



Dynamic Plant Defense Strategies Against Insect Herbivory: From Recognition and Signaling to Host Plant Resistance

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ABSTRACT

Herbivorous insects constantly attack plants, and plants have developed multi-layered defence system, which function in a pre-, during, and/or post-attack manner. These defenses consist of constitutive physical (trichomes, epicuticular waxes, lignification and latex), biochemical and molecular (secondary metabolites, proteinase inhibitors, defensive enzymes, reactive oxygen species (ROS) and phytohormonal signaling). Mechanical damage and herbivore- or oviposition-induced molecular patterns trigger rapid electrical, calcium and ROS signals and then induce a jasmonate-, salicylate- and ethylene-dependent pathway. Plants also protect themselves indirectly by producing herbivore-induced plant volatiles and the production of extrafloral nectar to attract predators and parasitoids. The chapter integrates these mechanisms and provides real-life examples from rice, maize, wheat and cotton to explain how they work. The integrated view presented here highlights the fact that plant resistance is not a function of a single trait, but rather an emergent property of interacting structural, chemical, signaling and ecological processes. This network can form the basis for host plant resistance breeding and incorporation of plant defence traits into sustainable insect pest management.

Keywords: *Host-Plant Resistance, Insect Herbivory, Secondary Metabolites, Jasmonic Acid, Herbivore-Induced Volatiles, Biological Control*

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1. INTRODUCTION

Plants and insects have coexisted for hundreds of millions of years, generating a continuing evolutionary interaction in which herbivores evolve mechanisms to locate, exploit and detoxify plant tissues while plants evolve traits that reduce herbivore preference, performance or damage. Plant defense is therefore best understood as a dynamic system rather

than as a collection of isolated traits. The material reviewed in the present chapter describes plant responses as a continuum beginning with attack perception, followed by rapid signaling, local and systemic defense activation, production of direct defenses and recruitment of indirect defenses. Host-plant resistance (HPR) represents the practical expression of plant defense in an agricultural crop.

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Resistance may involve antixenosis, in which plant traits reduce host acceptance, oviposition or feeding; antibiosis, in which plant characteristics adversely affect insect survival, growth, development or reproduction; and tolerance, in which the plant maintains productivity despite insect injury. Consequently, morphological barriers, biochemical constituents and molecular signaling pathways should be considered together when evaluating resistance. Plant defenses are commonly distinguished as constitutive and induced. Constitutive defenses are present before attack and include structural barriers and preformed chemical compounds. Induced defenses are activated or intensified following herbivory and include jasmonate- and ethylene-associated signaling, ROS bursts, defensive enzymes, secondary metabolites and volatile-mediated recruitment of natural enemies (Howe and Jander, 2008).

2. RECOGNITION OF INSECT ATTACK AND EARLY SIGNALING

The first requirement for effective defense is recognition of herbivory. Insects provide both mechanical and chemical information. Feeding causes cell-wall disruption and tissue deformation, while oral secretions, regurgitant, saliva, frass and oviposition-associated substances provide additional molecular information. Plants detect damage-associated molecular patterns (DAMPs) generated from injured tissues and herbivore-associated molecular patterns (HAMPs) derived from the attacker. Oviposition-associated molecular patterns (OAMPs) can also activate defense before larval feeding begins. Pattern-recognition receptors at the plant cell surface perceive extracellular danger signals and initiate rapid intracellular events. These include changes in ion fluxes, membrane depolarization, calcium signaling and production of reactive oxygen species. Chitin fragments, insect-derived proteins and other elicitors can contribute to this early recognition process. The response is not merely a local wound response: electrical and chemical signals can propagate to undamaged tissues, allowing systemic defense and priming. Priming refers to a physiological state in which a plant responds more rapidly or strongly to a subsequent challenge. Oviposition represents a particularly important recognition stage because it precedes larval feeding. Egg-associated chemicals may induce localized hypersensitive-like responses, ovicidal chemistry, tissue growth that interferes with

egg survival, and oviposition-induced plant volatiles that recruit egg parasitoids. Examples described in the source material include responses of Scots pine to *Diprion pini*, *Brassica* to *Pieris brassicae* and pea to *Bruchus pisorum*.

