

Recent Knowledge about the Relation Between Allelochemicals in Plant and the Insects

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INTRODUCTION

The acceptance or rejection of plants by herbivorous depends on their behavioral responses to plant features. These features may be physical or chemical. Plants produce a wide variety of chemical compounds, allelochemicals, which appear to function primarily as a defense against herbivory, although they may serve other functions in the plant as well

These compounds include alkaloids, mustard oils, flavonoids, terpenes and sesquiterpenes, cucurbitacins, phenolics and many others.

Increases in glucosinolates caused higher resistance of plants against specialist herbivores in several cases [1]. The distribution, concentration and composition of various toxic or bitter-tasting plant secondary metabolites such as glucosinolates are known to depend on many factors, e.g. nutritional state, age, tissue, genotype, population, or species [2, 3].

Plant allelochemicals have been shown to act as feeding deterrents or toxins to generalist and non-adapted specialist insects. In contrast, these same substances are consumed with no ill effects by adapted specialist insects

which may use these compounds as feeding or oviposition cues [4]. Some allelochemicals, glucosinolates and Cardenolides may be used as nutrient sources for specialist insects.

So capabilities of herbivores to detoxify noxious plants will allow them to diversify food resources. This is of prime importance for insects like locusts living in constraining conditions. *Schistocerca gregaria* (Forsk.) the desert locust which is adapted to live and breed in the Saharan region from India to the Atlantic coast will have sometime to feed successfully on plants high toxic to most herbivores (ex. *Hyoscyamus nrticus* containing atropine and other alkaloids). In many cases these compounds confer efficient defence against pathogens or herbivores [5].

Sites and concentrations of allelochemicals: Plant surface waxes are complex mixtures of fatty acids, esters, alkenes and other hydrocarbons and also contain varying quantities of many different secondary dependent on leaf age, damage, temperature, insulation, rain and dew. Flavonoid glycosides are the major chemicals on the leaf surface.

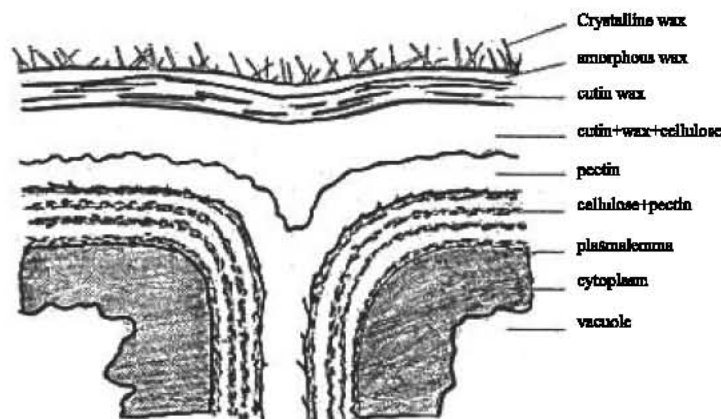


Fig. 1: Diagrammatic cross section of plant cuticle showing wax layers and parts of the epidermal cells [6]

Many secondary compounds present in plants are toxic, not only to potential herbivores, but also to the plant itself. For this reason, they are usually either compartmentalized and separated from cytoplasm, or they are stored in an inactive form. Anatomy is of particular importance in relation to the precise location of secondary metabolites in plants. Some alkaloids are sequestered in epidermal tissue vacuoles or in latex, other are to be found only in vacuoles of young tissue. Some, such as nicotine are manufactured in the roots and transported to the aerial parts, they are at high level in xylem. Others are deposited in cell walls and in trees may then end up in the bark. Non protein amino acids are usually in highest concentration in seeds. Coumarins tend to be localized in oil gland or in cells of the epidermis. Acetylenes and other lipid-soluble compounds may be secreted into the surface wax. Many species have glandular trichomes in which diverse terpenoids and phenols are sequestered.

Effect of some factors on allelochemicals concentration in host plants

1-Growing season: Concentration in leaves are generally high early in the growing season. Plants producing new leaves, which have higher concentration of allelochemicals, earlier in a new field season decreased the resistance of a native crucifer to adapted insect herbivores including a leaf mining fly, *Scaptomyza nigrita* [7].

