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Significance of Cyanogenesis in Arthropods

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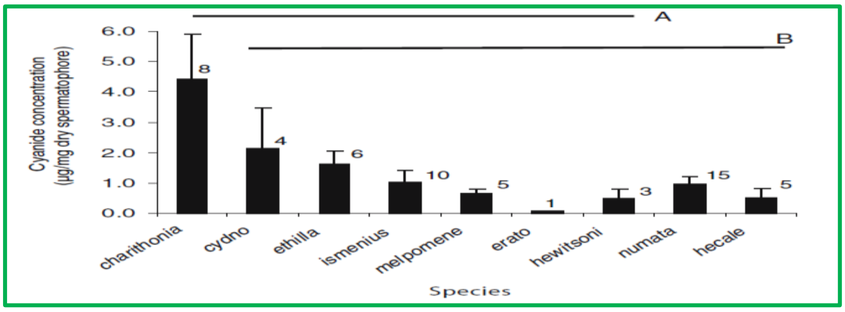
Chemical defences are key components in insect–plant interactions, as insects continuously learn to overcome plant defence systems by detoxification, excretion or sequestration. Cyanogenic glucosides (CNglcs) are important natural products in the chemical warfare between plants and arthropods. More than 60 different CNglcs structures are known. CNglcs are β-glucosides of α-hydroxynitriles derived from the aliphatic protein amino acids (valine, isoleucine and leucine), aromatic amino acids (phenyl alanine and tyrosine) and cyclopentenoid non-protein amino acid. CNglcs are found in a wide range of arthropods namely, millipedes, centipedes, mites, beetles, bugs, and especially butterflies and moths. The ability of living organisms to produce hydrocyanic acid (HCN) is termed as cyanogenesis (Zagrobelny *et al.*, 2018).

Biosynthesis of CNglcs from amino acids which will be subjected to two successive N-hydroxylations followed by decarboxylation catalyzed by cytochrome P450 monoxygenase enzyme and UDPG-glycosyltransferase. Catabolism of CNglcs is initiated through enzymatic hydrolysis by β-glucosidase to afford the α-hydroxynitrile which is unstable compound and it is converted to toxic HCN by α- hydroxynitrile lyase. HCN is a respiratory inhibitor, inhibits the cytochrome oxidase enzyme resulting in the inability of organisms to use oxygen (Naveena *et al.*, 2021).

CNglcs have acquired multiple physiological function in defence, intraspecific communication, host–insect recognition, assessment of mate quality, nuptial gift and recruited as storage compounds that are mobilised when needed to counteract imbalances in primary metabolism (Zagrobelny *et al.*, 2007). Linamarin and lotaustralin are present in all instars of Zygaenidae, which are able to biosynthesise the CNglcs *de novo* as well as to sequester them from larval food plants. Contraction of irritated segments results in the appearance of droplets on the cuticular surface of the larvae which contain CNglcs which help to avoid from predators and parasitoids. The oribatid mite, *Oribatula tibialis* (Nicolet) uses the cyanogenic aromatic ester mandelonitrile hexanoate (MNH) for HCN storage, which degrades *via* two different pathways, both of which release HCN. MNH is emitted from exocrine opisthonotal oil glands, which are potent organs for chemical defense in most of the oribatid mites (Bruckner *et al.*, 2016).



Average cyanide concentration (µg/mg spermatophore dry weight) of dissected spermatophores from mated *Heliconius* females.

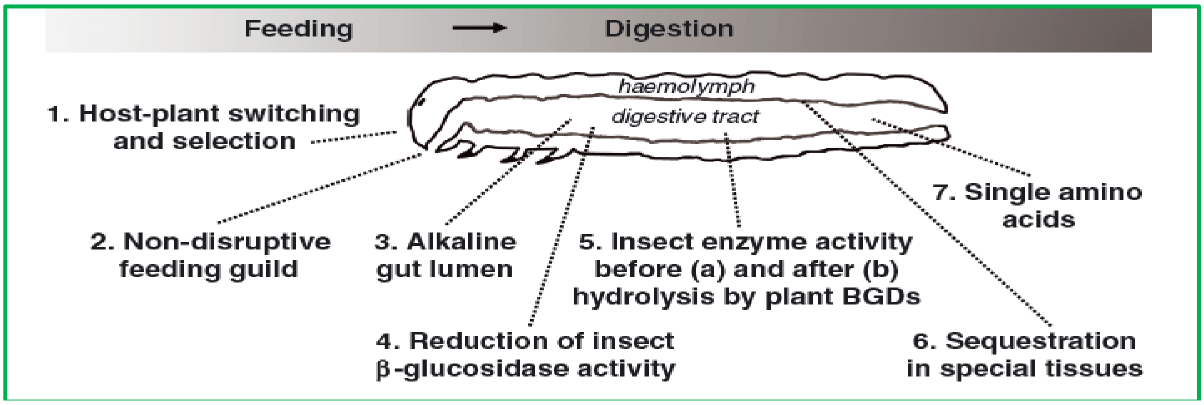
Males of several insect species transfer nuptial gifts to females during mating, typically in the form of a protein-rich spermatophore. Males of *Heliconius sp.* are known to transfer nutritional gifts to the females which contain CNglcs. Males with low linamarin and lotaustralin is rejected by females (Cardoso and Gilbert, 2007).

Zygaena filipendulae L., larvae combine behavioural, morphological, physiological and biochemical strategies at different time points during feeding and digestion to avoid toxic hydrolysis of the CNglcs present in their food plant. They found that high feeding rate limits the time for plant β-glucosidases to hydrolyse CNglcs. Larvae performed leaf-snipping, a minimal disruptive feeding mode and highly alkaline midgut lumen inhibited the activity of ingested plant β -glucosidases significantly (Pentzold *et al.*, 2014).

Adaptations to prevent self-intoxication in Arthropods

Insect herbivores have evolved different adaptation to counteract and overcome two-component plant chemical defence. These adaptations occur at different stages of herbivory in a temporal context: before feeding (1) during feeding (2) during digestion.

1) Before feeding: recognition, switching and selection of host plant.
2) During feeding: impact of feeding by modifying mouth parts, piercing and sucking, leaf snipping or leaf mining method.
3) during digestion: physiological and metabolically adaptation to counteract two component system defence.
   a) Alkaline gut pH inhibit plant β-glucosidase enzyme
   b) Reduction of endogenous insect β-glucosidase activity in the gut
   c) Specialized enzyme activity in insects
   d) Sequestration: spatial separation of plant β-glucosidase in the insect
   e) Single amino acid counteract plant β-glucosidase activity



In a nutshell, CNglcs are the important chemical components not only used for self defence but also offers several advantages to Arthropods mainly, intraspecific communication, nuptual gift, assesment of mate quality, storage and metabolism of nitrogen compounds. Therefore, knowledge regarding presence, biosynthesis, hydrolysis and detoxification of cyanogenic glucosides in arthropods is the need of the hour.

References

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