



Phyto-Antifeedants

9

Anandamay Barik

Contents

9.1	Introduction	285
9.2	Phyto-Antifeedants: Biochemical Diversity and Target Insects	286
9.2.1	Terpenes	287
9.2.1.1	Monoterpenes	287
9.2.1.2	Sesquiterpenes	287
9.2.1.3	Diterpenes	287
9.2.1.4	Triterpenes	290
9.2.2	Flavonoids	294
9.2.3	Alkaloids	304
9.2.4	Steroids	304
9.2.5	Coumarins	309
9.2.6	Other Compounds	310
9.3	Phyto-Antifeedants: Mode of Action	310
9.3.1	Cognition of Antifeedants	313
9.3.2	Validating the Action of Inhibitory Response	314
9.3.2.1	Carbohydrates Hide the Distasteful Taste of Secondary Plant Metabolites	314
9.3.2.2	Longer Dietary Exposure Helps the Gustatory System to Consume Nontoxic Unpalatable Substances	315
9.3.2.3	Longer Dietary Exposure Towards Toxic and Unpalatable Substances Causes Release of Detoxification Enzymes	315
9.4	Phyto-Antifeedant: Formulation	315
9.5	Phyto-Antifeedants: Potential Uses	317
9.6	Phyto-Antifeedants: Prospects for Commercial Use	319
9.7	Conclusions	320
	References	321

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283

Abstract

Plants possess primary and secondary metabolites. Primary metabolites are required to maintain their basic physiological processes, which also serve as essential sources of nutrients for herbivores, whereas secondary metabolites help to protect plants from herbivore damage. Phyto-antifeedants, a type of secondary metabolite, are recorded from 43 families of plants, but stress has been given in 4 families—Meliaceae, Asteraceae, Labiatae and Leguminosae. Terpenes are classified depending on isoprene units. Terpenes are divided into monoterpenes, sesquiterpenes, diterpenes and triterpenes, and many compounds among these groups act as antifeedants. Flavonoids, alkaloids, steroids and coumarins from plant sources could also act as antifeedants. The lepidopteran larvae possess chemosensilla on the maxillary palp, and the test cells in the sensillum act as deterrent. Some insects possess P450 detoxification enzymes in the midgut to detoxify the antifeedants. One of the most commonly used antifeedant is azadirachtin A from *Azadirachta indica*, which is applied against ca. 400 insect species belonging to Blattodea, Coleoptera, Diptera, Dermaptera, Ensifera, Homoptera, Heteroptera, Hymenoptera, Lepidoptera, Isoptera, Phasmida, Thysanoptera and Siphonaptera. One of the best strategies to apply an antifeedant is in water- or oil-based formulations. Latex may also be used to apply antifeedants. At present 1000 antifeedants have been isolated from plants in laboratory conditions, but the efficacies of antifeedants in the field are low due to either habituation of insects towards antifeedants or variations in responses among different insects. The major hindrance in developing phyto-antifeedants is that they are not broad spectrum or they may not be effective in field conditions. Therefore, basic research in combination with field trials of the isolated phyto-antifeedants at different doses are necessary to get ecofriendly safe products for insect pest management.

Keywords

Phytochemicals · Antifeedants · Pest control · Mode of action · Commercialization

Learning Objectives

1. Application of synthetic insecticides to control insect pests poses threat to human health, nontarget organisms and the environment. Recently the European Union prohibited the use of certain pesticides. Now the question is asked whether phytochemicals as antifeedants can replace the synthetic pesticides.
2. Plants produce a diversity of compounds called secondary metabolites to cope with the feeding damage caused by herbivorous insects. Since the early days, humans are using plant extracts comprised of specific secondary metabolites to modulate insect behaviour.
3. A number of secondary metabolites acting as antifeedants could be used for pest management strategies, but commercial success of botanical pesticides using

secondary metabolites is meagre except for plant extracted oils, pyrethrum and neem.

4. An improved understanding of secondary metabolites acting as antifeedants to insects is one of the major focuses in integrated pest management strategies in the present scenario.

9.1 Introduction

The present century focuses on protecting crop plants from insect herbivores to safeguard plants from herbivore feeding damage. Plants have evolved during Devonian Period ca. 400 million years back, and since the beginning of plant evolution, plants have evolved different compounds, which may deter from insect feeding. Green plants produce carbohydrates by photosynthesis which are stored as sugars and considered as primary energy source. A part of this energy is used to transform nitrogen to amino acids. Sugars are also employed to build in cell walls. Primary metabolites represent a greater part of plant biomass. The primary metabolites mainly consist of carbohydrates, proteins and lipids, which are responsible for basic physiological process of plants and serve as essential sources of nutrients for herbivores. Depending on the primary metabolism, plants have an array of metabolic pathways to generate diverse secondary plant substances. These secondary plant substances do not possess a role in primary metabolism. As plants cannot move during insect attack as well as do not possess adaptive immune system like vertebrates during various infections, plants produce an array of diverse secondary metabolites to protect them from herbivore damage. The secondary metabolites are evolved during natural selection in plants in such a way that these compounds may intervene the metabolism, neural transmission, development and reproduction of insect herbivores. Besides production of secondary metabolites, plants have developed various morphological defensive mechanisms, such as impervious cuticles, thorns, spikes, trichomes, etc. against insect herbivores.

Green plants produce a wide structural diversity of secondary metabolites, such as terpenoids, phenolics, alkaloids, cyanogenic glycosides, glucosinolates, quinones, amines, peptides, non-protein amino acids, organic acids, polyacetylenes and peptides. A cursory review of literature documents that more than 100,000 compounds are on records (Wink 1988, 2003). These plants produced secondary metabolites can act on different molecular targets at a particular time and frequently in a synergistic manner (Wink 2008, 2015; Mason and Singer 2015). Therefore, the mixtures of secondary metabolites vary between different organs and developmental stages of a plant as well as within populations of a species.

Insects are one of the most important agents causing damage in agroecosystems. The USA, EU, China and Brazil are the largest agricultural producers in the world, and these four countries used 827 million, 831 million, 1.2 billion and 3.9 billion pounds of pesticides in 2016, respectively. Despite application of insecticides, it is estimated that 18–20% crop losses due to arthropod attack occur across the globe and result in an estimated loss of more than a value of US\$ 400 billion. In India, crop

losses due to insect attack are estimated to be 15.7% at the present condition, and the agriculture sector of India loses an estimated value of about US\$ 36 billion. Food plants throughout the world are affected by 10,000 insect species, 30,000 weed species, 1000 nematode species and 100,000 diseases, which are due to the attack by fungi, viruses, bacteria and other microorganisms. About 10% of the insect pests are generally predicted to be major pests, and herbivorous insects are reported to cause one-fifth of the world's crop loss per annum. Four major and 26 minor crops are responsible for ca. 95% of human sustenance, indicating that many of these crop plants are cultivated for a long time, and thus, these crop plants provide food for a vast array of insect species with a high degree of adaptation to the crop plants. It is found that most of the insect species are specialist feeders—75% of temperate and 80% of tropical lepidopteran insect pests are monophagous or oligophagous.

Entomologists have been searching for safe and ecofriendly insect control measures by underpinning the idea that in real world, many plants protect themselves from insect attack by secreting unpalatable substances, and it is feasible to apply such compounds as feeding or oviposition inhabitants to protect the crop plants. The progress on this concept has been slow. The idea is that 'suppressants' inhibit insects against biting activity, while 'deterrents' avert insects from further feeding. Generally most of the times, we are unable to understand the phase of feeding when it is interrupted, and subsequently, many authors concomitantly employ 'antifeedants' as well as 'feeding deterrents' for compounds present in plant tissues that inhibit or avert insect feeding activity. In this context, the expression 'rejectant' could not be used as it does not make a distinction between suppressants and deterrents. The word 'repellent' implicates an oriented movement from the source of stimulus (Dethier et al. 1960). An ideal antifeedant would be nontoxic secondary metabolites, not phytotoxic and nontoxic to human, animals, beneficial insects and organisms, as well as suppresses the feeding activity of as many as insect pests, practically applicable to a crop, and ultimately, low cost for commercial production as well as high availability.

After reviewing crop yield losses by the herbivorous insects, it is interesting to discuss about the origin of antifeedants in the perspective of plant origin, mode of action, formulations and applications of phyto-antifeedants, including the drawbacks and prospects on the use of phyto-antifeedants for insect pest control, which is an essential step towards developing safe and economical as well as sustainable methods of pest management programme for the food security and also for the future. This chapter discusses about phyto-antifeedants, not about the derivative antifeedants, which are prepared from antifeedants of plant origin.

9.2 Phyto-Antifeedants: Biochemical Diversity and Target Insects

Antifeedants in plants differ to a great extent in their chemistry and are comprised of inorganic compounds as well as secondary metabolites. The prospective of plant taxa to show antifeedant activity of insects has been demonstrated to be definite to

certain insect species as well as the effectiveness may be determined by their genotype and ecological environment.

To date, the insect antifeedant activity has been recorded from 43 families of plants, but more research has been performed in families Meliaceae (Fagoonee and Lange 1981), Asteraceae (Zalkow et al. 1979; Rose et al. 1981), Labiatae (Miyase et al. 1981) and Leguminosae (Bentley et al. 1984). Future researches are required to search all potential local plants depending on visual as well as chemotaxonomic basis, while simultaneously the industrial waste products of plants should be tested since they may possess substantial amounts of inhibitory compounds or new antifeedants arising due to processing (Jermy et al. 1981).

9.2.1 Terpenes

Terpenes, the largest class of compounds, consist of more than 30,000 compounds and show a wide variety of structures comprising isoprene molecules. Each isoprene molecule (isoprene unit) possesses five carbon atoms with double bonds. The carbon skeleton of terpene is formed by an enzyme class, the terpene synthases, which converts the acyclic prenyl diphosphates including squalene into an array of cyclic and acyclic forms. The diversity of terpenes is due to the large number of various terpene synthases, and at the same time, some terpene synthases create multiple products. Terpenes are subdivided into acyclic or cyclic according to the structure. Acyclic terpenes are linear, such as β -myrcene (monoterpene), while cyclic terpenes are ring-like, such as *p*-cymene (monoterpene). Based on isoprene units, terpenes are divided into monoterpene, sesquiterpene, diterpene and triterpene.

9.2.1.1 Monoterpenes

The simplest terpenes are known as monoterpenes, which are comprised of two isoprene molecules. Monoterpenes (C-10 compounds) are highly volatile, which are abundant in plants, and act as strong feeding deterrence as well as deterrent to predators (Table 9.1 and Fig. 9.1).

9.2.1.2 Sesquiterpenes

Sesquiterpenes develop from farnesyl pyrophosphate (C₁₅) containing three isoprene units (C₅) and present in plant essential oils. Sesquiterpenes consist of a large diversity of cyclic compounds and non-cyclic farnesyl derivatives. The cyclic sesquiterpenes consist of monocyclic, bicyclic and tricyclic compounds including the sesquiterpene lactones. A list of sesquiterpenes (Table 9.2 and Fig. 9.2) and sesquiterpene lactones (Table 9.3 and Fig. 9.3) acting as phyto-antifeedants were presented below.

