https://doi.org/10.33451/florafauna.v29i1pp49-55
FLORA AND FAUNA ISSN 2456 - 9364 (Online)
2023 Vol. 29 No.1 PP 49-55 ISSN 0971 - 6920 (Print)

A Cognitive Behavioral Defense Mechanism of Plants Against Herbivory

***Priya Dilip Lokare, . Anil Kumar[1], Kul Bhaskar[2], Kamal Kant Patra[3], Sneh Agrawal[4], Sangita Jadhav[5], Devidas Narhar Patil[6] and Hrishikesh Haribhau Khodade[7]**

Department of Botany,
Loknete Ramdas Patil Dhumal Arts,
Science and Commerce College, RAHURI-413705,
AHMEDNAGAR (MAHARASHTRA) INDIA
[1]Department of Botany,
DDU Gorakhpur University, GORAKHPUR-273009 (UP) INDIA
[2]Department of Botany,
Government Degree College, Sukrauli-274207, KUSHINAGAR (UP) INDIA
[3]Nalanda College, BIHARSHARIF-803101, NALANDA (BIHAR) INDIA
[4]Department of Periodontology,
Bharati Vidyapeeth (Deemed to be university) Dental College and Hospital Sector-7,
BELPADA, NAVI MUMBAI-400061 (MAHARASTRA) INDIA
[5]Department of Botany, S.N. Arts, D.J.Malpani Commerce and B.N.Sarda Science College
Sangamner (Autonomous) Tal-SANGAMNER Dist-AHMEDNAGAR (MAHARASHTRA) INDIA
[6]Department of Botany,
Bhartiya Jain Sanghatana's Arts, Science and Commerce College,
WAGHOLI-412207 (MAHARASTRA) INDIA
[7]S. M. Joshi College, HADAPSAR-411028, PUNE (MS) INDIA
*Corresponding Author
E-mail: priyalokare2@gmail.com

Received : 28.03.2023; ***Accepted*** : 08.05.2023

ABSTRACT

Plants interactions with animals, insects, and pathogens is the need of ecosystem. Herbivory is the most critical part of food chain. In an ecosystem, the relationship between prey and predators and mutualism are inevitable breathing junctions. Plants are eaten by herbivores, but plants in return have evolved in such a way which affect herbivores and other organisms that come in contact with them at every level from basic biological interaction to genetics. In other words, plants have adapted strategies to defend themselves against herbivory.Mainly, there are two defense strategies, 1) direct defense responses and 2) indirect defense responses. The former one includes production of such enzymes which reduce the digestibility of consumed food,reallocation of resources, morphological adaptations, and the production of specialized bioactive molecules such as alkaloids, phenolics, terpenoids, glucosinolates.The later one includes the production of volatiles and extrafloral nectars to attract pollinators and other microorganisms to reduce enemy pressure and for their own benefit, pollination. All these strategies are to intoxicate or repel the insect herbivores and to reduce the herbivory.

Figure : 00 References : 58 Table : 00
KEY WORDS : Cognitive adaptations, Defense mechanisms, Herbivory.

Introduction

The relationship of land plants and herbivores is as old as 400 million years. During this long period of time, plants have evolved and adapted themselves in such ways which affect herbivores at every level from basic biological interactions to genetics and make them to not eat plants. Some of these reactions are for mutual benefits such as pollination but most of them are for defense against predators and herbivores. The plant as a host and insects as predators or herbivores relationship is so common that every plant is eaten by at least one herbivore. This gives rise to the origination of co-evolution theory[19] which could be the cause of so much diversity in plants as well as herbivores. The diversity in plants can vary from only few of the millimeters such as duckweed (Lemnaceae) to hundreds of meters such as California redwood tree. This diversity can also be seen in life cycle of plants that some of them last few weeks to thousands of years[35].

