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Biology and Integrated Management of the Cabbage Seedpod Weevil in Prairie Canola Crops

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Summary

The economic importance of the cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Marsham), increased rapidly in the prairies of western Canada following its discovery in canola near Lethbridge in 1995. Since 1999 outbreaks have occurred almost annually over thousands of hectares of cropland, necessitating applications of vast quantities of chemical insecticide. Both larvae and adults can damage the crop, with larvae developing within pods and feeding on seeds and adults feeding through pod pericarp late in the season to further reduce yield and quality. The development of sustainable control strategies has proceeded in several directions, including chemical, cultural, plant resistance, and biological control, and successes in each area have facilitated development of an integrated management approach for this pest. The chemical insecticide compounds and formulations with greatest effectiveness for reducing both adult and larval densities through foliar sprays and seed treatments were identified. Trap crop technology was tested under prairie field conditions, and seeding date recommendations were determined. New canola germplasm was produced that expresses both antibiotic and antixenotic (non-preference) resistance to the weevil. The mechanism of resistance was unraveled for the new germplasm, and has identified two key glucosinolate compounds that affect weevil behavior; these can drive future plant breeding programs to develop additional weevil-resistant germplasm. The species compositions and impact of indigenous natural enemies of the weevil were determined, and studies were conducted to assess European natural enemies for possible introduction to North America in a classical biological control program. Although the cabbage seedpod weevil remains an important component of the insect pest fauna of prairie canola crops, the knowledge now exists to enable producers to manage this pest in a sustainable manner.

Introduction

The cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Marsham) (Coleoptera: Curculionidae), is an alien species native to Europe that only recently invaded prairie cropland, but in a short time it has become a major pest of canola (*Brassica napus* L. and *Brassica rapa* L.). The weevil appears to have entered the continent via British Columbia because its first discovery in North America occurred in the southwestern region of the province in the early 1930's[1]. From there it spread south and eastward, so that by the early 1990's its range encompassed most of the continental U.S.A.[2] and the interior of British Columbia in the Okanagan and Creston Valleys[3]. It was first discovered in the prairies of western Canada in canola crops near Lethbridge, AB in 1995[4]. At least one other introduction of the cabbage seedpod weevil appears to have occurred in Québec, as determined through molecular analysis of mitochondrial DNA[5].

The cabbage seedpod weevil completes its larval development only in certain species of Brassicaceae, although adults may feed on nectar and pollen of a wide range of brassicaceous species[6,7,8]. It overwinters as an adult beneath the soil, primarily in wooded areas or grassy vegetation[9]. Overwintering survival is strongly associated with below-freezing temperatures. Cárcamo et al. (2009)[10] found that although the cabbage seedpod weevil has a supercooling point near -7ºC, its survival declined significantly at -5°C relative to 5°C, but lengthening the overwintering period had much less effect on mortality.

Adults emerge from their overwintering sites in spring, with peak emergence when soil temperatures reach approximately 15°C[9]. Following their emergence, adults fly to patches of early-flowering brassicaceous weeds, and are especially attracted to stands of wild mustard, *Sinapis arvensis* L., and volunteer

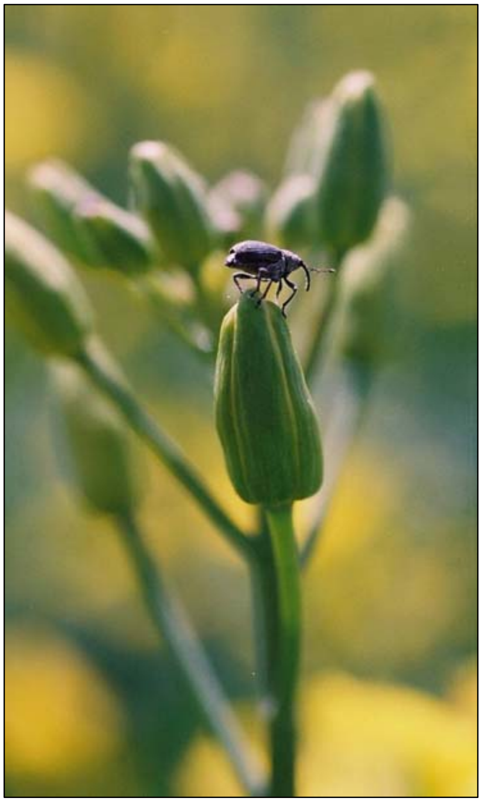

Figure 1. Adult of the cabbage seedpod weevil on a flower bud of canola.Photo credit: Lloyd Dosdall.

