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Does Canola Compensate for Lygus Bug Damage?

Final Report – Crop Years 2000, 2001

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Abstract

Canola's ability to compensate for herbivore damage is essential information for the management of lygus bugs. In Alberta, we studied plant architecture, seed yield and other vegetative and reproductive attributes potentially involved in compensation in two experiments, manipulating density and duration of infestation of lygus bugs during the bud through bloom period of *Brassica napus*. After seedling emergence, plants were individually caged and density treatments (0, 2, 4, 6 and 10 lygus bugs / cage) or duration treatments (0, 5, 10, 15, and 20 days, all with four bugs / cage) were applied at bud. At harvest, plants were retrieved for measures of stature and feeding damage. Yields were measured by seed size.

Density experiments showed that plants became more robust with increasing lygus density. Canola stem diameter, biomass, and branching were significantly increased by lygus treatments. Total seed weight increased at Beaverlodge in 2000: seed production in high-density treatments more than doubled (221%). In all other cases, seed weight was not significantly affected, either in total or by size class. No negative treatment effects on plant productivity were found. Duration treatments did not affect stem diameter, height, biomass, or total seed yield. Lygus-treated plants produced 23% more buds than controls, however. Greatest numbers of buds were produced after a 5-day exposure. Duration experiment small seed weight increased significantly (38% overall) in a stepped manner: small seed production increased at 5 days and again at 20. Damage to plants was significant: bud and pod abscission increased after15 days exposure possibly due to a decline in the ability of plants to produce new buds. Drought is implicated in these plant responses as an additive factor that did not interact with lygus treatments.

These induced defensive responses to lygus feeding were agronomically positive. Yield losses were not found although yield increases sometimes occurred. Bud "blast" was not a useful indicator of potential yield since losses in buds and pods occurred both when yields were improved and when no changes in yield could be detected.

We conclude that insecticidal control of lygus at early growth stages in canola is not a prudent strategy. In our experiments, plants with lygus bugs were more productive. Where growing conditions allow compensation for bud damage to occur, lygus bugs present in canola during bud through flowering stages do not pose a threat to yield. Early-season populations of lygus bugs are not pests – their feeding benefits canola plants through the release of apical dominance.

Introduction

Farmers concerned about the numbers of lygus in their canola applied insecticide to an estimated 1.4 million acres of canola in Alberta in 1998. Much of this insecticide treatment was outside the recommended application window of late flowering through early pod ripening (stages 4.4 - 5.2). Insecticide applications for lygus were general throughout the province and 1998 canola yield losses in Alberta were confounded by the combined impacts of drought and damage from other insects. Significant infestations of bertha armyworm occurred in the Manning area, for instance, along with drought and heavy infestations of lygus. It was not possible to determine the proportion of the damage due solely to lygus, however, the total treatment cost for the 1998 lygus infestation likely exceeded $12 million. The yield loss was unknown.

Insecticide treatment of canola for lygus infestation occurred for the first time in Alberta in 1996 when about 10,000 acres were treated in the Lethbridge-Vulcan area. In 1997, an estimated 200,000 to 400,000 acres of canola were treated for lygus primarily in central and southern Alberta. In 1998, about four million acres of canola were seeded in Alberta and a significant portion of the canola acres in the Peace River area of Alberta were subsequently heavily infested with lygus. Notable by its severity was the Grande Prairie infestation, at bud through early flowering, of fall-seeded and early spring-seeded canola. Surveys of lygus in canola, the first widespread surveys of lygus bugs conducted for the province, were conducted throughout Alberta during bolting (June 1998) and again in late bloom stage canola (July). These surveys confirmed high rates of infestation in the Peace. High infestation rates of lygus continued in the province throughout 1999.

It was previously recognized that Alberta had three primary pest lygus species in canola: *Lygus lineolaris* (Palisot de Beauvois), *L. borealis* Kelton , and *L. elisus* Van Duzee (Butts and Lamb 1990a). A survey of lygus in canola conducted in southern Alberta in 1997, however, found that an additional species, *Lygus schulli* Knight, was dominant that year (48% of specimens) (Peter Mason, personal communication). In a taxonomic revision of the genus, Lygus, *L. keltoni* Schwartz was recognized as a new species, replacing many of the records for *L. schulli*, including (in part) those from the 1997 survey (Schwartz and Foottit 1998).

The relative abundance of lygus species in canola and other crops has been observed to change abruptly. For instance, *L. lineolaris* went from being the least abundant lygus species in canola in Alberta from 1982 - 1985 to the most abundant species in 1986 (Butts and Lamb 1991b). All four species can occur together in canola (Schwartz and Foottit 1998) and may cause the same damage but this has not been demonstrated. The pest status of *L. keltoni* is uncertain and *L. schulli* has not been studied as a pest of canola.

Compensation is the process by which plants respond positively to recover from effects of pest injury on plant growth (Rubia-Sanchez *et al.* 1999). It is seen as one of fourteen host-plant resistance mechanisms known to moderate insect-plant interactions (van Emden 1997). In this scheme, compensation has been shown to involve mechanisms affecting quality of seed yield, resource allocation, plant phenology (particularly the timing of maturation), plant architecture, and other structural modifications. External factors, such as nutrients, frost, water and light levels, and the level of interspecific competition, are widely thought to modify these responses. Inadequate pollination, too, can be important although *Brassica napus* is mainly self-pollinating and outcrossing occurs at rates of 20 to 30% (Thomas 2000). But while good agronomic conditions should favour compensation, it has been proposed that selection for agronomic traits in crops may favour reproductive growth over vegetative growth (Meredith Jr. and Wells 1989) and decreased growth form plasticity ([Welter and Stegall 1993][Rosenthal and Welter 1995]). Both of these selection pressures could reduce a crop’s ability to compensate for arthropod herbivory. The processes that produce the compensation response are largely unknown but may contain a "biphasic" element in which increasingly severe herbivory eventually results in decreased plant growth or reproduction (Dyer *et al.* 1993; Lowenberg 1994; Rosenheim *et al.* 1997).

Tolerance, in artificially or naturally damaged vs. undamaged plants, is often equated with compensatory ability (e.g., Belsky 1986). Tolerance traits contribute to fitness by determining the amount of regrowth and reproduction occurring after damage. Undercompensation, in which damaged individuals have lower fitness than undamaged controls, is an expression of a plant's inability to tolerate damage (Marquis 1996) while overcompensation results in greater fitness for individuals than undamaged controls.

All lygus bugs overwinter as adults (Kelton 1975); pest species move into canola when buds form in the crop (Butts and Lamb 1991b). In most years, lygus damage is confined to spring-seeded canola but in 1998, fall-seeded canola was damaged in the spring by large numbers of overwintered lygus adults (Jones 1999b). Lygus bugs damage the buds, flowers and seeds of host plants by puncturing and lacerating tissue, injecting salivary gland secretions that liquefy cell contents, and then ingesting the fluids (Miles 1972). Symptoms of lygus feeding in canola include small brown lesions at feeding sites, bud abscission, shedding of injured flowers, seed coat punctures, partial to complete collapse of seeds, endosperm necrosis, and chalky spots surrounding the puncture (Butts and Lamb 1990b). Additionally, under heavy feeding pressure, sap was seen oozing from multiple feeding punctures per plant in many Alberta fields in

1997 and 1998. Lygus are pests of canola. Up to 30% seed loss occurred in southern Alberta in 1983 (mean about 6% regionally) (Butts and Lamb 1991a). From 1985 – 1990, an estimated 10 - 18% of seed was collapsed in southern Manitoba (Turnock *et al.* 1995). Shrivelled ('blasted') seed accounted for 10 - 50% of total canola yield harvested from fields in the Olds area of Alberta (Jones 1997; Phil Thomas, personal communication).

