Grasshoppers – Generalists to Specialists?

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Insects like the grasshopper have developed different mechanisms to protect themselves from the chemical defenses of plants. During evolution, grasshoppers which showed no preference for a particular food, developed these for plants whose chemical defenses they could tolerate.

Plants' Defence

How do plants, which do not move, protect themselves when attacked by predators? They produce substances, which are used for defense against predators, along with primary compounds necessary for their survival. The defensive chemicals are called secondary compounds and can be toxic or repellant to the predators. These include phenolics, terpenoids, alkaloids, cyanogenic glycosides, etc.; many plants permanently store such defensive compounds. The neem plant stores azadirachtin, which interferes with the hormonal system of insects and serves as an antifeedant. Similarly, desert plants contain numerous poisonous substances which deter herbivores from feeding on them.

Some plants produce defensive chemicals only on being attacked ('induced defense'). They also release volatile compounds into the air which attract predators and parasites that kill insects attacking them. This is like the tomato plant which makes itself less acceptable as a food source by producing inhibitors when attacked. These impede the insect's ability to break down proteins it ingests from the plant.

It has been established that when the plant, Sitka willow, *Salix sitchensis*, is attacked by insects, it produces compounds that reduce its leaf quality making it less acceptable to the insects. Along with this, the attacked plant also produces signals that inform the nearby willows of the impending danger.

Keywords
Antifeedants, co-evolution, cassava, tomatine, linamarin.

Insects Fight Back

If plants developed defenses against insects, then insects have also developed such defenses in retaliation, a process termed as co-evolution. This is a process in which two interacting species exert pressure on each other such that the properties and characteristics of one organism evolve in response to specific properties of the other.

Co-evolution helps both insects and plants develop their respective defense mechanisms.

How Grasshopper Senses Toxic Compounds in Plants

To protect themselves from toxic compounds, insects need to first sense them in their food. Grasshoppers use different parts of their body to evaluate the quality of the food. Chemoreceptors on leg parts and small feeler or antenna-like structures growing from lower lip play an important role in this process. Sensory organs of smell as also the mouth-part structures lying at the back of grasshopper's mandibles and sensory structures growing from them help in this evaluation (*Figure* 1). Chemoreceptors include cells which respond to toxic secondary compounds and to compounds which stimulate feeding ('phagostimulants'). The latter acts as a sweetener and masks the bitter taste of secondary compounds. Many nutrients, like sugars as well as some secondary compounds stimulate feeding. Amino acid mixtures found in plants show relatively weak stimulating effect, but when mixed with sucrose may stimulate feeding.

Grasshoppers use different parts of their body to evaluate the quality of the food.

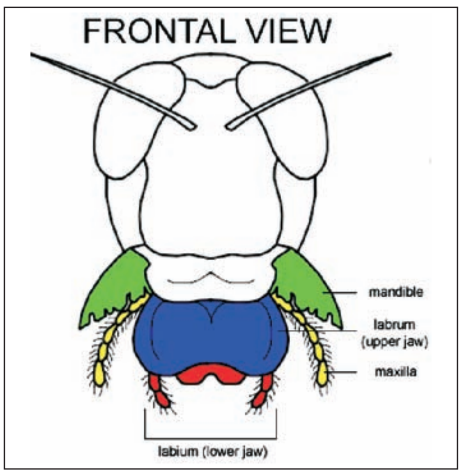


Figure 1. Frontal view of the mouth parts of a grasshopper.
Source: http://en.wikipedia.org/wiki/Image:Grasshopper_mouth.png

The relative concentration of phagostimulants and deterrents determine the acceptability of a plant for an insect.

The acceptability of a plant to an insect is dependent on the relative concentrations of phagostimulants and deterrents. If the concentration of deterrents is large, along with activating the deterrent sensitive cells, they can also suppress the activity of the responding cells. Thus, insects are unaware of the palatability of the plants. If the concentration of such phagostimulants is high, they may suppress the activity of deterrent sensitive cells. For example, tomatine (found in tomatoes) at 0.1% dry weight almost totally inhibits *Locusta migratoria* (migratory locust) from feeding on highly palatable wheat flour wafers, but large amounts of sucrose mask the bitter taste of tomatine making the wafers palatable.

Certain secondary compounds like non-protein amino acid, Canavanine (a behavioral deterrent for the American desert locust, *Schistocerca americana*) does not stimulate the deterrent cells. It, however, suppresses the activity of the sucrose sensitive cells so that the insect remains unaware of the palatable properties of any food containing it.

