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Assessment of *Sinapis alba*, *Brassica napus* and *S. alba* × *B. napus* hybrids for resistance to cabbage seedpod weevil, *Ceutorhynchus assimilis* (Coleoptera: Curculionidae)

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SUMMARY

Canola (*Brassica napus* L.), yellow mustard (*Sinapis alba* L.) and intergeneric crosses of *S. alba* × *B. napus* were assessed for resistance (antixenosis) to the cabbage seedpod weevil (*Ceutorhynchus assimilis* Paykull). Pod trichomes did not appear to be a major factor in the resistance of *S. alba* to weevils. The number of feeding punctures and eggs per pod in *S. alba* was not significantly different in pods with trichomes than in those where the trichomes had been removed. Choice and no-choice laboratory tests examining feeding punctures and eggs laid per pod suggested that resistance in *S. alba* is not conferred in the intergeneric cross, *S. alba* × *B. napus*. Similar data on feeding and weevil oviposition were found in field test plots. However, despite many eggs being laid in *S. alba* × *B. napus* hybrid plants, fewer cabbage seedpod weevil larvae developed to exit the intergeneric hybrid pods. Glucosinolate analyses of leaves, pods and seeds showed that *S. alba* plants have a high concentration of *p*-hydroxybenzyl glucosinolate in all three plant parts, but *B. napus* has no *p*-hydroxybenzyl. Interestingly the intergeneric hybrid examined in this study had 62% and 60% of *p*-hydroxybenzyl concentration in the leaves and seeds, respectively, than was found in the *S. alba* parent. However, pod tissues contained very little (3%) compared with the *S. alba* parent. It is possible, therefore, that the adult cabbage seedpod weevil feeds on the pods of the intergeneric hybrid and lays eggs in the pod, because of the low concentration of *p*-hydroxybenzyl glucosinolate, but the larvae then fail to develop as they feed on the seeds containing high concentrations of *p*-hydroxybenzyl glucosinolate. It should be noted also that this hybrid produced pods that were more similar in physical shape to canola pods and that this may also be a factor determining cabbage seedpod weevil feeding and subsequent egg laying. In addition, both *B. napus* and the intergeneric hybrid produced 3-butenyl and 4-pentenyl glucosinolates in their pods, and degradation products (3-butenyl, and 4-pentenyl isothiocyanates) from these glucosinolate types, are known to be stimulatory kairomones that attract cabbage seedpod weevil. Further studies are being conducted to examine these factors in more detail.

INTRODUCTION

The cabbage seedpod weevil is a major insect pest of spring- and autumn-planted oilseed rape throughout the Pacific Northwest and other production regions of the US (McCaffrey 1992) and Europe (Dmoch 1965; Free & Williams 1978). Cabbage seedpod weevil larvae can reduce yield by up to 35% in crops not treated with insecticides (McCaffrey *et al*. 1986). Ethyl parathion, historically the primary insecticide recommended for the control of cabbage seedpod weevil in the Pacific Northwest, was recently withdrawn and replaced by methyl parathion (McCaffrey *et al*. 1986). Canola and rapeseed are minor crops in the US and, consequently, insecticide registrations for the control of this pest are limited. Alternative control technologies must be pursued if canola or rapeseed are to be produced economically in areas infested with cabbage seedpod weevil.

The major oilseed rape species are *B. napus* L., *B. rapa* L., *B. carinata* Braun, and *B. juncea* L. Research

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at the University of Idaho has focused on developing edible (canola) and industrial (high erucic acid) oilseed varieties of *B. napus* and oilseed yellow mustard (*S. alba*). *Sinapis alba* has been shown to be tolerant to flea beetle (*Phyllotreta cruciferae* (Goeze)) attack on cotyledons and is resistant to pod feeding by the beetles (Lamb 1980, 1984; Bodnaryk & Lamb 1991; Brown *et al*. 1999*a*). Doucette (1947) reported that *S. alba* pods were immune to attack by cabbage seedpod weevil. This observation is supported by results in small plot studies assessing the effects of late season insect control on *S. alba* yields (Brown *et al*. 1999*b*). No-choice laboratory studies have verified that cabbage seedpod weevil does not oviposit on *S. alba* pods (Harmon & McCaffrey 1998). The trichomes of the pods have been shown to be responsible for the resistance of *S. alba* pods to flea beetle attack (Lamb 1980), and to a lesser degree attack by *Lygus* bugs (Bodnaryk 1996), and it is suspected that a similar mechanism may be responsible for the resistance of *S. alba* to cabbage seedpod weevil.