Despite this damage, canola has been found to compensate for 'indirect' losses – of buds and flowers (e.g., Tatchell 1983). However, data from studies in Alberta show that this result could not be predicted and that the amount of loss appeared to vary with growing conditions (Butts and Lamb 1990b). In that Alberta study, the relationship between growing conditions and feeding injury to the plant was complicated by an overcompensation response in which bud loss resulted in increased numbers of pods. Nonetheless, total seed weight was not always fully compensated. Overcompensation in pod numbers was apparently achieved in a dry year but not in a wet year (Butts and Lamb 1990b).

In Britain, Tatchell demonstrated compensation in canola using the pollen beetle, *Meligethes aeneus*, which causes bud and pod loss similar to that caused by lygus (Tatchell 1983). Although the author admitted that many factors were not controlled that could have affected bud loss, *Brassica napus* plants compensated with increased yield, increased numbers of axillary racemes and increased numbers of pods per raceme. Damage from beetle feeding and from artificial pruning of buds failed to demonstrate yield loss, regardless of the level of injury. The importance of plant nutrition was acknowledged but no mention was made in either of these studies of the soil fertility levels or of fertilizer applied.

Our project sought to determine the impact on canola yield and other components of plant compensation caused by lygus feeding during bud through bloom period. Lygus bug density and duration of lygus infestation were manipulated. A third experiment examined how levels of a balanced nitrogen-sulphur fertilizer influenced the compensation response.

Methods and Materials

Lygus Bug Density Experimental Design

Five subsample plants were selected from within plots using a stratified random sampling plan. Within plots, all subsample plants were caged individually and received the same treatment. Four replicate sets of treatment plots were used. Within cages, lygus bugs were introduced at 0 (the control), 2, 4, 6 or 10 adults per plant at the bud stage. Equal numbers of males and females of a single species were introduced to each cage. Cages were checked regularly and insects were replaced as necessary to maintain treatment numbers. Cages were removed at the end of the treatment period. To maintain plots free of insect pests from the end of treatment until harvest, plots were swept and, if needed, insecticide was applied.

Data were collected on soil fertility (pre-seeding soil samples were taken to determine fertility levels required). Compensation data measurements were taken post-harvest including plant biomass, yield (distribution of seed size and weight), and architectural measures (# racemes, # pods / raceme). Feeding injury was measured as the number and position of buds blasted. Growth stage observations were taken.

Duration of Lygus Infestation Experimental Design

Identical design to the density experiment but with infestation density treatments replaced by infestation duration treatments. In this experiment, a standard lygus density of four lygus bugs per plant was established on caged plants at the bud stage. As much as possible lygus were identified to species and two males and two females of a single species were used per cage. Insects were left on plants for 5, 10, 15, or 20 days. Control plants had no insects but were caged and otherwise treated identically. Cages were left in place until all treatments were completed. To maintain plots free of insect pests from the end of treatment until harvest, plots were swept and, if needed, insecticide was applied.

Impact of Sulphur Fertility Experimental Design

This experiment, performed in the Edmonton area only and on sites deficient in sulphur, used a standard infestation rate of four lygus bugs per plant (two males and two females of the same species) established on plants in bud. Treatments consisted of different rates of sulphur fertilizer to achieve 0%, 50% and 100% of optimal fertility). At Muir Lake in 2000 and Ellerslie in 2001 plots were fertilized to achieve 0-, 10-, and 20-kg plant available S / ha. Fertilizer treatments were banded with the seed. Plots were about 2.5 metres x 8.5 metres with five subsample plants caged per plot. The experiment was replicated in four blocks. Cages were removed at the end of the treatment period at which time insecticide was to be applied as needed to maintain plots free of insect pests. The same set of measurables as the above experiments was used.

Sites

Experiments were conducted at four sites in Alberta in three different ecozones. Lethbridge, the most southerly site, at 49E42' N, 112E50' W is in the brown soil zone of the Moist Mixed Grassland ecozone.

Ellerslie, at 53E33' N, 113E30' W near Edmonton in the black soil zone, is part of the Aspen Parkland ecozone. The Beaverlodge site, at 55E12' N, 119E27' W in the Alberta Peace River region, is on gray luvisol soil in the Peace Lowland ecozone. Selected sites were agronomically representative of fields in their areas. The density experiment was conducted at all three of the above locations, while the duration experiment was conducted at Lethbridge and Ellerslie. The sulphur experiment was conducted at Muir Lake (53° ' N, 114° ' W) in 2000 and at Ellerslie in 2001. Both of the latter sites were sulphur-deficient. At all sites, nitrate, phosphate, and sulphate fertility levels were determined by pre-seeding grid sampling. Number and spacing of soil samples taken depended on variability. Pre-seeding herbicides for annuals and volunteers were applied according to need at the sites.

Beaverlodge - Experiments were conducted on the Beaverlodge Research Farm. Plots were sown on 2000 May 15 on summerfallow using a Conserva-pac seeder with 9" row spacing. Fertilizer applied was 12-51-0 (50kg/ha). Significant flea beetle damage in seedling stand required control. Deltamethrin (Decis 5.0EC) was applied 2000 June 07. Lygus were introduced at 2000 July 08 to caged plants at early- to mid-bud (stage 3.1) and removed August 04 at mid-flower (stage 4.2). Insecticide applications were made twice (post-treatment) during August to prevent damage from flea beetles. Snowfall of 15 cm 2000 September 01 did no apparent harm to plants, which were harvested in late September.

Edmonton - The density and duration experiments were set up at the Ellerslie Research Station on barley stubble and The sulphur experiment at Muir Lake in 2000 on oat stubble and at Ellerslie in 2001 on barley stubble. Soil samples were taken at Ellerslie on 2000 May 08 and 2001 May 24, and at Muir Lake on 2000 May 03. The Ellerslie site was fertilized with 100 kg N / ha as urea, 30 kg P /ha as 0-45-0, and 20 kg S / ha as K_2SO_4. Muir Lake plots were fertilized with 60 kg N / ha (as urea pre-banded) and 0, 10 or 20 kg S / ha (as K_2SO_4). Canola was seeded 2000 May 22 and 2001 May 25 with a Fabro double-disc press drill equipped with on-row packers and eight-inch row spacing at a depth of 1.2 cm (0.5 in) and a rate of 6.7 kg / ha. Plot size was 2.4 by 8.5 m. Herbicides were applied 2000 June 20 (Ellerslie) and June 26 (Muir Lake) and 2001 June 19. Poast Ultra (150 ml / ac) + Muster (110 ml/ac) + Lontrel (227 ml/ac) + Merge surfactant (400 ml/ac) were applied by plot sprayer. Post-experiment insecticide treatment was not required. Plots were harvested at Ellerslie on 2000 Sep 20 and 2001 October 09 and at Muir Lake on 2000 Sep 21 using a small plot combine.

Lethbridge - The density and duration experiments were established at the Victory Church site of the Lethbridge Research Centre on land fallowed the previous year. Soil analysis indicated no need for additional fertilizer. Edge was applied for weed control after seedbed preparation by discing. Seeding of all plots at 7.8 lb./ac was done on the same day, 2000 May 02, with a Valmar air seeder, followed by two passes of a draw-bar harrow packer. Lack of rainfall after seeding resulted in poor moisture conditions and uneven, delayed germination. Plants were caged at the mid- to late-bud stage. Both experiments were re-stocked as required to maintain treatment numbers after searching for live bugs inside the cages. At the completion of experiments, plots were sampled for insect problems and treated with insecticide if required. Developmental stage of each plant was determined by opening a small portion of the bottom pod to examine the color of the seed. Ten pods from the main stem were collected from each of the caged plants. Plants were harvested on 2000 August 22 into cloth bags as they matured (yellow pods). At Lethbridge in 2000, harvested plants were so badly stunted by drought it was felt that there was little value in collecting architectural data. Because of the prolonged drought, experiments were not conducted in 2001 at Lethbridge.

