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POLLINATION STUDIES IN ALFALFA, MEDICAGO SATIVA L. (LEGUMINOSAE),
WITH SPECIAL REFERENCE TO THE ALFALFA LEAFCUTTER BEE, MEGACHILE
ROTUNDATA (F.) (APOIDEA)

by

BRENDA S. BROOKES, B.Sc.(Hons.)

A thesis submitted to the Faculty of
Graduate Studies and Research
in partial fulfilment of
the requirements for the degree of

Master of Science

Department of Biology

Carleton University

Ottawa, Ontario

Dec. 11, 1992

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in partial fulfilment of the requirements for
the degree of Master of Science

Thesis Supervisor

Chair, Department of Biology

Carleton University

Dec. 11, 1992

ABSTRACT

Flowers of alfalfa (Medicago sativa L.) have a remarkable pollination mechanism, apparently specialized for bees. The literature was surveyed, and it was found that hundreds of bee species have been recorded on alfalfa flowers, and that families and genera of bees differ in their preferences for alfalfa flowers. Over 500 collections of pollinating bees were made, and showed that the genera most attracted to Canadian alfalfa are Megachile, Bombus, and Halictus. Experiments indicated that increased visitation to alfalfa was related to: a) limited competition from surrounding sources of pollen and nectar during the alfalfa blooming season; b) limited size of the alfalfa plantation; and c) spill-over of pollinators from wildflowers surrounding and interspersed with the alfalfa. The alfalfa leafcutter bee strongly preferred alfalfa flowers over the flowers of most other species, and showed innate pollination behavior suiting it to the distinctive alfalfa flower. By contrast, honeybees strongly preferred flowers other than alfalfa.

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Introduction

Pollination biology is both of theoretical and practical interest. Theoretically, the analysis of adaptive relationships between pollinators and flowers provides an excellent opportunity for the study of evolution (Baker 1983). Depending on the degree of co-adaptation between flowers and their pollinating animals, from one to many pollen- and nectar-foraging insect species may visit particular plant species (LaPlaca Reese and Barrows 1980). In many cases floral morphology restricts the number and species of pollinators, depending on their sizes, tongue length, phenology, or behavior (LaPlaca Reese and Barrows 1980). Solitary bees are considered to be especially useful for studying adaptations to particular flowers (Steiner and Whitehead 1990). Practically, pollinators are responsible for much of the value of agricultural crops. For example, in the U.S. alone it has been estimated that pollinators generate as much as 20 billion dollars annually (Levin 1987, Torchio 1990). This study addresses the relationships between the specialized flowers of one of Canada's most important economic plants, alfalfa (Medicago sativa L., family Leguminosae) and bees that pollinate it, including native North American bees and the alfalfa leafcutter bee (Megachile rotundata (F.) (often incorrectly referred to as M. pacifica (Panzer); Roberts 1978), Hymenoptera; Megachilidae; Fig. 1).

Alfalfa

Alfalfa is considered to be the most widely adapted agronomic crop, the most energy-efficient crop to grow, and the

Fig. 1. Photographs of female (top) and male (bottom) alfalfa leafcutter bees.

most important source of protein yield per ha (Barnes et al. 1988). It is the principal hay plant in the United States (Hintz 1983) and the most important forage legume of Canada (Goplen et al. 1980) and the C.I.S. (formerly U.S.S.R.; Michaud et al. 1988). More than 10 million ha of alfalfa hay are harvested annually in the USA, and about 2 million ha annually in Canada (Rumbaugh 1991).

Although alfalfa is a perennial, alfalfa pastures lose their vigour after about 5 years, and therefore must be periodically replanted from seed (Goplen et al. 1980). Since the crop arises each year from perennial shoots, pollination and pollinators are not required in most years. Alfalfa is mostly an outcrosser, pollinated by bees, so bee pollination is critical for the production of seeds, and therefore ultimately for the forage crop. It is ironic that although more publications have been produced about the pollination biology of alfalfa than of any other plant (McGregor 1976), there has been only limited research on the evolutionary aspects of the highly evolved pollinating mechanism.

Alfalfa flowers have a rare floral mechanism that promotes cross-fertilization. The following summary of the mechanism of alfalfa pollination is based on Larkin and Graumann (1954). The parts of an alfalfa flower are shown in Fig. 2. There are three basic petal types: a large standard (vexillum) petal, which attracts pollinators; two smaller, flanking wing petals (ala, plural alae) on which insects commonly alight; and two petals

Fig. 2. Diagrams of alfalfa flower (after Brookes and Small 1988). A, intact, tripped flower of alfalfa. B, dissected flower.

A **B**

fused at one of their margins to form the keel (carina), which shelters the stamens. The staminal column consists of a free (vexillary) stamen opposite the standard, and nine additional stamens whose filaments are fused basally into a tube surrounding the ovary. The explosive tripping mechanism arises from pressure exerted by elongated "expansion-restrained" cells of the keel side of the staminal column. This pressure results in a curving of the staminal tube which arcs the sexual column towards the standard. A complicated arrangement of the keel and wing petals restrains the sexual column, preventing it from slapping against the standard petal. Portions of the wing petals called wing horns block the throat of the corolla, hindering pollinators from reaching the basal nectary. When a bee of appropriate dimensions pushes against these wing horns the sexual column is released and slaps against the insect (Fig. 15A). If the insect is carrying pollen from the flowers of another plant, the stigma may be cross-pollinated. Furthermore, pollen is deposited on the insect for transport to other flowers.

It is important to keep in mind that native New World bees are not the natural pollinators of alfalfa. Alfalfa is native to the Old World, most probably in western Asia. It was imported into South America in the 17th century, into the U.S. in the 18th century, and into Canada in 1871 (Michaud et al. 1988).

Managed pollinators: Honeybees

Native North American bees produced acceptable yields of alfalfa seed until about the end of the last century. However,

as the prairies were cleared and monocultures eliminated nesting sites of the unmanaged native bees, alfalfa seed yields declined dramatically (Parker et al. 1987), so that seed production became dependent on managed bees, principally the honeybee.

The honeybee is the only social bee currently managed commercially to pollinate alfalfa, although studies of the feasibility of using bumblebees are in progress (D. Fairey, personal communication). It has long been known that the honeybee is of limited practical value in alfalfa seed production in northern climates such as Canada's (McGregor 1976). Honeybees find alfalfa nectar attractive, and nectar-collecting bees readily visit alfalfa flowers. However, they quickly learn to rob the flower of its nectar without tripping the staminal column by inserting their proboscises in the side of the corolla tube. Several years of observations at Guelph, Ontario, showed that an average of only 76 flowers are tripped for every 10,000 visited by honeybees, and that most of the tripping was done by young and inexperienced workers that had not yet learned to rob (Smith 1960). Pollen-collecting honeybees find alfalfa pollen unattractive and prefer other plants. However, if alternative pollen sources are limited or unavailable, honeybees will collect alfalfa pollen, which is very difficult to obtain without tripping the flowers.

Honeybees pollinate alfalfa more effectively in hot dry climates, such as in interior valleys of California where alfalfa seed is raised, because the flowers trip more easily (Parker et

al. 1987). Consequently, native wild bees are relatively important in cooler, humid areas such as Canada, the northern United States, and most parts of Europe (Bohart 1958). Nye and Mackensen (1968) demonstrated that honeybees vary genetically in their predisposition to pollinating alfalfa, and that the bees can be selected for this trait, but their observation has not led to the selection of a honeybee suitable for alfalfa. Accordingly, in Canada honeybees play a minor role in alfalfa pollination.

Managed pollinators: alfalfa leafcutter bees

The following account of the natural and economic history of alfalfa leafcutter bees is based on Faurey et al. (1984) and Richards (1984). Megachile species occur on all the major land masses of the world. There are about 115 species in North America, of which 29 occur in Canada. The alfalfa leafcutter bee, Megachile rotundata (F.), is a Palearctic species, ranging from Europe and North Africa to Mongolia. Female alfalfa leafcutter bees are larger than the males, although the latter are about twice as frequent. Species of Megachile are solitary, although the alfalfa leafcutter bee is gregarious (i.e., tolerates a high concentration of nearby nests of other females). Females independently construct their own nests, collect provisions, and lay eggs. The males play no role except for fertilizing the females. The name leafcutter (or leafcutting) bee stems from the females' use of their serrated mandibles to cut round or oblong sections of leaves and petals. These are

shaped into thimble-like cells within an appropriate-sized tunnel, which they provision with a mixture of pollen and nectar.

Several characteristics of the behavior of alfalfa leafcutter bees make them suitable for commercial management. Their gregarious nature means they are unlikely to disperse. They accept man-made nesting sites. Emergence can be synchronized to coincide with alfalfa flowering. The limited flight range restricts the bees to the flowering crop provided. Bohart (1972) discusses these and additional advantages of using leafcutter bees.

The alfalfa leafcutter bee is bivoltine (Richards 1984) in warm climates. Since alfalfa flowering can extend over several months, the second generation could take advantage of this. The foraging period of the alfalfa leafcutter bee usually coincides with the blooming period of alfalfa in most climates (Bohart 1972), suggesting a possibly intimate evolutionary relationship between the plant and the bee.

Historical accounts of the alfalfa leafcutter bee's introduction and use are given in Free (1970), Ivanochko (1979), Klostermeyer (1982), Richards (1983) and Torchio and Parker (1975). The bee was inadvertently introduced from eastern Europe or western Asia to the east coast of North America about 1930. It is currently found throughout the northern United States, and extends north to southern Ontario as far as Ottawa (Ivanochko 1979). The bee is now used to produce alfalfa seed in the western U.S., Canada, New Zealand, and in South American and

European countries. In Canada, attempts to use leafcutter bees for producing alfalfa seed began in 1961 in southern Alberta, and since then there has been a steady expansion of not only the alfalfa seed industry but also an industry producing the leafcutter bees. As a result, western Canada no longer imports alfalfa seed, although seed is still imported into eastern Canada. Additionally, western Canada has become the world's leading supplier of alfalfa leafcutter bees, with exports mainly to the U.S., and also Argentina, Russia, and many European countries. In the past few years 150 to 300 million bees have been exported annually (Richards and Krunic 1990).

Richards (1989) summarized attempts to use the alfalfa leafcutter bee as a pollinator of crops other than alfalfa. While the bee has had some success on a variety of other crops (mostly on legumes), it is not nearly as useful as the honeybee. For example, the alfalfa leafcutter bee was observed to visit only 21 of 100 plants in bloom in a general plant nursery at the University of Guelph (Richards 1989).

Managed pollinators: alkali bee

The alkali bee (Nomia melanderi Ckll.) is an efficient pollinator used commercially to pollinate alfalfa in the northwest U.S. and in Canada (Southwick 1988). It is a solitary bee native to limited areas west of the Rocky Mountains, and while it is an excellent pollinator of alfalfa (Johansen and Mayer 1976), in Canada and in most areas it is not as good a pollinator of alfalfa as the alfalfa leafcutter bee. A possible

explanation for this might be the sympatric origin of the alfalfa leafcutter bee and alfalfa in central Asia and Europe, which may have led to the bee naturally evolving adaptations to the flowers. Since the alkali bee is native to North America, it could not have naturally evolved an affinity to alfalfa flowers.

Questions addressed in this study

There are several general areas of theoretical and practical interest regarding the pollination relationships of bees and alfalfa. This thesis deals with three of these areas, and is therefore divided into three major sections.

The most basic question is whether the thousands of known bee species are equally attracted to alfalfa flowers. This question is dealt with in Part A, which provides: a brief literature review of the bees recorded as good pollinators of alfalfa in various regions of the world; the first extensive literature survey of records of all bee pollinators reported on alfalfa, and an analysis of the comparative preferences for alfalfa by the different families and genera of bees; a list of native Canadian bee species observed to pollinate alfalfa during field work carried out for this study; and a comparison of the seed set resulting from pollination by wild bees and managed bees, using data from the literature.