Canola[8]. Flight dispersal by weevil adults is dependent on temperature and relative humidity[11]. The mean temperature required for a flight height of 1 m is 12°C, and flight height increases with ambient temperature. On the other hand, increases in relative humidity are associated with reduced flight heights and dispersal distances[11].

Adults invade canola crops in June, in the bud to early flowering stages and feed on canola pollen, nectar, buds, and racemes (Figure 1). Significant clustering of adults along field edges in early stages of invasion is followed by more homogeneous distributions as canola development proceeds to flowering and pod enlargement[12]. Mating occurs on canola plants and ovariole development requires that females feed on raceme tissue[13]. Most eggs are laid soon after flowering, when pods are 45 to 60 mm long[8]. During oviposition, a female makes an opening in the pod wall with her mouthparts, and then turns to deposit an egg into the opening[14]. The female then brushes her abdomen over the area, releasing a pheromone that deters other females from ovipositing in the same pod[15].

Within canola fields, cabbage seedpod weevil adults and larvae are not randomly distributed, but rather are found correlated with nitrogen and sulfur in canola leaf tissue[16]. Females prefer to feed and oviposit on plants with high levels of sulfur and low levels of nitrogen[16], although larval development time increases with increasing nitrogen levels[17]. Sulfur fertilization can result in increases in sulfur-containing glucosinolate compounds in plant tissue[18,19], and the breakdown products of these compounds are attractive to adult weevils[20,21]. As a result, weevils tend to cluster in fields where sulfur content is high in plant tissue. Larvae develop rapidly in spring canola, progressing through three larval instars in approximately 50 days in southern Alberta[22,8]. During this time, each larva consumes five to six canola seeds[23]. When mature, the larva chews an opening in the pod wall, drops to the soil, burrows in, and pupates in an earthen cell. Adults emerge about 14 days later[8].

Figure 2. Final-instar larva of the cabbage seedpod weevil within a pod of canola. Photo credit: Lloyd Dosdall.

Crop Damage and Yield Loss by Cabbage Seedpod Weevil

Crop damage occurs when larvae feed within pods and destroy developing seeds (Figure 2). In addition, when the new generation of adults emerges in late summer, weevils can feed through the pod walls in late-maturing fields to consume canola seeds, reducing yield and quality (Figure 3)[24,25]. Pods with exit holes shatter before harvest more frequently than non-infested pods, and exit holes may serve as entry points for fungal spores that can germinate to further reduce yield[25].

Figure 3. Adults of the new generation of cabbage seedpod weevils feeding on a ripening pod of canola. Photo credit: Lloyd Dosdall.

Few studies have assessed the relationship between weevil density and yield loss. Studies conducted in Scandinavia showed a negative relationship between increasing weevil density and yield loss[26,27]. In a study by Tulisalo et al. (1976)[26], two weevils per plant reduced yield by 50%, and at higher densities seed weights were considerably lower than in uninfested controls. Other studies in France[28] and the U.S.A.[29] determined that canola pod infestation levels below 26% (as indicated by exit hole counts) have no measurable effect on yield.

The co-occurrence of weevils with other pests can lower the economic threshold. Free et al. (1983)[30] determined that in England, densities below one weevil per plant caused fewer than 26% of pods to be infested, and on its own, this density did not warrant insecticidal intervention. However, in the presence of the pod midge, *Dasyneura brassicae* Winnertz (Diptera: Cecidomyiidae), yield losses were much higher so low weevil densities warranted control. In southern Alberta and Saskatchewan, the cabbage seedpod weevil often co-occurs with lygus bugs (*Lygus* spp.) (Hemiptera: Miridae) which are intermittent pests of canola. A study utilizing exclusion cages enclosing 10 plants within 0.8 m^2 was conducted near Lethbridge in 2000 and 2002 to determine the combined and separate feeding effects of these two insects on canola (Cárcamo, unpublished data). In both years, a combined density of two weevils and two lygus bugs (equal sex ratios) per plant reduced seed weight relative to that of plants from control cages without insects; however, lower densities of weevils and lygus bugs had no impact on yield. In 2002, a much more humid year than 2000, cabbage seedpod weevils alone reduced yield at densities of two adults per plant. The highest treatment combination of four lygus bugs and four weevils (each with two males and two females) per plant always had the lowest yield.