Experimental Animals - Lygus Bugs

Lygus populations vary considerably in abundance from year to year and regionally (Cárcamo *et al.* 2002), so experiments conducted in different geographic zones and over more than one year were expected to give the results wider applicability. Lygus bugs used at Ellerslie were swept from a nearby alfalfa field, collected individually into glass vials, sexed, and identified. Male and female lygus in equal numbers were introduced to cages and cages were monitored throughout the experiments to ensure constant infestation densities over the course of treatments. At Lethbridge, lygus were collected from various canola fields in the vicinity and were added to cages on July 22 and 23. Bugs were collected into large plastic bags held in iced buckets to prevent overheating. Bugs were stored at 12E C overnight, then taken to the field and transferred to cages using snap vials. Single species were not selected but equal sex ratios were added to cages.

Plants were caged and insect treatments applied after the formation of buds but before flowering. At the completion of treatments, lygus bugs were collected from cages and preserved in ethanol for later confirmation of species identity. Cages were then removed. From the end of treatments until harvest, sweeps of plots were conducted and insecticide was applied, if populations of lygus or other pests warranted, thereby avoiding the possibility of additional damage to plants.

Experimental Plants - Canola

Brassica napus variety Q2 seed for all sites was taken from a single bag and sorted by size using the standard soil sieve series #10 (2.00 mm opening) and #12 (1.70 mm opening). The middle fraction (< 2.00 and > 1.70 mm) was treated with fungicide (carbathiin, thiram and metalaxyl) before seeding. Plots were about 2.5 metres by 8.5 metres. Plots were seeded at about 6.7 kg/ha and at a seeding depth of 1.2 cm (0.5 in). Fertilizer was applied as required by soil test recommendations to achieve optimal, balanced fertility (Experiments 1 & 2).

At harvest, plant height was measured to the extended length of their uppermost branches. Plants were then cut at about 1 cm above ground level. Because canola stems are not necessarily round, multiple measures of basal stem diameter were taken at the cut end using calipers. At Ellerslie, roots of density and duration experiment plants were recovered from a soil volume of about 20-cm diameter by 25-cm depth. Roots were washed, measured for length, oven dried at 60°C for 48 hr. and weighed. Once raceme measurements were taken, all aboveground plant material was oven-dried, as above, before weighing. Additionally, at harvest in Lethbridge, the length of the lowest pod on the main stem was measured. After harvest, roots were collected by digging ca.10 cm radius around the plant; only the 20 bug/plant and control plots were selected.

In this report, plant stature attributes refer to stem diameter, plant height, aboveground biomass, and, where measured, total plant biomass (including root biomass). Plant reproductive attribute consist of seed yield (the weights of seed in the three size categories), and numbers of buds and pods per raceme. Architectural attributes consist of the numbers of primary, secondary and tertiary branches. Feeding damage is the number and position of abscised buds and pods. Lost buds could be differentiated from lost pods by their shorter, thinner pedicel. Growth stage observations were taken.

Statistical Analyses

Data were transformed using log (x + 1); mean values listed in this report are the untransformed, raw means. The General Linear Model procedure of SAS (SAS Institute Inc. 1988) was used to analyse single-site, single-year data sets with a fixed-effects model suitable for these randomized complete block designs. Levene's test was used for assessing homogeneity of variances (Cochrane and Cox 1992). Statistical testing of multiple-site and multiple-year data was performed with years, sites and their interaction terms specified as random effects. (Blocks, treatments and their interaction terms are thereby fixed effects.) The experimental error terms for all models were appropriate for testing main effects and interactions since subsample data were collected (Steel and Torrie 1980). Significant treatment effects were further investigated using orthogonal contrasts. These three tests compared the control group with the treated group (0 bugs vs. infested); the lowest with the highest treatment group (2-bugs/plant vs. 10-bugs/plant in the density experiment, and 5 days infestation vs. 20 days in the duration experiment); and the middle two lygus-treatment groups. Multiple means comparisons used were Student-Newman-Keuls for balanced data and Tukey for unbalanced data in the fixed effects model. Comparisons of least squares treatment means to the control were made using either the Dunnett or Dunnett-Hsu methods (for balanced or unbalanced data, respectively). A preliminary analysis of covariance showed that stem diameters and plant heights were significantly related. To distinguish the influence of plant height from the treatment effects on stem diameter, the covariate, height, was added to the analysis of variance stem diameter model. In the multiple-site data set for lost reproductive structures in 2000, analysis showed that density treatments did not interact with site, and the following reduced model was therefore indicated:

$$Y = \text{site} + \text{block(site)} + \text{treatment} + \text{treatment*block(site)} + \text{error}$$

During the first year of this research, 1999, we noticed that caged lygus bugs were able to feed through the netting on the bud clusters of neighbouring plants. We tried several techniques in that year to reduce extra-cage feeding. We found that by snapping the stems of neighbouring plants close to the ground, a portion of the neighbouring plant stem would remain horizontal. Subsequent vertical growth then tended to place the bud clusters of the neighbour out of contact with the experimental plant cage. Using this technique, competition for root-zone nutrients was maintained for experimental plants, thus better approximating normal cropping conditions, and extra-cage feeding was greatly reduced. The modified protocol was adopted for 2000 and 2001. Upon completion of the treatments and removal of the cages, experimental plants blended into the plot. Despite having experimental plants marked with flagging tape, we found that a metal detector was useful at harvest for finding the ground-level cage rings that encircled the experimental plants.

Results

As noted above, the original experimental protocol was modified after the 1999 crop year and so inclusion of 1999 data in this report would not be helpful. Results for the 1999 crop year have been reported elsewhere (Jones *et al.* 1999; Jones *et al.* 2000; Jones *et al.* 2001).

Lygus Species Used in the Experiments

Lygus bugs collected from cages at the termination of experiments were identified to species. The dominant species in 2000 were *L. borealis* and *L. elisus* at Lethbridge, and *L. borealis* and *L. lineolaris* in the Edmonton area. Throughout the province that year, the dominant species present were L. keltoni (65 %), L. borealis, and L. elisus (17 % each).

Density of Lygus Infestation

Plant Stature – Height, Stem Diameter, Biomass

Plants did not respond to lygus density treatments in 2000 through height (Table 1; Figure 1). In 2001 at Beaverlodge, however, plants in the highest density lygus treatment were significantly shorter than the 2-bugs/plant treatment ($P = 0.0007$, $F_{1,12}$=20.1; Figure 2). With no difference between the control and infested treatments, or between the 4- vs. 6-bugs/plant treatments, the contrast results showed a curvilinear plant height response to lygus density. In Ellerslie, there was a trend toward taller plants with increasing lygus numbers.

Stem diameters generally increased with increasing numbers of lygus (Table 1). As well, for all experiments showing significant treatment effects, plants with lygus had stem diameters significantly greater than the controls. At Beaverlodge in 2000, the 10-bugs/plant treatment had significantly thicker stem diameters than the 2-bugs/plant treatment. At Ellerslie, in 2000 (Figure 3), stem diameter for the highest density plants were 24% thicker than the controls. In 2001 (Figure 4), the highest density treatment plants had stems 38% thicker than the controls. On average over 2000 and 2001, infested plants at Ellerslie had 21% thicker stems than the controls. At Beaverlodge in 2000, treatments with lygus had plants with stems only 3% thicker than the controls ($P = 0.042$, $F_{1,12}$), while the highest lygus density plants had stems 19% thicker than the lowest ($P = 0.001$, $F_{1,12}$).

Treatments were found to have had a significant effect on aboveground vegetative biomass at Ellerslie in 2000, using total numbers of pods per plant as a covariate measure (P=0.016, $F_{4,12}$=4.73) (Table 2). Contrast comparisons indicated significantly greater biomass in lygus-treated plants than in the controls (P=0.002, $F_{1,12}$=15.3). Dunnett-Hsu comparisons of least squares means with the controls showed that the 6- and 10-bugs/plant treatment plants had significantly greater biomass than the controls (50% and 88% greater; P=0.015 and P= 0.0063, respectively) (Figure 5). In 2001, treatments at Ellerslie were again significant for vegetative biomass data (P=0.011, $F_{4,12}$=5.22) (Figure 6). Contrast testing detected that lygus-treated plants had significantly greater biomass (P=0.005, $F_{1,12}$=11.61) and that the highest lygus treatment plants were significantly more massive (by 40%) than the lowest (P= 0.037, $F_{1,12}$=5.53). The Beaverlodge experiment in 2000 showed a significant treatment effect using total numbers of racemes per plant as a covariate measure (P=0.031, $F_{4,12}$=3.85). Contrast testing found that lygus treated plants were significantly larger (by about 27%) than the controls (P= 0.003, $F_{1,12}$=13.5).

