Chapter 10 Arthropods of Legume Forage Crops

Juliana Soroka

Agriculture and Agri-Food Canada, Saskatoon Research Centre, 107 Science Place, Saskatoon, Saskatoon, Canada S7N 0X2

Jennifer Otani Agriculture and Agri-Food Canada, Beaverlodge Research Farm, Beaverlodge, Alberta, Canada T0H 0C0

Abstract. Forages occupy a major proportion of arable lands of North America. Because they are less intensely managed than other production systems, perennial legume forage fields can provide greater ecosystem stability than their annual crop counterparts. This stability promotes species diversity, and a vast array of arthropod species can be found in fields used for forage production. Despite this wealth of arthropod diversity, most species are not economic pests, and those that are pests are usually invasive alien species. This chapter summarizes features of the arthropod communities in leguminaceous forage crop agroecosystems on the prairies and describes the ecological roles of some of the most economically important members in these communities.

Résumé. Les cultures fourragères occupent une proportion importante des terres arables de l'Amérique du Nord. Comme ils font l'objet d'une gestion moins intense que d'autres systèmes de production, les champs de légumineuses fourragères vivaces constituent des écosystèmes plus stables que les champs de cultures annuelles. Cette stabilité favorise la diversité des espèces, et on peut donc trouver dans les champs de production de fourrages une grande variété d'espèces d'arthropodes. Malgré leur grande diversité, la plupart de ces arthropodes ne sont pas des ravageurs d'importance économique, et les espèces nuisibles sont habituellement des espèces exotiques envahissantes. Le présent chapitre résume les caractéristiques de ces communautés d'arthropodes dans les agroécosystèmes de cultures fourragères des prairies; il décrit les rôles écologiques de certains des membres de ces communautés les plus importants au plan économique.

Introduction

Grassland agriculture emphasizes the importance of forages in livestock production and land management. Forages consist of any high-fibre plant material, other than threshed grain, directly consumed by livestock or harvested and preserved as livestock feed (Barnes and Baylor 1995; Lamp et al. 2007). Forages occupy over half of the arable land area of the world and more than 430 million ha of cropland, pasture, and rangeland in North America (Lamp et al. 2007).

Forage crops fit into both agricultural and natural ecosystems. They are pivotal to sustainable agriculture, supplying feed for livestock to convert fibre into protein. Bacteria in legume root nodules convert atmospheric nitrogen into a form readily used by plants and, when used in crop rotations, forages may increase subsequent crop productivity. They provide feed for wildlife, stabilize and conserve soil, increase soil organic matter and water-holding capacity, improve water quality, and decrease wind and water erosion.

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Cultivated forages usually comprise grass and/or legume species and have several uses and forms. Species used for cultivated hay production are primarily perennials and include short- or long-lived cool or warm season grasses and perennial legumes. A few forage crops are annuals, such as annual rye grass, silage maize, and forage peas. Tame or improved pasture, land that is planted to specific grasses or grass-legume mixtures for animal grazing, is usually fenced and may receive improvements such as fertilization or weed control. Rangeland is grazing land that is composed of self-seeding, usually indigenous, grasses that are infrequently rejuvenated and instead managed as a natural ecosystem (Barnes and Baylor 1995).

Forage grasses have comparatively few major chronic insect pests, and forage legumes are also relatively pest free. There are several reasons for this. Legumes, especially indeterminate species, have comparatively high levels of compensatory ability. Only a small portion—perhaps 20%—of the numerous legume flowers protected from pest attack will form pods (van Emden 1980). Forage land has a lower value per unit area compared with that of other agricultural commodities. Forages typically represent a form of low-input, extensive rather than intensive agriculture, with little soil amendment because the plants themselves provide nitrogen for growth. Perennial species with infrequent tillage or soil disturbance are often used for forage production. In some areas, forages may remain in production for 20 years or more. Such longevity promotes a temporal stability rarely seen in other agricultural systems and provides the opportunity for the development of a diverse arthropod community structure (Summers 1998). Because of the environmental stability of forage crops, insect communities within them also tend to be stable.

One exception to arthropod stasis in forages is that of invasive alien species. Invasive alien species are organisms that successfully establish themselves in intact, pre-existing native ecosystems and then overwhelm them (Convention on Biological Diversity 2002). Factors that influence the invasiveness of a species may include relief from or reduction of the pressures of predators or parasites of its native country, being biologically "hardy" (such as having a short generation time and/or a generalist diet), or arriving in an ecosystem that has already been disturbed by humans (World Conservation Union 2008). Most arthropod pests of prairie forages are not native to this continent. They tend to be cosmopolitan in distribution and to decrease local biodiversity and ecosystem stability as they increase biological homogenization (Environment Canada 2008).

Arthropods are important components of forage production systems as direct competitors for forage resources and as pollinators essential for propagation of some forage species. This chapter describes forage types and the legume species most commonly grown for forage in the grasslands of the three prairie provinces. It provides an overview of the arthropod species occurring in legume forage crops in the Northern Great Plains and discusses the general features of these species, their trophic levels, and their impact on forage production. The distribution, bionomics, ecological roles, and natural control of six of the principal legume forage insects and insect complexes occurring on the Canadian prairies are described. Arthropods of pastures and rangelands are discussed elsewhere in this volume.

Forage Uses and Composition

The primary economic use of cultivated forages is as feed for livestock. Forage is grazed in the summer or is consumed in preserved form as hay, pellets, cubes, or silage for eight months of the year or more on the Northern Great Plains. Forages are also used as green manures—crops grown for a specific period and then incorporated into the soil to increase soil organic matter and nitrogen, improve water retention and aeration, suppress weeds, and remediate soil compaction and erosion. Legume green manures that flower before incorporation also provide forage for pollinating insects. Forages grown for seed production are managed quite differently than forages grown for hay, with more inputs and less tolerance for insect damage to floral structures.

Forage species composition varies with climate and usage. The major species of legume forage crops grown in Canadian grasslands are biennial, short-lived perennial, or perennial species. They include alfalfa (*Medicago* spp.), sweetclover (*Melilotus* spp.), sainfoin (*Onobrychis viciifolia* Scop.), birdsfoot trefoil (*Lotus corniculatus* L.), cicer milkvetch (*Astragalus cicer* L.), crown vetch (*Coronilla varia* L.), red clover (*Trifolium pratense* L.), white clover (*T. repens* L.), and alsike clover (*T. hybridum* L.) (Lamp *et al.* 2007).

Alfalfa is by far the most frequently grown legume forage crop worldwide, primarily because of its high feed value. At flower bud stage, the protein content of alfalfa can be as high as 10–20% (Marten *et al.* 1988). Having its origin in central and southwest Asia, alfalfa came to the New World with New England colonists and again with the Spaniards, spreading throughout North America by the mid-1800s. It is well adapted to cold winters, hot dry summers, and a variety of soil types. Because a stand of alfalfa can be productive for up to 30 years, it provides a stable environment for many species of arthropods, both phytophagous and entomophagous. Alfalfa is an important honey-producing crop on the Canadian prairies and serves as a source of nectar and pollen for many arthropods.

