Effect of Insect Herbivory on the Architecture and Seed Production of Canola, *Brassica napus* L.¹

H.A. Cárcamo²

Agriculture and Agri-Food Canada, Lethbridge Research Centre, 5403 First Ave., South, Lethbridge Alberta, Canada T1J 4B1

J. Entomol. Sci. 47(1): 44-55 (January 2012)

Abstract Several native *Lygus* spp. (Hemiptera: Miridae) feed on buds, flowers and immature seeds of canola. These plant resources are also exploited by a recent alien pest now established in southern Alberta, Canada: the cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Marsham) (Coleoptera: Curculionidae). A caged study was conducted with *Brassica napus* L. in 2000 and 2002 to determine if various combinations and densities of lygus and seedpod weevils (0, 10 + 10, 20 of either, 20 + 20, 40 + 40, individuals per cage) affected yield and its components such as number of branches, pods and seed weight. Under severely dry conditions, cages with the intermediate (20 + 20) and high (40 + 40) insect combinations had lower grain yield as well as number of racemes and pods per raceme relative to control cages with no insects added. Under more humid conditions in 2002, similar results were observed but the damage by the cabbage seedpod weevil at 20 adults per cage was more apparent than in 2000. These results suggest that in most years the weevil is a more serious pest than lygus bugs but low combined densities do not decrease yield. Furthermore, in southern Alberta at low or moderate densities, these late-season pests do not appear to stimulate plants to overcompensate. There was no indication of competition between these two insects.

Key Words *Brassica napus*, lygus bugs, cabbage seedpod weevil, *Ceutorhynchus obstrictus*, plant compensation

It is well established that plant responses to above ground herbivory, whether by vertebrates or arthropods, are nonlinear (Dyer et al. 1993) and are dynamic in time and space. Depending on environmental conditions, most plants compensate or overcompensate for some level of herbivory particularly during earlier growth stages (Gavloski and Lamb 2000). For example, during the vegetative stage, rice plants reduce the effects of the brown plant hopper, *Nilaparvata lugens* Stal (Homoptera: Delphacidae), feeding on the main shoot by translocating nutrients and assimilates from the primary tiller (Rubia-Sanchez et al. 1999). Canola plants, also known as oilseed rape (*Brassica napus L.*), compensate for moderate herbivory by flea beetles at the seed-ling stage (Gavloski and Lamb 2000), *Lygus* spp. during early flower (J. Jones unpubl. data), cabbage seedpod weevil (Free et al. 1983, Lerin 1984) and *Meligethes aeneus* F. (Tatchell 1983) during flower. Unraveling insect-plant interactions are necessary to develop more sophisticated insect thresholds in the advancement of integrated pest management (Allen et al. 2009).

¹Received 15 June 2011; accepted for publication 30 September 2011.

²Email: hector.carcamo@agr.gc.ca.

Canola is an important cash crop world wide and a major export crop for Canada where most of the production takes place in the western prairie ecoregion. The entomology of Brassica species, including canola, was reviewed by Lamb (1989). In the southern ecozone of the mixed grasslands of Alberta and Saskatchewan, canola is attacked by several insects such as flea beetles, Phyllotreta cruciferae (Goeze) (Coleoptera: Chrysomelidae), at the seedling stage (Lamb 1989), and cabbage seedpod weevils, Ceutorhynchus obstrictus (Marsham) (Coleoptera: Curculionidae) (Cárcamo et al. 2001) and lygus bugs, Lygus Hahn (Heteroptera: Miridae), during the flower and pod stages (Butts and Lamb 1991). The latter two pests immigrate to canola fields at the late-bud and early-flower stages to feed on these reproductive structures which lead to their abortion. However, it is the damage to the immature seeds that is considered economic. Ceutorhynchus obstrictus larvae feed on 3 - 6 seeds per pod (Cárcamo et al. 2005), and lygus bugs reduce seed weight by about 11% (Butts and Lamb 1990). Plant injury levels and economic thresholds have been established for lygus bugs (Wise and Lamb 1998a), but only nominal thresholds are in use for cabbage seedpod weevils (Dosdall et al. 2001). Integrated pest management of these two pests requires improved knowledge of the plant responses when they cooccur at various densities in southern Alberta.