2-Minerals: Sulfate fertilization increases concentrations of glucosinolates in cultivated Brassicaceae and native caper had also higher concentrations of glucosinolates and lower insect damage in drier soils [7].

3-Nitrogen: Nitrogen increases amino acid and subsequently glucosinolates.

4-Irrigation: Cultivated Brassicaceae has higher concentrations of GSL under drought conditions or intermittent irrigation than under continuous irrigation.

5-Herbivores attack: When host plant infested by their pests the allelochemicals are produced. The defense chemicals are produced only when plant are under attack and in many cases these responses could deter infestation [8].

6-UV light: Allelochemicals in most instances is greatly enhanced in the presence of UV light [9].

Insects behaviour and allelochemicals: The narrow host ranges of herbivores most commonly depend on the presence or absence of a variety of secondary metabolites in plants, so that plant chemotaxonomy is probably an important factor in understanding host ranges.

***Feeding response:** In fact host plant discrimination occurs within an assemblage of potential host plants and most likely reflects a complex balance between attractant and deterrent allelochemicals compound [10]. Many adapted herbivores tolerate or use these compounds to find their host plant. The evidence of the effect of allelochemicals on insect feeding behaviour tends to be a feeding preference for allelochemicals tested on artificial filter paper discs [11].

****Antifeedant effect:** Allelochemicals are defensive substances that inhibit food intake by non-specialized insects. Many studies have demonstrated the role of allelochemicals as antifeedant effect: Syringin and chlorojanerin from *Rhaponticum pulchrum* were shown to be good anti-feedants against the three species of the stored product insect pests *Sitophilus granarium*, *Trogoderma granarium* and *Tribolium confusum* [12]. The antifeedant action of the crude extract of *Solanum nigrum* was more effective on *Phthorimaea operculella* than *Lantana camara* extract. It is possible the allelochemicals of *S. nigrum* as known, solanidine have more diverse effects on insect behavior [13].

Break-down products of glucosinolates were more efficient in deterring the generalist locust than were glucosinolates, allyl-isocyanate a volatile compound was a 100-fold higher deterrent than is its substrate (Sinigrin). Deterrent or stimulate feeding depending on the concentration tested, Glucobrassicin, Epiprogoitrin and Sinigrin, when tested on filter paper discs, acted as phagostimulants at low concentrations and as deterrents at high concentrations. The deterrent effect of bis (3-indolyl) methane was still significant at 0.4 Mmol/g D.W., this compound was the most effective in locust feeding inhibition [14]. The higher concentration of Sinigrin treated on leaf disc was deterred to Chrysomelidae, isothiocyanates could be responsible for the repellency of the late instar wireworms *Limonius infuscatus*. Cyanide released from field grown sorghum is an effective plant defense and probably accounts for most of the unpalatability of this crop to acridids in West Africa and India [15, 16]. Quinolizidine Alkaloids (QAs) in lupines, they can be feeding deterrents for herbivores, the effect of QAs also include: (1) inhibition of plant virus,

bacteria and parasitic fungi (2) deterrent effects on insects (i.e. aphids and beetle), (3) allelopathic (i.e. inhibition of seed germination) [17]. Cucurbitacins and cardenolides have been implicated as part of feeding deterrence mechanism of unacceptably glucosinolate-containing plants for crucifer adapted Chrysomelidae flea beetles. Plant monoterpenes that deter herbivores are designated as allomones (compounds that are beneficial to the emitting species but not to the receiving species) [18].

The larvae of *S. exigua* in choice tests, left the furanocoumarin-containing diet more frequently by becoming more mobile after ingestion of the treated diet, as measured by time spent questing (in which larvae walk or lift their thoraxes and move from side to side in a searching motion) and number of questing occurrences [19].

