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Using plant chemistry and insect preference to study the potential of *Barbarea* (Brassicaceae) as a dead-end trap crop for diamondback moth (Lepidoptera: Plutellidae)

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ABSTRACT

Barbarea vulgaris R. Br. has been proposed as a dead-end trap crop for diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae), because its larvae do not survive on this plant species despite being highly preferred for oviposition. We compared plants of several species, varieties, and types in the genus *Barbarea* (Brassicaceae) to study their potential as trap crops for *P. xylostella*. In terms of insect behavior, *Barbarea* plants were assessed based on the criteria of high oviposition preference by *P. xylostella* moths (compared to other *Barbarea* plants and to three *Brassica oleracea* L. crop varieties) and low survival of *P. xylostella* larvae. *Barbarea* plants were also assessed based on the criteria of high content of glucosinolates, which stimulate adult oviposition and larval feeding in *P. xylostella*, and high content of saponins, which are detrimental to survival of *P. xylostella* larvae. All *Barbarea* plants tested were preferred over cabbage by ovipositing *P. xylostella*. Among *Barbarea* plants, few significant differences in oviposition preference by *P. xylostella* were found. Ovipositing *P. xylostella* preferred *B. vulgaris* plants containing mainly 2-phenylethylglucosinolate over *B. vulgaris* plants containing mainly (*S*)-2-hydroxy-2-phenylethylglucosinolate, and P-type *B. vulgaris* var. *arcuata* plants over *Barbarea rupicola* and *B. vulgaris* var. *variegata* plants. Despite containing a lower content of saponins than other *Barbarea* plants tested, *Barbarea verna* did not allow survival of *P. xylostella* larvae. Our studies show that, except for *B. rupicola* and P-type *B. vulgaris* var. *arcuata*, which allowed survival of *P. xylostella* larvae, all *Barbarea* plants tested have potential as dead-end trap crops for *P. xylostella*.

Introduction

The diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae), is considered one the most damaging insect pests of cruciferous crops throughout the world (Furlong et al., 2013; Zalucki et al., 2012). The ability of *P. xylostella* to develop resistance to insecticides, combined with general environmental and health concerns, have stimulated interest in developing alternative management techniques such as trap crops (Shelton and Badenes-Perez, 2006). One of the plant species proposed as a trap crop for *P. xylostella* is wintercress, *Barbarea vulgaris* R. Br. (Brassicaceae) (Badenes-Perez et al., 2004, 2005b; Idris and Grafius, 1994, 1996; Lu et al., 2004; Shelton and Nault, 2004), a biennial or short-lived perennial plant that occurs in temperate regions worldwide (MacDonald and Cavers, 1991; Uva et al., 1997). Given the choice between *B. vulgaris* and various cruciferous crops, *P. xylostella* greatly prefers to oviposit on *B. vulgaris*, even though its larvae do not survive on it (Badenes-Perez et al., 2004; Lu et al., 2004; Shelton and Nault, 2004). Trap crops like *B. vulgaris*, which are highly attractive to insects, but on which they cannot survive, are known as dead-end trap crops (Shelton and Badenes-Perez, 2006; Shelton and Nault, 2004). The resistance of *B. vulgaris* to *P. xylostella* is caused by the triterpenoid saponins 3-*0*-*β*-cellobiosylhederagenin (saponin 1) and 3-*0*-*β*-cellobiosyloleanolic acid (saponin 2), which act as feeding deterrents or are correlated with deterrency (Agerbirk et al., 2003a; Badenes-Perez et al., 2010; Shinoda et al., 2002) in *P. xylostella* larvae. The ability of saponins to permeate the cell membrane and to induce apoptosis also makes them cytotoxic to lepidopteran cells (De Geyter et al., 2012).

Barbarea vulgaris var. *arcuata* has been shown to have two morphologically-distinct forms, G and P, which have hairless (Glabrous) and hairy (Pubescent) leaves, respectively, differ in the content of glucosinolates and saponins, and are, genetically,