There are different strategies adopted by the plants to defend themselves against herbivores such as insects and mammals. Some plant species produce such chemicals and compounds which alter herbivores' preference of eating while other species affect their development and growth. Based on these traits, plants defend themselves from herbivores physically by developing morphological adaptations as well as chemically by producing aerosols and other compounds. Defense mechanisms of plants can be constitutive, or they would only be activated after the herbivores attack. As the defense mechanisms of plants are expensive so it is the matter of cost versus benefits. Plants always remined in dilemma of investing energy (such as limited resources such as nitrogen) in defense or development and growth[5]. There is also a challenge of producing chemical compounds because they can also be toxic to plants themselves. This review covers different defense mechanisms of plants to conserve themselves against herbivory.

2. Defense responses of plants against herbivory

Plants have evolved and adapted themselves to have such features which help them fight against predators and herbivores. These traits involve biological specialized compounds production, defense proteins production, resources reallocation to the site away from the wound, and various other morphological features. Moreover, there are some indirect defense responses including attraction and nourishing other predators to create a competition for herbivores.

2.1 Direct defense response

Direct defense mechanisms involve the physical barriers for herbivores including insect and animal herbivores. These mechanisms involve the production of compounds which act as antinutritive, repellent, or prove harmful for them. Some of the major direct defense responses are given below.

2.1.1 Specialized biological active compounds

There are two classes of chemical compounds which are produced by the plants, these are called primary and secondary metabolites. Primary metabolites are required for reproduction, development, and growth. While secondary metabolites have various other self-helping features such as to protect themselves from herbivores and pathogens. These specialized biological active compounds are not only required for defense, but they also attract seed-dispersing animals, flies and other insects for the purpose of pollination[5, 25]. These biological active specialized compounds are not only produced on induction but constitutively and their targets are digestive, nervous, and endocrine systems of herbivores[49]. In this category, two metabolites are involved in giving specific color, taste, and odor to the plants[25].

Generally, these compounds are used for general herbivores as repellent and for specialist herbivores as attractant[24]. Resultantly, generalist insect herbivores are intoxicated while specialist herbivores are compelled to invest for detoxification process. In this way, their development and growth slow down[36].

2.1.1.1 Alkaloids

Alkaloids are natural bioactive products found in 20% of vascular plants and more than 15000 in number have been discovered. Prevalently, these are found in Amaryllis, legumes, nightshade plants, and lilies species. They are well-researched in terms of their metabolic effects in mammals such as strychnine, morphine, nicotine, caffeine, and cocaine. They are also known as defense compounds for plants against herbivores[34]. True alkaloids are those which are synthesized in roots and above ground they are accumulated[57]. Sparteine and cytisine are alkaloids derived from quinolizidine and are actively used by plants to defend themselves from herbivores[13]. Demissine is an alkaloid produced by nightshade potato (*Solanum demissum*) which resists herbivore insects such as Colorado beetle (*Leptinotarsa decemlineata*) and potato leafhopper. Solanine_ a sterole derived pseudo alkaloid which is produced by *S. tuberosum* and can be detoxified by beetles[13, 28].

2.1.1.2 Glucosinolates

These are nitrogen and sulfur containing compounds and are abundantly found in *Capparales* and *Brassicaceae*. Glucosinolates(GSL) are amino acid-derived glucosides and there are more than 120 different types are known[33]. They repel generalist and attract specialist insect herbivores. Cabbage stem flea beetle (*Psylliodeschrysocephala), an insect which only feed on leaves of those plants which contain GSL*[26]. Toxins are produced by different plants with variety of metabolic diversity which determines diversity in mechanisms and strategies of defense against herbivores of different kinds including insects and pests. It can be imagined by the fact that 40 different GSL's breakdown found in *A. thaliana* produced more than 100 different types of products which can more efficiently defend plants[34]. For example, breakdown of indole GSL in the absence of myrosinase[6] can produce such products which can provide better defense as compared to stable aliphatic GSL[37]. Hopkins *et al.*[33], Halkier and Gershenzon[27].