3. CLASSIFICATION OF PLANT DEFENSE MECHANISMS

Plant defense against insects can be organized into four functionally interconnected categories: (i) physical or morphological defense, (ii) biochemical or chemical defense, (iii) molecular and signaling defense, and (iv) indirect ecological defense. Direct defenses act on the insect by reducing access, feeding, digestion, survival or reproduction. Indirect defenses reduce herbivory by recruiting predators, parasitoids and other natural enemies.

3.1 Physical and Morphological Defenses

Physical defenses constitute an important first barrier between a plant and a herbivore. Surface architecture, tissue hardness and chemical properties of the epidermis influence insect landing, attachment, movement, oviposition and feeding. Important traits include trichomes, cuticular waxes, lignification, suberization, sclerophylly, spinescence and latex-producing structures (Hanley et al., 2007; Sharma et al., 2009).

3.1.1 Trichomes

The defensive role of trichomes is related to density, length, orientation, shape and location. Mainly the non-glandular trichomes provide mechanical interference while the glandular trichomes may release sticky, toxic or deterrent compounds. The dense or elongate trichome may affect the movement and attachment of insects, oviposition and feeding, and the cost to the insect of accessing epidermal tissues. The source material also mentions the rice leaf-sheath trichomes in the context of resistance of brown planthopper, and explains the variability at the microscopic level between the rice genotypes. Resistance via trichomes does not always remain the same. In some species, herbivory may affect trichome density or defense chemistry, thus highlighting herbivory and constitutive/induced defense interactions. For instance, in black mustard, herbivory has been linked to changes in trichome and glucosinolate traits (Traw, 2002).

3.1.2 Cuticular and Epicuticular Wax

Cuticular and epicuticular waxes are the hydrophobic layer found on the surface of leaves and can affect insect behaviour and mechanical properties of the leaf surface. A waxy surface may decrease attachment and affect the movement of insects which rely on surface contact. Host recognition, settling, feeding efficiency and fecundity may also change with the difference in the composition of the waxes. In addition to having a physical barrier function, long-chain hydrocarbons, alcohols and aldehydes may play a role in chemical deterrence.

3.1.3 Lignification, Suberization and Sclerophylly

Lignification makes tissues stiffer by depositing lignin inside the cell wall, which makes them stiffer and less digestible. Selected tissues are covered with hydrophobic, protective barriers known as suberization. Leaf hardening (sclerophylly) also decreases tissue palatability and digestibility. These characteristics combined can make it more difficult to chew and tear the tissues in plant food and can decrease the nutritional value of the diet.

3.1.4 Spinescence and Latex

Spines, thorns and prickles are distinctive mechanical barriers which might impede access to young shoots and other vulnerable tissues. Latex is a physical defence that is different. If the tissues containing the latex are damaged, the latex may be burst out and coagulate and seal the wound. Sticky latex can paralyze or damage insect mouthparts or insect locomotion while the latex proteins and secondary metabolites may have other biological effects on herbivores (Ramos *et al.*, 2007).

3.2 Biochemical and Chemical Defenses

Biochemical defense comprises preformed and inducible compounds that reduce insect feeding, digestion, development or survival. The principal groups highlighted in the source material are secondary metabolites, protein-based defenses and defensive enzymes.

3.2.1 Secondary Metabolites

Secondary metabolites comprise of alkaloids, terpenoids and phenolic compounds. Alkaloids like nicotine may disrupt the insect's nervous system, and caffeine may deter insects from feeding. Terpenoids are compounds which possess repellent, toxic, antifeedant or ecological signalling properties; the examples mentioned in the source material are azadirachtin, pyrethrins, limonene, α -pinene, linalool and gossypol. Phenolics are comprised of tannins, flavonoids, coumarins and compounds associated with lignin and

may reduce appetites, block digestion and aid in strengthening tissues. Compounds that are linked to plant defence include phenolic acids such as gallic, caffeic, ferulic and chlorogenic acids. They can have direct effect by deterrence or toxicity, or indirect by being transformed in the tissues into toxic products.

