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Resistance to the cabbage root fly, *Delia radicum* (Diptera, Anthomyiidae), of turnip varieties (*Brassica rapa* subsp. *rapa*)

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Abstract The cabbage root fly *Delia radicum* L. (Diptera: Anthomyiidae) is one of the major pests of many *Brassica* crops in the temperate areas of Europe and North America. At present, turnip (*B. rapa* ssp. *rapa* L.) varieties resistant to the pest does not exist. With the aim to fill this gap, a no-choice tolerance test of 56 accessions among turnips, turnip tops and turnip greens was performed under controlled conditions by introducing *D. radicum* eggs. Plant survival, leaf and root conditions, pupae number and weight significantly varied among plant accessions. Ten putatively resistant and ten susceptible accessions (control group) were selected from this first screening, transplanted in the field and exposed to natural infestation to detect antibiosis and antixenosis mechanisms. Both in the laboratory and in the field, pupae number significantly varied within accessions and between resistant and susceptible group, although pupal weight did not, indicating the absence of antibiosis effect on this early stage. In the field, the number of galleries was significantly lower in the resistant group in comparison with the control. Resistant accessions had smaller size, and a smaller, white and mostly buried root. Within the resistant and susceptible accessions, larger plants harboured more pupae, however purple roots were those most preferred, and the hosted pupae weighed most. Three accessions from the resistant group (MBGBR0178, MBGBR0570 and MBGBR0371) stand out for resistance to *D. radicum* possibly through antixenosis mechanisms.

Keywords Antibiosis · Antixenosis · Brassicaceae · Tolerance · Turnip

Introduction

Turnip (*Brassica rapa* L.) is one of the oldest cultivated vegetables that has been used for human consumption in temperate Europe since 2500–2000 BC. According to the studies based on morphology, geographic distribution, isozymes and molecular data, Europe should be one primary centre of origin for oil and turnip types, whereas East Asia should be another primary centre for Indian oil types and Chinese leafy vegetables (Gómez-Campo and Prakash 1999; Vogl-Lukasser et al. 2007). In the Iberian Peninsula, this

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plant constitutes, together with cabbage (*B. oleracea* L. *capitata*), kale (*B. oleracea* L. *acephala*) and leaf rape (*B. napus* L. var. *pabularia*), an important supply of vegetables during the winter. In the coldest regions of Portugal and NW Spain the edible parts of *B. rapa* subsp. *rapa* include turnip greens (young leaves harvested in the vegetative period), turnip tops (fructiferous stems with the flower buds and the surrounding leaves) and turnips (roots), used for culinary profit as well as for winter fresh fodder (Padilla et al. 2005). The leaves are characterized by a particular bitter and pungent taste, which has been related to the degradation product of some glucosinolates such as gluconapin, glucobrassicanapin (Padilla et al. 2007) and progoitrin (Francisco et al. 2009a). The genetics and the phylogenetic relationship among cultivated types of *B. rapa* subsp. *rapa* have been studied (Zhao et al. 2005; Takuno et al. 2007; Soengas et al. 2011). Also, the variation of phytochemical contents (Krumbein et al. 2005; Padilla et al. 2007; Francisco et al. 2009b, 2012; Schreiner et al. 2011; Cartea et al. 2012; Thiruvengadam and Chung 2015), the agronomic characteristics (Padilla et al. 2005; Francisco et al. 2011a), and the sensorial traits (Francisco et al. 2009a, 2010) are well known. In addition, the nutritional properties have been also investigated because turnips, turnip tops and turnip greens are a good source of health-promoting bioactive compounds such as glucosinolates, vitamin A, vitamin C, vitamin K, flavonoids, hydroxycinnamic acids, folate and calcium (Fernandes et al. 2007; Francisco et al. 2010, 2011a, b). Resistance to diseases such as black rot (*Xanthomonas campestris* pv. *campestris* (Pammel) Dowson) has been assessed among turnip accessions (Lema et al. 2015). However, the plant–insect interactions are still poorly known.

The cabbage root fly, *Delia radicum* L. (Diptera: Anthomyiidae), is one of the major pests of many *Brassica* crops in the temperate areas of Europe and North America, and represents the most dangerous phytophagous for turnip (*B. rapa* ssp. *rapa)* and swede (*B. napus* var. *napobrassica* (L.) Reichb.) crops. This species is monovoltine in northern Europe and multivoltine in central Europe and U.S.A. (Biron et al. 2002). After emergence in spring, flies feed during 4–6 days on protein and carbohydrate of flowering fruit trees before mating. Females lay white, oblong, 1 mm long, grouped eggs around the base of young plants or in the soil surface. The eggs hatch into white maggots after about 4–6 days at 15–20 °C. The larvae feed for about 3 weeks on the roots and stems of the cabbage plants. Finally, they form reddish-brown pupae which develop in the soil and hatch into adult flies after approximately 20 days. Two pauses in development may take place: the first in summer (quiescence) when the ground is above 22 °C; the second in winter (diapause), beginning in September–October (Dreves et al. 2006). Direct damage to the plant, as a result of feeding by *D. radicum* larvae on root tissue, and indirect damage, by facilitating the entry of secondary root pathogens, reduce both yield and quality of the vegetables and eventually induce plant death (Griffith 1986). The most common feeding symptoms of cabbage maggot are plant yellowing, stunting and slow growth.