Yields – Seed Weight and Size Distribution

In 2000, a significant treatment effect was found for total seed production at Beaverlodge (P=0.032, $F_{4,12}$=3.79; Table 2). There, total seed weight increased with increasing numbers of lygus bugs (Figure 7). This response resulted from increased seed production in the lygus-treated plants relative to the control (P= 0.009, $F_{1,12}$= 9.71). Dunnett's comparison of least squares treatment means with the control showed significantly increased production in plants infested at the 4- and 10-bugs/plant levels (200% and 221%, respectively; Table 2). Total seed production in 2001 did not respond significantly to the lygus treatments. The apparent trend at Ellerslie in 2001 was non-linear, with increased production at the lower treatment levels. The trend at Beaverlodge in 2001 was also apparently non-linear, but in the opposite direction (Figure 8).

Seed weight for large seed was not responsive to treatment in any year or at any site (Table 3). In both 2000 and 2001 at Ellerslie, large seed weight was maximized in the 4-bugs/plant treatment, however. This was true as well at Beaverlodge in 2000, but in 2001, the greatest seed yield in the large size class was obtained in the 10-bugs/plant treatment (Figure 9). Seed weight for the medium and small size classes likewise did not show a treatment response and the trends across treatments at each site were similar for medium seed to those found for large seeds. Small seed weights tended to increase with increasing lygus numbers at both sites in 2000 but did not do so in 2001 (Figure 10). Treatment responses at Beaverlodge were consistent across size classes within years but differed among years.

Branching Patterns

Experiments at Ellerslie showed a significant treatment effect for total numbers of branches produced in 2000 (P = 0.026, $F_{4,12}$ = 4.06; Figure 11) and again in 2001 (P = 0.021, $F_{4,12}$ = 4.34; Figure 12) (Table 4). In both years, control plants produced the fewest branches. Significantly more total branches were produced by lygus-treated plants in 2000 (P=0.0424, $F_{1,12}$=5.15) and in 2001 (P=0.008, $F_{1,12}$=9.94) – 56 and 57% more, respectively. In addition, the analysis of 2000 data showed that the 10-bugs/plant treatment had almost double the branches of the 2-bugs/plant treatment (P=0.011, $F_{1,12}$=9.08, Figure 11). In 2001, lygus-treated plants at Ellerslie had 57% more total branches on average than the control plants (P=0.008, $F_{1,12}$=9.94, Figure 12).

The above data for total branches were broken down into branching levels. Numbers of main racemes (level 1 branches) per plant were not affected by treatments in 2000 but significant treatment differences occurred at Ellerslie in 2001 (P=0.011, $F_{4,12}$=5.30; Table 4). At that time, control plants had only 86% the number of main racemes as the lygus-treated plants (P=0.016, $F_{1,12}$=7.90; Figure 13). As with total numbers of branches, the trend of greater numbers of main racemes was evident for Beaverlodge plants in both years.

Secondary branches showed significant treatment differences on two occasions: in 2000 (P=0.023, $F_{4,12}$=4.25) and 2001 (P=0.001, $F_{4,12}$=9.25; Table 5) at Ellerslie. In 2000, the control treatment produced significantly fewer secondary branches, only 56% of the number produced on average by the lygus-treated plants (P=0.008, $F_{1,12}$=9.98). As well, contrast testing detected that the highest treatment rate produced 88% more secondary branches than the lowest treatment rate (P=0.028, $F_{1,12}$=6.29; Figure 14). In 2001 at Ellerslie, control plants had only 70% the number of secondary branches relative to the lygus-treated plants (P=0.0004, $F_{1,12}$=23.46). In addition, the lowest treatment level had significantly fewer branches, 71% of the highest treatment level (P=0.009, $F_{1,12}$=9.58; Figure 15).

Numbers of tertiary branches were unaffected by lygus treatments in 2000 but were significantly more numerous with increasing lygus density at Ellerslie in 2001 (P=0.010, $F_{4,12}$=5.31; Table 5). Contrast testing determined that this trend was due primarily to the difference between the control and lygus-treated plants (P=0.002, $F_{1,12}$=15.63; Figure 16).

In general, plants at Beaverlodge had greater numbers of branches at all levels than did plants at Ellerslie. Lygus treatment effects, when evident, indicated a response trend toward fewer branches with increasing numbers of lygus at Beaverlodge. The response was opposite in direction at Ellerslie, where increasing the numbers of lygus produced greater numbers of branches.

Damage Patterns

Analyses of variance of lost reproductive structures data by site-year showed significant treatment effects at Ellerslie in 2000 (P=0.035, $F_{4,12}$=3.69) and 2001 (P=0.020, $F_{4,12}$=4.45; Table 6). The damage trend at Ellerslie in both 2000 and 2001 showed increasing damage with increasing lygus densities. Contrast testing of the 2000 data showed a significant increase in numbers of lost structures in the high density treatment (more than doubled) compared with the low density (P=0.008, $F_{1,12}$=10.16; Figure 17). In 2001, numbers of lost structures at Ellerslie increased 48% on average in the lygus-treated plots compared with the controls (P=0.020, $F_{1,12}$=7.24; Figure 18).

Beaverlodge 2000 data showed no significant treatment effect (P=0.4204) although control plants at both Ellerslie and Beaverlodge sites had fewer lost structures than did plants in any of the lygus-treated plots.

In 2001, as well, treatments did not significantly affect numbers of lost buds and pods (P= 0.8221). While the trend in 2000 was toward greater numbers of lost structures with increasing numbers of lygus, the opposite seemed to be the case at Beaverlodge in 2001.

Plant responses for lost reproductive structures had similar forms at Ellerslie and Beaverlodge in 2000. As well, the data were found to have homogeneous site variances (P=0.6466). These data were then analyzed using a multiple-site analysis of variance (treatment P=0.0773) which showed that the site-by-treatment interaction was not significant (P=0.603). This finding was consistent with other site-by-treatment interactions for the density experiment variables and the site-by-treatment interaction term was removed from the model. The reduced model showed significant site differences (P=0.0008, $F_{1,6}$=38.20; Table 7). Beaverlodge had 92 lost structures per plant, averaged over all treatments, while Ellerslie plants averaged 51. The treatment effect was also significantly (P=0.019, $F_{4,28}$=3.50; Figure 19). Over both sites, control plants had 45% fewer lost structures (mean ± std: 52.9 ± 34.92) than lygus-treated plants (76.7 ± 59.32; P=0.020, $F_{1,28}$=6.12). As well, the contrast test for lowest vs. highest treatment rates was significant: the 2-bugs/plant treatment had 70% fewer lost structures than the 10-bugs/plant treatment (P=0.010, $F_{1,28}$=7.55).

The same process was applied to data for the total numbers of healthy (seed-bearing) pods by site-year and by year over both sites. No significant treatment effects were found for healthy pods at either Ellerslie or Beaverlodge when data were analyzed by site-year. The multi-site data set for 2000 were homogeneous for site variances (P=0.6466). The multi-site ANOVA showed significant differences between sites (P=0.0449, $F_{1,2.9}$=11.4): Beaverlodge plants produced 58% more seed-bearing pods than did plants at Ellerslie. Lygus treatments had a significant and positive effect on numbers of pods (P=0.0173, $F_{4,4}$=11.81): all lygus-treatment means were greater than the control (Table 7) although treatment means could not be separated.

Significant heterogeneity of variances existed in the lost-structures, healthy pods, and total-structures multiple-site data sets for 2001 (P=0.0015, P=0.0120, and P=0.0018, respectively) and these combined-site models were not tested.

