Lac ecosystem: Complex yet fascinating

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Lac insects belonging to the genus *Kerria*, family Tachardiidae, and order Hemiptera are commercially harnessed for resin, dye, and wax. Owing to their nontoxic and harmless nature lac products find an incredibly wide range of applications in food, pharmaceuticals, cosmetics, paints, varnishes, surface coating industry, confectionery industry, postal department, fruit and vegetable coating, soft drinks, *etc*. Due to its great demand in the international market, a significant portion of lac (7293.47 tonnes) in different forms was exported to foreign nations and earned foreign exchange of Rs. 405.51 crores during 2019-20 (Yogi et al., 2021). Shellac, a refined lac product, has been permitted as a food additive by the European Union (EU) with E number E904 and has also received a GRAS (Generally Recognized as Safe) status from the U.S. FDA (Srivastava and Thombare, 2017). Since lac resins represent a significant part of raw lac, they can be hydrolyzed into their constituent acids. One of the constituent acids, aleuritic acid is used as a precursor for the production of a variety of high value chemicals such as isoambrettolide. Another product, lac dye, which is poly hydroxy anthraquinone derivatives has brilliance and fastness and is used for dying silk and wool.

The lac insect is a unique species of scale insect that feeds on a particular class of plants called lac hosts. These host plants together with the lac insect make up an ecosystem that is a complex multitrophic web of flora and fauna. The flora and fauna of this lac environment are part of a complex, multi-trophic network that displays a great variety of biodiversity. In addition to the lac insects, it also includes host plants, several lac insect predators and parasitoids secondary parasitoids microbes, and a variety of host plant pests. The first trophic level in this ecosystem is made up of the host plants for lac insects, followed by the second by lac insects, pests of host plants, the third by primary parasitoids and predators of lac insects, and the fourth by hyperparasitoids of lac insect pests and the fifth by microbes inhabiting these flora and fauna and even soil.

Trophic level 1: Lac host plants

Lac insects thrive by sucking phloem sap from the delicate branches of the host plant. Lac insects can live on over 400 plant species that grow naturally in forests (Kapur et al.,1954). Lac production and quality are mainly dependent on the host plant and lac insect strain. As lac insect is immobile almost throughout its life (except for crawlers and adult males) and attaches to the host plant where it can obtain nourishment efficiently and with a greater affiliation, the host plant plays a critical role in the production and regulation of lac. The quality of lac pigment (erythrolaccin) present in the resin also relies upon the lac insect and the host plant on which the insect is growing (Mishra et al., 1999).

Lac host plants can be divided into numerous categories based on the degree of preference of lac insects for specific hosts and the quantity and quality of lac obtained by inoculating the host. Firstly, some species make notable hosts throughout the year and anywhere they exist. Secondly, some species are good hosts in certain restricted areas of the country, while in other areas these species are not suitable for lac cultivation. Thirdly, there are hosts which are major hosts for positive precise functions in certain specified seasons. Again, at the same time as one sole or sort of host species is a good host, another (which might be botanically indistinguishable from the first) may be a non-host (Sharma et al., 2024 under publication). Based on lac cultivation and use possibilities for domestic distribution, lac host plants are grouped into

3 categories (Srivastava, 2011) common host plant, occasional host plant, and rare host plant. Out of 400 identified lac hosts, few are of commercial importance. The traditional lac hosts in this country are *Schleichera oleosa* (*kusum*) (Fig. 1a), *Butea monosperma* (*palas*) (Fig. 1b) and *Ziziphus mauritiana* (*ber*) (Fig. 1c). *Flemingia semialata* (Fig. 1d) has gained popularity as a lac host due to its bushy nature, facilitating cultural operations easily. There are a few endemic hosts and recently diagnosed as potential hosts. Those include *Ficus* spp*., Samanea saman, Cajanus cajan* (pigeon pea), *Malvaviscus penduliflorus*, *Calliandra calothyrsus*, and *Calliandra surinamensis*. *Ficus* spp. generally act as broodlac savers during summer.