Intergeneric crosses between *S. alba* and *B. napus* (Brown *et al*. 1997) have recently been reported. The availability of this new germplasm provided an opportunity to assess whether the cabbage seedpod weevil resistance trait(s) of *S. alba* would be transferred to the hybrid progeny. The pods of the intergeneric crosses do not have trichomes, which may be a factor in mediating the response of the cabbage seedpod weevils to the hybrid pods (Lamb 1980).

Female cabbage seedpod weevils form a feeding puncture in the pod prior to oviposition; and thus, qualitative and quantitative differences in glucosinolate composition in the pods can make them more or less acceptable for oviposition by the female cabbage seedpod weevils (Smart & Blight 1997). *P*-hydroxybenzyl (sinalbin) glucosinolate has been shown to be one mechanism implicated in the resistance of *S. alba* seedlings to flea beetle, bertha armyworm (Bodnaryk 1991) and *Lygus* bugs (Bodnaryk 1996). The presence, both qualitative and quantitative, of specific glucosinolates, such as *p*-hydroxybenzyl, could mediate the ovipositional preferences of cabbage seedpod weevils. Negative association of oviposition and glucosinolate composition would suggest an association between glucosinolate profile and resistance.

With this in mind, the emphasis in this research was to determine: (1) whether the resistance factors of *S. alba* were conferred to the intergeneric hybrid progeny of crosses between *S. alba* and *B. napus*; (2) whether pod trichomes contributed to the resistance (antixenosis) of *S. alba* to cabbage seedpod weevil; and (3) whether glucosinolates were associated with this resistance.

MATERIALS AND METHODS

Assessment of S. alba *and* S. alba × B. napus *crosses for resistance to cabbage seedpod weevil in paired and no-choice tests*

Paired choice and no-choice ovipositional bioassays were conducted using 185 cm^3 cages. Test lines included: *B. napus* (cv. Cyclone), *Sinapis alba* (a numbered breeding line UI.535) and the hybrid *S. alba* (U.535) × *B. napus* (Cyclone). In the paired choice tests, one female cabbage seedpod weevil was confined with four pods (two of a test line and two of the standard *B. napus* (cv. Bridger) per cage. In the no-choice tests, one female cabbage seedpod weevil was confined with four pods of the same line per cage (Harmon & McCaffrey 1998).

All pods were excised from plants grown in a glasshouse. Previous studies suggest that the response of cabbage seedpod weevil to excised pods is similar to the response to attached pods (Harmon & McCaffrey 1998).

Cabbage seedpod weevils were collected from flowering winter rapeseed (*B. napus*) in Latah and Nez Perce Counties, Idaho. Field-collected cabbage seedpod weevils were put individually into several cages with one Bridger pod. Pods were dissected 24 h later to assess adult feeding and the presence of eggs in pods. Only females producing eggs were used in the bioassays. Each bioassay was conducted over a 4-day period under the laboratory conditions described above. Pods were changed daily and feeding punctures and eggs were recorded. Each test was replicated 20 times.

Assessment of pod trichomes as a source of resistance to the cabbage seed pod weevil

All the intergeneric hybrids produced had no trichomes on the pods. Paired choice ovipositional bioassays were conducted with: (1) *S. alba* pods with trichomes *v. S. alba* pods with trichomes removed (Lamb 1980); and (2) undamaged *S. alba* pods *v.* damaged *S. alba* pods, to determine the effect of *S. alba* trichomes on cabbage seedpod weevil resistance. All pods were excised from field-grown plants of the breeding line UI.535. Trichomes were plucked from the pods with forceps. Because trichome removal also caused physical damage to the pods, some pods did not have trichomes removed, but were damaged to simulate trichome removal by slitting the pods along each side with a razor blade, possibly releasing allelochemicals. Undamaged pods received neither trichome removal or damage. Adult cabbage seedpod weevils were field-collected from flowering rapeseed (*B. napus*). Cabbage seedpod weevils were put individually into several cages with one Bridger (*B. napus*) pod. The pods were dissected 24 h later to assess whether cabbage seedpod weevils had

