Changes in Pigment Content of Triticale Genotypes Infested With Grain Aphid *Sitobion avenae* (Fabricius) (Homoptera: Aphididae)

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The effect of feeding by the grain aphid *Sitobion avenae* (Fabricius) (Homoptera: Aphididae) on chlorophyll, carotenoid and flavonoid content was studied in waxy and waxless triticale genotypes. On both sampling dates (5 and 10 days after infestation), seedlings of infested waxy and waxless plants had lower chlorophylls and carotenoids and higher flavonoids than in uninfested plants.

Key words: Biotic stress, chlorophyll, carotenoid, flavonoid, *Triticosecale*, *Sitobion avenae*, waxes.

INTRODUCTION

Triticale (*Triticosecale* Wittmack) is a hybrid crop developed by crossing wheat (*Triticum aestivum* L.) and cereal rye (*Secale cereale* L.) (Salmon, 2004). One of the most serious pests of triticale plants is the grain aphid *Sitobion avenae* F., an important pest of cereals in Europe which can substantially reduce cereal yields and quality because of its capacity for extremely rapid population growth (Larsson, 2005). Damage from *S. avenae* is both direct, through mechanical damage and injection of chemical substances in saliva, and indirect, through the effect of honeydew and pathogenic fungi. *S. avenae* also is a highly efficient vector of barley yellow dwarf virus (Brault et al., 2007).

Everyone who cares for plants knows aphids (Homoptera: Aphididae). These small, fragile insects with famously powerful reproductive potential are of immense importance in agriculture and horticulture (Miles, 1989) as well as in nonagricultural ecosystems (Stadler et al., 1998; Wimp and Whitham, 2001). They are major pests in many crop and fruit species, as they remove plant assimilates (Miles, 1989), induce galls (Brown et al., 1991), transmit plant viruses (Sylvester, 1989), and excrete honeydew which acts as a growth medium for unwanted fungi (Rabbinge et al., 1981; Fokkema et al., 1983).

As producers of honeydew, some aphid species also provide a resource eagerly sought by beekeepers for the production of premium forest honey (Bauer-Dubau and Scheurer, 1993; Döring and Chittka, 2007). The feeding injury done by *S. avenae* to triticale also induced biosynthesis of secondary metabolites; generally these substances are thought to have an effect on insect behavior and performance (Bennett and Wallsgrove, 1994; Onyilagha et al., 2004; Wójcicka, 2010; Atayyat et al., 2012). Because carotenoids and flavonoids are recognized as active compounds that may play an important role in plant defense, we wanted to determine whether these allelochemicals in triticale tissues are related to grain aphid performance.

Insect infestations can trigger complex physiological responses in a plant. Feeding by herbivorous insects may change the photosynthetic activity of host plants. Where photosynthetic tissue is lost during insect feeding, both increased and decreased photosynthesis in the remaining leaf tissue may be observed. When no loss of photosynthetic tissues occurs, for example when piercing-sucking insects attack a plant, photosynthetic damage often is less apparent (Walter, 1989; Zangerl et al., 2002; Nabity et al., 2009; Velikova et al., 2010).

For the most part our understanding of the biochemical processes of seasonally occurring chloro-

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phyll degradation has outpaced advances in our knowledge about chlorophyll degradation associated with biotic stresses like herbivory. Loss of chlorophyll and other plant pigments caused by herbivore feeding is not clearly understood, although herbivory-elicited chlorophyll loss has been described in aquatic and terrestrial ecosystems (Spooner et al., 1994; Burd and Elliott, 1996). In this study we examined the effects of *S. avenae* feeding on chlorophyll, carotenoid and flavonoid levels in seedlings of waxy and waxless triticale genotypes.

MATERIALS AND METHODS

PLANT MATERIAL

We used plants of waxy triticale (RAH 122, DED 1137) and waxless triticale (RAH 325, RAH 366) obtained from the Institute of Plant Breeding and Acclimatization (Radzików/Błonie near Warsaw, Poland). Seed samples were germinated in a climate chamber and kept at $21\pm1°C$ and 70% RH under a 16 h photoperiod. The seedlings were grown in medium-nutrient fine-structure compost with sand in plastic pots ($7\times7\times9$ cm), one seedling per pot. The plants were regularly watered and no extra fertilizer was added.