2.1.1.3 Phenolics

Phenolics are the best defense compounds which defend plants from feeding herbivores by repelling them and inhibiting their enzymes which are important factors in the determination of metabolic efficiencies. Phenolic compounds also attract pollinators and seed dispersing animals. Reducing the growth of plants nearby and absorbing harmful UV radiations are plus points of phenolic compounds which add in the defense of plants against herbivory[10].

It is studied that phenolics-containing plants are much less attractive as compared to those plants which do not produce phenolics. Cereal aphids (*Rhopalosiphumpadi) d*o not eat wheat cultivars which contain phenolic compounds[39]. It was observed that willow plant *(Salix dasyclados)* in stressed conditions does not produce phenolics and becomes more attractive to *Galerucella lineola* (leaf beetle) as compared to non-stressed plant[38].

2.1.1.4 Terpenoids

Sesquiterpenes and terpenes are known as essential oils and are produced by many plants. Essential oils possess toxic and repellent effects on herbivores. Leafcutter ant (*Atta cephalotes)* is repelled by terpenoid known as limonene produced by citrus plants[11]. Monoterpenes are produced by many conifer plants which possess toxic effects on various herbivorous insects such as bark beetles[52].

2.1.2 Reduction in digestibility

Multiple dense proteins are produced by plants which reduce the ability of herbivores to digest the engulfed plant. Among them, there are anti-nutritive as well as anti-digestive proteins. Antinutritive proteins reduce the utilization of consumed food by changing the physical and chemical availability while anti-digestive proteins limit the digestion of engulfed plants by reducing enzymatic digestion potential[17, 52].á-amylase inhibitors, polyphenol oxidases, protein inhibitors, lectins, and chitinases are major classes of dense proteins[21]. In detail, these are given below[8].

2.1.2.1 Alpha amylase inhibitors

Cereal seeds and monocots contain á-amylase inhibitors (á-AI) such as (wheat) *Triticum spp. (barley) Hordeum vulgare, Z. mays, and s. bicolor.* á-amylases are found in herbivores insects and microorganisms are efficiently inhibited by the á-AIs while they seldom affect amylases[21]. These dense proteins (á-amylase inhibitors) can inhibit S*itophilus* spp. (wheat weevils), *Tribolium*spp. (flour beetle),*Tenebrio obscurus* (mealworm), and grain beetles (*Oryzaephilus* spp.) and complete protection in *Bruchuspisorum*(pea weevil), transgenic peas[42].

2.1.2.2 Polyphenol oxidases

Polyphenol oxidases (PPOs) are such enzymes which cause spontaneous cross-inking of *o-quinones* and polymerization which in turn cause browning of fruits, plants extracts, and especially damaged tissues of plants. Reactive oxygen species (ROS) are also produced by PPOs. These two processes depend on the disruption of compartmentalization of cell. As soon as this happens, PPOs react with phenolic substances from vacuoles after releasing from thylakoids[41]. Upon wounding, they are frequently being produced by plants, hence are considered to play a role in defense against herbivory. As they limit Lepidopteran larvae[9], grasshopper (*Melanoplus* spp.)[2], and *L. decemlineata,* insect herbivores feeding on plants in which PPOs are found[2, 22].

2.1.2.3 Proteinase inhibitors

Proteinases or endopeptidases are enzymes which are found in the gut of the insects which feed on plants and are used to break peptide bonds of plant proteins. There are four classes of endopeptidases. Among them most common are Lepidoptera, Coleoptera, and Orthoptera which have alkaline or neutral pHin the gut region. There are further subclasses of enzymes such as chymotrypsin-like, trypsin-like, and elastase-like. Herbivore insects which have more acidic content in their gut are found to have aspartic acid and cysteine proteases such as Hemiptera, Diptera, and Coleoptera. The smallest class of proteinases are metalloproteinases[12, 40]. *G. max* has trypsin inhibitors which are proved to be toxic against insect, *Tribolum confusum*.