oviposited. Only females producing eggs in this susceptible host were used in the bioassays. One cabbage seedpod weevil was confined with two pods, one of each test type (i.e. damaged with trichomes and without trichomes) in a 185 cm^3 cage. Bioassays were conducted at 20 ± 1 °C, 40–50% RH and 15:9 (L:D) photoperiod over a 4-day period with pods replaced daily. Feeding punctures and eggs were recorded. Each test was replicated 20 times.

Assessment of S. alba *and* S. alba × B. napus *crosses for resistance to the cabbage seedpod weevil in field tests*

Seedlings of tested lines were transplanted to the University of Idaho Plant Science Farm, Moscow, Idaho, USA. Seedlings of both parental lines *B. napus* (cv. Cyclone) and *Sinapis alba* (breeding line UI.535) and the intergeneric cross (*S. alba* (U.535) × *B. napus* (Cyclone)) were transplanted from glasshouse-propagated plants into two-row plots on 24 April 1994. Plots were 4·6 m long, with two replicates arranged in a randomized complete block design. Thirty pods per plot were removed on 22 May 1994 to record eggs laid and feeding punctures. Also, 200 pods per plot were removed from *S. alba* plants on 25 July and from *B. napus* and the hybrid line on 29 July to determine the incidence of larval exit holes within each test line.

Glucosinolate determination

Glucosinolate profiles of leaf, pod and seed tissues of *S. alba*, *B. napus* parents, and the intergeneric cross were determined by measuring the trimethylsilyl derivatives of desulphated glucosinolates using a modified version of the Canadian Grain Commission method (Daun & McGregor 1983). Leaf tissue was sampled from the youngest leaves at the beginning of flowering, and pod tissue was sampled *c.* 5 days after flower petal drop. Pod and leaf tissue was frozen at −20 °C immediately after sampling. Seed samples of 500 mg were each ground in 5 ml of hexane using a Raney seed crusher. Each sample was washed with an additional 5 ml of hexane and allowed to air dry. Frozen leaf and pod tissue samples were lyophilized and ground to pass through a 20-mesh sieve. 100 mg of each sample was placed in a test tube and heated to 100 °C in a heating block. After temperature equilibration, 6 ml of boiling water was added to denature endogenous thioglucosidase and extract glucosinolates. Hot water extraction provides an excellent denaturation of myrosinaese and subsequent protection of aliphatic glucosinolates from hydrolysis (D. I. McGregor, personal communication). In addition, glucosinolates are quite soluble in water, and would be well extracted by hot water. This study deals only with aliphatic and aromatic glucosinolates, rather than indolyl glucosinolates where methanol is a more appropriate extractant. One ml of 1 mM allyl glucosinolate water solution was added to each sample as an internal standard. After 5 min, 200 ml of 0·6 M lead-barium acetate was added. After mixing, the samples were centrifuged at 2000 ***g*** for 10 min. The supernatant was poured onto DEAE Sephadex A-25 anion exchange columns. Columns were washed with 3 ml of 0·5 M acetic acid followed by 2–3 ml washes of distilled water (green samples only) and a final wash of 3 ml of 0·02 M pyridine-acetate to remove neutral compounds. One ml of purified sulphatase type H-1 was added to the columns and allowed to stand overnight. The resulting desulpho-glucosinolates were eluted into 1·8 ml auto-sampler vials with 1·5 ml of distilled water. The aqueous samples were dried down at 60 °C on a heating block under a stream of air. The desulpho-glucosinolates were redissolved in 500 ml of a 1:1 mixture of pyridine and dimethylforamide, and 100 ml of *bis*(trimethylsilyl) trifluoroacetamide (BSTFA) containing 10% trimethyl-chlorosilane (TM) was added to derivitize the samples. The samples were placed in a heating block at 90 °C for 20 min to drive the derivatization reaction. After cooling, 1·0 ml samples were injected into a Varian model 3700 FID gas chromatography equipped with a Varian model 8000 auto-sampler and a 2 m × 2 mm i.d. glass column packed with 2% OV-7 on chromosporb AW DMCS 100/120 mesh. The glucosinolates were quantified with a Hewlett-Packard 3390A integrator using the peak area of the benzyl glucosinolate as an internal standard.