Preventive management practices to decrease *D. radicum* populations include: crop covering with mesh netting or exclusion fences (Bomford et al. 2000), trap cropping (Rousse et al. 2003), "push–pull strategy" (Kergunteuil et al. 2015), the avoidance of sowing/planting during the main egg-laying periods, tillage regime and row spacing (Dosdall et al. 1998). The biological control of the cabbage root fly population is exerted by generalist feeding epigeal predators, which consume immature stages of *D. radicum.* Among them, ground beetles (Coleoptera: Carabidae) and rove beetles (Coleoptera: Staphylinidae) are particularly effective (Eyre et al. 2009; Hummel et al. 2012). Several parasitoids (Hemachandra et al. 2007), entomopathogenic fungi (Bruck et al. 2005) and nematodes (Georgis et al. 2006) attacking *D. radicum* larvae and pupae have been also described. However, these control measures are not effective enough and, finally, the control of *D. radicum* mainly depends on the application of insecticides, such as the organophosphates trichlorfon and diazinon, which rarely provide 100% control (Cartea et al. 2010a). Actually, the use of chemicals is limited because they are hazardous to the environment, and also because pupae developing below-ground may escape the application (Joseph and Zarate 2015). In contrast, host plant resistance to insect herbivores may be a useful approach for *Brassica* vegetables (Felkl et al. 2005; Cartea et al. 2010b). High levels of resistance to the cabbage root fly have been reported especially in wild *Brassica* species (e.g. *B. incana*, *B. spinescens* and *B. fruticulosa*) (Jensen et al. 2002; Felkl et al. 2005; Shuhang et al. 2016), whereas moderate

resistance have been described within cultivated forms of *B. oleracea* (Ellis et al. 1999; Jyoti et al. 2001). Nevertheless, this level has not been considered high enough for a practical exploitation in breeding programmes. Previous studies on the resistance of *B. rapa* to *D. radicum* found that turnips were always the most susceptible plants in comparisons with other brassicaceous species such as *B. napus* L., *B. juncea* L., and *Sinapis alba* L. (Dosdall et al. 1994) and *B. carinata* L. and *B. nigra* L. (Dosdall et al. 2000). To our knowledge, no information is available on the existence of strongly resistant varieties of *B. rapa* subsp. *rapa* against the cabbage root fly.

Plant resistance is the heritable ability of plants to escape the herbivore enemies (Mitchell et al. 2016). It is generally categorized into three functional categories: antibiosis, antixenosis and tolerance (Smith 1989, 2005). Antixenosis (non-preference) describes the extent to which the plant will be able to escape herbivores due to its morphological and biochemical characteristics; antibiosis refers to the negative influence of the plant on the biology of the insect attempting to use that plant as host; and tolerance indicates the ability of the plant to grow and reproduce in spite of harbour a pest population. Tolerance, however, only involves plant characteristics and is not part of the insect-plant interaction.

Quantify antixenosis may be accomplished by counting how many eggs, larvae, pupae and adult the plant is harbouring, by measuring leaf eating and/or larvae food intake, and by scoring how much damage is suffered by the plant (Stenberg and Muola 2017). Antibiosis is usually expressed as fertility rate, development time and body weight. However, antixenosis and antibiosis are often correlated and difficult to disentangle. Insect herbivores choose to lay eggs on plants that are more palatable to their offspring, but the offspring survival and development may also depend on plant chemical defences, which is a matter of antibiosis (Stenberg and Muola 2017).

The Misión Biológica de Galicia (Spanish Council for Scientific Research) stores a collection of *B. rapa* subsp. *rapa* accessions as part of the *Brassica* genus germplasm bank. The objective of this study was to identify sources of resistance via tolerance, antibiosis or antixenosis mechanisms to *D. radicum* in 56 local varieties of turnips, turnip tops and turnip greens. To this end, no-choice tests, searching for tolerance and antibiosis/antixenosis evidence, were performed under controlled conditions. The best accessions selected from this first screening were transplanted in the field and exposed to natural infestation of *D. radicum*.

Materials and methods

Plant material

Fifty-one local varieties of *Brassica rapa* subsp. *rapa* from Galicia (NW Spain) and five from Asturias (N Spain) including 22 turnips (the root is the edible part), 31 turnip greens (the leaves harvested in the vegetative period) and 3 turnip tops (the fructiferous stems with the flower buds and the surrounding leaves) and kept at the *Brassica* germplasm bank at the Misión Biológica de Galicia (MBG-CSIC), were used in this study. Plants were initially grown in glasshouse at 20 °C, under natural photoperiod and 80% RH for 40 days, in 8 × 8 × 8 cm plastic pots filled with *Sphagnum* peat (GRAMOFLOR GmbH & Co., Drepholzer, Germany). Regular manual watering (without fertilization), was adopted.

Insects

A laboratory culture of *D. radicum* was established in 2010 from a population collected in turnip crops at the Misión Biológica de Galicia (Salcedo, Pontevedra province, NW Spain, 42°24′N, 8°38′W) and used to provide eggs for artificial infestation. The cabbage fly larvae were reared on small pieces of fresh turnips, whereas the adults were fed with a mixture of brewer's yeast:honey:water (1:1:2). The insectaries (mesh cages 65 × 65 × 65 cm) were maintained at 19 ± 1 °C, 60 ± 5% of RH and a photoperiod of L16:D8. Males and females were kept together for mating. Female flies laid eggs around pieces of turnip placed in plastic Petri-dishes with damp filter paper on the bottom. Eggs were collected with a fine camel hair paint brush.

Laboratory experiment

From October 2010 to November 2011, 56 *B. rapa* local varieties were tested for resistance to *D. radicum* larvae attack by using a no-choice test. Ten plants per variety were randomly arranged in a climatic chamber

at 19 ± 1 °C, 60 ± 5% of RH and a photoperiod of L16:D8. The plants were inoculated with five *D. radicum* eggs (2–3 day old), when they had reached the 5–6 true leaf stage. The eggs were gently laid close the plant stem with a fine paint brush. Upon hatching, larvae were allowed to feed on the taproots. The plants were scored daily for symptoms of attack, such as leaf wilting and plant collapse (death). For each plant, the number of days without collapse (tolerance) was recorded as well as the survival rate per accession after 20 and 30 days from the infestation. During the experiment, the plants were watered as they needed for their maintenance in turgid conditions. The experimental unit was the plant.