9.2.1.3 Diterpenes

These compounds are derived from C₂₀ isoprenoid geranylgeranyl pyrophosphate, which are heavy molecules with high boiling points. The diversity (structural and functional) of diterpenes is attributed to the different functions of diterpene cyclases

Table 9.1 A list of monoterpenes acting as phyto-antifeedants

Sl No.	Monoterpenes	Test insect	Origin	References
1	Ipolamiide	<i>Locusta migratoria</i>	<i>Stachytarpheta mutabilis</i>	Bernays and De Luca (1981)
		<i>Schistocerca gregaria</i>		
		<i>Spodoptera littoralis</i>		
2	Catalpol + catalposide	<i>Poanes hobomok</i>	<i>Catalpa speciosa</i>	Chang and Nakanishi (1983)
3	Specionin	<i>Choristoneura fumiferana</i>		
4	Xylomollin	<i>Spodoptera exempta</i>	<i>Xylocarpus moluccensis</i>	Kubo and Nakanishi (1977), Mabry et al. (1977)
5	Verbenone	<i>Hylobius abietis</i>		Klepzig and Schlyter (1999), Lindgren et al. (1996)
		<i>Dendroctonus ponderosae</i>		Gillette et al. (2014)
		<i>Leptinotarsa decemlineata</i>		Ortiz de Elguea-Culebras et al. (2017)
6	Carvone	<i>Hylobius abietis</i>	Essential oils of many plants and conifer plants	Klepzig and Schlyter (1999), Lindgren et al. (1996), Schlyter et al. (2004)
		<i>Hylobius pales</i>	<i>Carum carvi</i> , <i>Mentha spicata</i>	Schlyter et al. (2004)
7	Thymol	<i>Spodoptera litura</i>	<i>Thymus vulgaris</i> , <i>Origanum vulgare</i>	Hummelbrunner and Isman (2001), Erler and Tunc (2005), Kim et al. (2010), Ortiz de Elguea-Culebras et al. (2017)
		<i>Ephestia kuehniella</i>		
		<i>Tribolium castaneum</i>		
		<i>Leptinotarsa decemlineata</i>		
		<i>Myzus persicae</i>	<i>Senecio palmensis</i>	González-Coloma et al. (2002)
		<i>Diuraphis noxia</i>		
		<i>Rhopalosiphum padi</i>		
		<i>Metopolophium dirhodum</i>		
	<i>Sitobion avenae</i>			
8	<i>trans</i> -Anethole	<i>Spodoptera litura</i>	<i>Pimpinella anisum</i>	Hummelbrunner and Isman (2001)
9	Limonene	<i>Spodoptera litura</i>	<i>Chloroxylon swietenia</i>	Kiran et al. (2006)

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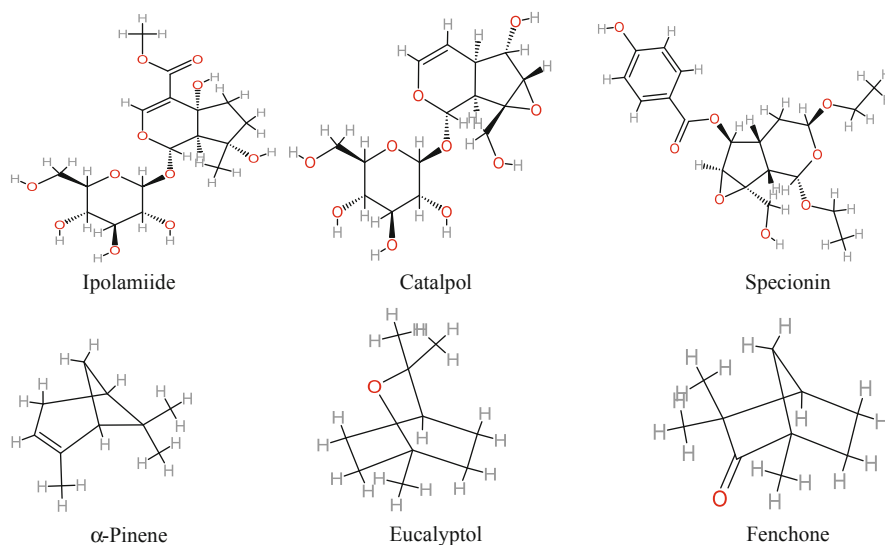
Table 9.1 (continued)

Sl No.	Monoterpenes	Test insect	Origin	References
		<i>Leptinotarsa decemlineata</i>		Khorram et al. (2011)
10	Carvacrol	<i>Ephestia kuehniella</i> <i>Tribolium castaneum</i> <i>Leptinotarsa decemlineata</i>	<i>Ocimum basilicum</i> , <i>Eugenia caryophyllus</i>	Erlar and Tunc (2005), Kim et al. (2010), Saroukolai et al. (2014), Ortiz de Elguea-Culebras et al. (2017)
11	γ -Terpinene	<i>Ephestia kuehniella</i>		Erlar and Tunc (2005)
12	Terpinen-4-ol	<i>Ephestia kuehniella</i> <i>Sitophilus zeamais</i> <i>Leptinotarsa decemlineata</i>		Erlar and Tunc (2005) Yildirim et al. (2013) Ortiz de Elguea-Culebras et al. (2017)
13	α -Pinene	<i>Leptinotarsa decemlineata</i> <i>Tribolium castaneum</i>		Rodilla et al. (2008), Khorram et al. (2011) Kim et al. (2010)
14	β -Pinene	<i>Leptinotarsa decemlineata</i>		Rodilla et al. (2008)
15	Eucalyptol	<i>Leptinotarsa decemlineata</i>		Rodilla et al. (2008)
16	Myrcene	<i>Tribolium castaneum</i> <i>Leptinotarsa decemlineata</i>		Kim et al. (2010) Khorram et al. (2011)
17	Terpinolene	<i>Myzus persicae</i> <i>Choristoneura fumiferana</i> <i>Tribolium castaneum</i> <i>Sitophilus zeamais</i>	<i>Piper hispidinervum</i>	Andrés et al. (2017) Kumbasli and Bauce (2013) Wang et al. (2009) Wang et al. (2009)
18	Pyrethrins	<i>Bemisia tabaci</i> , <i>Myzus persicae</i>	Pyrethrum	Prota et al. (2014)
19	Camphor	<i>Leptinotarsa decemlineata</i>		Ortiz de Elguea-Culebras et al. (2017)
20	Linalool	<i>Tribolium castaneum</i> , <i>Rhyzopertha dominica</i> , <i>Sitophilus oryzae</i>	Lamiaceae, Lauraceae	Kanda et al. (2017)

(continued)

Table 9.1 (continued)

Sl No.	Monoterpenes	Test insect	Origin	References
21	Menthone	<i>Sitophilus oryzae</i>	<i>Mentha piperita</i>	Rajkumar et al. (2019)
		<i>Tribolium castaneum</i>		
22	Menthol	<i>Sitophilus oryzae</i>		
		<i>Tribolium castaneum</i>		
23	1,8-Cineole	<i>Leptinotarsa decemlineata</i>		
24	Fenchone			
25	γ -Terpinene			

**Fig. 9.1** Structure of some monoterpenes

as well as chemical modification of enzymes. Table 9.4 presents a list of diterpenes and the structure of some common diterpenes (Fig. 9.4) that act as phyto-antifeedants.

9.2.1.4 Triterpenes

Triterpenoids represent the largest groups in nature possessing 30 carbon atoms composed of 6 isoprene units. The extensive occurrence in plants is one of the main reasons for considerable interest with more than 14,000 compounds identified (Hamberger and Bak 2013). Triterpenoids are formed by cyclization of oxidized squalene predecessors by oxidosqualene cyclases, forming over 100 various cyclical

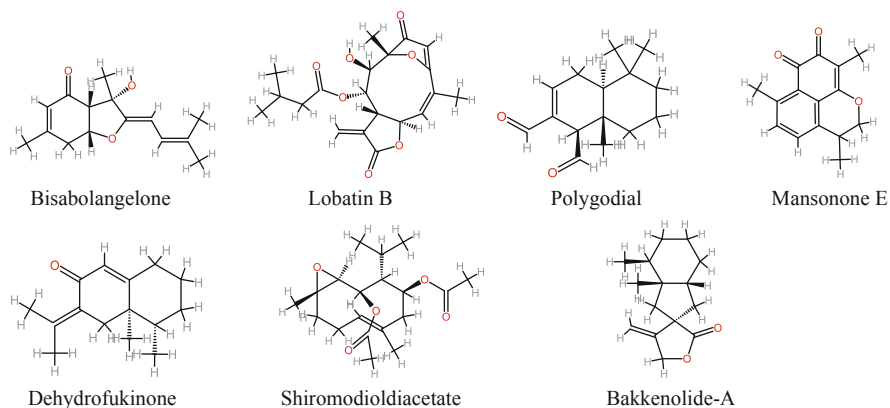
Table 9.2 A list of sesquiterpene acting as phyto-antifeedants

Sl No.	Sesquiterpenes	Test insect	Origin	References
1	Shiromodioldiacetate	<i>Spodoptera litura</i>	<i>Parabenzoin trilobum</i>	Wada et al. (1968)
2	Shiromodiolmonoacetate			
3	Plagiochiline A	<i>Spodoptera exempta</i>	<i>Plagiochila fruticosa</i> , <i>P. hattoriana</i> , <i>P. ovalifolia</i> and <i>P. yokogurensis</i>	Asakawa et al. (1980)
4	Drimanes	<i>Myzus persicae</i>		Caprioli et al. (1987), Gutiérrez et al. (1997)
5	Bisabolanes	<i>Myzus persicae</i>		
6	Bisabolangelone	<i>Peridroma saucia</i> <i>Mamestra configurata</i>	<i>Angelica sylvestris</i>	Nawrot et al. (1991)
7	Bakkenolide-A	<i>Peridroma saucia</i> <i>Coptotermes fornosanus</i>	<i>Homogyne alpina</i>	Isman et al. (1989) Kreckova et al. (1988)
8	Celanguilin	<i>Spodoptera exempta</i>	<i>Celastrus angulatus</i>	Wakabayashi et al. (1988)
9	11 β -Acetoxy-5 α -angeloyloxysilphinen-3-one	<i>Leptinotarsa decemlineata</i>		González-Coloma et al. (1995, 1997)
10	11 β ,5 α -Dihydroxysilphinen-3-one	<i>Leptinotarsa decemlineata</i>		
11	11 β -Acetoxy-5 α -isobutyryloxysilphinen-3-one	<i>Myzus persicae</i> <i>Diuraphis noxia</i> <i>Rhopalosiphum padi</i> <i>Metopolophium dirhodum</i> <i>Sitobion avenae</i>	<i>Senecio palmensis</i>	González-Coloma et al. (2002)
12	Germacranolides	<i>Spodoptera litura</i>	<i>Neurolaena lobata</i>	Passreiter and Isman (1997)
13	Neurolenin A, B, C, D	<i>Spodoptera litura</i>		
14	Lobatin A			
15	Lobatin B			
16	Polygodial	<i>Bemisia tabaci</i> <i>Myzus persicae</i> <i>Leptinotarsa decemlineata</i> <i>Spodoptera littoralis</i>	<i>Drimys winteri</i>	Prota et al. (2014) Kubo and Ganjian (1981), Caprioli et al. (1987),

(continued)

Table 9.2 (continued)

Sl No.	Sesquiterpenes	Test insect	Origin	References
		<i>Spodoptera exempta</i>		Zapata et al. (2009)
17	Drimane sesquiterpenoids	<i>Spodoptera littoralis</i>		Kubo and Ganjian (1981), Caprioli et al. (1987)
18	Drimendiol			Zapata et al. (2009)
19	Isodrimeninol			
20	Isotadeonal			
21	Mansonone E	<i>Spodoptera litura</i>	<i>Mansonia gagei</i>	Mongkol and Chavasiri (2016)
22	Dehydrofukinone	<i>Myzus persicae</i> <i>Spodoptera littoralis</i>	<i>Senecio adenotrichius</i>	Ruiz-Vásquez et al. (2017)
23	11-Hydroxyeremophila-6,9-dien-8-one	<i>Myzus persicae</i>		
24	Ligudicin A	<i>Myzus persicae</i> <i>Spodoptera littoralis</i>		

**Fig. 9.2** Structure of some sesquiterpenes

triterpene scaffolds. These scaffolds are the initiators to create the wide diversity of triterpenoids followed by wide-ranging diversification, particularly by oxygenation and glycosylation (Cárdenas et al. 2019). On the other hand, the oxygenated terpenes are called limonoids, which are characterized by a 4,4,8-trimethyl-17-furanysteroid skeleton. The first tetranotriterpenoid is limonin isolated from citrus, and the term limonoid is originated from limonin. Limonoids are created by the deletion of four