APHIDS

The grain aphids *Sitobion avenae* Fabricius (Hemiptera: Aphididae) used in the experiments came from a stock culture maintained at the University of Natural Sciences and Humanities in Siedlce. Parthenogenetic clones of *S. avenae* were reared on winter wheat cv. Tonacja in an environmental chamber ($21\pm1°C$, 70% RH, 16:8 h L:D), transferred to the studied genotypes for one generation (Apoblaza and Robinson, 1967), and then the adult apterous females were used in the experiments.

ENTOMOLOGICAL OBSERVATIONS

The aphids were observed on isolated plants in plastic cylinders ($30\times15\times15$ cm) in an environmental chamber ($21\pm1°C$, 70% RH, 16:8 h L:D). Plants of each of the four triticale genotypes were infested with 10 *S. avenae* 5 days after planting (one wingless female was kept on one plant with the use of a small brush). Uninfested seedlings were also caged to ensure uniformity of microenvironmental conditions, especially light. At two intervals of infestation (5 and 10 days) the grain aphids (adult apterae, larvae and adult alatae) were counted on 10 plants of each triticale genotype.

CHEMICAL ANALYSES

The content of chlorophyll, carotenoids and flavonoids in tissues of the triticale seedlings (infested, and uninfested as control) was determined spectrophotometrically.

Determination of chlorophyll and carotenoids

Acetone solution (80%) was used to wash material. The solutions were kept in the dark by wrapping the flask in aluminum foil. The absorbance of the solution was evaluated at 470 nm, 646.8 nm and 663.2 nm. Acetone solution (80%) was used to blank the spectrophotometer. The pigment concentration in the solutions was determined according to Lichthenthaler (1987), using the following equations:

$$\text{Total chlorophyll} = 7.15 \times A663.2 + 18.71 \times A646.8$$

$$\text{Carotenoids} = \frac{1000 \times A470 - 1.82 \times A_{663.2} - 85.02 \times A_{646.8}}{198}$$

Determination of flavonoids

Flavonoid content was determined spectrophotometrically using $AlCl_3$ reagent. Freeze-dried samples were extracted with methanol. The concentration of flavonoid was determined as described by Kreft et al. (2002). Briefly, 0.2 ml 5% $AlCl_3$ in methanol or 0.2 ml methanol was added to 2 ml diluted sample. After 30 min the absorbance at 420 nm was measured in both solutions. The concentration was calculated from the difference between measurements and compared with a rutin standard.

STATISTICS

Differences in pigment content between infested and uninfested triticale plants were subjected to two-tailed unpaired Student's t-tests. Differences in the number of aphids on the studied triticale genotypes were tested by one-way ANOVA followed by Duncan's test. Linear correlations between the concentrations of the chemical compounds and aphid population density on the plants were calculated (Pearson correlations).

RESULTS

Chemical analyses showed that aphid infestation altered the levels of the studied pigments. Infestation significantly reduced the mean values of chlorophylls. In uninfested seedlings at the first measurement it ranged from 2.29 mg g^{-1} in waxy genotype RAH 122 to 2.63 mg g^{-1} in waxless genotype RAH 366, and at the second measurement from 1.9 mg g^{-1} in

TABLE 1. Changes in total chlorophyll concentration (mg g^{-1} f.w ±SE) in uninfested and infested seedlings of triticale genotypes 5 days after grain aphid infestation

Studied genotype		Total chlorophyll	
		Uninfested plants (control)	Infested plants
waxless	RAH 325	2.55±0.07	1.96±0.06*
	RAH 366	2.63±0.05	2.01±0.01*
waxy	DED 1137	2.31±0.07	1.76±0.003*
	RAH 122	2.29±0.05	1.73±0.06*

Asterisked values differ significantly from control values: *P<0.001 (Student's *t*-test).

TABLE 2. Changes in total chlorophyll concentration (mg g^{-1} f.w ±SE) in uninfested and infested seedlings of triticale genotypes 10 days after grain aphid infestation

Studied genotype		Total chlorophyll	
		Uninfested plants (control)	Infested plants
waxless	RAH 325	2.46±0.08	1.51±0.01*
	RAH 366	2.58±0.05	1.59±0.03*
waxy	DED 1137	2.00±0.05	1.43±0.0*
	RAH 122	1.90±0.02	1.40±0.04*

Asterisked values differ significantly from control values: *P<0.001 (Student's *t*-test).

