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Research Article

Resistance against Insect Pests by Plant Phenolics and their Derivative Compounds

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Abstract

The chemical nature of plant phenolics varies from a simple monomeric unit to highly polymerized structures of varying proportions of monomeric aglycon units. Phenolics are aromatic benzene ring compounds with one or more hydroxyl groups produced for protection against biotic stresses. The functions of phenolic compounds in plant physiology are difficult to overestimate. The phenolics provide structural integrity and scaffolding support to plants. Importantly, phenolic phytoalexin secreted by wounded or otherwise perturbed plants, repel or kill many insect pests. Insects represent adaptive characters that have been subjected to natural selection during evolution. Plants synthesize a greater array of secondary compounds than animals, since plants cannot rely on physical mobility to escape their predators and have therefore evolved a chemical defense against such predators. This article reviews the role of plant phenols and polyphenols, interactions and their concern to resistance mechanisms against the insect pest stresses.

Keywords: Phenol, Resistance, Interaction, Brinjal, Biotic

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Introduction

Plants have prepared various secondary metabolites for resistance to biotic agents like the resistance against *Leucinodes orbonalis* by phenolic compounds of brinjal *S. melongena* [1]. Similarly the defensive plant proteins play a significant role in direct interactions between herbivores and plants; the role of non-protein secondary metabolites is just as big. The term ‘secondary’ is used to contrast them with metabolites that are directly involved in growth, development or reproduction, although it is not always possible to determine the precise physiological role of each metabolite. Across the plant kingdom, there is a staggering diversity of secondary metabolites, and they can be distinct for small phylogenetic groups. Many secondary metabolites have been implicated in plant defenses or are stress-related. Despite the rich diversity of secondary metabolites, their biosynthetic origins allow them to be classified into three basal groups: (1) the phenolics; (2) the isoprenoids; and the (3) N-containing compounds.

Kant *et al*. [2] reviewed that for the plants to preserve their fitness when attacked by herbivores, it can employ complex strategies that include reallocation of resources and the production of defensive metabolites and structures, which can be either prefabricated or be produced only upon attack. In addition to the herbivore resistance, the phenolic compounds had also been reported to have antimicrobial activity against different pathogenic micro-organisms [3].

What are Phenolics

Phenolic compounds are secondary metabolites which are synthesize in plants and possessbiological prosperitieslike antefedent [4], antioxidant, antiapoptosis, anti-aging, anticarcinogen, anti-inflammation,anti-artherosclerosis, cardio vascular protection, inhibition of angiogenesis and cell proliferation activity. Phenolics consist of an aromatic ring with one or more hydroxyl groups. Two pathways are responsible for the majority of plant phenolics: (1) the phenylpropanoid pathway [5], which converts the aromatic amino acid phenylalanine into phenolics. Phenylpropanoid are a diverse chemical class with immense health benefits that are biosynthesized from the aromatic amino acid L-phenylalanine, and (2) the acetate/malonate (polyketide) pathway [6]. Single phenolics can be polymerized to form polyphenols and both can be subjected to additional modifications, giving rise to a vast quantity (>9000) of chemically diverse metabolites, which include benzoquinones, phenolic acids, coumarins, flavonoids, lignins and tannins [7]. Most of these biological actions have beenattributed to their intrinsic reducing capabilities [8].Rich dietary sourcesof phenolics include fruits, tea, coffee, cocoa, and processed foods derived from these, suchas wine. At high levels, and in particular when sugar levels are low, phenols impart an astringency, bitterness, and color to foods like brinjal. Phenolicsin grapes and wines include many different substances: phenolic acids (e.g., hydroxybenzoic acids such as gallic acid, hydroxyl-cinnamic acids found in grape juice), three classesof flavonoids found in the skins and seeds (red anthocyanins, the flavonols, and the abundant flavan-3-ols, comprise the monomeric catechins), oligomeric pro-anthocyanidins, and polymeric condensed tannins.Plant foods like brinjal [4] have phenolic compounds, which affect their: appearance, taste, odor and oxidative stability. In cereal grains, these compounds are located mainly in the pericarp [9]. The major phenolic acids in cereals are ferulic and p-coumaric acids [10,11]. Anthocyanins are water-soluble pigments mostly studied in cereals [12].

Phenolics have various functions in primary metabolism; for instance, they protect plants from UV radiation [13] or form, as lignins, an integral part of the secondary cell wall in vascular plants [14]. Furthermore, flavonoids are crucial for reproduction because they are required for pollen development [15] and provide many of the visual and volatile cues used by flowers [16] and fruits [17] to attract pollinators and seed dispersers, respectively. Plants use phenolics to resist attacks from herbivores because of their deterrent [18] and toxic [19] nature. Hence, they are often constitutively present at or near the cell surface or stored as inactive compounds away from activating enzymes (e.g. in vacuoles or specialized cells, or bound to the cell wall) [20].