The second general question addressed whether competition for native pollinators differs between native vegetation and planted alfalfa, in both eastern and western Canada. This was not originally planned as a major investigation, but as field

work progressed it became increasingly obvious that the ability of alfalfa to attract wild pollinators differed considerably according to spatial relationships with surrounding wildflowers. This is important in evaluating to what extent native bees can be exploited as pollinators of alfalfa in different regions of Canada. Therefore, Part B deals with the ability of alfalfa to attract native Canadian bee pollinators with respect to: different spatial relationships with wildflowers, comparative attractiveness of some other flowering plants, and different flower colors. Also, alfalfa seed yield by wild pollinators in the Ottawa area was compared with records of seed yield produced by managed leafcutter bees.

The third general question dealt with whether alfalfa leafcutter bees are more compatible with alfalfa flowers than with flowers of other species. As noted later, this specific relationship is the basis of a multimillion dollar industry, which is suggestive of a unique relationship, although almost no comparative experimental studies have been conducted to determine whether or not this is the case. Therefore, Part C includes experimental and observational studies of the comparative attractiveness of a variety of different plant species, including alfalfa, primarily to the alfalfa leafcutter bee, but also to some other insects; observations on foraging times of alfalfa leafcutter bees and honeybees on different flowers, and an examination of foraging time in relation to flower size; and observations of behavioral differences of leafcutter bees on

several different types of flowers.

PART A: SURVEYS OF DIFFERENT POLLINATORS ON ALFALFA FLOWERS

Introduction

This section addresses the comparative attractiveness of bee species to alfalfa flowers, by conducting literature and field surveys. The assumption is that the recorded presence of a bee foraging on alfalfa is an indication of attractiveness. Because an extensive survey of bee species observed pollinating alfalfa has not been published, I have attempted a more comprehensive summary of information from the world's literature than presently available. Such a survey is desirable because very few bees have been commercially exploited for the purpose of pollinating alfalfa, and it is quite possible that additional species may be useful. Also, this information provides the opportunity for taxonomic and geographical analysis. The geographical information may be helpful in indicating where the pollinators may be obtained for experimental purposes.

In addition to the examination of the world literature with regard to alfalfa, collections of bees on alfalfa were made during the field work conducted for Part B of this study. This provided the opportunity to examine the relative preferences of bee families in Canada for alfalfa, as done above for North America.

In a brief listing of some major surveys conducted up to 1957, Bohart (1957) concluded that for North America, the most species attracted to alfalfa occurred in the bee-rich areas west of the Rockies; that for northern Europe, limited numbers of

species of wild bees are attracted to alfalfa; and that in southeastern Europe and central Asia, where alfalfa originated, surveys of wild bees visiting alfalfa are limited.

Methods

Various sources were utilized to compile a comprehensive world list of bee species recorded on alfalfa flowers, including computer literature searches, examination of Hymenopteran reference works, review of about 500 scientific publications dealing with various aspects of Hymenoptera, alfalfa, or pollination, and personal communication with about 50 Hymenopterists. A species of bee was included on the list only if that bee was reported to be actually foraging on alfalfa flowers. In many cases, presence of a given species on alfalfa has been independently reported by different researchers. For simplicity, however, only one reference was recorded for each species (Table 1). Based on this table, frequencies of families and genera of pollinating bees on alfalfa were found for North America, Europe, and Asia (Table 2), and a Chi-square test was performed on the data to examine whether there were any significant differences among these frequencies. (Since frequencies of pollinating bee families and genera were not available for Asia and Europe, they were assumed to be equal. Frequencies were available for North America, and are used in the Chi-square test discussed below). Information indicating whether the pollinator was important or merely an occasional visitor was usually not available. However, this information was available

for a number of the most important pollinators of alfalfa in different regions of the world, and is summarized in Table 3. Geographical occurrence in the main north temperate regions (North America, Europe, Asia) was also recorded, where the information was available (Table 1). And, taxonomic position (by family and genus) and distribution (in North America, Europe, and Asia) of the 149 species was also determined (Table 1).

The relative occurrence of bee families on alfalfa was examined for North America. The numbers of species of bees in North America (north of Mexico) were obtained for the eight families of bees present in North America from Hurd (1979), and are shown in Table 4 (comparable information does not seem to be available for other areas or for the world). The numbers of species of bees in Canada for each of these families is also indicated in Table 4, after Masner et al. 1979. The percentage of species within each bee family represented by the bees recorded on alfalfa (in Table 1) was calculated for North America (Table 4). A chi-square test was performed on the frequency data for numbers of bee species on alfalfa for the eight families in comparison to the expected frequencies.

Collection of bees in eastern and western Canada is described in Part B. All Hymenoptera foraging in 20 alfalfa sites were collected, including non-pollinators (mostly wasps). Identifications were made, as far as possible, employing Mitchell's (1962) Bees of the Eastern United States. Considerable help with identifications was provided by L.

Dumouchel of Agriculture Canada and by R. Owen of the University of Calgary. For the pollinating bees collected, genera were examined with respect to a) their fidelity to alfalfa (i.e., relative occurrence at the 20 alfalfa sites examined); and b) their relative occurrence as a percentage of all pollinators collected. The order of frequency of occurrence of genera at the 20 Canadian sites was compared with the order of occurrence for the world, taken from the literature.

Results

Based on examination of the literature, a total of 149 species in 25 genera of bees are recorded on alfalfa flowers in Table 1. Of these genera, those with the most species recorded foraging on alfalfa were: Megachile (43 species), Bombus (21 species), Halictus (16 species), Osmia (12 species), Andrena (11 species), Eucera (9 species), and Nomia (5 species). Table 2 shows frequencies of families and genera of the alfalfa-pollinating bees compiled in Table 1, for North America, Europe, and Asia. The chi-square test performed (omitting Melittidae due to its very limited representation) gave a total chi-square statistic of 8.34 which is not significant at $P = 0.05$; that is, no significant differences for these frequencies was found.

The numbers of species of bees in North America (north of Mexico) for the eight families of bees present in North America are shown in Table 4. No records in North America of alfalfa visitation were found for three of the bee families (Colletidae, Oxaeidae, and Melittidae). Of the 3465 described species of

North American bees, 76 species have been recorded on alfalfa flowers. Table 4 shows expected numbers for the eight families of bees. A chi-square test gave a chi-square of 45.47, which is significant at $P = 0.001$. That is, there are very highly significantly different frequencies than expected by chance alone. The social bee family (the Apidae) had a remarkable 31.90% of the species recorded on alfalfa. Of the bee families that are predominantly or entirely solitary in life style (all but the Apidae), the Megachilidae had the highest percentage (5.93) of species recorded on alfalfa.

A list of the genera of Hymenoptera collected during this study is given in Table 5 (wasps collected are identified in Appendix 2). Vouchers of all collections are cited in Appendix 2, and deposited in the Canadian National Collection of Insects, Arachnids and Nematodes (CNC) in Ottawa. Six hundred and four collections of Hymenoptera were made (Appendix 2). Of these, 545 collections were pollinating Apoidea, belonging to 13 genera (Table 6). The frequency of occurrence in the 20 sites examined (i.e., percentage of sites in which the genera occurred), and the relative occurrence of these 13 genera (i.e. percentage of occurrences of a genus relative to total recorded occurrences of all pollinating bees), are shown in Table 6. The order of frequency of these 13 genera is compared in Table 6 for the field studies conducted in Canada and for the literature studied. As can be seen in Table 6, for both the literature of the world and the field studies in Canada, Megachile was the most frequently

recorded or collected alfalfa-pollinating genus, followed by Bombus and Halictus. Andrena was the fourth most collected genus in Canada and the fifth most recorded genus reported in the literature.

TABLE 1

Recorded occurrences of bee species on alfalfa
flowers in North America, Europe and Asia.

SPECIES	DISTRIBUTION		REFERENCE
	N.A.	Eur. Asia	
Superfamily: APOIDEA			
Family: HALICTIDAE			
Subfamily: Halictinae			
Genus: <u>Halictus</u>			
<u>H. eurygnathus</u> Bluthg.	*	*	Móczar 1959
<u>H. farinosus</u> Smith	*		Nye 1980
<u>H. germinatus</u> Per.	*		Móczar 1959
<u>H. glabriventris</u> Cwfd.	*		Linsley 1946
<u>H. incompletus</u> (Cwfd.)	*		Linsley 1946
<u>H. leucozonius</u> Schenck	*	*	Dochkova et al. 1987
<u>H. ligatus</u> Say	*		Bohart 1958
<u>H. malachurus</u> Kby.	*	*	Popov 1956
<u>H. marchali</u> Bluthg.	*	*	Dochkova et al. 1987
<u>H. nitidus</u> Panz.	*		Dochkova et al. 1987
<u>H. parallelus</u> Say	*		Nye 1980
<u>H. quadricinctus</u> (F.)	*	*	Dochkova et al. 1987
<u>H. rubicundis</u> (Christ)	*	*	Móczar 1959
<u>H. scabiosae</u> Rossi	*		Dochkova et al. 1987
<u>H. simplex</u> Bluthg.	*		Dochkova et al. 1987
<u>H. tripartitus</u> Ckll.	*		Linsley 1946

TABLE 1 (continued)

SPECIES	DISTRIBUTION		REFERENCE
	N.A.	Eur. Asia	
Genus: <u>Lasioglossum</u>			
<u>L. pauxillum</u> (Schr.)	*		Banaszak and Manole 1987
Genus: <u>Nomiodes</u>			
<u>N. variegata</u> (Olivier)	*		Wafa et al. 1975
Genus: <u>Rhophites</u>			
<u>R. canus</u> Eversm.	*	*	Dimitrov et al. 1987
Subfamily: Nomiinae			
Genus: <u>Nomia</u>			
<u>N. diversipes</u> Ckll.	*	*	Popov 1956
<u>N. melanderi</u> Ckll.	*		Menke 1952
<u>N. nevadensis</u> Cress.	*		Linsley 1946
<u>N. peninsularis</u> Ckll.	*		Linsley 1946
<u>N. ruficornia</u> Spin.	*		Parker et al. 1987
Family: ANDRENIDAE			
Subfamily: Andreninae			
Genus: <u>Andrena</u>			
<u>A. albofasciata</u> Thoms.	*	*	Anasiewicz 1975
<u>A. candida</u> Smith	*		Youssef and Bohart 1960
<u>A. decipiens</u> Schenck	*		Banaszak and Manole 1987
<u>A. edwardsii</u> Cress.	*		
<u>A. flavipes</u> Panz	*	*	Pesenko 1976
<u>A. gelriae</u> Vecht.	*		Banaszak and Manole 1987
<u>A. ilerda</u> Cam.		*	Randhawa and Yunus 1974

TABLE 1 (continued)

SPECIES	DISTRIBUTION			REFERENCE
	N.A.	Eur.	Asia	
<i>A. labialis</i> Kby.		*	*	Ózbek 1976
<i>A. ovatula</i> Kby.		*	*	Wafa et al. 1975
<i>A. piperi</i> Viereck	*			
<i>A. wilkella</i> (Kby.)	*	*		Banaszak 1983
Subfamily: Panurginae				
Tribe: Melitturgini				
Genus: <i>Melitturga</i>				
<i>M. clavicornis</i> Latr.		*	*	de la Sierra & Ibanez 1980
Tribe: Panurgini				
Genus: <i>Calliopsis</i>				
<i>C. andreniformis</i> Smith	*			Bohart 1958
Family: MELITTIDAE				
Subfamily: Melittinae				
Genus: <i>Melitta</i>				
<i>M. leporina</i> Panz.		*	*	Tigari 1971
Family: MEGACHILIDAE				
Subfamily: Megachilinae				
Tribe: Anthidiini				
Genus: <i>Anthidium</i>				
<i>A. edwardsii</i> Cress.	*			Linsley 1946
<i>A. florentinum</i> Latr.		*	*	Batra 1976

TABLE 1 (continued)