Trophic level 2

A. Lac insects

Out of the reported nine lac insect genera and 101 species in the world, two genera and 28 species are found in our country, representing 27.7% of the known lac-insect species diversity (Sharma et al., 2024 under publication). Under the *Kerria* genera 24 species are found in India (Garcia et al. 2016). *Kerria lacca* is the most important and widely cultivated commercial lac insect in India. *Kerria chinensis* and *Kerria sharda* are also cultivated to some extent. Based on the life cycle, lac insects are particularly divided into two strains, *rangeeni* and *kusmi*. Both the strains are categorized into two crops each i.e., for *kusmi*,theyare *aghani*(from June/July to January/February) and *jethwi* (from January/February to June/July) and its main host plant is *S. oleosa*, and for *rangeeni*, they are *katki* (from May/June to October/November) and *baisakhi* (from October/November to May/June) and its main host plant is *B. monosperma*. *Kusmi* strain secretes superior quality resin compared to *rangeeni* and it is indigenous to India.

Life cycle of lac insects: Lac insects are ovoviviparous insects that produce juveniles after hatching within the mature female cell. Biologically, lac insect's life cycle is divided into three stages: nymph, pupa and adult and practically as crawler, settled nymph and adult. Crawlers are tiny boat-shaped nymphswith three pairs of legs and a pair of antennae, as they come out of the female insects and crawl throughout the tree branch in search of soft branch to get settled so that they can feed by piercing the shoot with their long proboscis and do not move afterward.

Following one to two days of settlement, settled nymphs begin secreting resin through resin glands that are located throughout the cuticle region. They gradually transform into males and females through three moultings although in distinct ways of metamorphosis. For example, only males go through complete metamorphosis, whereas females do not go through the pupal stage. After the first moult, both of them lose legs, eyes, and antennae and transform into second instar. Then second instar male lac insects get transformed into pre-pupa and later undergo metamorphosis into pupa where they stop feeding where the degeneration of internal organs from larval stage starts and histogenesis begins. Male and female can now be distinguished at this moult stage as the male is elongated or cigar-shaped while the female is round-shaped. After that, those who get transformed into males (both winged and wingless) come out from the encrustation sacrificing their piercing mouth part. Then males fertilize female lac insects which cost them their life as without nutrition they survive for a few days and die. After fertilization, females secrete more resin and continue to grow bigger to accommodate the young ones. After attaining maturity, eggs are laid in the cavity by shrinking of the female cells, which are identified by yellow dots on the lac encrustations. Each female is capable of laying 200–500 eggs which hatch immediately inside the encrustation and emerge out of the female. This is called swarming, and the life cycle goes on (Fig. 2).

B. Lac host associated fauna

Like other plants, lac host plants are also subjected to attack by hordes of insect pests. There are different types of lac host plant pests available which are also components of the second trophic level. They include sap sucking insects, defoliators, pod borers, seed borers *etc*. which damage host plants. Since the productivity of lac depends on the availability of healthy shoots on host plants, damage done by insect pests has direct bearing on it. According to reports, significant lac host plants are infested by 61 sporadic and minor pests, including roughly 19 major pests (Sharma and Ramani, 2001). A pest complex of about 32 insect pests belonging to six orders and 20 families has been recorded on *Flemingia semialata* (Meena et al*.,* 2014). Egyptian cottony cushion scale, *Icerya aegyptiaca*, scale insect, *Aulacaspis* sp., leafhopper, *Amrasca biguttulla*, weevils, *Amblyrrhinus poricollis* Schoenherr and *Peltotrachelus* sp., sweet potato bug, *Physomerus grossipes* Fabricius, soapberry bug, *Leptocoris augur* (F.) have been reported as pests on *kusum* (Singh et al., 2014).

Trophic level 3

Lac crop is destroyed by a number of major and minor pests, which not only dramatically reduces the yield but also has an impact on the quality of the lac. Since lac insects are sedentary, they are more vulnerable to predators and parasitoids. Predators include both vertebrate and invertebrate species, while the parasitoids are all insects. On average, loss to the lac crops by these predators and parasitoids results in 35-40% of the damage annually. Twenty species of lac insect predators, 30 species of primary parasitoids, 45 species of secondary parasitoids are known (Das, 1990).