Plants Synthesize Phenolics

Phenolics are often produced and accumulated in the sub-epidermal layers of plant tissues exposed to stress and pathogen attack [21]. The concentration of a particular phenolic compound within a plant tissue is dependent on season and may also vary at different stages of growth and development [4,22]. Several internal and external factors, including trauma, wounding, drought and pathogen attack, affect the synthesis and accumulation of phenolics [23]. Furthermore, the biosynthesis of phenolics in chloroplasts and their accumulation in vacuoles are enhanced on exposure to light [23]. Photo-inhibition, as well as nutrient stresses, such as deficiencies in nitrogen, phosphate, potassium, sulphur, magnesium, boron and iron, also triggers the synthesis of phenyl-propanoid compounds in some plant species, which include members of the flavonoid biosynthetic pathway [7].

Phenolics for Defence

Phenolics serve a dual function of both repelling [1,4] and attracting different organisms in the plant's surroundings, while as sugars do reverse of it (**Figure 1**). They act as protective agents, inhibitors, natural animal toxicants and pesticides against invading herbivores, nematodes, phytophagous insects, and fungal and bacterial pathogens [24].

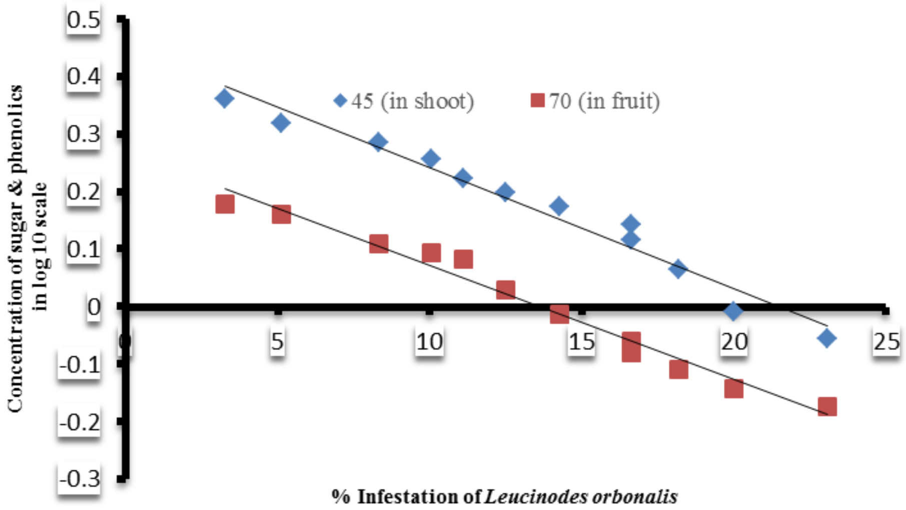

Figure 1 Relationship between the *Leucinodes orbonalis* (Guenee) infestation and phenol and sugar content in brinjal shoot and fruits at different phonological stages of vegetative and reproductive growth [4]