SPECIES	DISTRIBUTION			REFERENCE
	N.A.	Eur.	Asia	
Tribe: Megachilini				
Genus: <u>Ashmeadiella</u>				
<u>A. bigelovia</u> (Ckll.)	*			Krombein 1967
<u>A. californica</u> (Ashmead.)	*			Michener 1936
Genus: <u>Chalicodoma</u>				
<u>C. ericetorum</u> Lep.		*		de la Sierra 1979
<u>C. mucorea</u> F.		*		Parker et al. 1987
<u>C. siculum</u> Rossi			*	Wafa et al. 1975
Genus: <u>Megachile</u>				
<u>M. alpicola</u> Alfk.		*		Ruszkowski et al. 1980
<u>M. apicaulis</u> Spin.	*	*		Stephen 1987
<u>M. argentata</u> Fab.		*	*	Parker et al. 1976
<u>M. bonbycina</u> (Pall.)		*		Ruszkowski et al. 1980
<u>M. branchella</u> Curtis			*	D'Albore 1984
<u>M. brevis</u> Say	*			Michener 1953
<u>M. centuncularis</u> K.	*	*	*	Móczar 1959
<u>M. circumcincta</u> (K.)		*		Ruszkowski et al. 1980
<u>M. concinna</u> Smith	*	*	*	Butler and Wargo 1963
<u>M. coquilletti</u> Ckll.	*			Linsley 1946
<u>M. dentitarsus</u> Sladen	*			Hobbs et al. 1961
<u>M. ericetorum</u> Lep.		*		Ruszkowski et al. 1980
<u>M. femorata</u> Smith			*	Kapil and Jain 1986
<u>M. flavipes</u> Spin.			*	Abrol 1988b

TABLE 1 (continued)

SPECIES	DISTRIBUTION			REFERENCE
	N.A.	Eur.	Asia	
<i>M. frigida</i> Smith	*			Hobbs et al. 1961
<i>M. genalis</i> Mor.		*		Ruszkowski et al. 1980
<i>M. gentilis</i> Cress.	*			Linsley 1946
<i>M. inermis</i> Prov.	*			Pengelly 1953
<i>M. integra</i> Cress.	*			Mitchell 1962b
<i>M. laechella</i> Curtis		*		Kapil and Jain 1980
<i>M. lanata</i> (Fab.)	*		*	Kapil et al. 1974
<i>M. latimanus</i> Say	*			Pengelly 1953
<i>M. ligniseca</i> (K.)		*		Ruszkowski et al. 1980
<i>M. manifesta</i> Cress.	*			Linsley 1946
<i>M. maritima</i> Kby.		*	*	Popov 1956
<i>M. melanophaea</i> Smith	*			Hobbs and Lilly 1954
<i>M. mendica</i> Cress.	*			Ivanochko 1979
<i>M. montivaga</i> Cress.	*			Ivanochko 1979
<i>M. nana</i> Bingh.			*	Abrol 1988a
<i>M. nivalis</i> Freise	*			Ivanochko 1979
<i>M. octosignata</i> Nyl.		*		Ruszkowski et al. 1980
<i>M. onobrychidis</i> Ckll.	*			Ivanochko 1979
<i>M. perihirta</i> Ckll.	*			Hobbs et al. 1961
<i>M. pilidens</i> Alf. k.		*		Marletto et al. 1988
<i>M. pugnata</i> Say	*			Pengelly 1953
<i>M. relativa</i> Cress.	*			Medler and Koerber 1958
<i>M. rotundata</i> (Fab.)	*	*	*	Klostermeyer 1982

TABLE 1 (continued)

SPECIES	DISTRIBUTION			REFERENCE
	N.A.	Eur.	Asia	
<i>M. saussurei</i> Rad.			*	Popov 1956
<i>M. sidalceae</i> Ckll.	*			Linsley 1946
<i>M. submucida</i> Alfkr.			*	Wafa et al. 1975
<i>M. texana</i> Cress.	*			Pengelly 1953
<i>M. vidua</i> Smith	*			Linsley 1946
<i>M. willoughbiella</i> Kby.		*		de la Sierra 1979
Genus: <i>Osmia</i>				
<i>O. caerulea</i> (L.)	*	*		Tasei 1972
<i>O. cornifrons</i> (Rad.)	*		*	Batra 1979
<i>O. cornuta</i> Latr.		*		Torchio & de la Sierra 1985
<i>O. excavata</i> Alfken	*			Rust 1974
<i>O. latreillei</i> Spin.		*		Lupo 1984
<i>O. lignaria lignaria</i> Say.	*			Rust 1974
<i>O. lignaria propinqua</i> Cr.			*	Torchio and Tepedino 1980
<i>O. nigrifrons</i> Cress.	*			Rust et al. 1974
<i>O. rufa</i> Latr.		*	*	Holm 1973
<i>O. sanrafaelae</i> Parker	*			Parker 1989
<i>O. seclusa</i> Sandh.	*			Bohart 1955
<i>O. subfasciata</i> Cress.	*			Krombein 1967

Family: ANTHOPHORIDAE

Subfamily: Anthophorinae

Tribe: Eucerini

TABLE 1 (continued)

SPECIES	DISTRIBUTION			REFERENCE
	N.A.	Eur.	Asia	
Genus: <u>Eucera</u>				
<u>E. chrysophaga</u> Per.	*			Popov 1956
<u>E. cinera</u> Lep.		*		Ózbek 1976
<u>E. clypeata</u> Erichs.	*	*		Dochkova et al. 1987
<u>E. interrupta</u> Baer.	*	*		Dochkova et al. 1987
<u>E. longicornis</u> L.	*	*		Akerberg and Lesins 1949
<u>E. nigrifacies</u> Leb.				Popov 1956
<u>E. nitidiventris</u> Mosc.	*			Móczar 1959
<u>E. pollinosa</u> Schmidt	*			Móczar 1959
<u>E. tuberculata</u> F.	*	*		Delaude and Tasei 1972
Genus: <u>Florilegus</u>				
<u>F. condignus</u> (Cress.)	*			Laberge and Ribble 1966
Genus: <u>Hemisia</u>				
<u>H. rhodopus</u> (Ckll.)	*			Bohart 1958
Genus: <u>Melissodes</u>				
<u>M. lupina</u> Cress.	*			Linsley 1946
<u>M. timberlakei</u> Ckll.	*			Linsley 1946
Genus: <u>Tetralonia</u>				
<u>T. edwardsii</u> Cress.	*			Bohart 1958
<u>T. tricineta</u> Eversm.	*	*		Móczar 1959
Tribe: Anthophorini				
Genus: <u>Anthophora</u>				
<u>A. forinosa</u> Klug.		*		Randhawa and Yunus 1974

TABLE 1 (continued)

SPECIES	DISTRIBUTION			REFERENCE
	N.A.	Eur.	Asia	
<i>A. furcata</i> Cress.	*			Pengelly 1953
<i>A. kaufmannii</i>			*	Ôzbek 1976
<i>A. magnilabris</i> Fedt.			*	Bohart 1958
<i>A. occidentalis</i> Cress.	*			Hobbs and Lilly 1954
<i>A. urbana urbana</i> Cress.	*			Linsley 1946
Subfamily: Xylocopinae				
Tribe: Ceratinini				
Genus: <i>Ceratina</i>				
<i>C. binghami</i> (Ckll.)			*	Goyal and Atwal 1975
Genus: <i>Pithitus</i>				
<i>P. smaragdula</i> (Fabr.)		*	*	Bohart 1972
Tribe: Xylocopini				
Genus: <i>Xylocopa</i>				
<i>X. aestuans</i> L.		*	*	Randhawa and Yunus 1974
<i>X. californica</i> Cress.	*			Bohart 1958
Family: APIDAE				
Subfamily: Apinae				
Tribe: Apini				
Genus: <i>Apis</i>				
<i>A. dorsata</i> Fab.			*	Randhawa and Yunus 1974
<i>A. florea</i> Fab.		*		Kapil et al. 1974
<i>A. mellifera</i> L.	*	*	*	Benedek 1972
Subfamily: Bombinae				

TABLE 1 (continued)

SPECIES	DISTRIBUTION			REFERENCE
	N.A.	Eur.	Asia	
Tribe: Bombini				
Genus: <u>Bombus</u>				
<u>B. agrorum</u> F.		*	*	Popov 1956
<u>B. americanorum</u> (F.)	*			Holm 1966
<u>B. armenicus</u>			*	Ôzbek 1976
<u>B. californicus</u> Smith	*			Hobbs et al. 1961
<u>B. crotchii</u> Cress.	*			Bohart 1956
<u>B. fervidus</u> (F.)	*			Hobbs and Lily 1954
<u>B. griseocola</u> (De Geer)	*			Pengelly 1953
<u>B. hortorum</u> (L.)		*		Dochkova et al. 1987
<u>B. impatiens</u> Cress.	*			Pengelly 1953
<u>B. incertus</u>			*	Ôzbek 1976
<u>B. lapidarius</u> L.		*		Móczar 1959
<u>B. lederi</u>			*	Ôzbek 1976
<u>B. lucorum</u> (L.)	*	*	*	Banaszak and Manole 1987
<u>B. morrisoni</u> Cress.	*			Bohart 1958
<u>B. nevadensis</u> Cress.	*			Hobbs and Lily 1954
<u>B. occidentalis</u> Greene	*			Hobbs et al. 1961
<u>B. pennsylvanicus</u> (DeGeer)	*			Mitchell 1962
<u>B. ruf. lineatus</u> Cress.	*			Hobbs and Lily 1954
<u>B. sylvarum</u> (L.)		*	*	de la Sierra 1979
<u>B. terrestris</u> (L.)	*	*	*	de la Sierra 1979
<u>B. terricola</u> Kby.	*			Hobbs et al. 1961

TABLE 2

Frequencies of families and genera of pollinating bees
recorded visiting alfalfa flowers North America, Europe, and
Asia (based on TABLE 1).

BEE SPECIES	N. AMERICA	EUROPE	ASIA
Halictidae			
<u>Halictus</u>	7	10	5
<u>Lasioglossum</u>	0	1	0
<u>Nomiodes</u>	0	0	1
<u>Rhophites</u>	0	1	1
<u>Nomia</u>	4	1	1
Total	11	13	8
Andrenidae			
<u>Andrena</u>	4	7	5
<u>Melitturga</u>	0	1	1
<u>Calliopsis</u>	1	0	0
Total	5	8	6
Melittidae			
<u>Melitta</u>	0	1	1
Megachilidae			
<u>Anthidium</u>	1	1	1
<u>Ashmeadiella</u>	2	0	0
<u>Chalicodoma</u>	0	2	1
<u>Megachile</u>	25	16	12
<u>Osmia</u>	8	4	3
Total	36	23	17

TABLE 2 (continued)

BEE SPECIES	N. AMERICA	EUROPE	ASIA
Anthophoridae			
<u>Eucera</u>	0	7	6
<u>Florilegus</u>	1	0	0
<u>Hemisia</u>	1	0	0
<u>Melissodes</u>	2	0	0
<u>Tetralonia</u>	1	1	1
<u>Anthophora</u>	3	0	3
<u>Ceratina</u>	0	0	1
<u>Pithitis</u>	0	1	1
<u>Xylocopa</u>	1	1	1
Total	9	10	13
Apidae			
<u>Apis</u>	1	2	2
<u>Bombus</u>	14	6	7
Total	15	8	9

TABLE 3

The most important wild pollinators of alfalfa reported in the literature and the region in which they are important.