A. Predators

The lepidopteran predator makes a tunnel inside the lac and makes a hole while adult emergence damaging the resin cover. On lac, there are three main predators *Eublemma amabilis* (Fig. 3a)*, Syncola* sp. (Jadhav et al., 2020; Fig. 3b)*, Chrysopa* sp. (Fig. 3c); the first two cause severe damage compared to *Chrysopa* sp. (Bhattacharya et al., 2005). Relative abundance of the major lac predators differs with the strains of lac insects. The number of *E. amabilis* is higher than that of *Syncola* sp. on *rangeeni* lac insects, whereas it was just the reverse on *kusmi* insects. Another predator, *Chrysopa* sp. was recorded only from *kusmi* lac insects casually and in low numbers. The abundance of lac predators is very much dependent upon the availability of food as their number increases in the growth of lac insects which finally attain a size 6-8 times that of larva at birth. Predators are more numerous during the summer crops (*baisakhi* and *jethwi*) than in those passing through rainy seasons (*katki* and *aghani*). There are a few vertebrate predators of lac insects, including monkeys, squirrels, rats, woodpeckers, and birds (Lalita, 2020). These vertebrate predators indirectly help in carrying the lac insects to newer locations.

B. Parasitoids

Parasitoids harm the lac insect by laying their eggs inside the lac cell and larvae hatch from the eggs, feed on the lac insect and destroy the whole crop. *Aprostocetus purpureus* (Fig. 3d) is the most abundant species followed by *Tachardiaephagus tachardiae* (Fig. 3e) and these together constitute 84.19% of the lac pest population (Sharma et al., 1997). The numbers of other parasitoids particularly *Parechthrodryinus clavicornis*, *Coccophagus tschirchii, Eupelmus tachardiae* are low and do not differ much among themselves within the crop. *Rangeen*i strain crops are more damaged during the damp season (*katki* crop) because they are more susceptible to pest attack rather than *kusmi*. In *kusmi* and *rangeen*i strains, the amount of resin was reduced by 17.92% and 17.44%, while fecundity was reduced by 32.55% and 34.71%, respectively due to parasitoids (Sharma and Ramani, 2001). Damage caused by parasitoids varies depending upon the virulence of outbreak and the stage of development of lac insect at which damage is inflicted.

Trophic level 4: Hyperparasitoids

Hyper parasitism is the development of secondary insect parasitoid at the expense of primary insect parasitoid. Insect hyperparasitoids, the most diverse members of insect food web therefore attack another insect developing or developed in or on another insect host, which can affect the biological control of the pest. There are two types: i. True hyperparasitoids which parasitize the larvae of their hosts (parasitoids), reaching these larvae with their ovipositor through the herbivore that hosts the parasitoid larva. ii. Pseudohyperparasitoids which attack the pupae by laying their eggs on the parasitoid (pre)pupae.

The common lac hyperparasitoids are *Elasmus claripennis*, *Eurytoma pallisdiscapus, Brachymeria tachardiae, Apanteles tachardiae* (Fig. 4a)*, Apanteles* sp., *Bracon greeni* (Fig. 4b) and *Pristomerus sulci* (Mohanasundaram et al., 2016). *E. claripennis* is a parasitoid of the important lac predator, *E. amabilis* which emerges to be an implicit biotic agent in the natural control; it has a short life cycle 11-20 days in summer and rainy season, and 20-32 days in winter, a favorable female ratio (84.3%), relatively high fecundity (on an average 28.4, and a maximum of 118 eggs/female), an adult life (approx. 26 days for female and 8 days for males), activity which is well synchronized with that of the host, has no hyperparasites and parasitizes the host larvae in their early instars (Meena and Sharma, 2018). Since hyperparasitoids have the potential of biological lac pest control, they are positive players in lac cultivation.

Trophic level 5: Microbes

Insects and plants have partnerships with microbes to develop novel useful functionalities. Bacteria perform a variety of advantageous tasks for their hosts, such as boosting stress resistance, protecting against adversaries, and even developing resistance to insecticides, *etc*. However, the supply of dietary supplements is the most typical host advantageous characteristic. The microbial partners which are symbionts to host insects (including lac insects, lac predators, parasitoids, hyperparasitoids, and lac host pests) are called endosymbionts, and those are symbionts to host plants are endophytes.