The health status of the plants was checked twice, at 20 and 30 days after the infestation. Leaf wilting was evaluated by using a subjective rating scale from 1 to 5 points (1 = all the leaves are green and turgid; 2 = one leaf is wilted; 3 = the 50% of the leaves are wilted; 4 = more than 50% of the leaves are wilted; 5 = 100% of the leaves are wilted).The roots were carefully examined to determine the existence of feeding injury by using a rating scale from 1 to 5 points (1 = all the roots are healthy; 2 = the surface of the main root shows some feeding marks; 3 = the main root is injured and the secondary roots are scarce; 4 = the main root is seriously injured and the secondary roots are missing; 5 = the main root is dead, completely withered). At the end of experiment, 30 days after the infestation, plants were removed from the pots and the pupae per plant were scored and weighed to the nearest 0.1 mg with an electronic high precision balance (COBOS PrecisionAX 120). The plants that received the highest point at the rating scale for both leaves and roots were considered dead. Each variety was considered putatively resistant (via tolerance evaluation) when they satisfied all the following criteria: (1) a mean of 28–30 days without collapse, (2) more than 80% of survival plants at 30 days after infestation; (3) the average rating scale for leaves and roots ranged between 1 and 2 at 20 and 30 days after infestation. Those varieties which exhibited tolerance below the standards required were considered putatively susceptible. The existence of significant differences among the varieties was statistically assessed. Successively, the most representative, non-ambiguous, ten putatively resistant accessions along with ten susceptible ones (control group) were selected to confirm their resistance under field conditions and to investigate the existence of antixenosis/antibiosis elements.

Field experiment

Plants were initially grown in multi-pot trays in a greenhouse at 20 °C for 40 days under the above mentioned conditions. On September 2012, then they were transplanted into the field (Salcedo, Pontevedra province, NW Spain, 42°24′N, 8°38′W), under natural conditions, at the 5–6 true leaf stage. Soil at the experimental plots is acid (pH 5.3), with very high content of organic matter (6.6%), and mostly sandy-loam textures. During the experiment, from September 2012 to June 2013, the mean temperature was 11.5 ± 1 °C, with 83.4% of mean RH and 190.26 ± 33.3 mm of rain. Environmental parameters were obtained from an official climate station of the regional Government (Conselleria de Medio Ambiente, Xunta de Galicia). The varieties were evaluated in a randomized complete block design with two replications. Each experimental block consisted of twenty rows of 10 plants each (one variety per row, randomly assigned). Rows were spaced 0.8 m apart and plants within rows were spaced 0.5 m apart. No insecticide of fungicide was applied to the plants. On April 2013, root position in the soil was scored by using a rating scale from 1 to 5 points (1 = completely buried, 2 = mostly buried, 3 = half buried, 4 = largely above soil line, 5 = above soil line), root diameter was measured at widest point, root colour was evaluated (1 = white, 2 = purple), and plant stem diameter was measured at the base (IBPGR 1990). Measurements were done with a digital calliper. On June 2013, all the plants were collected and transported to the laboratory to assess the root damage as the number of galleries per root. It was assumed that each gallery referred to one larva, according to our previous observations during the *D. radicum* rearing. To assess the existence of antixenosis or antibiosis, all the larvae and pupae found in the roots and/or in the soil around the plant were counted and individually weighed.

Statistical analysis

The count data, such as the number of root galleries and pupae, were square root transformed prior the analysis of variance. Rating scales were transformed

as $\log_{10}(x + 1)$ prior to be subjected to the tests to stabilize the variance.

For the experiment developed in the climatic chamber, the existence of significant differences for the number of days without collapse (tolerance), pupae number (antixenosis) and pupal weight (antibiosis) among the 56 plant accessions (fixed factor) was obtained with a one-way ANOVA. The survival rate at 20 and 30 days after infestation was subjected to a Generalized Linear Model (GLM) with binomial distribution and logit link function, with main effect from the variety. Significant differences for leaves and roots damaged after 20 and 30 days among the varieties (fixed factor) by using a visual scale were evaluated with a Kruskal–Wallis one-way analysis of variance. When the putatively resistant (R) and susceptible (S) groups were constituted, the same statistical tests were repeated to assess the existence of significant differences within each group and between them.

For the field experiment, firstly we tested the existence of differences among the accessions within the R and S groups for root position, root colour, root diameter, plant diameter, number of galleries, pupae number and pupal weight (response variates) by using the ANOVA analysis. Successively, comparisons between R and S groups were done by using an unbalanced ANOVA. The means were separated by Fisher's least significant difference (LSD). Blocks were considered as random factor. Finally, to investigate the relationships between the agronomical characters and the indicators of *D. radicum* performance, such as the number of galleries (antixenosis), pupae number (antixenosis) and pupal weight (antibiosis) found within the R and S groups, a multiple regression analysis was performed.

Significance was declared at $P < 0.05$. Statistical tests were performed using the software GenStat12.1 (VSN International Ltd., Hemel Hempstead, UK).

Results

Laboratory experiment

The fifty-six tested varieties were significantly different for the number of days without collapse, the survival rate at 20 and 30 days, leaf damage at 20 and 30 days, root damage at 20 and 30 days, the number of retrieved pupae and pupal weight (Supplementary Table S1). Based on these data and on the criteria to evaluate the tolerance under controlled conditions, the plants were categorized into putatively resistant (R) and susceptible group (S). Ten, non-ambiguous, putatively resistant accessions were selected for the field experiment. Data showed significant differences between the R and S groups for all the variables, with the exception of the pupal weight (Table 1). In addition, within the R group, the accessions performed similarly, without differences for tolerance or survival rate, whereas within the S group, there were significant differences for all the tested variables (Table 1).