BEE TAXA	REGION(S)	REFERENCE(S)
<u>Megachile</u> spp.	N. America, Europe	Bohart 1958, Holm 1966
<u>Bombus</u> spp.	N. America, Europe	Bohart 1958, Holm 1966
<u>Andrena</u> spp.	n. U.S., cent. Asia	Banaszak & Manole 1987
<u>A. wilkella</u> (Kby.)	Great Lakes region	Banaszak 1983
<u>Anthophora magnilabris</u> Fed.	cent. Asia	Bohart 1958
<u>A. urbana</u> Cress.	Utah	Stephen 1987
<u>Calliopsis andreniformis</u> Sm.	Nebraska	Bohart 1958
<u>Eucera</u> spp.	cent. Asia	Popov 1956
<u>E. clypeata</u> Erichs	Russia	Dochkova et al. 1987
<u>E. longicornis</u> L.	Scandinavia	Ackerberg & Lesins 1949
<u>Florilegus condignus</u> (Cress.)	cent. U.S.	Laberge and Ribble 1966
<u>Halictus</u> spp.	w. U.S., cent. Asia	Nye 1980, Bohart 1958
<u>Hemisia rhodopus</u> (Ckll.)	Arizona, s. Utah	Bohart 1958
<u>Melissodes</u> spp.	w. U.S.	Linsley 1946
<u>Melitta leporina</u> Panz.	Europe, w. Asia	Tigari 1971
<u>Melitturga clavicornis</u> Latr.	cent. Asia	de la Sierra & Ibanez 1980
<u>Nomia melanderi</u>	U.S. Intermountain Region	Menke 1952
<u>N. diversipes</u> Latr.	cent. Asia	Popov 1956
<u>Osmia sanrafaelae</u> Parker	s. Utah	Parker 1989
<u>O. seclusa</u> Sand.	Utah and Idaho	Bohart 1958

TABLE 3 (continued)

BEE TAXA	REGION(S)	REFERENCE(S)
<u>Rhopites canus</u> Eversm.	cent. and e. Europe,	Dimitrov et al. 1987
<u>Tetralonia edwardsii</u> Cress.	Utah, Idaho	Bohart 1958
<u>T. tricineta</u> Eversm.	cent. Asia	Móczar 1959
<u>Xylocopa</u> spp.	sw U.S., Israel	Randhawa and Yunus 1974

TABLE 4

Representation of families of bees in North America (north of Mexico) in relation to occurrence on alfalfa.

BEE FAMILY	TOTAL NUMBER OF BEE SPECIES IN NORTH AMERICA ¹	NUMBER RECORDED ON ALFALFA ²	NUMBER EXPECTED ON ALFALFA ³	% OF BEE FAMILIES IN NA
Colletidae	153 (45 ⁴)	0	3.356	0.00
Oxaeidae	4 (0)	0	0.088	0.00
Halictidae	506 (110)	11	11.098	2.17
Andrenidae	1199 (250)	5	26.298	0.42
Melittidae	30 (2)	0	0.658	0.00
Megachilidae	607 (150)	36	13.314	5.93
Anthophoridae	919 (135)	9	20.157	0.98
Apidae	47 (47)	15	1.031	31.90
TOTALS	3465 (739)	76	76.020	-----

¹ Number of described species, after Hurd (1979).

² Based on Table 1.

³ Expected number of the 76 bees recorded on alfalfa in proportion to the relative number of bees in the family in relation to the 3465 bee species.

⁴ Numbers of described species in Canada, after Masner et al. (1979).

TABLE 5

List and taxonomy of pollinating Hymenoptera genera collected on alfalfa flowers in eastern and western Canada during this study.

Superfamily: APOIDEA

Family: COLLETIDAE

Subfamily: Hylaeinae

Genus: Hylaeus

Family: HALICTIDAE

Subfamily: Halictinae

Genus: Agapostemon

Genus: Halictus

Genus: Lasioglossum

Genus: Evyllaeus

Genus: Dialictus

Family: ANDRENIDAE

Subfamily: Andreninae

Genus: Andrena

Family: MEGACHILIDAE

Subfamily: Megachilinae

Tribe: Megachilini

Genus: Megachile

Genus: Hoplitis

Genus: Osmia

Genus: Coelioxys¹

TABLE 5 (continued)

Family: ANTHOPHORIDAE

Subfamily: Anthophorinae

Genus: Melissodes

Family: APIDAE

Subfamily: Apinae

Tribe: Apini

Genus: Apis

Subfamily: Bombinae

Tribe: Bombini

Genus: Bombus

¹ This is a parasitic megachilid, not a pollinator, and is not included in analyses of pollinators

TABLE 6

Importance of genera of bees as pollinators, showing for the present study: relative occurrence in 20 sites, relative occurrence of total of 545 pollinators collected, order of importance, and order of importance based on literature survey (examined previously).¹

GENUS	OCCURRENCE AS % OF SITES	RELATIVE OCCURRENCE AS %	ORDER OF OCCURRENCE	LITERATURE ORDER OF OCCURRENCE
<u>Hylaeus</u>	10	0.37	8	
<u>Agapostemon</u>	10	0.73	7	
<u>Halictus</u>	15	13.00	3	3
<u>Lasioglossum</u>	10	0.37	8	
<u>Evyllaes</u>	10	0.37	8	
<u>Dialictus</u>	10	1.83	6	
<u>Andrena</u>	45	11.01	4	5
<u>Megachile</u>	40	47.89	1	1
<u>Hoplitis</u>	5	0.37	8	
<u>Osmia</u>	5	0.18	9	4
<u>Melissodes</u>	5	0.37	8	
<u>Apis</u>	30	3.49	5	
<u>Bombus</u>	55	20.00	2	2

¹ Collecting times varied from 1/2 to 10 hrs, with more time spent at sites with relatively many pollinators.

Discussion

The list of 149 species of bees recorded on alfalfa in the literature is incomplete. In fact, during the field work for this study several genera not previously recorded on alfalfa were recorded, including Hylaeus, Agapostemon, Evyllaeus, Dialictus, and Hoplitis. Bohart (1958) conjectured that several hundred species of pollinators occur on alfalfa, and future surveys will likely at least double the number of species presently recorded.

Linsley (1958) noted that families of solitary bees generally differ somewhat in their floral preferences. For example, anthophorine and megachilid bees usually choose a different series of flowers from colletid and andrenid bees. The percentage of species within each bee family represented by the bees recorded on alfalfa was found to be very highly significantly different for North America, demonstrating different preferences for alfalfa by the families of bees. The social bee family (the Apidae) represented about 32% of the species recorded on alfalfa. In the field work conducted in Canada, two genera of Apidae, Apis and Bombus, represented about a quarter of the collected pollinators. However, this does not indicate a special affinity for alfalfa flowers, but rather the versatility of social bees on a wide variety of types of flowers (Hobbs et al. 1961). Solitary bees are more likely to collect pollen (and hence trip alfalfa flowers) than social bees because solitary bees are much less dependent on nectar stores. Of the solitary bee families, the Megachilidae showed an affinity for

alfalfa flowers. The high frequency of species of Megachile particularly reflected a special relationship between this genus and alfalfa. Bohart (1958) noted that megachilids are reputed to be efficient on alfalfa. Megachile was the most frequently collected genus of pollinators, both in the literature surveyed and in the field work conducted (Table 6).

PART B: COMPETITION OF ALFALFA WITH NATIVE VEGETATION FOR NATIVE
POLLINATORS

Introduction

The preceding section dealt with the question of how well alfalfa attracts different pollinators. This section considers the question of how well cultivated alfalfa competes with native vegetation for native pollinators. Both topics examined are critical limiting factors to the success of alfalfa in setting seed, and therefore require exploration. This section deals with three aspects of the competitive ability of alfalfa to attract native Canadian bee pollinators: spatial relationships with wildflowers, comparative attractiveness of alfalfa and other flowering plants, and attractiveness of different flower colors. And, as a measure of just how attractive alfalfa can be, seed yield of the alfalfa site found to be most attractive to wild pollinators was compared with records of seed yield produced by managed leafcutter bees.

Relatively little attention has been given to the problem of attracting pollinators to crops when surrounding wildflowers compete for the pollinators. It is known that the attractiveness of plant species to insects depends both on their abundance (i.e., the total floral display) and the attractiveness of given plant species to given pollinators (Baker 1983). There is evidence that certain wildflowers, such as sweetclover and mustard (both examined in this study), are especially attractive to honeybees, and therefore draw away potential pollinators from

crops (Bohart 1957). For example, most species of bumblebee prefer red clover to alfalfa, especially as a pollen source, and it is very difficult to attract bumblebees to alfalfa when red clover is nearby (Bohart 1958). Honeybees also have been observed to frequent wildflowers in strong preference to alfalfa, and normally visit alfalfa only when competing flowers are in low numbers (Bohart 1958).

Both absolute numbers and species diversity of pollinators attracted to alfalfa are of interest. No studies have been reported on the comparative ability of alfalfa and surrounding wildflowers to attract local pollinators, either in absolute numbers or in terms of species diversity. Since the pollination mechanism of alfalfa is so specialized, it would seem that a smaller range of bee species would find it attractive in comparison to other flowers. It was therefore of interest to compare the diversity of pollinators on alfalfa with the diversity of pollinators on other species.

Flower color has often been proposed as one of the factors in attractiveness of bees to alfalfa. Flowers of purple-flowered alfalfa (*M. sativa* subsp. *sativa*) and yellow-flowered alfalfa (*M. sativa* subsp. *falcata* (L.) Arcangeli) are shown in Fig. 3. Goplen and Brandt (1975) stated that reports on the relative attractiveness of yellow and purple alfalfa flowers are conflicting and inconclusive. In a study of comparative seed set by Goplen and Brandt (1975), purple-flowered alfalfa was found to set more seed than yellow-flowered alfalfa when exposed to

Fig. 3. Inflorescences of purple-flowered (right) and yellow-flowered (left) alfalfa.

leafcutter bees.

Seed yields of alfalfa commercially pollinated by honeybees have been reported to range from 390 to 670 kg/ha in the northwestern U.S. In the southwestern U.S.A., honeybees have produced yields of greater than 1120 kg/ha (Robinson et al. 1988). As noted previously, honeybees are unsuitable pollinators of alfalfa in Canada, where alfalfa leafcutter bees are used for commercial pollination of alfalfa. Seed yields of alfalfa commercially pollinated by alfalfa leafcutter bees in the southern prairie region of Canada have been reported to range from 300 to 900 kg/ha under irrigation, while yields of 150 to 300 kg/ha are considered satisfactory without irrigation (Goplen et al. 1980). Little information has been published on Canadian alfalfa seed yields outside of the Prairie Provinces, where 95% of Canada's production of alfalfa seed is found. Trials at New Liskeard in northern Ontario produced an average yield of 331 kg/ha using commercial methods, but this increased to 783 kg/ha based on careful hand harvesting (Skepasts and Taylor 1984).

Methods

Pollinating bees were collected from 16 alfalfa populations in the Ottawa area of Ontario, and four in the Peace River region of northwestern Alberta and northeastern British Columbia. A total of 81 hours was spent collecting bees at the 20 alfalfa locations. The Ottawa sites (1 - 16) and the Peace River sites (20-23) are described in Appendix 1. (Sites 17-19 and 24 were used for other purposes, as explained later.) I attempted to

collect specimens in a standard fashion under similar weather conditions, so that the sites could be compared with respect to diversity and absolute numbers of bee pollinators. Collections were made during peak flowering times (late June to mid July), on warm days (21° - 28° C), with limited or no wind, and under sunny or slightly overcast skies. At each site, I used an insect net to collect as many bees and wasps as possible. Bees were collected only after I observed them foraging on the alfalfa flowers. Times spent at each site were recorded. The bees and wasps were killed using ethyl acetate, and mounted on pins, following methods described by Martin (1977). All collections were deposited in the National Insect Collection of Agriculture Canada in Ottawa.

It became apparent during preliminary studies that pollinator density varied considerably depending on the spatial relationship of the alfalfa and surrounding wildflowers. To illustrate these differences, I classed the field sites into five groups (note Fig. 4): (1) centre of large alfalfa monoculture; (2) small monoculture surrounded by wild vegetation; (3) periphery of large alfalfa monoculture surrounded by wild vegetation; (4) intermixture of alfalfa and wild vegetation; and (5) small isolated alfalfa monoculture. Analysis of variance was performed on the collected data for these groups, omitting situation 5, since only one site of this class was examined. To meet the assumptions of the analysis of variance the data were log-transformed. A Duncan multiple range analysis was conducted

Fig. 4. Diagrams of five categories of spatial relationships of alfalfa (A) and wildflowers (W) recognized in this study. 1: centre of large monoculture; 2: small monoculture surrounded by competing wildflowers; 3: edge of large monoculture adjacent to wildflowers; 4: intermixed alfalfa and wildflowers; 5: isolated small monoculture.

