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Defensive Role of Plant Latex on Insect Pests' Suppression: A Critical Review

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Abstract

Over 350 million years have passed since the documentation of the first interaction between plants and insects. Numerous plant defense qualities and associated counter-adaptive features have developed as a result of these interactions between insects and plants. These characteristics might be either morphological or biological in nature. One of the most significant and useful biochemical characteristics in plants is latex. Latex has a sticky property due to presence of secondary metabolites in it, which aids in entangling or sealing the mouthparts of small insects. These metabolites also chemically interact with the insects interfering with crucial bodily processes. Plant latex has amazing properties that help protect plants from insects and inhibit them in general. It may be possible to control insect pests in a natural, secure, and long-lasting manner by correctly identifying plant latex with strong insecticidal properties and developing formulations of plant latex.

Keywords

Plant Latex, Insect Herbivory, Plant Defence, Insect-Plant Interactions

1. Introduction

Co-evolution of insects and plants has been ongoing for millions of years. Plants and herbivorous insects are engaged in a constant, quiet conflict. Insects are ready to create counter-adaptations because plants are constantly looking for new methods to fend off insect pests. This complex interaction has resulted in the evolution of certain plant defence qualities, as well as their counter-adaptive characteristics in insects. To counteract one another's tactics, both plants and insects have developed morphological and physiological defence characteristics. However, given their dynamic character, biochemical interactions are thought to be more significant and effective than morphological ones.

The employment of safe and sustainable methods to improve agricultural yield and lessen dependency on chemical pesticides is becoming increasingly important in modern times. When establishing a pest control approach, it is crucial to comprehend and include the many naturally present defensive features that plants have against insect herbivory. In order to create and implement management techniques to outwit the insect pests, it is equally vital to comprehend how the insect pests have adapted to these defensive features. The current essay will concentrate on latex, one of these plant defensive characteristics.

2. What Is Latex?

The root, stem, leaves, and fruits of all angiosperms contain plant latex [1], a natural polymer released as a milky fluid by cells with a high level of specialisation called laticifers [2] (**Figure 1**). It is an emulsion-like sticky substance that resembles white glue. It is released from many plant parts in response to a small tissue injury. Normal latex colours include white, yellow, orange, and red; however, they change when exposed to air. It is a complex mixture of various phytochemicals, mostly secondary metabolites like flavonoids, alkaloids, triterpenes, acetogenins, and saponins. It also contains starch, sugars, oils, tannins, resins, sterols, fatty acids, resins, and gums that coagulate when exposed to air. A variety of enzymes and inhibitors, including thrombins, plasmins, papain, hevein, allergens, toxins, and lectins are present in latex [3]. Numerous functions, including the elimination of waste metabolites, protecting damaged tissue, fending off herbivores, and fending off infections are performed by the plant latex. The protective function of plant latex against various insect pests will be covered in this article.

2.1. Brief History about Latex

The term "latex" was first used by English physicians in the 1600s, who compared its functions with animal lymphatic veins [4]. Later, James [5] projected a defensive function of latex in his article describing North American milkweeds. He opined that milkweed carries disagreeable properties of becoming a better

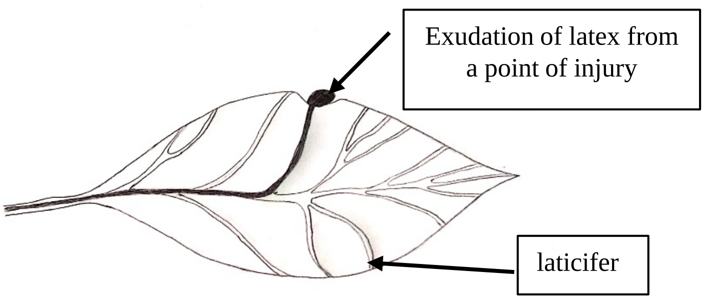

Figure 1. Exudation of latex from laticifers from a point of injury.

protection from enemies than its prickles or hairs. The sap of this plant has grown to be so profuse and noxious that it plays a crucial role in its defence. A few years later, German scientist Kniep [6] conducted an experiment to demonstrate the latex's resistance property. He repeatedly slashed the leaves of a Euphorbiaceae plant until the latex stopped flowing from the fresh cuts. Slugs willingly consumed these leaves, but they turned down the undamaged leaves that had not yet lost all of their latex. Almost a century later, Dussourd and Eisner [7] suggested that most mandibulate milkweed herbivores routinely sever the laticifers before meals in order to disarm their latex response.

2.2. Distribution of Latex Producing Plants

According to Lewinsohn [8], 10% of all angiosperm, *i.e.* more than 20,000 plant species from over 40 families exude latex. When conifers and plants that exude resin are taken into account, the number rises to 35,000 species [8] [9] [10] [11]. In general, plant families and species that thrive in tropical environments have higher proportions of laticiferous tissues than plant families and species that thrive in temperate environments. Plant families that produce profuse quantities of latex include Euphorbiaceae, Asclepiadaceae, Moracea, Apocynaceae, Lactuceae, Asteraceae, etc. Among the plant families, Euphorbiaceae is one of the most diverse and largest families of the angiosperms that contain maximum latex-producing species [12]. Since the interactions between plant and herbivorous insects are more intense in tropical regions than in temperate regions, the frequent occurrence of laticiferous plants is interrelated with the defensive roles of latex and laticifer against herbivores [3]. In fact, just 6% of temperate plant species produced latex, compared to 14% of tropical plant species.