Feeding Aversion Learning

Before feeding on a plant, grasshoppers repeatedly touch a leaf surface with peg-like sensory organs present on the tips to evaluate the quality of the food – if it senses something unpalatable it rejects the food without biting and thus gets protected from the toxicity of the deterrents. But if it comes across some new plant, the grasshopper sometimes bites it to evaluate its quality. On subsequent encounters, however, rejection or acceptance of the plant is based on the grasshopper's prior experience with it. 'Feeding aversion learning' occurs when grasshoppers learn to associate some unpalatable internal constituent of the leaf with the characteristics of its surface compounds and thus avoid it.

If an insect senses something unpalatable it rejects the food and learns to avoid it in future as well.

There are some toxic compounds like unsuitable sterols which grasshoppers are unable to detect on palpation. However, learnt avoidance to such toxic compounds may occur due to some noxious effects. If *Schistocerca americana* is given spinach leaves (which contain only unsuitable sterols), duration of subsequent meals on the leaves will decrease and finally the insect will reject it. This happens because the grasshopper learns to associate spinach with some post-ingestive noxious effect it has experienced in the past and thus avoids it.

Figure 2. The cassava plant. Source:http://en.wikipedia. org/ wiki/Image:Cassava.jpg

How Grasshopper Copes with Secondary Compounds in its Diet

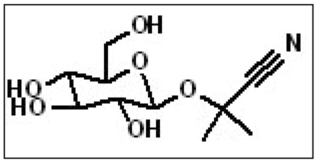
Toxic secondary compounds are present in almost all plants. If grasshoppers become averse to all plants, they would eventually starve to death. To prevent this, they have evolved various mechanisms to detoxify some secondary compounds in their diet. Thus, generalist grasshoppers, which have no feeding preferences, become specialists in detoxifying certain secondary compounds.

Figure 3. The cassava root. Source:http://en.wikipedia.org/ wiki/Image: Manihot_esculenta_ dsc 07325.jpg

Grasshoppers which can feed on any plant belonging to different families like *Schistocerca americana, Schistocerca gregaria,* etc., have structures corresponding to their stomach/intestine consisting of extensive back and front arms ('posterior' and 'anterior arms') (*Figure* 2). Probably the arms at the back portion are concerned with detoxification of secondary compounds as they absorb the solid food entering the midgut**,** owing to their large surface area. In addition, in some species, the uppermost layer of back cecal arm consists of deep pockets lined with an envelope which accumulates macromolecules like tannic acid. Its contents are thrown out along with the feces.

Many grasshoppers prefer food with small amounts of secondary compounds, less than the threshold concentration (concentration above which the compounds can be very toxic). These compounds can be detoxified owing to various modifications in the midgut regions, like *Zonocerus variegatus*, a polyphagous West African species which often feeds on cassava (*Manihot esculenta*) (see *Figures* 2, 3). The cassava[1] plant contains cyanogenic glycoside-Linamarin (Structure 1) which itself is not a deterrent for the insect. When an insect bites a healthy leaf it is repelled by a puff

[1] The cassava plant is found in Kerala in India. Its edible part is the root which is eaten only after boiling it two to three times (to remove cyanogenic glycoside). It is considered the poor man's food and is rich in carbohydrates.



Structure 1. Linamarin.

of hydrogen cyanide (HCN) produced by enzymatic action on linamarin. But the insect has become a specialist in avoiding HCN by feeding on wilted leaves (rather than healthy leaves) as these produce low concentration of HCN which is not enough to deter the insect from feeding on it. The plant wilts due to various reasons like old age, lack of water in the environment and even due to multiple bites by the insects.

The grasshopper is repelled by a puff of hydrogen cyanide (HCN) when it bites a healthy leaf of the cassava plant.

Locusta migratoria prefers older sorghum (*jowar*) leaves. Grass-feeding species find seedling grasses less palatable than mature grasses, as these contain high concentrations of secondary compounds. As the plants mature, the level of secondary compounds in them decline and they become more palatable. Something similar is seen in *Taeniopoda eques* (Burmeister) (*Figure* 4) which is a highly mobile species and consumes many different species of small herbaceous annuals in one day so as to receive enough nutrition. This also prevents the insect from ingesting large quantities of poisonous compounds. The insect keeps switching between food items with different secondary compounds as it has a predilection for new compounds. Successive meals on the same plant species (even a highly nutritious plant) become successively smaller, but as soon as the insect switches to a new plant species (even if it is relatively deterrent) it eats a large meal again. Through this mechanism it can include initially unpalatable but highly nutritious plants in its diet. A similar behavior is also seen in the grasshopper *Schistocerca gregaria* (desert locust).

These feeding habits imply that a certain threshold concentration of secondary compounds is required to deter insects from feeding. This concentration is not be the same for all species.