(1)

```

      W      W      W
    W  W      W      W  W
  W  W  AAAAAAAAAA  W
    W  AAAAAAAAAA
      W  AAAAAAAAAA  W
        AAAAAAAAAA  W
        AAAAAAAAAA  W
        AAAAAAAAAA  W
        AAAAAAAAAA  W
        AAAAAAAAAA  W
        AAAAAAAAAA  W
        AAAAAAAAAA  W
      W      W      W  W
    W      W      W
  
```

(2)

```

      W  W
    W      W
  W  AAAAAA  W
    W  AAAAAA
  W  AAAAAA  W
    W  AAAAAA  W
      W  W  W
        W  W
  
```

(3)

```

      W      W
    W  W      W      W
  W  W  AAAAAAAAAA  W
    W  AAAAAAAAAA
      W  AAAAAAAAAA  W
        AAAAAAAAAA  W
        AAAAAAAAAA  W
        AAAAAAAAAA  W
        AAAAAAAAAA  W
        AAAAAAAAAA  W
        AAAAAAAAAA  W
      W      W      W  W
    W      W      W
  
```

Arrows in diagram (3) point to the top-left 'W' and the bottom-left 'W' of the central block.

(4)

```

      W      W
    W  A  W  A  W
  W  A  W  A  W
    W  A  W  A  W
      W  A  W  A  W
        W  A  W
          W  W
  
```

(5)

```

  AAAAAA
  AAAAAA
  AAAAAA
  AAAAAA
  
```

in order to assess which of the classes were significantly different.

The density and diversity of native pollinators attracted to some native plant species were also examined in order to compare their relative attractiveness to alfalfa. The variety of pollinators visiting Virginia creeper (Parthenocissus quinquifolia (L.) Planch.), narrow-leaved meadowsweet (Spiraea alba Du Roi), and white clover (Trifolium repens L.) was compared with the variety of pollinators visiting alfalfa. Meadowsweet, Virginia creeper and alfalfa grew in close proximity at Site 16 on the Central Experimental Farm, and white clover was about a km away (Site 24). In all cases, hundreds of plants and thousands of flowers were available in a fairly small area, and were the most attractive flowers visible in that area. Collecting procedures were as described above.

The comparative attractiveness of purple-flowered alfalfa (M. sativa subsp. sativa) and yellow-flowered alfalfa (M. sativa subsp. falcata (L.) Arcangeli) was examined at Site 16 by collecting visiting Hymenoptera (as described previously). A total of five hours was spent collecting on each of the two colors of flowers, alternating every half hour. Collecting techniques and ambient conditions were as described above. A Monte-Carlo contingency test was performed to examine whether there were significant differences in attractiveness to alfalfa for the nine genera of bees collected.

At Site 15, breeder seed of the alfalfa cultivar 'Comsel' is

maintained. Dr. A. McElroy, who is responsible for this cultivar, kindly supplied the total weight of seeds harvested in 1991 for this site. I measured the area and calculated the yield/area.

Results

Six hundred and four collections of Hymenoptera were obtained at the 20 alfalfa sites. Identification of these was dealt with in Part A and Appendix 2.

Comparative numbers of pollinators captured while visiting alfalfa in the five spatial arrangements with surrounding wildflowers are given in Table 7, and illustrated in Figs. 4 and 5. Large monocultures were the least attractive, drawing very few species, in fact very few bees. By contrast, an isolated small monoculture was the most attractive. Analysis of variance showed that there were significant differences among the classes of spatial arrangement in terms of attractiveness to pollinators (Table 8, Fig. 6). A Duncan multiple range analysis is shown in Table 9.

The numbers of bees of the 13 pollinating genera that were collected, is given for each of the five spatial arrangements in Table 10. The situation attracting the largest number of genera of bees was the intermixture of alfalfa and wildflowers, which yielded 11 of the 13 genera. Of particular interest is the observation that the genus Megachile, which produced the largest number of individuals in the study, was completely absent from the centres of large monocultures.

Fig. 5. Comparative abundance of pollinators on alfalfa in various spatial arrangements (1-5) with native flowering plants (centre of large monoculture, small monoculture surrounded by competing wildflowers, edge of large monoculture adjacent to wildflowers, intermixed alfalfa and wildflowers, isolated small monoculture), and on narrow-leaved meadowsweet, Virginia creeper, and white clover. Standard errors are indicated for three of the spatial arrangements; data for the centre of large monocultures were invariable, while one sample only was available for remaining situations.

Alfalfa arrangements and some species

It was found that purple-flowered alfalfa attracted more pollinators than the yellow-flowered alfalfa (Table 11). The Monte-Carlo contingency test performed produced a probability level of 0.024, i.e., there was a significant (at $P = 0.05$) difference in attractiveness for at least one of the genera of bees collected. As shown in Table 12, the difference was mostly with respect to attractiveness to the most common genus, Megachile, with purple-flowered alfalfa attracting more than twice as many bees of this genus as did yellow-flowered alfalfa.

Virginia creeper, narrow-leaved meadowsweet, and white clover all attracted larger numbers of pollinators than alfalfa, and the first two species attracted about the same number of genera of bees as did alfalfa. (note hourly capture rate in Table 11; also see Table 12 and Fig. 7). (Numbers of genera shown in Table 12 are based on different collection times and are therefore not directly comparable. However, they give a crude indication of relative diversity.) Most of the genera of pollinators occurred on flowers of most of the plant species examined. White clover attracted only the honeybee and one Andrena. The honeybee was attracted to Virginia creeper, meadowsweet, and white clover, but completely avoided both purple-flowered and yellow-flowered alfalfa.

A yield of 240 kg/ha was calculated for alfalfa at Site 15.

TABLE 7

Hourly rate of capture of wild Hymenopteran pollinators on alfalfa, indicating comparative pollinator abundance in various spatial relationships of alfalfa and wild flowering vegetation.

SITUATION	SITES	TOTAL COLLECTING TIME (h)	TOTAL NO. POLLINATORS CAPTURED ON FLOWERS	HOURLY RATE OF CAPTURE
Centre large monoculture	1-9	33	20	0.6
Small monoculture surrounded by wildflowers	10,11	10	24	2.4
Monoculture edge next to wildflowers	20-23	9	73	8.1
Intermixed alfalfa and wildflowers	12-14,16	19	191	10.1
Isolated small monoculture	15	10	236	23.6

TABLE 8

Analysis of variance of the means of the foraging rates of alfalfa leaf-cutter bees on legume flowers in various spatial relationships (compare Table 7).

<u>SOURCE</u>	<u>DF</u>	<u>SUM OF SQUARES</u>	<u>MEAN SQUARE</u>	<u>F-VALUE</u>	<u>P-VALUE</u>
Alfalfa arrangement	4	6.579	1.645	37.401	0.0001
Residual	15	0.660	0.044		

Fig. 6 Plot of means, and standard errors, of the foraging rates of alfalfa leaf-cutter bees on legume flowers in various spatial relationships (compare Table 8).

TABLE 9

Duncan multiple range test of the alfalfa leafcutter bees' foraging rates on alfalfa in various spatial relationships (compare Table 7).

SPATIAL RELATIONSHIP	NUMBER OF SITES	MEAN FORAGING RATE	DUNCAN MULTIPLE RANGE TEST ^{1,2}
Monoculture centre	9	0.184	1
Monoculture edge	2	0.537	2
Intermixed	4	0.764	2,3
Small monoculture	4	0.917	3

¹ P=0.05

² Numbers denote groups among which means are significantly different and within which means are not significantly different.

TABLE 10

The numbers of bees of each of the pollinating genera that were collected for each of the five spatial arrangements.

GENUS	NUMBERS COLLECTED ON ALFALFA FLOWERS IN VARIOUS SPATIAL ARRANGEMENTS ¹				
	1	2	3	4	5
<u>Hylaeus</u>	1			1	
<u>Agapostemon</u>				2	2
<u>Halictus</u>				11	60
<u>Lasioglossum</u>	1			1	
<u>Evylaeus</u>	1				1
<u>Dialictus</u>				9	1
<u>Andrena</u>	4	3	2	37	14
<u>Megachile</u>		4	21	121	114
<u>Hoplitis</u>				2	
<u>Osmia</u>				1	
<u>Melissodes</u>				2	
<u>Apis</u>	7		12		
<u>Bombus</u>	6	17	38	4	22
TOTAL NUMBER OF					
POLLINATING GENERA	6	3	4	11	7

¹ 1) Centre of large monoculture.

2) Small monoculture surrounded by wildflowers.

3) Monoculture edge next to wildflowers.

4) Intermixed alfalfa and wildflowers.

5) Isolated small monocultures.

TABLE 11

**Comparison of rate of capture of pollinators on purple
-flowered and yellow-flowered alfalfa, Virginia creeper,
narrow-leaved meadowsweet (Site 16), and white clover
(Site 24) in Ottawa.**

GROUP	TOTAL COLLECTING TIME (hr.)	TOTAL NO. OF BEES CAPTURED	HOURLY RATE OF CAPTURE
Purple-flowered alfalfa	5	91	18.2
Yellow-flowered alfalfa	5	63	12.6
Virginia creeper	3	101	33.7
Narrow-leaved meadowsweet	2	51	25.5
White clover	1	89	89.0

TABLE 12

Numbers of collections of pollinating bees on purple- and yellow-flowered alfalfa, meadowsweet, and Virginia creeper, all at Site 16 and on white clover at nearby Site 24.

GENUS	PURPLE ALFALFA (5 hrs)	YELLOW ALFALFA (5 hrs)	MEADOWSWEET (2 hrs)	VIRGINIA CREEPER (3 hrs)	WHITE CLOVER (1 hr)
<u>Hylaeus</u>		1			
<u>Agapostemon</u>				6	
<u>Halictus</u>	5	5	1	1	
<u>Lasioglossum</u>			1	1	
<u>Evylaeus</u>				21	
<u>Dialictus</u>	4	5	12	15	
<u>Andrena</u>	5	14	7	5	1
<u>Megachile</u>	71	33	5	15	
<u>Hoplitis</u>	2				
<u>Osmia</u>	1				
<u>Heriades</u>				22	
<u>Melissodes</u>	1	1			
<u>Apis</u>			10	9	89
<u>Bombus</u>	1	1	15	6	
TOTAL NUMBER OF GENERA	8	7	7	10	2

Fig. 7. Comparative diversity of pollinators on alfalfa in various spatial arrangements (1-5) with native flowering plants (centre of large monoculture, small monoculture surrounded by competing wildflowers, edge of large monoculture adjacent to wildflowers, intermixed alfalfa and wildflowers, isolated small monoculture), and on narrow-leaved meadowsweet, Virginia creeper, and white clover. Standard errors are indicated for three of the spatial arrangements; data for the edge of large monocultures were invariable, while one sample only was available for remaining situations.

Alfalfa arrangements and some species.

Discussion

It was found that very different numbers of native pollinators were attracted to alfalfa depending on its spatial arrangement with surrounding wildflowers. The clearest result was with respect to the centre of large monocultures, which attracted significantly fewer pollinators than the other spatial arrangements. How can the differences in attractiveness among the spatial arrangements be explained? First, it needs to be remembered that native pollinators require nesting sites, which are found in the natural landscape. This means that the pool of native pollinators for plantings of alfalfa can only be drawn from the surrounding environment. So, the surrounding wildflowers compete for the attention of the pollinators. Also, the flight distances of many species, especially of the smaller solitary bees, are limited, and they will forage only short distances away from their nesting sites (Bohart 1972). These considerations can be used to explain the differences in pollinator density and diversity observed among the five spatial situations recognized above, as follows (see Table 13).