Field experiment

The comparisons among the accessions within the R and S groups showed the existence of significant differences for all the studied variables (Table 2). In particular, within the R group, the accessions MBGBR0178, MBGBR0570 and MBGBR0371, stand out for the low number of galleries (Table 2; Fig. 1).

When the R and S groups were compared, it was found that the mean number of galleries per plant (2.12 ± 0.23) was significantly lower in the first group than in the second one (4.15 ± 0.37) (Table 2) and the mean number of pupae collected per plant was significantly higher in the S group (0.49 ± 0.10 and 1.38 ± 0.26, respectively) (Table 2; Fig. 2). The pupal weight did not vary between resistant (8.09 ± 0.67 mg) and susceptible plants (9.3 ± 0.34 mg) (Table 2; Fig. 2). Root diameter, root position, root colour and plant diameter were significantly different between R and S group. The putatively resistant plants had in general smaller size, smaller and mostly buried roots and the proportion of white roots was higher than in the susceptible group (94 and 64%, respectively) (Table 2; Fig. 2).

The proportion of successfully developing larvae (i.e. the ratio between the pupae number found per plant and the number of galleries) should account for antibiosis to *D. radicum*, although these data should be taken with caution because in the field many other factors could lead to pupal mortality. However, for both R and S groups, the result was similar (31 and 31.6%, respectively). The existence of a relationship between pupae number and pupal weight could account for the presence of antibiosis mechanism

Table 1 Mean values ± SD of the putatively resistant (R) and susceptible (S) varieties (N = 10 plants per accession) subjected to infestation of five *D. radicum* eggs per plant in the climatic chamber and observed during 30 days

Groups	Plant accession number	Days without collapse	Pupae/plant	Pupal weight/plant (mg)	% survival (20 days)	% survival (30 days)	Leaf status (20 days)	Leaf status (30 days)	Root status (20 days)	Root status (30 days)
R	MBGBR 0140	30 ± 0.00	1.50 ± 0.27	8.91 ± 1.22	100 ± 0	100 ± 0	2.10 ± 0.31	2.31 ± 0.30	1.90 ± 0.23	2.42 ± 0.27
R	MBGBR 0154	30 ± 0.00	0.91 ± 0.38	6.76 ± 0.58	100 ± 0	90 ± 10	1.30 ± 0.21	1.81 ± 0.44	1.20 ± 0.13	1.70 ± 0.40
R	MBGBR 0163	30 ± 0.00	2.60 ± 0.43	7.81 ± 0.74	100 ± 0	100 ± 0	1.00 ± 0.00	2.50 ± 0.27	2.20 ± 0.36	2.80 ± 0.44
R	MBGBR 0173	30 ± 0.00	2.20 ± 0.20	6.30 ± 0.21	100 ± 0	100 ± 0	2.80 ± 0.20	2.90 ± 0.18	1.50 ± 0.16	1.80 ± 0.20
R	MBGBR 0178	30 ± 0.00	2.40 ± 0.43	6.5 ± 0.18	90 ± 0	90 ± 10	2.40 ± 0.34	2.80 ± 0.39	2.00 ± 0.39	2.50 ± 0.40
R	MBGBR 0183	30 ± 0.00	0.90 ± 0.31	6.70 ± 0.11	100 ± 0	100 ± 0	2.10 ± 0.10	2.12 ± 0.10	1.71 ± 0.30	1.71 ± 0.30
R	MBGBR 0194	30 ± 0.00	1.00 ± 0.37	9.30 ± 0.88	100 ± 0	100 ± 0	1 ± 0.00	1.73 ± 0.30	1.51 ± 0.17	1.71 ± 0.30
R	MBGBR 0371	28.10 ± 1.51	2.81 ± 0.33	5.18 ± 1.37	90 ± 13	90 ± 13	1.81 ± 0.53	2.20 ± 0.51	2.40 ± 0.50	2.50 ± 0.48
R	MBGBR 0469	29.10 ± 0.90	1.53 ± 0.37	8.67 ± 1.87	90 ± 10	90 ± 10	1.40 ± 0.40	2.70 ± 0.30	2.00 ± 0.39	2.32 ± 0.40
R	MBGBR 0570	28.10 ± 2.90	2.51 ± 0.37	8.81 ± 1.14	90 ± 10	90 ± 10	1.60 ± 0.40	1.70 ± 0.40	2.30 ± 0.34	2.43 ± 0.34
P-values		P = 0.518	P < 0.001	P = 0.062	P = 0.402	P = 0.570	P < 0.001	P = 0.049	P = 0.152	P = 0.049
S	MBGBR 0571	25 ± 3.33	2.10 ± 0.38	11.51 ± 0.76	80 ± 13	80 ± 13	2.00 ± 0.52	2.60 ± 0.40	2.40 ± 0.45	2.40 ± 0.45
S	MBGBR 0581	26.8 ± 2.31	2.50 ± 0.45	9.20 ± 1.12	80 ± 13	80 ± 13	2.40 ± 0.37	2.81 ± 0.42	2.35 ± 0.42	2.70 ± 0.40
S	MBGBR 0104	26.6 ± 2.27	1.00 ± 0.21	7.76 ± 0.75	80 ± 13	80 ± 13	1.80 ± 0.53	2.31 ± 0.47	2.55 ± 0.45	2.44 ± 0.48
S	MBGBR 0124	19.5 ± 3.45	1.10 ± 0.35	6.83 ± 0.64	40 ± 16	30 ± 15	3.71 ± 0.60	3.81 ± 0.61	3.51 ± 0.62	3.86 ± 0.61
S	MBGBR 0215	25 ± 3.33	2.00 ± 0.47	7.01 ± 0.23	80 ± 13	80 ± 13	1.80 ± 0.53	2.50 ± 0.45	2.80 ± 0.44	2.64 ± 0.48
S	MBGBR 0232	5.50 ± 1.50	3.31 ± 0.52	6.36 ± 0.92	0 ± 0	0 ± 0	5.00 ± 0.00	5.00 ± 0.00	5.00 ± 0.00	5.00 ± 0.00
S	MBGBR 0288	24.31 ± 2.90	2.71 ± 0.40	7.50 ± 0.23	70 ± 15	70 ± 15	2.31 ± 0.60	2.53 ± 0.56	2.94 ± 0.48	2.96 ± 0.48
S	MBGBR 0433	29.60 ± 0.40	3.24 ± 0.47	8.10 ± 0.70	90 ± 10	90 ± 10	2.40 ± 0.37	3.00 ± 0.26	3.10 ± 0.38	3.00 ± 0.37
S	MBGBR 0451	22.52 ± 3.82	2.81 ± 0.40	11.03 ± 0.77	90 ± 10	90 ± 10	2.20 ± 0.47	2.75 ± 0.34	2.35 ± 0.40	2.60 ± 0.31
S	MBGBR 0485	26.41 ± 1.83	3.00 ± 0.42	11.09 ± 1.09	70 ± 15	70 ± 15	2.70 ± 0.54	2.80 ± 0.51	3.33 ± 0.40	3.40 ± 0.37
P-values		P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001	P < 0.001
P-values (R/S)		P = 0.002	P = 0.012	P = 0.198	P = 0.017	P < 0.001	P < 0.001	P = 0.003	P < 0.001	P < 0.001