Table 9.3 A list of sesquiterpene lactones acting as phyto-antifeedants

Sl No.	Sesquiterpene lactones	Test insect	Origin	References
1	Schkuhrin I	<i>Spodoptera exempta</i>	<i>Schkuhria pinnata</i>	Pettei et al. (1978)
		<i>Epilachna varivestis</i>		
2	Schkuhrin II	<i>Spodoptera exempta</i>		
		<i>Epilachna varivestis</i>		
3	Vernodalin	<i>Spodoptera exempta</i>	<i>Vernonia amygdalina</i>	Ganjian et al. (1983)
4	Vernodalol			
5	11,13-Dihydrovernodalol	<i>Spodoptera exempta</i>		
6	Alantolactone	<i>Sitophilus granarius</i>	<i>Inula helenium</i>	Nawrot et al. (1986)
		<i>Tribolium confusum</i>		
		<i>Trogoderma granarium</i>		
7	Britanine	<i>Sitophilus granarius</i>	<i>Inula caspica</i>	Adekenov et al. (2015)
		<i>Tenebrio molitor</i>	<i>Inula caspica</i>	
8	Glaucolide-A	<i>Spodoptera eridania</i>	<i>Vernonia gigantea</i> , <i>V. glauca</i>	Mabry et al. (1977)
		<i>Spodoptera frugiperda</i>		
9	Parthenolide	<i>Spodoptera litura</i>	<i>Neurolaena lobata</i>	Passreiter and Isman (1997)
10	Buddlein A			
11	Neuroenin B			
12	(1 <i>S</i> ,6 <i>R</i>)-2,7(14),10-Bisabolatrien-1-ol-4-one and (+)-7(14),10-bisaboladien-1-ol-4-one	<i>Locusta migratoria</i>	<i>Cryptomeria japonica</i>	Kashiwagi et al. (2007)
13	Cubebol and ferruginol		<i>Cryptomeria japonica</i>	Wu et al. (2008)
14	Inuchinenolide C	<i>Tenebrio molitor</i>	<i>Inula caspica</i>	Adekenov et al. (2015)
15	Arglabin		<i>Artemisia glabella</i>	Adekenov et al. (2015)
16	Bilobalide	<i>Hyphantria cunea</i>	<i>Ginkgo biloba</i>	Pan et al. (2016)
17	Eupatolide 13- <i>O</i> - β -d-glucopyranoside (eupatolide-II)	<i>Phyllotreta striolata</i>	<i>Inula salsoloides</i>	Bai et al. (2018)

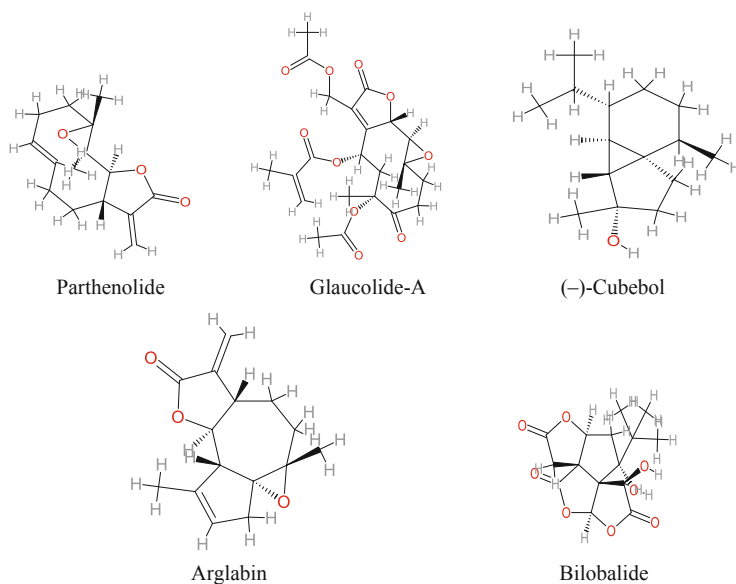


Fig. 9.3 Structure of some sesquiterpene lactones

carbon atoms from the terminal chain of apotirucallane or apoeuphane skeleton and changed to furan ring (Fang et al. 2011). The presence of limonoids is reported from plant families (Meliaceae and Rutaceae and sometimes in Cneoraceae and Simaroubaceae) of order Riales (Roy and Saraf 2006). One-third of 300 limonoids isolated from plants is from *Azadirachta indica* (neem) and *Melia azedarach* (Chinaberry). Scientifically, the inhibitory feeding activity of neem tree was described first. In 1952, Heinrich Schmutterer exhibited that the desert locust [*Schistocerca gregaria* (Forsk.)] refused to consume neem. David Morgan (Butterworth and Morgan 1968) isolated the active ingredient azadirachtin from the seeds of *A. indica*. Tables 9.5 and 9.6 present the lists of triterpenes and triterpene limonoids, respectively, which act as phyto-antifeedants, and some common structures of triterpenes are presented in Fig. 9.5.

9.2.2 Flavonoids

Flavonoids are compounds (1) consisting of derivatives of a phenyl-substituted propylbenzene containing a C15 skeleton; (2) having a C16 skeleton, which contain phenyl-substituted propylbenzene derivatives; and (3) flavonolignans containing derivatives of phenyl-substituted propylbenzene compressed with C6-C3 lignan precursors (Yonekura-Sakakibara et al. 2019). More than 9000 flavonoid compounds are identified having C6-C3-C6 carbon framework containing the structure of chromane or chromene, such as flavans, flavones, flavonols and

Table 9.4 A list of diterpenes acting as phyto-antifeedants

Sl No.	Diterpene clerodanes	Test insect	Origin	References	
1	Tafricanin A, B	<i>Locusta migratoria</i>	<i>Teucrium africanum</i>	Hanson et al. (1982)	
2	Clerodin (I)	<i>Spodoptera litura</i>	<i>Caryopteris divaricata</i> , <i>Scutellaria altissima</i>	Hosozawa et al. (1973, 1974)	
		<i>Leptinotarsa decemlineata</i>	<i>Caryopteris divaricata</i> , <i>Scutellaria altissima</i>	Bozov and Georgieva (2017)	
3	Caryoptin (II)	<i>Spodoptera litura</i>	<i>Caryopteris divaricata</i>	Hosozawa et al. (1973, 1974)	
4	Dihydroclerodin-I (V)				
5	Dihydrocaryoptin (VI)				
6	Clerodin hemiacetal (VII)				
7	Caryoptin hemiacetal (VIII)				
8	Caryoptinol (IX)				
9	Dihydrocaryoptinol (X)				
10	Ajugacumbins A, B, C, D	<i>Pareba vesta</i>	<i>Ajuga decumbens</i>	Min et al. (1989)	
11	Jodrellin A, B	<i>Spodoptera littoralis</i>	<i>Scutellaria woronowii</i>	Anderson et al. (1989)	
12	Ajugarin I		<i>Ajuga remota</i>	Simmonds et al. (1989)	
13	6,19-Diacetylteumassilin	<i>Helicoverpa armigera</i>	<i>Ajuga remota</i>		
		<i>Spodoptera littoralis</i>	<i>Teucrium</i>		
				14	Deacetyl ajugarin II
				15	Teucjaponin B
16	12-Epl-teucvm				
17	Rhodojaponin III	<i>Leptinotarsa decemlineata</i>	<i>Rhododendron molle</i>	Klocke et al. (1991)	
		<i>Spodoptera frugiperda</i>			
18	3,13E-clerodien-15-oic acid	<i>Reticulitermes speratus</i>	<i>Detarium microcarpum</i>	Lajide et al. (1995)	
19	4(18), 13E-clerodien-15-oic acid				
20	18-Oxo-3,13E-clerodien-15-oic acid				
21	2-Oxo-3,13E-clerodien-15-oic acid				
22	Ryanodol	<i>Spodoptera litura</i>	<i>Persea indica</i>	González-Coloma et al. (1996)	
23	Ryanodol 14-monoacetate	<i>Spodoptera litura</i>	<i>Persea indica</i>		
24	Cinnzeylanol	<i>Spodoptera litura</i>	<i>Persea indica</i>		
25	Cinnzeylanone	<i>Spodoptera litura</i>	<i>Persea indica</i>		

(continued)

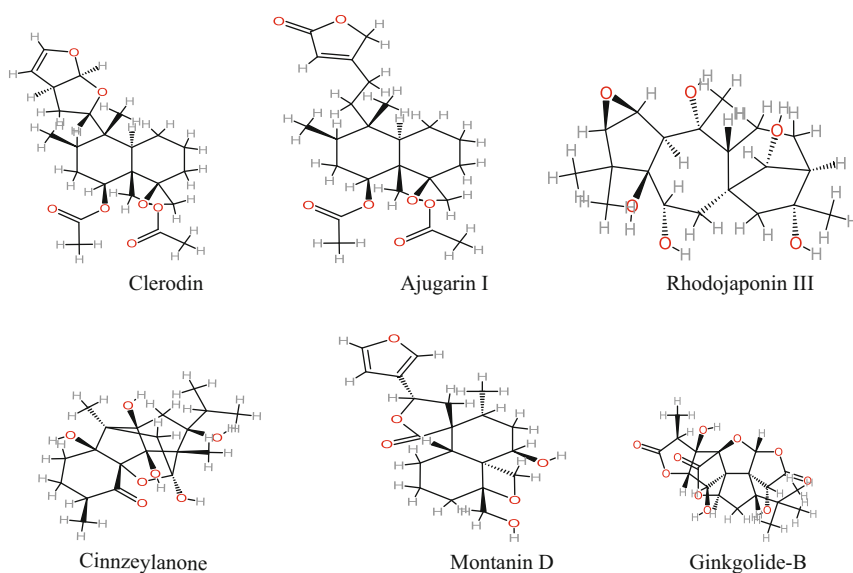
Table 9.4 (continued)

Sl No.	Diterpene clerodanes	Test insect	Origin	References
26	Epicinnzeylanol	<i>Spodoptera litura</i>	<i>Persea indica</i>	
27	Tanabalin (=12S-acetoxyhautriwaic acid)	<i>Pectinophora gossypiella</i>	<i>Tanacetum balsamita</i>	Kubo et al. (1996)
28	Ajugapitin	<i>Spodoptera littoralis</i>	<i>Ajuga chamaepitys</i> , <i>Salvia lineata</i>	Belles et al. (1985)
29	Indicol	<i>Spodoptera litura</i>	<i>Persea indica</i>	Fraga et al. (1997)
30	Vignaticol			
31	Perseanol			
32	14,15-Dehydroajugareptansin	<i>Spodoptera littoralis</i>	<i>Ajuga reptans</i>	Bremner et al. (1998)
33	Scutecepyrol B	<i>Spodoptera littoralis</i>	<i>Scutellaria rubicunda</i>	Bruno et al. (1999)
		<i>Spodoptera frugiperda</i>		
		<i>Mamestra brassicae</i>		
		<i>Pieris brassicae</i>		
		<i>Helicoverpa armigera</i>		
34	Isofruticolone	<i>Spodoptera littoralis</i>	<i>Teucrium fruticans</i>	
35	Clerodin	<i>Spodoptera littoralis</i>	<i>Caryopteris divaricata</i>	Hosozawa et al. (1974)
36	Caryoptin	<i>Spodoptera littoralis</i>		
		<i>Henosepilachna vigintioctopunctata</i>		
37	Dihydroclerodin-I	<i>Spodoptera littoralis</i>		Hosozawa et al. (1974)
38	Dihydrocaryoptin			
39	Clerodin hemiacetal			
40	Caryoptin hemiacetal			
41	Sideroxol	<i>Spodoptera frugiperda</i>	<i>Sideritis akmanii</i> , <i>S. rubriflora</i>	Bondi et al. (2000)
42	14,15-Dihydroajugapitin		<i>Ajuga iva</i>	
43	Ivain IV	<i>Spodoptera littoralis</i>	<i>Ajuga iva</i>	
		<i>Spodoptera frugiperda</i>		
44	Montanin D	<i>Spodoptera littoralis</i>	<i>Teucrium arduini</i>	Bruno et al. (2002)
45	6 β -Hydroxyteuscordin			
46	<i>Cis</i> -cleroda-15,16-dihydroxy-3,13(Z)-dien-18-O-[β -D-galactopyranosil]-peracetylester	<i>Tenebrio molitor</i>	<i>Baccharis sagittalis</i>	Cifuentes et al. (2002)

(continued)

Table 9.4 (continued)

Sl No.	Diterpene clerodanes	Test insect	Origin	References
47	<i>Cis</i> -cleroda-3,13(14)-dien-15,16-olide-18- <i>O</i> -[β -D-galactopyranosyl]-peracetylexer			
48	Hastifolins A, B, C	<i>Spodoptera littoralis</i>	<i>Scutellaria hastifolia</i>	Raccuglia et al. (2010)
49	Clerodin	<i>Helicoverpa armigera</i>	<i>Clerodendrum infortunatum</i>	Abbaszadeh et al. (2014)
50	15-Methoxy-14,15-dihydroclerodin			
51	15-Hydroxy-14,15-dihydroclerodin			
52	Ginkgolide	<i>Hyphantria cunea</i>	<i>Ginkgo biloba</i>	Pan et al. (2016)
53	Scutecyprin	<i>Leptinotarsa decemlineata</i>	<i>Scutellaria altissima</i>	Bozov and Georgieva (2017)
54	11-Epi-scutecolumnin C			

**Fig. 9.4** Structure of some diterpenes

anthocyanidins (Anderson and Markham 2006). However, auronones, chalcones and dihydrochalcones are also under flavonoids in a wide sense, but truly not in a limited sense (Yonekura-Sakakibara et al. 2019). Table 9.7 presents a list of flavonoids, which act as phyto-antifeedants (Fig. 9.6).