Previous research has determined than when more than 25% of pods are damaged by cabbage seedpod weevil, yield reduction is substantial and insecticidal control is warranted[28,29]. In 2002, the Lethbridge study validated these results as all treatments with densities of two or more weevils per plant had significantly less yield than the controls, and resulted in 40 to 64% of canola pods infested with larvae (Cárcamo, unpublished data). Data from this study should be interpreted with caution, however, because plants grown at a density of only 10 per 0.8 m^2 develop more branches and pods per plant than at higher densities; the latter may better tolerate insect feeding.

Control of Cabbage Seedpod Weevil in Canola

Investigations have been conducted on several fronts to manage infestations of this pest, including chemical, cultural, host plant resistance, and biological control strategies. In western Canada, two pyrethroid insecticides are currently registered for reducing adult populations of cabbage seedpod weevil in canola[69]. A nominal economic threshold of three to four adult weevils per 180° sweep net sample when the crop is at 10 to 20% flower is recommended before applying chemical insecticide[25]. Using the estimates of sweep net efficiency developed for lygus bugs by Wise and Lamb (1998)[31], it appears that this threshold is approximately one to two weevils per plant.

Chemical Control. A study in southern Alberta that compared 11 insecticidal compounds using methods that varied from small enclosure cages to small plot studies and field-scale trials concluded that pyrethroid insecticides provided the most consistent control[32]. The insecticide compounds evaluated as seed treatments (lindane, imidacloprid, acetamiprid) did not reduce weevil damage compared to plants that developed from untreated seed. However, in Washington State, U.S.A., treatment of canola seed with the neonicotinoid compound, imidacloprid, caused reductions in cabbage seedpod weevil exit holes of 88 to 100%, and seed yields from plants grown from imidacloprid-treated seed were 1.9 to 2.4 times greater than those of the untreated controls[33]. Using large field enclosure cages that were stocked with high densities of cabbage seedpod weevil and excluded other potential pest species, Dosdall (2009)[6] found that mean numbers of second- and third-instar larvae were significantly greater in plants that developed from seed treated with lindane than plants treated with the neonicotinoid compounds, clothianidin and imidacloprid, even though weevil oviposition was similar for all treatments. Emergence of new generation adults was reduced by 52 and 39% for plants treated with clothianidin and imidacloprid, respectively, compared with emergence from plants treated with lindane.

Cultural Control. The observation that early in crop invasions by the cabbage seedpod weevil, adults are initially clustered along field edges[34,35,12] has prompted researchers to explore trap cropping as a cultural practice for reducing damage from this insect pest. Buntin (1998)[36] investigated temporal trap cropping by seeding, in fall, a spring canola cultivar along the field perimeter and a winter cultivar in the middle of a 0.35 ha plot. The spring cultivar grew faster and concentrated more weevils, but the study results were inconsistent and did not prevent weevil damage and yield loss.

Trap crops were investigated for control of cabbage seedpod weevil in southern Alberta from 2001 to 2004 using large commercial fields with a main crop of *B. napus* and the perimeter planted at the same time to a *B. rapa* cultivar[37]. *B. rapa* flowered about one week earlier than the main crop of *B. napus* and effectively concentrated weevils where they could be controlled with a pyrethroid insecticide to prevent their movement into the main crop (Figure 4). This trap crop strategy worked well in large square fields that were 1.6 by 1.6 km even when weevil populations were high. However, this approach was not as effective when fields were smaller and narrow, especially when weevil densities far exceeded the economic threshold. The advantages of trap cropping can include substantial savings in costs of insecticide and fuel from reduced spraying applications, and the method has the potential to conserve populations of natural enemies and other beneficial insects in the main crop area which may comprise up to 90% of the field. A requirement for successful implementation of a trap crop strategy is to carefully monitor the trap crop so that insecticide can be applied before beetles disperse in large numbers to the main crop.

Figure 4. Trap crop of early-flowering *Brassica rapa* planted around the perimeterof a main crop of *Brassica napus* to control infestations of the cabbage seedpodweevil in southern Alberta. Photo credit: Héctor Cárcamo.

Seeding date can be important for the cultural control of cabbage seedpod weevil infestations. Early seeding of canola (in late April in the southern prairies) can predispose canola crops to higher infestation levels of the weevil than for crops seeded later (in early May)[38]. Adult weevils emerge from their overwintering sites in spring before canola is in the vulnerable bud to early flowering stages, so early-seeded crops can be especially attractive to invading weevils. Seeding early can enable crops to take advantage of higher levels of residual soil moisture from snow melt than are available later in the season, but this benefit can be lost if yield is compromised by greater weevil attack. Seeding later in spring, at recommended seeding rates, can help reduce weevil infestations and damage[38].