The independent impacts of lygus bugs and cabbage seedpod weevils on Brassica crops have been studied in detail in various temperate regions. Butts and Lamb (1990) estimated an 11% reduction in seed weight from direct lygus feeding in northern and central Alberta. However, they suggested that canola may compensate for damage to buds and flowers because there were no differences in pod production among insect treatments that included control at earlier and later growth stages. Wise and Lamb (1998a) reported yield losses of 20% in field cages and 14% in field plots in southern Manitoba. Similar yield reduction was suggested in previous studies by Turnock et al. (1995). In these studies the dominant lygus bug was the tarnished plant bug, L. lineolaris (Palisot de Beauvois). Wise and Lamb (1998a) also reported that with adequate rainfall (100 mm from bud to end of flower) canola partially compensates for lygus bug feeding. In another study conducted at multiple sites in Alberta, individual canola plants were caged with varying densities of lygus bugs during the bud to early flower stages only (Jones et al., unpubl. report), and they concluded that lygus bugs induced higher vegetative growth such as thicker stems, higher branching and in some cases increased yield. It is worth noting that the complex of lygus bugs in canola can be variable (Cárcamo et al. 2002), and Wise and Lamb (1998a) reported a higher reproductive rate for L. lineolaris relative to L. borealis. In the drier regions of the prairies such as southern Alberta and Saskatchewan, L. lineolaris is very rare and is replaced by other species such as L. elisus or L. keltoni near the Alberta foothills (Schwartz and Foottit 1998).

Cabbage seedpod weevil effects on Brassicaceous plants are well known in Europe where it is a common native pest and to a lesser extent, in North America, where it is an invasive pest. Studies with winter canola in the UK showed that with adequate growing conditions, canola plants tolerate up to 60% of bud and flower blasting and can fully compensate for the feeding damage by adult weevils (Williams and Free 1979, Free et al. 1983). Using cages, researchers have shown that less than 1 weevil per plant does not result in sufficient yield loss to warrant spraying although interactions with a pod midge magnified the problem (Sylven and Svenson 1975, Free et al. 1983). In another study from Scandinavia it was clear that plants could not compensate to prevent yield losses from 2 weevils per plant (Sylven and Svenson 1975,

Tulisalo et al. 1976). However, if the level of pod infestation is less than 25%, compensation is complete and control measures were not warranted (Lerin 1984, Buntin 1999). In southern Alberta, several insecticide trials have been conducted to test various chemicals but no significant effects on yield were found (Cárcamo et al. 2005).

The main objective of this study was to compare single species effects and various combinations of lygus bugs and cabbage seedpod weevils on canola yield and plant growth characteristics including branching and pod production.

Materials and Methods

The study site was located 2 km east of the Lethbridge Research Center (49°42′N; 112°44′W) (LRC). On 2 May 2000 the land was disced to prepare the seedbed and Edge[™] (Dow AgroSciences Canada Inc, Calgary, Alberta, Canada) granular herbicide (ethalfluralin 5%) was incorporated for preplant weed control. On the same day, the canola variety Q2 (untreated seed, except for fungicide) was planted using a John Deer pan drill at the rate of 5.5 kg/ha, 15 cm row spacing and at 1 cm depth. Moisture at seeding was poor and by 15 May germination was patchy.

Flea beetle pressure at the site was extremely high and cotyledon consumption was estimated to be over 50% in some plots; therefore, Decis 5EC[™] (Bayer Cropscience Inc., Calgary, Alberta, Canada) (deltamethrin) at 148 mL/ha was sprayed on 23 May. Drought conditions throughout the seedling stage, plus flea beetle pressure, created a patchy stand (range of 25 - 55 plants/sq m) and variable growth stages (as of 19 July: 10% bud, 45% early flower and 45% mid-to-late flower). In 2001 the experiment was planted but was abandoned because of extreme drought but it was repeated in 2002 at a nearby site about 0.5 km north of LRC.

Experimental design. A randomized block design with 4 replicate blocks (6 plots per block, 2 cages per plot) with the following 6 treatments was used (abbreviation codes are used hereafter): (1) control with no insect pests (LW0), (2) low densities of 10 lygus and 10 weevils per cage (LW10), (3) intermediate densities of 20 lygus and 20 weevils per cage (LW20), (4) high densities of 40 lygus and 40 weevils per cage (LW40), (5) 20 lygus bugs (L20) only, and (6) 20 weevils only (W20). In 2002, plants growing in plots outside of the cages also were sampled and processed. The insect densities selected were expected to represent values below (10/cage), near (20/ cage), and above (40/cage) economic thresholds for lygus bugs according to a previous study that had used the same cages (Wise and Lamb 1998a). Weevil densities were somewhat arbitrary because they were based on preliminary data suggesting a sweeping efficiency of 20% (Cárcamo, unpubl. data) or about double that of lygus bugs (i.e., sweep nets catches represent only 20% of the total weevil density in an area) and the assumption that flowering canola, where the weevils are concentrated, is easier to sample than canola at the pod stage recommended for lygus sampling. Using Wise and Lamb's (1998b) estimate that one arc (effectively 90°) with a sweep net covers approximately 0.66 m², 0.20 sweeping efficiency and a nominal economic threshold of 4 weevils per sweep, the density of weevils at threshold was estimated at 30 weevils per m² (4 weevils/sweep/0.66 m²/0.20). This translates to 24 weevils for a cage 0.81 m² or approximately 2 weevils per plant with 10 plants per cage.