Figure 4. *Taeniopoda eques* (also called the 'horse lubber' because of its horse-shaped cuticle).
Source: http://fireflyforest.net/firefly/2007/11/02/horse-lubber-grasshoppers/

***Habituation*:** Habituation is the decrease in response to a stimulus with repeated exposure to it. Some grasshoppers can get used to (habituate) certain compounds due to (i) desensitization of deterrent sensitive cell to the compounds or (ii) induction of some detoxifying enzymes in the midgut of the grasshoppers or (iii) both.

Some grasshoppers can get addicted to nicotine!

This helps the insect in specializing in long-term adaptations to some but not all noxious foods. *Schistocerca gregaria* can get habituated to nicotine hydrogen tartrate (NHT) on repeated exposure to the compound and thus can eat NHT-treated food, as readily as normal food without experiencing any harmful effects. Habituation, however, does not occur in all grasshoppers – *Locusta migratoria* does not get habituated to NHT.

***Utilization of secondary compounds by grasshoppers*:** Some grasshoppers have developed mechanisms in the strong midgut region to sequester plant secondary compounds and metabolize them into some useful form. The compounds help in their growth and development or in protection against predators. Certain grasshoppers 'advertise' their intrinsic toxicity by the bright coloration and distinctive markings on their wings. The grasshopper, *Poekilocerus bufonius*, defends itself by ejecting a spray, which contains two major cardiac active compounds (*Figure* 5).

Some grasshoppers even spray their predators to cause heart attacks in them!

It extracts these two toxins, that can severely disrupt normal cardiac function, from milkweed plants on which it exclusively feeds. The tree locust, *Anacridium melanorhodon*, exhibits increased growth on a tannin containing diet. It retains most of the

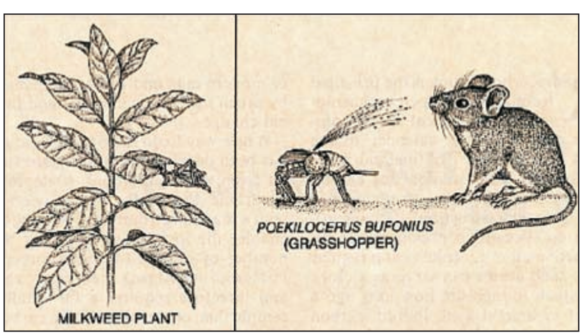


Figure 5. The grasshopper, *Poekilocerus bufonius,* uses the cardenolides produced by milkweed plants for defense against predators like rats. Source: http://www.uky.edu/~garose/link100.htm

tannins which bind to the sclerotized cuticle, stabilizing the proteins there.

Box 1.

Grasshoppers themselves are a highly prized item of human food in countries like Tanzania. During swarms many people collect the insects which are then salted, fried or roasted to make a spicy crunchy snack serving as a good source of income to many people. The average retail price per kg of this insect in Kampala in 2008 was US $2.80, which compared favourably with that of the goat meat, which sold at US $2.30 per kg.

Conclusions

Plants produce many secondary compounds like alkaloids, phenols and terpenes for their defense. Some plants permanently store the metabolites, which are toxic or repellant to predators and others secrete the compounds only when attacked. In ecological retaliation, insect herbivores develop their own defenses through the process of co-evolution like developing the midgut region to detoxify small amounts of secondary compounds or getting habituated to them. Thus, generalist grasshoppers become specialists in combating the toxicity of certain chemical defenses of plants and also using them for their own benefits. A constant tug of war goes on between plants and insects in which sometimes plants and sometimes insects win.

If secondary metabolites are capable of protecting plants, can't they be used as insecticides for crops? In fact, some of the ecdysone agonists are already available in the market such as Tebufenozide RH-5992 (Rohm and Haas Company). Some neem -based insecticides are also commercially available.

Studies on chemical ecology can make important contributions to the efforts for developing environmentally safe pesticides. It should be possible to exploit natural compounds which are toxic only to pests (not to mammals or beneficiary animals) and deter them from feeding on crops.

Suggested Reading

[1] **S V Eswaran, Why Does the Grasshopper Not Eat Spinach, *Resonance*, p.978, 2009.**

[2] **E A Bernays and R F Chapman, Plant Secondary Compounds and Grasshoppers: Beyond Plant Defenses, *Journal of Chemical Ecology*, Vol.26, No.8, pp.1773–1794, 2000.**

[3] **Video, 64 km clouds of grasshopper!, http://in.youtube.com/watch?v=kcArEEvQZ-M.**

[4] **Video, How locusts perceive the signal to swarm, http://in.youtube.com/watch?v=uURqcI08IC4.**

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