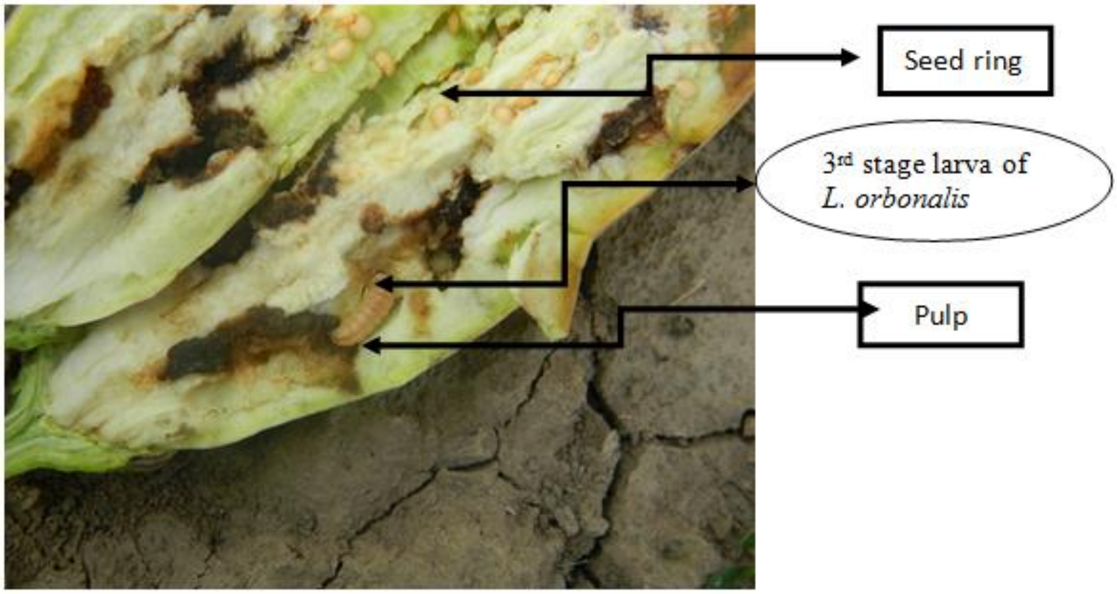

Figure 2 Infestation of the *Leucinodes orbonalis* to pulp of the brinjal fruit [4]

In brinjal the seed ring contains high content of phenolic compounds, so infestation by the *L. orbonalis* is least in that region, while as in pulp the concentration of the phenolics is less and sugars are more so attack is accordingly more (Figure 2). The thickness of the pulp is more, and the pest remains continue to feed on it till several larval stages (4 stages). However, the pest feed less in the seed ring, and move back to the pulp.

Tannins

Plants synthesized different types of phenolics with diverse functions that they perform against biotic stresses. In KSUAST-K, Srinagar the chemical constituent namely lignin were observed to have exhibited a clear correlation negative with the *Leucinodes orbonalis* incidence. Genotypes, Shalimar Brinjal Hybrid-1 and Shalimar Brinjal Hybrid-2 showed minimum content of lignin. Varieties, Brinjal-85 were found least attacked by the *L. orbonalis* and recorded the shoot damage of 2.34 and total moisture, and lignin content of 78.72per cent and 34.24 mg/100g dry wt. respectively. In Brinjal Highest lignin and crude fiber content were observed in Brinjal-85 and lowest in Shalimar Brinjal Hybrid-1 [1].

Allelochemicals and Plant Competition

In different families of plants, various types of phenolics found are as: Umbelliferone, p-hydroxybenzoic acid, vanillyl alcohol and isoflavones. Chemoattractants in Rhizobium Sinapinic acid, syringic acid, ethylsyringamide, propylsyringamide, carbethoxyethylen syringamide, para-hydroxybenzoate, ferulic acid *vir* gene inducers. In Agrobacterium, Vanillyl alcohol, bromo acetosyringone

Inhibitors of *vir* gene induction in Agrobacterium: Acetosyringone, a-hydroxyacetosyringone, p-Hydroxybenzoate. Chemoattractants in Agrobacterium and Rhizobium, and *vir* gene inducers in Agrobacterium Salicylic acid Quorum quencher in Agrobacterium Hydroquinones.

Allelochemicals like Coumarins, xanthones, anthocyanidins are phenolic derivatives and are most common in plants.Phenolics act as determinants of colour and attractants of pollinators in plants.Caffeic acid *vir* gene inducer in Agrobacterium 3,4-Dihydroxybenzoic acid Protocatechuic acid, b-resorcylic acid, protocatechuate, p-resorcylate, catechol vir gene inducer in Agrobacterium Chlorogenic acid. Precursor for lignin and suberin synthesis in plants are Lignin, tannins and suberins. Further phenolics act like the structural components of plant cells

Catechins Plant defence

Flavonoids, flavonols, flavones, genistein, daidzein, O-acetyldaidzein, 6-O-malonylgenistin, 6-O-malonyl daidzin, glycitin, 6-O-malonylglycitin nod gene inducers in *Rhizobium Apigenin*, naringenin, luteolin Chemoattractants in Agrobacterium and Rhizobium, and nod gene inducers in Rhizobium Gallate, gallic acid, pyrogallic acid, syringic acid, kaempferol vir gene inducers in *Agrobacterium Flavanones*, quercetin nod gene inducers in Rhizobium Isoflavonoids. Chemoattractants and nod gene inducers in *Rhizobium Cajanin*, medicarpin, glyceoline, rotenone, coumestrol, phaseolin, phaseolinin, limonoids, tannins, flavonoids Phytoalexins, phytoanticipins and nematicides in plant defenceacid.

Center to defence mechanism

Against microbial invaders. Phenolics are synthesized when plant pattern recognition receptors recognize potential pathogens by conserved pathogen-associated molecular patterns (PAMPs), leading to PAMP-triggered immunity. As a result, the progress of the infection is restricted long before the pathogen gains complete hold of the plant.