Sweetclover is a drought and cold tolerant, rapid-growing, introduced biennial legume that is used for pasture, hay, silage, and soil improvement. It is a superior green manure crop because it has the largest amount of dry matter and nitrogen production of any common forage (Byers and Stromberg 1987). Sweetclover was one of the principal forage legumes grown in North America until the middle of the last century, but production has since declined, largely because of the rise of the sweetclover weevil, *Sitona cylindricollis* Fåhr., a prominent pest of the crop (Bird 1947; Craig 1978).

Sainfoin and birdsfoot trefoil are non-bloating perennial legumes grown for pasture, hay, or silage. Both species are resistant to feeding by the alfalfa weevil (Lamp *et al.* 2007). Cicer milkvetch and crown vetch are winter-hardy perennial legumes grown over small areas on the prairies, principally for soil conservation and in pasture mixtures. Possibly because of their small areas of production, these crops have few insect pests. Red clover, white clover, and crimson clover are short-lived perennials that are grown in moister areas of the prairies. Used in hay, pasture, or green manure production, the true clovers have a suite of specialist and generalist insects feeding on them.

Forage grasses and legumes grown for hay are among the least intensively managed of any cultivated crops, often with minimal input and management and greater tolerance to insects and other stresses than crops with higher economic value. Most forage legumes have relatively high insect pest economic thresholds, partly because of their plant physiological characteristics and partly because many legumes are not grown as cash crops. Even in seed production, insect economic thresholds in legume forages are often greater than in other crops. In prairie alfalfa hay production, control of lygus bugs (*Lygus* spp. Miridae) is not recommended, because it is not economically feasible. In alfalfa crops grown for seed, the economic threshold for lygus bugs at bud and early bloom is eight bugs that are third instar or older per 180° sweep of an insect net. In contrast, the economic threshold of lygus bugs in canola production is one to two lygus bugs per sweep (Saskatchewan Ministry of Agriculture 2010).

Forage Arthropods

Just as the grasslands ecosystem is more suitable for some forages than others, it is also more suitable for some insects than others. There is a significant xerophilic component to the arthropod fauna of grasslands, with many acridids and formicids flourishing. Similar taxa are dominant in xerophytic legume ecosystems around the world. In a list of 446 insects and mites collected from alfalfa grown in Alberta, Harper (1988) recorded the greatest number of species in the family Miridae (Hemiptera). Similarly, Miridae and Lygaeidae comprised the greatest number of arthropods in the 103 species collected in alfalfa in Saudi Arabia (Alsuhaibani 1996). The predator composition in alfalfa fields in the United States is similar to that found in alfalfa in Europe (Wheeler 1977) and Saudi Arabia (Alsuhaibani 1996).

Over 1,000 species of arthropods are associated with legume forages in North America (van den Bosch and Stern 1952). Many are transients, herbivores, predators, or parasitoids. Harper's (1988) list of insects and mites found in Alberta alfalfa fields includes herbivores (48% of taxa), predators and parasitoids (37%), pollinators (4%), and others (11%) such as saprophages, scavengers, and fungivores. The entomofauna of alfalfa in Saudi Arabia is similar, comprising herbivores (48%), predators and parasitoids (26%), pollinators (22%), and others (5%) (Alsuhaibani 1996).

Feeding by most species of phytophagous arthropods on forage hay crops rarely causes economic loss. Some species, however, may require control. This is especially true when crops are being established. Perennial crops in the year of their establishment are generally more vulnerable to herbivory than when they are well-established, and they have higher potential lifetime productivity than the same crop in later years. Even in established crops, alfalfa weevils and plant bugs can greatly decrease forage biomass and seed yields. In other cases, insect damage to forages may be subtle and cumulative over time, making it difficult to distinguish from losses due to drought, grazing or cutting pressure, or root diseases.

Forage Insect Case Studies

About 10 insect species limit alfalfa production in North America (Council for Agricultural Science and Technology 1986). The first five species discussed in the following case studies are the most common insect pests of alfalfa on the Canadian prairies. The sixth case study discusses the alfalfa leafcutting bee (*Megachile rotundata* Fab.), the insect that is most important for alfalfa seed production worldwide.

Foliage Feeders

Foliage feeding by arthropods can lead to defoliation of forage and loss of plant biomass, accelerated leaf senescence, plant architecture modification, and, under heavy feeding pressure, plant stunting, stand reduction, and death (Lamp *et al.* 2007). Many of the defoliators of greatest concern in forage legumes are monophagous or oligophagous, and preferentially feed on one or a few host species.

Alfalfa Weevil

Palearctic in origin, the alfalfa weevil, *Hypera postica* (Gyllenhal) (Coleoptera: Curculionidae), was first noted in North America near Salt Lake City in 1902 (Titus 1911), likely from alfalfa used as packing in furniture shipments from Italy (Stewart 1926). Two

other populations were discovered, one near Yuma, Arizona, in 1939, which was thought to have originated from Egypt (Wehrle 1940), and the other in Maryland in 1951 (Poos and Bissell 1953). The weevil was reported first in Canada in the Milk River Valley of Alberta in 1954 (Hobbs *et al.* 1959) and then in the southwestern and south-central agricultural areas of Saskatchewan in the same year (MacNay 1957; Beirne 1971), soon spreading throughout southern Alberta and southwestern Saskatchewan to about the 51st parallel. It was introduced into southern Ontario (Beirne 1971) and southwestern Quebec in the 1960s (Brown 1968, cited in Loan 1971), likely from the eastern United States. In the mid-1990s, it expanded its distribution eastward and northward from southwestern Saskatchewan (Soroka and Goerzen 2002) and is now established in the alfalfa-seed-growing regions of northeastern Saskatchewan and Manitoba.

The alfalfa weevil develops on several legume species, including *Medicago sativa*, *M. lupulina*, *Melilotus alba*, *M. officinalis*, *Trifolium pratense*, *T. repens*, *T. hybridum*, and *T. incarnatum* (Titus 1911). Currently, it is one of the most important insect pests of alfalfa in North America and is especially destructive in areas of alfalfa seed production with a short growing season, where the crop is not mowed prior to seed initiation (Lauderdale 1991). Such areas include the Canadian prairies.

Univoltine in Canada, the alfalfa weevil overwinters as an adult in alfalfa crowns or debris in or near alfalfa fields. Weevils emerge from hibernation in spring as alfalfa starts to regrow. They feed, mate, and lay eggs, at first on leaves, in leaf sheaths, buds, or petioles and later in alfalfa stems. Eggs are laid in clusters of 5–20, and each female weevil can lay from 400 to 800 eggs over four or more weeks. Both adults and larvae are foliage feeders, but the larvae are more injurious, feeding on buds and unexpanded leaves at stem terminals. Older larvae feed on expanded leaves and, under heavy feeding pressure, leaves can be shredded, with only leaf fragments and stems remaining (Fig. 1). Larval feeding is heaviest at pre-bloom to early bloom stages of alfalfa. Larvae develop through four instars, dropping to the ground to pupate in mid-summer. Adults emerge in late summer to feed and seek out overwintering sites.

Because the weevil is not native to North America, classical biological control with natural enemies from areas of its origin was thought to be an ideal way of managing the pest. Several parasitoids of *H. postica* were introduced into Utah from Europe from 1911 to 1914, resulting in the establishment of the larval parasitoid *Bathyplectes curculionis* (Thomson) (Hymenoptera; Ichneumonidae) (Maund and Hsiao 1991). In Europe, this species deposits its eggs in small alfalfa weevil larvae in the spring, takes about 30 days to become an adult, and then begins a second generation that overwinters as pupae in cocoons (Martelli, cited in Titus 1911).

