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EFFECT OF PEA APHID INFESTATION ON ACTIVITY OF AMINO ACID DECARBOXYLASES IN PEA TISSUES

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The study examined changes in lysine decarboxylase (LDC), ornithine decarboxylase (ODC) and tyrosine decarboxylase (TyDC) activity in tissues of pea (*Pisum sativum* L.) infested by the pea aphid (*Acyrthosiphon pisum* Harris). The aphid induced increased ODC activity after one day and at two weeks. The effect was clearly systemic. TyDC activity increased after one day and at one week at feeding sites (aerial parts), while LDC activity increased only after one day of infestation and then decreased. Attack by aphids also affected enzyme activity in root tissues not directly damaged by the herbivores. The mechanisms of the response induced by pea aphid infestation in pea are discussed.

Key words: *Acyrthosiphon pisum*, *Pisum sativum*, lysine decarboxylase, tyrosine decarboxylase, ornithine decarboxylase, polyamines.

INTRODUCTION

Amino acid decarboxylases are key enzymes of biogenic amine biosynthesis in plant cells. For example, ornithine decarboxylase (EC 4.1.1.17) is a common enzyme catalyzing transformation of ornithine to putrescine in plant and animal tissues (Walters, 2003). Another diamine, cadaverine, is synthesized in plants of the families Fabaceae, Poaceae and Solanaceae through decarboxylation of lysine with the participation of lysine decarboxylase (EC 4.1.1.18) (Bagni and Tassoni, 2001). Aromatic amino acid decarboxylases such as tyrosine decarboxylase (EC 4.1.1.25) are also involved in biosynthesis of important classes of defensive secondary plant metabolites (Facchini et al., 2000).

Information on the involvement of polyamines (PAs) and aromatic monoamines in insect-plant interactions is limited despite numerous data on their role in the plant defense against pathogens (Walters, 2003). A few published reports have rather suggested anti-arthropod activity of their hydroxycinnamic acid derivatives (HCAAs) which may paralyze skeletal muscles and block synaptic transmission (Klose et al., 2002). Defense action of these compounds has been observed in the interaction between *Capsicum annuum* L. and the leaf miner *Liriomyza trifolii* (Burgess), as well as between *Nicotiana attenuata* (Torr. ex Wats.) and such insect species as *Manduca sexta* (L.), and *Spodoptera littoralis* (Boisduval) (Tebayashi et al., 2007; Bassard et al., 2010). Free polyamines and α-difluoromethyl-ornithine (a known inhibitor of PA biosynthesis) disturbed the sensitivity of *Plutella xylostella* L. antennae to odors, influencing its behavior (Zhang et al., 2008). On the other hand, tyramine was found to stimulate oviposition of *Papilio polyxenes* F. on *Pastinaca sativa* L. (Carter et al., 1998).

Our earlier studies showed that such free PAs as agmatine and cadaverine (at 0.01% concentration) and agmatine, cadaverine, putrescine, spermidine and spermine (at 0.1% concentration) reduced the quantity of assimilated food, body mass and survival of the grain aphid (*Sitobion avenae* F.) (Sempruch et al., 2010a). Putrescine, spermidine and spermine (at 10 mM concentration) disturbed the settling behavior of bird cherry-oat aphid (*Rhopalosiphum padi* L.) on triticale (Sempruch et al., 2011). Aphid feeding affected the amount of amine in triticale tissues, and these changes were dependent on the susceptibility of the host plant and

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the duration of infestation (Sempruch et al., 2012). After two weeks of infestation the amine level was reduced in more susceptible triticale, while in less sensitive plants the content of cadaverine, spermidine and tryptamine increased, with a simultaneous decrease of the putrescine concentration. It has been suggested that the changes in amine content in triticale plants infested by cereal aphids were at least partly the result of altered activity of key enzymes of amine biosynthesis, such as ODC, LDC and TyDC (Sempruch et al., 2008, 2009, 2010b). However, there are no data on the participation of the amines and their metabolic transformation in the interaction between host plants and other aphid species.

Here we examine the changes in activity of amino acid decarboxylases in tissues of pea (*Pisum sativum* L.) infested by the common pea aphid (*Acyrthosiphon pisum* Harris). Enzyme activities were analyzed in aphid-infested aerial parts and in roots not directly damaged by the insects. The changes were assessed in terms of possible systemic effects of *A. pisum* infestation in pea seedlings.

