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Review/Fórum

Influence of abiotic factors on the resistance of plants to insects

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Abstract. Plant resistance is considered as an important pillar of Integrated Pest Management (IPM), being a highly targeted method since is a less harmful method to the environment, if compared to other tactics such as chemical control. Abiotic factors are those related to the environment and have a direct influence on the dynamics of interaction between insects and plants. The abiotic factors such as altitude, temperature, humidity, luminosity, wind and soil fertility, among others, do not act alone, but in a complex net that leads insect population dynamics in agroecosystems. How the variations of these factors can be studied in the same context? First, it is important to consider how each abiotic factors act separately and then in a coexistence influence over the populations dynamics of insects and plants. In this study, the literature about the influence of abiotic factors on insect herbivory has been reviewed, focusing mainly on the mechanisms in which the plants use in the defense against insects.

Keywords: Interaction; Mechanisms; Population dynamics.

Influência de fatores abióticos na resistência de plantas a insetos

Resumo. A resistência de plantas é considerada um importante pilar no contexto do Manejo Integrado de Pragas (MIP), sendo um método bastante visado por ser menos nocivo ao meio ambiente, quando comparado a outras táticas como o controle químico. Os fatores abióticos são aqueles relacionados ao ambiente e têm influência direta na dinâmica de interação entre insetos e plantas. Os fatores abióticos como altitude, temperatura, umidade, luminosidade, ventos e fertilidade do solo, por exemplo, não atuam sozinhos, mais sim em um complexo de fatores coexistentes que regem as dinâmicas populacionais nos diversos agroecosistemas. Como as variações destes fatores podem ser estudadas em um mesmo contexto? Primeiramente, é importante conhecer como cada uma atua individualmente para então contextualizar em uma situação de coexistência sobre as dinâmicas populacionais de insetos e plantas. Neste artigo, a literatura sobre a influência de fatores abióticos na herbivoria de insetos foi revisada, focando principalmente nos mecanismos em que as plantas utilizam na defesa contra insetos.

Palavras-chave: Dinâmica populacional; Interação; Mecanismos.

The coadaptation of arthropods and plants dates back more than 350 million years (São João & Raga 2016), and both plants and herbivorous insects have adapted to the defense strategies developed mutually. This adaptive race between insects and plants has resulted and will continue to result in a complex plant defense system, adapted to recognize exogenous compounds or damaged cell signals, which activates the plant's immune response against herbivorous insects (Hare 2011). Recent studies have shown that in plants there is a form of signaling very similar to the nervous system of animals, responsible for signaling the attack of herbivores (Toyota *et al.* 2018; Muday & Brown-Harding 2018).

As defensive weapons against herbivorous insects, plants have specialized morphological structures, secondary metabolites or proteins with toxic, repellent and/or anti-nutritional activity (War *et al.* 2012). Furthermore, plants interact with insects directly affecting their host preference, survival or reproduction, or indirectly, attracting natural enemies (War *et al.* 2012; Poelman 2015). In general, when the plant perceives the presence of an aggressive agent, the induced defense mechanisms are activated. One of these forms of perception occurs when defense-inducing molecules binds to specific receptors located in cell membranes or in the cell nucleus (Pinto *et al.* 2011).

Methods of pest control are essential in order to achieve a profitable and quality production in agriculture. Among the methods available for pest control, the plant resistance method consists of "cultivating plants that presents in their constitution, genes that express phenotypic traits that make them less injurious than others (susceptible) under equal conditions" (Souza 2014). The characteristics expressed by resistant plants may provide changes in the behavior, physiology or biology of phytophagous insects, or may present only a greater capacity to withstand their attack (Boiça Júnior *et al.* 2013).

Several biotic and abiotic factors may influence the expression of resistance in plants in a different way. These factors include

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those inherent in plants, the insect and the environment. In addition to the forms of inherent defense in plants, several exogenous factors directly influence the response of plants against herbivory (Boiça Júnior 2018).