How Herbivores Cope with Plant Defences

Plants and herbivores have coevolved for over 400 million years. While plants have evolved signaling networks to regulate induced defences and diversity in their palette of secondary metabolites [25], herbivores have been under pressure to evade defences [26]. Hence, behavioural adaptions have evolved that allow herbivores to avoid defended plant tissues [27-29] as much as possible or to dismantle defensive structures, like trichomes [30] and latex channels [31]. However, herbivores have also evolved a variety of mechanisms to cope with deterrent substances produced by their host plants. Given the enormous economic impact of herbivore resistance to agrochemicals, a large part of our knowledge of adaptations to xenobiotics comes from the field of pesticide resistance [32]. However, the mechanisms (Fig 3) at play are similar to those that enable them to resist defensive phytotoxins, and a functional overlap between adaptation to agrochemicals and to phytotoxins has been suggested [33].

The Insect Resistance Response Shown Diagrammatically

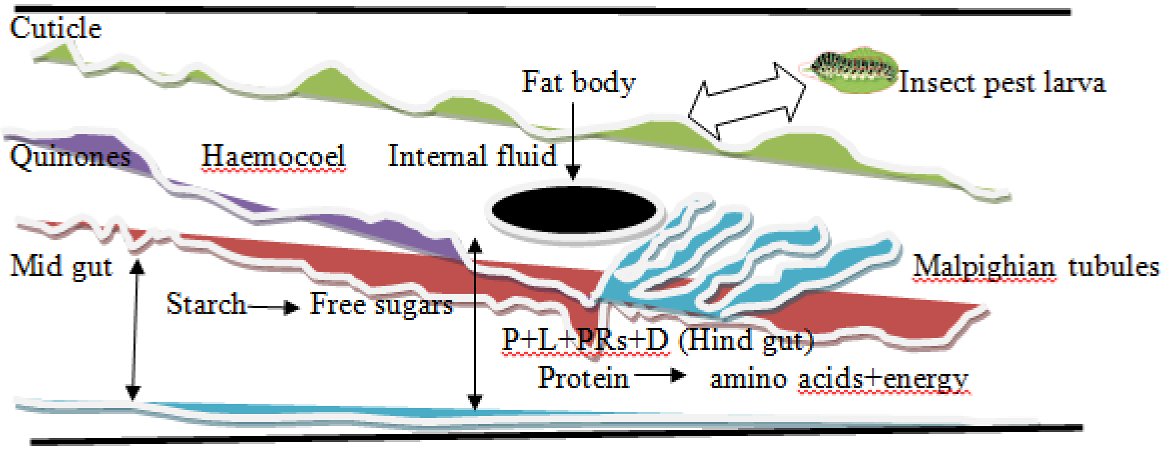

Figure 3 above showed the response of herbivores towards the defensive secondary metabolites[33]

Phenolics—Molecules for Cross-Talk in the Rhizosphere

The plant rhizosphere is a dynamic ecosystem of different species, representing flora, fauna and microbes that interact with each other in a variety of complex reactions. These interactions are mainly governed by a diverse array of phenolics exuded by the growing roots of plants, together with a host of other chemicals [34]. The functions performed by phenolics in the plant rhizosphere have been aptly termed the 'rhizosphere effect [35]. The root exudates generally include ions, free oxygen, water, enzymes, mucilage, a number of carbon-containing primary and secondary metabolites and, most importantly, plant phenolics. The released phenolics differ from species to species and also with time, space and location. Their concentrations in the soil range from 2.1 to 4.4% in monocotyledonous plants and 0.1 to 0.6% in dicotyledonous plants. Phenolics trigger redox reactions in soils and selectively influence the growth of soil microorganisms that colonize the rhizosphere. Microorganisms break down phenolics into elements that contribute towards the mineralization of soil nitrogen and the formation of humus [36]. The phenolics chelate metals and improve soil porosity, providing active absorption sites and increasing the mobility and bioavailability of elements, such as potassium, calcium, magnesium, copper, zinc, manganese, molybdenum, iron and boron, for plant roots [37]. Although plants exude different phenolic compounds that are toxic to most microorganisms, Agrobacterium and Rhizobium have evolved mechanisms to counteract, nullify and even utilize these defences fortheir own advantage [38]. The most significant of these mechanisms that involve phenolics are: (i) chemotaxis; (ii) activation of the bacterial nodulation (nod) and virulence (*vir*) gene networks; (iii) xenobiotic detoxification; and (iv) quorum signalling.