MATERIAL AND METHODS

PLANTS

The pea plants used in the experiments were grown from seeds supplied by the Lobelia II seed company (Chrzanów, Poland). The cultivar is labelled "six-week peas" by the company.

APHIDS

A multiclonal parthenogenetic population of pea aphid was reared on pea seedlings in a climate chamber at 24°C/18°C (day/night) and 70% RH under a 16 h photoperiod. Wingless *A. pisum* females were used in the experiments.

PLANT INFESTATION WITH APHIDS AND SAMPLING

Pea seeds were germinated in a climate chamber at 24°C/18°C (day/night) and 70% RH under a 16 h photoperiod. Plants were grown individually in medium-nutrient fine-structure compost with sand in 8.0 × 9.5 cm plastic pots, regularly watered.

Nine 7-day-old seedlings were individually infested with ten wingless *A. pisum* females. Control plants (without aphids) were similarly grown in another climate chamber under the same conditions. Three infested and control seedlings were collected 24 h, one week and two weeks after the beginning of the experiment. The aphids on the seedlings at the time of plant material collection were counted. Colony density was calculated as the average number of aphids per plant. For chemical analyses the collected seedlings were divided into aerial parts and roots.

ENZYME ASSAYS

The fresh plant material was homogenized with 0.2 M phosphate buffer (pH 8.2) with the addition of β-mercaptoethanol and ethylenediaminetetracetic acid (EDTA) for ODC extraction, 0.2 M Tris-HCl buffer (pH 5.6) for LDC extraction, or 0.5 M acetate buffer (pH 5.6) for TyDC extraction. The obtained enzymatic extracts were filtered through two layers of cheesecloth and centrifuged at 18,000 × g at 5°C.

Enzyme activities were assayed by spectrophotometric methods as described by Ngo et al. (1987) for ODC and Phan et al. (1982, 1983) for LDC and TyDC. The assays employed a Hewlett Packard 8453 UV-Vis spectrophotometer. Enzyme activity is expressed as μM putrescine (ODC), cadaverine (LDC) or tyramine (TyDC) generated during 1 h enzymatic reaction with 1 mg enzymatic protein. The protein quantity in the enzymatic extracts was estimated according to the method of Lowry et al. (1951).

STATISTICS

The data on the number of aphids on artificially infested seedlings and the activity of the analyzed enzymes in plant tissues come from three independent experiments. The distribution of obtained data was verified with the chi-square test. The Kruskal-Wallis test, as a non-parametric alternative to ANOVA, was applied when the data distribution deviated from normality (LDC activity in pea roots, TyDC and ODC activity in aerial parts). One-way ANOVA was used for data with a normal distribution (aphid density, LDC activity in aerial parts, TyDC and ODC activity in roots). The significance of differences in enzyme activity between control and aphid-infested seedlings was checked with the Mann-Whitney U-test or Student's t-test. Changes in pea aphid number during particular intervals of the experiment were subjected to Tukey's post-hoc test. Interactions between aphid density on artificially infested seedlings and enzyme activity were analyzed with Pearson's line correlation or Spearman's rank correlation, depending on the data distribution. $P \leq 0.05$ was taken to indicate statistical significance.

The results given in the tables are arithmetic means with standard errors. All statistical analyses used Statistica for Windows ver. 9.0 (2010).

RESULTS

NUMBER OF PEA APHIDS ON PEA SEEDLINGS

The number of pea aphid individuals on infested pea seedlings significantly fluctuated during experimental period ($F_{2,6} = 5.93$ at $P = 3.80 \times 10^{-2}$). An increase in aphid colony density in the first week of the experiment and a subsequent decrease in the

second week were observed (Fig. 1). As a consequence, *A. pisum* number was significantly higher after the first week than at the other time points.