2.3. Composition and Role of Plant Latex

In addition to a variety of proteins, including proteases, oxidases, lectins, chitin-binding proteins, chitinases, glycosidase, and phosphatase, latex contains a variety of secondary metabolites, including alkaloids, terpenoids, cardenolides, rubber, phenolics, furanocoumarins, and starch, in highly concentrated amounts. Various compounds and proteins that are found in plant latex, along with the varieties of plants that contain them are presented in **Table 1**.

The most popular theories for the function of latex in plants include sealing injured tissues, excreting waste metabolites, protecting against herbivores, and fending off diseases [3]. There is a lot of evidence to support the defensive roles of latex against herbivores [9]. The first proof was published in the early 20th century by a German scientist named Kniep, who saw that slugs quickly ate damaged Euphorbiaceae plant leaves after completely draining them of their latex content, but not those with intact latex [6].

A half-century or so later, Dussourd and Eisner offered more evidence when they discovered that many insects consuming milkweeds had evolved a specialised vein-cutting behaviour to deactivate laticifer and avert the exudation of latex [7]. They discovered that when milkweed latex was intentionally placed on

Table 1. Chemicals and proteins found in plant latex that have confirmed or potential defensive role against herbivorous insects.

Category	Compounds and proteins	Name of the compound/protein	Plant species and references
Chemicals	Alkaloids	Morphine	*Papaver somniferum* (Papaveraceae) [23] [24]
		Cheledonine, Sanguinarine, Copticine	*Chelidonium majus* (Papaveraceae) [25]
		Lobeline	*Lobelia cardinalis* (Campanulaceae) [26]
		Sugar-mimic alkaloids, D-AB1, DNJ, etc	*Morus australis*, *Morus* spp. (Moraceae) [18]
		Phenanthroindolizidin alkaloids	*Ficus* spp.
	Terpenoids	Lactucin, Lactucopicrin, Lettucenin A	*Lactuca* spp., *Lactuca sativa* (Asteraceae) [27] [28] [29]
		Phorbol	*Euphorbia* spp., *Euphorbia biglandulosa* [30] [31]
	Cardenolides	Voruscharin, Ushcharidin, Usharin, Calotropagenin, etc.	*Asclepias* spp., *Asclapias curassavica*, etc. *Calotropis procera* (Apocynaceae) [32] [33] [34] [35]
		Toxicariosides	*Antiaris toxicaria* (Moraceae) [36]
	Rubber	Rubber (cis-1,4-isoprene polymer)	*Hevea brasiliensis* (Euphorbiaceae), *Ficus* spp. (Moraceae), *Alstoia boonei* (Apocynaceae), *Parthenium argentatum*, *Lactuca* spp. (Asteraceae) [37] [38]
	Phenolics	p-Coumaric acid hexadecyl, octadecyl eicosyl esters	*Ipomoea batatas* (Convolvulaceae) [39]
		Urushiol	*Rhus* (*Toxicodendron*) spp. (Anacardiaceae, Resin) [40]
	Furanocoumarins	Bergapten, Xanthotoxin, Angelicin	*Petroselium crispum*, *Pastinica sativa* (Apiaceae, resin oil) [41] [42] [43] [44]
Proteins	Proteases	Cysteine protease	*Carica papaya* (Caricaceae), *Ficus carica* (Moraceae), *Morrnia brachystephana*, *Calotropis procera*, *Asclepias barjoniifolia* (Apocynaceae), *Mangifera indica* (Anacardiaceae, resin) [19] [22] [35] [45] [46] [47] [48]
		Serine protease	*Ficus elastica* (Moraceae), *Hevea brasiliensis*, *Euphorbia sapina* (Euphorbiaceae), *Wrightia tinctoria* (Apocynaceae), *Ipomoea carnea* (Convolvulaceae), *Mangifera indica* (Anacardiaceae, resin) [48]-[53]
	Protease inhibitors	Cysteine protease inhibitor	*Calotropis procera* (Apocynaceae), *Cucurbita maxima* (Cucurbitaceae, phloem sap) [22] [54] [55]
		Serine protease inhibitor (Trypsin inhibitor and chymotrypsin inhibitor),	*Ficus carica* (Moraceae), *Carica papaya* (Caricaceae), *Hevea brasiliensis* (Euphorbiaceae), *Cucurbita maxima* (Cucurbitaceae) [54] [55] [56] [57]
		Aspartic protease inhibitor	*Cucurbita maxima* (Cucurbitaceae) [54] [55]
	Oxidase	Polyphenol oxidase (PPO)	*Hevea brasiliensis* (Euphorbiaceae), *Taraxacum kok-saghyz*, *Lactuca sativa* (Asteraceae), *Mangifera indica* (Anacardiaceae, Resin) [58] [59] [60]
		Peroxidase (POD)	*Ficus carica* (Moraceae), *Ipomoea carnea* (Convolvulaceae), *Lactuca sativa* (Asteraceae), *Mangifera indica* (Anacardiaceae, Resin) [48] [56] [60] [61]
		Lipoxygenase (LOX)	*Cucurbita maxima* (Cucurbitaceae, phloem sap) [54]