The climate is constituted by a set of abiotic factors that plays a central role in the multi-trophic relations in the most diverse agroecosystems. The temperature is one of the most important abiotic factors, since it directly influences the modification of physiological processes, growth, development, reproduction, mortality and plant phenology (Jamieson *et al.* 2012). Even so, other abiotic factors such as soil and air humidity, plant nutritional status, wind incidence, rainfall and fertilization directly influence the biology of insects and may cause resistance effects. Thus, the present study aims to expose the importance of abiotic factors in plant resistance to herbivorous insects, with emphasis on the mechanisms involved.

ABIOTIC FACTORS

Abiotic factors are variations in the environment in which plants are developing, affecting the physiological state of them. For example, plants that grows under different light conditions have different growth rates (Gupta & Agarwal 2017). Likewise, variations in temperature, nutritional levels and water conditions also plays a key role in the defense of plants against herbivory (Gouinguené & Turlings 2002; Dicke & Baldwin 2010). Although there are still few studies regarding the interference of abiotic factors in the herbivory capacity of insects, some studies reported how environmental factors affect the production of chemical compounds for the defense of plants (De Lucia *et al.* 2012; Jamieson *et al.* 2012; Rasmann *et al.* 2014).

ALTITUDE

Most studies related to elevation have focused on the environmental interference on herbivory rate, focusing on the presence of all community of insects in a certain altitude in only one species of plants; analysis of the herbivory of all community of insects in all plants of the community at a certain altitude, or; analysis of herbivory variation according to a gradient of elevation focusing on different species that compose the community (Rasmann *et al.* 2014). In general, herbivory decreases as altitude increases, but the pattern is quite variable (Hodkinson 2005; Pellisier *et al.* 2012).

A classical theory says that altitude plants suffer less damage from herbivory but are expected to have lesser degrees of active defense mechanisms compared to similar plants at lower altitudes (Coley & Barone 1996). This theory was confirmed in a study performed by Pellissier *et al.* (2012), where the authors observed that general herbivores have accelerated growth rate when fed with plants obtained from higher altitude. Even so, the exact reasons for this pattern are just speculated, and the probable reasons raised by the authors are the decline of the defenses and the higher nutritional quality of the plants. In a subsequent study performed by Pellissier *et al.* (2014), the authors concluded that altitude plants reduce energy expenditure with defense against herbivory.

TEMPERATURE AND CO_2

High CO_2 levels and changes in temperature are two primary factors in the interactions between plants and insects. For example, the acceleration of plant phenological stages by global warming may generate a temporal asynchrony between the flowering of plants and the occurrence of pollinating insects. In addition, high levels of CO_2 combined to high temperatures, increase the carbohydrate concentration in the leaves and reduce the efficiency of nitrogen utilization, reducing the nutritional value of the plants and stimulating herbivorous insects to consume more to meet their physiological needs (De Lucia *et al.* 2012).

Even though most herbivorous insects do not respond directly to the concentration of CO_2 in the atmosphere, they are very sensitive to changes in temperature, which affects their life cycle, population size and geographical distribution (Bale *et al.* 2002; Rosenblatt & Schmitz 2016). Herbivorous insects typically respond to the temperature increase with an acceleration in their reproductive rate, winter survival, and number of generations within a season. An example is the southern pine beetle *Dendroctonus frontalis* Zimmermann (Coleoptera: Curculionidae), which has almost 100% of mortality when the air temperature reaches -16ºC, but with the increase of the average temperature, the insect survives through the winter and causes severe damages to the forests in the north hemisphere (Ayres & Lombardero 2000).

Temperature has a profound effect on all life forms, especially in poikilotherms, including insects and plants, which body temperature depends on caloric energy available in the environment (Watt *et al.* 2016, Johnson & Züst 2018). The association of high temperatures and high concentrations of CO_2 alters the nutritional composition of the plants, which in some cases may even improve the nutritional quality, attracting different species of insects (Sharma *et al.* 2016).