Table 9.5 A list of triterpenes acting as phyto-antifeedants

Sl No.	Triterpene	Test insect	Origin	References
1	Betulin	<i>Myzus persicae</i>	<i>Betula</i> species	Schoonhoven and Derksen-Koppers (1976)
2	Harrisonin	<i>Eldana saccharina</i> <i>Maruca testulalis</i>	<i>Harrisonia abyssinica</i>	Hassanali et al. (1986)
3	Obacunone	<i>Eldana saccharina</i> <i>Maruca testulalis</i>		
4	Salannin	<i>Epilachna varivestis</i>	<i>Pieris brassicae</i>	Schwinger et al. (1984), Kraus et al. (1987)
5	Momordicine II	<i>Aulacophora foveicollis</i> <i>A. nigripennis</i> <i>Epilachna admirabilis</i> <i>E. boisduvali</i> <i>A. femoralis</i>	<i>Momordica charantia</i>	Chandravadana (1987) Abe and Matsuda (2000)
6	3,7,23-Trihydroxycucurbita-5,24-dien-19-al	<i>Aulacophora foveicollis</i>		Chandravadana (1987)
7	Betulinic acid	<i>Spodoptera litura</i>	<i>Zizyphus xylopyrus</i>	Jagadeesh et al. (1998)
8	Oleanolic acid	<i>Sitophilus oryzae</i> <i>Heliothis zea</i>	<i>Junellia aspera</i>	Pungitore et al. (2005) Argandoña and Faini (1993)
9	Asiatic acid	<i>Oxya fuscovittata</i>	<i>Shorea robusta</i>	Sanjayan and Partho (1993)
10	Salannin	<i>Spodoptera litura</i> <i>Pericallia ricini</i> <i>Oxya fuscovittata</i>	Neem oil	Govindachari et al. (1996)
11	Nimbin	<i>Spodoptera litura</i> <i>Pericallia ricini</i> <i>Oxya fuscovittata</i>		
12	Deacetylnimbin	<i>Spodoptera litura</i>		

(continued)

Table 9.5 (continued)

Sl No.	Triterpene	Test insect	Origin	References
		<i>Pericallia ricini</i>		
		<i>Oxya fuscovittata</i>		
13	Momordicine I	<i>Aulacophora nigripennis</i>	<i>Momordica charantia</i>	Abe and Matsuda (2000)
		<i>Epilachna admirabilis</i>		
		<i>Epilachna boisduvali</i>		
14	Methyl 6,11 β -dihydroxy-12 α -(2-methylpropanoyloxy)-3,7-dioxo-14 β ,15 β -epoxy-1,5-meliacadien-29-oate	<i>Spodoptera littoralis</i>	<i>Trichilia pallida</i>	Simmonds et al. (2001)
		<i>Spodoptera exigua</i>		
		<i>Heliothis virescens</i>		
		<i>Helicoverpa armigera</i>		
15	Betulinic acid	<i>Achaea janata</i>	<i>Vitex negundo</i>	Chandramu et al. (2003)
16	Ursolic acid			
17	Maslinic acid	<i>Sitophilus oryzae</i>	<i>Junelia aspera</i>	Pungitore et al. (2005)
18	Xylogranatins F, G, R	<i>Mythimna separata</i>	<i>Xylocarpus granatum</i>	Wu et al. (2008)
19	Catunarosides A, B, C, D	<i>Plutella xylostella</i>	<i>Catunaregam spinosa</i>	Gao et al. (2011)
20	Swartziatrinoside			
21	Araliasaponin V			
22	Araliasaponin IV			
23	Ginsenoside	<i>Pieris rapae</i>	<i>Panax ginseng</i>	Zhang et al. (2017)
24	Ginsenosides (Rg1, Re, Rf, Rb1, Rg2, Rc, Rb2, Rb3 and Rd)	<i>Plutella xylostella</i>		Yang et al. (2018)
25	Ginsenosides Rb1, Rb2, Rc, Rd, Re and Rg1 [Rb1, Rb2, Rc, Rd, Rh2 and Rg3]	<i>Ostrinia furnacalis</i>		Liu et al. (2020)
26	Ginsenosides Re, Rg1 and Rg2			
27	Saponin CP4	<i>Plutella xylostella</i>	<i>Clematis aethusifolia</i>	Tian et al. (2021)
28	Clematoside S			
29	3-O- β -D-ribofuranosyl-(1 \rightarrow 3)- α -L-rhamnopyranosyl-(1 \rightarrow 2)-[β -D-glucopyranosyl-(1 \rightarrow 4)]- β -D-xylopyranosyl hederagenin			
30	Lupeol	<i>Corcyra cephalonica</i>	<i>Hemidesmus indicus</i>	Pillai et al. (2020)

Table 9.6 A list of triterpene limonoids acting as phyto-antifeedants

Sl No.	Limonoids	Test insect	Origin	References
1	Toonacilin, toonacilid	<i>Epilachna varivestis</i>	<i>Toona ciliata</i>	Kraus et al. (1978)
2	Meliantriol	<i>Schistocerca gregaria</i>	<i>Melia azedarach</i>	Kraus et al. (1981)
3	Limonin	<i>Spodoptera frugiperda</i> <i>Heliothis zea</i>	Citrus, grapefruit seeds	Klocke and Kubo (1982)
4	Sendanin	<i>Heliothis zea</i>	<i>Trichilia roku</i>	Nakatani et al. (1985a, b)
5	7-Acetyltrichilin A	<i>Spodoptera eridania</i>		
<i>Epilachna varivestis</i>				
<i>Spodoptera littoralis</i>				
6	Limonin	<i>Eldana saccharina</i>	Citrus, grapefruit seeds	Hassanali et al. (1986)
<i>Maruca testulalis</i>		Alford and Bentley (1986)		
<i>Chortstoneura fumiferana</i>		Alford et al. (1987)		
<i>Leptinotarsa decemlineata</i>		Mendel et al. (1991)		
<i>Leptinotarsa decemlineata</i>				
7	Azadirachtin	<i>Schistocerca gregaria</i>	<i>Azadirachta indica</i>	Butterworth and Morgan (1968), Mordue (Luntz) and Nisbet (2000)
8	Obacunone	<i>Leptinotarsa decemlineata</i>	Grape fruit seeds	Mendel et al. (1991)
9	Nomilin			Mendel et al. (1991)
10	Sandoricin	<i>Spodoptera frugiperda</i>	<i>Sandwicum koetjape</i>	Powell et al. (1991)
11	Cedrelone	<i>Peridroma saucia</i> , <i>Mamestra configurata</i>	<i>Toona ciliata</i>	Koul and Isman (1992)
12	1-Deoxy-3-trigloyl-11-methoxymeliacarpinin	<i>Spodoptera exigua</i>	<i>Melia azedarach</i>	Nakatani et al. (1993)
13	Humilinolides A–D	<i>Tenebrio molitor</i>	<i>Swietenia humilis</i>	Segura-Correa et al. (1993)
14	Toosendanin	<i>Peridroma saucia</i>	<i>Melia toosendan</i> , <i>M. azedarach</i>	Chen et al. (1995)
15	Nimboldins B, C, D, E	<i>Spodoptera eridania</i>	<i>Melia toosendan</i>	Nakatani et al. (1996)

(continued)

Table 9.6 (continued)

Sl No.	Limonoids	Test insect	Origin	References
16	Salannin			Zhou et al. (1996)
17	Trichilins H, I, J, K and L			
18	Azedarachin A and 12- <i>O</i> -acetyl-azedarachin B			
19	Ichangensin	<i>Leptinotarsa decemlineata</i>	Citrus molasses	Murray et al. (1999)
20	Melianoninol, melianone	<i>Pieris rapae</i>	<i>Melia azedarach</i>	Wang et al. (1994)
21	Melianol, meliandiol			
22	Meliantriol, toosendanin			
23	Trichilins B, D, H			
24	Lignanes	<i>Rhodnius prolixus</i>		Nakatani et al. (1994)
25	Piscidinol B-F	<i>Spodoptera exigua</i>	<i>Walsura piscidia</i>	Govindachari et al. (1996)
26	Azedarachin C	<i>Spodoptera exigua</i>	<i>Melia azedarach</i>	Huang et al. (1995)
27	Azadirachtin	<i>Spodoptera litura</i>	<i>Azadirachta indica</i>	Li et al. (1995)
28	Toosendanin	<i>Peridroma saucia</i>	<i>Melia toosendan</i>	Xie et al. (1995)
29	Salannin, nimbin	<i>Spodoptera litura</i>	<i>Melia azedarach</i>	Govindachari et al. (1996)
30	Ruageanins A, B	<i>Spodoptera frugiperda</i>	<i>Ruafea fglabra</i>	Mootoo et al. (1996)
31	Azedarachin A, salannin	<i>Spodoptera eridania</i>	<i>Melia toosendan</i>	Nakatani et al. (1996)
32	Nimboldins C–E	<i>Spodoptera eridania</i>	<i>Melia toosendan</i>	
33	Trichilins K, L, I, J, H	<i>Spodoptera eridania</i>	<i>Melia toosendan</i>	Zhou et al. (1996)
34	Azadirachtin	<i>Spodoptera littoralis</i>	<i>Azadirachta indica</i>	Mordue (Luntz) and Nisbet (2000)
		<i>Spodoptera frugiperda</i>		
		<i>Heliothis virescens</i>		
		<i>Helicoverpa armigera</i>		
		<i>Pieris brassicae</i>		

(continued)

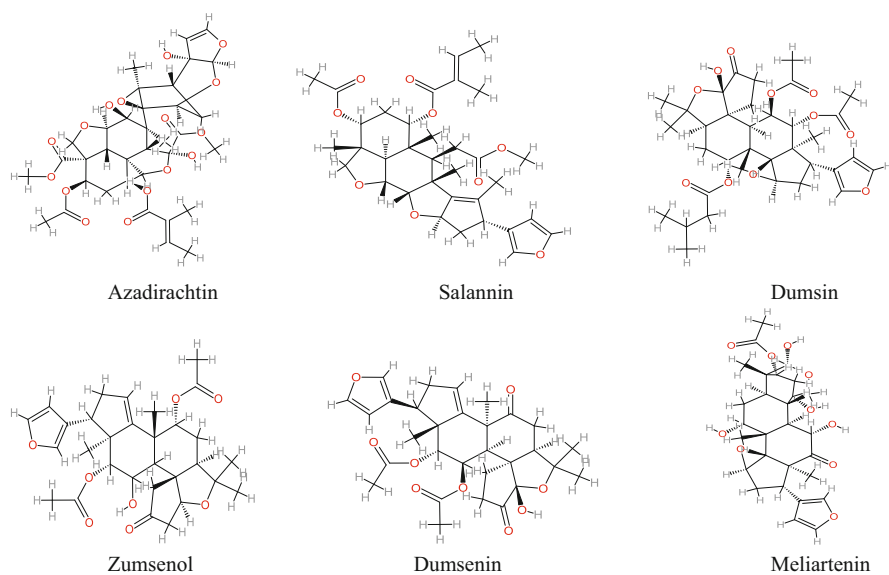
Table 9.6 (continued)