A. Endophytes

Endophytes are diverse group of microbes that usually impact plant communities by increasing fitness which is achieved through conferring of abiotic and biotic stress tolerance, increasing biomass, decreasing water consumption. Endophytes produce a broad range of phyto-hormones, such as auxins, cytokinins, and gibberellic acids to assist proper growth of the plants. They are also capable of synthesizing bioactive compounds that are used by plants for defense against pathogens and some of these compounds have proven to be useful for novel drug discovery as well as in industries, and agriculture. Depending on how they interact with their host plant, they might be categorized as advantageous, neutral, or harmful. Endophytes are often found in the vascular tissues and intercellular space of plants. The endophytes *Agrobacterium larrymoorei*, *Rhizobium sp*., *Sphingomonas sp*., and *Priestia megaterium* have been identified from the phloem sap of lac host plants, *Flemingia* spp. (unpublished data from our lab). Bacterial strains were isolated from the root nodules of *Flemingia* spp. and are classified as *Bacillus* (55%), *Rhizobium* (10%), *Pseudomonas* (10%), *Agrobacterium* (4%), *Brevibacillu*s (4%), *Ensifer* (4%), *Lysobactor* (4%) and new (10%) based on 16S rDNA genotyping. Rhizobial culture-treated plants showed significant increase in plant height, nodule count on roots, and leaf area by 62%, 32%, and 50%, respectively (Tribhuvan et al., 2017). Endophytes with positive impact on plant growth and health would have a beneficial role in lac production.

B. Endosymbionts

Interaction of insects and microbes are from obligate mutualism to facultative parasitism. Insects shelter symbiotic bacteria on the integument, in the digestive tract, and in some unique structures within their body. The role of endosymbionts in insects includes digestion (of recalcitrant food), nutrition (supplementation of vitamins and other essential nutrients), protection (production of anti-fungal agents, detoxification of pesticides), resistance (against predators, parasites and pathogens), inter and intra-specific communication (pheromone production), increasing efficiency as disease vectors, host insect morphogenesis and temperature tolerance (Dillon and Dillon, 2004).

Lac insects are associated with both bacteria and fungi. Bacteria are mostly symbiotic and sometimes pathogenic. *Wolbachia* is the most ubiquitous endosymbiotic bacteria of insects, which is present in lac insects and may have been held responsible for its putative role in lecanoid chromosome system of sex determination and in the biased sex ratio of *K. lacca* population (Jaipuriar et al., 1985). *Wolbachia* mainly undergoes vertical transmission from mother to offspring. Other than *Walbachia*, *Pantoea* sp. was found to be another dominant bacterial genus found in lac insects (Kandasamy et al., 2022). It was also found that the bacterial diversity varies between different life stages of lac insect and lac insects grown on different host plants. *Bacillus kochii, Bacillus oceanisediminis, Bacillus amyloliquefaciens*, *Bacillus nakamurai*, and *Enterobacter cloacae* were observed on *kusmi* lac insects collected from *kusum. Klebsiella quasipneumoniae* subsp. *similipneumoniae, Citrobacter amalonaticus*, *Providencia vermicola* and *B. nakamurai* were found in lac insects collected from *ber. Enterobacter ludwigii, B. nakamurai* and *Enterobacter cancerogenus* were found in lac insects collected from *F. semialata* (Thamilarasi et al., 2018).

C. Fungal growth on lac insects

Lac insect association with fungi is not always beneficial. Being phytosuccivorous in habit, lac insects excrete large quantity of sugar-rich honeydew which becomes a major cause of fungal contamination. *Capnodium*, *Fumago*, *Conidiocarpus*, *Polychaeton* sp. *Aspergillus awamori* Nakazawa, *Aspergillus terricola* and *Penicillium citrinum* are some of the fungi present on lac crop (Sharma and Jaiswal, 2011). A complex of fungal species inhabits the lac insects and causes sooty mold disease of lac crop. Fungal infection affects lac yield by inhibiting respiration, mating process and larval emergence (Sharma and Kandasamy, 2023).

Others

Besides fungal growth, honeydew serves as an excellent medium for bacterial growth. *Enterobacter sp., Klebsiella variicola*, *Stenotrophomonas maltophilia, Pantoea cypripedii*, *Pseudomonas stutzeri, Pantoea dispersa, Bordetella trematum* and *Cedecea davisae* were isolated from lac insect honeydew (Shamim et al., 2019).

The honeydew that the lac insect excretes is naturally consumed by several ant species, honeybees, and other insect species, preventing losses due to fungal infestation. This illustrates the importance of honeydew in the development of tri-trophic interactions between plants, insects, and their natural enemies.

Conclusion

Lac insects are one of the most fascinating insects known to mankind and such is the ecosystem in which they exist. This article described only the biotic components of the lac ecosystem; however, abiotic components also have a remarkable role in lac production. Systemically studying lac ecosystem provides clues to the researchers in increasing lac production and also to control lac insect pests and diseases. Although the lac ecosystem is studied greatly, still more studies are needed to further explore the lac ecosystem and tweak the system in more fruitful ways.