Analysis of Ellerslie data over the two-year period, 2000-2001, showed that the lygus treatments significantly increased total numbers of pods (P=0.0425, $F_{4,4}$=7.04; Table 8). Contrast testing further indicated that infested plots had significantly greater numbers of pods than controls (P=0.0208, $F_{1,24}$=6.12). Numbers of lost reproductive structures (buds and pods) were similarly analyzed. The multi-year data for bud and pod loss at Ellerslie were not homogeneous over years. Numbers of total reproductive structures produced by plants (healthy, seed-bearing pods plus abscised buds and pods) increased on Ellerslie plants due to lygus density treatments (P=0.0141, $F_{4,4}$=13,25). This increase was due primarily to greater bud production in lygus-treated plants (P=0.0100, $F_{1,24}$=7.82; Figure 20). Only the lost-structures data over both years at Beaverlodge could be analyzed; No multi-year treatment effects were found for Beaverlodge.

Duration of Lygus Infestation

Plant Stature – Height, Stem Diameter, Biomass

Plant height was not significantly affected by the duration treatments in either 2000 or 2001 (Table 9). Inspection of the means indicated that Ellerslie plants in both 2000 and 2001 were shortest in the control plots although this was not the situation at Lethbridge where the shortest plants were in the 10-day treatment (Figure 21). The differences in height between shortest and tallest treatments at each site-year were about 4-8%. A two-year ANOVA conducted for the stem diameter data (Table 10, Figure 22) found smaller treatment probabilities, although changes remained insignificant.

Basal stem diameters were not responsive to treatments and no significant differences were found in single site-year ANOVAs (Table 9). Smallest stem diameters were found in the 20-day treatments at Lethbridge (13% smaller than the thickest stems) but in the control groups in both years at Ellerslie. At Ellerslie in 2000, control plant stems were 6% thinner than the thickest, 10-day treatment plants and, in 2001, were 8% thinner than the thickest, 5-day treatment plants (Figure 23). Stem diameter treatment means could not be separated with a combined analysis of 2000 and 2001 data (Table 10). Over both years, the thickest stem diameters were in the 5-day treatment group, the thinnest diameters in the controls.

Vegetative, aboveground biomass data for both sites showed response levels similar to height and stem diameter - no significant differences were found. The smallest treatment biomass means at Ellerslie were the controls while the smallest treatment biomass means at Lethbridge were in the longest-duration treatment (Table 9). At Lethbridge, the largest treatment (15-day) biomass was twice the smallest treatment mean (20-day). At Ellerslie, the largest treatment means were the 20-day and 5-day treatments (in 2000 and 2001, respectively) which were 23% and 14% larger than controls, respectively (Figure 24). Multiple-year analysis showed lygus treatments did not significantly affect the biomass changes. The smallest biomass plants were in the controls and the largest biomass plants were in the 5-day treatment group (Table 10).

Yields – Seed Weight and Size Distribution

Total seed yield was not significantly affected by the duration of lygus treatment in any of the single site-year ANOVAs (Table 11). The trend in seed production at Lethbridge in 2000 was essentially flat but at Ellerslie, there was a trend toward increased yield productivity with longer exposure times to lygus

(Figure 25). Lowest yields for Ellerslie in 2000 were found in the control treatment plots, while the lowest yields at Ellerslie in 2001 were in the 15-day treatment plots. Data for the two years showed different trends at Ellerslie. In 2000, all lygus-treated plots showed yields greater than controls while in 2001, all lygus-treated plots were either approximately equal to or lower than the controls.

Analyses of large, medium and small seed yields from the Ellerslie site for 2000 and 2001 all showed no significant treatment effects (Table 11). Total seed weight and seed weights by size class were analyzed over the two-year period. The ANOVA indicated a significant treatment effect for the small size category ($P=0.0291$, $F_{4,4}=8.81$) but significance testing using contrasts and multiple least squares means tests did not uncover further separation of these data (Table 12). Small seed weights had significantly larger treatment means with increasing duration of exposure to lygus over both 2000 and 2001 (Figure 26) but large and medium seed data did not show significant treatment effects.

Branching Patterns

No significant treatment effects were found for total branches per plant or for primary, secondary, or tertiary branches per plant when these data were analyzed by year (Table 13). The trends evident for the branching variables indicated the possibility of increased total branching in lygus-treated plots relative to controls in both 2000 and 2001 and a trend in 2000 of greater branching with increasing lygus treatment duration (Figure 27).

Multiple-year analyses of total, primary, and secondary branching showed no significant treatment effects although the probability level for total branches (using log-transformed data, $P=0.0790$) indicated a strong trend toward greater branching in lygus-treated plants than the controls (Figure 27). However, all lygus-treated plots had tertiary branching means greater than control plots (Figure 28) and the 20-day treatment mean greater than other means. In addition, years had a significant effect on the degree of total, secondary, and tertiary branching. Branching was reduced for year 2000 plants by 29, 24, and 49%, respectively compared with 2001 levels (all $P<0.0001$).

Damage Patterns

Lost reproductive structures – aborted buds and pods that had either abscised or remained shrivelled on the plant – were evident on the harvested plants. Single site-year analyses of the numbers of healthy (seed-bearing) pods, abscised and aborted structures, and the total of these (total structures) showed that lygus duration treatments were significant only for abscised structures in 2000 ($P=0.0297$, $F_{4,12}=3.90$; Table 15).

Contrast testing established that control plants had significantly fewer abscised structures than lygus-treated plants (P=0.0081, $F_{1,12}$=10.05). In both years, the lowest level of abscised structures in the lygus-treated plots occurred in the 10-day treatment. The contrast test for 10 vs. 15 days in 2000 showed a trend of lower abscission levels in the 10-day treatment (P=0.0737, Figure 29). The same trend of highest abscission rates in the 15-day treatment and lowest in the 10-day occurred in 2001 as well. Two-year analyses of these data for Ellerslie showed significant year effects in the numbers of productive pods, lost structures and total structures (Table 16). Plants produced more buds and pods in 2001 than in 2000 and more of these were lost to lygus treatments in 2001 than in 2000. Plant production of total structures was significantly greater because of the duration treatments (P=0.0048, $F_{4,5}$=16.59; plant height covariate P<0.0001) although contrast testing and means separation tests did not identify the source of this difference. Similarly, total lost structures were significantly affected by lygus treatments (P=0.0004, $F_{4,4}$=81.71) and although there was some evidence that losses in the lygus-treatments were greater than in the control, the data were not significantly different (P=0.0651). Analysis of data for abscised structures showed that duration of lygus infestation was significant (P=0.0052) with significantly fewer abscised pods in the controls than in the lygus-treated plants (P=0.0059, $F_{1,24}$=9.13). As well, the 10-day treatment had significantly fewer abscised pods than the 15-day treatment (P=0.0174, $F_{1,24}$=6.52; Figure 30).

Impact of Sulphur Fertility

Repair and replacement of nets consumed more resources for these experiments in 2001 than in other years of the project. Severe wind and heavy rain destroyed netting for many cages on two occasions. On July 17, many nets were destroyed by high winds and heavy rain in the Ellerslie area. On July 28 and 29, we again had very heavy rains and high winds throughout the area and many cages were ripped open. We made the decision to scuttle the sulphur trial and so salvage the density and duration studies with the remaining nets. Repairs to cages were made and lygus restocked so that the density and duration experiments could continue. The results reported below are from the study conducted at Muir Lake in 2000.

Sulphur deficiency symptoms were present, although not as pronounced as they had been at Hubbles Lake the previous year. No significant differences were found among the plant stature attributes: height, stem diameter, and biomass. Plants having no additional sulphur were as tall, weighed as much, and had stems and roots as thick as the plants with added sulphur (Table 18). Tertiary- and quaternary-level branches and total branches per plant were all significantly greater in the control plants than in the plants with additional sulphur. Primary and secondary branches of control plants also had mean numbers greater than both sulphur-treatment means but not significantly so (Table 19). Damage to reproductive structures was evident in the numbers of aborted buds and abscised pods. Control plants lost significantly more buds and pods than plants with additional sulphur. Reproductive potential – the total number of buds produced – was also significantly greater in the controls. This effect, though less dramatic, was present also in the numbers of seed-bearing pods. No significant difference was found in the numbers of healthy pods on sulphur-treated and untreated plants although these were lowest on the controls (Table 20).