3.2.2 Protein-Based Defense

Protein-based defense includes proteinase inhibitors and regulated changes in protein abundance. Proteinase inhibitors interfere with digestive proteases in the insect gut and thereby reduce the efficiency with which dietary proteins are utilized. The resulting nutritional imbalance can retard larval growth and development. At the cellular level, plants regulate defense proteins through transcriptional, post-transcriptional and translational mechanisms and remove damaged proteins through autophagy and ubiquitin-proteasome pathways.

3.2.3 Peroxidase

Peroxidase (POD) is an important defense-associated enzyme that uses hydrogen peroxide as an oxidant to catalyze oxidation of phenolic and other substrates. Herbivory can increase ROS production and stimulate POD activity. POD-mediated oxidation contributes to cell-wall cross-linking, lignification, suberization and wound sealing while also participating in ROS homeostasis. Thus, POD links biochemical signaling with reinforcement of physical barriers (Gulsen *et al.*, 2010; Almagro *et al.*, 2009).

3.2.4 Polyphenol Oxidase

Polyphenol oxidase (PPO) catalyzes oxidation of phenolic substrates to quinones after cellular compartmentation is disrupted by wounding or herbivory. Quinones are highly reactive and can interact with amino acids and other nucleophilic compounds, reducing nutrient availability and potentially impairing digestive processes in herbivores. PPO therefore represents an important biochemical link between tissue damage, phenolic chemistry and insect performance.

3.2.5 Phenylalanine Ammonia-Lyase

Phenylalanine ammonia-lyase (PAL) occupies a central position in phenylpropanoid metabolism. It converts phenylalanine to trans-cinnamic acid, from which pathways leading to flavonoids and lignin-related compounds proceed. Because phenylpropanoids participate in both chemical defense and structural reinforcement, PAL activity can influence multiple components of host resistance.

3.3 Molecular Defense and Hormonal Signaling

Induced defense requires coordination between perception, signaling and gene regulation. Jasmonic acid (JA), salicylic acid (SA) and ethylene (ET) form major regulatory nodes, while calcium signaling, ROS and electrical signals provide rapid information transfer. Their effects are context-dependent and are best viewed as an integrated network rather than three independent pathways.

3.3.1 Jasmonic Acid Signaling

JA biosynthesis begins with membrane-derived linolenic acid. Lipoxygenase catalyzes formation of hydroperoxy intermediates, followed by formation of 12-oxo-phytodienoic acid in chloroplast-associated steps and subsequent metabolism in the peroxisome to JA. JA can be conjugated to isoleucine to form the bioactive jasmonoyl-isoleucine (JA-Ile). Under non-stress conditions, JAZ proteins repress JA-responsive transcription factors. Following herbivory, JA-Ile promotes interaction of JAZ proteins with the SCF-COI1 complex, leading to JAZ ubiquitination and proteasomal degradation. Release of transcription factors activates JA-responsive genes and redirects resources toward defense. This pathway is particularly important for responses to herbivory and wounding.

3.3.2 Salicylic Acid Signaling

The synthesis of SA occurs through isochorismate pathway and a phenylalanine pathway. While systemic immune responses and resistance to numerous biotrophic pathogens depend on SA signaling, other herbivore-induced signaling may also interact with SA signaling. Systemic defense as described in the source material is the enhancement of resistance following the initial attack and at sites remote from the initial attack and priming refers to the increased resistance at a later time.

3.3.3 Ethylene Signaling

Ethylene is involved in the methionine/ Yang cycle and is a gaseous regulator of stress responses. It is context-dependent in its herbivory function and often acts in conjunction with JA signaling. Ethylene can reinforce responses resulting from wounds and modulate the expression of transcription programs involved in defence and stress responses. is synthesized through the methionine/Yang cycle and acts as a gaseous regulator of stress responses. Its role in herbivory is highly context dependent and frequently interacts with JA signaling. Ethylene can reinforce wound-associated responses and regulate transcriptional programs associated with defense and stress adaptation

3.3.4 Hormonal Crosstalk

Hormonal Crosstalk is a dynamic network of signals between JA, SA and ET. JA-SA interactions can be antagonistic, enabling plants to allocate different types of defence, while JA and ET can have synergistic effects in specific responses. SA-ET interactions are dependent on context. This crosstalk facilitates a balance between defense specificity and energetic cost and a need to respond to multiple stresses simultaneously.

