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Defense Traits and Tolerance Strategies of Plants against Herbivores

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Abstract

Plants exposes to various types of biotic and abiotic stresses. It received various signals called Herbivore-associated molecular patterns (HAMPs) and induces defence mechanism against insects. Defense system, by this plant mitigates the adverse effects of herbivore, consisting of various morphological, biochemical, and molecular mechanisms. The trichomes, epidermis, cuticle, and bark tissues are important physical barriers to herbivores. Various secondary metabolites reduces digestibility in insect. The cysteine protease overexpression in maize retard the growth of *S. frugiperda*. In *Arabidopsis*, release of green-leaf volatiles by overexpression of *hpl* gene increases, which increases attraction of parasitoid *Cotesia glomerata* that increases mortality of larva of *Pieris rapae*. The application of plant hormones like JA, SA, and Ethylene etc. also induces defence system in the plant against insect. However, the exact defensive mechanism is still not understood. Studying the level of molecular mechanism of induced resistance against insect could be an important tool for the pest management.

Keywords: defense traits, tolerance strategies, plants against herbivores

Introduction

Plants face various types of biotic and abiotic stresses. Drought, salinity and heat stress are most important abiotic stresses to the plants while pathogens, bacteria and specially insects are most important biotic stress to the plant. Although, insects are small in size but they are considered as very dangerous threat to plant survival, due to their abundance, diversity and highly capable to induce insecticide tolerance in nature. Plants took millions of year to evaluate efficient defence system against insects. Many scientists are extensively studying the ecology and evolution of plant-insect interactions (Goodspeed *et al.*, 2012) [1]. In this review we focus primarily on the major biomolecules, different genes and tolerance strategies involved in defence system against insect. These approaches are to understand biochemical and molecular mechanism of plant-insect interaction and defence system in plant against insects.

Toxic Secondary Metabolites

Plants synthesize huge number of various secondary metabolites, which reduces digestibility in insect. In *Arabidopsis* mutations in genes of activation and regulation of GS biosynthesis make the *Arabidopsis* highly susceptible to chewing type of insect. While in several insects acclimatize to GS, some level of resistance provide by the metabolites synthesized from the phenylpropanoid pathway. In *Arabidopsis* mutant for *fah1-7* confirm high number of *P. brassicae* (Onkokesung *et al.*, 2016) [2]. Besides, *MYB75* overexpressing lines showed reduced levels of kaempferol 3,7-dirhamnoside that increases the performance *P. brassicae* (Onkokesung *et al.*, 2014) [3].

In mutated tobacco lines dropping nicotine content increases the performance of not only *M. sexta*, *S. exigua*, but also to other native herbivores. This increased performance was reduced after nicotine application (Machado *et al.*, 2016) [4], (Steppuhn *et al.*, 2004) [5]. In maize mutant line for *bx1* reduces level of benzoxazinoids, DIMBOA-Glc and HDMBOA-Glc, as a result feeding was increased by *S. exigua* and *S. littoralis* (Maag *et al.*, 2016) [6]. Another important secondary metabolite sesquiterpene 7 epizingiberene also involved in resistance development in plant e.g. tomato against to *M. sexta* (Bleeker *et al.*, 2012) [7].

In *Arabidopsis*, mutant for diterpene rhizathalene A synthesis by terpene synthase significantly increases feeding by *Bradysia* sp. (Vaughan *et al.*, 2013)^[8].

In dandelion (*Taraxacum officinale*), sesquiterpene lactone taraxinic acid β -D-glucopyranosyl ester formation in root latex tolerate attachment of *Melolontha melolontha*, whereas mutation in germacrene A synthase *ToGAS1*, which catalyzes sesquiterpene lactone taraxinic acid β -D-glucopyranosyl ester, enhances attractiveness to *Melolontha melolontha* (Huber *et al.*, 2016)^[9].

The role of secondary metabolites against phloem-feeding insects is less clear. The aphid, one of the major pests of agriculture, has contrasting performance in a mutant altering indole GS level (Barth and Jander, 2006)^[10], (Pfalz *et al.*, 2009)^[11]. In *Arabidopsis* camalexin increases tolerance to aphids but its mutant for camalexin by silencing *pad3* is susceptible to aphids (Kusnierczyk *et al.*, 2008)^[12]. Furthermore, callose inducibility directly regulated by benzoxazinoids which are toxic and acts against to chewing and phloem-feeding type of insects. In *bx13* mutant of maize feeding by *S. exigua*, and *S. littoralis* and leaf aphid, *Rhopalosiphum maidis* was increased (Handrick *et al.*, 2016)^[13].

Defense Proteins

Protease inhibitors are usually efficient antiherbivore proteins in defense mechanism (Johnson *et al.*, 1989)^[14]. Further study with knockout genes in several plant species has confirmed the important role of protease inhibitor against various herbivores. The cysteine protease overexpression retard growth of *S. frugiperda* in maize (Pechan *et al.*, 2002)^[15].

Another efficient defense strategy against insects is the depletion of essential amino acids in insect diets. Transgenic tomato deficient in threonine deaminase (TD2), which catalyzing conversion of L-threonine into alpha-ketobutyrate and ammonia, are more vulnerable to *S. exigua* and *T. ni* (Gonzales-Vigil *et al.*, 2011)^[16]. Threonine deaminase inhibited by isoleucine. Interestingly, in insect midgut the proteolytic activation enhances TD efficiency (Chen *et al.*, 2005)^[17]. Similarly, *N. attenuata* lines deficient in threonine deaminase are more susceptible to *M. sexta* (Kang *et al.*, 2006)^[18]. Finally, in tomato overexpression of arginase drastically reduces this enzyme content in larval midgut of *M. sexta* and makes the tomato more resistant to *M. sexta* (Chen *et al.*, 2005)^[17].