Host Plant Resistance. Not all species of Brassicaceae are equally susceptible to infestation by the cabbage seedpod weevil. For instance, *B. rapa* is more susceptible than *B. napus* and susceptibility of *Brassica juncea* (L.) Czern. is approximately equivalent to *B. napus* [39,40]. *Sinapis alba* L. is resistant to the weevil[41,40], and this resistance has provided the foundation for research to develop weevil-resistant canola. Dosdall and Kott (2006)[42] evaluated intergeneric canola germplasm, produced by using embryo rescue to cross *S. alba* with *B. napus* and then backcrossing progeny to the *B. napus* parent, as potential sources of resistance to the weevil. In field assessments, some of the intergeneric genotypes expressed substantial weevil resistance with infestation levels that were 2.5 to 8.3 times less than those observed in susceptible lines[42]. The resistant germplasm developed with this approach expressed both antibiotic and antixenotic resistance to the weevil: weevils preferred not to feed or oviposit on the resistant lines, and when they did, larval development times were longer and larval biomass was less than for larvae reared on susceptible genotypes[42,43]. Overwintered females that fed upon the resistant germplasm had reduced egg development compared with females reared on weevil-susceptible canola[43].

The novel weevil-resistant germplasm differed from susceptible canola in the olfactory cues it produced. Odours from whole flowering plants, flowering racemes and cauline leaves (leaves on the upper part of the plant stem below the flowers) of susceptible genotypes were significantly more attractive to both male and female weevils than those of resistant genotypes[44], indicating chemical differences among genotypes. Shaw et al. (2009)[45] determined that genotypes susceptible and resistant to the cabbage seedpod weevil differed in the amounts of an uncharacterized glucosinolate contained in seeds of immature pods. Using High Performance Liquid Chromatography, Shaw et al. (2009)[45] found that the peak height or quantity of this glucosinolate was 3.5 times greater in susceptible canola than in resistant material. Tansey et al. (2010c)[44] found that the genotype-specific peak heights of this compound also correlated with weevil olfactory responses, and inferred that the identity of the attractive compound was 2-phenylethyl glucosinolate. The lowered amount of this compound in resistant germplasm appears to be responsible for its reduced attractiveness to cabbage seedpod weevil. In addition, the weevil-resistant canola was found to have levels of 1-methoxy-3-indolylmethyl glucosinolate that were approximately three-fold greater in resistant than susceptible germplasm. This glucosinolate is known to have a repellent effect on cabbage seedpod weevil adults and has been correlated with lower larval weights and longer larval development times[43,44].

The visual appearance or light reflectance properties of flowers and foliage of resistant and susceptible canola also differed, and this influenced attractiveness of the plants to adults of the cabbage seedpod weevil[46]. Flowers of susceptible genotypes reflected more yellow than those from resistant genotypes, and were more attractive to the weevil. Flowers of resistant genotypes were less attractive to females than those of susceptible genotypes. Tansey et al. (2010d)[46] found that significant differences occurred in the amounts of yellow, green, blue, and ultraviolet light reflected among genotypes, and that female weevils responded especially to amounts of yellow and ultraviolet light reflected from flowers. Floral visual cues therefore have great importance in the selection of oviposition sites by the cabbage seedpod weevil, and this trait is an important characteristic of the weevil-resistant canola[46].

When resistant genotypes were grown in the field intermixed with a susceptible line of canola, the resistant lines disrupted cabbage seedpod weevil host selection and lessened the attractiveness of susceptible canola[47]. Weevil numbers and egg-laying in pods of susceptible genotypes were reduced in the presence of the resistant plants. This result was consistent with associational resistance as defined by Tahvanainen and Root (1972)[48] where reductions in herbivore feeding occurred on otherwise suitable plants because they were grown in proximity with genetically distinct and less attractive co-habitants.

Biological Control. Parasitoids were observed to attack larvae of the cabbage seedpod weevil soon after its invasion of western North America. Surveys by various researchers[49,50,51,52] found that several hymenopteran ectoparasitoids attacked weevil larvae, and early species identifications of these parasitoids suggested that the dominant natural enemy fauna of Europe also occurred in North America. However, subsequent examinations of voucher specimens from the early collections and more recent sampling determined that the North American fauna is relatively distinct, comprising a mixture of Nearctic and Palearctic species[53].