3.3.5 Oxidative Burst and ROS

ROS like hydrogen peroxide can be damaging oxidants as well as signaling molecules. On herbivore attack, she will undergo a quick oxidative burst and activate antioxidant and defense enzymes. There is a need for proper regulation -too much ROS is harmful to membranes and proteins, but just enough ROS is good for inducing defense genes and strengthening cell walls. Thus, the ROS production/detoxification/signaling balance is an important aspect of plant resilience.

3.4 Indirect Defenses and Tritrophic Interactions

Indirect defenses reduce herbivory by recruiting the natural enemies of herbivores. Two mechanisms emphasized in the source material are herbivore-induced plant volatiles (HIPVs) and extrafloral nectar (EFN). These mechanisms expand plant defense beyond the plant itself and establish a tritrophic interaction among plant, herbivore and natural enemy.

3.4.1 Herbivore-Induced Plant Volatiles

HIPVs are the volatile organic compounds that are released or amplified after herbivore attack. These are terpenoids, green leaf volatiles and aromatic compounds. Damage by mechanical forces, and insect oral secretions, can start the signaling and volatile production process. These air-borne chemical signals may draw parasitoids and predators to herbivores, thus increasing the chances of herbivores being attacked. HIPVs are therefore an ecological signal that plants damaged by attack lead to biological control agents being recruited (Huffaker *et al.*, 2011; Kost and Heil, 2008).

3.4.2 Extrafloral Nectaries

Extrafloral nectaries are structures that produce nectar that are not part of the flower. They are an attractive source of carbohydrates for ants and other insect predators to reward and keep herbivores at bay. The source material outlines a sequence of insect feeding leading to JA associated signaling, increased

EFN release, recruitment of predator, and then herbivore pressure reduction (Gish et al., 2015).

4. CASE STUDIES DEMONSTRATING DYNAMIC PLANT DEFENSE

4.1 *Jasmonic Acid-Mediated Protection in Wheat*

In the first case study, the authors compared the wheat varieties Fareed-2006 and Paktoon-2016 under aphid stress and treatment with JA (1 mM and 100 μ M foliar application) and found that aphid stress caused a decline in root fresh weight, shoot fresh weight, root length and plant height, while JA treatment increased fresh weight, length and height of wheat plants. The treatment of 1 mM had the most prominent response and Paktoon-2016 had the highest growth than Fareed-2006. JA application also resulted in higher levels of total soluble protein, phenolics and H₂O₂ compared to the stressed plants in the reported comparison and lower aphid numbers. The case thus demonstrates that an exogenous activation of a defense-signaling pathway can lead to changes in plant performance and herbivore population dynamics. The results are applicable to the experimental system used and are not necessarily the optimum JA concentration for all crops or pests.

4.2 *Flavonoid-Mediated Defense in Maize Against Corn Earworm*

Maize near-isogenic lines that vary in the level of flavonoids accumulation were used in the second case study to look at the effects on *Helicoverpa zea*. Larval mortality and surviving larval weight were greatest for high-flavonoid tissues. Neonates on U-E silks had 43.33% mortality, whereas those on B73 control silks had 10.0% mortality. Also, ZmY1 silks had 30.0% mortality compared to 13.3% mortality of NS control silks. Larvae feeding on U-E and ZmY1 husks had mortality rates of 53.33% and 30.0%, respectively, versus 10.0% and 6.6% for the respective controls. Larvae that survived were also significantly smaller. The source material also provides evidence of disruption of the larval peritrophic matrix in larvae fed on high-flavonoid husks and a mechanism of gut integrity and digestion impairment. There were important candidate compounds found to be elevated flavan-4-ols and 3-deoxyanthocyanidins. The study shows that variation in secondary metabolism that is genetically associated with it can actually be seen as a measurable antibiosis.