*****Stimulant effect:** Allelochemicals and their metabolites compound were acted as feeding stimulants. Behavioural responses to allelochemicals by individuals of any one insect usually depend on concentrations. Glucosinolates volatiles are rather known as feeding stimulants than as repellents. Sinigrin crucifer plant has a stimulant effect on feeding activity of the larvae of *plutella maculipennis*. Allyl isothiocyanate is strong attractant for *meligethes aeneus* and phenyl isothiocyanate seemed to attract males of *Dasyneura brassicae* and isothiocyanate volatile product is attractive for many insects specialist on crucifer plant [20]. Epiprogoitrin and Glucocheirolin are more stimulant for *P. maculipennis* feeding than other glucosinolates. In general, glucosinolates and not their break-down products are implicated as the active contact stimuli in larval feeding specificity and glucosinolates are often gustatory stimulants for the young of adapted insects [21]. For specialist insects, cyanide and cyanogenic compounds can also serve as kairomones. For example all *Spodoptera eridania* larva grow as well or better when cyanide, as KCN, is present in the diet than when it is absent [22]. Plant monoterpenes that attract herbivores are designated as kairomones, the monoterpenes of the plant could become attractants for this species), although still serving as allomones toward other herbivores. Larvae of *Helicoverpa armigera* preferred to feed on plant tips and boring into squares and bolls of cotton plants, related to nutrition and depended mainly on the contents of terpenoids and tannis [23].

******Food consumption and growth:** Phytophagous insects exhibit some degree of selectivity in food they eat.

Host plant selection involves not only choosing the right species of plant, but also selecting an individual plant within that species that is suitable for feeding, survival and development.

Following observation [24], it has been determined that insect nutritional indices are affected by both experimental condition and physiology of plant material. For example, the consumption rate, Approximate Digestibility (AD) and efficiency of conversion of digested food (EC I) of adult male grasshopper *Melanoplus sanguinipes* fed on wheat, Oates and kochia are significantly different [25]. Nutritional indices of *Poeciloceris bmtionius* nymphs on *Calotropis procera* are increased as compared with that on wheat seedling [26]. Feeding of the grasshopper, *Eupreopcnemis plorans* on Lupine or horse-bean resulted in higher relative consumption rate (RCR), longer nymphal duration and lower values of AD, EC I, ECD (efficiency of conversion of digested food) and RGR (relative growth rate) compared to clover, these results may be due to the allelochemicals compounds found in Lupine and horsebea (quinolizidine alkaloid and cyanogenic glycoside (HCN) and non amino acids, respectively). Lower weight gain and higher food consumption of grasshoppers fed on Lupine or horsebean was related to malassimilation caused by allelochemicals present in these plants, which exert chronic toxicity on their digestive enzymes [27]. Cardenolides in the leaves of *C. procera* have the stimulant effect on the feeding of grasshopper, *P. bmtionius* [26].

The relative growth rate, ECI and ECD were reduced after feeding the cutworm on *Melia toosendan* or extracts containing the limonoid toosendammin [28]. Weight gain in *E. plorans* fed on Lupin and horsebean was lower than in those fed on clover. This is probably because of the time and the energy required to degrade alkaloid or HCN, which compromises the digestion of the food, or the chronic toxicity of plants allelochemicals [27]. Ingested food of one year old leaves of *Pinus sylvestris*, contain low phenolic, by the larvae of European pine sawfly was higher [29]. Larval growth of *Spodoptera litura* was influenced by azadirachtin, may be due to the presence of antifeedant allelochemicals [30]. Larvae of *Zygaena filipendulae* reared on cyanogenic *Lotus corniculatus* develop faster compared to larvae reared on transgenic *L. japonicus* [31]. Pupal weight, growth rate, female longevity of the European grapevine moth, *Lobesia botrana* were increased on the alternative hosts, *Daphne gnidium*, *Olea europaea* and *Tanacetum vulgare* than *Vitis vinifera* [32].

Oviposition response: Visual, odor and taste cues are all important in host-seeking for food by phytophagous Lepidoptera larvae. However, female adults seem to be less dependent on plant odor for oviposition. And water-soluble leaf chemicals, appear to be major stimulants in some instances. The importance of allelochemicals as larval feeding stimulants for some specialist insects suggested that ovipositing females would use these compounds as cues for appropriate place to lay their eggs. Such was the case for females of buckeye butterfly, *Junonia coenia*. These butterflies would oviposit on agar discs if they contained powdered host plant material or pure iridoid glycosides typical of the host plant *J. coenia* preferring to oviposit on plants higher in iridoid glycoside content may have offspring that develop more quick [33]. The role of allelochemicals appeared when the gravid females of *Busseola fusca* laid equal or higher numbers of eggs on the surrogate stems than on susceptible maize stem [34].