TABLE 3. Changes in carotenoid concentration (mg g^{-1} f.w ±SE) in uninfested and infested seedlings of triticale genotypes 5 days after grain aphid infestation

Studied genotype		Carotenoids	
		Uninfested plants (control)	Infested plants
waxless	RAH 325	0.69±0.01	0.51±0.003*
	RAH 366	0.73±0.01	0.53±0.01*
waxy	DED 1137	0.46±0.003	0.34±0.01*
	RAH 122	0.44±0.01	0.32±0.00*

Asterisked values differ significantly from control values: *P<0.001 (Student's *t*-test).

TABLE 4. Changes in carotenoid concentration (mg g^{-1} f.w ±SE) in uninfested and infested seedlings of triticale genotypes 10 days after grain aphid infestation

Studied genotype		Carotenoids	
		Uninfested plants (control)	Infested plants
waxless	RAH 325	0.65±0.02	0.41±0.01*
	RAH 366	0.66±0.01	0.42±0.003*
waxy	DED 1137	0.42±0.01	0.29±0.00*
	RAH 122	0.40±0.00	0.27±0.00*

Asterisked values differ significantly from control values: *P<0.001 (Student's *t*-test).

TABLE 5. Changes in flavonoids concentration (mg g^{-1} f.w ±SE) in uninfested and infested seedlings of triticale genotypes, 5 days after grain aphid infestation.

Studied genotype		Flavonoids	
		Uninfested plants (control)	Infested plants
waxless	RAH 325	1.34±0.03	1.86±0.00*
	RAH 366	1.33±0.03	1.72±0.01*
waxy	DED 1137	1.82±0.01	3.05±0.01*
	RAH 122	1.60±0.01	3.47±0.003*

Asterisked values differ significantly from control values: *P<0.001 (Student's *t*-test).

TABLE 6. Changes in flavonoids concentration (mg g^{-1} f.w ±SE) in uninfested and infested seedlings of triticale genotypes, 10 days after grain aphid infestation.

Studied genotype		Flavonoids	
		Uninfested plants (control)	Infested plants
waxless	RAH 325	1.31±0.02	2.04±0.04*
	RAH 366	1.29±0.03	1.97±0.03*
waxy	DED 1137	1.73±0.01	3.65±0.03*
	RAH 122	1.48±0.01	4.01±0.01*

Asterisked values differ significantly from control values: *P<0.001 (Student's *t*-test).

waxy genotype RAH 122 to 2.58 mg g^{-1} in waxless genotype RAH 366. For infested seedlings the corresponding values were 1.73 mg g^{-1} (day 5) and 1.40 mg g^{-1} (day 10) in waxy genotype RAH 122, and 2.01 mg g^{-1} (day 5) and 1.59 mg g^{-1} (day 10) in waxless genotype RAH 366 (Tabs. 1, 2).

Carotenoid content trended similarly. For uninfested seedlings at the first measurement it ranged from 0.44 mg g^{-1} in waxy genotype RAH 122 to 0.73 mg g^{-1} in waxless genotype RAH 366, and at the second measurement from 0.40 mg g^{-1} in waxy genotype RAH 122 to 0.66 mg g^{-1} in waxless genotype RAH 366. For infested seedlings the corresponding values were 0.32 mg g^{-1} (day 5) and 0.27 mg g^{-1} (day 10) in waxy genotype RAH 122, and 0.53 mg g^{-1} (day 5) and 0.42 mg g^{-1} (day 10) in waxless genotype RAH 366 (Tabs. 3, 4).

Aphid infestation also altered the flavonoid levels, which significantly increased under the stress of *S. avenae* 5-day and 10-day infestation in tissues of waxy and waxless triticale seedlings (Tabs. 5, 6). The effect was more pronounced in genotype RAH 122, which produced almost three times more flavonoids than uninfested plants did.

TABLE 7. Abundance (mean ±SE) of grain aphids on the studied triticale genotypes

Studied genotype		Days after infestation	
		5 days	10 days
waxless	RAH 325	179.1±3.20[c]	231.3±7.71[b]
	RAH 366	210.0±5.76[b]	272.2±9.54[a]
waxy	DED 1137	96.1±1.81[de]	126.1±2.92[d]
	RAH 122	90.2±1.32[e]	115.0±2.26[d]

Values bearing different letters differ significantly at $P \leq 0.01$ (Duncan's test). Values are means from 10 plants on the sampling date for each genotype.

