

A Review of the Part Chemicals Plant Defense Mechanism Plays

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ABSTRACT

Some plants protect themselves from insect herbivores by emitting chemical signals that attract parasitic wasps. Plant chemical defenses generally are classified as nonnitrogenous, nitrogenous, and elemental. Ecologically, the distinction between nonnitrogenous and nitrogenous defenses reflects the availability of C versus N for allocation to defense at the expense of maintenance, growth, and reproduction. Each of these categories is represented by a wide variety of compounds, many differing only in the structure and composition of attached radicals. Elemental defenses are conferred by plant accumulation of toxic elements from the soil.

KEYWORDS: Chemical Defenses, Nonnitrogenous, Nitrogenous, And Elemental.

Nonnitrogenous Defenses

Nonnitrogenous defenses include phenolics, terpenoids, photooxidants, insect hormone or pheromone analogs, pyrethroids, and aflatoxins. Phenolics, or flavonoids, are distributed widely among terrestrial plants and are likely among the oldest plant secondary (i.e., nonmetabolic) compounds. Although phenolics are perhaps best known as defenses against herbivores and plant pathogens, they also protect plants from damage by ultraviolet (UV) radiation provide support for vascular plants (lignins), compose pigments that determine flower color for angiosperms, and play a role in plant nutrient acquisition by affecting soil chemistry. Phenolics include the hydrolyzable tannins, derivatives of simple phenolic acids, and condensed tannins, polymers of higher molecular weight hydroxyflavonol units. Polymerized tannins are highly resistant to decomposition, eventually composing the humic materials that largely determine soil properties. Tannins are distasteful, usually bitter and astringent, and act as feeding deterrents for many herbivores. When ingested, tannins chelate N-bearing molecules to form indigestible complexes. Insects incapable of catabolizing tannins or preventing chelation suffer gut damage and are unable to assimilate nitrogen from their food. Some flavonoids, such as rotenone, are directly toxic to insects and other animals.

Rhoades (1977) reported that the foliage surface of creosote bushes, *Larrea tridentata* from the southwestern United States and *L. cuneifolia* from Argentina, is characterized by phenolic resins, primarily nordihydroquaiaretic acid. Young leaves contained about twice as much resin (26% d.w. for *L. tridentata*, 44% for *L. cuneifolia*) as did mature leaves (10% for *L. tridentata*, 15% for *L. cuneifolia*), but the amounts of nitrogen and water did not differ between leaf ages. Leaf-feeding insects that consume entire leaves all preferred mature foliage. Furthermore, extracting resins from foliage increased feeding on both young and mature leaves by a grasshopper generalist, *Cibolacris parviceps*, but reduced feeding on mature leaves by a geometrid specialist, *Semiothisa colorata*. Insect developmental hormones and examples of their analogues in plants. From Harborne (1994). laboratory experiments. These results suggested that low levels of resins in mature leaves may be a feeding stimulant for *S. colorata*. Terpenoids also are widely represented among plant groups. These compounds are synthesized by linking isoprene subunits. The lower molecular weight monoterpenes and sesquiterpenes are highly volatile compounds that function as floral scents that attract pollinators and other plant scents that herbivores or their predators and parasites use to find hosts. Some insects modify plant terpenes for use as pheromone. Terpenoids with higher molecular weights include plant resins, cardiac glycosides, and saponins.

Terpenoids usually are distasteful or toxic to herbivores. In addition, they are primary resin components of pitch, produced by many plants to seal wounds. Pitch flow in response to injury by insect feeding can physically push the insect away, deter further feeding, kill the insect and associated microorganisms. Becerra (1994) reported that the tropical succulent shrub *Bursera schlechtendalii* stores terpenes under pressure in a network of canals in its leaves and stems. When these canals are broken during insect feeding, the terpenes are squirted up to 150 cm, bathing the herbivore and drenching the leaf surface. A specialized herbivore, the chrysomelid, *Blepharida* sp., partially avoids Examples of pyrethroid and aflatoxin defenses. From Harborne (1994). this defense by severing leaf veins before feeding but nevertheless suffers high mortality and may spend more time cutting veins than feeding, thereby suffering reduced growth. Cardiac glycosides are terpenoids best known as the milkweed (Euphorbiaceae) compounds sequestered by monarch butterflies, *Danaus*

plexippus. Ingestion of these compounds by vertebrates either induces vomiting or results in cardiac arrest. The butterflies thereby gain protection against predation by birds.