In the late 1950s, 13 European species of parasitic wasps were released to control the weevil in the eastern United States (Brunson and Coles 1968). The eight species that became established include two egg parasitoids, *Pattasson luna* (Girault) and *Peridesmia discus* Walker (Pteromalidae); three larval parasitoids, *B. curculionis* and *B. anurus* (Thomson) (Ichneumonidae) and *Tetrastichus incertus* Ratzberg (Eulophidae); and two parasitoids of adult weevils, *Microctonus aethiopoides* Loan and *M. colesi* Drea (Braconidae) (Abu and Ellis 1976). *Microctonus aethiopoides* and *B. anurus* are largely responsible for reducing alfalfa weevil populations below damaging levels in the northeastern and mid-Atlantic states (Day 1981; Kingsley *et al.* 1993; Radcliffe and Flanders 1998; Kuhar *et al.* 1999). Six parasitoid species were released into southern Ontario in 1970 and 1971: *Bathyplectes curculionis*, *B. anurus*, *B. stenostigna* (Thomson), *T. incertus*, *M. aethiopoides*, and *M. colesi* (Harcourt and Guppy 1984). These species and the egg parasitoid *P. luna*, which



Fig. 1. Fourth instar alfalfa weevil *Hypera postica* larva on a shredded alfalfa leaflet. Photo courtesy of Agriculture and Agri-Food Canada.

spread naturally from the United States, are now established in Ontario and provide effective control of the weevil (Harcourt and Guppy 1984). In areas where three or more of the parasitoid species are established, alfalfa weevil is seldom of economic importance (Weeden *et al.* 2007), even in areas once requiring multiple applications of insecticide (Hogg 1994).

Biological control of the alfalfa weevil has not met with equal success in western North America. This may reflect differences in the establishment success of certain parasitoid species, and/or differences between strains of the weevil. *Bathyplectes anurus*, which has a 50% greater reproductive potential than does *B. curculionis*, is not well-established in the west (Maund and Hsiao 1991). Also, the western strain of alfalfa weevil is infected with *Wolbachia* bacteria that confer resistance to parasitism by *M. aethiopoides*. This parasitoid is effective against eastern and Egyptian strains of the weevil, which are not infected with *Wolbachia* (Hsiao 1996).

Other Forage Weevils

The weevil family Curculionidae is the largest insect family in the world, with over 40,000 known and probably many unknown species. However, with only 600 species recorded in the country, the Curculionidae is essentially a southern group that is not well represented in Canada (Bright 1993).

The relatively few species of curculionids on the prairies include some of the most destructive pests of agriculture (Arnett 1993). In addition to the alfalfa weevil *H. postica*, the lesser clover leaf weevil (*H. nigrirostris* (F.)) and the clover leaf weevil (*H. punctata* (F.)) also inflict considerable damage on legume forage crops. Of the 11 *Sitona* species known to occur in North America (Bright 1994), the sweetclover weevil (*S. cylindricollis*), two species of clover root curculio (*S. flavesens* (Marsh.) and *S. hispidulus* (F.)), alfalfa

curculio (*S. lineellus* Bonsdorff (= *S. scissifrons* (Say))), and pea leaf weevil (*S. lineatus* (L.)), have been recorded as pests of prairie forages (Beirne 1971). The sweetclover weevil may be the principal reason for the decline of sweetclover as a major forage species in western North America from its heyday in the middle of the last century (Bird 1947, 1949). Traditionally thought to be of little economic importance (Beirne 1971), pea leaf weevil recently has become a major threat to the pulse industry of Alberta and is spreading eastward (Vankosky *et al.* 2009). Other curculionids affecting prairie forages include the clover seed weevils *Tychius picrirostris* (F.), *T. meliloti* Stephens, and *T. stephensi* Schonh (Anderson and Howden 1994). With the exception of *S. lineellus*, all of these are invasive alien species, and little is known about their native biological control agents.

Sap Suckers

Pea Aphid

The pea aphid *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae) is cosmopolitan in distribution in temperate climates. Believed to be Palearctic-Oriental in origin (Blackman and Eastop 1984), it was first found in Canada in Ottawa at the end of the 19th century (Johnson 1900).

In Canada, the pea aphid is holocyclic, or sexually reproductive, overwintering principally as a diploid egg on leaves and stems of alfalfa, clovers, and perennial wild legumes (Harper 1975). The stem-mother fundatrix emerges from the egg in the spring, and then parthenogenetically and viviparously produces a generation of daughters on the overwintering host. The daughters parthenogenetically produce wingless (apterous) or winged (alate) female progeny. Winged forms are produced in response to declining host quality and physical contact or crowding. Winged aphids migrate to other hosts, including other alfalfa stands or annual legumes such as field peas. On the summer hosts, many generations of apterous females are produced parthenogenetically and viviparously, without mating or an egg stage, and enormous populations can build up within a week or two under favourable warm, dry conditions. Pea aphids can also appear as migrants to the prairies when alates are carried on winds from source areas to the south (Smith and Mackay 1989). Such migrations occasionally cause aphid outbreaks in late May or early June, but usually the populations of pea aphids on the prairies peak in late July or early August. In autumn, shorter photoperiods and lower temperatures stimulate parthenogenetic females to produce a single sexual generation of oviparae, or sexual females and males. These mate and the oviparous females lay eggs on the winter hosts, completing the life cycle (Lees 1961; Harper 1979).

Damage by pea aphid is caused by the withdrawal of sap from leaves, stems, blossoms, and pods during feeding (Gyrisco 1958). This removes photosynthate available for plant growth and may cause leaf chlorosis or abscission, wilting, stunting, reduced flowering and seed production (Cuperus *et al.* 1982), and overwintering mortality (Beirne 1972). Pea aphids are the most important insect vector of legume viruses, including verticillium wilt (*Verticillium alboatrum* Reinke and Berth.), the most destructive disease of alfalfa in Europe that was recently introduced into North America (Huang *et al.* 1983). In Canada, *A. pisum* is considered a rare pest of dryland alfalfa or red clover grown for hay (Mackauer 1971), but may be more of a problem on alfalfa grown for dehydration or seed production (Harper and Lilly 1966).

The most common arthropod predators of pea aphids are species of ladybird beetles (Coccinellidae), hover flies (Syrphidae), lacewings (Chrysopidae), minute pirate bugs

(Anthocoridae), and damsel bugs (Nabidae) (Fluke 1925; Gyrisco 1958; Harper and Lilly 1982). Larvae and adults of the introduced ladybird beetle, *Coccinella septempunctata* L., and the native *Hippodamia convergens* G.-M. are especially voracious feeders of pea aphids (Summers *et al.* 2008). In some jurisdictions, treatment thresholds for aphids are based in part on the number of lady beetle adults and larvae present (e.g., Summers and Goodell 2007). Predators usually accumulate when prey numbers become noticeably abundant and will leave an area when prey becomes scarce. Thus, a predator guild can cause an immediate decline in numbers of pea aphids in a field, but not exert density-dependent control, so that aphid populations often increase over time in the presence of predators alone (Snyder and Ives 2003).