Cages (0.81 m² and 1.2 m tall) were placed in areas with at least 10 plants of similar growth stage (prebud to insure little damage by insects) on 4 and 5 July, and any lygus bugs and cabbage seedpod weevils were removed on the same dates. All

cages were inspected again for unwanted insects on 11 July prior to stocking (14 and 15 July), and cages in the check treatment (no insects) were further cleaned of contaminants on 1 August. The species composition of lygus bugs stocked was 40% each for *L. keltoni* and *L. elisus* and 20% *L. borealis*. On 29 August 2000, when the plants were at the mature pod stage 5.4 (Harper and Berkenkamp 1975), all lygus, seedpod weevils and other insects were collected from each cage using a hand-held battery operated aspirator. Levels of flea beetles and aphids were categorized into heavy, moderate or light infestation. On 30 August, 4 caged plants from each plot were bagged individually to quantify pod blasting and cabbage seedpod weevil exit holes. The remaining plants were harvested to estimate plant and seed biomass.

In 2002, the study was conducted at a site 0.5 km north of LRC ($49^{\circ}42.525'N$; $112^{\circ}45.485'W$). Canola variety Q2 coated with Vitavax RS (containing Lindane) was seeded at 7 kg/ha on 13 May, after Edge herbicide was soil incorporated the same day. Plants were caged on 27 June and thinned to 10 plants on 4 July and insects were removed from all cages. Cabbage seedpod weevils were collected from canola fields in the area, and the cages were stocked on 5 July at the late bolting to early flower stage. Lygus bugs, also from surrounding farms, were added from 10 - 12 July when plants were at the early to mid flower stage. Two of the four blocks received 100% *L. keltoni* but the other two had 30 - 40% *L. elisus*. Species identifications were done in the field with the naked eye. Some hail damage to cages took place on 10 August 2002 but the cages were repaired promptly. Caged plants were harvested from 4 - 20 September; a cool end of summer delayed plant maturation. To attempt to collect as many insects as possible from each cage post harvest, they were inspected periodically until 7 October.

Statistical analysis. Results were analyzed as a randomized block design with two cages and plants nested in each replicate plot. A mixed model ANOVA was performed using SAS (SAS 2003) with the type of insect combination as the fixed factor and replicate as the random factor to analyze whole plant variables such as total branches, pods produced, cabbage seedpod weevil damage per plant, and number of aborted pods. Log (x + 1) transformed data were used in an attempt to normalize data or, where this failed, ranked data were used. Each branch per plant was classified according to the branching level from primary to tertiary (fourth and fifth level branches were not numerous enough for analysis). This variable was used as a second fixed factor in the mixed analysis of variance to address possible interactions of insect combinations and branch level that might affect some of the response variables. Differences (SAS 2003); with a probability value of 0.05 considered significant for pairwise comparisons if overall model results suggested significant effects.

Results

Growing conditions and treatment establishments. Southern Alberta had drought in 2000 with < 61 mm rainfall until the end of flowering. On 12 July each cage received 28 L of water by hand irrigation. Due to poor moisture conditions in 2000, plants were small and senesced prematurely. These conditions likely benefited lygus bug development but were detrimental for cabbage seedpod weevils. The average number of adult weevils retrieved from the cages ranged from 0 (LW0) to 5 (W20) (Table 1). Treatment LW40 had an average of 2.5 adult weevils per cage. The average number of lygus ranged from 9 (LW0) to 116 (LW20) (Table 1). Lygus numbers in

to a	issess ins	sect nen	Sivory en	ects on	canola.			
		200	00		2002			
	Lyg	us	Weev	/ils	Lyg	us	Wee	vils
Treatment*	Mean	SE	Mean	SE	Mean	SE	Mean	SE
LW0	9.3	5.6	0.0	0.0	21.0	4.4	6.5	4.6
LW10	67.3	15.5	1.6	0.8	84.7	10.0	37.6	14.4
LW20	116.4	39.6	1.8	0.8	124.1	50.9	72.8	18.8
LW40	94.0	35.4	2.5	2.0	153.9	45.7	165.5	42.4
L20	99.4	30.5	0.4	0.4	72.4	22.9	4.5	2.4
W20	7.6	3.1	5.5	3.2	21.6	4.7	96.4	29.5

Table 1. Average number of lygus bugs and cabbage seedpod weevils retrievedfrom the cages at harvest time at the study near Lethbridge, AB Canadato assess insect herbivory effects on canola.