Sl No.	Limonoids	Test insect	Origin	References
		<i>Epilachna varivestis</i>		
		<i>Locusta migratoria</i>		
		<i>Melanoplus sanguinipes</i>		
35	Meliartenin	<i>Spodoptera eridania</i>	<i>Melia azedarach</i>	Carpinella et al. (2002)
		<i>Epilachna pannelata</i>		
		<i>Epilachna paenulata</i>	<i>Melia azedarach</i>	Carpinella et al. (2003)
36	Dumsin	<i>Pectinophora gossypiella</i>	<i>Croton jatrophioides</i>	Nihei et al. (2002)
		<i>Spodoptera frugiperda</i>		
37	Zumsin	<i>Pectinophora gossypiella</i>		
		<i>Spodoptera frugiperda</i>		
38	Meliartenin	<i>Epilachna paenulata</i>	<i>Melia azedarach</i>	Carpinella et al. (2003)
39	Musidunin	<i>Pectinophora gossypiella</i>	<i>Croton jatrophioides</i>	Nihei et al. (2004, 2005, 2006)
		<i>Spodoptera frugiperda</i>		
40	Musiduol	<i>Pectinophora gossypiella</i>		
		<i>Spodoptera frugiperda</i>		
41	Zumketol	<i>Pectinophora gossypiella</i>		
		<i>Spodoptera frugiperda</i>		
42	Zumsenin	<i>Pectinophora gossypiella</i>		
		<i>Spodoptera frugiperda</i>		
43	Zumsenol	<i>Pectinophora gossypiella</i>		
		<i>Spodoptera frugiperda</i>		
44	Dumnin	<i>Pectinophora gossypiella</i>		

(continued)

Table 9.6 (continued)

Sl No.	Limonoids	Test insect	Origin	References
		<i>Spodoptera frugiperda</i>		
45	Dumsenin	<i>Pectinophora gossypiella</i> <i>Spodoptera frugiperda</i>		
46	Xylogranatins F, G and R	<i>Mythimna separate</i>	<i>Xylocarpus granatum</i>	Wu et al. (2008)
47	2-Acetyl soymidin B	<i>Spodoptera litura</i> <i>Achaea janata</i>	<i>Soymida febrifuga</i>	Yadav et al. (2014)
48	Soymidin D	<i>Spodoptera litura</i> <i>Achaea janata</i>		
49	Soymidin E	<i>Spodoptera litura</i> <i>Achaea janata</i>		
50	Trichanolid F	<i>Spodoptera litura</i>	<i>Trichilia connaroides</i>	Solipeta et al. (2020)

**Fig. 9.5** Structure of some triterpenes

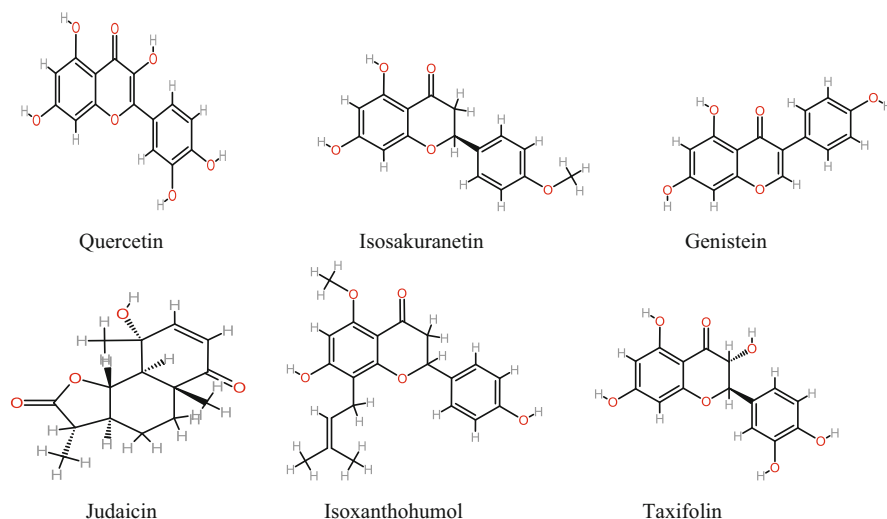


Fig. 9.6 Structure of some flavonoids

9.2.3 Alkaloids

Alkaloid compounds (nitrogen incorporated into a heterocyclic ring) are naturally occurring low-molecular-weight organic compounds. It was reported that ca. 20–30% of all alkaloids arise in higher plants, mostly in dicotyledonous angiosperms at concentrations of ca. 0.01% of the dry weight or more (Seigler 1998). These compounds could be stored in any part of the plant at different concentrations; they are most often intense in the most nutritious tissues, such as seed tissues (Bernays and Chapman 1994). It is reported that ca. 10% of plant species produce alkaloids as secondary metabolites, and these compounds primarily help to protect against herbivores as well as pathogens. Till date more than 16,000 alkaloids have been identified (Murphy 2017). However, some of them act as phyto-antifeedants (Table 9.8 and Fig. 9.7).

9.2.4 Steroids

Steroids possess the tetracyclic 1,2-cyclopentanoperhydrophenanthrene (5 α - or 5- β -gonane) carbon skeleton, normally having methyl substituents at C-10 and C-13 and an alkyl substituent (side chain) at C-17. An array of diverse steroid compounds arises due to different oxidation states of carbons of its tetracyclic core and CH₃ groups and the framework of the side chain. All steroids are derived from *S*-squalene-2,3-epoxide (Gunaherath and Gunatilaka 2014). The major plant steroids are phytosteroids, withanolides, brassinosteroids, phytoecdysteroids, and steroidal alkaloids. Table 9.9 shows a list of steroids, which act as phyto-antifeedants (Fig. 9.8).

Table 9.7 A list of flavonoids acting as phyto-antifeedants

Sl No.	Flavonoids	Test insect	Origin	References			
1	5-Hydroxy-3,6,7,8,4'-pentamethoxyflavone	<i>Spodoptera litura</i>	<i>Gnaphalium affine</i>	Morimoto et al. (2000, 2003)			
2	5-Hydroxy-3,6,7,8-tetramethoxyflavone						
3	5,6-Dihydroxy-3,7-dimethoxyflavone						
4	4,4',6'-Trihydroxy-2'-methoxychalcone						
5	5-Hydroxy-3,6,7,8,4'-heptamethoxyflavone						
6	5-Hydroxy-3,6,7,8-tetramethoxyflavone						
7	5,6-Dihydroxy-3,7-dimethoxyflavone						
8	Quercetin	<i>Coptotermes formosanus</i>	<i>Bobgunnia madagascariensis</i>	Ohmura et al. (2000)			
		<i>Tribolium castaneum</i>		Adeyemi et al. (2010)			
9	Taxifolin	<i>Coptotermes formosanus</i>		Ohmura et al. (2000)			
10	Naringenin						
11	Isosakuranetin						
12	Aromadendrin						
13	Phloretin						
14	Myricetin						
15	Sakuranetin						
16	Eriodictyol						
17	Genistein	<i>Coptotermes formosanus</i>	<i>Trifolium pratense</i>	Ohmura et al. (2000)			
		<i>Acyrthosiphon pisum</i>		Goławska and Łukasik (2012)			
		<i>Hylastinus obscurus</i>		Quiroz et al. (2017)			
18	Formononetin	<i>Hylastinus obscurus</i>					
19	Fisetin	<i>Coptotermes formosanus</i>		Ohmura et al. (2000)			
20	Kaempferol				<i>Sitophilus oryzae</i>	<i>Calotropis procera</i>	Nenaah (2013)
					<i>Rhizopertha dominica</i>		
21	Catechin	<i>Coptotermes formosanus</i>		Ohmura et al. (2000)			
22	Catechinic acid						
23	Judaicin	<i>Helicoverpa armigera</i>	<i>Cicer judaicum</i>	Simmonds and			

(continued)

Table 9.7 (continued)

Sl No.	Flavonoids	Test insect	Origin	References
		<i>Spodoptera litura</i>		Stevenson (2001)
		<i>Spodoptera frugiperda</i>		
24	Maackiain	<i>Helicoverpa armigera</i>		
		<i>Spodoptera litura</i>		
		<i>Spodoptera frugiperda</i>		
25	Luteolin	<i>Acyrtosiphon pisum</i>		Goławska and Łukasik (2012)
26	3-O-Rutinosides of quercetin	<i>Sitophilus oryzae</i>	<i>Calotropis procera</i>	Nenaah (2013)
		<i>Rhyzopertha dominica</i>		
27	3-O-Rutinosides of isorhamnetin	<i>Sitophilus oryzae</i>		
		<i>Rhyzopertha dominica</i>		
28	5-Hydroxy-3,7-dimethoxyflavone-4'-O- β -glucopyranoside	<i>Sitophilus oryzae</i>	<i>Calotropis procera</i>	Nenaah (2013)
		<i>Rhyzopertha dominica</i>		
29	Tephroapollin-F	<i>Sitophilus oryzae</i>	<i>Tephrosia apollinea</i>	Nenaah (2014)
		<i>Rhyzopertha dominica</i>		
		<i>Tribolium castaneum</i>		
30	Isoxanthohumol	<i>Myzus persicae</i>		Stompor et al. (2015)
31	Formononetin	<i>Hylastinus obscurus</i>		Quiroz et al. (2017)

Table 9.8 A list of alkaloids acting as phyto-antifeedants

Sl No.	Alkaloids	Test insect	Origin	References
1	Isoboldine (I)	<i>Spodoptera litura</i>	<i>Cocculus trilobus</i>	Munakata (1975)
		<i>Abraxas miranda</i>		
2	Wilforine	<i>Pieris rapae</i>	<i>Maytenus rigida</i>	Monache et al. (1984)
		<i>Locusta migratoria</i>		
3	Pterocarpan	<i>Maruca testulalis</i>	<i>Tephrosia hildebrandtii</i>	Lwande et al. (1985)
4	Hildecarpin			
5	Vasicine	<i>Aulacophora foveicollis</i>	<i>Adhatoda vasica</i>	Saxena et al. (1986)
		<i>Epilachna vigintioctopunctata</i>		
6	Vasicinol	<i>Aulacophora foveicollis</i>	<i>Adhatoda vasica</i>	Saxena et al. (1986)
		<i>Epilachna vigintioctopunctata</i>		
7	Vasicinone	<i>Aulacophora foveicollis</i>	<i>Adhatoda vasica</i>	Saxena et al. (1986)
		<i>Epilachna vigintioctopunctata</i>		
8	Tylophorine	<i>Spilosoma obliqua</i>	<i>Tylophora asthmatica</i>	Tripathi et al. (1990)
9	Dithyreanitrile	<i>Spodoptera frugiperda</i>	<i>Dithyrea wislizenii</i>	Powell et al. (1991)
		<i>Ostrinia nubilalis</i>		
10	3'-Acetyltrachelanthamine	<i>Leptinotarsa decemlineata</i>	<i>Heliotropium floridum</i>	Reina et al. (1997)
11	Europine	<i>Spodoptera littoralis</i>		Reina et al. (1995)
12	Cardiopetamine	<i>Spodoptera littoralis</i>	<i>Delphinium cardiopetalum</i>	González-Coloma et al. (1998)
13	15-Acetylcardiopetamine	<i>Leptinotarsa decemlineata</i>	<i>Delphinium cardiopetalum</i>	
14	Lycopsamine	<i>Leptinotarsa decemlineata</i>	<i>Heliotropium megalanthum</i>	Reina et al. (1998)
		<i>Spodoptera littoralis</i>		
15	Berberine	<i>Hyphantria cunea</i>	<i>Coptis japonica</i>	Park et al. (2000)
		<i>Agelastica coerulea</i>		
16	Palmatine	<i>Hyphantria cunea</i>	<i>Coptis japonica</i>	Park et al. (2000)
		<i>Agelastica coerulea</i>		
17	Coptisine	<i>Hyphantria cunea</i>	<i>Coptis japonica</i>	Park et al. (2000)
		<i>Agelastica coerulea</i>		