Chemotaxis

As in several other soil bacteria, phenolics play a pivotal role in the chemotactic responses of Agrobacterium and Rhizobium in their search for growth substrates and hosts. These serve as excellent models for signal transduction and plant–microbe interactions [39]. Diverse plantphenolic compounds with varying substitution patterns determine the chemotactic movement of Agrobacterium or Rhizobium across chemical gradients towards higher levels of potential nutrients and lower levels of inhibitors. Althoughacetosyringone and umbelliferone are inhibitors of nod geneinducers, *R. leguminosarum* exhibits an exaggerated chemotacticresponse to high concentrations of phenolic compounds [40]. Probably, the complex nature of the root exudates of different plants in the rhizosphere [41] necessitates such negative regulation by some phenolics. For example, it might be required to prevent competing rhizobia from targeting the same host plant and also for creating a favourable ecological niche for each of the species, therefore preventing nodule initiation in the vicinity of clover root tips by umbelliferone, is a good example of such negative rhizospheric interactions [41]. Aceto-syringone and hydroxyl aceto-syringone exuded from plant wounds are potent chemo-attractants at very low concentrations, and they also act to induce the *vir* genes of Agrobacterium [42]. In addition to aceto-syringone, a number of other phenolics and sugars are effective as chemo-attractants [43,44].

Activation of the bacterial nod and vir-gene networks

Microbial gene expression following chemotaxis is influenced by a diverse array of substituted plant phenols. These plant-derived signals are termed ‘host recognition factors’ or ‘xenognosins’ [45]. In both the symbiotic Rhizobium and pathogenic Agrobacterium, the same phenolics that act as chemoattractants may also regulate the expression of nod and vir genes, respectively.

Detoxification and biotransformation:

Phenolics act as antimicrobial compounds because of their ability to disrupt nonspecifically the structural integrity of bacterial membranes and to inhibit specifically bacterial enzymes involved in electron transport [46]. It is natural that bacteria would counteract or even nullify these toxic compounds. Many bacteria are endowed with the ability to degrade and utilize toxic phenols as a source of carbon [47,48].

An important mechanism by which members of Rhizobiaceae monitor their environment is quorum sensing [49]. The production, release and sensing of homoserine lactones (HSLs) or their acylated forms (AHL) are important for quorum sensing [50]. Quorum sensing allows bacterial cell–cell communication and promotes an advantageous lifestyle for both the survival and maintenance of pathogenic or symbiotic relationships within a range of environmental niches [51]. In quorum sensing, cell density dependent regulation of gene expression enables bacteria to coordinate certain adaptive processes that cannot be performed by an individual microbe.

How Plants Overcome Insect Pests

Quorum sensing helps rhizobia to synchronize themselves to phenolic signals on a population-wide scale and to function as multi-cellular organisms for successful symbiosis. Plants recognize herbivores by their molecular patterns or their elicitors. It is hypothesized that polyphosphoinositides generated at the plasma membrane play an important role as second messengers, just as they do during pathogenesis [52]. The most rapid measured responses are ion (e.g.

Ca2þ and Kþ) fluxes across the plasma membrane, followed by changes in the plasma membrane potential. Subsequently, a protein kinase cascade can activate the production of ROS such as hydrogen peroxide by activating an NADPH-dependent oxidase. Hydrogen peroxide can have a direct effect on herbivores or enter the cell, thus changing its redox status. The rapid increase in cytosolic Ca2þ can also give rise to increased nitric oxide-mediated processes that precede the upregulation of JA levels [53]. These responses occur not only locally, but also in unattacked neighbouring cells and in distal tissues. Herbivory, the application of oral secretions to wounded leaves and aphid probing have been shown to give rise to membrane depolarization due to an electrochemical gradient between the interior and the exterior of the attacked plants cells. This membrane depolarization can travel with a speed of up to 40cms–1 through the entire plant and mutant plants with attenuated wound-induced surface potential changes exhibit a reduced JA response in distal leaves [3].

Conclusion

Finally, it is appealing to think of attack suppression as a primitive adaptation of the plants. However, some studies suggest this may not always be the case. Therefore, generally it has negative and less efficient consequences also. In a plant–herbivore context such 'mafia behaviour' would mean that herbivores increase feeding upon experiencing induced plant defense. Although empirical studies of mafia behaviour are scarce, the costs of mounting an induced defense response under certain circumstances can be higher than its benefit. For example, when exposed to herbivore, some plants (tobacco) typically initiate a JA-induced accumulation of nicotine, but the accumulation of nicotine is costly and decreases the competitive ability of the plant. Hence, when larvae of the nicotine-tolerant herbivore *M. sexta* feed on tobacco, the plant responds by down regulating the accumulation of nicotine. Therefore, it is argued that this response likely reflects an adaptation of the plant to shut down an inefficient and costly defense response, because using this energy to compete with conspecifics may be more rewarding.

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