Photooxidants, such as the quinones and furanocoumarins, increase epidermal sensitivity to solar radiation. Assimilation of these compounds can result in severe sunburn, necrosis of the skin, and other epidermal damage on exposure to sunlight. Feeding on furanocoumarin-producing plants in daylight can cause 100% mortality to insects, whereas feeding in the dark causes only 60% mortality. Insect herbivores can circumvent this defense by becoming leaf rollers or nocturnal feeders (Harborne 1994) or by sequestering antioxidants (Blum 1992). Insect development and reproduction are governed primarily by two hormones, molting hormone (ecdysone) and juvenile hormone. The relative concentrations of these two hormones dictate the timing of ecdysis and the subsequent stage of development. A large number of phytoecdysones have been identified, primarily from ferns and gymnosperms. Some of the phytoecdysones are as much as 20 times more active than the ecdysones produced by insects and resist inactivation by insects (Harborne 1994).

Schmelz *et al.* (2002) reported that spinach, *Spinacia oleracea*, produces 20-hydroxyecdysone in roots in response to root damage or root herbivory. Root feeding by the fly *Bradysia impatiens* increased production of 20-hydroxyecdysone by 4–6.6-fold. Fly larvae preferred a diet with a low concentration of 20-hydroxyecdysone and showed significantly reduced survival when reared on a diet with a high concentration of 20-hydroxyecdysone.

Plants also produce some juvenile hormone analogues (primarily juvabione) and compounds that interfere with juvenile hormone activity. The antijuvabione hormones usually cause precocious development. Plant-derived hormone analogues are highly disruptive to insect development, usually preventing maturation or producing imperfect and sterile adults (Harborne 1994). Some plants produce insect alarm pheromones that induce rapid departure of colonizing insects. For example, wild potato, *Solanum berthaultii*, produces (E)-β-farnesene, the major component of alarm pheromones for many aphid species. This compound is released from glandular hairs on the foliage at sufficient quantities to induce departure of settled colonies of aphids and avoidance by host-seeking aphids (R. Gibson and Pickett 1983). Pyrethroids are an important group of plant toxins. Many synthetic pyrethroids are widely used as contact insecticides (i.e., absorbed through the exoskeleton) because of their rapid effect on insect pests. Aflatoxins are toxic compounds produced by fungi. Many are highly toxic to vertebrates and, perhaps, to invertebrates (G. Carroll 1988, Harborne 1994). Higher plants may augment their own defenses through mutualistic associations with endophytic or mycorrhizal fungi that produce aflatoxins.

Nitrogenous Defenses

Nitrogenous defenses include nonprotein amino acids, cyanogenic glucosides, glucosinolates, and alkaloids. These compounds are highly toxic as a result of their interference with protein function or physiological processes. Nonprotein amino acids are analogues of essential amino acids.

Their substitution for essential amino acids in proteins results in improper configuration, loss of enzyme function, and inability to maintain physiological processes critical to survival. Some nonprotein amino acids are toxic for other reasons, such as interference with tyrosinase (an enzyme critical to hardening of the insect cuticle) by 3,4-dihydroxyphenylalanine (L-DOPA). More than 300 nonprotein amino acids are known, primarily from seeds of legumes (Harborne 1994).

Toxic or other defensive proteins are produced by many organisms. Proteinase inhibitors, produced by a variety of plants, interfere with insect digestive enzymes (Kessler and Baldwin 2002, Thaler *et al.* 2001).

The endotoxins produced by the bacterium *Bacillus thuringiensis* (Bt) have been widely used for control of several Lepidoptera, Coleoptera, and mosquito pests. Because of their effectiveness, the genes coding for these toxins have been introduced into a number of crop plant species, including corn, sorghum, soybean, potato, and cotton, to control crop pests, raising concerns about potential effects of outcrossing between crop species and wild relatives or non-Bt refuges (Chilcutt and Tabashnik 2004) and potential effects on nontarget arthropods (Hansen Jesse and Obrycki 2000, Zangerl *et al.* 2001). However, subsequent studies have indicated minimal effect on nontarget species and long-term regional suppression of major pests with Bt crops has greatly reduced the use of insecticides (Carrière *et al.* 2003). Cyanogenic glycosides are distributed widely among plant families. These compounds are inert in plant cells. Plants also produce specific enzymes to