The aphid *Macrosiphum euphorbiae* Thomas (Hemiptera: Aphidae) attacks various Solanaceae species, such as the medicinal plant *Solanum dulcamara* (L.). Flynn *et al.* (2006) explored the effect of temperature and CO_2 on the aphid/host interaction. The number of aphids in *S. dulcamara* tends to increase under high CO_2 contents associated with high temperatures. Despite this, it was observed that the mean insect weight was lower under higher temperatures and higher CO_2 content. This reduction in weight may be an accelerated development effect, which reduces insect feeding time (Bale *et al.* 2002).

WATER STRESS

Based on the dynamics of psyllids under water stress in eucalyptus, White (1969) formulated a hypothesis, which states that insect cycle break is the result of physiological changes of the plant, especially in relation to the availability of nitrogen during long periods of water deficit.

Huberty & Denno (2004) made a bibliographical survey of the effects of water stress on sucking and chewing insects. The authors observed that suckers and chewers respond differently to plant stress, where most suckers have inferior performance in plants under water stress and chewers were little influenced by water stress.

In fact, the resistance of plants facing water deficit will depend on the intensity of the stress and the ability of the insect to accept certain situation. For instance, *Spodoptera exigua* Hübner (Lepidoptera: Noctuidae), feeding on *S. dulcamara,* presented a better performance in flooded plants than in plants submitted to water deficit (Nguyen *et al.* 2016), corroborating with observations of Huberty & Deno (2004).

Not only the water deficit can change the dynamics between plant and insect but the excess of water also has a direct influence on such interactions (Mody *et al.* 2009). The mechanisms involved in triggering the systemic resistance in the leaves are better understood than those mechanisms that part from the roots (Erb *et al.* 2009). One of the few papers dealing with this, performed by Erb *et al.* (2009), proved that the synthesis of abscisic acid in maize, triggered by herbivory of *Diabrotica specisa* Germar (Coleoptera: Chrysomelidae), induces resistance of the plant against *Spodoptera litorallis* Boisduval (Lepidoptera: Noctuidae) on the leaves. An important detail of this study is that the resistance was attributed to the change in leaf water content, which reduced its nutritional quality.

Not only the induction of resistance mediated by chemical compounds is activated, but morphological changes in plants are also induced by water stress. For instance, varieties of elm susceptible to the leaf beetle *Pyrrhalta luteola* Müller (Coleoptera: Chrysomelidae), submitted to water stress have more trichomes in the abaxial portion of the leaves, reducing insect attack (Bosu & Wagner 2014).

WIND

Wind can influence insects both physically and physiologically, as well as being an important agent of insect dispersal. Few studies relate the incidence of wind to the resistance of plants to insects. One of the main studies that correlates the incidence of winds with the application of jasmonic acid was carried out by Cipollini & Redman (1999). In their study, jasmonic acid was applied to tomato plants of different ages under various wind programs. The aim of the research was to check the induction of resistance of tomato against *Manduca sexta* L. (Lepidoptera: Sphingidae). First, the authors observed that tomato treated with jasmonic acid, induced the activity of several oxidative enzymes, such as peroxidases and polyphenol oxidases. In addition, the authors verified that plants of 4-6 and 8 weeks induced more oxidative enzymes and reduced *M. sexta* growth. In turn, the incidence of winds increased the activity of peroxidases, thus *M. sexta* tends to have a slower growth as more wind incidence.

The direct influence of winds is related to the reduction of plant weight, increase of the larval period of pests such as *Plutella xylostella* L. (Lepidoptera: Pluellidae) and the reduction of prey capture by predators such as *Parus major* L. (Passeriformes: Paridae) (Chen *et al.* 2018). Therefore, winds may influence indirectly plant-insect interaction (Carmona *et al.* 2011). On the other hand, some studies have shown that variations in the concentration of amino acids and free carbohydrates in cruciferous leaves, influenced by wind, have no influence on the biology of generalist pests such as *P. xylostella* (Gols & Harvey 2009; Chen *et al.* 2018).