2.1.2.4 Lectins

Storage organs such as vacuoles and protective plant structures such as Leguminosae have sugar-binding proteins called lectins. There is huge diversity in lectins, and it is difficult to classify them. So far, lectins have been classified into six families based on CRD (Carbohydrate Recognition Domain) such as cereal lectins, legume lectins, P-, C-, and S-type lectins, and pentraxins[4]. Legume and cereal lectins are found in plants. Nutrition absorption inhibits when lectins encounter inner lining of insect herbivores which is made up of glycoproteins. However, the mechanism of toxicity is yet to be studied.

2.1.3 Resources relocation

Reallocation of resources is the redistribution of the valuable food and nutrients to other parts of the plant upon attack by herbivores. When sulfur knapweed moth attack on plant, spotted knapweed (*Centaurea maculosa),* it shifts more nitrogen supply towards shoots[44]. Higher photosynthetic growth is maintained by plants in this way. Study showed that Guatemalan potato moth (*Tecianso lanivora)* larvae attack on *S. tuberosum* potato tubers increases non-attacked tuber mass of potato[47].From shoots to roots can also be the path of reallocation of food resources. When *M.* sexta attack on leaves of *N. attenuate*, its oral secretion triggers the carbon redistribution from shoots to roots[50]. From leaves to roots path of food resources reallocation is adopted by quaking aspen (*Populus tremuloides)* when JA is applied on leaves exogenously. It was observed that when JA is applied half of the root system of *H. vulgare,* carbon allocation is increased to those parts which are non-treated[32]. The carbon reallocation might be due to the change in invertase activities, but the reason behind reallocation of nitrogen is still unknown. The production is different above and below parts of the plant and that could be the reason of reallocation. Carbon acquisition is easy in aerial parts as compared to roots where nitrogen is more easily accessible[20].

2.1.4 Morphological adaptation

Herbivore encounter different plant parts to get feed. Plants have adopted number of strategies as a defense to conserve themselves. Various morphological adaptation such trichomes, crystals and wax films, toughness of leaves and roots, resin and laticifers flow, and spines.

2.1.4.1 Crystals and waxes

Most the vascular plants have cuticles which are covered with films and crystals made of epicuticular. These covering, though, provide protection against pathogens and harsh conditions such as desiccation tolerance, but they also provide slipperiness which resist insects to populate on leaf surface[43]. During plant development the composition and biosynthesis of these waxes and films vary and with the change of temperature and seasons, physical and chemical properties change. Recently, it was studies that *P. brassicae* positioning on *A. thaliana* triggers the increase in fatty acids in waxes, hence affecting the composition[7].

2.1.4.2 Trichomes and thorns

Spines and thorns are grown by the plants on their surfaces to defend themselves from mammals and trichomes (hair) against insect herbivory[58]. Removal of thorns and spines result in increase of herbivory by mammals while insect herbivores attack and feeding increases by the removal of trichomes. In response to the feeding by insect herbivores, trichomes have been observed to increase in numbers. Bioactive volatile or non-volatile natural products are produced by glandular trichomes which deter, poison, or repel insects[23].

2.1.4.3 Toughness in leaves and roots

Toughness of leaves and roots hinders the penetration by piercing and sucking insects and causes mandibular damage in chewing or biting herbivores[48]. For an examples, fungi can easily grow on the leaves of ice-cream-bean *(Inga edulis)* beside their toughness, but fungus-growing ants (*Atta cephalotes)* can't grow on them.The tough and mature leaves may be avoided as younger leaves are expanding though they have higher levels of chemicals[48]. Cell walls of plant cells are strengthened by reinforcement of cellulose, callose, lignin, and suberin along with phenolics and silicon.

2.1.4.4 Oleoresins and laticifers

Laticifers and oleoresin ducts are network of channels in vascular tissue of several plants. Resin and latex are stored inside these channels. These resins and latex secreted when channels are broken and intoxicate or entrap herbivores.