control hydrolysis of the glycoside. When crushed plant cells enter the herbivore gut, the glycoside is hydrolyzed into glucose and a cyanohydrin that spontaneously decomposes into a ketone or aldehyde and hydrogen cyanide. Hydrogen cyanide is toxic to most organisms because of its inhibition of cytochromes in the electron transport system (Harborne 1994). Glucosinolates, characteristic of the Brassicaceae, have been shown to deter feeding and reduce growth in a variety of herbivores (Renwick 2002, Rotem *et al.* (2003) reported that young larvae of the cabbage white butterfly, *Pieris rapae*, a specialized herbivore, showed reduced growth with increasing glucosinolate concentration in *Brassica napus* hosts, but that older larvae were relatively tolerant of

glucosinolates. Alkaloids include more than 5000 known structures from about 20% of higher plant families (Harborne 1994).

Molecules range in size from the relatively simple coniine of poison hemlock to multicyclic compounds such as solanine. Familiar examples include atropine, caffeine, nicotine, belladonna, digitalis, and strychnine. They are highly toxic and teratogenic, even at relatively low concentrations, because of their interference with major physiological processes, especially cardiovascular and nervous system functions. D. Jackson *et al.* (2002) reported that larval weights and survival of tobacco budworm, *Helicoverpa virescens*, were negatively related to pyridine alkaloid concentrations among tobacco, *Nicotiana tabacum*, cultivars. Survivorship after 8 weeks declined from 60% to 0% as total alkaloid concentration increased from 0% to 2% w.w. Shonle and Bergelson (2000) found that generalist herbivore feeding on *Datura stramonium* was negatively correlated with hyoscyamine concentration; however, feeding by specialist herbivores, flea beetles, *Epitrix* spp., was positively correlated with concentrations of scopolamine, indicating that this compound has become a phagostimulant for these adapted herbivores.

Elemental Defenses

Some plants accumulate and tolerate high concentrations of toxic elements, including Se, Mn, Cu, Ni, Zn, Cd, Cr, Pb, Co, Al, and As (Boyd 2004). In some cases, foliage concentrations of these metals can exceed 2% (Jhee *et al.* 1999). Although the function of such hyperaccumulation remains unclear, some plants benefit from protection against herbivores. Boyd and Martens (1994) found that larvae of the cabbage white butterfly fed *Thlaspi montanum* grown in high Ni soil showed 100% mortality after 12 days, compared to 21% mortality for larvae fed on plants grown in low Ni soil. Hanson *et al.* (2004) reported that Indian mustard, *Brassica juncea*, can accumulate Se up to 1000 mg kg⁻¹ d.w., even from low-Se soils. Green peach aphids, *Myzus persicae*, avoided Se-containing leaves when offered a choice of foliage from plants grown in Se or non-Se soil. In nonchoice experiments, aphid population growth was reduced 15% at 1.5 mg Se kg⁻¹ d.w. and few, if any, aphids survived at leaf concentrations >125 mg Se kg⁻¹. Jhee *et al.* (1999) found that young larvae of *Pieris napi* showed no preference for high- or low-Zn leaves of *Thlaspi caerulescens*, but later-instar larvae showed highly significant avoidance of high-Zn leaves. Jhee *et al.* (2005) concluded that Ni accumulation could protect *Streptanthus polygaloides* plants from chewing herbivores but not sap-sucking herbivores.

Defensive compounds may be energetically expensive to produce, and their production competes with production of other necessary compounds and tissues. Some, such as the complex phenolics and terpenoids, are highly resistant to degradation and cannot be catabolized to retrieve constituent energy or nutrients for other needs. Others, such as alkaloids and nonprotein amino acids, can be catabolized and the nitrogen, in particular, can be retrieved for other uses, but such catabolism involves metabolic costs that reduce net gain in energy or nutrient budgets. Few studies have addressed the fitness costs of defense. Baldwin (1998) evaluated seed production by plants treated or not treated with jasmonate, a phytohormone that induces plant defenses. Induction of defense did not significantly increase seed production of plants that came under herbivore attack but significantly reduced seed production of plants that were not attacked.

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