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Fig. 1a. *Kusum* tree

Fig. 1b. *Palas* tree

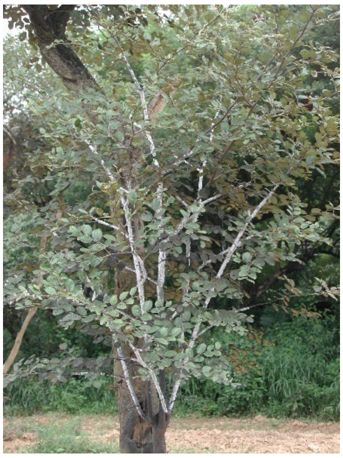

Fig. 1c. Lac insects on *ber* tree

Fig. 1d. Lac insects on *Flemingia semialata*

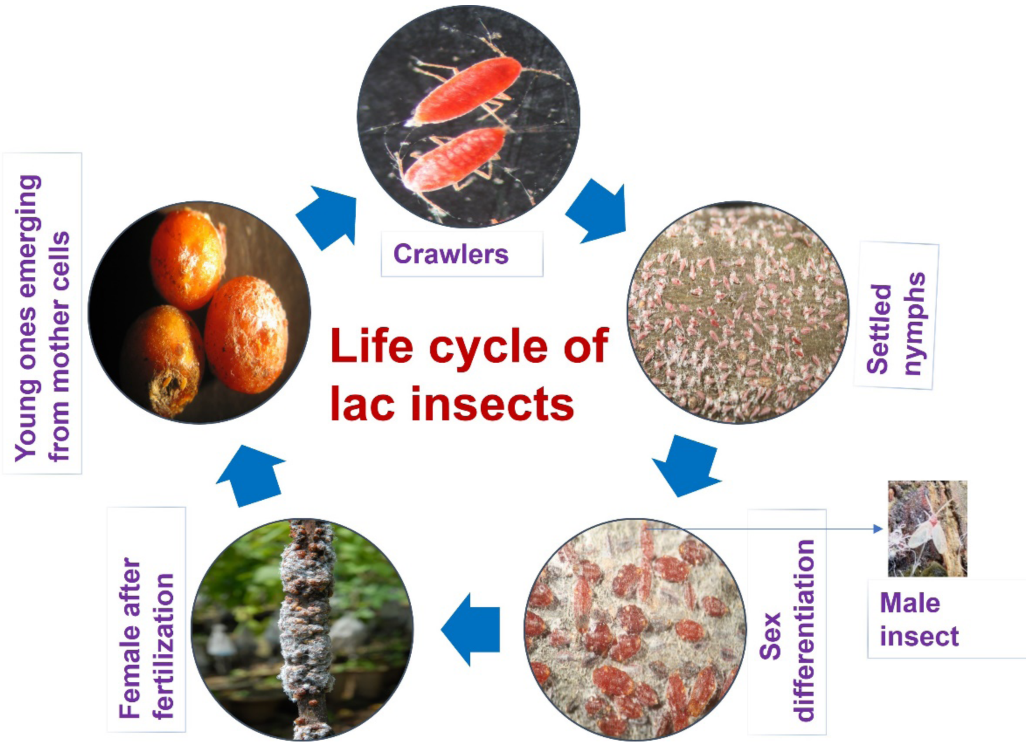

Fig. 2. Life cycle of lac insects

Fig. 3a. *Eublemma amabilis*

Fig. 3b. *Syncola* sp.

Fig. 3c. *Chrysopa* sp.

Fig.3d. *Aprostocetus purpureus*

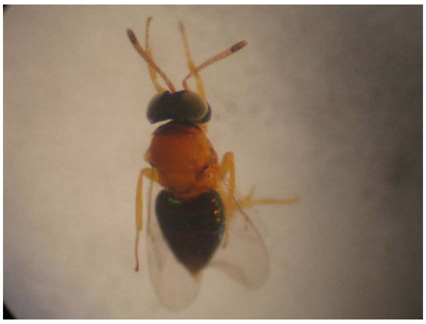

Fig. 3e. *Tachardiaephagus tachardiae*

Fig. 4a. *Apanteles tachardiae*

Fig. 4b. *Bracon greeni*

All figures courtesy: Dr. A. Mohanasundaram

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