More than 10% of the angiosperm plants, especially in tropical plants, latex laticifers are found to be abundant[1]. Among latex producing plants, milkweed (*Asclepias)* species are the most studied. *Cryptostegia grandiflora* (rubber wine) produces latex which can be transported upwards of about 70 cm to where insects and other herbivores have attacked and trap small insect herbivores by coagulation[18].

2.2 Indirect defense responses

To reduce enemy pressure, plant attracts and nourishes other organisms; it is termed as indirect defense[15]. This included the production of extrafloral nectar, food bodies, and volatiles.

2.2.1 Volatiles

VOCs (volatile organic compounds) are released from vegetative part of the plant, flowers, and roots. More than 1000 VOCs are recorded to have in number including esters, alcohols, terpenoids, and aldehydes[46]. These specialized organic compounds perform various functions including attracting pollinator, repelling herbivores, and as communication molecules within and between plants[16]. VOCs released abundantly when plants are attacked by herbivores[53]. GLVs are green-leaf volatiles are formed from 13-hydroperoxylinolenic acid and are isomers of hexanol acetate[45, 54].The variety in synthesis of volatiles comes with different strategies adopted by herbivores to get feed. For an example, piercing and sucking insect herbivores triggers the production of esters, sesquiterpenes, and monoterpenes along with SA-mediated pathway while leaf-eater insect herbivores induce JA signaling pathway[54, 56].

Production of VOCs is also parts dependent. The VOCs produced by roots are different from leaves. For an instance, when *D. virgifera* attacks on roots of *Z. mays,* sesquiterpenes along with small amount of caryophyllene and á-humulene are released. On the other hand, leaves of maize produce over 30 different VOCs when attacked by leafhopper, *Euscelidius variegatus.* Among those VOCs include aromatic compounds, homo-, mono and sesquiterpenes, and *GLVs*[3].

VOCs are used by plants to make their defense tuned fine according to the need. This is done with the help of carnivores that differentiate between damaged and undamaged plants by using VOCs[3, 14]. As an example, *H. virescens*larvae are fed by *N. tabacum* by releasing variety of VOCs during day and night. During day, VOCs are used to attract parasitoids and during night,egg laying females are repelled. Moreover, when tobacco plants are attacked by nicotine-insensitive herbivores, they start producing VOCs and suppress the production of nicotine. In addition, attacked plants can communicate with other plants to alert them of possible ganger. That's why those plants respond strongly when attacked.

2.2.2 Extrafloral nectar

More than 70 species of plants including gymnosperms, ferns, and angiosperms produce extrafloral nectar (EFN). Evolutionary studies proved that it is more ancient than floral nectar[29]. To attract parasitoids and predators, EFN is secreted on shoots and leaves in Contact to floral nectar which is used to attract pollinators. EFN also has repellent functionality[55].

Cotton*(Gossypium herbaceum)*, cashew *(Anacardium occidentale)*, passion flowers*(M. esculenta)*, castor oil*(Ricinus communis)*, and Leguminosae species are studied to produce EFN[30]. EFN contains mainly carbohydrates, but it does also consist of proteins, lipids, mineral nutrients, antioxidants, and natural biological active products such as phenolics, alkaloids, and VOCs.However, composition of EFN varies among different species of plants, even different types of nectars are produced by the same plant species. Though EFN consists of biological active natural products, but it does not always act toxic or repellent. And if one herbivore insect is getting affected by an EFN doesn't mean, it is toxic to everyone[51].

The production of EFN depends on the process of herbivory. More EFN is produced in herbivory as compared to the absence of herbivory. In response to the VOCs from damaged plants, the production of VOCs increases as is studied in case of *P. lunatus*[31].

Conclusion

Conservation and reproduction are the key and important roles that every living being needs to play and it has proven to be the instinctual. Adaptations of different strategies to defend themselves against their preys is one way to conservation. Plant species have evolved and, so far, very interesting defense trategies have been adapted. This process continues and plants evolve various behavioral and cognitive adaptations.