The number of days without collapse (tolerance), pupae number and pupal weight, and the proportion of the survived plants after 20 and 30 days were recorded. The health status of the leaf was checked at 20 and 30 days after infestation by using a subjective 1–5 points rating scale (1 = all the leaves are green and turgid, 2 = one leaf is wilt; 3 = a half of the leaves are wilt; 4 = more than a half of the leaves are wilt; 5 = all the leaves are wilt). Feeding-injury on the roots was evaluated at 20 and 30 days by using a 1–5 points rating scale (1 = all the roots are healthy; 2 = the surface of the main root has some feeding marks; 3 = the main root is injured and the secondary roots are scarce; 4 = the main root is seriously injured and the secondary roots are missing; 5 = the main root is dead, completely withered). P-values = statistical differences within resistant (R) and susceptible (S) groups. P values (R/S) = statistical differences between resistant (R) and susceptible (S) groups

Table 2 Mean values ± SD for the number of pupae, pupal weight, and the mean number of galleries retrieved from the selected accessions categorized as resistant (R) and susceptible (S), tested under field conditions after natural *D. radicum* infestation

Groups	Plant accession number	Pupae/plant	Pupal weight/plant (mg)	Galleries/plant	Root diameter (mm)	Root position (1–5)	Root colour (1–2)	Stem diameter (mm)
R	MBGBR 0140	0.05 ± 0.22	11.20 ± 0.00	1.84 ± 2.04	19.55 ± 6.06	3.79 ± 0.71	1.00 ± 0.00	14.84 ± 3.70
R	MBGBR 0154	1.40 ± 2.01	8.36 ± 3.52	2.00 ± 3.04	26.07 ± 8.06	2.50 ± 1.00	1.05 ± 0.22	21.57 ± 7.15
R	MBGBR 0163	0.68 ± 1.11	7.63 ± 3.47	2.74 ± 2.30	23.35 ± 6.92	1.95 ± 0.70	1.10 ± 0.32	16.52 ± 5.93
R	MBGBR 0173	0.50 ± 1.24	10.49 ± 4.11	2.25 ± 2.17	24.74 ± 7.04	1.80 ± 0.83	1.00 ± 0.00	19.57 ± 6.38
R	MBGBR 0178	0.29 ± 0.77	9.10 ± 2.55	0.88 ± 1.83	32.68 ± 13.33	3.94 ± 1.03	1.06 ± 0.24	17.55 ± 5.13
R	MBGBR 0183	0.73 ± 1.52	8.23 ± 4.93	1.37 ± 3.09	33.37 ± 10.93	3.26 ± 0.81	1.00 ± 0.00	16.11 ± 4.34
R	MBGBR 0194	0.25 ± 0.78	7.08 ± 4.54	2.30 ± 2.38	22.73 ± 7.65	2.65 ± 0.81	1.00 ± 0.00	13.73 ± 4.32
R	MBGBR 0371	0.10 ± 0.44	9.45 ± 2.33	0.55 ± 1.28	26.02 ± 13.49	2.80 ± 1.15	1.00 ± 0.00	19.07 ± 6.95
R	MBGBR 0469	0.80 ± 3.05	5.27 ± 4.97	1.58 ± 2.18	45.37 ± 22.31	2.83 ± 1.20	1.5 ± 0.51	23.00 ± 10.34
R	MBGBR 0570	0.26 ± 0.93	9.76 ± 6.47	0.84 ± 1.46	41.65 ± 13.94	2.32 ± 0.75	1.31 ± 0.48	19.87 ± 4.40
Mean values		0.49 ± 0.10	9.3 ± 0.34	2.12 ± 0.23	29.75 ± 1.01	2.88 ± 0.08	1.09 ± 0.02	19.49 ± 0.62
P-values		$P = 0.010$	$P < 0.001$	$P = 0.009$	$P < 0.001$	$P < 0.001$	$P < 0.001$	$P < 0.001$
LSD		0.1350	0.2740	0.2059	7.5460	0.0724	0.0293	3.924
S	MBGBR 0571	2.10 ± 3.19	8.32 ± 5.10	5.40 ± 5.19	68.56 ± 25.03	3.47 ± 1.12	1.74 ± 0.45	26.60 ± 11.07
S	MBGBR 0581	0.65 ± 1.87	5.18 ± 4.80	2.44 ± 2.28	71.31 ± 22.62	3.60 ± 1.14	1.55 ± 0.51	17.13 ± 5.38
S	MBGBR 0104	1.2 ± 2.57	5.93 ± 3.60	1.71 ± 3.00	20.50 ± 4.02	3.71 ± 0.82	1.00 ± 0.00	17.14 ± 5.48
S	MBGBR 0124	1.50 ± 3.19	9.14 ± 6.20	5.71 ± 5.91	46.65 ± 21.99	3.36 ± 0.79	1.59 ± 0.50	21.77 ± 10.76
S	MBGBR 0215	0.11 ± 0.33	11.85 ± 0.00	2.28 ± 4.42	30.46 ± 7.02	2.00 ± 0.50	1.00 ± 0.00	17.98 ± 7.10
S	MBGBR 0232	1.20 ± 2.59	9.38 ± 2.20	6.44 ± 6.51	33.89 ± 12.76	3.00 ± 0.86	1.25 ± 0.44	24.20 ± 9.68
S	MBGBR 0288	0.10 ± 0.48	15.36 ± 0.00	1.29 ± 1.62	33.48 ± 12.43	3.65 ± 0.87	1.95 ± 0.22	17.07 ± 9.12
S	MBGBR 0433	4.27 ± 6.52	9.12 ± 4.21	9.33 ± 5.92	38.13 ± 10.36	3.06 ± 1.05	1.00 ± 000	48.68 ± 10.04
S	MBGBR 0451	3.10 ± 5.84	7.34 ± 5.61	8.74 ± 8.10	69.46 ± 23.52	3.45 ± 0.88	1.00 ± 0.00	36.48 ± 15.93