In contrast to predators, parasitoids can cause large declines in pea aphid populations (Snyder and Ives 2003). In Manitoba, pea aphid is parasitized by three endemic species of Hymenoptera: *Praon occidentale* Baker, *P. pequodorum* Viereck, and *Aphidius piivorus* (Smith) (Aphidiidae) (Wylie *et al.* 2005). Of several exotic parasitoids imported by the United States Department of Agriculture, the two solitary endoparasitoid species, *Aphidius smithi* Sharma and Subba Rao, and *A. ervi* Haliday, are now established. Significant economic control of pea aphid was achieved by these introduced species in eastern North America and by *A. smithi* in California (Hagen *et al.* 1976). *Aphidius smithi* was also introduced into Canada (Mackauer 1971), and both it and *A. ervi* are now established in most regions, including the prairie provinces of Manitoba and Alberta (Harper 1988; Wylie *et al.* 2005). In Manitoba in 2001, over three-quarters of the *Aphidius* emerging from aphid mummies were *A. ervi*, whereas *A. smithi* is believed to occur at densities too low to have an agriculturally useful effect on the pest (Wylie *et al.* 2005).

The entomophthoran fungus *Pandora neoaphidis* Rem. and Henn. (*=Entomophthora aphidis* Hoff.) is one of the most important pathogens of the aphid (Hutchison and Hogg 1985; Gutierrez and Pickering 1991). The presence of predators and parasitoids such as *C. septempunctata* and *A. ervi* can enhance transmission of *P. neoaphidis* to nearby aphids. This is thought to be a result of aphid escape movements in response to attack, resulting in greater contact with *P. neoaphidis* conidia (Baverstock *et al.* 2008). Because dry climates inhibit the survival of this fungal pathogen, its effectiveness in controlling the aphid on the dry prairies is likely less than it is in more humid areas.

Other Legume Aphids

Originating in North Africa, the spotted alfalfa aphid *Therioaphis maculata* (Buckton) was introduced into North America in the early 1950s (Stern and van den Bosch 1959) and first recorded in Alberta in 1979 (Alberta Agriculture, Food, and Rural Development 1983). Unlike the pea aphid, the spotted alfalfa aphid injects a salivary toxin as it feeds that can kill young susceptible alfalfa plants and stunt mature plants. An early symptom of alfalfa toxicity is veinal yellowing or clearing on leaflets. Spotted alfalfa aphids produce much greater amounts of honeydew than do pea aphids. The honeydew can promote growth of sooty mould on alfalfa foliage, reducing its palatability and quality. Spotted alfalfa aphid is relatively heat tolerant (Davis 1985) and can complete a generation in about seven days at 27 °C (Messenger 1964), making it eminently suitable for the occupation of the warm, dry grasslands of the prairies. Ongoing attempts to control the aphid in California were unsuccessful, for within two years of its discovery in the state, the aphid had developed resistance to several organophosphate insecticides (Stern and van den Bosch 1959). Although the widespread use of parathion, malathion, and tetraethyl pyrophosphate gave excellent control of the aphid initially, their indiscriminate toxicity also largely eliminated

natural enemies of the aphid. In the absence of biological control agents, the few aphids that survived chemical application rapidly multiplied to become a serious economic threat despite repeated chemical treatments. Chemical control of *T. maculata* decreased only when an integrated pest management program was implemented with resistant alfalfa cultivars, imported biological control agents, cultural practices, and chemical control measures that were compatible with beneficial species (Holtkamp *et al.* 1992).

Other aphids on prairie legumes include yellow clover aphid (*Therioaphis trifolii* (Monell)), sweetclover aphid (*T. rheimi* (Borner)), and clover aphid (*Nearctaphis bakeri* (Cowan)). *Nearctaphis bakeri* is native to North America but now occurs in Europe and North Africa. Although its secondary hosts are species of clover (Leguminosae), its primary hosts are species in the family Pomaceae such as *Crataegus, Cydonia,* and *Malus* (Heie 1992). These aphids generally are of minor economic importance to prairie forages. However, *N. bakeri* can vector soybean dwarf virus from clovers to clovers, as well as from clovers to soybean (Harrison *et al.* 2005). This economically important virus is endemic to forage legumes in the United States.

More Sap Suckers

Danks (1988) stated that herbivores in the orders Hemiptera, Lepidoptera, Orthoptera, and many Coleoptera are especially common in the Canadian grasslands. This is particularly true of Hemiptera in legume forages.

Lygus Bugs

In a collection of insects and mites from Alberta alfalfa fields, Harper (1988) found 41 of the 437 species collected to be in the hemipteran plant bug family Miridae, the greatest number in any insect family. The genus *Lygus* comprised the greatest number of species of mirids in this survey.

Lygus bugs (*Lygus* spp., Hemiptera: Miridae) are native to North America, with 16 of the 31 endemic species present in the southern areas of the prairie provinces (Table 1). Nine of these species are pests of alfalfa and other legume crops (Schwartz and Foottit 1998). The most common species in prairie alfalfa fields are the tarnished plant bug (*L. lineolaris* (Palisot de Beauvois)), the pale legume bug (*Lygus elisus* Van Duzee), and *L. borealis* (Kelton). Several *Lygus* species have two or more generations per year in southern prairie latitudes. Within a species, voltinism can vary directly with accumulated temperatures above 10 °C (Champlain and Butler 1967). *Lygus lineolaris* and *L. borealis* are univoltine at latitudes below approximately 50°N (Schwartz and Foottit 1992). Some *Lygus* species have a wide host range. *Lygus lineolaris* feeds on over 300 plant species from diverse families (Young 1986).

The life history of economically important species of lygus bugs was summarized by Kelton (1955). In grasslands, adult lygus bugs emerge from winter diapause when temperatures increase in spring. Early in the season, they feed on forbs and shrubs such as willows, snowberry, or caragana. They then disperse to feed and oviposit on herbaceous weeds, alfalfa, and other crops. Later in the summer, several species of lygus bugs will move onto species of *Aster, Solidago*, and *Artemisia* (Asteraceae) (Schwartz and Foottit 1992). The particular species of host plant may be less important than its physiological state, with preference given to plants that are in reproductive stage (Fye 1980, 1982; Domek and Scott 1985).