(1) Native pollinators generally prefer wildflowers over alfalfa and in the complete absence of nearby attractive wildflowers there is little incentive for bees to fly into the centre of a large monoculture. As well many solitary bees are small and will not fly long distances, and so even if they accept alfalfa flowers they will not fly the long distances to reach the centre. Since almost no pollinators were found in the centres of

the nine large monocultures examined, it is clear that native pollinators cannot or will not forage in this location.

Megachile, the most frequently encountered genus, is an excellent example of this, as it was completely absent from the centre of large monocultures, although found in all of the other kinds of spatial arrangements.

(2) Small monocultures surrounded by competing wildflowers attracted very few native pollinators, in the two such sites examined. Clearly the pollinators find the native wildflowers more attractive, although there seems to be some spill-over from the wildflowers to the alfalfa.

(3) The edge of large monocultures adjacent to wildflowers proved moderately attractive in the four sites examined. This greater attractiveness in comparison to small monocultures may be explained by the ease with which bees may simply fly over the small monocultures (i.e., "the grass is greener on the other side"). By contrast, once within the periphery of a large plantation, the pollinators are more likely to encounter alfalfa flowers than wildflowers.

(4) Four of the sites examined had an intermixture of alfalfa and wildflowers. The wildflowers seemed to provide a high density of pollinators near the alfalfa flowers, and spill-over to the alfalfa seemed to account for the appreciable number of bees observed on the alfalfa.

(5) The spatial situation attracting the most bees to alfalfa was a small monoculture of alfalfa isolated (at least

TABLE 13

Interactions of alfalfa, surrounding wildflowers, and native pollinator pool.

SITUATION	PLANT SPECIES PRESENT		COMPETITIVE PROCESSES	RESULT
	ALFALFA	OTHERS		
1) Centre of large mono-culture	Yes	No	No competition but few pollinators; pollinators cannot fly or those that are able, do not find the large expanse of alfalfa attractive	Virtually no pollinators available
2) Small monoculture surrounded by competing wildflowers	Yes	Yes	Strong competition; pollinators find surrounding vegetation attractive but spillover occurs	Very few pollinators available
3) Edge of large mono-culture adjacent to wildflowers	Yes	Yes	Strong competition; pollinators find vegetation on the periphery more attractive but once among alfalfa see more alfalfa	Few pollinators available
4) Intermixed alfalfa and wildflowers	Yes	Yes	Strong competition; but considerable spillover	Many pollinators for few flowers
5) Isolated small monoculture	Yes	No	Weak competition; pollinators have little choice but the available alfalfa	Many pollinators for few flowers

seasonally) by a considerable distance from competing flowers, but with habitats providing nesting sites for bees. Probably in this situation the bees occupying a considerable area had little choice for forage except alfalfa within their normal flight distance.

It is interesting that the indigenous species of plants were much more attractive to the indigenous species of Hymenoptera than were the non-native alfalfa and white clover. Virginia creeper and narrow-leaved meadowsweet are native to Canada, and white clover is naturalized from Europe. White clover attracted only the honeybee, which is not native to Canada.

However, it may be noted that at least one introduced plant species is extremely attractive to bees. The introduced plant, red clover (Trifolium pratense L.), was observed to be remarkably competitive in drawing bees away from alfalfa. At Sites 8 and 9 in Ottawa, honeybees were seen in large numbers on a few red clover plants, while several hundred thousand surrounding alfalfa plants attracted almost none. At Sites 20 and 21 in northern Alberta, the same phenomenon was observed, but for bumblebees instead of honeybees.

The observation that purple-flowered alfalfa is more attractive to pollinators than yellow-flowered alfalfa is consistent with Goplen (1970) and Goplen & Brandt (1975), who found that yellow-flowered plants were pollinated to a lesser extent and set fewer pods and seeds than purple-flowered plants. By contrast, experiments examining the relative attractiveness of

honeybees to alfalfa flower color have produced contradictory results. For example, Kauffeld and Sorensen (1971) found that honeybees preferred light-colored to dark-colored alfalfa flowers, while Clement (1965) and Hanson et al. (1964) did not find any evidence that flower color was significant in attracting honeybees. The two subspecies of alfalfa differ not only in flower color but also in flower size (Part C, Table 23, and so the question arises whether this contributes to the difference in attractiveness of yellow and purple alfalfa flowers. Flowers of the purple-flowered subspecies averaged 9.08 mm while those of the yellow-flowered subspecies averaged 7.07 (Table 23), and so the comparative attractiveness of the former may be due to the 22% difference in length. Another consideration is ease of tripping yellow-flowered alfalfa. According to Hely and Zorin (1977) "resistance to tripping...is often so great that even bees actively seeking pollen are deterred from working its flowers, even in the absence of alternative pollen sources". Scientific studies of these factors have not yet been conducted with alfalfa leafcutter bees. Flower color and aroma, nectar volume and quality, volatiles in flower petals, and ease of tripping have all been implicated in the attraction of honeybees to alfalfa flowers (Kauffeld and Sorensen 1980), and the same may be true for alfalfa leafcutter bees.

As noted above, Site 15 provided ideal conditions for attracting surrounding pollinators, including fairly small size of plantation, and surrounding habitats where wild bees can nest

but where potentially competing flowers were absent. Clearly the considerable number and diversity of native pollinators visiting this site (Figs. 4 and 7) were sufficient to produce the moderate yield calculated. Although this occurred in a park-like setting (the large Experimental Farm area), it is of interest that this appreciable yield was possible in the centre of Ottawa.

Furthermore, after the seed harvest (in mid-July), the plants flowered a second time, and developed a considerable number of seeds.

The idea is widespread in North America that "most species that trip alfalfa flowers are either too scarce in alfalfa seed areas or too uncommon as alfalfa visitors to be important" (Pedersen et al. 1972). Smith (1960) reviewed the situation for Ontario and stated "intensive farming practices have, in recent years, been largely responsible for a decline in the wild bee population." It does seem true that in most areas of the U.S. and Canada where alfalfa seed is currently raised, most of the land has been cleared and is currently used for agriculture and for urban development. Therefore with the loss of their habitats, wild pollinators are relatively scarce. However, there are extensive wild areas in much of eastern and northern Canada, and indeed many abandoned farm areas returning to native vegetation, that provide suitable habitat for wild bees, and hence provide potential areas for raising alfalfa seed through the use of wild pollinators. According to Kevan (1987), "It was not long ago, as some farmers remember, that Ontario exported

alfalfa seed by the boxcar. Now, almost all of the seed planted in Ontario is imported from the Prairies". It may well be that a revival of the use of native pollinators to produce alfalfa seed in Ontario is possible.

PART C: EXPERIMENTAL STUDIES OF COMPARATIVE ATTRACTIVENESS
OF DIFFERENT PLANT SPECIES, INCLUDING ALFALFA, TO
ALFALFA LEAFCUTTER BEES

Introduction

The preceding sections dealt with the questions of how well alfalfa attracts different pollinators, and how well it competes with native vegetation for native pollinators. The relationships of many bee species to alfalfa were examined, and it was concluded that megachilids, including the alfalfa leafcutter bee, are especially attracted to alfalfa. The following considers whether alfalfa leafcutter bees are more compatible with alfalfa flowers than with flowers of other species, a topic for which almost no comparative experimental studies have been conducted. Experimental and observational studies of the comparative attractiveness of a variety of different plant species, including alfalfa were carried out. This was done primarily for the alfalfa leafcutter bee, but also for some other insects. Related studies included observations on foraging times of alfalfa leafcutter bees and honeybees on different flowers, and an examination of foraging time in relation to flower size; and observations of behavioral differences of leafcutter bees on several different types of flowers.

After the discovery that the alfalfa leafcutter bee was an excellent pollinator of alfalfa, attempts were made, with various degrees of success, to employ this bee as a pollinator of other crops (e.g. Richards 1989). The measure of usefulness was seed

set, i.e. a criterion from the plant's point of view. In the present study, time limitations did not permit seed set to be measured, and a criterion from the pollinator's point of view was examined, i.e., attractiveness to the bees.

The present study examined floral preferences of leafcutter bees by presenting the bees with a choice of a number of plant species. The only experimental study of a similar nature that I was able to find is that of Ayers et al. (1987), who examined the relative attractiveness of 54 plant species to honeybees. They found large differences in attractiveness of the plants, and recommended that the most attractive species be used for honey production.

Efficiency of pollination is commonly measured by the number of flowers visited per minute (e.g. Kapil and Jain 1986). Foraging times could be important as indicators of the ease with which nectar and pollen collection are accomplished (i.e. short times would be preferable), or of the attractiveness of the flower (i.e. long times could be required if much pollen or nectar is present).

Methods

The experiments conducted were carried out at the Beaverlodge Research Station in northwestern Alberta, where colonies of both leafcutter bees and honeybees are available (note Fig. 7). I made a preliminary examination to see if bouquets of given species placed near a leafcutter bee shelter with a large number (20,000) of bees differed notably in

Fig. 8. Author in front of leafcutter bee shelter at
Beaverlodge Research Station, Alberta.

attractiveness to insects under two circumstances: a) alone (without any competition from bouquets of other species), and b) in proximity to bouquets of other species. No substantial differences were evident, and it was therefore obvious that a surplus of pollinators was available near the shelter, and proximity to flowers of other species made little difference. Nevertheless some slight differences seemed evident. When an attractive species was placed next to an unattractive one, the unattractive one benefitted slightly by obtaining some spill-over of pollinators from the attractive species. Consequently the following trials were replicated with bouquets of the species distributed randomly.

Trial #1 (12 July 1991). Inflorescences of 10 different species, including three color variants of alfalfa (Tables 14, 17), were freshly collected and placed in 5 cm diameter jars of water. The species were as follows: yellow sweetclover (Melilotus officinalis (L.) Lam.), white sweetclover (Melilotus alba Desr.), white-flowered, purple-flowered, and yellow-flowered alfalfa (Medicago sativa L.), sainfoin (Onobrychis viciifolia Scop.), birdsfoot trefoil (Lotus corniculatus L.), alsike clover (Trifolium hybridum L.), red clover (Trifolium pratense L.), white clover (Trifolium repens L.), narrow-leaved meadowsweet (Spiraea alba Du Roi), and dandelion (Taraxacum officinale Weber). An attempt was made to have about an equal area of flowers in the bouquets. The bouquets were positioned randomly in a row in a north-south direction about 3 m from an

alfalfa leafcutter bee shelter with 20,000 bees, on a sunny day with limited wind. The experiment was conducted within foraging distance of honeybee hives, so that it was possible to examine the relative attractiveness of the bouquets to honeybees at the same time as the experiment was being conducted with reference to leafcutter bees. During the experiment, from 1300-1500 hr, shade temperature was about 25°C. Twenty successive counts of bees alighting on the flowers were made, each count taking two minutes. Then the 12 bouquets were randomly interchanged in position and another 20 measurements made as before.

Trial #2 (16 July 1991). Inflorescences of 16 different species (including the same 10 species and three color variants of alfalfa used above, as well as cicer milkvetch (Astragalus cicer L.), shrubby cinquefoil (Potentilla fruticosa L.), yarrow (Achillea millefolium L.), goldenrod (Solidago gigantea Ait.), canola (Brassica campestris L.), and bluebell (Campanula rotundifolia L.) were employed (Fig. 9), as on the 12th of July. The experimental conditions and procedures were as above.

Data analysis was conducted on the 12 species of plants that were measured on both days, for a total of four replicates. First, the mean numbers of pollinators visits were log-transformed, to meet the assumptions of the analysis. Then, an analysis of variance was conducted, followed by a Duncan multiple range test.

At Site 17 at Beaverlodge Research Station a demonstration plot had been set up, planted in 1987, with several legume

Fig. 9. Experimental bouquets of flowers in front of plantation at Beaverlodge Research Station, used in study of attractiveness of flowers of various species to bees.

forages. This was 50 m away from the alfalfa leafcutter bee shelter at Site 18. The forages were in an east-west sequence with each particular species occupying a north-south row 7 m by about 1 m. Therefore, the demonstration plot provided a means of comparing attractiveness of several of the plant species to leafcutter bees in situ with the bouquet experiments. This does not provide a statistical design with replicates and a means of accounting for position effects. Only species with similar displays of flowers were compared, namely, yellow- and purple-flowered alfalfas, white and Alsike clovers, and birdsfoot trefoil. In each case the number of pollinators observed in one minute was examined in sequence and this was repeated five times on July 8 and again on July 9.