On other hand: the oviposition repellent was reported by many authors: (Elsayed [13]) found that the extracts of *lantana camara* and *Solanium nigrum* on tubers affected the discrimination of oviposition site by the females of *Phthorimaea operculella*. The effect of these plant extracts seemed to be concentrations dependent. Such an effect may be a chemical excitatory cue emitted by the plant extracts and acted as an oviposition repellent. Cardenolides are extremely effective inhibitors of oviposition by foraging of the *Pieris rapae* and *P. brassicae* [35]. Coating of chickpea seeds (*Cicer arietinum*) with a 0.05% (w/v) solution of plant lectins caused a significant reduction in egg laying of cowpea weevil, *Callosobruchus maculatus* [36]. Plant lectins caused high deterrent activity to Homoptera [37].

Fecundity and fertility of *E. plorans* grasshoppers fed on clover was significantly higher than that of *E. plorans* fed on either lupin or horsebean. The lower reproduction rates are attributable to lower production of yolk protein in the haemolymph of *E. plorans* may be by allelochemicals in lupin or horsebean leaves [27]. In similar experiments, fecundity and fertility of *P. bntoni* reared on *C. procera* leaves were significantly higher than when reared on *Zygophyllum simplex* and *Pulicaria crispa* [38].

Hatchability of *P. operculella* decreased as the concentration of *L. camara* and *S. nigrum* extracts increased on *Aphis faba*. The bioactivity of plant extracts sprayed on *Phthorimaea operculella* eggs, may be attributed that, allelochemicals of crude extracts have the ability of eggs penetration and prevented the development of the embryo [13].

Survival and malformation: Toxicity of allelochemicals is often the main argument to accept defensive functions allelochemicals in plant herbivore interactions. The defensive Potential of having more than one category of compounds is conceptually straight forward. Several compounds many act synergistically and be much more effective together than alone. Alternately, atypical compounds may allow a plant characterized by glucosinolates to escape from its glucosinolate-adapted herbivores by having a toxin to which these herbivores are not adapted [39].

After feeding of *E. plorans* on three diets, mortality increased on horsebean and lupin, which may be the result of the toxic effect of alkaloid and HCN present [27]. *Schouwbia* leaves containing GSL caused chronic toxicity to *S. gregaria* [14].

Flavone glycoside kill or impair the growth of many of the major insect pests of maize [41]. Aromatic plants allelochemicals in legume seeds are used as direct toxicity to adults of beetle also inhibition of reproduction [41]. Monoterpenes in conifer resins appear to function as important defenses against infestation by bark beetles. Both conifer resins and individual resin monoterpenes have been shown to repel beetle attack and to be toxic to egg. Larval and adult stages [42].

Short feeding of *E. plorans* on horsebean induced morphogenetic effects. Two types of malformations were observed; partially emerged hind legs and partially emerged abdomen. These malformations occurred in 10% of the adult emerged [27]. Bis (3-diindolylmethane), show that high concentration exhibited not only considerable nymph mortality but also the individuals which survived the utilized concentration showed different grades of latent effect expressed by the morphogenetic system as adult malformation [14].

Application of plant extract to some insect was associated with several aspects of disordered metamorphosis. Extracts of neem seeds, neem kernel and leaves inhibited pupal development and failure of emergence in *Leptinotarsa decemlineata* [28]. Larval mortality of the European grapevine moth, *L. botrana* on the *V. vinifera* was higher than that on the alternative hosts, *D. gnidium*, *O. europaea* and *T. vulgare* [32].

Adaptation for plant allelochemicals:

Insect metabolism of plant allelochemicals enter in three phases:

- Absorption by the gut.

- Transport from the gut to the haemolymph.
- Deposition in organs and other sites of storage.

Epilachna beetles are able to feed extensively on cucurbitacin-containing plants by using novel behavioral adaptation to reduce their exposure to cucurbitacins during feeding-in squash leaves, herbivore damage usually leads to rapid increases in the concentrations of cucurbitacins at the site of feeding, presumably due to translocation from other parts of the plant. However, *Epilachna* beetles chew a circular trench around the area in which they are about to feed, cutting through all leaf tissues but lower epidermis. This behavior prevents cucurbitacin accumulation at the feeding site by blocking influx from other tissues. Sawflies exhibit a number of characteristics typical of other specialist herbivores that feed on plants with high concentrations of chemical defenses (terpenoids): (1) They are at least partially resistant to host defenses, particularly at certain stages of development; (2) they avoid feeding on tissues with relatively high concentrations of defensive substances; and (3) these have appropriated host defenses for their own use in this case as protective agents [43].