(continued)

Table 9.8 (continued)

Sl No.	Alkaloids	Test insect	Origin	References
18	Leptine	<i>Leptinotarsa decemlineata</i>	<i>Solanum chacoense</i>	Rangarajan et al. (2000)
19	Strychnine	<i>Spodoptera litura</i>	<i>Neurolaena lobata</i>	Passreiter and Isman (1997)
		<i>Diabrotica virgifera virgifera</i>		Simmonds (2003)
20	Matrine	<i>Coptotermes formosanus</i>	<i>Sophora flavescens</i>	Mao and Henderson (2007)
21	Oxymatrine	<i>Coptotermes formosanus</i>		
22	Atropine	<i>Spodoptera litura</i>	<i>Datura stramonium</i> , <i>Datura ferox</i> , <i>Datura innoxia</i>	González-Coloma et al. (2004)
		<i>Leptinotarsa decemlineata</i>	<i>Datura stramonium</i> , <i>Datura ferox</i> , <i>Datura innoxia</i>	
23	Atropine + Nicotine	<i>Lymantria dispar</i>	<i>Datura stramonium</i> , <i>Datura ferox</i> , <i>Datura innoxia</i>	Shields et al. (2008)
24	3-O-Acetyl-narcissidine	<i>Spodoptera littoralis</i>	<i>Hippeastrum puniceum</i>	Santana et al. (2008)
25	(+)-11 β -Methoxy-10-oxoerysotramidine		<i>Erythrina latissima</i>	Cornelius et al. (2009)
26	(+)-10,11-Dioxoerysotramidine			
27	(+)-Erysotrine			
28	(+)-Erysotramidine			
29	(+)-Erythraline			
30	(+)-11 β -Hydroxyerysotramidine			
31	Taxol	<i>Lymantria dispar</i>	Yew plant	Hu et al. (2011)
32	α -Chaconine	<i>Trogoderma granarium</i>	<i>Solanum tuberosum</i>	Nenaah (2011)
33	α -Solanine	<i>Trogoderma granarium</i>	<i>Solanum tuberosum</i>	Nenaah (2011)
34	(3 β ,7 α)-Stigmast-5-ene-3,7-diol	<i>Leptinotarsa decemlineata</i>	<i>Echium wildpretii</i>	Santana et al. (2012)
35	(3 β ,7 α)-7-Methoxystigmast-5-en-3-ol			

(continued)

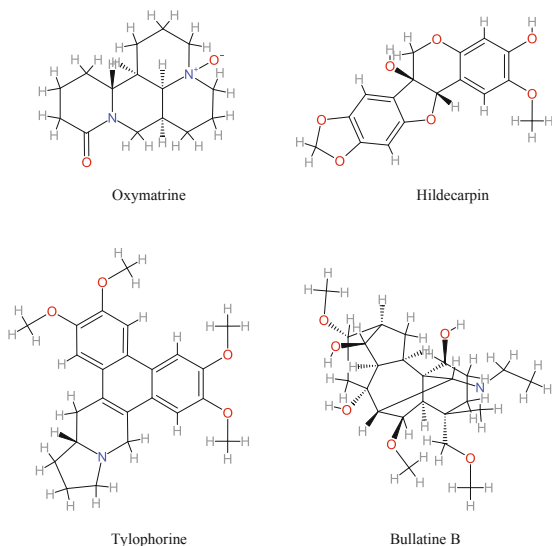
Table 9.8 (continued)

Sl No.	Alkaloids	Test insect	Origin	References
36	7-Demethoxytylophorine	<i>Plutella xylostella</i>	<i>Cynanchum komarovii</i>	Guo et al. (2014)
37	6-Hydroxyl-2,3-dimethoxy phenanthroindolizidine			
38	Vasicine acetate		<i>Adhatoda vasica</i>	Paulraj et al. (2014)
39	2-Acetyl-benzylamine			
40	Pubescensine	<i>Pieris rapae</i>	<i>Aconitum soongaricum</i> var. <i>pubescens</i>	Chen et al. (2015)
41	3-Deoxyaconitine			
42	Aconitine			
43	15- α -Hydroxyneoline			
44	Taurenine			
45	Bullatine B			
46	Chasmanthinine	<i>Spodoptera exigua</i>	<i>Aconitum franchetii</i> var. <i>villosulum</i>	Zhang et al. (2017)
47	Apetalidine A	<i>Spodoptera litura</i>	<i>Aconitum apetalum</i> , <i>Aconitum franchetii</i> var. <i>villosulum</i>	
48	Apetalidine E		<i>Aconitum apetalum</i> , <i>Aconitum franchetii</i> var. <i>villosulum</i>	
49	Chasmaconitine		<i>Aconitum apetalum</i> , <i>Aconitum franchetii</i> var. <i>villosulum</i>	
50	Indaconitine		<i>Aconitum apetalum</i> , <i>Aconitum franchetii</i> var. <i>villosulum</i>	

9.2.5 Coumarins

Coumarin compounds are in the family of benzopyrones (1,2-benzopyrones or 2H-1-benzopyran-2-ones), which is a class of lactones containing a benzene ring fused to α -pyrone ring (Matos et al. 2015). The name ‘coumarin’ is derived from the French term of Tonka bean (*coumarou*), seeds of *Dipteryx odorata* (*Coumarouna odorata*) (Fabaceae/Leguminosae), which was first isolated in 1820. A list of coumarins is presented in Table 9.10. Figure 9.9 provides some structure of coumarins.

Fig. 9.7 Structure of some alkaloids



9.2.6 Other Compounds

Aglaroxin A isolated from the twigs with bark of *Aglaia elaeagnoidea* (syn. *A. roxburghiana*) had potent antifeedant activity against the gram pod borer, *Helicoverpa armigera* (Hübner) and Asian armyworm, *Spodoptera litura* (Fabricius) (Lepidoptera: Noctuidae) (Koul et al. 2005).

Ononitol monohydrate, a class of glycoside, isolated from *Cassia tora* (Fabaceae) leaves showed antifeedant activity against the third instar larvae of *H. armigera* and *S. litura* (Baskar and Ignacimuthu 2012).

9.3 Phyto-Antifeedants: Mode of Action

The antifeedant effects of compounds on insects are generally measured by determining nutritional indices, such as consumption, digestion and growth rate of insects after consuming the foods provided. However to measure accurate estimate of nutritional indices, a series of control experiments with weighed quantity of food would have to be provided to determine whether the compound of interest has resulted in a reduction in food consumption.

In feeding inhibitory test of a compound, different methods have been employed, such as spraying of the compound on natural food (leaf disks), incorporating it with dried food (wheat flour for locusts) and adding it in artificial diets, which is palatable (mostly with sucrose). For chewing insects, sucrose is mixed with agar or agar cellulose substrates; filter paper or glass fibre disks have been employed, while an artificial medium in parafilm sachets is used for sucking insects. For heteropteran and lepidopteran larvae and coleopteran insects, antifeedants are provided in drinking water sources.

Table 9.9 A list of steroids acting as phyto-antifeedants

Sl No.	Steroids	Test insect	Origin	References
1	Withanolide E	<i>Spodoptera littoralis</i>	<i>Physalis peruviana</i> , <i>Withania somnifera</i>	Ascher et al. (1980)
		<i>Epilachna varivestis</i>	<i>Physalis peruviana</i> , <i>Withania somnifera</i>	
2	Nicalbin A, B	<i>Epilachna varivestis</i>	<i>Nicandra physalodes</i>	
3	4 β -Hydroxywithanolide E	<i>Epilachna varivestis</i>	<i>Physalis peruviana</i>	
4	Nic-1 (nicandrenone)	<i>Epilachna varivestis</i>	<i>Nicandra physalodes</i>	
5	Azedarachol	<i>Agrotis segetum</i>	<i>Melia azedarach</i>	Nakatani et al. (1985b)
6	Conessine	<i>Spodoptera litura</i>	<i>Holarrhena antidiysenterica</i>	Thappa et al. (1989)
		<i>Pieris brassicae</i>	<i>Holarrhena antidiysenterica</i>	
7	Salpichrolide A, C, G	<i>Musca domestica</i>	<i>Salpichroa origanifolia</i>	Mareggiani et al. (2000)
8	Leptine I	<i>Leptinotarsa decemlineata</i>		Hollister et al. (2001)
9	Leptinines			
10	Luciamin	<i>Schizaphis graminum</i>		Dayan et al. (2009)
11	20-Hydroxyecdysone	<i>Phyllotreta striolata</i>	<i>Ajuga nipponensis</i>	Xu et al. (2009)
12	(3 β ,7 α)-Stigmast-5-ene-3,7-diol	<i>Leptinotarsa decemlineata</i>	<i>Echium wildpretii</i>	Santana et al. (2012)
13	(3 β ,7 α)-7-Methoxystigmast-5-en-3-ol	<i>Leptinotarsa decemlineata</i>	<i>Echium wildpretii</i>	

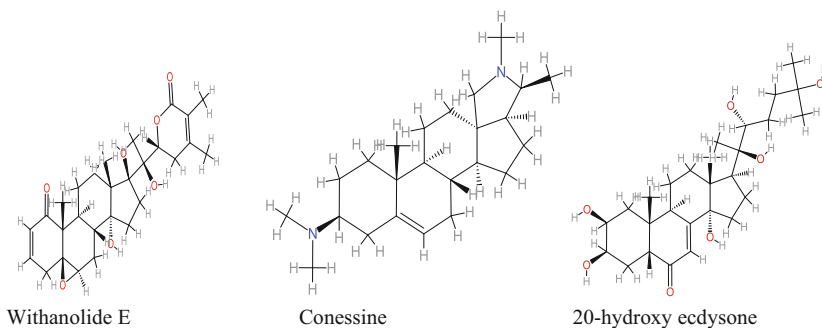
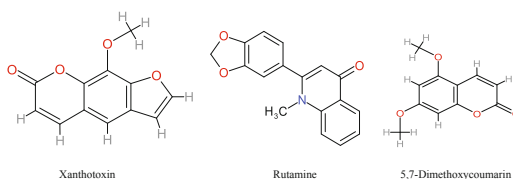
**Fig. 9.8** Structure of some steroids

Table 9.10 A list of coumarins acting as phyto-antifeedants

Sl No.	Coumarins	Test insect	Origin	References
1	Xanthotoxin	<i>Spodoptera litura</i>	Umbelliferae	Yajima and Munakata (1979)
		<i>Spodoptera exigua</i>		Berdegue et al. (1997)
		<i>Trichoplusia ni</i>		Akhtar and Isman (2004)
2	8-Methoxypsoralen	<i>Spodoptera littoralis</i>	<i>Tetradium daniellii</i>	Stevenson et al. (2003)
		<i>Heliothis virescens</i>		
3	5-Methoxypsoralen	<i>Spodoptera littoralis</i>		Sbegen-Loss et al. (2011)
		<i>Heliothis virescens</i>		
		<i>Cryptotermes brevis</i>		
4	5,8-Dimethoxypsoralen	<i>Spodoptera littoralis</i>		Stevenson et al. (2003)
		<i>Heliothis virescens</i>		
5	5-Geranyloxypsoralen	<i>Spodoptera littoralis</i>		
		<i>Heliothis virescens</i>		
6	Xanthotoxin	<i>Trichoplusia ni</i>	Umbelliferae plants	Akhtar and Isman (2004)
7	3(2'',2''Dimethyl butenyl) 3'-hydroxydihydrofuropsoralen	<i>Spodoptera littoralis</i>	<i>Ruta chalepensis</i>	Emam et al. (2009)
8	Rutamine	<i>Spodoptera littoralis</i>	<i>Ruta chalepensis</i>	
9	5,7-Dimethoxycoumarin	<i>Cryptotermes brevis</i>	Total citrus wax	Sbegen-Loss et al. (2011)

Fig. 9.9 Structure of some coumarins

In choice tests, the screening method is much sensitive. The peach aphid *Myzus persicae* feeds on artificial foods containing different allelochemicals, whereas in a choice experiment the aphids could not distinguish between the control without the test allelochemicals and substance with allelochemicals. This study indicated that experimental conditions would have to be chosen after careful considerations. According to Ma (1977), the threshold value of *Spodoptera exempta* towards warburganal was 1000 times higher when applied in sucrose-agar diet than warburganal present in natural leaf surface (Kubo et al. 1976). These results suggested that the compound mixed in agar caused the receptors to contact at lower concentrations than that present in the leaf surface. Further, the increased food intake may be due to poor nutritional value of agar (Dethier 1982).