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Lygus Species	Distribution	Host Range
atritibialis Knight	Central Great Plains, BC, MB	Artemisia canadensis
borealis (Kelton) *	Widely in northern North America	Asteraceae, Brassicaceae, Fabaceae
convexicollis Reuter	Western sp.	Gum weeds, tar weeds
elisus Van Duzee *	Throughout prairies	Prefers weedy Brassicaceae
hesperus Knight *	Western North America	Broad host range
keltoni Schwartz *	Western sp., southern AB	Broad host range, especially Asteraceae
<i>lineolaris</i> (Palisot de Beauvois) *	Most widely distributed Lygus sp. in North America	Over 300 recorded hosts
plagiatus Uhler	East of Rockies, southern prairies	Ambrosia artemisifolia
potentillae Kelton	Transcontinental	Potentilla fruticosa
robustus (Uhler)	Montane, Lethbridge	Artemisia, Achillia, Asteraceae
rubrosignatus Knight *	Boreal, with southern collections	<i>Senecio</i> , several crops
rufidorsus (Kelton) *	Most agricultural areas of Canada	Solidago spp.
shulli Knight *	Western montane	Herbacious Asteraceae and Fabaceae
solidaginis (Kelton)	Prairies, parkland, Peace River	Symphorocarpos, Solidago spp.
unctuosus (Kelton) *	Transcontinental, especially northern prairies	Stinging nettle Urtica dioica
vanduzeei Knight	West to SK	Asteraceae. esp. Solidago

Several lygus bug species occurring in the grasslands are oligophagous and live on one or a few xeric hosts typical of the region, such as *Artemisia* spp., *Ambrosia* spp., *Potentilla fruiticosa* L., *Achillia millefolium* L., *Solidago* spp., and *Symphoricarpos occidentalis* Hook. Schwartz and Foottit (1998) list four records of *L. convexicollis* Reuter occurring in southern Alberta and Saskatchewan. This species breeds on a group of resinous glandular plants commonly called gumweeds or tarweeds, which occur in arid regions in western North America. *Lygus convexicollis* is well-suited to feeding on hosts such as *Brickellia oblongifolia* Nutt., *Hemizonia luzulaefolia* DC, and *Madia* spp. (Asteraceae) because it has a relatively long labrum that can penetrate to the plant structures beneath the sticky exudates (Schwartz and Foottit 1998).

With their piercing, sucking mouthparts, *Lygus* species preferentially feed on plant tissues high in nutrients, such as apical meristems and leaf primordia, or developing reproductive tissues. Extensive *L. lineolaris* feeding can delay alfalfa regrowth and reduce plant height (Newton and Hill 1970), but lygus bug damage to alfalfa hay is of much less economic importance than is feeding on reproductive tissues, which causes seed loss. Feeding on reproductive tissue causes bud blast; blossom, pod, or fruit abscission; fruiting abnormalities; and seed shrivelling or loss (Soroka 1991). In some plants, in addition to damage from puncture wounds and plant sap extraction, a phytotoxic response also occurs caused by the digestion of plant tissue by the enzyme polygalacturonase present in *Lygus* saliva (Strong 1970). This enzyme is associated with the lacerate and flush method of *Lygus* feeding, and its presence is characteristic of the family Miridae (Wheeler 2001). This toxic response causes necrotic areas and secondary rots at feeding sites on plants such as alfalfa, beans, potatoes, celery, and asparagus.

Several generalist predators feed on lygus bug eggs and/or nymphs. Big-eyed bugs such as *Geocoris pallens* Stål and *G. bullatus* (Say) (Lygaeidae), damsel bugs (*Nabis* spp.), ladybird beetles (Coccinellidae), minute pirate bugs (Anthocoridae), assassin bugs (Reduviidae), and various spiders are predators of lygus bugs commonly found in alfalfa seed fields (Mayer and Johansen 1991; Jorgensen 2005; Blodgett 2009a). Although ladybird beetles will attack lygus bug nymphs (JS, pers. obs.), species such as *Hippodamia convergens* and *Coccinella septempunctata* preferentially prey upon pea aphids (Jorgensen 2005). Given a choice of either lygus bugs or pea aphids, damsel bugs and crab spiders preferentially consume lygus bug nymphs (Jorgensen 2005).

Five native species of *Peristenus* (Hymenoptera: Braconidae) parasitize lygus plant bugs on the prairies (Goulet and Mason 2006) (Fig. 2). Parasitism of lygus bugs in alfalfa by native wasps generally ranges from 0 to 20% (Day 1987), but can be as high as 70% (Braun *et al.* 2001).

Other Plant Bugs

The alfalfa plant bug *Adelphocoris lineolatus* (Goeze) (Miridae) was introduced into North America from Europe early in the 20th century (Knight 1922). It is increasing in economic importance in alfalfa production on the prairies, principally as a seed production pest (Craig 1971) and secondarily as a pest of forage production (Newton and Hill 1970). Two generations per year are common in the southern prairies, but a second generation is rarely completed at latitudes above approximately 51°N. When a second generation is completed, it occurs when very warm spring temperatures permit the rapid development of the first generation (Craig 1963; Soroka and Murrell 1993). Alfalfa plant bugs overwinter as eggs in legume stubble and field trash, develop into adults by late June or early July, and leave alfalfa fields shortly after egg laying. This mirid is oligophagous to slightly polyphagous,



Fig. 2. Parasitoid *Peristenus* near *mellipes* parasitizing from a fifth instar nymph of lygus bug *Lygus borealis*. Photo courtesy of Agriculture and Agri-Food Canada.

feeding on alfalfa, sweetclover, trefoil (Wipfli *et al.* 1990), some vegetables and fruits (Day 1987), and occasionally canola, *Brassica rapa* L. and *B. napus* L. The principal damage from the bug in alfalfa occurs as bud blasting. The superb plant bug (*A. superbus* (Uhler)), the rapid plant bug (*A. rapidus* (Say)), and *Plagiognathus brunneus* Provancher (*=P. medicagus* Arrand) (Miridae) have also been historically problematic in prairie alfalfa seed production (Beirne 1972; Smoliak *et al.* 1981). However, possibly because their overwintering eggs and young nymphs are readily destroyed by cultural operations (Beirne 1972), all three of these species have decreased in prominence as pests of alfalfa seed production across the prairies.

A minority of the Hemiptera occurring in legume fields on the prairies are predacious. *Orius tristicolour* (White) (Anthocoridae) is the most common insect predator in Alberta alfalfa fields, feeding on an assortment of aphids, mites, thrips, plant bugs, and small Lepidoptera (Harper 1988). Species of *Deraeocoris* (Miridae), ambush bugs (Phymatidae), and assassin bugs (Reduviidae) are generalist predators that feed on pests, but also on beneficial species such as honey bees (Harper 1988).

Seed Chalcids

Several species of small wasps in the family Eurytomidae feed on legume seeds. As their names indicate, the larvae of the alfalfa seed chalcid (*Bruchophagus roddi* (Gussakovsky)), clover seed chalcid (*B. gibbus* (Boheman)), trefoil seed chalcid (*B. platypertus* (Walker)),

and sainfoin seed chalcid (*Eurytoma onobrychidis* Nikolskaya) are host specific. Similar in appearance, they are usually identified by the host plant in which they are found.

The alfalfa seed chalcid is thought to be Eurasian in origin, like its host plant, and was first reported to occur as a pest of alfalfa in Canada by Treherne (1919). However, it and the other chalcids listed earlier are now cosmopolitan in distribution (Muesebeck *et al.* 1951). The first Canadian record of sainfoin seed chalcid was from Alberta in 1980 (Hanna 1980). Because this observation occurred shortly after the alfalfa crop was introduced to North America, the insect was likely imported with seed from the Kazakhstan region of Asia in the 1970s.

Seed chalcids are attracted to their flowering host by host odours (Kamm and Buttery 1986). A female will oviposit from 15 to 65 eggs in soft, developing seeds, one egg per seed, over a period of one month or longer. The eggs hatch after about 10 days. Larvae feed on the seed endosperm, develop through five instars and complete their growth in about three weeks, and then pupate in the hollowed-out seed coat. After a short pupation, adults chew their way out of the seed coat, leaving small round exit holes that are diagnostic for the pests. Larvae of this second generation normally overwinter in a pre-pupal stage within the ripened seed (Nielson 1976). Although legume seed chalcids are generally bivoltine on the prairies, three generations of chalcids are common in Oregon and Montana (Carillo and Dickason 1963; Blodgett 2009*b*). Because of the protracted emergence and egg laying of females in the spring to summer, all stages of the chalcid may co-occur.