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strongly divergent (Agerbirk et al., 2003a, 2001; Augustin et al., 2012; Hauser et al., 2012; Kuzina et al., 2009, 2011; Nielsen et al., 2010a). G-type *B. vulgaris* var. *arcuata* contains saponins 1 and 2 and does not allow survival of *P. xylostella* larvae (Agerbirk et al., 2003a; Badenes-Perez et al., 2010). P-type *B. vulgaris* var. *arcuata* does not contain saponins 1 and 2, although it contains other saponins (Kuzina et al., 2011), and allows survival of *P. xylostella* larvae (Agerbirk et al., 2003a; Badenes-Perez et al., 2010). *B. vulgaris* var. *variegata* also contains saponins 1 and 2, which makes this variety resistant to *P. xylostella* (Badenes-Perez et al., 2011; Shinoda et al., 2002). Within *B. vulgaris*, two different chemotypes that are morphologically indistinguishable have also been found (van Leur et al., 2006). BAR- and NAS-type *B. vulgaris* plants have (*S*)-2-hydroxy-2-phenylethylglucosinolate (S2OH2PE, glucobarbarin) and 2-phenylethylglucosinolate (2PE, gluconasturtiin), respectively, as their main glucosinolates (van Leur et al., 2006). The preference and performance of insects on BAR- and NAS-type *B. vulgaris* has been tested with the crucifer specialists *Pieris rapae* L. (Lepidoptera: Pieridae) and *Delia radicum* L. (Diptera: Anthomyiidae), and with the generalist *Mamestra brassicae* L. (Lepidoptera: Noctuidae) (van Leur et al., 2008a,b). Significant differences have been found in the performance of these insects, which performed better either on BAR-type (*D. radicum*) or on NAS-type plants (*M. brassicae*) (van Leur et al., 2008a,b). It is not known if there are differences in the content of saponins in BAR- and NAS-type plants and if these two chemotypes could differ in the preference and performance of *P. xylostella*.

Saponins 1 and 2 are also responsible for the resistance of G-type *B. vulgaris* var. *arcuata* to larvae of the flea beetle *Phyllotreta nemorum* L. (Coleoptera: Chrysomelidae) (Kuzina et al., 2009; Nielsen et al., 2010a), which is another insect specialized on glucosinolate containing-plants (Nielsen, 1977, 1978). In G-type *B. vulgaris* var. *arcuata*, the genes for resistance to *P. nemorum* and saponin production seem to be the same (Kuzina et al., 2011). Besides G-type *B. vulgaris* var. *arcuata*, full resistance to *P. nemorum* has been found in *B. vulgaris* var. *vulgaris*, while partial resistance has been found in *B. verna* (Mill.) Asch. and *B. intermedia* Boreau (Agerbirk et al., 2003b). Analysis of the genetic relatedness between G- and P-type *B. vulgaris* var. *arcuata* and *B. verna* has shown more relatedness between G-type *B. vulgaris* var. *arcuata* and *B. verna* than between between G- and P-type *B. vulgaris* var. *arcuata* (Toneatto et al., 2012). The similarity in the resistance mechanism to *P. nemorum* and to *P. xylostella* suggests that other *Barbarea* spp. resistant to *P. nemorum* could also be resistant to *P. xylostella*.

Using a *Barbarea* plant that is very attractive to *P. xylostella* and, additionally, has a high content of saponins 1 and 2, is crucial to ensure its effectiveness as a dead-end trap crop. Here we compare different *Barbarea* spp., varieties, and types to test which ones could have the highest potential as a dead-end trap crop for *P. xylostella*. The *Barbarea* spp. tested were *B. rupicola* Moris, *B. verna*, and *B. vulgaris*. Two varieties of *B. vulgaris* were tested, *B. vulgaris* var. *arcuata* and *B. vulgaris* var. *variegata*. Within *B. vulgaris* var. *arcuata*, we tested G- and P-type plants. We also tested BAR- and NAS-type *B. vulgaris* plants. Larval survival and oviposition preference for *P. xylostella* was compared among these *Barbarea* lines and between three crucifer crops (cabbage, *Brassica oleracea* L. var. *capitata*, broccoli, *B. oleracea* var. *italica*, and Chinese cabbage, *B. rapa* L. var. *pekinensis*). For each plant type and treatment, we also determined the content of glucosinolates and saponins 1 and 2. Since some differences in glucosinolate content and herbivory by *P. nemorum* have been found between *Barbarea* spp. collected at different locations (Agerbirk et al., 2003b; Hauser et al., 2012), additional larval survival and two-choice oviposition tests with *P. xylostella* were conducted with plants of the same type (G and P) collected from different locations in Denmark, Germany, and the US.