*Abbreviations: L = lygus bugs, W = cabbage seedpod weevils, numbers refer to the number of insects.

Treatments LW40 and L20 were similar (90 - 100 bugs) and slightly higher than cages of LW10 (Table 1).

In 2002, growing conditions were more favorable for plant growth, although heavy precipitation in June deposited around 250 mm of rainfall in a short period. Weevil reproduction was much higher than in 2000: 5 - 6 per cage for LW0 and L20 and up to 166 in cages of LW40 (Table 1). The number of weevils retrieved from the intermediate combination treatments ranged from 38 - 98 (Table 1). The number of lygus bugs in the cages in 2002 was comparable to those obtained in 2000, except that the highest number (154) was obtained from the LW40 treatment. Treatment LW20 had 124 lygus, which was very close to 2000 (116). Treatment L20 produced slightly fewer lygus than Treatment LW10. Cages that had no lygus added (LW0, W20) still produced 21 bugs at the end of the study (Table 1).

Yields. In 2000, about 3 of the 10 plants per cage died or did not produce pods because of the severe drought. Average canola seed weight per cage ranged from 10 - 20 g per cage (0.81 m²). Mean plant seed weight was higher in the control treatment without insects than in the two treatments with highest insect combinations of 20 or 40 of each species; other treatments did not differ (Table 2).

In 2002, plants sampled outside of the cages had a low seed yield per plant (6.7 g) and were comparable to Treatment LW40 (Table 2). Plants from Treatment L20 had similar yields to those from Treatment LW0, but the former had significantly higher yield than Treatments W20 or LW40. Plants from Treatment LW40 had lower yield than other treatments except for Treatment LW20 (FPLSD P < 0.05, after Proc Mix ANOVA: F = 7.08; df = 6, 16; P = 0.0009). Average yields were comparable among Treatments LW10, L20 and W20.

Biomass. In 2000, average plant biomass ranged from 9 - 14 g with no significant differences among treatments (Table 2). In 2002 there were no predictable differences in plant biomass among cage treatments, although Treatment L20 had significantly higher biomass than the Treatment LW10 (Table 2). Plants in cages with the highest insect densities had similar biomass as those with no insects. All plants grown inside

						2000						
	Se	eed weight (g)	(g)	Pla	Plant biomass	ss (g)	Race	Racemes per plant	ant	Weev	Weevil holes per pod	poo
Treatment	Mean*	SE		Mean	SE		Mean	SE		Mean	SE	
LW0	3.5	0.6	٩	13.8	2.2	A	9.1	1.3	A	0.00	0.001	0
LW10	2.2	0.6	AB	10.7	2.1	A	6.8	1.2	AB	0.07	0.021	ш
LW20	1.0	0.2	ш	12.3	2.4	٩	4.5	0.5	ш	0.13	0.026	۲
L20	2.2	0.5	AB	9.1	1.4	٨	6.1	0.8	AB	0.01	0.006	U
W20	2.3	0.5	AB	10.1	1.5	٩	5.8	0.8	AB	0.08	0.020	AB
LW40	1.3	0.3	Ш	11.3	2.3	٨	4.6	0.7	В	0.09	0.023	AB
Open	·			ı	ı		ı			ι		
							2002					
LWO	15.4	2.0	AB	46.0	4.2	AB	18.4	1.58	AB	0.02	0.005	O
LW10	15.9	1.6	AB	36.4	3.1	Ш	17.4	1.27	Ш	0.16	0.021	U
LW20	10.8	1.3	BC	43.9	3.5	AB	20.0	1.18	AB	0.44	0.036	ш
L20	17.9	1.4	٩	47.3	3.3	٩	20.6	1.11	٩	0.03	0.006	O
W20	12.9	1.4	Ш	40.3	3.2	AB	19.2	1.37	AB	0.40	0.029	Ю
LW40	6.7	0.8	o	40.6	3.5	AB	17.3	1.05	В	0.64	0.033	A
Open	9.9	0.4	o	15.6	1.2	o	5.91	0.40	ပ	0.13	0.009	O
* Means within year and columns not sharing letters are significantly different, FPLSD P < 0.05	ear and column	ıs not sharinç	j letters are :	significantly di	ifferent, FPL	-SD P < 0.0	ú					

Table 2. Average plant seed weight, dry plant biomass, racemes and cabbage seedpod weevil larval holes per pod per plant in 0000

CÁRCAMO: Insect Herbivory on Canola

cages had higher biomass than plants grown in the open area adjacent to the cages (Table 2).