Seed chalcids do not affect production of forage, but damage by larvae can reduce seed yields by more than 50%. This damage may go unnoticed because the attacked seeds are lighter in weight and may be lost during combining and seed cleaning. Damage to dryland crops can be twice that in irrigated fields, and old seed fields can be two to three times more heavily infested with seed chalcids than new fields (Antonova and Bazyleva 1974). The level of chalcid infestation and seed yields of alfalfa are correlated with temperature, rain, and degree-day data from the year of and the year preceding seed collection (Soroka and Spurr 1998). The infestation level of B. roddi is most closely correlated with the temperature and rainfall in July and August, with the proportion of damaged seed being highest in years following warm and dry summers. Alfalfa cultivar also influences the infestation levels. Winter-hardy cultivars that become dormant early in the autumn have lower levels of chalcid-damaged seeds than do less hardy cultivars that maintain growth later in the season (Soroka and Spurr 1998). Likewise, high variability occurs in the damage caused by trefoil seed chalcid between years (Peterson et al. 1991). This variability is related to weather conditions, mainly temperature and humidity, and the amount of non-harvested seeds remaining in the field.

Although legume seed chalcids are considered host specific, members of the parasitoid complexes associated with them are not. Several species of parasitic wasps attack legume seed chalcids. *Bruchophagus roddi* is parasitized by *Pteromalus sequester* (Walker) (*=Habrocytus medicaginis* Gahan) (Pteromalidae), *Baryscapus bruchophagi* (Gahan) (Eulophidae), and *Idiomacromerus* spp. (Torymidae) (Artokhin 1983; Thoenes and Moffett 1987; Aeschlimann and Vitou 1989). *Tetrastichus bruchophagi* Gahan, *Trimeromicrus maculatus* Gahan, *P. sequester* (Pteromalidae), and *Liodontomerus longfellowi* (Girault) (Torymidae) were reared from clover seed samples in Oregon (Carillo and Dickason 1963). *Aprostocetus bruchophagi* (Gahan) (Eulophidae), *Eupelmus allynii* (French) (Eupelmidae), *Eupelmella vesicularis* (Retzius) (Eupelmidae), *Mesopolobus bruchophagi* Gahan (Pteromalidae), *L. plexus* Gahan, *T. maculatus*, and *P. sequester* parasitize trefoil seed chalcid in North America (references in Peterson *et al.* 1991); two of these are found

in Ontario (Ellis 1991). Richards and Hanna (1982) found *P. sequester, E. vesicularis*, and *L. perplexus* parasitizing sainfoin seed chalcids near Lethbridge, Alberta. Richards (1989*a*) concluded that many of the parasitoids that commonly parasitize legume seed chalcids in the genus *Bruchophagus* in western Canada likely parasitize *E. onobrychidis* as well.

Parasitism of legume seed chalcids may be extremely variable. Carillo and Dickason (1963) found levels of parasitism of alfalfa seed chalcids in Oregon alfalfa samples to average 23%, whereas clover seed chalcids were parasitized at a rate of 3.2%. Nikolskaya (1933) reported 98% infestation of sainfoin seed chalcid in Ukraine, whereas Richards (1989*a*) reported parasitism of less than 6% near Lethbridge. In 2007, 9.5% of cleaned sainfoin seed from a field near Aberdeen, Saskatchewan (JS, unpublished) was infested by *E. onobrychidis*. Of the recovered chalcids, 0.15% were parasitized by *T. sequester* (G. Gibson, pers. comm.). Chalcid populations often remain high despite the presence of their parasitoids.

Alfalfa Blotch Leafminer

A native of Europe, the alfalfa blotch leafminer *Agromyza frontella* (Rondani) (Diptera: Agromyzidae) was first recorded in North America in Massachusetts in 1968 (Miller and Jensen 1970) and along the eastern seaboard shortly thereafter. Spreading north and westward, it was found in the Maritimes, Quebec, and eastern Ontario by 1974 (Harcourt *et al.* 1987); in Manitoba in1998 (Lundgren *et al.* 1999); in Saskatchewan in 2001 (JS, unpublished); and near Brooks, Alberta, in 2005 (Meers 2005). Its rapid spread can be attributed to movement of adults aided by prevailing winds and storm events and by the transport of infested alfalfa.

The leafminer overwinters as a puparium in plant litter at the soil surface. Adults emerge in spring when temperatures rise above 4-7 °C, at approximately the same time that alfalfa starts to develop (Venette et al. 1999). Female flies lay up to three eggs within a leaflet close to the adaxial surface, ovipositing on a total of 150-200 leaflets and marking them with an oviposition-deterring pheromone in the process (McNeil and Quiring 1983). Newly emerging larvae tunnel through the leaflets, develop through three instars, and make feeding mines within the leaf mesophyll in shapes characteristic of each instar. The first instar forms a narrow, linear mine with frass laid down in two parallel lines, the second instar larva forms a transitional mine with frass evacuated in a semicircular pattern, and the third instar larva forms a blotch mine with frass in irregular patches oriented toward the centre of the leaflet (Helgeson and Baxendale 1978). The feeding pattern of all three instars combined appears as characteristic question mark-shaped mines on alfalfa leaflets. Once they mature, the leafminer larvae emerge from their blotches and drop to the ground to pupate at the soil surface. A generation lasts about a month, with several generations per year, depending on seasonal temperatures. Three generations are common in Ontario (Guppy 1981) versus two in northern Minnesota (Venette et al. 1999).

Primary forage losses are caused by larval feeding, but female adults also contribute to alfalfa biomass reduction. Females puncture alfalfa leaflets with their ovipositors to create characteristic circular pinholes and then feed on the exuding plant sap. In extreme infestations, there may be more than 250 pinholes per trifoliate, causing the leaves to become brittle and have little forage value. New infestations of alfalfa blotch leafminer may reduce alfalfa yields by 7–20% and protein content of the hay by 10–20% (Venette *et al.* 1999). Thirty or more large mines per stem have been associated with yield losses of 11% (Hendrickson and Day 1986). Feeding by *A. frontella* may also predispose alfalfa

to attack by pathogens. Richard and Guibord (1980) noted an association of leafminer pinholes with the occurrence of spring black stem, *Phoma medicaginis* Malbr. and Roum. Effects of the leafminer on alfalfa seed production are unknown.