S	MBGBR 0485	0.71 ± 2.02	7.23 ± 8.82	2.87 ± 2.90	47.75 ± 24.94	3.06 ± 1.14	1.29 ± 0.47	31.83 ± 22.10
Mean values		1.38 ± 0.26	8.09 ± 0.67	4.15 ± 0.37	44.34 ± 1.73	3.26 ± 0.08	1.33 ± 0.03	24.16 ± 1.02
P-values		$P < 0.001$	$P = 0.011$	$P < 0.001$	$P < 0.001$	$P = 0.002$	$P < 0.001$	$P < 0.001$
LSD		0.2283	0.3079	0.2948	13.21	0.07421	0.0447	8.563
P-values (R/S)		$P = 0.005$	$P = 0.904$	$P < 0.001$	$P < 0.001$	$P < 0.012$	$P < 0.001$	$P < 0.001$

Table 2 continued

Groups	Plant accession number	Pupae/plant	Pupal weight/plant (mg)	Galleries/plant	Root diameter (mm)	Root position (1–5)	Root colour (1–2)	Stem diameter (mm)
LSD (R/S)		0.0593	0.0954	0.0827	4.120	0.2285	0.0145	2.425

Root position was assessed by using a 1–5 points rating scale (1 = completely buried, 2 = mostly buried, 3 = half buried, 4 = largely above soil line, 5 = above soil line), root diameter was measured at widest point, plant diameter at the basis, and root colour by a 1–2 points rating scale (1 = white, 2 = purple). P-values = statistical differences within resistant (R) and susceptible (S) groups. P values (R/S) = statistical differences between resistant (R) and susceptible (S) groups. LSD = Fisher's least significant differences

through larval competition for the resources. By using a linear regression analysis, we found that a significant and negative relationship does exist only among the R accessions ($F < 0.001$, $r = -0.41$).

The accessions of the R group, showed significant and positive correlations between plant diameter and pupae number ($P = 0.001$, $r = 0.45$), root colour and pupae number ($P = 0.020$, $r = 0.49$) and root colour and pupal weight ($P = 0.007$, $r = 0.48$), which indicates that purple roots had a larger number of pupae with higher body weight. Among the S accessions, a similar trend was found for the correlation between plant diameter and pupae number ($P = 0.001$, $r = 0.52$), root colour and pupae number ($P = 0.020$, $r = 0.45$) and root colour and pupal weight ($P = 0.007$, $r = 0.49$). In addition, plant diameter ($P = 0.048$, $r = 0.54$) and root position ($P = 0.025$, $r = 0.49$) did account for the higher number of galleries among the susceptible plants.

Discussion

Knowledge of mechanisms of host plant resistance to insect pests is a crucial first step in developing insect resistant cultivars. Indeed, the combination of more elements of resistance is highly desirable because it ensure a good control of a resident pest population. The existence of both antixenosis and antibiosis increase the probability of a long-lasting resistance to insect herbivores, in comparison with antibiosis or antixenosis alone (Jyoti et al. 2001). However, the relative importance of antibiosis and antixenosis may depend also on the type of herbivore (generalist vs. specialist) and the lifetime of the plant. Generalist herbivore are not always able to make the optimal plant choice. Also, if the plant live longer than the generation time of the herbivore, antibiosis gains more importance than antixenosis because the initial plant choice become less significant (Stenberg and Muola 2017). It is well known that environmental conditions can affect the outcome of evaluations aimed at identifying insect resistant varieties, and especially when natural infestation is used one runs the risk of susceptible plants escaping infestation. To prevent this, we firstly used a no-choice test to eliminate the obviously susceptible accessions. Plant performance observed in the field, especially among the putatively resistant accessions, mostly agreed with the results