FERTILIZATION

Plant resistance is a result of several factors that influence insect growth, fecundity and survival. Even if the resistance has a strong base in the plant genotype, its expression can be influenced by environmental factors, including soil fertility. In a review published by Waring & Cobb (1992), it was concluded that fertilization increased the growth, fecundity, survival and population density of insects in most studies. Depending on the form and amount of fertilizer applied, a reduction in the concentration of secondary metabolites in plants may occur (Koricheva *et al.* 2004; Clemensen *et al.* 2017).

The nutritional quality of plants plays a central role in their resistance against insects. Nitrogen, a central element in protein composition, is a limiting nutrient for both plants and animals. The growth and reproduction of phytophagous insects generally increases according to the nitrogen rates (Fischer & Fiedler 2000; Veromann *et al.* 2013; Clemensen *et al.* 2017).

The beneficial effects of silicon have been demonstrated in several species of plants, and in the case of phytosanitary problems, this element is able to increase the resistance of plants against the attack of insects and pathogens (Epstein 2001; Reynolds *et al.* 2016; Bakhat *et al.* 2018). Silicon can confer resistance to plants by the way it is deposited on the cell wall of the cells, forming a mechanical barrier (Goussain *et al.* 2002; Bakhat *et al.* 2018). The use of silicon, regardless of the form of application and the source used, increases the resistance of the potato plants to *Diabrotica speciosa* Germar (Coleoptera: Chrysomelidae) and *Liriomyza* spp., possibly due to its accumulation and polymerization in the cell wall , increasing the stiffness of the foliar tissues and hindering chewing by the insects (Gomes *et al.* 2009).

Another important feature of silicon is that this element may have the role of elicitor in the induced resistance process (Gomes *et al.* 2005; Gomes *et al.* 2009; Reynolds *et al.* 2016). For instance, it has been proven that silicon induces increased peroxidase, polyphenoloxidase and phenylalanine ammoniumase enzymes activity (Gomes *et al.* 2005). Thus, the benefits provided by silicon fertilization may result in reduced crop losses due to reduced insect attack (Villegas *et al.* 2017). However, the induction of resistance in plants allocates resources for the synthesis of defense compounds, making it necessary to verify possible decreases in productivity (Vargas-Ortiz *et al.* 2013).

TRANSGENERATIONAL INDUCTION OF RESISTANCE

Biotic and abiotic stresses induce resistance not only in the parent plants, but also indirectly in the offspring. This maternal resistance induction (transgenerational immunity), although little studied, has been shown to provide protection against herbivores to the progeny of some plants (Agrawal 2001; Agrawal 2002).

To illustrate, *Raphanus raphanistrum* L. injured by *Pieris rapae* L. (Lepidoptera: Pieridae) or treated with jasmonic acid produces an offspring with a high degree of resistance against these insects (Agrawal 2002). *Arabidopsis thaliana* (L.) Heynh exposed to abiotic stress such as cold, heat or impaction, has changes in the methylation of the DNA, which confers resistance to insects in the next generation (Boyko *et al.* 2010).

Research on insect/plant interaction should be focused not only on genetic effects, but also on the epigenetic regulation of metabolic pathways of plant defenses and insect response, since many evidences are related to siRNA signaling and DNA methylation (Holeski *et al.* 2012). Thus, the understanding of induced transgenerational resistance could account for many responses regarding the ability of plants to deal with herbivory damage (War *et al.* 2012).

FUTURE PERSPECTIVES

Several abiotic factors, including those inherent in plants, insects and the environment may negatively or positively influence the expression of resistance in plants. A single abiotic factor can affect the entire ecological web, and it is important to know the consequences of each factor and the interaction between them to seek answers regarding pest control in agricultural systems. One of the future challenges is the exploration of the defense elicitors and genes encoding proteins that regulate plant response to herbivorous attack in plants for pest management. However, before effectively using an elicitor in agricultural systems, it is important to understand chemical changes induced in the plant due to herbivorous attack and variations in the environment. It is expected that the knowledge of plant defenses along with factors that optimize them may contribute to the development and adoption of new methods for pest control in a sustainable agriculture and a consolidated integrated pest management.

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