Continued

Lectins, Chitin-binding proteins, and Chitinases	Lectin (inhibited by lactose and D-galactose)	*Euphorbia lactea*, *Euphorbia hermentiana*, etc. (Euphorbiaceae) [49]
	GlcNAc-binding (Chitin-binding) protein (non-hevein like)	Cucurbita maxima (Cucurbitaceae, phloem sap) [54] [55] [61] [62] [63]
	Chitinase (also chitin-binding)	*Calotropis procera* (Apocynaceae), *Morus alba* (Moraceae) [22] [64]
Others	Lipase	*Euphorbia characias* (Euphorbiaceae), *Asclepias curassavica* (Apocynaceae), *Carica papaya* (Caricaceae) [65] [66] [67]
	Glutamyl cyclase	*Carica papaya* (Caricaceae) [57]
	Gum arabic glycoprotein	*Acacia senegal* (Fabaceae) [68]
	Phenyl alanine ammonia lyase (PAL)	*Lactuca sativa* (Asteraceae) [60]
	Phosphatase	*Euphorbia esula*, *Euphorbia splendens* (euphorbiaceae) [69]
	Linamarase (b-glucosidase)	*Manihot esculenta* (Euphorbiaceae) [70]

the mandibles of beetles (*Tetraopes* spp.), the latex adhered to the teeth and caused them to become stuck [7]. Additionally, they observed that the mandibles of caterpillars trying to consume *Lactuca* sp. (Family: Asteraceae) leaves or the entire body of aphids walking on the plant's surface would get stuck in the latex when the creatures were feeding in their natural settings [13] [14]. Additionally, it was discovered that a significant portion of freshly emerged monarch butterfly larvae (*Danaus plexippus*) were caught in milkweed latex [15] [16] [17]. Usually, the sticky plant latex shields plants from herbivorous insects by capturing and immobilising them.

On the other hand, other chemicals found in latex, like as the alkaloid morphine found in poppies and the cardenolides found in milkweed, are harmful to animals, especially insects, and are thought to have protective roles [9]. However, some latex and or exudates, such as the latex of mulberry trees, *Morus* spp., are not sticky enough to capture insects [18]. Recent research has shown that a number of latex components, particularly latex proteins, are essential for defence against insect herbivory [18] [19] [20] [21] [22]. The protective actions of diverse plants' latex against different insect pests are shown in **Table 2** and **Table 3**.

2.4. Mode of Action of Plant Latex

The amounts of numerous secondary metabolites and proteins found in plant latex, exudates (including phloem sap), and resins are usually substantially higher than those found in leaf sap. Many of these substances are physiologically active and offer herbivores protection through toxicity or antinutritive effects, while others make things sticky and can trap insect herbivores. Following is a discussion of common latex components, their mechanisms of action, and potential biological impacts on herbivore resistance.

Table 2. Plant defensive proteins against insect pests [71].

Putative defence protein	Plant species	Insect species
Protease inhibitors (PIs)	*Sorghum bicolor*	*Schizaphis graminum*
		Manduca sexta
	Solanum lycopercisum	*Helicoverpa armigera*
	Gossypium hirsutum	*Manduca sexta*
	Solanum nigrum	*Spodoptera littoralis*
	Nicotiana attenuata	*Spodoptera exigua*
	Transgenic Arabidopsis/oil seed rape	*Spodoptera exigua*
	Transgenic Arabidopsis/ tobacco	*Plutella xylostella*
		Mamesrra brassicae
		Spodoptera littoralis
Lipoxygenases (LOXs)	*Cucumis sativus*	*Spodoptera littoralis*
	Nicotiana attenuata	*Bemisia tabaci*
	Alnus glutinosa	*Agelastica alni*
	Triticum aestivum	*Sitobion avenae*
	Solanum lycopercisum	*Macrosiphium euphorbiae*
		Myzus persicae
	Nicotiana attenuata	*Myzus nicotianae*
Peroxidases (PODs)	*Alnus glutinosa*	*Agelastica alni*
	Arabidopsis thaliana	*Bemisia tabaci* (whitefly)
	Bouteloua dactyloides	*Blissus oxiduus*
	Populus sp.	*Lymantria dispar*
	Medicago sativa	*Aphis medicaginis*
	Zea mays	*Spodoptera littoralis*
	Oryza sativa	*Spodoptera frugiperda*
Polyphenol oxides (PPOs)	*Solanum lycopercisum*	*Manduca sexta*
	Bouteloua dactyloides	*Blissus oxiduus*
	Solanum lycopercisum	*Spodoptera frugiperda*,
		Helicoverpa armigera
Chitinases	*Sorghum bicolor*	*Schizaphis graminum*
Hevein-like protein	*Arabidopsis thaliana*	*Bemisia tabaci*
Catalase	*Bouteloua dactyloides*	*Blissus oxiduus*
Superoxide dismutase (SOD)	*Medicago sativa*	*Aphis medicaginis*

Table 3. Biological activities of chemical compound isolated from latex of different plant species [72].

Latex plant	Compound isolated	Biological activity
Papaver somniferum	1-deoxynojirimycin	Insecticidal
Anabasis aphylla	Anabasine, lupinine	Mosquitocidal
Morus alba	Chitinase	Defence against herbivore insects
Lactuca virosa	Lactctopicrin, lactucin	Neurotoxic to insects
Anabasis aphylla	Nicotine, anabasine, lupinine	Mosqiutocidal
Papaver somniferum	Opium	Glycosidase inhibition in insects
Papaver somniferum	Opium alkaloids	Narcotic and insecticidal
Hevea brasiliensis	Profillins, hevamine	Insecticidal
Euphorbia lactea	Tirucallo1 a triperpene	Insecticidal
Papaver bracteatum	Glycosidase inhibitors 1,4-dideoxy-1,4-imino-darabinit ol (d-AB1)	Insecticidal
Asclepias humistrata	Cardiac glycoside	Insecticidal
Ficus virgata	Cysteine protease	Insecticidal
Calotropis procera	Cysteine protease	Insecticidal and defensive
Calotropis procera	Procerin, calotropin	Insecticidal
Calotropis procera	Methomyl and cardinolides	Pesticidal and acaricidal
Calotropis procera	Quercetin-3-rutinoside	Toxic, poisonous
Calotropis procera	Triterpenoid saponins	Toxic, pesticidal
Calotropis procera	C-24 diepimer of stigmast-4-en-6B-o 1-3-one	Insecticidal
Calotropis procera	Calotropinol	Larvicidal and repellent
Calotropis gigantiea	Cardenolides	Pesticidal and acaricidal
Catharanthus roseus	Vinblastine, vincristine	Oviposition inhibitor
Carica papaya	DELTA 1-piperidene alkaloids	Insecticidal
Annonaceous plants	Acetogenins	Insecticidal
Annona spinescens	Pessoine and spinosine	Insecticidal
Annona glabra	Annoglacins A and B	Insecticidal
Calophyllum lanigerum	Pyrannocoumarins	Insecticidal
Jatropha curcas	2-epihydroxy isojatrogrossidion	Larvicidal
Aloe harlana	Anhrone (Aloin)	Larvicidal