References

1. Agrawal AA, Konno K. Latex: a model for understanding mechanisms, ecology, and evolution of plant defense against herbivory. *Annu. Rev. Ecol. Evol. Syst.* 2009; **40**(311-331.
2. Alba-Meraz A, Choe HT. Systemic effects on oxidative enzymes in *Phaseolus vulgaris* leaves that have been wounded by the grasshopper *Melanoplus differentialis* (Thomas) or have had a foliar application of jasmonic acid. *International journal of plant sciences.* 2002; **163**(2): 317-328.
3. Ali JG, Alborn HT, Stelinski LL. Constitutive and induced subterranean plant volatiles attract both entomopathogenic and plant parasitic nematodes. *Journal of Ecology.* 2011; **99**(1): 26-35.
4. Arason GJ. Lectins as defence molecules in vertebrates and invertebrates. *Fish & Shellfish Immunology.* 1996; **6**(4): 277-289.
5. Baldwin IT. An ecologically motivated analysis of plant-herbivore interactions in native tobacco. *Plant physiology.* 2001; **127**(4): 1449-1458.
6. Barth C, Jander G. *Arabidopsis myrosinases* TGG1 and TGG2 have redundant functions in glucosinolate breakdown and insect defense. *The Plant Journal.* 2006; **46**(4): 549-562.
7. Blenn B, Bandoly M, Küffner A, Otte T, Geiselhardt S, Fatouros NE, Hilker M. Insect egg deposition induces indirect defense and epicuticular wax changes in *Arabidopsis thaliana. Journal of Chemical Ecology.* 2012; **38**(7): 882-892.
8. Bowles DJ. Defense-related proteins in higher plants. *Annual Review of Biochemistry.* 1990; **59**(1): 873-907.

9. Castanera P, Steffens J, Tingey W. Biological performance of Colorado potato beetle larvae on potato genotypes with differing levels of polyphenol oxidase. *Journal of Chemical Ecology.* 1996; **22**(1): 91-101.

10. Cheeke PR Toxicants of plant origin: alkaloids, Vol. 1. (CRC Press, 1989).

11. Cherrett J. Some factors involved in the selection of vegetable substrate by *Atta cephalotes* (L.)(Hymenoptera: Formicidae) in tropical rain forest. *The Journal of Animal Ecology.* 1972; 647-660.

12. Coppedge B, Jones J, Felton G, Stephen F. Examination of midgut proteinases of the adult Southern Pine Beetle (Coleoptera: Scolytidae). *Journal of Entomological Science.* 1994; **29**(4): 457-465.

13. D'Mello JF, Duffus CM, Duffus JH Toxic substances in crop plants. (Woodhead Publishing, 1991).

14. Dicke M. Local and systemic production of volatile herbivore-induced terpenoids: their role in plant-carnivore mutualism. *Journal of Plant Physiology.* 1994; **143**(4-5): 465-472.

15. Dicke M, Sabelis MW, Takabayashi J, Bruin J, Posthumus MA. Plant strategies of manipulating predatorprey interactions through allelochemicals: prospects for application in pest control. *Journal of chemical ecology.* 1990; **16**(11): 3091-3118.

16. Dicke M, van Poecke RM, de Boer JG. Inducible indirect defence of plants: from mechanisms to ecological functions. *Basic and applied ecology.* 2003; **4**(1): 27-42.

17. Duffey SS, Stout MJ. Antinutritive and toxic components of plant defense against insects. *Archives of Insect Biochemistry and Physiology: Published in Collaboration with the Entomological Society of America.* 1996; **32**(1): 3-37.

18. Dussourd DE. Behavioral sabotage of plant defense: do vein cuts and trenches reduce insect exposure to exudate? *Journal of Insect Behavior.* 1999; **12**(4): 501-515.