The role of defense proteins against phloem-feeding insects is less clear. In *Arabidopsis* Overexpression of *PP2-A1*, reduces *M. persicae* infestation. This might be due to clogging sieve pores (Zhang *et al.*, 2011)^[19]. Chaperone also known to plays an important role in defense system. The recently identified chaperone, SLI1, may avoid piercing of stylet into the sieve tubes. In *Arabidopsis* mutant deficient in SLI1 demonstrate increased feeding and infestation by *M. persicae* (Kloth *et al.*, 2017)^[20].

Volatiles as Attractants of Herbivore Natural Enemies

In response to herbivores attack plants releases various volatile compounds. Some of these are known in defense system since they affect herbivores interaction and increases attraction to natural enemies of herbivores i.e. parasites. Additionally these volatiles promote plant herbivores interaction. In *Arabidopsis*, the overexpression of hydroperoxide lyase gene (*HPL*) increases the release of green-leaf volatiles, which increases attraction of parasitoid

Cotesia glomerata that increases mortality of larva of *Pieris rapae* (Shiojiri *et al.*, 2006)^[21]. In *N. attenuate* mutant lines deficient in *HPL* contains low number of egg predator *Geocoris punctipes* (Halitschke *et al.*, 2008)^[22].

Silencing the marker enzyme of jasmonic acid biosynthesis (*LOX2*) reduces attachments of predator and increases damage by *M. sexta* (Schuman *et al.*, 2012)^[23]. The overexpress the maize terpene synthase *TPS10* in *Arabidopsis* releases sesquiterpenes and thus *Arabidopsis* become more attractive to *Cotesia marginiventris* (Schnee *et al.*, 2006)^[24]. Jasmonic acid (JA) is well known to induce defence system against insect. In maize JA treatment induces the expression of APETALA 2 (AP2)/ERF *EREB58* transcription factor which binds to *TPS10* promoter and regulate the volatile sesquiterpenes production (Li *et al.*, 2015)^[25]. In rice *S*-linalool increases attraction of the parasitoid *Anagrus nilaparvatae*. In mutant rice in which *S*-linalool synthase was silenced reduces attraction of *Anagrus nilaparvatae* leading to increase in BPH (Xiao *et al.*, 2012)^[26].

Physical Barriers

The trichomes, epidermis, cuticle, and bark tissues are important physical barriers to herbivores. On *Arabidopsis lyrata* mutant line for *GLABROUS1*, key gene regulating trichome development, high number of leaf-chewing insects occurs (Kivimäki *et al.*, 2007)^[27]. Whereas, *Arabidopsis* mutant line for *g11* showed more susceptibility to *S. littoralis* (Reymond *et al.*, 2004)^[28]. Remarkably, an *Arabidopsis* mutant for decreased cuticular wax and cutin shows more resistant *S. littoralis* (Blanc *et al.*, 2018)^[29].

Tolerance Strategies

The capacity of plants to repair, regrow and reproduce after insect attack is known as tolerance. It varies from plant to plant and species to species. Such capacity is important for plant to survival against insects. However the chemistry of plant tolerance to herbivores still remains poorly studied. Herbivores attacked the plants and uptake the nutrients. Herbivores attack on *N. attenuate* reduces not only the carbohydrate in roots but also the regrowth capacity of defoliated plants. The JA application on *N. attenuate* recovered the plant from above threat against insect (Machado *et al.*, 2013)^[30]. In solanaceae species that exhibit a lower JA showed the greater defoliation tolerance (Machado *et al.*, 2017)^[31]. Furthermore, in *N. attenuata* silencing the *SnRK1* increases carbon transport to the roots and prolongs flowering, this *SnRK1* silencing may positively regulate the depletion of carbohydrate root and increase tolerance (Schwachtje *et al.*, 2006)^[32].

Progress with Genomics Approaches

Whole-genome analyses of plants infected by herbivores have produced an unbiased transcriptional profile in defense signaling pathways. Insects of the same feeding pattern showed overlapping transcriptome signatures, some of these are clearly specific to chewing larvae and phloem-feeding insects (Kusnierczyk *et al.*, 2008)^[12]; (Reymond *et al.*, 2004)^[28]. Plants, in response to herbivores attack, synthesize JA which along with functional COI1 induces expression of responsive genes (Reymond *et al.*, 2004)^[28], (Schweizer *et al.*, 2013)^[33].

Genetic approaches like QTL (quantitative trait locus) mapping and genome-wide association have most potential for uncovering novel molecular players in defense system. One of the novel proteins SLI1 impairs phloem ingestion

(Kloth *et al.*, 2017) [20]. In *Arabidopsis* genome-wide association study determine loci that control variation in GS profiles under biotic and abiotic stresses (Brachi *et al.*, 2015) [34], (Chan *et al.*, 2011) [35]. Whole-genome analyses may prove valuable tool for discovering novel and important defense genes.

Conclusion

The continuous efforts to understand molecular mechanism of plant-herbivore interactions and responsive defense system by numbers of scientist from glob unveiled an important molecular players involved in defense system in plant against insects. Genomic approaches allow understanding the role defense genes in intricate signaling network and mechanisms of herbivore tolerance in plant.

Future challenges include how signals from insect is perceived, how it activate downward defense system in plant and how specificity is obtained against different herbivory and pathogenesis. Herbivores evaluate themselves via biochemical and behavioral adaptations against plant, which in turn plants also evaluate defense regulation and expression patterns. Understanding the molecular mechanisms of such phenomena holds the key to appreciate fully the beauty and diversity of plant-herbivore interactions.

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