2.4.1. Secondary Metabolites

1) Rubber

Approximately 300 genera and 8 plant families produce latex that contains the terpenoid rubber (cis-1,4-polyisoprene), which is present in many plant species

[11] [37] [38]. Both the white colour and stickiness of latex are result of the rubber particles that are present in it. Variation in colour of the latex is due to the presence of varied ingredients which has no significant correlation with insect resistance [3]. Typically, the main function of rubber in latex is to produce stickiness that captures whole insects [13] [14], or smothers their mouthparts [7]. Rubber also aids in securing leaf wounds, stopping further latex leaking and possibly warding off pathogen infestation.

2) Alkaloids

Alkaloids, reported from the latex of many species, are sporadically distributed among angiosperm families, such as Papaveraceae and Moraceae. For example, isoquinoline alkaloids such as chelidonine, sanguinarine, and copticine make up about 20% fresh mass of the latex in *Chelidonium majus* [25]. Sanguinarine interferes with neurotransmission by inhibiting choline acetyl transferase, various neuroreceptors, and also DNA synthesis [73]. In latex of mulberry species (*Morus* spp., Family: Moraceae), sugar-mimic alkaloids, also known as imino sugars, have been found which act as potent inhibitors of various glycosidases and sugar-metabolizing enzymes [74]. These substances prevent the digestive enzymes sucrase and trehalase from working properly, preventing the uptake of sucrose and the utilisation of trehalose, resulting in toxicity and growth retardation of insects [75] (**Figure 2**).

3) Cardenolides

Cardenolides are a class of cardiac-active steroids found in milkweed (*Asclepias* spp.) and oleander latex, among other Apocynaceae plants. Cardenolides, also known as cardiac glycosides, are extraordinarily hazardous to a variety of species because they inhibit Na^+/K^+-ATPases, which are crucial for maintaining the electric potential in most animal cells [33].

4) Terpenoids

Compounds called terpenoids are produced from isoprene units, which have five carbons. They are a very broad set of substances that play a variety of roles in plant defence, primary metabolism, and pollinator attraction. According to Noack *et al.* [30], phorbol and its derivatives, as well as diterpenoids, which are

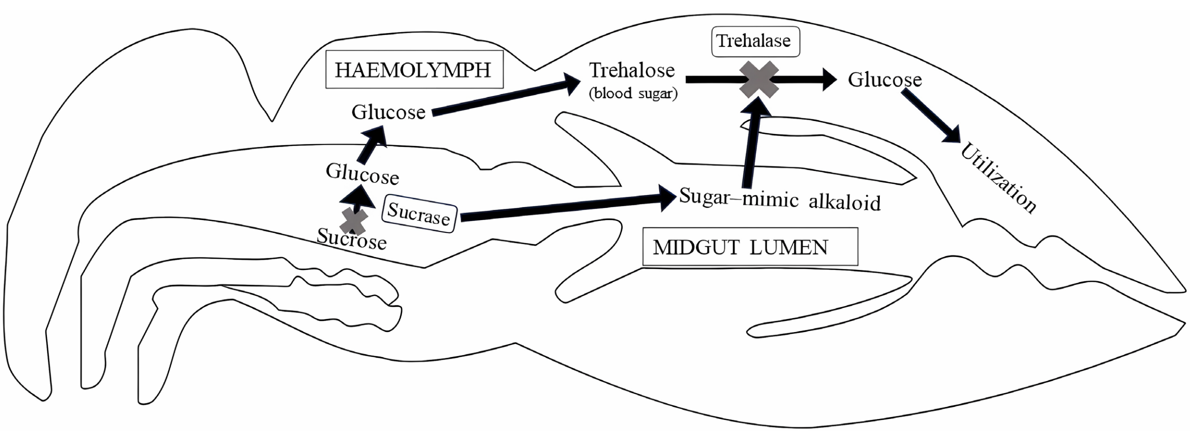

Figure 2. Action of sugar-mimic alkaloid on insect body.

poisonous to insects and herbivores, are found in the latex of the Euphorbia species (*Euphorbia biglandulosa* and allied species).

5) Phenolics

It has been recognised that phenolic compounds, such as tannins, lignins, and diphenols (catechol), serve as plant defences. Hexadecyl, octadecyl, and eicosyl esters of p-coumaric acids are found in large concentrations in the latex of the sweet potato *Ipomea batatas* (Family: Convolvulaceae) [39]. The quantities of (Z)-isomers of C16, C18, and C20 coumarates show an inverse relationship with weevil acceptance, suggesting that (Z)-coumarate esters may help protect sweet potatoes against insect herbivores [39].