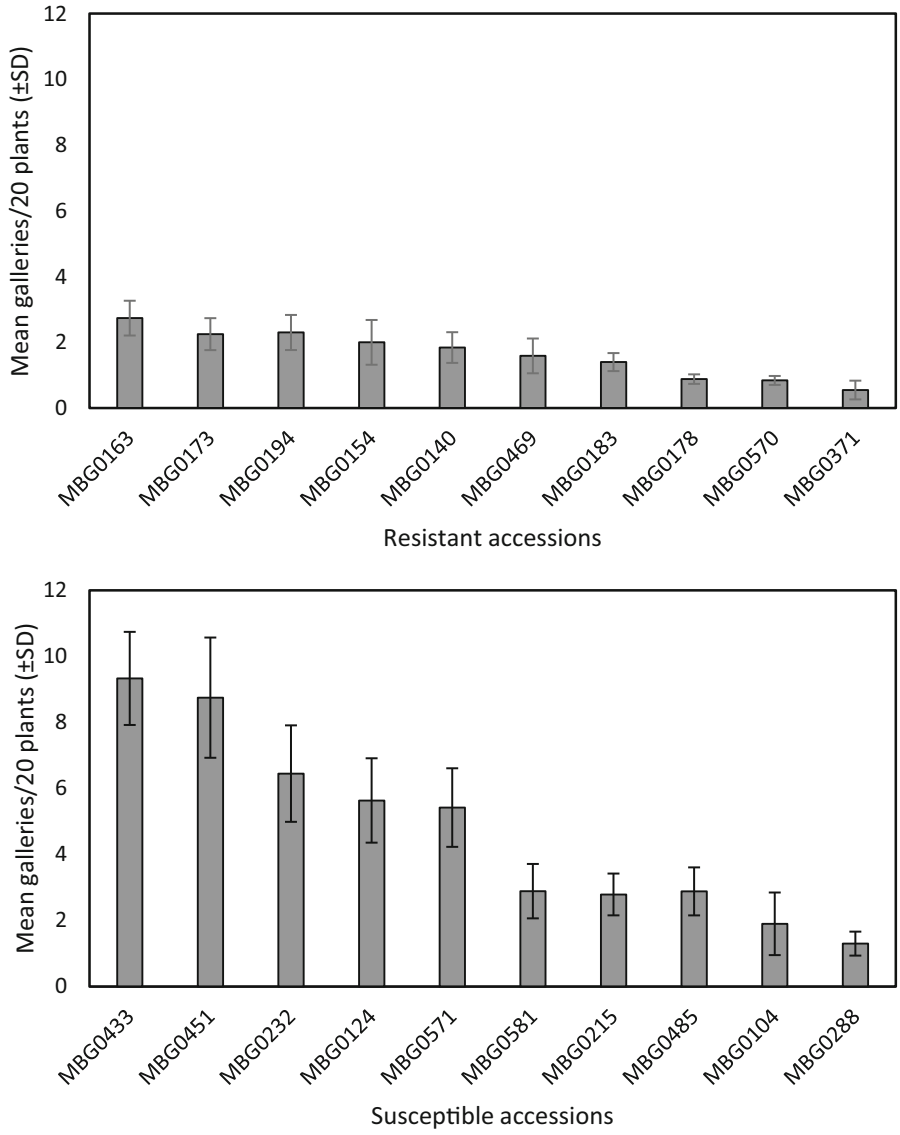

Fig. 1 Mean number of galleries per plant of putatively resistant and susceptible accessions subjected to *D. radicum* attack in the field

obtained under controlled conditions by *D. radicum* egg infestation, which shows that the adopted indicators of plant resistance, such as plant tolerance, survival rate, leaf wilting and collapse, and root damages were effective.

Antibiotic effect on insect herbivores could be due to single or multiple traits including low nutritional value of the host plant, the presence of biologically active inhibitory plant chemicals or morphological traits. Antibiosis typically increases mortality or, in alternative, surviving individuals may experience small body size, low weight, prolonged developmental period, and low female fecundity (Mithöfer and Boland 2012). We did not find evidence of antibiosis effect on the pupal weight under controlled conditions and in the field. Nonetheless, the lower pupae number found among the putatively resistant accessions subjected to the no-choice test may indicate certain level of antibiosis/antixenosis, for example through reduced feeding efficiency or plant palatability (Mitchell et al. 2016). In the field, where the plants were exposed to natural infestation, the scarce number of pupae retrieved from resistant accessions could indicate the existence of both antibiosis and antixenosis elements, possibly through increased larval mortality and low attractiveness to egg laying. The existence of a