4.3 *Morphophysiological and Biochemical Defense in Cotton Against Whitefly*

The third case study involved comparing the highly tolerant cotton genotypes, Bio-100 BG-II and GCH-3, with the susceptible ones KDCHH-9810 BG-II and HS-6 at 45, 60, 75 and 90 days after sowing under whitefly stress. The leaf area, specific leaf weight, photosynthetic rate, relative water content, total chlorophyll and electrolyte leakage were affected by whitefly infestation. This effect was more pronounced in susceptible genotypes. Biochemical responses indicated increased levels of phenols, tannins, and H₂O₂ and PPO activity after infestation. Tolerant genotypes showed lower accumulation of ROS and higher activity of PPO indicating an effective regulation of the oxidative stress and higher availability of products associated with defence mechanisms which are produced from phenolic substrates. It has been made clear that for tolerance to occur, it does not need to be associated with the absolute increase in one metabolite, but it could be related to the efficiency of oxidative and enzymatic responses.

5. INTEGRATION OF DEFENSE MECHANISMS

The fundamental lesson that can be learned from these examples is that plant defense is integrated. A dense cover of trichomes can limit initial herbivore contact, a waxy surface can modify the attachment, tissue strengthening can increase the difficulty of feeding, perception of feeding can stimulate calcium, ROS and hormonal signals, secondary metabolites and proteinase inhibitors can decrease herbivore performance, and volatile signals can attract natural enemies. Therefore, resistance is frequently a network property that is due to the interaction of constitutive barriers and induced responses. This integration also brings about possibilities for compromises. The defense efforts expend carbon, nitrogen, sulfur and energy, and over allocation of resources can hinder growth. These costs can be lowered with induced defenses, so that plants can invest in defenses conditionally. Priming also offers a strategy where plants are constantly 'primed' to respond to attack without consistently using the maximum defense response.

6. IMPLICATIONS FOR HOST-PLANT RESISTANCE AND INTEGRATED PEST MANAGEMENT

The processes discussed in this chapter are relevant to breeding and integrated pest management. Combinations of structural, biochemical and physiological features should be used in screening programs rather than just one. Additional traits like thickness of trichome layer, trichome tissue texture, resistance of the tissues to breaking, phenol content, or defensive enzyme activity and inducible signaling capacity can contribute to complementary information. Resistant cultivars can be used in combination with biological control and ecological engineering for sustainable pest management. There is a potential to use varieties with a HIPV property that are maintained or improved in the presence of parasitoids and predators. Similarly, characteristics that promote natural-enemy recruitment can be used in concert with direct antibiosis and help to minimize reliance on insecticides. Evaluation of plant defense traits should, therefore, be done in relation to not only their effect on pests but also their compatibility with beneficial organisms.

7. FUTURE PROSPECTS

Breeding and selection of dense trichome and tougher tissues, along with preferring the specific chemistry of the plant. Application of elicitors, priming agents and biostimulants to trigger endogenous defense reactions with minimal metabolic expenditure. High throughput phenotyping and AI image analysis to quickly measure morphological and damage related resistance traits. QTL mapping and dissection of complex, quantitative resistance traits using genomic tools. Identification of chemical profiles for diagnostics of defense metabolites by metabolomics assisted breeding. Combination of genomics, transcriptomics, proteomics and metabolomics to establish defense phenotype to molecular mechanisms. RNA interference and other molecular methods for targeted suppression of key insect genes, as technically and regulatory feasible. Development of integrated management approach for crop protection including predator and parasitoid conservation.

8. CONCLUSION

Host plants have a complex and an extremely well-orchestrated defence mechanism against insect herbivores. The first line of defense is constituted by the constitutive structures, like trichomes, waxes,

lignified tissues and latex, and biochemical barriers are made up of secondary metabolites, proteinase inhibitors and defensive enzymes. Herbivore perception triggers early calcium and ROS induction and subsequently JA-, SA- and ET-dependent pathway activation leading to local, systemic and primed responses. Ecologically, HIPVs and extrafloral nectar attract natural enemies and/or spread plant defense beyond the plant. The case studies in wheat, maize and cotton show that resistance can emerge from a variety of structural, biochemical and signaling properties. The future of host-plant resistance is thus in understanding and harnessing the networks of defenses, not single universal resistance factors. The classical breeding of plants with the aid of phenomics, molecular genetics, metabolomics, and ecological pest management is a promising path forward for crops that are productive, resilient, and fit for sustainable insect pest management.

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