2.4.2. Proteins

1) Proteases

All living things contain proteases, which are enzymes that break down proteins into their simpler parts. Proteases (= peptidases), the most common and abundant proteins come in a variety of forms in diverse plant latex, are key molecules involved in plant defense mediated by laticifers. Cysteine and serine peptidases are most common in laticifer fluids [76]. For instance, serine proteases from the plant families Moraceae, Euphorbiaceae, Apocynaceae, and Convolvulaceae [45] [46] [47], as well as cysteine proteases from the latex of plant families Caricaceae, Moraceae, and Apocynaceae are reported [51] [52] [53]. A strong toxicity of papaya and wild fig (*Ficus virgata*) leaves against the Eri silkworm, *Samia ricini*, and the cabbage worm, *Mamestra brassicae*, infers that the toxicity vanished when latex was drained out of the leaves or when E-64, a cysteine protease-specific inhibitor, was coated on the surface of leaves [19]. This experiment acted as the straight proof for showing the connection of cysteine proteases in plant resistance against herbivores. The cysteine proteases degrade the peritrophic membrane of the insect midgut, which consists of proteins and chitin [77]. The dead bodies of caterpillars mired in latex of papaya, fig, and milkweed turn black and soft [78] indicate that all tissues of insects are a potential target of digestion by proteases in latex.

2) Protease inhibitors (PIs)

PIs bind to proteases and prevent the ingestion of protein and are believed to act as anti-nutritive secondary metabolites. Trypsin (serine protease) inhibitors are found in latex of *Ficus carica* [56] and *Carica papaya* [57]. Gene expression of trypsin inhibitors is also in the laticifers *of Hevea brasiliensis* [79]. Also, the latex-like phloem sap of *Cucurbita maxima* (Family: Cucurbitaceae), contains various types of protease inhibitors including trypsin, chymotrypsin, and cysteine or aspartic inhibitors [54] [55].

3) Lectins and hevein-like chitin-binding proteins

Lectins are carbohydrate-binding proteins that have attraction towards specific sugar parts, which often show toxicity against animals including insects [63]. Numerous types of lectins have been found in latex of plant families such as Euphorbiaceae, Moraceae, Apocynaceae, and phloem sap from Cucurbitaceae.

Of these, *H. brasiliensis* contains havein, which is a major latex protein, is vital in the adhesion of rubber particles [80]. Upon exposure to air, hevein binds to cross-linked rubber particles and receptor proteins, thus instigating coagulation of latex. Coagulation of cucurbit phloem sap not only stops exudation but also glues mouth parts of beetles and can inhibit feeding [81].

4) Chitinases

Chitinases are enzymes that breakdown chitin, an important component of insects' gut peritrophic membrane. Chitinases are extensively found in plant latex from several plant families including Caricaceae, Moraceae and Euphorbiaceae [69] [82]. Expression of chitinases in the latex of *F. carica* and *C. papaya* increases in response to wounding [57]. Chitinases of poplar trees are released in response to herbivory and provide protection against subsequent attack [83].

5) Oxidases

Polyphenol oxidase (PPO) and peroxidase (PO) are common plant oxidases testified from the families Euphorbiaceae, Moraceae and Anacardiaceae [48] [58]. The wide distribution of PPOs and POs in many plant species is suggested by frequent browning of latex upon exposure to air. PPOs and some POs oxidize to mono- or di-hydroxyphenolics that are finally converted to o-quinones, which then covalently bind to amino acids such as cysteine and lysine, making them inaccessible, and reduce the nutritive value of leaf protein [84] [85]. Thus, they are sometimes regarded as plant anti-herbivore defence proteins.

2.5. Pesticidal Activity of Plant Latex

Plant latex is extremely toxic to insects and kills a large percentage of their larvae, pupae, and adults. Latex functions as both a systemic and a contact toxin, depending on the type and length of the treatment. Larvae, caterpillars, pupae, and sap-sucking adult insects commonly suffer from stomach poisoning brought on by latex. After successful treatment, latex components prevent numerous insect species from feeding, oviposition, laying eggs, growing, and reproducing [86] [87] [88], primarily mosquitoes *Aedes aegypti* [89]. In larval stages, its sub-lethal dose has negative effects on pupae and larvae, reduces body weight, and prevents moulting [90]. Latex-induced toxicity also impacts pupation rates and lengthens pupal duration [90].

Plant latex from *C. procera* [90], *A. squamosa* [91], *H. brassiliensis* [92], *C. papaya*, *Goniothalamus macrophyllus* [93] and *Asclepias humistrata* (sandhill milkweed) showed strong insecticidal activity against larvae and caterpillars of herbivorous insects [64] [94]. Latex from *A. humistrata* kills newly hatched monarch butterfly caterpillars by traping. Similarly, mulberry latex showed very high toxicity [75] and feeding inhibition in *Bombyx mori* [18]. It shows anti-feedant activity in herbivorous insects due to presence of unpalatable substances such as toxins, enzymes and immune allergens. Persian poppy (*Papaver bracteatum*) and opium poppy (*P. somniferum*) latex contains glycosidase inhibitors 1,4-dideoxy-1,4-imino-darabinitol (d-AB1) and 1-deoxynojirimycin (DNJ) which show insecticidal properties. Similarly, cysteine protease in latex of papaya (*C. papaya*) and wild fig (*F. virgata*) latex have shown high toxicity to caterpillars of herbivorous insects. Lectin from barks of *H. brasiliensis* shows insecticidal activity.