Statistical analyses

Protected L.S.D.s or Student's *t*-tests (SAS Institute 1989) were used to assess differences among treatments for multiple comparisons or paired choice tests, respectively.

RESULTS AND DISCUSSION

Assessment of S. alba *and* S. alba × B. napus *hybrids for resistance to cabbage seedpod weevil*

In paired choice tests, pods from *S. alba* had significantly ($P < 0{\cdot}001$) fewer feeding punctures and contained significantly ($P < 0{\cdot}001$) fewer eggs per pod than the *B. napus* standard (Table 1). *B. napus* (Cyclone) and *B. napus* (Bridger) had a similar number of feeding punctures; although significantly more ($P < 0{\cdot}001$) eggs were observed in Cyclone pods than in those from Bridger. The intergeneric hybrid had significantly fewer feeding punctures but significantly ($P < 0{\cdot}05$) more eggs per pod than the *B. napus* standard.

In no-choice tests, significantly more ($P < 0{\cdot}05$) feeding punctures were observed on *B. napus* (Bridger) than on the other lines tested (Table 2). Feeding punctures on the intergeneric hybrid were not significantly different ($P < 0{\cdot}05$) from the *B. napus* (Cyclone) parent. Significantly fewer ($P < 0{\cdot}05$)

Table 1. *Feeding and oviposition of cabbage seedpod weevil on* B. napus, S. alba *and* S. alba × B. napus *hybrid plants in paired choice tests*

Paired choice test	Feeding punctures/pod/day			Eggs/pod/day		
	Mean ± S.E.*	*t*†	*P*	Mean ± S.E.	*t*	*P*
B. napus (Bridger)	9·84 ± 0·79	1·18	0·244	1·22 ± 0·13	3·11	0·004
B. napus (Cyclone)	8·73 ± 0·51	—	—	1·97 ± 0·21	—	—
B. napus (Bridger)	13·14 ± 0·78	16·76	< 0·001	2·08 ± 0·15	13·99	< 0·001
S. alba (UI.535)	0·03 ± 0·01	—	—	0·00 ± 0·00	—	—
B. napus (Bridger)	10·46 ± 0·76	4·48	< 0·001	1·39 ± 0·11	2·88	0·007
S. alba × *B. napus*	6·54 ± 0·44	—	—	2·00 ± 0·18	—	—

* $n = 20$.
† Treatment means compared using paired Student's *t*-test (SAS Institute 1989).

Table 2. *Feeding and oviposition of cabbage seedpod weevil on* B. napus, S. alba *and* S. alba × B. napus *in no-choice tests*

Line	Feeding punctures/pod/day ± S.E.	Eggs/pod/day ± S.E.	*n*
B. napus (Bridger)	9·36 ± 0·03	1·96 ± 0·15	20
B. napus (Cyclone)	8·03 ± 0·52	2·23 ± 0·16	20
S. alba (UI.535)	0·73 ± 0·07	0·00 ± 0·00	20
S. alba × *B. napus*	7·44 ± 0·45	1·99 ± 0·13	20

Eggs, D.F. = 6 and 188; $F = 50{\cdot}25$, $P = 0{\cdot}0001$; Feeding punctures, D.F. = 6 and 188; $F = 48{\cdot}17$, $P = 0{\cdot}0001$ (SAS Institute 1989).

feeding punctures were observed on *S. alba* pods than on the other lines. No eggs were found in *S. alba* pods although the number found in both *B. napus* lines and in the *S. alba* × *B. napus* hybrid were not significantly different ($P < 0{\cdot}05$).

From the paired-choice and no-choice tests, the relative susceptibility of the intergeneric crosses was similar to that of the *B. napus* parental line rather than the *S. alba* parent.

In these choice tests the intergeneric cross *S. alba* × *B. napus* was as susceptible to cabbage seedpod weevil feeding and oviposition as the *B. napus* parent. Although the intergeneric hybrid did not have hairy pods, trichomes do not appear to be the major factor mediating the resistance of *S. alba* to cabbage seedpod weevil.