A stop watch measuring to 1/100th of a second was used to examine the time spent foraging, from time of alightment to time of departure, on a variety of crop species (Tables 19, 21). If the bee seemed to be merely resting or grooming the observation was not included. Most observations were made on plants in situ, but a few were made on plant bouquets. Observations for leafcutter bees (Table 19) were made at approximately 25°C between 1300 and 1600 h. Observations for honeybees (Table 21) were made at approximately 20°C between 1100 and 1200 h. (I did not have time to make observations for honeybees and leafcutter bees at the same temperature.) The data were log-transformed to better meet the assumptions of the following analyses. Analysis of variance was conducted to see if there were significant

differences among the means. And, a Duncan multiple range test was used to analyse which means were significantly different (separately for leafcutter bees and for honeybees). For the eight legume species for which the visitation times by leafcutter bees were recorded, the correlation of visitation times and mean flower length (measured as described below) was found.

For five collections of alfalfa (two yellow-flowered, two purple-flowered, and one white-flowered), and for eight additional legume species, mean flower length was found based on 20 flowers, each taken from a different plant (Table 23). Measurements were made from the base of the calyx to the tip of the standard petal. Significance of differences of the log-transformed means was examined by analysis of variance, and subsequently which of the 13 means differed from each other was examined by Duncan's multiple range test.

The comparative pollinating behavior of alfalfa leafcutter bees on the flowers of alfalfa and several other legume species was carefully studied. It was found that the relatively complicated behavior of the alfalfa leafcutter bee on the alfalfa flower could be observed more readily under cool conditions. The alfalfa leafcutter bee does not initiate flight until the ambient temperature has reached between 17°C and 20°C; the lower the intensity of radiation of the sun the higher the required ambient temperature (Klostermeyer 1982). In the mornings, when temperatures were about 20°C, the bees carried out pollination slowly. This slow motion facilitated observation of the sequence

of behavior.

Results

Differences in the attractiveness of the bouquets were found with respect to leafcutter bees, honeybees, bumble bees, some other visiting Hymenoptera, and flies (Tables 14, 17). However, statistical analysis was carried out only for alfalfa leafcutter bee visits, on the 12 species for which four replicates were available (Fig. 10). As shown in Table 15, there were very highly significant differences among the species visitation rates, while differences among the four replicates were not significant. The Duncan multiple range test (Table 16) showed two distinctive groupings: the alfalfas and sweetclovers in one group, and another group with the remaining species in four overlapping subgroups.

White sweetclover was the only species attractive to honeybees (Table 17). Flies were attracted only to the flowers of species of Compositae that were tested (Table 17).

The leafcutter bees were attracted to the sweetclovers and alfalfas immediately upon their presentation. It was as if either experience or instinct were influencing this behavior, with little evidence that the bees were inspecting the flowers to judge whether or not they provided nectar or pollen. By contrast, the unattractive species of flowers were for the most part not even inspected. Once again it was as if instinct or learning allowed the bees to perceive at a distance the likely pollen or nectar rewards.

Although of much less importance, the results of an examination of a forage plot of five rows of legume species may also be mentioned. The resulting total numbers of observations for the five species (Table 18) provides a rough measure of their relative attractiveness. As indicated in Table 18, purple-flowered alfalfa was slightly more attractive to the alfalfa leafcutter bee than was yellow-flowered alfalfa. These were somewhat more attractive than birdsfoot trefoil and considerably more attractive than the clovers.

The times leafcutter bees spent foraging on purple-flowered and yellow-flowered alfalfa and on seven other species are shown in Table 19 and Fig. 11. The longest average time observed (7.46 seconds) was on purple-flowered alfalfa, almost twice as long as on yellow-flowered alfalfa (3.53 seconds). The reasons for the difference are unclear, and could relate to such factors as different pollen production and nectar availability. The shortest times were spent on the white and yellow sweetclovers. Analysis of variance (Table 20) showed that there were significant differences present among the mean foraging times. As revealed by the Duncan multiple range test (Table 19), many but by no means all of the plant species differ significantly in foraging times of the bee.

The times honeybees spent foraging on four legumes, including alfalfa, are shown in Table 21 (compare Fig. 12). The results are fairly similar. Analysis of variance (Table 22) showed the presence of significant differences among the mean

foraging times. And, the Duncan multiple range test (Table 21) showed that some, but not all of the means were significantly different. Consistent with alfalfa leafcutter bee foraging times discussed above, the honeybees spent the least time on the most preferred plant (Table 17), white sweetclover.

Analysis of variance of flower lengths of legumes examined is given in Table 24, and showed significant differences among the means at a probability of greater than 0.0001. Means and standard errors of flower lengths are given in Table 23, and the same information, log-transformed, is given in Fig. 13. As revealed by the Duncan multiple range test, all of the 13 tested groups had significantly different mean lengths, except the following: the two yellow-flowered alfalfa collections; the weedy purple-flowered alfalfa collection from Ottawa, a weedy white-flowered alfalfa collection from Beaverlodge, and white clover; and birdsfoot trefoil and cicer milkvetch.

The correlation coefficient between mean corolla length and mean foraging times was $r = 0.823$, which is significant at $P = 0.05$. The amount of variation accounted for by the correlation coefficient is $r^2 = 0.678$, i.e. 67.8%. Corolla length is plotted against foraging time in Fig. 14.

The following records observations of the behavior of leafcutter bees as they foraged on flowers of three different legumes:

(A) Alfalfa

A characteristic behavior of alfalfa leafcutter bees was

observed on alfalfa flowers. The bee alights on the wing petals, her head oriented toward the throat of the flower. The flower is tripped by using a clawing motion of her front legs on the 'thumb and pocket' region of the corolla and a simultaneous pressing down of the wing petals with the hind legs. After tripping, the sexual column slaps against the ventral surface of the bee, depositing pollen, and pressing the standard away from the keel, thus opening the throat of the flower. The bee then inserts her proboscis down the throat of the flower and imbibes the nectar. During her floral visits the bee periodically pauses to groom pollen from her body onto the abdominal scopa. Newly emerged adults that were placed near alfalfa flowers exhibited the precise sequence described above for experienced adults.

(B) Birdsfoot trefoil

The bee alights on the wing petals, pushes its head into the throat of the corolla, imbibing nectar. Once the bee is in this position the apex of the keel contacts the bee. The characteristic pump mechanism of the trefoil flower is activated with pollen being forced out of the tip of the keel. The scopa is positioned here and thus accumulates pollen. The rear legs of the bee apparently groom the pollen from the tip of the keel directly to the scopa.

(C) Sainfoin

The bee alights on the wing petals, pushes its head into the throat of the corolla, and imbibes nectar. Once the bee is in this position the hinge mechanism typical of the sainfoin flower

deploys. The weight of the bee depresses the keel and the wings and so the sexual column passively contacts the bee's abdomen. The abdomen flexes in order to accommodate the curvature of the flower. The anthers directly deposit the pollen on the scopa.

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TABLE 14

Numbers of leafcutter bee visits to standard bouquets of flowers placed near a leafcutter bee shelter (Site 18).

FAMILY	SPECIES	12 JULY			16 JULY			GRAND TOTALS ¹
		2-3	3-4	TOTAL	4-5	5-6	TOTAL	
Legumi- nosae	Yellow sweetclover	71	34	105	71	70	141	246
	White sweetclover	47	47	94	62	52	114	208
	White. alfalfa	42	30	72	54	40	104	176
	Purple alfalfa	23	33	56	41	20	61	117
	Yellow alfalfa	21	27	48	32	22	54	102
	Sainfoin	2	10	12	24	9	33	45
	Birdsfoot trefoil	0	4	4	12	17	29	33
	Alsike clover	4	3	7	13	8	21	28
	Red clover	2	4	6	3	2	5	11
	White clover	1	5	6	0	0	0	6
	Cicer milkvetch				2	8	10	
Rosaceae	Shrubby cinquefoil				3 ²	3 ²	6 ²	
	Meadowsweet	0	0	0	0	0	0	0
Compos- itae	Dandelion	5	7	12	1	2	3	15
	Yarrow				0	0	0	
	Golden rod				0	0	0	
Crucif.	Canola				48	33	81	
Campan.	Bluebell				0	0	0	

¹ Indicates where measured for both dates.

² Bees were cutting petals, not foraging for nectar or pollen

TABLE 15

Analysis of variance of mean number of leafcutter bee visits to standard bouquets of flowers placed near a leafcutter bee shelter (Site 18) (compare Table 14, Fig. 10).

<u>SOURCE</u>	<u>DF</u>	<u>SUM OF SQUARES</u>	<u>MEAN SQUARE</u>	<u>F-VALUE</u>	<u>P-VALUE</u>
Time	3	0.272	0.091	1.390	0.2631
Species	11	15.390	1.399	21.460	0.0001
Residual	33	2.151	0.065		

Fig. 10. Plot of mean numbers, and standard errors, of leafcutter bee visits to standard bouquets of flowers placed near a leafcutter bee shelter (Site 18) (compare Table 14).

TABLE 16

Duncan multiple range test of the numbers of leafcutter bee visits to standard bouquets of flowers placed near a leafcutter bee shelter (Site 18) (compare Table 14).

PLANT SPECIES	COUNT	MEAN	DUNCAN MULTIPLE RANGE TEST ^{1,2}
Meadowsweet	4	0.000	1
White clover	4	0.270	1,2
Red clover	4	0.564	2,3
Dandelion	4	0.615	2,3,4
Birdsfoot trefoil	4	0.767	3,4
Alsike clover	4	0.850	3,4
Saifoin	4	0.979	4
Alfalfa yellow flower	4	1.417	5
Alfalfa purple flower	4	1.464	5
Alfalfa white flower	4	1.619	5
White sweetclover	4	1.722	5
Yellow sweetclover	4	1.777	5

¹ P=0.05

² Numbers denote groups among which means are significantly different and within which means are not significantly different.

TABLE 17

Numbers of insect visits to standard bouquets of flowers during experiment reported in Table 14.

FAMILY	SPECIES	HONEY BEES	BUMBLE BEES	OTHER HYMEN- OPTERA	FLIES
Legumi- nosae	Yellow sweetclover				
	White sweetclover	32	1		
	White alfalfa		1		
	Purple alfalfa				
	Yellow alfalfa				
	Sainfoin				
	Birdsfoot trefoil				
	Alsike clover				
	Red clover				
	White clover		1		
	Cicer milkvetch				
Rosaceae	Shrubby cinquefoil				
	Meadowsweet				
Compos- itae	Dandelion		1		2
	Yarrow			2	1
	Golden rod			7	4
Crucif- iferae	Canola				
Campan- ulaceae	Bluebell		1		

TABLE 18

Number of leafcutter bees counted in a forage legume demonstration plot (Site 17) at Beaverlodge Research Station. Based on 20 square metres of forage in flower, five 1 minute counts, on warm (ca. 25°C), mostly sunny afternoons with limited wind.

FORAGE LEGUME SPECIES	DATE		
	JULY 8	JULY 9	TOTAL
Alfalfa 'Peace' (purple-flower)	33	39	72
Alfalfa 'Anik' (yellow-flower)	29	38	67
Birdsfoot trefoil 'Leo'	22	24	46
Alsike clover 'Aurora'	6	9	15
White clover 'Nora'	5	9	14

TABLE 19

Comparison of foraging times of alfalfa leafcutter bees on various forages at 25°C and Duncan multiple range test of significance of differences of means (based on 40 measurements).