Plant architecture variables. In 2000, plants in the control cages had more racemes (9 versus 4) than those grown in treatments LW20 or LW40 (FPLSD, transformed data, P < 0.05, Table 2). In 2002, average number of racemes in the various insect combination treatments ranged from about 17 - 21 and there was no predictable pattern of significant differences (Table 2). Uncaged plants had much fewer branches than those caged.

Fewer pods formed on secondary and tertiary racemes compared with primary racemes. There was an interaction between branch level and insect combination treatment only in 2002 (Fig. 1). The average number of pods produced in the 'LW40' treatment was significantly lower than the control or the '20 - 20' treatment. Insect combination treatment did not affect pod abortion which was always higher in primary than in secondary racemes (data not shown).

Weevil damage to pods. In 2000, the number of cabbage seedpod weevil larvae produced per pod in treatments with weevils was 2-fold higher in the LW20 treatment than in the LW10 treatment (Table 2). The LW40 treatment produced intermediate levels of weevil larvae per pod. In 2002, however, this treatment had significantly higher exit holes per pod (0.64) than all other treatments; the two treatments that had 20 weevils added, regardless of lygus presence had similar larval exit holes per pod and higher than the LW10 treatment and the controls (Table 2).

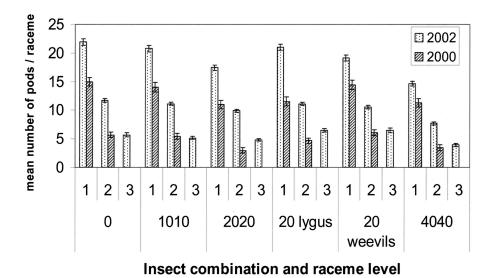


Fig. 1. Effect of combined or single species herbivory by lygus bugs and cabbage seedpod weevils at various densities (numbers refer to densities, '1010' = 10 of each, etc.) on the average number of pods produced per raceme (1 = primary, 2 = secondary, 3 = tertiary) in canola plants confined with cages in 2000 and 2002 near Lethbridge, Alberta, Canada.

Discussion

The range of lygus bug reproduction in the treatment with only 20 lygus was much lower than those reported by Wise and Lamb (1998a) for their inoculation of only 10 lygus. This difference can be explained by the lower rate of reproduction of the lygus species found in the current study compared with *L. lineolaris* which had a 25-fold rate of increase in the Manitoba field study. One of the dominant species added to this cage experiment was *L. keltoni*, which has an average lifetime reproductive potential of 133 nymphs in the laboratory (Cárcamo et al. 2006).

In this study, lygus bugs alone did not have a consistent negative effect on canola yield as reported elsewhere in Canada. Severe yield depression was expected in cages with lygus bugs in 2000 because the plants suffered from extreme moisture stress. All of the cages with lygus bugs reached densities at harvest that would translate to field abundance greater than 2 per sweep [using Wise and Lamb's (1998a) conversion of 250 per cage = 78 per 10 sweeps]. Even if lygus bugs at the critical early pod stage, 2 - 3 weeks earlier, were only half of these densities one would still expect yield reductions because of the moisture stress. In 2002 in fact, the highest numerical yield per plant was observed in the treatment with 20 lygus and no weevils, which was significantly higher than treatments with 20 weevils or more. These results disagree with most past publications on lygus bugs from other regions in the prairies but unique growing conditions each year and the low plant density in the current study makes it difficult to make generalizations.

Studies by Butts and Lamb (1991) suggested similar damage potential by L. elisus and L. lineolaris. Lygus keltoni was the dominant species retrieved from the cages in 2002 (62%) but its pest potential to canola compared with L. lineolaris remains to be determined. Lygus development time in relation to crop stage is a possible reason for lygus bugs being an intermittent pest in southern Alberta (Cárcamo, unpubl. data). Most years, lygus bugs reach high densities toward the end of the growing season when canola plants are at the mature pod stage and are ready for harvest (Cárcamo, unpubl. data). Usually, only late-seeded fields are at risk for lygus damage. In the current study there was a major difference in lygus developmental stages inside and outside the cages. A sample of 170 bugs swept from around the cages revealed 82% were nymphs when the crop was at the 5.3 stage (late pod). This suggests that most lygus bugs would have been too young to cause damage to the uncaged plants. However, inside the cages, 81% were adults at the time of harvest. It is possible that many of these adults were at least third or older instars at the time the crop was at the susceptible 5.1 stage. Hail or rainfall, as shown elsewhere (Day 2006), may have reduced populations of lygus bugs outside cages, hence explaining the developmental differences between lygus in caged and open plants.