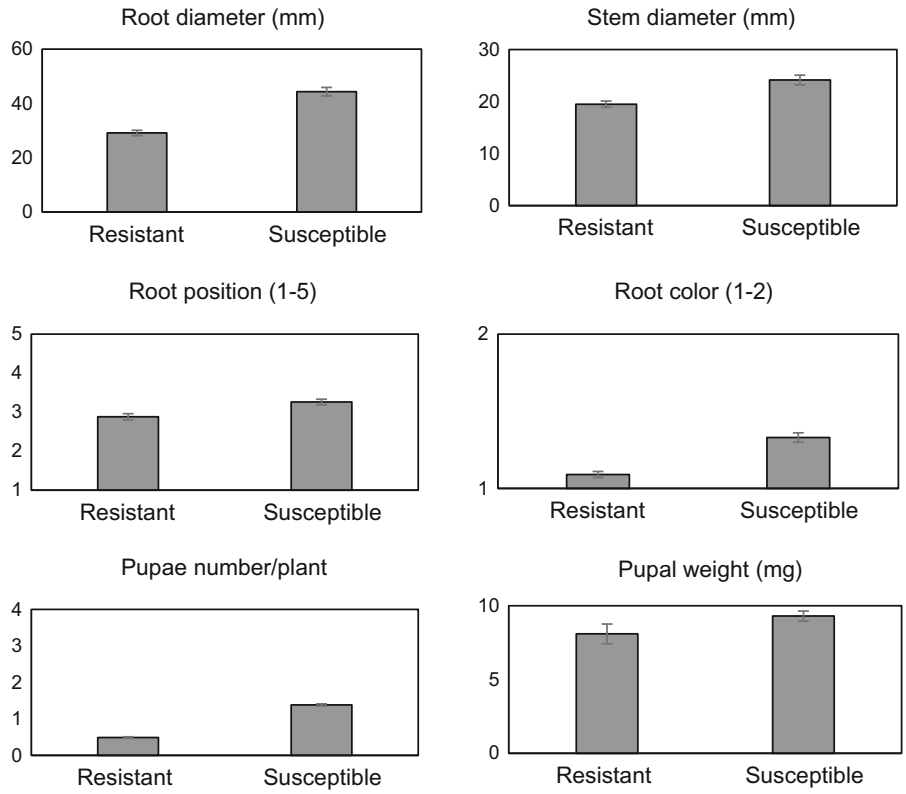

Fig. 2 Mean values of root diameter at the widest point, plant diameter, root position in the soil, root colour, number of pupae and pupal weight of resistant (N = 20 plants/accession) and susceptible (N = 20 plants/accession) plants subjected to *D. radicum* attack in the field. Root position in the soil was described by using a 1–5 points rating scale (1 = completely buried, 2 = mostly buried, 3 = half buried, 4 = largely above soil line, 5 = above soil line). Root colour was described as 1 = white, 2 = purple. Error bars mean SD

negative relationship between pupae number and pupal weight among the resistant accessions, suggests the existence of a mechanism of antibiosis, possibly through larval competition for the resources. Anyway, precaution should be adopted in the interpretation of this result from the field, because the immature stages of the cabbage root fly may suffer certain rate of mortality due to soil conditions, drought or flooding, and predator or parasitoid attack. Indeed, for the future, the use of other insect traits primarily related to antibiosis, such as egg-to adult development time and the proportion of the enclosed flies should provide more reliable results (Shuhang et al. 2016). Actually, the scarce evidence of resistance based on antibiosis mechanisms among our accessions was expected because of this kind of resistance to *D. radicum* among *Brassica* crops is very low in comparison to wild *Brassica* species (Ellis et al. 1999; Jensen et al. 2002; Felkl et al. 2005; Shuhang et al. 2016).

D. radicum larvae feeding usually damage the tissue of the root epidermis and phloem and xylem parenchyma, provoking plant wilting and collapse. We did not check for such symptoms among the plants in the field as a measure of tolerance, as we did in the climatic chamber, because under natural conditions it should be caused by several other biotic and abiotic factors (Shuhang et al. 2016). However, at the end of the field experiment the 9% of the putatively resistant plants died, in contrast to the 18% for the susceptible ones. Resistant varieties had in the field a significantly small number of root injuries by *D. radicum* than the susceptible ones. Dosdall et al. (1994) showed that root damage is generally correlated with oviposition rate, which imply that the mechanism of resistance by brassicaeous plants to *D. radicum* is mainly by antixenosis or non-preference mechanisms.

Antixenosis is characterized by the presence of morphological or chemical plant factors that significantly alter insect behaviour and the selection of the host plant. This may depend to morphological characters that create physical barriers to pest attachment, feeding and oviposition, such as glandular trichomes or leaf waxes, or to the presence of chemicals that repel insect from oviposition and larval feeding (Jyoti et al. 2001; Mitchell et al. 2016). The study of turnip agronomical characters revealed significant

differences within and between R and S group. Because plants tested belong to the same plant species, we avoided differences due to different leaf and root morphology and/or plant phenology. The resistant accessions had a smaller, white, mostly buried root, and lower plant diameter in comparison to susceptible varieties, which implies that these agronomic traits may protect the plants to the cabbage root fly attack. Multiple regression analyses showed that larger plants and purple roots were mostly preferred for egg laying, because they harboured a significant higher number of pupae in both R and S groups. Host plant finding for oviposition by *D. radicum* female is mainly based on visual cues, such as leaf colour, plant shape and size, on the detection of host-finding cues such as isothiocyanates and on oviposition stimulant such as sinigrin (Nottingham 1988; Städler and Schöni 1990; Baur et al. 1996; Roessingh et al. 1997). Further investigation should be directed to assess whether biochemical differences between white and purple root does exist. Three turnip varieties from the putatively resistant group (MBGBR0178, MBGBR0570 and MBGBR0371), stand out for resistance to *D. radicum* through antixenosis mechanisms, because they had the lowest number of galleries per plant. Selection of the most resistant individuals within these accessions could provide the better candidates for a breeding programme against the cabbage root fly.

To conclude, the present study represents a first approach to find *B. rapa* subs. *rapa* local varieties that represent a potential source of desirable traits in order to develop a resistance breeding programme against the cabbage root fly. Several accessions tested in this work are promising genotypes and should be deeply investigated to unravel the genetics of the resistance and for identification of repellent or deterrent factors which interfere with oviposition stimulants. In addition, glucosinolate content and root sugar content, particularly sucrose, which is an important insect phagostimulants (Hopkins et al. 1999), should be also quantified in the selected varieties, unveiling whether biochemical contents of purple root may differ from the white roots.

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