Several indigenous parasitoids attack the invasive leafminer in Canada (Guppy and Meloche 1989). They include Diglyphus intermedius (Gault) (Coote and Ellis 1986) and Chrysocharis giraulti Yashimoto (Eulophidae), both of which also parasitize economically important *Liriomyza* species (Lasalle and Parrella 1991). However, parasitism rates of the leafminer by native species are low and poorly synchronized with A. frontella development (Hendrickson and Barth 1979; Guppy et al. 1988). The United States Department of Agriculture introduced 14 species of exotic parasitoids of A. frontella to Delaware, Pennsylvania, and New Jersey in the 1970s, of which three, Dacnusa dryas Nixon (Braconidae), Chrysocharis punctifaces Delucchi (Eulophidae), and Miscogaster hortensis Walker (Pteromalidae), quickly became established (Drea and Hendrickson 1986). Dacnusa dryas, in particular, became an effective biological control agent against the leafminer, reducing pest populations by up to 84% in Ontario shortly after introduction in 1979 (Harcourt et al. 1988) and generally keeping the pest below economic injury levels when the two species occur sympatrically. Dacnusa dryas has become established in much of the present range of A. frontella. In 2008, populations of the leafminer were reported to be heavily parasitized in fields near Brooks, Alberta (Meers 2008), by an as yet unidentified parasitoid that may be D. dryas. This parasitism level was seen three years after the first record of the pest in the region.

Pollinators

Alfalfa, like most legumes, is primarily insect pollinated. Peck and Bolton (1946) found 10 species of native *Megachile* and three species of *Coelioxis* leafcutting bees (Megachilidae), 13 species of *Bombus* and three species of *Psithyrus* bumble bees (Apidae), the honey bee *Apis mellifera* L. (Apidae), and *Anthophora furcata* Pz. (Anthophoridae) pollinating flowers of alfalfa in alfalfa fields in northern Saskatchewan. This series of pollinators represent the species present before the introduction of the domesticated leafcutting bee *M. rotundata* Fab. Later, Harper (1988) recorded 15 species of pollinating Hymenoptera present in alfalfa fields in Alberta: six species of leafcutting *Megachile* bees, eight species of *Bombus* bumblebees, and the honey bee.

Honey bees were the most common bees found in an early Saskatchewan survey of alfalfa fields, but were considered to be poor pollinators of the crop (Knowles 1943). This perception may be in part due to the mechanism of pollination, or "tripping," of an alfalfa flower, and in part to the learning ability of the honey bee.

The corolla of the alfalfa flower is typical of legumes. It consists of the basal petal or standard, which acts as a landing platform for insects, two smaller side or wing petals, and two fused top petals that form the keel, which is directly opposite the standard. The keel encloses, under considerable tension, a reproductive column formed by the stigma and 10 anthers. This column is normally non-functional unless it is released from the keel. Pressure on the petals causes the keel to release the reproductive column and it springs forward to land on the standard (Larkin and Graumann 1954), similar to the action of the metal bar of a mouse trap. The release of the alfalfa reproductive column is so sudden and has such force that observers describe it as an explosion (Reinhardt 1952). Once released or tripped, the alfalfa column does not return to its former position within the keel as in other legumes.

The length of its tongue or proboscis determines in part the amount of time a bee requires to land on a flower and extract nectar (Plowright and Laverty 1984). Honey bees have relatively short tongues (Waddington and Herbst 1987) and are not well-suited to extracting nectar from long, tubular corollas typical of alfalfa flowers. Reinhardt (1952) anthropomorphically described the alfalfa flower as a trap for honey bees trying to extract nectar from the nectaries within the corolla. When a honey bee is caught in a tripped flower, considerable effort is needed on the part of the bee to extricate itself. Naive honey bees will occasionally trip alfalfa flowers, but experienced bees avoid doing so, indicating a learning ability in the species (Reinhardt 1952). Most nectar-gathering honey bees avoid alfalfa flower tripping by "robbing" the flower, inserting their proboscis at the side of the flower and gathering nectar without landing on the standard or transferring pollen.

Bumble bees are fairly efficient pollinators of alfalfa flowers (Peck and Bolton 1946), but their numbers in comparison to other pollinators in Saskatchewan alfalfa fields have been low (Knowles 1943) and may be getting lower throughout western North America (Grixti *et al.* 2009). Many bumble bees prefer to visit native prairie dicotyledonous species (Clinebell 2001), red clover, or sweetclover rather than alfalfa (Harper 1988).

Megachilid leafcutting bees, represented by 22 species in western Canada (Richards 1989b), are the most efficient pollinators of alfalfa (Knowles 1943; Richards 1989b). They nest in sod, soil, holes in trees or rotting tree stumps, old insect burrows or mud dauber wasp nests, or any other suitable cavity that is from 2.5 cm to approximately 100 cm deep. Unlike honey bees, there is no queen or division of labour. Although they often nest in close proximity to one another, each female maintains its own nest. Leafcutting bees, as their name implies, construct nests out of a series of circular or elliptical pieces of leaves or other suitable material such as flower petals. Some species have strong preferences in the choice of plant material used to line the nest and cell. One species, Megachile umatillensis Mitchell, native to the western United States, cuts pieces only from the petals of evening primrose Oenethera pallida (Bohart and Youssef 1972). Alfalfa leafcutting females (Fig. 3) prefer to cut pieces from leaves of plants with "soft" foliage such as alfalfa, clover, buckwheat, rose, lamb's quarters, or canola petals. They cut pieces 0.6-0.12 mm in size from the leaf edges with their sharp mandibles, and then hold the pieces next to their body as they fly back to their nest, transporting one leaf piece per flight. They construct cigarlike nests that contain several to many overlapping thimble-shaped cells, each about the size of a pencil eraser. Each cell is composed of about 15 leaf pieces, with two or three more pieces capping the end of the cell once it has been provisioned and the egg is laid. Cells contain a provision ball of stored pollen and nectar mixed together and a single egg is inserted into the ball.

Megachilidae have their brush-like, pollen-carrying scopa on the ventral surface of the abdomen and not on the hind legs as does the honey bee. Females force apart an alfalfa flower, insert their tongues into the corolla, and extract nectar. This action causes the stamens to flip up, striking the bee under the head and on the thorax. The bees transfer pollen collected on their bodies to their scopa and move on to the next flower, cross-pollinating as they travel. When they return to their nests, they enter the cell that they are provisioning headfirst, regurgitate the nectar into the cell, back out of the nest, turn around and back into the nest, and then scrape off the pollen into the nectar (Richards 1989*b*). Unlike honey bees, megachilids are not deterred by the explosiveness of alfalfa flower tripping and will return to alfalfa flowers numerous times.

Megachilid bees are among the world's most efficient pollinators, in one study tripping an average of 17.3 alfalfa flowers per minute (Knowles 1943). This is in part



Fig. 3. Alfalfa leafcutting bee *Megachile rotundata*, the principal commercial pollinator of alfalfa in North America. Photo courtesy of Agriculture and Agri-Food Canada.

because their long tongues allow them to reach the nectar in tubular flowers with ease, in part because the "swimming" or vibrating movements at flowers facilitates effective pollen transfer, and in part because of their high frequency of flower visits. Ironically, leafcutting bees are efficient pollinators because they are inefficient nest provisioners and may require 15–27 flower visits to gather sufficient resources to provision a single brood cell (Richards 1989*b*).

Several features of alfalfa leafcutting bees make them amenable to domestication. In addition to being efficient pollinators, they prefer to visit alfalfa or other legume blossoms and restrict their foraging to a small area of a few hectares. In contrast, honey and bumble bees forage on many plants over great distances. Megachilids are much less aggressive than honey bees, stinging only when physically trapped or attacked. They do not defend their nests against invaders. Their venom is less toxic than that of the honey bee. They are solitary but gregarious and will live their separate lives in close proximity to other leafcutting bees. They will live in man-made structures, and their life cycle can be

synchronized with pollination requirements. Unlike native leafcutting bees, *M. rotundata* will stay where placed. Although less cold tolerant than bumblebees, they will visit flowers at colder temperatures than will honey bees.