19. Ehrlich PR, Raven PH. Butterflies and plants: a study in coevolution. *Evolution.* 1964; 586-608.

20. Erb M, Lenk C, Degenhardt J, Turlings TC. The under estimated role of roots in defense against leaf attackers. *Trends in plant science.* 2009; **14**(12): 653-659.

21. Falco MC, Marbach PAS, Pompermayer P, Lopes FCC, Silva-Filho MC. Mechanisms of sugarcane response to herbivory. *Genetics and Molecular Biology.* 2001; **24**(113-122.

22. Felton G, Donato K, Broadway R, Duffey S. Impact of oxidized plant phenolics on the nutritional quality of dietar protein to a noctuid herbivore, *Spodoptera exigua. Journal of Insect Physiology.* 1992; **38**(4): 277-285.

23. Fordyce JA, Agrawal AA. The role of plant trichomes and caterpillar group size on growth and defence of the pipevine swallowtail *Battus philenor. Journal of Animal Ecology.* 2001; **70**(6): 997-1005.

24. Fraenkel GS. The Raison d'Etre of Secondary Plant Substances: These odd chemicals arose as a means of protecting plants from insects and now guide insects to food. *Science.* 1959; **129**(3361): 1466-1470.

25. Fürstenberg-Hägg J, Zagrobelny M, Bak S. Plant defense against insect herbivores. *International journal of molecular sciences.* 2013; **14**(5): 10242-10297.

26. Hajek A, St. Leger R. Interactions between fungal pathogens and insect hosts. *Annual review of entomology.* 1994; **39**(1): 293-322.

27. Halkier BA, Gershenzon J. Biology and biochemistry of glucosinolates. *Annual review of plant biology.* 2006; **57**(1): 303-333.

28. Harborne JB Introduction to ecological biochemistry. (Academic press, 2014).

29. Heil M. Indirect defence—recent developments and open questions. *Progress in botany.* 2008; 359-396.

30. Heil M. Indirect defence *via* tritrophic interactions. *New Phytologist.* 2008; **178**(1): 41-61.

31. Heil M, Koch T, Hilpert A, Fiala B, Boland W, Linsenmair KE. Extrafloral nectar production of the ant-associated plant, *Macaranga tanarius,* is an induced, indirect, defensive response elicited by jasmonic acid. *Proceedings of the National Academy of Sciences.* 2001; **98**(3): 1083-1088.

32. Henkes GJ, Thorpe MR, Minchin PE, Schurr U, Roese US. Jasmonic acid treatment to part of the root system is consistent with simulated leaf herbivory, diverting recently assimilated carbon towards untreated roots within an hour. *Plant, Cell & Environment.* 2008; **31**(9): 1229-1236.

33. Hopkins RJ, van Dam NM, van Loon JJ. Role of glucosinolates in insect-plant relationships and multitrophic interactions. *Annual review of entomology.* 2009; **54**(57-83.