EFFECT OF APHID INFESTATION ON ENZYME ACTIVITY IN PEA TISSUES

As compared with control plants, LDC activity increased after one day of infestation and decreased after one week in the aerial parts and roots of the pea seedlings (Tab. 1). Enzyme activity decreased significantly in aerial parts and increased nonsignificantly in roots after two weeks of aphid feeding. TyDC activity significantly rose in aerial parts after one day and one week of infestation, and fell after two weeks, but the changes were not statistically significant (Tab. 2). Root tissues showed fluctuations of TyDC activity during the experimental period. It increased slightly versus the control at the beginning of artificial infestation, decreased after one week and increased again after two weeks. The changes after one and two weeks were statistically significant. *A. pisum* infestation induced activity in aerial parts of the pea plants; the effect was significant after one day and two weeks (Tab. 3). ODC activity in root tissues decreased versus the control after one day and increased in the next intervals of the experiment, showing a systemic effect on the activity of this enzyme.

Enzyme activity also fluctuated in the aerial part and roots of control pea seedlings during the experimental period (Tabs. 1, 2, 3). Generally, decarboxylase activity was relatively low after one day, increased after one week and decreased again after two weeks. These changes were especially evident for LDC.

The changes in enzyme activity were statistically significant for LDC ($F_{5,12} = 66.96$ at $P < 10^{-14}$ for aerial parts; $H_{(5, N = 18)} = 16.39$ at $P = 5.80 \times 10^{-3}$ for roots) and TyDC ($H_{(5, N = 18)} = 14.70$ at $P = 1.17 \times 10^{-2}$ for aerial parts; $F_{5,12} = 22.33$ at $P = 1.10 \times 10^{-5}$ for roots) (Tabs. 1, 2). The differences in ODC activity were statistically significant in aerial parts ($H_{(5, N = 18)} = 12.28$ at $P = 3.12 \times 10^{-2}$) but not in roots ($F_{5,12} = 2.35$ at $P = 0.11$) (Tab. 3).

Generally, *A. pisum* infestation activated the studied decarboxylases in pea seedling tissues after one day of infestation (Fig. 2). TyDC activity increased and LDC activity decreased after one week. After two weeks, ODC activity was stimulated while the activity of the other decarboxylases was inhibited.

Statistical analyses of the interaction between number of aphids on plants and enzyme activity in pea tissues showed a positive correlation for LDC in aerial parts of aphid-infested seedlings ($r_9 = 0.72$ at $P = 2.81 \times 10^{-2}$). This relationship was not significant for the other analyzed decarboxylases.

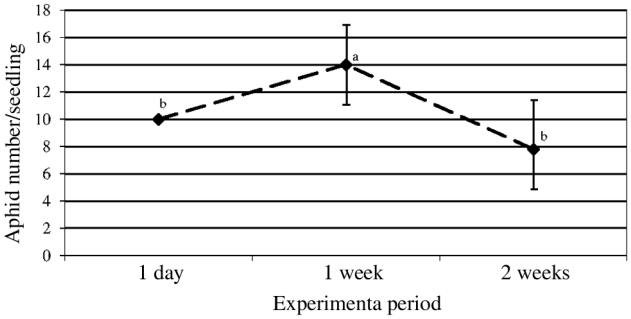

Fig. 1. Density of pea aphid (number of aphids/plant) on pea seedlings during collection of plant material for enzymatic analyses. Values bearing different letters differ significantly at P≤0.05 (Tukey's test).

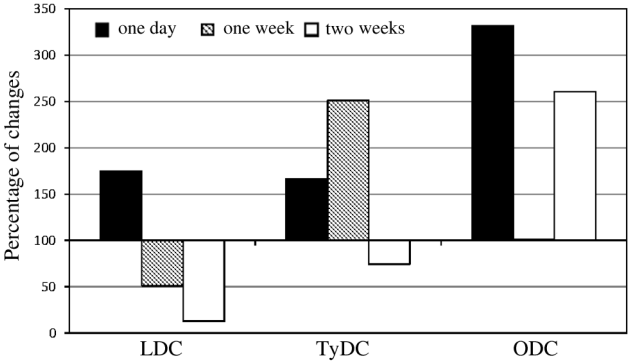

Fig. 2. Changes in activity of lysine decarboxylase (LDC), tyrosine decarboxylase (TyDC) and ornithine decarboxylase (ODC) (% change versus control as 100%) caused by *A. pisum* feeding in aerial parts of pea seedlings.