Discussion

As in Tatchell's experiments, we found that canola plants can compensate for herbivory in several ways, including increased seed production for indirect loss of buds and flowers (Tatchell 1983). Overcompensation, also seen in our experiments, is thought to be accomplished through the release of apical dominance and its associated increase in growth from nonapical meristems (Aarssen 1995; Rosenheim *et al.* 1997; Trumble *et al.* 1993; Watson 1995). Whether plants compensate fully or overcompensate, the degree is thought to be influenced by environmental factors. For instance, in one set of experiments, overcompensation for lygus damage was apparently achieved in a dry year but not in a wet year (Butts and Lamb 1990b). Tatchell looked at compensation using the pollen beetle, *Meligethes aeneus*, which causes bud and pod loss similar to lygus. In his experiments, *Brassica napus* plants also compensated for pod feeding by increased yield, increased numbers of axillary racemes and increased numbers of pods per raceme (Tatchell 1983). Our experiments sought to determine whether canola could compensate for damage due to lygus bug feeding that occurred between bud and mid to late flowering stages, a damage period that had not been previously examined in canola using lygus. We tested for compensation by manipulating the severity of herbivory in two ways – holding the duration of infestation constant while varying the density of lygus, and holding the density constant while varying the duration of infestation.

Site differences - Characterisation of site differences enhanced our understanding of how plant productivity was affected by local site effects when plants are under stress from lygus feeding. In both experiments, analyses of compensation variables often showed significant site effects. For instance, multi-site analyses conducted on numbers of lost reproductive structures, showed these were greater at Beaverlodge. The proportions of lost structures to the total numbers of buds produced per plant were similar for both sites, however, indicating that the process underlying abortion of buds and pods was the same regardless of site (Table 21).

Year differences – Within-site, multi-year analyses showed that plant characters varied significantly in their structural or yield responses to changes in year-to-year environmental conditions. Considering the drought conditions prevalent, particularly at Lethbridge throughout the experimental period and at Ellerslie in 2001, this is not surprising. What is important, however, is that year-by-treatment interactions were never significant even though the year effects often were. In other words, canola responded to lygus bugs in the same manner regardless of environmental conditions while the impact of drought on canola overrode the impact of the bugs.

Density of Infestation Experiments

Canola compensated for lygus damage at all sites and years. The nature of the compensation was shown to consist of responses in both reproductive and vegetative parameters. Significant treatment responses were found in a number of the parameters tested (summarized in Table 8). Further, these responses were all positive, that is, increases in lygus density produced increases in the response parameters.

Using yield as the primary measure of crop productivity, canola overcompensated for lygus damage in one of the five site-years – *i.e.,* 20% of the time more canola seed was produced in the plots with lygus than in the plots that had no lygus. In that same site-year when yield overcompensation occurred, lygus bug treatments also caused significant losses in buds and pods. In the remaining four site-years, no significant change in yield could be found while, at the same time, two of those four site-years showed significant losses in buds and pods. (Plant structure data were not collected from drought-affected Lethbridge plants in 2000.) Loss of buds from lygus feeding was not, therefore, a useful indicator of potential yield, since significant increases in numbers of lost structures were observed both when yields were improved and when no changes in yield could be detected.

Using biomass and plant structure data as measures of plant productivity to judge the impact of lygus feeding told a somewhat different story. In 2000, Beaverlodge plants showed increased stem diameters in response to lygus density increases while total seed weight also significantly increased. In 2001, only plant height was found to change in response to treatments at Beaverlodge, a measure that in itself does not indicate increased productivity. At Ellerslie in 2000, stem diameters, total branching, and secondary branching all increased in response to treatments. In 2001, Ellerslie lygus-treated plants had significantly greater aboveground biomass while branching at all levels and stem diameters also increased significantly. Over both years, treatments significantly increased numbers of seed-bearing pods produced by Ellerslie plants. Lethbridge plants were significantly drought-affected and no response to treatments could be found. From these five site-years of density experiment data then, sixty per cent clearly showed increased productivity in canola plants without yield loss. Enhanced apical dominance through increased branching appears to be the primary mechanism by which canola compensates for the loss of buds due to lygus feeding. Increases in stem diameter and biomass follow as a natural outcome of branching.

An important measure of yield quality is seed size which we tested but found no evidence that seed size was affected, either in the case of overcompensation or in the cases of full compensation (Table 8). There were trends of increasing weight of small seed with increases in lygus density at both Ellerslie and Beaverlodge in 2000 (Figure 10), in medium seed at Beaverlodge that year and in large seed at both Ellerslie and Beaverlodge. These results for 2000, although hardly conclusive, do not indicate a trade-off in one seed size over another. Rather, it seems that while all size classes showed a tendency to increase in lygus-treated plots relative to controls, this was more pronounced in the small and medium sizes than in the large. On the other hand, control plots had significantly less large seed than lygus-treated plots. Years made little difference in the impact of lygus feeding on yield or seed size. As well, multi-year analyses for each size class and for yield in total showed no significant treatment or year-by-treatment effects. Only the small size class showed a significant year effect – small seed weight tripled at Ellerslie in 2001 compared with 2000. Clearly, drought-stressed canola plants were unable to fill a significant portion of their seed. Under the more normal moisture conditions present elsewhere in our experiments, however, we found no significant issues of seed size in plants under lygus attack about which producers need be concerned.

We found no evidence either of a biphasic response in compensation. Higher densities of lygus tended to produce a greater response than lower densities. This was certainly so for direct damage measures caused by lygus feeding but also for the indirect, induced responses. Many parameters showed significant control vs. lygus-treatment differences, indicating that, under our experimental conditions, as few as two lygus bugs per plant could produce a response. The plant responses observed are consistent with induced defense – “those induced responses that currently decrease the negative fitness consequences of attacks on plants” (Karban and Baldwin 1997). We know that lygus bugs are important pests of canola (*e.g.,* Wise and Lamb 1998b; Wise and Lamb 1998a) yet, field scale economic studies of this impact had been previously conducted only on late flowering through podding stage plants. Our studies found no evidence that lygus feeding on canola at stages earlier than late flowering would result in economic loss. Rather, it appears strongly that economic loss from lygus feeding in canola is restricted to later growth stages when canola plants are no longer able to compensate for damage. Economic thresholds covering late bloom and podding periods likely achieve their effectiveness because canola’s defensive responses, including production of branches from dormant meristems and the subsequent production of additional reproductive structures, are decreased or have ceased functioning. As well, we found no evidence to indicate that any of the lygus densities we tested, over the period from bud through bloom, presented an economic threat. Indeed, all of the parameters measured indicated a positive agronomic response even when damage to reproductive structures was significant.

Duration of Infestation Experiments

Seven duration experiment plant parameters showed significant year-to-year differences. All but one of these indicated an increase in 2001, a severe drought year at Ellerslie. Branching was significantly affected by the growing conditions in 2001 – secondary, tertiary, and total branching were all significantly greater in 2001 (by 32, 95, and 41%, respectively) compared with 2000. In fact, all control plot means and treatment means were higher in 2001 than in 2000. If all else were equal, dry conditions, in the presence of lygus bugs, apparently augmented the compensatory response. The total of all reproductive structures produced – buds, flowers, and pods – also increased by 14% in 2001 relative to 2000. Production of seed-bearing pods increased by 6%, while bud and pod losses increased by 33% (Table 15). Both production of reproductive structures and canola's response to lygus feeding on these structures were greater in the drought conditions of 2001. Although total seed yield was not significantly different between the two years, production of seed greater than 2.00-mm diameter was significantly reduced in 2001 to 18% of the amount produced in 2000. Production of small seed showed the opposite trend, almost tripling in 2001. The drought clearly had a marked impact on seed quality, as measured by size, in 2001. In addition, however, the branching and budding responses of plants to years (drought) appeared to be on the same scale as the responses to lygus treatments.