34. Howe GA, Jander G. Plant immunity to insect herbivores. *Annual review of plant biology.* 2008; **59**(1): 41-66.
35. Howe GA, Schaller A in Induced plant resistance to herbivory 7-29 (Springer, 2008).
36. Kessler A, Baldwin IT. Plant responses to insect herbivory. *Annu Rev Plant Biol.* 2002; **53**(299-328.
37. Kim JH, Jander G. Myzus persicae (green peach aphid) feeding on Arabidopsis induces the formation of a deterrent indole glucosinolate. *The Plant Journal.* 2007; **49**(6): 1008-1019.
38. Larsson S, Wirén A, Lundgren L, Ericsson T. Effects of light and nutrient stress on leaf phenolic chemistry in Salix dasyclados and susceptibility to *Galerucella lineola* (Coleoptera). *Oikos.* 1986; 205-210.
39. LeszczyDski B, WarchoB J, Niraz S. The influence of phenolic compounds on the preference of winter wheat cultivars by cereal aphids. *International Journal of Tropical Insect Science.* 1985; **6**(2): 157-158.
40. Macedo MR, Freire MdGM. Insect digestive enzymes as a target for pest control. *Invertebrate Survival Journal.* 2011; **8**(2): 190-198.
41. Mahanil S, Attajarusit J, Stout MJ, Thipyapong P. Over expression of tomato polyphenol oxidase increases resistance to common cutworm. *Plant science.* 2008; **174**(4): 456-466.
42. Morton RL, Schroeder HE, Bateman KS, Chrispeels MJ, Armstrong E, Higgins TJ. Bean ±-amylase inhibitor 1 in transgenic peas *(Pisum sativum)* provides complete protection from pea weevil *(Bruchus pisorum)* under field conditions. *Proceedings of the National Academy of Sciences.* 2000; **97**(8): 3820-3825.
43. Müller C. 13 Plant–Insect interactions on cuticular surfaces. *Annu Plant Rev Biol Plant Cuticle.* 2008; **23**(398.
44. Newingham BA, Callaway RM, BassiriRad H. Allocating nitrogen away from a herbivore: a novel compensatory response to root herbivory. *Oecologia.* 2007; **153**(4): 913-920.
45. Paré PW, Tumlinson JH. De novo biosynthesis of volatiles induced by insect herbivory in cotton plants. *Plant physiology.* 1997; **114**(4): 1161-1167.
46. Pichersky E, Noel JP, Dudareva N. Biosynthesis of plant volatiles: nature's diversity and ingenuity. *Science.* 2006; **311**(5762): 808-811.
47. Poveda K, Jiménez MIG, Kessler A. The enemy as ally: herbivore induced increase in crop yield. *Ecological Applications.* 2010; **20**(7): 1787-1793.
48. RAUPP MJ. Effects of leaf toughness on mandibular wear of the leaf beetle, *Plagiodera versicolora*. *Ecological Entomology.* 1985; **10**(1): 73-79.
49. Rosenthal GA, Berenbaum MR Herbivores: their interactions with secondary plant metabolites: ecological and evolutionary processes, Vol. 2. (Academic Press, 2012).
50. Schwachtje J, Minchin PE, Jahnke S, van Dongen JT, Schittko U, Baldwin IT. SNF1-related kinases allow plants to tolerate herbivory by allocating carbon to roots. *Proceedings of the National Academy of Sciences.* 2006; **103**(34): 12935-12940.
51. Stephenson AG. Iridoid glycosides in the nectar of *Catalpa speciosa* are unpalatable to nectar thieves. *Journal of Chemical Ecology.* 1982; **8**(7): 1025-1034.
52. Trapp S, Croteau R. Defensive resin biosynthesis in conifers. *Annual Review of Plant Physiology and Plant Molecular Biology.* 2001; **52**(1): 689-724.
53. Tumlinson J, Paré P, Lewis W. Plant production of volatile semiochemicals in response to. *Insect-plant interactions and induced plant defence.* 1999; **223** p 95.
54. Turlings TC, Lengwiler UB, Bernasconi ML, Wechsler D. Timing of induced volatile emissions in maize seedlings. *Planta.* 1998; **207**(1): 146-152.
55. Wagner D, Kay A. Do extrafloral nectaries distract ants from visiting flowers? An experimental test of an overlooked hypothesis. *Evolutionary Ecology Research.* 2002; **4**(2): 293-305.
56. Walling LL. The myriad plant responses to herbivores. *Journal of plant growth regulation.* 2000; **19**(2): 195-216.
57. Ziegler J, Facchini PJ. Alkaloid biosynthesis: metabolism and trafficking. *Annual review of plant biology.* 2008; **59** p-735.
58. Zvereva EL, Kozlov MV, Niemelä P. Effects of leaf pubescence in *Salix borealis* on host plant choice and feeding behaviour of the leaf beetle, *Melasoma lapponica. Entomologia experimentalis et applicata.* 1998; **89**(3): 297-303.