Different methods have been applied by various researchers to describe antifeedant effects, such as the effect of antifeedants in concentrations (ppm—implicating a reduction in food intake by 50%) which reduce food intake by 50%, while a group of researchers reported that the effect of antifeedants would be taken into account when the compound of interest inhibited feeding of the insect pest between 80% and 100%; antifeedants in the context of leaf surface area are not fed by an insect (protective concentrations, PC) and the intensity of insect starvation (starvation concentration, SC), i.e., the effective antifeedant concentration was not taken into account when these values are below 95% level. Jermy et al. (1981) used a log 2 concentration series to state antifeedant activity in effective threshold concentrations. However, a number of reviews suggested that bioassays to observe the antifeedant effect of an insect towards a compound will not be more than 6 h as lower feeding for long-term test could cause post-ingestive toxicity rather than behavioural basis.

9.3.1 Cognition of Antifeedants

Different mechanisms are used by various insects at the sensory level for the cognition of antifeedants. Phytophagous insects possess taste cells to detect inedible and/or toxic secondary metabolites of plant origin, and specialized receptors are stimulated by the substances, or the activities of receptors are modified by tuning the other compounds, and in this way insects adjust the sensory code (van Loon and Schoonhoven 1999).

In lepidopteran larvae, the bitter-receptor (deterrent) taste cells possess four types of chemosensilla—the lateral and medial styloconic sensilla, epipharyngeal sensilla and gustatory sensilla, which are located on the maxillary palp. Each sensillum possesses three to four taste cells. One of the taste cells in each sensillum acts as deterrent. Overlapping molecular receptive ranges (MRRs) are present in some bitter-receptor taste cells (van Loon and Schoonhoven 1999). A bitter-receptor taste cell can respond to various secondary plant metabolites by the co-localization of a set of signalling pathways, each with distinct MRRs, such as the bitter-receptor taste cell located in the lateral styloconic sensillum of *M. sexta* and had at least two signalling pathways: one pathway reacts to phenolic glycosides (salicin and helicin)

and methylxanthines (caffeine, theophylline and theobromine), while the other pathway reacts to aromatic nitro derivatives (aristolochic acids) (Glendinning and Hills 1997). For example, caffeine—a deterrent to the monophagous larva of *Danaus plexippus*—responds to all eight receptors located in the maxillary sensilla styloconica. A number of literatures reveal that direct gated ion channels and G protein-coupled receptors are involved in sugar signalling pathways for dipteran taste cell (Murakami and Kijima 2000; Ishimoto et al. 2000; Dahanukar et al. 2001).

Phytophagous insects may employ post-ingestive response to detect toxic compounds in food, e.g. the larvae of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) initially start feeding on foods containing indole-3-carbinol (a toxic compound), which is present in cruciferous plants, but the larvae did not consume after 2–3 min and become motionless (Glendinning and Slansky 1995). This observation suggests that indole-3-carbinol does not deter the larvae initially through pre-ingestive (i.e. gustatory or olfactory) mechanism, and this compound deter the larvae to feed through post-ingestive response. Similar results were recorded in the case of *M. sexta* larvae. Larvae of *M. sexta* when provided with artificial diet mixed with nicotine then they initially consumed rapidly, but they did not feed after 24–30 s, and subsequently, the larvae started to tremble aggressively. The above fact is not an incident of pre-ingestive response but post-ingestive response of the *M. sexta* larvae, which is proved by these four facts: (1) taste-mediated inhibitory responses in the larvae generally onset more rapidly (in <6 s); (2) destroying the gustatory and olfactory chemosensilla of larvae had no effect on the time course or the nature of inhibitory response to the diet containing nicotine; (3) nicotine did not stimulate the deterrent taste cells in the larvae (Glendinning 1996); and (4) the larvae aggressively tremble when nicotine trespasses the central nervous system (Morris 1984).

9.3.2 Validating the Action of Inhibitory Response

Phytophagous insects tackle the inhibitory response of secondary metabolites by at least three different mechanisms—two are performed by the taste system, while the third is mediated by detoxication enzymes present in the midgut. It seems that these three mechanisms are helpful to combat against a wide array of secondary plant metabolites.

9.3.2.1 Carbohydrates Hide the Distasteful Taste of Secondary Plant Metabolites

When inedible secondary plant metabolites are provided with carbohydrates (sugars or sugar alcohols), then this mechanism is functional. The carbohydrates in the food can override the inedible taste of some plant secondary metabolites, which causes the inedible food to become edible or palatable food (Glendinning et al. 2000). The peripheral taste system helps to detect the mechanism as several reports are available, which proved that carbohydrates inhibit the response mechanism of deterrent taste cells (Blaney and Simmonds 1990; Shields and Mitchell, 1995a, b). Among the

two possibilities, one is that carbohydrate-sensitive taste cell inhibits the activity of deterrent taste cell present in the same chemosensillum, while in another possibility, carbohydrates attach to the receptor molecules, resulting in the inhibition of the response of the taste cells.

9.3.2.2 Longer Dietary Exposure Helps the Gustatory System to Consume Nontoxic Unpalatable Substances

If phytophagous insects are provided a diet with nontoxic unpalatable substances, then insects will repetitively check the diet, and after 12–48 h of tasting the diet, insects will ultimately adapt their inhibitory response towards these substances. In *M. sexta*, a diet containing caffeine has been provided for 24 h; then, the insect put an end to inhibitory response towards caffeine. This mode of mechanism is mediated peripherally as the prolonged exposure to the diet helps to desensitize all caffeine-response taste cells towards caffeine. Similar results were obtained if salicin is provided for 24 h, but this mechanism is performed centrally because of the absence of desensitization of salicin-response taste cells. Both these results suggest that the larvae of *M. sexta* employ peripheral and central gustatory mechanisms to adapt nontoxic unpalatable substances.

9.3.2.3 Longer Dietary Exposure Towards Toxic and Unpalatable Substances Causes Release of Detoxification Enzymes

It is common that phytophagous insects can overcome the inhibitory responses of toxic plant secondary metabolites by inducing the detoxification enzymes present in the midgut (Zangerl and Berenbaum 1993; Glendinning and Slansky 1995).

The larvae of *M. sexta* can overcome the neurotoxic effects caused by nicotine in the diet. Initially for a period of 30 h, the larvae deter from feeding towards ecologically relevant concentration of nicotine, but after that the midgut wall produces a huge amount of P450 detoxification enzymes, which catabolize the nicotine to excretal substance with less toxicity (Negherbon 1959; Morris 1983, 1984; Snyder et al. 1993, 1994). The above statement is supported by two reasons: (1) feeding of low amount of nicotine in diet does not induce release of P450 detoxification enzymes (Snyder and Glendinning 1996), and (2) when nicotine-fed larvae were provided piperonyl butoxide (PB) (an inhibitor of P450 detoxification enzymes), it results in consumption of nicotine at a lower rate that is similar to that of uninduced larvae.

9.4 Phyto-Antifeedant: Formulation

The use of natural antifeedants is growing in the world, and the choice of the ideal formulation is dependent on a series of factors: type of antifeedants (natural or synthetic), pharmaceutical forms (dust and spray), duration of action time (short or long) and environment of exposure. The most used antifeedant is azadirachtin A from *A. indica*. Other azadirachtin isomers are also reported to act as antifeedants, but activity of azadirachtin A is higher than other isomers. This compound is

effective against ca. 400 insect species belonging to Blattodea, Coleoptera, Diptera, Dermaptera, Ensifera, Homoptera, Heteroptera, Hymenoptera, Lepidoptera, Isoptera, Phasmida, Thysanoptera and Siphonaptera (Koul and Wahab 2004).

Liquid formulations of commercial neem-based insecticides—(1) Agroneem (Ajay Bio-Tech, Pune, India), (2) Ecozin (AmVaC, Los Angeles, CA) and (3) Neemix 4.5 (Certis, Columbia, MD)—and a neem seed extract formulation containing 1036, 16,506, 471 and 223 µg/ml azadirachtin, respectively, caused lower feeding punctures by the gravid female boll weevils *Anthonomus grandis grandis* Boheman on the treated cotton square compared to control treatments (Showler et al. 2004). If the formulations are applied in outdoor environment 24 h before weevils were in touch, a decrease of 46–60% feeding compared with controls was recorded (Showler et al. 2004), indicating that repeated applications are needed to get the best result. A significant reduction in the feeding activity of the diamondback moth, *Plutella xylostella*, larvae was recorded by feeding on Agroneem, Ecozin and Neemix (Liang et al. 2003).

AgriDyne Technologies Inc. (ATI) has developed a formulation, Align™ (an emulsifiable concentrate containing 3% azadirachtin), which is diluted with water before spraying to control insect pests of fruits and vegetables. The application of Align™ resulted in a significant reduction in feeding activity of cabbage looper, beet armyworm, diamondback moth, Colorado potato beetle, sweet potato whitefly, grape leafhopper, green peach aphid and onion thrips. Further, AgriDyne has formulated two neem-based insecticides, Azatin® EC and Turplex™, to control insect pests of greenhouse and ornamental plants, respectively.

In India, several neem-based products are available, such as Azadit; Biosol; Godrej; Achook [containing 2800 ppm of the compounds azadirachtin (aza) (0.03%; 300 ppm), azadiradione, nimbocinol and epinimbocinol]; Field Marshal (azadirachtin-enriched neem extract—water-miscible); neem-based emulsifiable concentrate, dust, water dispersible powder and granule (25% WDP are effective against *H. armigera*, *S. obliqua* and *E. cnejeus*, while 5% dust are effective against *S. obliqua*, and 3.5% and 10% granules on China clay against sorghum stem borer, *Chilo partellus*); Neemhit prepared by Ayurvedic formula (effective against cotton, sugarcane, peanut, soybean, sunflower, corn, pulses, rice, vegetables, fruit trees, flowers and plantation crops according to manufacturer); Neem Oil Emulsion; Neem Plus; Neem Top; Neemark (water-miscible concentrate containing 80% neem biomass—give an emulsion on dilution with water); Neemasol; Neemgold; Neemguard; etc. Further, four neem-based insecticides—Neemix® (0.25% EC at 20 mg azadirachtin/litre), Ecozin® (3% EC at 20 mg azadirachtin/litre), Agroneem® (0.15% EC at 4.8 mg azadirachtin/litre) and neem oil (0.25% EC azadirachtin at 20 mg azadirachtin/litre)—are effective antifeedants against the larvae of *Pieris brassicae* (Hasan and Ansari 2011).

Zuleta-Castro et al. (2017) formulated the emulsion containing 0.76% p/p ethanolic extract using *A. indica* cell culture extract, 0.72% 8-hydroxyquinoline, 1% anthraquinone and epichlorohydrin, 0.20% Tween 8 and 50/50 aqueous phase/oil phase to control *S. frugiperda* insects, and the metabolite did not degrade in the light, which causes death of the insect pests in the field.