Assessment of pod trichomes as a source of resistance to the cabbage seedpod weevil

Table 3. *Feeding and oviposition of cabbage seedpod weevil on* S. alba (*UI.535*) *pods in paired choice tests*

Paired choice test	Feeding punctures/pod/day		Eggs/pod/day	
	Mean ± S.E.*	*t*†	Mean ± S.E.	*t*
Trichomes no damage	0·16 ± 0·07	1·26	0·0 ± 0·0	—
Trichomes with damage	0·06 ± 0·04	—	0·0	—
Trichomes	0·23 ± 0·08	4·63	0·03 ± 0·02	0·59
Trichomes removed	1·48 ± 0·26	—	0·01 ± 0·01	—

* $n = 20$.
† Treatment means compared using paired Student's *t*-test (SAS Institute 1989).

No eggs were laid in *S. alba* pods with trichomes intact, with or without damage (Table 3). Although significantly ($P < 0{\cdot}05$) more feeding punctures were recorded on pods without trichomes compared to damaged pods with trichomes, the number of eggs per pod was generally very low and no significant differences ($P > 0{\cdot}05$) in egg numbers were found in *S. alba* pods with or without trichomes. This suggests that trichomes are not a major factor in the resistance to cabbage seedpod weevil found in *S. alba*.

Table 4. C. assimilis *feeding*, *oviposition*, *and exit holes on* B. napus, S. alba *and* S. alba × B. napus *hybrid in field plots*

Line	Feeding punctures/pod Mean ± S.E.*	Eggs/pod Mean ± S.E.	Exit holes/100 pods Mean ± S.E.
B. napus (Cyclone)	3·25 ± 0·55	0·40 ± 0·07	65·0 ± 0·5
S. alba (UI.535)	0·00 ± 0·00	0·00 ± 0·00	0·0 ± 0·0
S. alba × *B. napus*	2·80 ± 0·40	0·65 ± 0·08	25·0 ± 14·0

* $n = 2$.
Exit holes, D.F. = 4 and 5, $F = 10{\cdot}07$, $P = 0{\cdot}0131$; Eggs, D.F. = 4 and 5, $F = 5{\cdot}36$, $P = 0{\cdot}0471$; Feeding punctures, D.F. = 4 and 5, $F = 15{\cdot}59$, $P = 0{\cdot}005$ (SAS Institute 1989).

Table 5. *Glucosinolate profiles of* S. alba, B. napus *and* S. alba × B. napus *hybrid pods*, *leaf and seed tissues*

Part	Line	BUT*	PENT	HYBUT	HYPENT	HYBENZ
		(μmol/g plant tissue)				
Leaves	*B. napus* (Cyclone)	0·0	0·0	0·0	0·0	0·0
	S. alba (034585)	0·0	0·0	0·1	0·0	13·7
	S. alba × *B. napus*	0·0	T†	0·0	0·0	8·5
Pods	*B. napus* (Cyclone)	T	T	0·0	0·0	0·0
	S. alba (034585)	0·0	0·0	0·5	0·0	24·7
	S. alba × *B. napus*	T	T	0·0	0·0	0·8
Seeds	*B. napus* (Cyclone)	1·0	0·0	1·3	0·0	0·0
	S. alba (034585)	1·3	0·0	6·2	0·0	170·6
	S. alba × *B. napus*	2·3	0·2	11·5	0·1	101·7

* BUT = 3-butenyl glucosinolate; PENT = 4-pentenyl glucosinolate; HYBUT = 2-hydroxy-3-butenyl (progoitrin) glucosinolate; HYPENT = 1-hydroxy-4-pentenyl glucosinolate; HYBENZ = *p*-hydroxybenzyl (sinalbin) glucosinolate.
† T = Trace.