Latex from few plant families such Annonaceae, Solanaceae Asteraceae, Cladophoraceae, Labiatae, Meliaceae, Oocystaceae and Rutaceae, possess phytochemicals, which show insecticidal activity. It shows toxic effects against *Culex quinquefasciatus*, *Sarcophaga haemorrhoidalis* and *Musca domestica.* Latex of *C. procera* also affects gonotrophic cycles of *A. aegypti* and shows inhibitory effects on egg hatching and larval development. Similarly, bark extract of *G. macrophyllus* is used as mosquito repellent while leaves and seeds of *Annonaceous acetogenins* show antifeedant and insecticidal properties (**Table 4**). Similarly, latex *of Calotropis procera* and *Ficus racemosa* were found effective against fourth instar larvae of the lymphatic filariasis vector *Culex quinquefasciatus* (Diptera: Culicidae). Plant latex from the Russian weed, *Anabasis aphylla* contains alkaloids like nicotine, anabasine, methyl anabasine and lupinine and kill larvae of *Culex pipiens* Linn., *C. territans* Walker, and *C. quinquefasciatus*.

Table 4. Insecticidal activity of latex bearing plant species with its common and scientific name [102].

Common name	Botanical name	Family	Pesticidal activity reported	Effective against life stage
Wild fig	*Ficus virgata*	Moraceae	Insecticidal	Larvicidal and growth inhibitory
Sandhill milkweed	*Asclepias humistrata*	Asclepiadaceae	Insecticidal	Adulticidal and repellent
Aak/madar	*Calotropis procera*	Asclepiadaceae	Insecticidal	Insecticidal, growth inhibitory
Aak	*Calotropis gigantea*	Asclepiadaceae	Insecticidal	Insecticidal, growth inhibitory
Madar	*Calotopis procera*	Asclepiadaceae	Insecticidal	Toxic, growth inhibitory and antifeedant
Milkweeds	*Asclepias angustifolia*	Asclepiadaceae	Insecticidal	Effective against herbivorous insects
Milkweeds	*A. barjoniifolia*	Asclepiadaceae	Insecticidal	Effective against herbivorous insects
Milkweeds	*A. fascicularis*	Asclepiadaceae	Insecticidal	Effective against herbivorous insects
Papaya	*Carica papaya*	Caricaceae	Insecticidal	Oviposition and development inhibitor
Tut	*Morus alba*	Moraceae	Insecticidal	Toxic to larvae of lepidopteran insects
Rubber plant	*Ficus elasica*	Moraceae	Insecticidal	Inhibit egg hatching and larval development
Bargad	*Ficus bengalensis*	Moraceae	Insecticidal	Inhibit egg hatching and larval development
Chalate	*Ficus insipida*	Moraceae	Insecticidal	Inhibit egg hatching and larval development
Ficus	*Ficus racemosa*	Moraceae	Insecticidal	Inhibit egg hatching and larval development
Wild fig	*Ficus virgata*	Moraceae	Insecticidal	Inhibit egg hatching and larval development
Gazyummaria	*Ficus microcarpa*	Moraceae	Insecticidal	Inhibit egg hatching and larval development
Gular	*Ficus glomerata*	Moraceae	Insecticidal	Inhibit egg hatching and larval development
Pipal	*Ficus religiosa*	Moraceae	Insecticidal	Inhibit egg hatching and larval development
Anjir	*Ficus carica*	Moraceae	Insecticidal	Inhibit egg hatching and larval development
Pakar	*Ficus rumphi*	Moraceae	Insecticidal	Toxic, antifeedant and antidote to snake bite

Continued

Jackfruit	*Artocapus heterophyllus*	Moraceae	Insecticidal	Growth inhibitory and toxic
Opium poppy	*Papaver sommeniferum*	Euphorbiaceae	Insecticidal	Effective against eggs and larvae
Spurge	*Euphorbia lacteal*	Euphorbiaceae	Insecticidal	Effective against eggs and larvae
Sudha	*Euphorbia nerrifolia*	Euphorbiaceae	Insecticidal	Effective against eggs, larvae and pupae
Tridhara	*Euphorbia antiqunum*	Euphorbiaceae	Insecticidal	Effective against eggs and larvae
Splendens	*Euphorbia splendens*	Euphorbiaceae	Insecticidal	Post-embryonic development of *Megaselia scalaris*
Badi dudhi	*Euphorbia hirta*	Euphorbiaceae	Insecticidal	Inhibitor of egg hatching, embryonic development
Biodiesel plant	*Jatropha curcas*	Euphorbiaceae	Insecticidal	Effective against eggs, larvae and pupae
Hierba mala	*Euphorbia cotimfolia*	Euphorbiaceae	Insecticidal	Effective against eggs, larvae and pupae
Mohan	*Euphorbia rogleana*	Euphorbiaceae	Insecticidal	Effective against eggs, larvae and pupae
Hyaena poison	*Hyaenanche globosa*	Euphorbiaceae	Insecticidal	Effective against eggs, larvae, pupae and adults
Persian poppy	*Papaver bracteatum*	Euphorbiaceae	Insecticidal	Mosquito and house fly larvae and eggs
Croton	*C roton sparciflorus*	Euphorbiaceae	Insecticidal	Mosquito and house fly larvae and eggs
Pili kaner	*Thivetia nerrifolia*	Euphorbiaceae	Insecticidal	Effective against eggs and larvae
Rubber tree	*Hevea brasiliensis*	Euphorbiaceae	Insecticidal	Effective against eggs and larvae
Persian poppy	*Papaver bracteatum*	Euphorbiaceae	Insecticidal	Toxic and repellent
Safed arand	*Jatropha curcas*	Euphorbiaceae	Insecticidal	Highly toxic to larvae, pupae and adults
Indian spurge tree	*Euphorbia. nivulia*	Euphorbiaceae	Insecticidal	Toxic and repellent
Antique euphorbia	*Euphorbia antiquorum*	Euphorbiaceae	Insecticidal	Toxic and repellent
Gobur champa	*Plumeria rubra*	Apocynaceae	Insecticidal	Repellent and antifeedant
Oleander	*Nerium oleander*	Apocynaceae	Insecticidal	Effective against eggs and larvae
Sapthaparna	*Alstonia macrophylla*	Apocynaceae	Insecticidal	Effective against eggs and larvae
Pili kaner	*Thevetia nerifolia*	Apocynaceae	Insecticidal	Effective against eggs, larvae, pupae and adults
Kaner	*Nerium indicum*	Apocynaceae	Insecticidal	Toxic, antifeedant and repellent
Dudhi	*Nerium tinctorum*	Apocynaceae	Insecticidal	Toxic, antifeedant and repellent
Sadabahar	*Vinca rosea*	Apocynaceae	Insecticidal	Effective against eggs, larvae, pupae and adults
Rubber vine	*Cryptostegia grandiflora*	Apocynaceae	Insecticidal	Toxic, antifeedant and repellent
Plumeria	*Plumeria alba*	Apocynaceae	Insecticidal	Effective against eggs and larvae
Sharifa	*Annona squamosa*	Apocynaceae	Insecticidal	IV instar larvae of lepidopteran insects
Mexican poppy	*Argemone ochroleuca*	Papaveraceae	Insecticidal	Adults and eggs of *Culex* sp.
Maulsari	*Mimusops elengi*	Sapotaceae	Insecticidal	Effective against eggs, larvae, pupae and adults