DISCUSSION

The increased activity of decarboxylases after one day of infestation suggests their participation in the short-term local response elicited by pea aphid feeding. The importance of the hypersensitive response (HR) in aphid-plant interactions has been noted by other authors (Goggin, 2007; Morkunas et al., 2011). During earlier HR events in response to some aphid species, reactive oxygen species (ROS) such as superoxide anion (O_2^-) and hydrogen peroxide (H_2O_2) are generated (Thompson and Goggin, 2006). Polyamines prevent plant damage caused by oxidative stress but may also generate large quantities of H_2O_2, inducing the next steps of stress responses (Mohapatra et al., 2009). Oxidative degradation of polyamines by diamine oxidase (DAO) and polyamine oxidase (PAO) generated H_2O_2 during the hypersensitive response of tobacco to tobacco mosaic virus (TMV) (Cona et al., 2006; Yoda et al., 2009). A similar mechanism could be involved in the induc-

TABLE 1. Effect of *A. pisum* infestation on lysine decarboxylase (LDC) activity (μM cadaverine × mg^{-1} protein × $hour^{-1}$) in pea seedlings

Experimental variant		Duration of infestation		
		One day $\bar{X} \pm SE$	One week $\bar{X} \pm SE$	Two weeks $\bar{X} \pm SE$
Shoots	Control	62.77 ± 13.70	384.76 ±10.04	208.66 ± 32.79
	Infested	109.61 ± 6.73	196.76 ± 9.28	26.90 ± 2.59
	t_3; p	3.07; 3.73×10^{-2}	13.75; 1.62×10^{-4}	5.53; 5.25×10^{-3}
Roots	Control	171.83 ± 6.14	467.92 ±55.43	25.44 ±10.55
	Infested	221.17 ±12.86	304.19 ± 2.75	60.32 ±15.36
	U_3; p	0.00; 4.95×10^{-2}	0.00; 4.95×10^{-2}	1.00; 0.13

Student's t-test comparing LDC activity in shoots of aphid-infested plants with LDC activity in control shoots. Mann-Whitney U-test comparing LDC activity in roots of aphid-infested plants with LDC activity in control roots.

TABLE 2. Effect of *A. pisum* infestation on tyrosine decarboxylase (TyDC) activity (μM tyramine × mg^{-1} protein × $hour^{-1}$) in pea seedlings

Experimental variant		Duration of infestation		
		One day $\bar{X} \pm SE$	One week $\bar{X} \pm SE$	Two weeks $\bar{X} \pm SE$
Shoots	Control	98.38 ± 4.66	104.54 ± 10.72	91.21 ±14.06
	Infested	163.73 ± 2.89	262.56 ± 8.65	67.90 ±7.51
	U_3; p	0.00; 4.95×10^{-2}	0.00; 4.95×10^{-2}	1.00; 0.13
Roots	Control	224.77 ± 8.10	446.76 ± 24.24	314.28 ± 18.74
	Infested	248.03 ±40.03	188.78 ± 1.99	526.70 ±41.89
	t_3; p	0.57; 0.60	7.88; 1.40×10^{-3}	4.63; 9.82×10^{-3}

Mann-Whitney U-test comparing TyDC activity in shoots of aphid-infested plants with TyDC activity in control shoots. Student's t-test comparing TyDC activity in roots of aphid-infested plants with TyDC activity in control roots.

TABLE 3. Effect of *A. pisum* infestation on ornithine decarboxylase (ODC) activity (μM putrescine × mg^{-1} protein × $hour^{-1}$) in pea seedlings

Experimental variant		Duration of infestation		
		One day $\bar{X} \pm SE$	One week $\bar{X} \pm SE$	Two weeks $\bar{X} \pm SE$
Shoots	Control	52.23 ± 29.32	157.41 ± 6.48	56.49 ± 0.93
	Infested	173.15 ±17.59	159.26 ± 2.45	147.23 ± 9.76
	U_3; p	0.00; 4.95×10^{-2}	3.50; 0.66	0.00; 4.95×10^{-2}
Roots	Control	82.41 ±10.92	87.97 ±12.04	46.30 ± 6.68
	Infested	62.89 ±6.63	94.45 ±22.45	94.44 ± 10.51
			ns	

Mann-Whitney U-test comparing ODC activity in shoots of aphid-infested plants with control shoots. ns – non significant difference between ODC activity in shoots of aphid-infested plants and ODC activity in control shoots (ANOVA: $F_{5,12} = 2.35$; $P = 0.11$).

tion of decarboxylases in pea tissues soon after *A. pisum* infestation began, which may have resulted in overaccumulation of PAs and intensification of their next transformations (e.g., oxidative degradation). This phenomenon needs to be studied in terms of the biochemical interactions between the oxidative burst and the metabolism of PAs in aphid-infested plants.