The effect of cabbage seedpod weevil on yield depression was consistently more important than lygus bugs, especially in 2002. In 2000 very few weevils were retrieved as adults at harvest and very few exit larval holes were recorded. However, there likely was some feeding damage by the larvae during early pod but these may have failed to reach maturity and exit from the dry pods as seen in other fields nearby (L. Dosdall, pers. comm.). In 2000 only the treatments with the two highest combinations with 20 or 40 insects of each species reduced plant seed weight. In 2002, moist conditions probably favored the weevil's development because pods matured more slowly and considerably more weevils and exit holes were observed than in 2000. Even the treatments with only 20 weevils and no lygus

caused significant seed weight reduction per plant compared with the treatment with only 20 lygus.

Validating economic thresholds for weevils and in combinations with lygus and relating them to field conditions is a challenging task because of the inherent constraints of cage studies where stand densities and growing conditions differ from commercial farms. Previous researchers have suggested a critical threshold of 1 weevil per plant (Free et al. 1983) for winter canola in Europe. The treatments in the current study reflected this density for the 10 caged plants. However, these plants had about 2 - 3 times more pods available for weevils to oviposit than those growing in more natural stands outside the cages and also 2 - 3 times more plant biomass than the uncaged plants. Therefore, a conservative estimate would be to consider that caged treatments were only about half of the densities compared with natural conditions. On the other hand, canola yields are not strongly affected by stand density because plants can take up open spaces (Angadi et al. 2003), and one may choose to simply use a density of weevils per square meter. In either case for this cage study, the nominal threshold recommended of 4 weevils per sweep seems to be correct regardless of area or number of plants. Assuming a 20% efficiency of sweeping, a density of 20 weevils added to a cage at early flower (0.81 m²) translates to 3.3 per sweep (if 1 sweep ~0.66 m², Wise and Lamb 1998b); therefore, one can recommend maintaining the current thresholds of 4/sweep. Therefore, there is no need to spray if one finds 10 insects of each species in a sweep net at early flower. Making this assumption seems reasonable because the treatment with 10 weevils (effectively about 0.5/plant) produced pod infestations of 13%. Pod infestations below 25% do not result in yield losses (Lerin 1984). The yield results in this study are in agreement with this concept because there was no yield reduction in the '10 - 10' treatment in either year. At densities of 20 or 40 weevils per cage (effectively 1 - 2/plant) pod infestations were greater than 25% in the more normal year (2002), and there were reductions in yield as predicted by the thresholds used in Europe for winter oilseed rape.

The measurements of plant architecture and pod production patterns conducted in this study were aimed to improve our understanding on the mechanism of canola yield reduction by lygus and cabbage seedpod weevils. It was interesting that in 2000, the number of racemes was more than twice in the control cages than in the highest insect treatments with 40 of each species. But this was only observed in the dry year. It seems that under good moisture conditions the number of racemes is not affected by insect pressure. However, the number of pods per branch was lower in the treatment with the most insects than in the controls both years, although only significantly so in 2002. There was no trend toward higher branching or more pods at low or intermediate insect densities relative to the control with fewer insects. Therefore, there was no suggestion that insects "stimulated" the plants to overcompensate as observed in other studies.

The result of fewer racemes and pods per plant in the treatment with the highest density of cabbage seedpod weevils was opposite to the finding by Tulisalo et al. (1976). These authors reported a consistent trend of more racemes and pods per plant along with a decrease in grain yield and 1000 seed weight, as they increased densities of cabbage seedpod weevils per cage. The authors concluded that plants compensated for adult feeding though not to the extent observed for *Meligethes aeneus* F., a more important oilseed rape pest in Scandinavia (Tulisalo et al. 1976, Tatchell 1983). Lack of an over-compensatory response at low or moderate levels of insect herbivory by weevils or lygus alone or in combination in the present study may be

related to the specific growing conditions of spring-planted canola where plants have a shorter growing season than winter cultivars of canola planted in Europe.