Plant latex significantly inhibits moulting in larval instars or transformation into next instar or larval stadia by slowing down the larval development. Latex induced toxicity significantly decreased the percentage of pupation, pupal weight and survival and prolonged the pupal duration [90]. Latex treatment also affects gonadotrophic cycles in *A. aegypti* female insects [95] and displays inhibitory effects on egg hatching and larval development [87]. It increases the postembryonic development period of larvae and pupae, reduces the F1 emergence [96] [97] and delays the formation of adults. Similar effects were also noted in blowfly *Chrysomya megalocephala* (Diptera: Calliphoridae) post-embryonic development at 1.0% (w/v) dose of *Parahancornia amapa* latex (Family: Apocynaceae) [98]. It shortened the postembryonic development period of larvae, pupae and newly hatched larvae to adults whereas 3.0% latex has provoked a prolongation of these periods [98]. Crude latex from *Euphorbia splendens* var. *hislopii* (Family: Euphorbiaceae) affects post-embryonic development time and viability of *Megaselia scalaris* under laboratory conditions at various doses ranging from 5 - 20, μg/mL [99]. Rubber plant *H. brasiliensis* latex heavily deters beetle, *Luprops tristis* and inhibits development and reproductive efficiency of parental adults [100]. Latex of the milkweed *Hoodia gordonii* proved deterrent to larval feeding and adult oviposition by generalist cabbage loopers (*Trichoplusia ni*) [101]. Latex almost completely inhibits feeding of *Diabrotica balteata* beetles when painted on leaves of lima beans.

Due to massive lethality and reproductive or post-reproductive inhibition of insect, latex and its components can be considered as potent natural insecticidal constituents for safe and eco-friendly control of insect pests [72].

2.6. Herbivore Adaptations for Feeding on Latex-Bearing Plants

Numerous herbivorous insects, mainly specialists, have evolved defence mechanisms to counteract or avoid latex's negative effects. These modifications fall into two categories: 1) Physiological modifications and 2) Behavioural modifications.

2.6.1. Physiological Adaptations

In order to consume the milkweed plants' latex, which is known to contain cardenolides, monarch butterfly larvae have evolved specialised Na^+/K^+ ATPases that are insensitive to cardenolides [102]. Other insect groups, such as *Chrysochus* beetles eating Apocynum, convergently developed this ability [103]. *Bombyx mori*, a type of silkworm that feeds exclusively on mulberries (*Morus* spp.), whose latex contains sugar-mimicking alkaloids, has acquired a susceptibility to sucrose and trehalose as well as to other sugar-mimicking alkaloids [75] [104]. The cysteine protease inhibitor activity that cabbage looper has acquired in its digestive juice blocks cysteine-protease activity, which is present in the latex of many plants and prevents the digestion of proteins in the peritrophic membrane [105].

2.6.2. Behavioural Adaptations

The laticifer system depends upon the ability to transport defence substances, hence, their purposes are lost when the transport routes are interrupted [7] [13] [106]. Wounding of the laticifers at a single location of feeding can disable all downriver activities. Many mandibulate herbivores of latex-bearing plants with non-articulated laticifers consequently engage in vein-cutting behaviour [7] [9]

[13] [14]. Vein-cutting is observed in Orthoptera (Tettigoniidae), Coleoptera (Cerambycidae, Chrysomelidae, Curculionidae), and Lepidoptera (Arctiidae, Gelechiidae, Noctuidae, Nymphalidae, Pyralidae). On common milkweed (*Asclepias syriaca*) in eastern North America, vein-cutting is commonly exercised by Arctiidae, Cerambycidae, Chrysomelidae, Curculionidae, and Nymphalidae [7] [107].

Plants with articulated laticifers (net or web type) show improved protection from herbivory because, even when insects cut veins, there are other paths for latex to go downstream of the cut. Insects feeding on leaves with articulated laticifers characteristically show a behaviour called trenching, in which insects cut a leaf-wide trench or circle trench [13] [14] [108]. Trenching is observed in Coleoptera (Coccinellidae, Chrysomelidae) and Lepidoptera (Noctuidae, Nymphalidae, Sphingidae) [106] [109]. Whether herbivores use vein cutting or trenching depends upon the types of laticifer (that is, non-articulated or articulated) of their host plants [106] (**Figure 3**).