The impact of drought was also apparent in the differences between sites in 2000. Plants at Lethbridge and Ellerslie were as different in stature and productivity as were the plants grown in 2000 and 2001 at Ellerslie. Drought-affected plants grew poorly regardless of location.

No year by treatment interactions were found –indicating that the impact of lygus-duration treatments on canola was independent of year, despite the very different growing conditions prevalent in 2000 and 2001.

By manipulating the length of time that lygus bugs infested plants, we were able to show that a minimum feeding period could be linked to observed changes in plant productivity. We found that duration of lygus exposure had a significant impact on several plant productivity parameters.

Total number of reproductive structures produced by plants was greater in the lygus-treated plots relative to controls. The response was not incremental (Figure 31), the greatest number of buds being produced after a 5-day exposure of plants to lygus (although the means for the 5-day and 20-day treatments were virtually identical in both 2000 and 2001). An exposure period of five days was, therefore, sufficient to induce the largest response. An additional five days of exposure to lygus produced a decline in the numbers of buds produced – the smallest lygus-treatment mean was in the 10-day treatment group in both years. This suggests there may have been a bud production limit reached. Further bud production may have been temporarily halted if the plant was unable to meet metabolic demands for additional structures, or if new bud positions (dormant meristems) were unavailable because of the structural limitations of new growth.

Small seed increased but treatment means could not be separated. The apparently stepped trend showed one increase in small seed with 5 to 15 days exposure to lygus (Figure 26) and a second increase in both years at 20 days. Flowering had ceased by 20 days in 2001 and so it is likely that the increase at 20 days is due to the failure of plants to fill seeds in the presence of lygus.

Abscised pods were most abundant in the lygus-treated plots relative to controls. The increase in abscised pods was not incremental and the same non-linear ranking of treatment means was seen in both years. The 10- vs. 15-day treatment contrast in the multi-year ANOVA showed significantly fewer buds abscised on plants exposed to lygus bugs for 10 days. Possible explanations for this result include a change in feeding behaviour (perhaps a decrease in feeding or in the numbers of feeding locations during that period) and a decrease in the susceptibility of injured buds to abscise.

One physiological mechanism by which compensation is thought to occur is the shunting of plant metabolites (from an injured organ to an uninjured one). Two-year mean increases in small seed weight after twenty days and concurrent decreases in medium and large seed weights certainly point to a loss in the plant's ability to fill seed. Drought conditions would have augmented this effect although because lygus treatments did not interact with yearly environmental changes, the two process seem not to be interdependent.

Sulphur Response Experiment

Sulphur is an essential plant nutrient. Canola is more demanding of sulphur for protein and chlorophyll production than are cereals. Alberta's soil types differ widely in their inherent levels of plant-available sulphur and about 35% of the 3 million acres of land seeded to canola each year in Alberta is sulphur deficient. Grey wooded soils are mostly sulphur-deficient, whereas brown soils tend not to be. Black soils have intermediate levels of sulphur for growing canola. Sulphur deficiency symptoms include delayed and prolonged flowering, pale yellow to white flowers, reduced seed set, thin or short pods, erect plant stature due to poor pod filling, delayed maturity, and increased susceptibility to disease (Grant *et al.* 1996). Sulphur availability is particularly important during bud and flower production. Both nitrate and sulphate are water-soluble and their uptake in plants is enhanced by adequate soil moisture while excessive soil moisture results in lower availability through leaching. Nitrogen and sulphur must be applied in the proper balance for plant nutrition: a N:S ratio of 7:1.is optimal. Addition of N to marginally sulphur-deficient soils can magnify or induce sulphur-deficiency symptoms. Available research indicates that damage to canola reproductive structures by lygus bug feeding may be compensated although the role of plant nutrition in this process is unclear. The current study briefly examined whether management of sulphur levels in the presence of lygus feeding could affect the ability of canola to compensate for bud loss and damage to pods and seeds.

Sulphur management of canola clearly affected branching and budding processes. More branches and buds were produced in sulphur-deficient plants but more of those buds and immature pods were subsequently dropped. Numbers of seed-bearing pods were nominally increased with increasing levels of sulphur. That sulphur management did not have a significant impact on this aspect of productivity is in keeping with other sulphur trials – they tend to be highly subject to the effects of year. In canola trials generally, the density of lygus bugs and the timing and duration of their feeding are usually not reported and probably go unnoticed unless dramatic.

In light of our findings of the impact of lygus density and infestation duration on both growth and reproduction of canola, it would clearly be inappropriate to ascribe the branching and budding effects found solely to the impact of sulphur management. We feel it is important, therefore, to recognize the interplay of insects and growing conditions on canola productivity, to monitor and report insect abundance in canola trials, and to consider how induced responses to insect feeding may affect the outcome of canola trials.

Conclusions

Canola’s response to lygus bugs was broadly the same at each of the sites and years tested (that is, there were no site by treatment or year by treatment interactions) in spite of large differences in environmental conditions. The impact of severe drought superseded canola’s ability to compensate for lygus damage. We found significant increases in numbers of lost structures both when yields were improved and when no changes in yield could be detected. Therefore, in-field assessments of the damage potential of lygus feeding during bud and flowering using reproductive structure loss (bud, flower, and pod “blanks”) may not provide useful information about yield potential. We found no evidence of detrimental impact of lygus density during bud and flowering. We did, however, find evidence for short duration, bud-period sensitivity to lygus feeding. Bud production and small seed weight increased after an exposure period of five days. Canola’s induced defenses nullified the putative negative impact of lygus bug feeding at the Alberta sites studied. In 20% of our density trials, yields were increased due to lygus feeding. Otherwise, yields were unaffected. All agronomic indicators showed that productivity was either enhanced or not significantly affected by lygus feeding during bud and flowering. Control plants without lygus bugs were less productive than lygus-treated plants. Lygus populations that occur in canola during bud and early to mid bloom do not pose a threat to yield. Insecticide intervention for lygus control during these periods is likely to be counter-productive. Current economic thresholds for lygus cover late bloom and podding periods. They apparently achieve their effectiveness because canola's defensive responses to herbivory, including production of branches from dormant meristems and the subsequent production of additional reproductive structures, are decreased or have ceased functioning due to normal maturity. Lygus bugs occurring in early growth stage canola are non-pests and have been found to be agronomically beneficial.

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References

Aarssen LW. 1995. Hypotheses for the evolution of apical dominance in plants: Implications for the interpretation of overcompensation. *Oikos* 74: 149-156

Belsky AJ. 1986. Does herbivory benefit plants? A review of the evidence. *American Naturalist* 127: 870-892

Butts RA, Lamb RJ. 1990a. Comparison of oilseed Brassica crops with high or low levels of glucosinolates and alfalfa as hosts for three species of Lygus (Hemiptera: Heteroptera: Miridae). *Journal of Economic Entomology* 83: 2258-2262

-----. 1990b. Injury to oilseed rape caused by mirid bugs (Lygus) (Heteroptera: Miridae) and its effect on seed production. *Annals of Applied Biology* 117: 253-266

-----. 1991a. Pest status of Lygus bugs (Hemiptera: Miridae) in oilseed Brassica crops. *Journal of Economic Entomology* 84: 1591-1596

-----. 1991b. Seasonal abundance of three Lygus species (Heteroptera: Miridae) in oilseed rape and alfalfa in Alberta. *Journal of Economic Entomology* 84: 450-456

Cárcamo HA, Otani J, Herle C, Dolinski MG, Dosdall LM, Mason P, Butts RA, Kaminski L, Olfert OO. 2002. Variation of Lygus Species Assemblages in Canola Agroecosystems in Relation to Ecoregion and Crop Stage. *Can Ent* 134: 97-111

Cochrane, WG, Cox, GM. 1992. *Experimental Designs*. John Wiley & Sons, Inc

Dyer MI, Turner CL, Seastedt TR. 1993. Herbivory and its consequences. *Ecological Applications* 3: 10-16

Grant C, Solberg E, Thomas P, Underwood N. 1996. Canola Nutrient Management Guide. *Lighthouse* Version 1.0

Jones, JW. 1997. Alberta Insect Pest Report for 1997.*Western Forum on Pest Management, Crowne Plaza Hotel, Edmonton, AB.* Edmonton, Alberta: Western Committee on Crop Pests

Jones, JW. 1999b. Alberta Insect Pest Report for 1999.*Western Committee on Crop Pests, 39th Annual Meeting, Penticton, British Columbia,*

Jones JW, Cárcamo HA, Otani JK, Butts RA, McKenzie RH, Solberg ED, DeMulder J. 1999. Does Canola Compensate for Lygus Damage? *Proc Ent Soc AB* 47th Annual Meeting, Waterton, Alberta 1999 October 14-16

-----. 2000. Does Canola Compensate for Lygus Damage? *Proc Ent Soc Can* Joint Annual Mtg 2000 ESQ/ESC/ESA

-----. 2001. Does Canola Compensate for Lygus Damage? Report for 1999 Crop Year. *Canola Council of Canada Project #AG99-20*: 37 pp.