The results from this cage study suggested lack of competition or intraguild predation between the two species. Average numbers of lygus bugs collected at the end of the experiment were similar among treatments that had 20 of each species alone or combinations of 20 each. Likewise, cabbage seedpod weevil adults at plant harvest or exit holes from pods were similar between these treatments. Lygus bugs have been listed as potential opportunistic predators of herbivores (Ehler 2004) with a rather omnivorous feeding habit. The results from the current study do not provide any indication that they were feeding on weevil larvae inside canola pods. Rosenheim et al. (2004) also reported lack of predation behavior in L. hesperus under field conditions. Although weevils and lyous adults fed on reproductive structures about the same time during the middle of the flowering and early pod stages, it seems that resources were not limiting for them to compete. This is supported by the fact that abortion of such structures was similar across all insect combinations and did not differ from the controls that had much fewer insects. Also, natural flower abortion rates in canola are very high and plants are known to compensate for it (Tommey and Evans 1992); therefore, insects feeding on flowers have little impact on the plant as these structures are very abundant.

In conclusion, the cage study did not find a clear and consistent impact of lygus bugs on canola yield although peculiar growing conditions make it difficult to generalize the results. The cabbage seedpod weevil appeared to be more important than lygus bugs as it clearly reduced seed yield during the wet year. This result was consistent with the finding of Brown et al. (1999) who concluded that this insect was a key component of the late season pest complex of canola in northern Idaho. During dry years, lygus bugs are likely more important in southern Alberta but drought effects on yield would render insect damage insignificant. Low densities of the two pests in combination, such as 1 of each per sweep, are not likely to reduce yield to warrant spraying the crop. At very high densities of both insects there was a reduction of yield both years of the study and none of the plant architecture parameters or plant biomass suggested that plants overcompensated for insect feeding at low or moderate densities. Although these two insects overlap in time and exploit the same canola reproductive structures, there was no indication of competition. Studies at the commercial farm scale are required to validate cage and plot studies and further refine pest management recommendations for this pest complex in canola.

Acknowledgments

The author thanks C. Herle, T. Larson, N. Schmold, the field crew of the Lethbridge Research Centre and many other students for technical support. This study was funded in part through a grant awarded to HC by the Canola Council of Canada, Alberta, Saskatchewan and Manitoba Canola Commissions and through the Matching Investment Initiative and Abase program of Agriculture and Agri-Food Canada. The author thanks K. Floate and P. Harris for constructive comments on an earlier draft.

References Cited

Allen, K. C., R. G. Luttrell and C. D. Parker Jr. 2009. Influence of within-season densities of Heliothines and tarnished plant bugs on variability in end-of-season cotton yield mapping. J. Cotton Sci. 13: 11-22.