Figure 5. Larva of a hymenopteran ectoparasitoid feeding on a larva of the cabbage seedpod weevil within a pod of canola. Photo credit: Lloyd Dosdall.

Extensive sampling of canola fields in southern Alberta and Saskatchewan from 2001 to 2006 revealed a total of 15 parasitoid species attacking the weevil, representing five families of Hymenoptera[54,53,12,55]. Small numbers of adult weevils were parasitized by *Microctonus melanopus* (Ruthe), a braconid wasp found in southern Alberta[54]. However, the dominant natural enemy fauna of cabbage seedpod weevil in the prairies is comprised of 14 species of larval ectoparasitoids (Figure 5), with >90% of parasitism inflicted by the pteromalids *Trichomalus lucidus* (Walker), *Chlorocytus* sp., and *Pteromalus* sp., and the eulophid *Necremnus tidius* (Walker) [53,12,55]. Parasitism of cabbage seedpod weevil larvae increased from 0.1% in 2002 to 5.0% in 2004[12], and increased further from 2004 to 2005, but total parasitism was usually less than 15% [56,55]. These parasitism levels are considerably lower than those common in Europe, where rates can reach 50 to 90% [57,58,59].

The lower parasitism levels in western North America than in Europe indicate a parasitoid fauna that did not coevolve with the weevil, but instead is comprised of native species that expanded their host ranges to exploit the abundant populations of cabbage seedpod weevil larvae in canola fields [12,55]. For instance, both *T. lucidus* and *N. tidius* were reared from larvae of the Nearctic weevil, *Ceutorhynchus neglectus* Blatchley[56], indicating that *C. neglectus* is an indigenous host of these parasitoids. As a consequence of the large numbers of *T. lucidus* and *N. tidius* occurring in canola fields, populations of the native weevil may be endangered in portions of its range that overlap with the cabbage seedpod weevil[56].

The relatively low parasitism levels of North American populations of the cabbage seedpod weevil has prompted research to evaluate partial reconstruction of the natural enemy complex of this pest in a classical biological control program. Classical biological control was attempted previously, in British Columbia in 1949 with the release of three European parasitoids [60,61]. Recent surveys conducted near the release sites found that only one species established, *Stenomalina gracilis* (Walker) [60,61], but unfortunately this species is non-specific in the range of weevil hosts it attacks[62].

An important consideration in the implementation of a classical biological control program is to ensure compatibility between weed and insect pest biocontrol [63]. A number of weevil species in the subfamily Ceutorhynchinae have been released in North America for the biological control of various weed species, or are under evaluation for release. Parasitoids selected for release to control cabbage seedpod weevil should not also attack these beneficial weevils. For instance, *Mesopolobus morys* (Walker) and *Trichomalus perfectus* (Walker) are the most effective parasitoids for cabbage seedpod weevil biocontrol in Europe[64], and both are under consideration for release in Canada[65]. However, their release in the prairies could be damaging if the parasitoids caused mortality to weevils released for weed biocontrol. The weevils, *Hadroplontus litura* (Fabricius) and *Microplontus edentulus* (Schultze), are established in North America as biological control agents for Canada thistle, *Cirsium arvense* L. (Scop.), and scentless chamomile, *Tripleurospermum perforatum* (Mérat) Laínz, respectively, and both weeds have the same geographical range as the cabbage seedpod weevil. Muller et al. (2011) [62] found that although a single specimen taxonomically similar to *T. perfectus* was reared in Europe associated with *M. edentulus*, neither *T. perfectus* nor *M. morys* were associated with *H. litura*. The risk of harm to beneficial weevils is therefore minimal, although studies still need to be conducted to determine possible effects of the parasitoids on indigenous weevil species such as *C. neglectus* [66].

Conclusion

In summary, although the cabbage seedpod weevil is a relatively recent invasive species on the prairies, it appears destined to remain a prominent pest of canola in the future. Its range continues to expand, especially to the east, and when its physiological and ecological requirements were incorporated in a bioclimatic model, all areas of canola production across the prairies were predicted to be capable of sustaining its populations[67]. Moreover, modeling various climate change scenarios suggested that its pest status will increase in future years as more area becomes suitable for its development, reproduction, and overwintering [68,10]. However, in view of the substantial progress that has been achieved to develop chemical, cultural, biological, and host plant resistance strategies for its control, it is apparent that the capability exists for managing this pest in a manner that is economically and environmentally sustainable.

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