Some decarboxylases whose activity was affected later in the aphid infestation (e.g., TyDC induced

after one week, ODC after two weeks) may participate in the long-term systemic defense. Expression of the genes encoding key enzymes of polyamine biosynthesis is regulated by jasmonates, which are known to be signalling molecules involved in plant responses to wounding and defenses against herbivorous insects. ODC transcript levels increased in transgenic tobacco in response to treatment with methyl jasmonate (MeJA) (Xu et al., 2004). In transgenic rice, exogenous MeJA inhibited the expression of arginine decarboxylase (*OsAdc1*), S-adenosylmethionine decarboxylase (*OsSamdc*) and spermidine synthase (*OsSpds*) genes (Peremarti et al., 2010). The level of free polyamines fell and the concentration of their conjugates increased up to tenfold in roots and shoots of potato plants after jasmonic acid treatment (Mader, 1999). In tobacco, MeJA lowered the levels of free putrescine, spermidine and spermine with a simultaneous increase of arginine decarboxylase and ornithine decarboxylase activity (Biondi et al., 2001). These phytohormone also induced the accumulation of conjugated polyamines and the activity of ornithine and S-adenosylmethionine decarboxylases but not arginine decarboxylase in tobacco leaves (Biondi et al., 2003). Induction of TyDC and ODC during longer infestation (one and two weeks), as well as the changes in enzyme activity in root tissues not directly damaged by the aphids suggests at least partial participation of the amino acid decarboxylases in the systemic pea response to *A. pisum* infestation. More work is needed to find out how the signaling pathways typical for the plant defense induced by herbivorous insects are involved in this mechanism.

We found significant fluctuations of decarboxylase activity in control pea seedlings during the experimental period. These changes seem related to intensive plant development during seedling growth; polyamines are considered plant growth regulators in some reports (Kusano et al., 2008).

Amino acid decarboxylation is an important part of the biochemical defense developed by triticale in response to grain aphid infestation (Sempruch et al., 2008, 2009, 2010b, 2012). *Sitobion avenae* reduced LDC activity in triticale tissues except after two weeks of infestation when the enzyme's activity increased in the less susceptible cultivar. The aphid generally caused TyDC activity to increase except at one week in the more sensitive cultivar and after one day of infestation in the less sensitive seedlings. ODC activity decreased during the first week of *S. avenae* infestation and increased later. In the pea plants we studied, after two weeks of *A. pisum* infestation the pattern of changes in LDC and ODC activity in the aerial parts of seedlings resembled the pattern in the more susceptible triticale cultivar described above. These changes can be linked to the pea plant's high nutritive value to the pea aphid. According to Goławska et al. (2007) the feeding behavior of the pea aphid on pea and broad bean is characterized by a higher share of phloem sap ingestion and shorter duration of peripheral tissue penetration than on alfalfa, clover and bean. Our data suggest that this may be related to amino acid metabolism through an increase of the lysine level and a decrease of cadaverine in consequence of reduced LDC activity. Also, the increase of ODC activity may have disturbed the balance between ornithine and polyamine levels. High ornithine levels impaired the development of the *S. avenae* population on winter wheat cultivars (Ciepiela and Sempruch, 1999). In transgenic rice plants, overexpression of cDNA for human ODC caused significant changes in putrescine, spermidine and spermine content in seeds and vegetative tissues (Lepri et al., 2001). However, other alternative metabolic pathways such as arginine decarboxylation and S-adenosylmethionine decarboxylation are involved in polyamine biosynthesis in plant tissues.

We found that *A. pisum* feeding modified the activity of the studied amino acid decarboxylases in pea plant tissues. The direction and intensity of these changes depended on the duration of infestation. The changes in LDC activity were positively correlated with aphid density on the infested plants, and the changes in ODC activity reflected a systemic effect. The patterns of the observed changes indicate local and partly systemic biochemical responses.

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