- Angadi, S. V., H. W. Cutforth, B. G. McConkey and Y. Gan. 2003. Yield adjustment by canola grown at different plant populations under semiarid conditions. Crop Sci. 43: 1358-1366.
- Brown, J., J. P. McCaffrey, B. L. Harmon, J. B. Davis, A. P. Brown and D. A. Erickson. 1999. Effect of late season insect infestation on yield, yield components and oil quality of *Brassica napus*, *B. rapa*, *B. juncea* and *Sinapis alba* in the Pacific Northwest region of the United States. J. Agric. Sci. 132: 281-288.
- Buntin, G. D. 1999. Damage loss assessment and control of the cabbage seedpod weevil (Coleoptera: Curculionidae) in winter canola using insecticides. J. Econ. Entomol. 92: 220-227.
- Butts, R. A. and R. J. Lamb. 1990. Injury to oilseed rape caused by mirid bugs (Lygus) (Heteroptera: Miridae) and its effect on seed production. Ann. Appl. Biol. 117: 253-266.
- Butts, R. A. and R. J. Lamb. 1991. Pest status of lygus bugs (Hemiptera: Miridae) in oilseed Brassica crops. J. Econ. Entomol. 84: 1591-1596.
- Cárcamo, H. A., L. Dosdall, M. Dolinski, O. Olfert and J. R. Byers. 2001. The cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Coleoptera: Curculionidae) - a review. J. Entomol. Soc. B.C. 98: 201-210.
- Cárcamo, H. A., L. M. Dosdall, D. A. Johnson and O. O. Olfert. 2005. Evaluation of foliar and seed-coated insecticides for control of the cabbage seedpod weevil (Coleoptera: Curculionidae) in canola. Can. Entomol. 137: 476-487.
- Cárcamo, H. A., T. R. Larson, C. E. Herle and J. K. Otani. 2006. Life history of *Lygus keltoni* (Hemiptera: Miridae) in the laboratory. Can. Entomol. 138: 871-874.
- Cárcamo, H., J. Otani, C. Herle, M. Dolinski, L. Dosdall, P. Mason, R. Butts, L. Kaminski and O. Olfert. 2002. Variation of Lygus species assemblages in canola agroecosystems in relation to ecoregion and crop stage. Can. Entomol. 134: 97-111.
- **Day, W. H. 2006.** The effect of rainfall on the abundance of tarnished plant bug nymphs [*Lygus lineolaris* (Palisot)] in alfalfa fields. Trans. Am. Entomol. Soc. 132: 445-450.
- Dosdall, L. M., D. Moisey, H. Cárcamo and R. Dunn. 2001. Cabbage seedpod weevil factsheet: [Edmonton], Agdex 622-21. Alberta Agriculture, Food and Rural Development, Edmonton, 4 pp.
- Dyer, M. I., C. L. Turner and T. R. Seastedt. 1993. Herbivory and its consequences. Ecol. Appl. 3: 10-16.
- Ehler, L. E. 2004. An evaluation of some natural enemies of *Spodoptera exigua* on sugarbeet in northern California. BioControl 49: 121-135.
- Free, J. B., A. W. Ferguson and S. Winfield. 1983. Effect of various levels of infestation by the seed weevil (*Ceutorhynchus assimilis* Payk.) on the seed yield of oil-seed rape (*Brassica napus* L.). J. Agric. Sci. Cambridge. 101: 589-596.
- Gavloski, J. E. and R. J. Lamb. 2000. Compensation for herbivory in cruciferous plants: Specific responses to three defoliating insects. Environ. Entomol. 29: 1258-1267.
- Harper, F. R. and B. Berkenkamp. 1975. Revised growth stage key for *Brassica campestris* and *B. napus*. Can. J. Plant Sci. 55: 657.
- Lamb, R.J. 1989. Entomology of oilseed Brassica Crops [online]. Annu. Rev. Entomol. 34: 211-229.
- Lerin, J. 1984. Assessment of yield loss in winter rape due to seedpod weevil (*Ceutorhynchus assimilis* Payk.) II. Yield loss in a cage experiment. Agronomie 4: 147-154.
- Rosenheim, J. A., R. E. Goeriz and E. F. Thacher. 2004. Omnivore or herbivore? Field observations of foraging by *Lygus hesperus* (Hemiptera: Miridae). Environ. Entomol. 33: 1362-1370.
- Rubia-Sanchez, E., Y. Suzuki, K. Miyamoto and T. Watanabe. 1999. The potential for compensation of the effects of the brown planthopper *Nilaparvata lugens* Stal (Homoptera: Delphacidae) feeding on rice. Crop Prot. 18: 39-45.
- SAS. 2003. SAS Institute Inc., Cary, NC, USA.
- Schwartz, M. D. and R. G. Foottit. 1998. Revision of the Nearctic species of the genus *Lygus* Hahn, with a review of the Palaerctic species (Heteroptera:Miridae). Associated Publishers, Gainesville, FL.
- Sylven, E. and G. Svenson. 1975. Relationship between density of *Ceutorhynchus assimilis* Payk. (Col.) and damage by *Dasyneura brassicae* Winn. (Cec.) in a cage experiment in summer turnip rape. Statens Vaxtskyddsanst Medd. 16: 53-60.

- Tatchell, G. M. 1983. Compensation in spring-sown oil-seed rape (*Brassica napus* L.) plants in response to injury to their flower buds and pods. J. Agric. Sci. 101: 565-573.
- Tommey, A. M. and E. J. Evans. 1992. Analysis of post-flowering compensatory growth in winter oilseed rape (*Brassica napus*). J. Agric. Sci. Cambridge. 118: 301-308.
- Tulisalo, U., S. Korpela and A. Pohto. 1976. The yield loss caused by the seedpod weevil *Ceutorhynchus assimilis* Payk, (Col., Curculionidae) on summer turnip rape in cage experiments. Ann. Entomol. Fennici. 42: 98-102.
- Turnock, W. J., G. H. Gerber, B. H. Timlick and R. J. Lamb. 1995. Losses of canola seeds from feeding by Lygus species [Heteroptera: Miridae] in Manitoba. Can. J. Plant Sci. 75: 731-736.
- Williams, I. H. and J. Free. 1979. Compensation of oil-seed rape (*Brassica napus* L.) plants after damage to their buds and pods. J. Agric. Sci. 92: 53-59.
- Wise, I. L. and R. J. Lamb. 1998a. Economic threshold for plant bugs, *Lygus* spp. (Heteroptera: Miridae), in canola. Can. Entomol. 130: 825-836.
- Wise, I. L. and R. J. Lamb. 1998b. Sampling plant bugs, Lygus spp. (Heteroptera: Miridae), in canola to make control decisions. Can. Entomol. 130: 837-851.