There were clear differences in grain aphid population development between the triticale genotypes. The number of grain aphids was higher on waxless than on waxy seedlings (Tab. 7). In all four genotypes the level of total chlorophylls was positively correlated with *S. avenae* population size (at 5 days: r=0.9958, $P \leq 0.01$; at 10 days: r=0.9823, $P \leq 0.05$). Carotenoids also correlated positively with number of *S. avenae* (at 5 days: r=0.9870, $P \leq 0.05$; at 10 days: r=0.9825, $P \leq 0.05$). Flavonoid levels correlated negatively with *S. avenae* population size (at 5 days: r=−0.9868, $P \leq 0.05$; at 10 days: r=−0.9830, $P \leq 0.05$).

DISCUSSION

The chemical composition of plants is not only affected by abiotic factors (Germ et al., 2010) but may also be influenced considerably by biotic factors such as herbivory. This study yielded basic data on the effect of *S. avenae* feeding on the levels of chlorophyll, carotenoids and flavonoids in waxy and waxless triticale. The changes in pigment content in response to *S. avenae* feeding suggest a feeding-induced stress response in all genotypes. Stress under aphid feeding led to lower chlorophyll and carotenoid content in triticale tissues. Photosynthetic pigment degradation is a complex phenomenon which often accompanies insect feeding damage to plants (Ni et al., 2002). Piercing-sucking herbivores may feed on sap of xylem, phloem or other plant cells. The feeding site and amount of tissue damage may vary considerably (Walling, 2000; Velikova et al., 2010). Photosynthesis is not compromised when cotton leaves are attacked by aphids for a few hours (Gomez et al., 2006), but such damage occurs after herbivores attack a plant for several days (Raddall et al., 2004). In terrestrial ecosystems, two well-known aphid species that elicit chlorophyll loss are the Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Hemiptera:

Aphididae) on wheat *Triticum aestivum* L. (Burd and Elliott, 1996; Burd and Elliott 1998) and the greenbug *Schizaphis graminum* (Rondani) on sorghum *Sorghum bicolor* (L.) Moench (Girma et al., 1998) and wheat. Unfortunately, the physiological mechanisms of photosynthetic pigment loss elicited by these sap-feeding herbivores have not been described (Ni et al., 2001).

According to Wilkaniec (1990), aphid feeding causes changes in the metabolism of host plants, which in turn disturbs photosynthesis, speeds tissue aging, and causes morphological deformations. This is connected with the direct harm done by aphids inserting saliva into plant tissues and blocking stomata with the honeydew they produce, but the exact mechanism by which aphids affect plant metabolism is not fully understood. Heng-Moss et al. (2003) speculated that by feeding mainly on phloem tissue *D. noxia* elicits a change in pH either on the luminal side of the thylakoid membrane, preventing the formation of zeaxanthin, or on the stromal side where regeneration of violaxanthin takes place (Heng-Moss et al., 2003). Both of these carotenoids are responsible for nonphotochemical quenching of exciton energy (Heldt, 1997). Because carotenoids serve as cellular membrane protectants, removal of carotenoid pigments may result in membrane degradation (Timko, 1998). Heng-Moss et al. (2003) stated that the reduction of chlorophyll *a* and *b* and carotenoid content after *D. noxia* feeding supports the suggestion by Fouche et al. (1984) that such herbivory negatively impacts the stacked region of thylakoid membranes. Carotenoids participate in light harvesting and protect the photosynthetic apparatus from photooxidative damage by quenching triplet-state chlorophyll molecules and scavenging reactive oxygen species such as singlet oxygen (Biswal et al., 1994; Malkin and Niyogi, 2000), so the patterns I found for all three photosynthetic pigments are not surprising.