Karban, R. and Baldwin, I. T. 1997. *Induced Responses to Herbivory*. London: Univ. Chicago Press

Kelton LA. 1975. The lygus bugs (genus *Lygus* Hahn) of North America (Heteroptera: Miridae). *Mem Ent Soc Can* 95: 101 pp.

Lowenberg GJ. 1994. Effects of floral herbivory on maternal reproduction in *Sanicula arctopoides* (Apiaceae). *Ecology* 75: 359-369

Marquis RJ. 1996. Plant architecture, sectoriality and plant tolerance to herbivores. *Vegetatio* 127: 85-97

Meredith Jr. WR, Wells R. 1989. Potential for increasing cotton yields through enhanced partitioning to reproductive structures. *Crop Science* 29: 636-639

Miles PW. 1972. The saliva of Hemiptera. *Advances in Insect Physiology* 9: 183-255

Rosenheim JA, Wilhoit LR, Goodell PB, Cardwell-Grafton EE, Leigh TF. 1997. Plant compensation, natural biological control, and herbivory by *Aphis gossypii* on pre-reproductive cotton: The anatomy of a non-pest. *Entomol. exp. appl.* 85: 45-63

Rosenthal JP, Welter SC. 1995. Tolerance to herbivory by a stemboring caterpillar in architecturally distinct maizes and wild relatives. *Oecologia* 102: 146-155

Rubia-Sanchez E, Suzuki Y, Miyamoto K, Watanabe T. 1999. The potential for compensation of the effects of the brown planthopper *Nilaparvata lugens* Stal (Homoptera: Delphacidae) feeding on rice. *Crop Protection* 18: 39-45

SAS Institute Inc. 1988. *SAS/STAT User's Guide*. Cary, NC: SAS Institute Inc.

Schwartz, MD, Foottit, RG. 1998. *Revision of the nearctic species of the genus Lygus Hahn, with a review of the palaearctic species (Heteroptera: Miridae)*. Memoirs on Entomology, International Vol. 10 Florida, USA: Associated Publishers

Steel, RGD, Torrie, JH. 1980. *Principles and Procedures of Statistics. A Biometrical Approach. 2nd Edition*. Toronto: McGraw-Hill

Tatchell GM. 1983. Compensation in spring-sown oilseed rape (*Brassica napus* L.) plants in response to injury to their flower buds and pods. *Journal of Agricultural Science* 101: 565-573

Thomas, P. 2000. Outcrossing Between Canola Varieties - A Volunteer Canola Control Issue. Alberta Agriculture, Food and Rural Development. http://www.agric.gov.ab.ca/crops/canola/outcrossing.html

Trumble JT, Kolodnyhirsch DM, Ting IP. 1993. Plant Compensation for Arthropod Herbivory. *Annu Rev Entomol* 38: 93-119

Turnock WJ, Gerber GH, Timlick BH, Lamb RJ. 1995. Losses of canola seeds from feeding by Lygus species (Heteroptera: Miridae) in Manitoba. *Can. J. Plant Sci.* 75: 731-736 van Emden HF. 1997. Host-Plant Resistance in Insect Pests. pp. 129-152 *in* D Pimentel (Ed.). *Techniques for Reducing Pesticide Use. Economic and Environmental Benefits* N.Y.: Wiley & Sons.

Watson MA. 1995. Sexual differences in plant developmental phenology affect plant-herbivore interactions. *Trends in Ecology and Evolution* 10: 180-182

Welter SC, Stegall JW. 1993. Contrasting the tolerance of wild and domesticated tomatoes to herbivory: agroecological implications. *Ecological Applications* 3: 271-278

Wise IL, Lamb RJ. 1998a. Economic Threshold for Plant Bugs, *Lygus* spp. (Heteroptera: Miridae), in Canola. *Can Ent* 130: 825-836

Wise IL, Lamb RJ. 1998b. Sampling plant bugs, Lygus spp. (Heteroptera: Miridae), in canola to make control decisions. *Can Ent* 130: 837-851

Presentations, Reports, and Papers Arising from this Project

Jones, JW, Cárcamo, HA, Otani, JK, Butts, RA, McKenzie, RH, Solberg, ED, and DeMulder, J. 1999. Does Canola Compensate for Lygus Damage? Proceedings, Entomological Society of Alberta. 47th Annual Meeting, Waterton, Alberta 1999 October 14-16

-----. 2000. Does Canola Compensate for Lygus Damage? Proceedings, Entomological Society of Canada. Joint Annual 50th Meeting Société d'entomologie du Quebéc / Entomological Society of Canada / Entomological Society of America, held 2000 December 3-7, at Palais de Congrès de Montréal, Québec.

Cárcamo, HA, Jones, JW, Otani, JK, and Butts, RA. 2001. Advances in the Lygus battle. Proceedings, Agronomy Update Conference, 2001. Meeting held at Lethbridge Lodge Hotel, Lethbridge, Alberta. pp. 155-161.

Jones, JW. 2001. What's Bugging Us Now? Proceedings, Farm Tech 2001. Meeting held at Westerner Park, Red Deer, Alberta. pg. 25.

Dosdall, LM, Jones, JW, Cárcamo, HA, and Otani, JK. 2001. Cabbage Seedpod Weevil and Lygus Bugs: New Research Developments on their Biology and Control. Proceedings, Western Canada Agronomy Workshop. Meeting held 2001 July 4-6 at Lethbridge, Alberta. 5: 48-52.

Jones, JW, Cárcamo, HA, Otani, JK, Butts, RA, McKenzie, RH, Solberg, ED, and DeMulder, J. 2001. Does Canola Compensate for Lygus Damage? Canola Council of Canada Project #AG99-20. Report for the 1999 Crop Year. 37 pp.

Jones, JW and Yang, R-C. 2001. A Tale of Two Bugs: Lygus and SAS GLM. Proceedings, Canadian Prairie SAS User Group. Meeting held at Alberta Research Council, Edmonton, Canada.

Jones, JW, Cárcamo, HA, Otani, JK, Butts, RA, McKenzie, RH, Solberg, ED, and DeMulder, J. 2002. Does Canola Compensate for Lygus Damage? Presentation to Alberta Canola Industry Meeting held 2002 April 10 at Alberta Research Council, Edmonton, Alberta.

-----. 2002. Lygus Bug Feeding Induces Increased Productivity in Canola. Seminar presentation, given 2002 May 22 at Saskatoon Research Centre, Saskatoon, Saskatchewan.

-----. 2003. Lygus Bug Feeding Induces Increased Productivity in Canola. Proceedings, Entomological Society of Alberta. 50th Annual Meeting held 2002 October 24-26 at Ramada Inn, Lethbridge, Alberta.

-----. 2003. Lygus Bug Feeding Induces Increased Productivity in Canola. (Manuscript in prep).

-----. 2003. Does Canola Compensate for Lygus Damage? Guest lecture, Integrated Pest Management course, University of Alberta, Department of Agricultural, Foods and Nutritional Sciences, 2003 January 20.