Assessment of S. alba *and* S. alba × B. napus *crosses for resistance to the cabbage seedpod weevil in field tests*

There were no significant differences ($P > 0{\cdot}05$) in the number of feeding punctures per pod or the number of eggs per pod observed in the *B. napus* (Cyclone) parent compared to the *S. alba* × *B. napus* hybrid (Table 4). No cabbage seedpod weevil eggs were found in *S. alba* pods. The *B. napus* parent (Cyclone) had significantly ($P < 0{\cdot}05$) more cabbage seedpod weevil exit holes than either the *S. alba* or the intergeneric hybrid. It is interesting to note that *B. napus* and the *S. alba* × *B. napus* hybrid had similar egg numbers per pod but significantly fewer ($P < 0{\cdot}05$) cabbage seedpod weevil larvae developed to exit intergeneric hybrid pods, suggesting expression of antibiosis in the hybrid.

Glucosinolates

As expected (Bodnaryk 1991), the primary glucosinolate found associated with *S. alba* leaves, seeds and pods was *p*-hydroxybenzyl (sinalbin) glucosinolate. High concentrations were found in leaves and pods (13·7 and 24·7 μmol/g of dry weight, respectively), with very high concentrations in the seed (Table 5). *B. napus* (Cyclone) contained no *p*-hydroxybenzyl in either leaves, pods or seed, but trace concentrations of 3-butenyl (gluconapin) and 4-pentenyl (glucobrassicanapin) glucosinolates were detected in leaves and pods. *B. napus* seeds contained low concentrations of 3-butenyl and 2-hydroxy-3-butenyl (progoitrin) glucosinolate. The intergeneric hybrid contained relatively high concentrations of *p*-hydroxybenzyl in the leaves and seeds (62 and 60 % of the concentration in the *S. alba* parent) but a lower concentration in the pod tissue (only 3 % of the concentration found in the *S. alba* parent pods). The intergeneric hybrid also contained some of all five glucosinolates examined and contained almost twice the concentration of 2-hydroxy-3-butenyl glucosinolate in the seed than the *S. alba* parent.

Despite many eggs being laid in *S. alba* × *B. napus* hybrid plants, significantly fewer cabbage seedpod weevil larvae developed to exit the intergeneric hybrid

pods as compared with the *B. napus* parent. Glucosinolate analyses of leaves, pod walls and seeds showed that *S. alba* plants have high concentrations of *p*-hydroxybenzyl glucosinolate in all three plant parts while *B. napus* has no *p*-hydroxybenzyl. Interestingly the intergeneric hybrid examined in this study had 62 and 60% the *p*-hydroxybenzyl concentration in the leaves and seeds, respectively, than was found in the *S. alba* parent. However, pod tissues contained very little *p*-hydroxybenzyl (3%) compared to the *S. alba* parent. It is possible, therefore, that the adult cabbage seedpod weevil feed on the pods of the intergeneric hybrid and lay eggs in the pod because of a low concentration of *p*-hydroxybenzyl glucosinolate. However, larvae fail to develop as they feed on the high *p*-hydroxybenzyl glucosinolate seeds.

Cabbage seedpod weevil resistance to *S. alba* may also result from the lack of stimulatory kairomones, such as 3-butenyl and 4-pentenyl glucosinolates, in the pods (Larsen *et al*. 1985) or their degradation products, 3-butenyl and 4-pentenyl isothiocyanate, respectively (Evans & Allen 1992; Bartlet *et al*. 1993). These glucosinolates were found in *B. napus* and in the intergeneric hybrid but not in the leaves or pods of *S. alba*. Alternatively, low numbers of exit holes in the field trial could be due to increased parasitism, whereby the hybrid plants release more isothiosinates (due to higher glucosinolate content) and parasitoids of crucifer-feeding insects can be attracted by isothiosinates (Murchie *et al*. 1997).

As well as glucosinolates and related by-products, physical factors such as pod wall thickness and pod size (Doucette 1947) and chemical factors such as waxes may also be important in mediating host acceptance by the cabbage seedpod weevil.

S. alba × *B. napus* hybrids with a wider variation of glucosinolate concentrations and profiles in different plant parts than the hybrid examined here have been developed. Genotypes from these intergeneric hybrids have been selected with pod shapes similar to *B. napus* while others have been selected with *S. alba* pod shapes. Further studies focusing on ovipositional behaviour of the cabbage seedpod weevils using these progeny types may help to elucidate further the mechanisms associated with host acceptance and plant resistance.

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