Neem seed extracts inhibited the feeding of rose aphid, *Macrosiphum rosae* (L.), and chrysanthemum aphid, *Macrosiphoniella sanborni* (Gillette), and subsequently resulted in a reduction in the aphid populations on host plants, while EC50 values were 0.88% and 0.96% for *M. rosae* and *M. sanborni*, respectively (Koul 1999).

It is essential that antifeedants must have properties like insecticides, i.e., effective only against the target insect pest (compounds that are nontoxic against mammals and nontarget mechanisms, such as beneficial insects), and they must possess residual property, so that crops can be protected against insect pests through its window of exposure. It is common problem of antifeedants that these compounds had been suffering from higher interspecific variations in bioactivity; for example, azadirachtin is an effective antifeedant against the desert locust (inhibiting feeding by 50% at a 0.05 ppm concentration), but the migratory grasshopper (a pest of cereal crops and rangeland grasses in North America) does not deter feeding at a concentration of 1000 ppm (Champagne et al. 1989). Further, the EC50 values of azadirachtin varied more than 30-fold between species; for example, the tobacco cutworm (*Spodoptera litura*) is the most sensitive, and the black army cutworm (*Acteobia fennica*) is the least (Isman 1993).

González-Coloma et al. (2002) demonstrated that the antifeedant activities of silphinene sesquiterpenes are species dependent, such as the cotton leaf worm (*S. littoralis*), Colorado potato beetle (*L. decemlineata*) and five aphid species (*M. persicae*, *Diuraphis noxia*, *Rhopalosiphum padi*, *Metopolophium dirhodum* and *Sitobion avenae*). Several reports revealed that insects show habituation on antifeedants though these compounds initially act as antifeedants on the insects; for example, the larvae of tobacco cutworm initially did not feed on azadirachtin, but the antifeedant activity of this compound becomes half after prolonged exposure of the insect for 5 h (Bomford and Isman 1996). The antifeedant activity of toosendanin is destroyed after 4.5 h. These observations suggest that the application of antifeedants on plants might only protect the plant from insect pests during initial attack, but after that the antifeedants become ineffective.

According to Isman (2002), the habituation was observed in the armyworm larvae (*P. unipuncta*) when they were provided xanthotoxin or thymol alone, but larvae did not show habituation when they were exposed to a blend of these two compounds. It was also shown that the larvae of *S. litura* showed habituation on azadirachtin, but the larvae did not become habituated when they were exposed to neem extract containing the same amount of azadirachtin (Bomford and Isman 1996). In the same way, the larvae showed habituation to toosendanin (95%), but they did not show habituation to a blend of limonoids containing 60% toosendanin.

9.5 Phyto-Antifeedants: Potential Uses

The best method to apply an antifeedant is in water- or oil-based formulations like the application of an insect pesticide. It is noted that the beneficial effects of antifeedants are dependent on applying these compounds in more strategic ways. Latex, a natural hydrocarbon polymer, is a nontoxic material, which is used in paints,

surface coatings, furniture, packaging, textiles, construction and pharmacy. Further, pharmaceutical industries apply them to put together in controlled release drug delivery systems to protect dosage forms from UV exposure and moisture (Shtykova et al. 2008). Shtykova et al. (2008) used the latex dispersion Eudragit copolymer (EC) to prepare the coatings on the antifeedants 2,6-di-tert-butyl-4-methylphenol (BHT) and cisdihydropinidine (Alk), which were efficient to deter the feeding activity on conifer bark by *Hylobius abietis* (pine insect) both in laboratory and in fields. The applications of essential oils as antifeedants are not so fruitful because of the degradation and volatilization of the active ingredients in essential oils. El Asbahani et al. (2015) formulated essential oils as microspheres or microcapsules to protect them from degradation. The ethanolic crude extract of *Annona mucosa* Jacq. (ESAM) seeds contains a mixture of alkaloids, triglycerides and acetogenins, which is a prospective source of insecticidal compounds against agricultural pests (Ansante et al. 2015; Souza et al. 2017). Souza et al. (2019) demonstrated that the combination of ESAM and acetogenin-based commercial bioinsecticide Anosom® 1 EC had marked antifeedant and growth inhibitory activities on the larvae of *H. armigera*. Skuhrovec et al. (2020) prepared encapsulated formations of essential oils using anise (*Pimpinella anisum* L. [Apiales: Apiaceae]) against one of the major insect pests of potato, the Colorado potato beetle.

The strategy 'stimulo-deterrent diversion' (also called 'push-pull strategy') employs 'push' intercrop and 'pull' edge crop to protect crops from insect pests by promoting biocontrol agents. This strategy is applied to manage pea leaf weevils by applying neem antifeedant (push) to keep away the insect pest and edge planting of winter peas as trap crops (pull) to attract the insect pest (Smart et al. 1994). Aggregation pheromone can be applied on the edge trap crop to increase the attraction of insect pests. Clover can also be grown as trap crop instead of winter pea (Cook et al. 2007). Neem-based antifeedants (push) can be applied in stimulo-deterrent diversion strategy to control *L. decemlineata* by early boundary planting of trap crop (potato as pull) to attract the insect pests and natural enemies of the insect pests (Martel et al. 2005). The western flower thrips, *Frankliniella occidentalis*, are one of the major insect pests of greenhouse-grown chrysanthemums. The thrips were deterred from chrysanthemums by spraying the antifeedant procured from the plant, Dorrigo pepper on the main crop, and concentrating them onto trap plants (cv. 'springtime' of chrysanthemum is the most attractive) (Bennison et al. 2002).

Another approach is the joint action of antifeedant and insect growth regulators (IGRs) to control the insect pests (Griffiths et al. 1991). A blend of *Ajuga* spp. leaf extract (antifeedant) and teflubenzuron (IGR) was effective against *Phaedon cochleariae* (mustard beetle) and the larvae of *Plutella xylostella* feeding on mustard plants. The antifeedant inhibited feeding of the insects, while insect growth regulator did not inhibit feeding for the first 48 h of application, but caused the death of beetles and larvae after 2 weeks (Griffiths et al. 1991). The joint action of antifeedant and IGR is the application of antifeedant on the tender leaves of a plant and IGR on the lower leaves of the same plant. Application of antifeedant caused the beetles to move

on the lower parts of mustard plant, but when the insects were in contact with the IGR on the lower leaves of the plant, it resulted in death of the insect pests.

9.6 Phyto-Antifeedants: Prospects for Commercial Use

Till date, in excess of 1000 compounds of plant origin as antifeedants have been isolated and tested against a number of insect species, and more compounds are being added as antifeedants in laboratory conditions (Koul 2005, 2008). At present, the efficacies of the antifeedants in field conditions are very few due to variations in responses among different insect pests and habituation of insect pests towards antifeedants as well as quick degradation of the antifeedant compounds in the field conditions. A major concern is that most of the commercial synthetic pesticides are broad spectrum, and the antifeedants will be broad spectrum in characteristics like synthetic pesticides. Most of the phyto-antifeedants act only on a limited number of insect pests, and when these compounds are applied in the field, these antifeedant compounds can act on specific insect pests, but, on the other hand, the antifeedant compounds may not be effective, and other insects present in the field may be attracted towards the crop plant, which ultimately lowers the crop production. Further, the cost of developing a particular antifeedant for a specific pest is a big question. This is the reason that only neem as antifeedants is commercially available in the market.

Polygodial or methyl salicylate as antifeedants resulted in a reduction in aphid populations, and subsequently, an increase in the production of winter wheat was recorded in IARC Rothamsted. The reduction in aphid population after application of polygodial is equal to that of application of pyrethroid insecticide cypermethrin (Pickett et al. 1997). Another limonoid antifeedant, toosendanin, obtained from the bark of the toosendan and *M. azedarach* has got much attention throughout the world as a commercial biopesticide by the scientists (Chiu 1989; Isman 1994; Chen et al. 1995; Koul et al. 2002). Due to public awareness that botanical pesticides are safer than synthetic ones, the applications of botanical pesticides are increasing throughout the world. The production of biopesticides is estimated ca. 2% of the US \$60 billion global pesticide market. However, microbial insecticides, such as products from *Bacillus thuringiensis*, dominate among the biopesticides. At present, the productions of biopesticides are increasing at a rate of 16% per annum, while the synthetic pesticides are increasing at a rate of 5.5% per annum (Miresmailli and Isman 2014). The use of some essential oils as biopesticides without regulatory review by the US Environmental Protection Agency (EPA) provided in the list [25 (b)] of the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA) has paved the way to commercialize some essential oils. Further research on the effects of antifeedants in the insect sensory systems and formulations of antifeedant compounds in such a way that these compounds could not be degraded in the environmental conditions as well as development of broad-spectrum antifeedant compounds similar to that of synthetic pesticides are needed to get the most effective results of phyto-antifeedants against insect pests in the crop fields.

9.7 Conclusions

Application of antifeedants from plant parts helps us to utilize plant defense mechanisms and subsequently, helps to reduce the use of synthetic pesticides. To get the best results by using phyto-antifeedants, the following criteria should be considered: categorization of the natural sources, maintenance of quality, adoption of standardization strategies and modification of regulatory constraints; if these four criteria are properly addressed, the phyto-antifeedants could be as competitive and successful as the synthetic ones. Limonene at lower concentration acts as an antifeedant, but this compound causes allergic reaction on the human skin at higher concentration. Hence, basic research in combination with field trials of the isolated phyto-antifeedant at different doses is necessary to get environment-friendly safe products for insect pest control. However, most of the research on phyto-antifeedants presents that crude plant extracts could act as antifeedant on a particular insect species in the laboratory. This is the major drawback of basic research on phyto-antifeedants, which should be avoided. It is better to identify the compound from plant sources, which acts as insect antifeedant. If it is not possible to identify the compound of interest, scientists should be in collaboration with farmers for application of plant-based crude extracts for insect pest control in the field, which is more valuable than that of laboratory studies. To obtain the best results of the application of phyto-antifeedants, it is prerequisite that (1) proper technique should be adopted to maintain the integrity of phytochemical mixtures; (2) development of broad-spectrum phyto-antifeedants, which is similar to that of synthetic ones in action and the production cost of phyto-antifeedants, would be lower than that of synthetic ones; and (3) application of advanced technologies and delivery methods, such as nanotechnology, and micro- and nano-encapsulation techniques may provide qualitative and quantitative release of phyto-antifeedants for insect pest control.

Points to Remember

- About 10% of the insect pests are major pests, and insect herbivores cause one-fifth of the world's crop loss per year throughout the globe.
- Four major and 26 minor crops are responsible for ca. 95% of human sustenance, indicating that many of these crop plants are grown for a long time.
- Application of phyto-antifeedants helps us to make use of natural plant defense mechanisms, which is essential to reduce the use of synthetic pesticides. However, it is prerequisite that phyto-antifeedants should have to be broad spectrum, like the available synthetic compounds.
- Most of the phyto-antifeedants are from 43 families of plants. However, four families—Meliaceae, Asteraceae, Labiatae and Leguminosae—are more exploited for identification and extraction of compounds, which are acting as insect antifeedants.
- The known phyto-antifeedants belong to groups, like various terpenes (monoterpenes, sesquiterpenes, diterpenes and triterpenes), flavonoids, alkaloids, coumarins, steroids, etc., and each species of insect may employ these compounds in an idiosyncratic manner, so that the same compound may have

altered fates in different species of insects, implicating that different mechanisms are involved in antifeedant action.

- The four criteria—categorization of the natural sources, maintenance of quality, adoption of standardization strategies and modification of regulatory constraints—are necessary to obtain the best results of the application of phyto-antifeedants.
- The formulation of antifeedant compounds including large-scale field trials would help to encourage farmers to use natural antifeedants.
- Phyto-antifeedants can be combined with natural plant substances, such as physiological toxins, to manipulate insect behaviour in integrated pest management strategy.

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