Adaptation mechanisms of insects against their host plant allelochemicals include, sequestration, storage and detoxification.

Sequestration of plant allelochemicals may involve metabolism of the compounds prior storage in the appropriate tissue. In addition there may be selective sequestration of a subset of the allelochemicals sequestered by insect herbivores may be different from that found in its host plant [44].

These defensive compounds, glucosinolates are found in the feces of *S. gregaria* after feeding on *S. purpurea*, nymphs excreted more glucosinolates in their feces than adult and this trend was dependent on the type of food, i.e. adult are more capable of metabolic dealing with GSL of food than nymphs [14]. Generally plant secondary substances were stored in fat body, haemolymph and other tissues. In *Cycina inopinatus* cardenolids were sequestered into the haemolymph and maintained at very high levels throughout larval development on *Asclepias humistratia*, an elimination of cardenolides occurs mainly via the larval exuviae [45]. The turnip sawfly, *A. rosae* larvae sequester certain glucosinolates of their host plants within their haemolymph [46]. Specialist insect that sequester allelochemicals must prevent auto toxicity of these compounds. In some way this may be accomplished by isolating the compounds in glands [47]. The generalist

herbivore *Vanessa cardui* contain very low levels of iridoid glycosides in their haemolymph, where the specialist *Junonia coenia* levels are 50 to 150 fold higher [48].

Glutathione transferase and MFOs of Oligophagous insects attack the allyl and benzl-isothiocyanates when fed on plants containing GSL. Direct excretion occurs in some adapted crucifer-feeding insects, GSL are metabolized in less toxic compounds which are excreted [49].

Low excretion of GSL in the feces of *S. gregaria* confirmed that the insect was adapted to *S. purpurea* [14].

Many insects possess metabolic mechanisms for detoxifying plant monoterpenes that allow them to feed on plant containing monoterpenes without apparent effects. A frequently cited example of monoterpene detoxification involves the microsomal, cytochrome P-450 dependent oxygenases found in the guts of *Lepidopteran* larvae [50].

Allelochemicals as insect protectants: Plant allelochemicals can have profound effect not only on plant-herbivore interactions but on herbivore-natural enemy interaction as well [51]. Plant allelochemicals may be able to reduce the extent of herbivore damage by attracting natural enemies of its herbivores, such as predators, parasitoids, parasitoids, or pathogens. Cucumber beetle employ cucurbitacins in their own defense, sequestering them in haemolymph, eggs and other body tissues to gain protection from predators [52]. The larvae of two species of *Penstemon sp* use the iridoid glycoside as warningly colored black and white from sequester iridoid glycosides [52]. Larvae of the catalpa sphinx are warningly colored black and yellow by using the iridoid glycoside in their food. Butterflies feeding on flavone-containing plants accumulate flavones and their utilization by the insect for protection against bird predation [43].

Dietary terpenoids are some time sequestered by insects in their body tissues as defenses against predators and other enemies.

Tobacco budworm larvae fed high concentrations of gossypol are s favorable hosts for development of the parasitoid, *Campoletis onorensis* [53]. Plant defensive toxins such as cardenolides that are sequestered by specialist herbivores can be an extremely effective defense against their natural enemies, grasshopper, *P. bmtionius* using cardenolides in their food (*C. procerca*) in defence against the birds [26]. Larvae of *Zygaena filipendulae* use cyanogenic glucosides in defence

against predators [54]. Larvae of *A. rosae* using the glucosinolates for their own defence [55].

Allelochemicals and insect pheromones: The initial attraction of bark beetles to their host trees is often due to volatile monoterpenes emanating from the tree, when the first individuals begin boring into a tree, volatile aggregation pheromones are released that attract other for a mass synchronized attack. These aggregation pheromones are frequently allylic-oxidation products of host monoterpenes. Mating pheromone of *Utetheisa ornatrix* was synthesized from pyrrolizidine alkaloids that were sequestered from host plant *Crotalaria* sp [56]. Some glucosinolates in the diet of mustard aphid are concentrated in the body for further use, as alarm pheromone production [57].

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