Trenching and vein-cutting is a phenotypically plastic behaviour. Many species will not exhibit this behaviour while feeding on an already depressurized leaf. It has been discovered recently, that trenching and vein-cutting behaviour is also specifically activated by compounds in latex and exudates [29] [107] [110]. The cabbage looper, *Trichoplusia ni*, cut trenches on plants that produce exudates such as *Lactuca sativa* (latex), parsley (*Petroselinum crispum*, Apiaceae, oil from oil ducts), cucumber (*Cucumis sativus*, Cucurbitaceae, exudates from phloem), and cardinal flower (*Lobelia cardinalis*, Campanulaceae, latex), but it does not trench on plantain (*Plantago lanceolata*, Plantaginaceae), which does not produce an exudate. When exudates from the above species were applied orally to the cabbage looper beforehand, the loopers trenched on plantain leaves

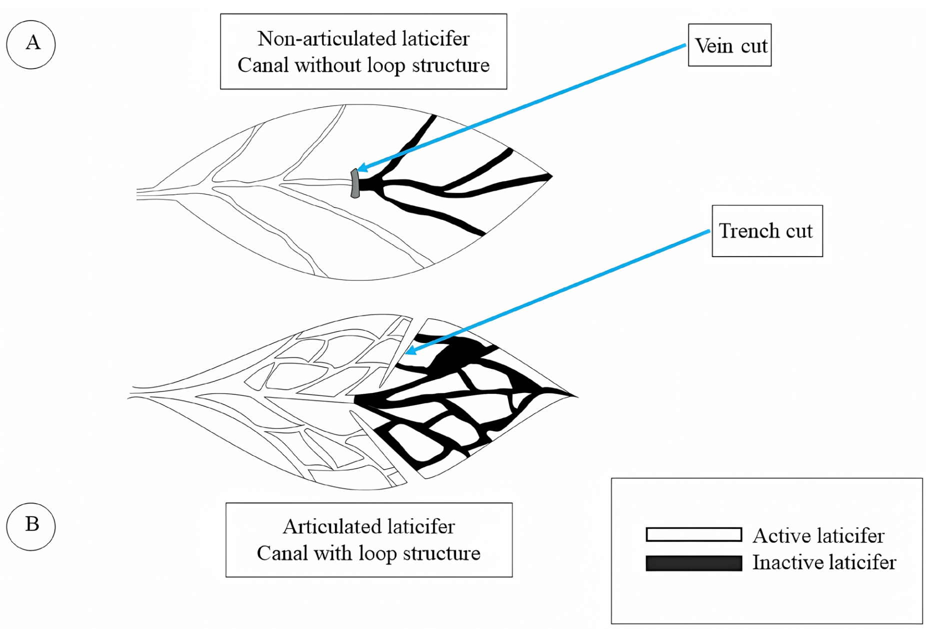

Figure 3. Vein cutting or trenching depends upon the types of laticifer of the host plant.

[29] [110].

Not all herbivores on laticiferous plants trench or cut veins, such as the milkweed leaf miner (*Liriomyza asclepiadis*), which feed without coming into contact with latex [44]. Likewise, most sap suckers (Hemiptera) do not come in contact with latex because of their intercellular feeding, and so they do not need any adaptations for feeding on latex-bearing species.

3. Conclusions and Future Perspective

Latex consists of a number of secondary metabolites which have unique mode of action and are sufficient to fight insect enemies single-handedly. So, when these secondary metabolites come together as a unit, they make even small amounts of latex very powerful in combating insect pests. There are a few ways in which plant latex can be used on a commercial scale to defend plants against insect pests without causing adverse environmental effects. However, till date, there is a paucity of information on the availability of plant latex-based insecticide on a commercial scale and so it can be regarded as an untapped resource treasure that can be used to solve many insect pests-related problems in a sustainable way.

It can be used in the following ways:

- As bio-insecticide by simply diluting it with water and spraying wherever required.
- The secondary metabolites present in latex can be individually extracted using different polar or non-polar solvents. These extracts can then be formulated and used.
- By using as paints to paint the surface of such plants that do not produce their own latex, thus, making them non-palatable to insects.
- Coating of seeds with latex to prevent egg laying.

Plant latex has incredible potential to be used as a bio-insecticide on a commercial saleable scale. A scope of research on identification of latex having insecticidal properties, development of formulation and launching of new latex-based insecticide is huge in the present day of organic agriculture. We may reduce reliance on chemical insecticides for pest control and may develop a new, sustainable and safe method of pest control by exploiting the defensive power of latex against insects.

Authors' Contribution

The idea for the article was conceived by **Maimon Soniya Devi** and **Tamoghno Majumder**. **Abhismita Samajder** and **Moumita Modak** did the preliminary literature survey. A detailed literature survey was done by **Amitava Banerjee**, **Anirban Sarkar** and **Lakshman Chandra Patel**. Drafting of the article and drawing or sketching of relevant figures were done by **Kriti Singh**, **Tamoghno Majumder**, **Aivi Mallick** and **Shanowly Mondal Ghosh**. The concept of the article was fine-tuned and the entire manuscript was critically revised by **Kusal Roy** and **Kriti Singh**.

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Conflicts of Interest

- The authors have no relevant financial or non-financial interests to disclose.
- The authors have no competing interests to declare that are relevant to the content of this article.
- All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.
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