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Research article

Role of phenolic compounds during antioxidative responses of winter triticale to aphid and beetle attack

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ABSTRACT

One of the earliest responses of plants to insects' attack is generation of reactive oxygen species. However, the elevated level of ROS can elicit oxidative burst within plant tissues, and plants employ antioxidant systems against these radicals. Due to their chemical structures, polyphenols are able to diminish the level of ROS. Thus, we investigated the role of phenolic compounds in oxidative stress within winter triticale caused by *Sitobion avenae* and *Oulema melanopus*. It was found, that infestation by insects induced a high increase in the content of hydrogen peroxide and superoxide anion radical within resistant Lamberto cv. 24 hpi, whereas in sensitive Marko cv., an increase in H_2O_2 content was found within two days of aphid feeding. Moreover, resistant plants showed earlier and much greater induction of L-phenylalanine and L-tyrosine ammonia lyases and chalcone synthase activities, as well as accumulation of phenolic compounds in response to insect feeding than susceptible Marko. On the other hand, strong positive influence of hydrogen peroxide and superoxide radical contents on chalcone synthase activity and furthermore flavonoid biosynthesis was detected in the susceptible cultivar. Negative relationships between level of o-coumaric acid or flavonoid compounds and content of hydrogen peroxide or superoxide radical suggest their antioxidant capacity. Luteolin and *o*-coumaric acid may attend in scavenging of hydrogen peroxide, whereas quercetin, apigenin and (+)-catechin probably participate in reduction of superoxide anion radical content.

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1. Introduction

Plants defend themselves against insect attacks using different mechanisms. Three types of resistance to arthropods are commonly referred to plant - insect interactions. The effects of resistant plants on arthropods can be manifested as antibiosis, in which the biology of the pest is adversely affected; or antixenosis, in which plant acts as poor host so the insect shifts to another plant. Besides that, the ability to withstand or recover from insect damage is possible in plants and it is expressed as tolerance. Thus, both constitutive and induced defenses may contribute to the protection of a plant against its herbivorous enemies (Smith, 2005). On the other hand, resistance reactions against aphids are mediated by plant hormones in which salicylic acid (SA), jasmonic acid (JA), and ethylene (ET) play key roles. However, PAD4 (PHYTOALEXIN DEFICIENT 4) may be required for induction of ROS-mediated cell death and expression of defense responses after aphid attack (Lei et al., 2014).

One of the earliest responses of plants to infestation with aphids is a generation of reactive oxygen species (ROS) (Van Breusegen et al., 2001; Maffei et al., 2007). ROS comprises both free radicals (superoxide anion radical, $O_2^{\bullet-}$; hydroxyl radical, $\bullet OH$; perhydroxyl radical, $HO_2\bullet$; and alkoxyl radical, $RO\bullet$) and non-radical (molecular) forms (hydrogen peroxide, H_2O_2; and singlet oxygen, $^1O_2$). The photosystem is the major source of ROS, since chlorophyll may act as a photosensitizer forming singlet oxygen; however, ROS formation can also occur in other compartments, such as the mitochondria, microsomes and peroxisomes (Bailey et al., 2005; Gill and Tuteja, 2010). Further, these substances may be produced in plant cells during normal developmental growth (Mittler et al., 2004) as well the levels of hydrogen peroxide, superoxide anion radicals and hydroxyl radicals may increase within plants in response to both

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biotic and abiotic stresses. The intensity and magnitude of ROS generation within plant tissues after insect feeding can elicit oxidative burst and lead to hypersensitivity reactions (Lamb and Dixon, 1997; Radville et al., 2011; Sytykiewicz et al., 2014). On the other hand, ROS are known to act as signals involved in the regulation of growth, cell cycle, pathogen and insect defense, and programmed cell death (Couto et al., 2016).

The superoxide anion radical is produced upon reduction of O_2 during electron transport along the noncyclic pathway in the electron transport chain. Nevertheless, Scarpeci et al. (2008) suggest that $O_2^{\bullet-}$ leads to the activation of genes involved in abiotic stress responses and down-regulation of genes encoding PSI and PSII components. Moreover, the generation of $O_2^{\bullet-}$ may trigger the formation of other ROS such as •OH. The hydroxyl radical is produced through the Haber-Weiss mechanism or the Fenton reaction in the presence of transition metals, such as copper or iron (Halliwell, 2006; Karuppanepandian et al., 2011). Hydroxyl radical is able to react with lipids, proteins and nucleic acids and, in the absence of the enzymatic mechanism for the elimination of this radical, excess production of •OH ultimately leads to cell death (Vranova et al., 2002).

Hydrogen peroxide is produced from the univalent reduction of $O_2^{\bullet-}$. This molecule is moderately reactive and has a relatively long life in relation to other ROS, such as $O_2^{\bullet-}$, •OH and $^1O_2$ (Pillay et al., 2016). Hydrogen peroxide plays a dual role in plants – at low concentrations, it acts as a signaling molecule involved in various biotic and abiotic stresses, whereas excess H_2O_2 production in plant cells leads to oxidative stress and programmed cell death (Tewari et al., 2006; Quan et al., 2008).