Results

Analysis of glucosinolates and saponins in foliage of Barbarea spp., varieties, and types

The glucosinolates found in the plants analyzed are shown on Table 1. The glucosinolate profiles were consistent with those recorded in previous studies of *Barbarea* (Agerbirk et al., 2001; Badenes-Perez et al., 2011; van Leur et al., 2006). The dominant glucosinolates were 2PE in *B. rupicola*, *B. verna* and NAS-type *B. vulgaris*; S2OH2PE in G-type *B. vulgaris* var. *arcuata*, *B. vulgaris* var. *variegata* and BAR-type *B. vulgaris*; and (*R*)-2-hydroxy-2-phenylethylglucosinolate (R2OH2PE, glucosibarin) in P-type *B. vulgaris* var. *arcuata*. Comparison of the total glucosinolate content among *B. rupicola*, *B. verna*, G- and P-type *B. vulgaris* var. *arcuata*, *B. vulgaris* var. *variegata*, and BAR- and NAS-type *B. vulgaris* plants showed statistically significant differences ($F_{6,95} = 8.44$; $P \leqslant 0.001$) (Fig. 1). Plants of G-type *B. vulgaris* var. *arcuata* and NAS-type *B. vulgaris* had lower glucosinolate content than the other *Barbarea* plants analyzed ($P \leqslant 0.05$). The highest glucosinolate content of all plants analyzed was in *B. rupicola*, which had significantly higher glucosinolate content than G-type *B. vulgaris* var. *arcuata*, *B. vulgaris* var. *variegata*, and BAR- and NAS-type *B. vulgaris* ($P \leqslant 0.05$). There were also significant differences in individual glucosinolate content among plants ($P \leqslant 0.001$). The highest content of R2OH2PE was found in P-type *B. vulgaris* var. *arcuata*; the highest content of S2OH2PE was found in *B. vulgaris* var. *variegata* and BAR-type *B. vulgaris*; the highest content of indol-3-ylmethylglucosinolate was found in BAR- and NAS-type *B. vulgaris*; and the highest contents of 2PE and 4-methoxyindol-3-ylmethylglucosinolate were found in *B. rupicola* and *B. verna*. G-type *B. vulgaris* var. *arcuata* plants from Svebølle had lower glucosinolate content (23.4 ± 1.2, as mean ± SE μmol/g of plant dry weight) than G-type plants from Blaufelden-Raboldshausen (39.3 ± 2.6 μmol/g of plant dry weight), Suserup (33.5 ± 3.9 μmol/g of plant dry weight), and Ithaca (32.5 ± 1.5 μmol/g of plant dry weight) ($F = 8.67$; df = 3, 10; $P \leqslant 0.001$). There were no significant differences in total glucosinolate content among G- and P-type *B. vulgaris* var. *arcuata* plants from Blaufelden-Raboldshausen (1.5 ± 0.2, as mean ± SE μmol/g of plant fresh weight), Jena (1.3 ± 0.2 μmol/g of plant fresh weight), Store Vildmose (1.8 ± 0.2 μmol/g of plant fresh weight), and Tissø (1.8 ± 0.3 μmol/g of plant fresh weight) ($F_{3,18} = 1.05$; $P = 0.395$).

Comparison in the content of saponins among the different *Barbarea* spp., varieties, and types showed statistically significant differences for both saponin 1 ($F_{5,42} = 43.47$; $P \leqslant 0.001$) and saponin 2 ($F_{5,42} = 33.09$; $P \leqslant 0.001$) (Fig. 2). We did not find saponins 1 and 2 in P-type *B. vulgaris* var. *arcuata*. There were no significant differences in content of saponins 1 and 2 among G-type *B. vulgaris* var. *arcuata*, BAR- and NAS-type *B. vulgaris* plants ($P > 0.05$), but these *B. vulgaris* plants contained more than 3 times higher content of saponin 1 and more than 50 times higher content of saponin 2 than *B. rupicola* and *B. verna* ($P \leqslant 0.05$). *B. verna* contained approximately 15 times more saponin 1 than *B. rupicola* ($P \leqslant 0.05$). *B. rupicola* did not contain any detectable amount of saponin 2 and *B. verna* contained only traces of it (less than 0.1 μmol/g of plant dry weight).

Oviposition preference of P. xylostella among different Barbarea spp., varieties, types, and locations

In terms of oviposition preference indexes for the different *Barbarea* plants tested, there were no significant differences among them when compared with cabbage ($F_{6,35} = 0.50$, $P = 0.804$), broccoli ($F_{3,16} = 1.55$, $P = 0.240$), and Chinese cabbage, ($F_{3,16} = 0.21$, $P = 0.885$). The *Barbarea* plants tested were preferred