The biology of the domesticated alfalfa leafcutting bee on the prairies is similar to that of its wild relatives, albeit it lives in an artificial domicile. The insect overwinters as a pre-pupa in its leaf cocoon, with leaf cells stored in bulk at optimum temperatures of 5–8 °C. About 21 days before crop pollination is needed, the bee cells are removed from refrigeration and incubated in trays at 30 °C. The adult bees emerge from 20 to 31 days after the initiation of incubation. Approximately half of the males emerge before the first females, and about 60% of a brood is male. Some leafcutting bee producers "bleed off," or remove, most of the largely unnecessary male bees before colony placement. As emergence of female bees commences, the trays of cells are transported to shelters in the fields. These shelters contain nesting material, usually polystyrene foam or wooden blocks with holes or tunnels drilled into them, in which the females create cells for their young. Although males can mate several times, females mate once, shortly after emergence. Adult females forage, usually downwind, to a short distance from the nest box, and return to the same nest box to lay their eggs. They live up to two months or more, and lay some 35–40 eggs during this time, each in its own leaf cell. Producers remove nest boxes from the field once they are approximately 75% full of capped cells and store them for the winter. If a nest box becomes full and few empty tunnels are available for nesting, a female leafcutting bee will deconstruct a cell already created by another female, eject the egg or larva that was inside, and lay her own egg in the cell. On the prairies, there is usually one generation per year (Richards 1989b).

More than two dozen species of predators, parasitoids, nest destroyers, and pathogens attack leafcutting bees (Baird *et al.* 1991). The most common parasitoid of the bee on the prairies is *Pteromalus venustus* Walker (Pteromalidae), an external gregarious parasite of the pre-pupal to late pupal stage of the leafcutting bee, as well as of many native bees and wasps. Also of Eurasian origin, the parasitoid female pierces the bee pupal cocoon with her ovipositor, anaesthetizes the developing bee, and oviposits between it and the cell lining. Because parasitism of bee larvae usually results in the death of both the host and the wasp, *P. venustus* prefers to parasitize pre-pupal to late pupal stages of the leafcutting bee (Tepedino 1988). After feeding, parasitoid larvae, which may number over 30 per bee (Hobbs and Krunic 1971), develop into adults if temperature and day length are suitable, or overwinter as pre-pupae in the bee cocoon. In the spring, the parasitoid adults emerge from about day 8 to day 13 of incubation and mate and parasitize other unparasitized, developing bees. The species is multivoltine on the prairies.

Species in the chalcid genera *Monodontomerus* (Torymidae), *Tetrastichus*, and *Melittobia* (Eulophidae) attack the alfalfa leafcutting bee and other native solitary and social bees and wasps. The cleptoparasitic wasp *Sapyga* spp. (Sapygidae) lays her eggs in the cells of the leafcutting bee, and the larger wasp larva consumes the provisions meant for the bee. Stored product pests can destroy cells (Hobbs 1968), and various ants, dragonflies, yellowjacket wasps, and pollen-eating mites are known to attack leafcutting bee larvae and adults (Richards 1989*b*).

The chalkbrood fungus (*Ascosphaera aggregata* Skou.) was first found in *Megachile* spp. in Nevada in 1973. It spread in wild and domestic leafcutting bee populations throughout western North America. Chalkbrood is currently well-established in southern Alberta (Murrell and Goerzen 1994) and is present at extremely low levels in Saskatchewan and Manitoba. Chalkbrood spores become incorporated into the cells of the bee larvae, and

then germinate and grow in the gut of the larvae that consume them, eventually leading to the demise of the bees before they reach maturity. Larvae become hardened and appear chalky, cream coloured, gray, or black. In areas where chalkbrood is prevalent, bee mortality may be 50% or higher.

The domestication of the leafcutting bee was the catalyst for the development of the alfalfa seed industry in western North America. It also illustrates an interesting facet of population ecology, that of physiological plasticity. Native to much of Eurasia, M. rotundata was first identified in North America from the District of Columbia and Virginia in 1947, but specimens were found in Kansas in 1950 and in California in 1949, suggesting multiple introductions or a much earlier arrival (Stephen 1991). Populations slowly grew, and by 1959 the bee's proclivity to gregariousness and to alfalfa pollination specificity were noted in alfalfa fields ranging from Utah to Oregon. When leafcutting bees were first imported into Alberta by Hobbs in 1962, they pollinated alfalfa only when temperatures were at or greater than about 21°C, which was a serious limitation to the bee's usefulness as a pollinator. A report from the Canada Department of Agriculture Saskatoon Research Station in 1964 stated that the alfalfa leafcutting bee was an interesting anomaly, but its inability to work at cooler temperatures rendered it impractical as an alfalfa pollinator on the Canadian prairies. Through natural and managed selection, the bee's cold tolerance has increased, and now pollination begins at 18 °C or even lower, and the bee has become well adapted to life on the prairies. The leafcutting bee production and export industry is now a thriving industry on the Canadian prairies, with Saskatchewan and Manitoba producing about 3.25 billion leafcutting bees annually for use around the world.

The success of domestication of *M. rotundata* in North America led workers to investigate the potential of the bee as an alfalfa pollinator in Europe and Asia. Reports from eastern Europe indicated that endemic *M. rotundata* populations were low in number, were difficult to trap and manage, were heavily parasitized, and were not particularly loyal to alfalfa (Stephen 1991). The subsequent successful reintroduction of Canadian *M. rotundata* to many areas of the world led to the demise of endemic populations of the bee or to interbreeding with Canadian populations. One of the few remaining native populations of *M. rotundata* in France was found to have significant behavioural and morphological differences from Canadian bees (Tasei 1982). How these changes arose is uncertain, but they may have resulted from an unknown "founder event" occurring at the time of establishment of the bee in North America (Stephen 1991).

Integrated Pest Management of Forages

The practice of integrated pest management in forages arose largely as a result of the need to conserve beneficial insects, including pollinators, predators, and parasites. The alfalfa and clover hay and seed industries were early adopters and implementers of the integrated pest management concept. In the United States, the first multi-state integrated pest management program was set up in alfalfa crops in 1976 in an effort to protect populations of beneficial insects (Fick and Lamp 1995). Alfalfa is now the model for forage and other crop-integrated pest management programs (Summers 1998). An integrated pest control regimen that includes insect monitoring, use of economic thresholds, and insecticide selectivity has been developed for alfalfa seed production on the prairies (Soroka *et al.* 2008). The sweep net has become an integral tool for many alfalfa seed producers or their scouts. Ecosystem stability may be one reason for the success of integrated management of arthropods in forage production in North America.

Conclusions

Forage crops constitute one of the most stable of any grassland agricultural production systems and contain some of the most diverse arrays of arthropods in the grassland biome. In part because of the agronomic practices unique to legume forage production and in part because of the characteristics innate to the plants themselves, arthropods, although numerous in species, infrequently reach pest status in forage crops. The majority of the few arthropod pest taxa of forages on the Canadian prairies are invasive alien species, as exemplified by four of the five pests discussed in this chapter.

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