Burd and Elliott (1996) showed that *D. noxia* feeding could reduce protein synthesis, blocking electron transport on the acceptor site of the photosystem II reaction center, causing over-reduction in the system. The process of chlorophyll degradation in senescent plants occurs by one of two pathways: the pheophorbide pathway (Matile et al., 1999) or the oxidative bleaching pathway (Janave, 1997). Ni et al. (2001) showed that feeding by chlorosis-eliciting *D. noxia* or the non-chlorosis-eliciting bird cherry-oat aphid *Rhopalosiphum padi* did not cause any changes in the oxidative bleaching pathway or chlorophyllase activity versus uninfested plants. However, Russian wheat aphid feeding caused significant losses of chlorophylls *a* and *b* and carotenoids in the damaged regions of wheat leaves (Ni et al., 2002). Interestingly, undamaged regions of *D. noxia*-infested leaves showed significantly higher

chlorophylls *a* and *b* and carotenoids than in uninfested plants on both dates of sampling (6 and 12 days) (Heng-Moss et al., 2003). Ni et al. (2002) inferred that undamaged regions of *D. noxia*-infested leaves compensated for the pigment losses in the damaged regions, and that Mg-dechelatase activity changed dynamically from a localized to a systemic response as the infestation period lengthened. After long infestation, Mg-dechelatase activity in both *D. noxia*-damaged and non-damaged regions increased significantly versus the respective regions of uninfested and *R. padi*-infested leaves. These results demonstrate the dynamic nature of plant responses to aphid feeding: initially a localized response limited to the site of feeding, and then transformed into a whole-leaf response. Ni et al.'s (2002) work also suggested that *D. nexia* elicits signal transduction between damaged and undamaged regions of infested leaves.

In this study the carotenoid and chlorophyll concentrations in the four triticale genotypes followed similar trends under feeding by *S. avenae*, suggesting that the two types of pigments were similarly affected by that stress. Haile et al. (1999) and Heng-Moss et al. (2003) reported a significant decline of photosynthesis in aphid-injured leaves and speculated that it may have resulted from increased synthesis of chemical defense compounds in response to herbivory. My results show an increase of flavonoids in tissues of the triticale genotypes under the stress of aphid feeding. Flavonoids are a large class of secondary metabolites encompassing more than 10,000 structures. Several lines of evidence demonstrate that they have antioxidant functions in higher plants challenged with a range of environmental stresses (Winkel-Shirley, 2002; Germ et al., 2010; Agati and Tattini 2010; Agatiet al., 2012). Flavonoids are of great interest for their bioactivities, basically related to their antioxidant properties (Cao et. al., 2013). The stress reactions of the four triticale genotypes point to the negative effect of aphid infestation and to activation of protective mechanisms such as an increase of flavonoid content. Tevini et al. (1991) showed that accumulation of these pigments in rice lessened the damage to the photosynthetic activity of mesophyll chloroplasts. My results also indicate that the waxy plants, which contained high levels of flavonoids, were less accepted by the grain aphid. Leiss et al. (2009) showed that resistant hybrids contained higher amounts of the flavonoid kaempferol glucoside. Flavonoids are generally involved in plant resistance to herbivores (Bennett and Wallsgrove, 1994; Onyilagha et al., 204; Kirk et al., 2005; Wu et al., 2007). Kaempferol glucosides also have a negative effect on aphids. Aphid-resistant cow pea lines contained significantly higher amounts of flavonoids, including kaempferol, than susceptible lines (Lattanzio et al.,

2000). Under infestation by feeding stinkbugs *Murgantia histrionica*, photosynthesis decreased rapidly and substantially in *Brassica oleracea* and *Phaseolus vulgaris* but in savoy cabbage leaves emission of mono- and sesquiterpenes was induced (Velikova et al., 2010). The different time-course of the induction of these two classes of terpenes apparently reflects induction of two different biosynthetic pathways and points to different roles of these terpenoids in tritrophic interactions.

The present results suggest that the level of photosynthetic pigments is crucial to the resistance of winter triticale genotypes to grain aphid. The total chlorophyll and carotenoid concentrations were correlated with the plants' resistance to infestation, that is, with aphid population density, on the waxy and waxless plants. The number of aphids was lowest on the waxy triticale plants, indicating that they are less attractive to *S. avenae*. Triticale responded to aphid feeding by increasing flavonoid production, a protective reaction in plants exposed to *S. avenae* feeding.

These data on the effect of *S. avenae* feeding on total chlorophyll, carotenoid and flavonoid concentrations in triticale tissues show changes in pigment concentrations in response to *S. avenae* feeding, and suggest a feeding-induced stress response in the studied triticale genotypes.

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