To protect themselves against these toxic oxygen intermediates, plants employ antioxidant defense systems. The main ROS scavenging system in plants uses antioxidant enzymes such as catalase, ascorbate peroxidase and superoxide dismutase (Maffei et al., 2007). Moreover, ascorbic acid, tocopherols and carotenoids decrease oxidative burst in plant cells. Due to their chemical structures, polyphenolic compounds, particularly phenylpropanoid acids and flavonoids, are strong antioxidant agents, thus they are able to diminish level of reactive oxygen species. Flavonoids also possess high tendency to chelate transition metals, such as iron and copper, and suppress the Fenton reaction. Moreover, *ortho*-diphenols can be oxidized by polyphenol oxidase (PPO) or peroxidase (POD), and these reactions may function as a detoxification arm against H_2O_2 in plants (Hernandez et al., 2009; Prochazkova et al., 2011).

Phenolic acids and flavonoids are groups of secondary metabolites derived from phenylpropanoids and the first step in their biosynthesis is the elimination of ammonia from aromatic L-amino acids. These reactions are catalyzed by phenylalanine ammonia lyase (PAL, EC 4.3.1.24) and tyrosine ammonia lyase (TAL, EC 4.3.1.23), and *trans*-cinnamic and *p*-coumaric acids are produced. Further, chalcone synthase (CHS, EC 2.3.1.74) catalyses the condensation of three acetate units with *p*-coumaroyl-CoA, and different subclasses of flavonoids are produced and can generally be classified into one of the following groups: flavones, flavonols, flavandiols, isoflavonoids, anthocyanins and proanthocyanidins (Supplemental Fig. 1) (Ferrer et al., 2008).

The grain aphid, *Sitobion avenae* F. (Hemiptera, Aphididae) is an important pest of cereals in Europe. Aphids ingest phloem sap from sieve elements and secrete various toxic compounds in their saliva. They are also capable of inoculating plants with the barley yellow dwarf viruses BYDV-MAV and BYDV-PAV (Brault et al., 2007). Moreover, aphids cause oxidative stress in plant cells, by inducing the generation of ROS (Sytykiewicz et al., 2014) and the production of quinone radicals (Mai et al., 2013). During the last decade, there are numerous occurrences of cereal leaf beetle (*Oulema melanopus* L., CLB) were observed in cereal crops. The CLB is a chewing insect that wounds plants and erodes mesophyll, thus reducing the assimilative surface of leaves and facilitating infection by fungi (Ulrich et al., 2004).

In this study, we investigated the role of flavonoids and its biosynthesis in oxidative stress caused by feeding of pierce-sucking (*S. avenae*) and chewing (*O. melanopus*) insects in winter triticale (× *Triticosecale* Wittm. ex A. Camus) plants. Generation of hydrogen peroxide and superoxide anion radicals, as well as accumulation of phenolics (phenolic acids and flavonoids) and the activities of enzymes that participate in their biosynthesis (PAL, TAL and CHS), were assessed. The degree of triticale resistance to insects was also examined based on entomological observations.

Thus, results of this work could help to understand (i) which variables influence the activity of chalcone synthase and furthermore biosynthesis of flavonoids during oxidative stress caused by insects feeding; (ii) what are the relationships between the content of ROS generated in stress conditions and accumulation of phenylpropanoid acids or flavonoids.

2. Materials and methods

The all entomological and infestation experiments were carried out in a climatic chamber (16:8 h light:dark photoperiod, temperature 24:18 °C and 65% relative humidity). Fluorescent lamps (cool white: day light 3:1) were attached to the growth chamber which provided 240 μmol m^{-2} s^{-1} light intensity (measured with Delta OHM HD2102.2 photo radiometer equipped with quantum-radiometric probe LP471PAR, Caselle, Padova, Italy).

2.1. Aphid

Adult wingless female of the grain aphid (*Sitobion avenae* F.) (green colour form) were collected from a stock culture raised on winter wheat seedlings cv. Tonacja at the Department of Biochemistry and Molecular Biology at the Siedlce University of Natural Sciences and Humanities. Parthenogenetic morphs were reared on the seedling of wheat in a climatic chamber.

2.2. Cereal leaf beetle (CLB)

Larvae of cereal leaf beetle (*Oulema melanopus* L.) were collected from field crops of wheat near Siedlce district, Poland (52°09′54″N; 22°16′17″E). They were transferred to the Department of Biochemistry and Molecular Biology, Siedlce University of Natural Sciences and Humanities and reared on the seedlings of common wheat cv. Tonacja.

2.3. Plant material

Two cultivars of winter triticale (× *Triticosecale* Wittm. ex A. Camus) – Lamberto (relatively resistant) and Marko (susceptible) – which were preselected from field observations, were used in the entomological and biochemical experiments. Triticale seeds were sown in plastic pots (12 cm diameter × 10 cm height) filled with the general-purpose horticultural substrate without additional fertilization. Seedlings of triticale cultivars were grown in a climatic chamber.

2.4. Adverse effects of host plants on insects

2.4.1. Antibiosis

The level of antibiosis of the winter triticale cultivars to *S. avenae* was examined, as described by Chrzanowski et al. (2012). Seven-

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