FORAGE SPECIES	MEAN TIME (sec.)	STANDARD ERROR	SHORTEST TIME (sec.)	LONGEST TIME (sec.)	DUNCAN MULTIPLE RANGE TEST ^{1,2}
White sweetclover	1.14	0.113	0.34	4.29	1
Yellow sweetclover	1.14	0.048	0.56	1.89	1,2
White clover	1.36	0.088	0.30	2.84	2
Alfalfa yellow	1.66	0.112	0.58	3.53	3
Alsike clover	2.00	0.173	0.85	4.87	3,4
Birdsfoot trefoil	1.92	0.133	0.43	5.34	3,4
Alfalfa purple	2.37	0.233	0.83	7.46	4
Sainfoin	3.04	0.225	0.86	6.10	5
Canola	3.66	0.239	1.01	7.23	6

¹ P=0.05

² Numbers denote groups among which means are significantly different and within which means are not significantly different.

TABLE 20

Analysis of variance of mean foraging times of alfalfa leafcutter bees on various forages (compare Table 19, Fig. 11).

<u>SOURCE</u>	<u>DF</u>	<u>SUM OF SQUARES</u>	<u>MEAN SQUARE</u>	<u>F-VALUE</u>	<u>P-VALUE</u>
Species	8	9.903	1.238	32.146	0.0001
Residual	351	13.516	0.039		

Fig. 11. Plot of mean foraging times, and standard errors, of alfalfa leafcutter bees on various forages (compare Table 19).

TABLE 21

Comparison of foraging times of honeybees on various forages at 20°C, and Duncan multiple range test of significance of differences of means (based on 40 measurements at Site 20, 10 July, 1991, 1100-1200 hrs).

FORAGE SPECIES	MEAN TIME (sec.)	STANDARD ERROR	SHORTEST TIME (sec.)	LONGEST TIME (sec.)	DUNCAN MULTIPLE RANGE TEST ^{1,2}
White sweetclover	1.04	0.062	0.53	2.29	1
Alsike clover	1.10	0.075	0.31	2.29	1,2
Alfalfa purple	1.36	0.106	0.33	3.57	2
White clover	1.69	0.121	0.77	3.96	3

¹ P=0.05

² Numbers denote groups among which means are significantly different and within which means are not significantly different.

TABLE 22

**Analysis of variance of mean foraging times of honeycreepers
on various forage ; at 20°C (compare Table 21, Fig. 12).**

<u>SOURCE</u>	<u>DF</u>	<u>SUM OF SQUARES</u>	<u>MEAN SQUARE</u>	<u>F-VALUE</u>	<u>P-VALUE</u>
Species	3	1.009	0.336	9.447	0.0001
Residual	156	5.552	0.036		

Fig. 12. Plot of mean foraging times, and standard errors, of honeybees on various forages at 20°C (compare Table 21).

TABLE 23

Means and standard errors of lengths of flowers of legume species and Duncan multiple range test of significance of means (based on 20 flowers, each from a different plant).

FORAGE SPECIES	FLOWER COLOUR	MEAN LENGTH (mm)	STANDARD ERROR	DUNCAN MULTIPLE RANGE TEST ^{1,2}
White sweetclover	white	4.72	0.0595	1
Yellow sweetclover	yellow	6.39	0.0523	2
Alfalfa 'Anik'	yellow	7.07	0.0987	3
Alfalfa yel. (Ottawa Site 16)	yellow	6.93	0.0906	3
Alsike clover 'Aurora'	wh/pink	7.41	0.1120	4
Alfalfa wht. (Beaverlodge)	white	8.28	0.1085	5
Alfalfa pur. (Ottawa site 16)	purple	8.30	0.0993	5
White clover 'Nora'	white	8.28	0.1085	5
Alfalfa 'Peace'	purple	9.08	0.1410	6
Cicer milkvetch 'Oxley'	pink/wh	10.44	0.1113	7
Birdsfoot trefoil	yellow	10.19	0.1501	7
Sainfoin	pink	11.10	0.1744	8
Red clover 'Altaswede'	red	13.23	0.1581	9

¹ P=0.05

² Numbers denote groups among which means are significantly different and within which means are not significantly different.

TABLE 24

**Analysis of variance of mean lengths of flowers of legume species
(compare Table 23, Fig. 13).**

<u>SOURCE</u>	<u>DF</u>	<u>SUM OF SQUARES</u>	<u>MEAN SQUARE</u>	<u>F-VALUE</u>	<u>P-VALUE</u>
Plant species	12	3.255	0.271	4.36E2	0.0001
Residual	247	0.154	0.001		

Fig. 13. Plot of mean lengths of flowers, and standard errors, of legume species (compare Table 23).

Discussion

The phenomenon of pollinator preference for the flowers of certain plants was demonstrated by the substantial differences observed in attractiveness of the flowers of the experimental plant species for leafcutter bees, honeybees, bumblebees, other Hymenoptera, and even flies.

The data obtained here for relative visitation of bees to a variety of flowers proved consistent between the replicates, and the grand totals shown in Tables 14 and 17 represent a reasonable assessment of preferences under the particular conditions of the experiments. The two sweetclover species were the most attractive to leafcutter bees and the white sweetclover attracted almost all of the honeybees observed. Next in attractiveness were the three colour variants of alfalfa studied. The three clover species and the other legume species attracted few pollinators. These results were so clear, it seems unlikely that the relative ranking of preferences would change under different conditions, but the possibility exists. In any event, it is interesting that the sweetclover and alfalfa species were significantly more attractive to leafcutter bees than any of the remaining species, since sweetclover and alfalfa are fairly close taxonomically.

A strong preference for alfalfa by the alfalfa leafcutter bee has been reported previously. Stephen and Torchio (1961) found that the alfalfa leafcutter bee preferred alfalfa to all other species examined in the northwestern United States.

However, I observed that although the alfalfa leafcutter bee shows a strong preference for alfalfa, nevertheless it prefers several other pollen sources. This is consistent with Packer (1970), who surveyed preferences by examining visitation on a variety of flowers, and found several species preferred more than alfalfa.

As indicated by the grand total in Table 14, white-flowered alfalfa was more attractive than either purple-flowered or yellow-flowered alfalfa. However, the means were not significantly different (Table 16, Fig. 10). Results in the literature have been contradictory with respect to relative attractiveness of flower color. It has been found that honeybees prefer light-colored flowers to dark-colored flowers (Kauffeld and Sorensen 1971). However, this contradicts Pedersen (1967), who found that white-flowered alfalfa was less attractive than purple-flowered alfalfa in attracting leafcutter bees. Steiner et al. (1992) found that white-flowered alfalfa was more attractive than yellow-flowered.

As noted above, there was some evidence that proximity of unattractive flowers of one species to attractive flowers of another species resulted in some spill-over of pollinators from the attractive to the unattractive. This subject was discussed earlier (Part B), where it was pointed out that the spatial relationships of alfalfa plantations in relation to surrounding wildflowers affected the attractiveness of the pollinators to alfalfa. That is, while competition from surrounding wildflowers

can draw away potential pollinators of alfalfa, in some circumstances nearby attractive flowers of competing species may actually result in a spill-over of pollinators onto the crop. Practically speaking it may be feasible to lay out a crop and wildflowers in a pattern that benefits the crop in terms of pollination.

Both the alfalfa leafcutter bee and the honeybee foraged more quickly on sweetclover flowers than on any other flowers examined. Furthermore, the sweetclover species have the smallest flowers of the plants examined (Table 23). This suggests that the small size of the flowers facilitates collection in some way, or alternatively that the small flowers have less nectar and so require less collection time. It may also be noted that sweetclover flowers are simpler in construction than all of the other types of legume flowers examined, and therefore may require less handling time by the bees. A significant positive correlation of foraging and flower length was found (Fig. 14). The reason for this is unclear, but may be related to larger flowers simply being more difficult to handle for the relatively small leafcutter bee. Alternatively, larger flowers may simply have more nectar, and the bees are choosing to spend more time imbibing.

The present study of foraging times also suggests that honeybees are faster and seem relatively consistent in times spent on a variety of flowers in comparison to leafcutter bees. The apparent consistency of honeybees may be related to their

Fig. 14. Relationship in legume flowers of mean length of flower (corolla length) and mean times spent collecting (foraging time) by alfalfa leafcutter bees.

1. White sweetclover
2. Yellow sweetclover
3. White clover
4. Yellow-flowered alfalfa 'Anik'
5. Alsike clover
6. Birdsfoot trefoil
7. Purple-flowered alfalfa 'Peace'
8. Sainfoin

generalist (polylectic) foraging behavior. Such bees need to be able to handle diverse flowers fairly well.

The description of alfalfa leafcutter bee pollination of alfalfa presented above conforms to the description in the literature (see Introduction and Fig. 15A) except for the following observation, not previously recorded. The bee does not simply force her way into the throat of the flower in her quest for nectar; she first employs her legs in an apparently deliberate fashion (at the risk of sounding anthropomorphic) precisely on the "trigger" region of the explosive flower, while simultaneously pushing, also in an apparently deliberate fashion, down on the wing petals, and thereby separating the keel petals. These two actions both promote tripping. This behavior of the bee obviously seems adaptive, particularly when contrasted with the behavior of the bee on other types of flowers, described below.

The observation that just-emerged bees, when placed near alfalfa flowers, soon exhibited the precise sequence of behavior described for experienced bees, shows that the behavior is innate and instinctive. This is very important in interpreting the evolutionary relationship of the alfalfa leafcutter bee and the alfalfa flower, almost certainly indicating that the bees behavior is an adaptation that evolved specifically to the rather rare mechanism of the alfalfa flower.

Birdsfoot trefoil and sainfoin flowers are quite different from the alfalfa flower. The flower of birdsfoot trefoil is an

Fig. 15. Diagrammatic comparison of alfalfa leafcutter bee pollinating explosive alfalfa flower (A) and non-explosive sweetclover flower (B). In A, the bee has clawed against the wing horns triggering the explosive mechanism of the flower (described in the text, Part C), so that the sexual column slaps against the bee, depositing pollen on it and possibly resulting in a transfer of pollen, previously collected by the bee, to the stigma of the flower. In B, the bee's weight on the wing petals has resulted in the passive lowering of the bee and the wing petal by its hinge so that the bee's body passively contacts the sexual column.

A **B**

example of a highly specialized pollination system, the pump mechanism. The flower of sainfoin has the same basic system of the majority of legumes, the hinge mechanism (Fig. 15B). On birdsfoot trefoil, the alfalfa leafcutter bee exhibited a behavior that allowed it to collect pollen quickly from the peculiar pump mechanism. That is, it positioned its scopa near the pump, where it could groom pollen quickly directly onto the scopa, while positioning its head near the nectary, where it could drink nectar. On sainfoin, the bee simply alighted on the keel petals like most legume-visiting bees, with the weight of the bee automatically lowering it to the anthers where pollen is passively transferred directly on to the scopa. Although sainfoin is a rather generalized flower, the bee showed some behavior specific to this flower, flexing its abdomen to match the curvature of the flower. Two aspects of the alfalfa leafcutter bee's behavior on these non-alfalfa flowers need to be emphasized. First, in neither case did the bee exhibit the stereotyped behavioral sequence it exhibits on the alfalfa flower. And second, the bee has considerable flexibility of behavior, and is able to handle other specialized as well as generalized legume flowers efficiently.

Perhaps the most significant point in these behavioral studies is the variety of responses of the bees to different flowers. This is clearly adaptive for the bees, which can use a different collecting strategy to maximize their efficiency on different types of flowers. This behavioral flexibility seems to

indicate some limitation on the possible evolutionary relationship between the alfalfa leafcutter bee and the alfalfa flower. It might be suggested that these two species co-evolved, the bee evolving specifically to the flower and vice-versa. However, it now seems clear that this can only be a partly correct explanation. Since the bee is capable of utilizing a variety of floral types efficiently, and even prefers other types of flowers (i.e. of sweetclover), it is improbable that the bee's evolution was completely dependent on adapting to the type of flower that alfalfa has. As well, since a variety of bees can pollinate alfalfa, it is improbable that the plant's flowers evolved solely to accommodate the leafcutter bee. Nevertheless, the remarkable stereotyped behavioral adaptation of the alfalfa leafcutter bee to the alfalfa flower, and the efficiency of alfalfa pollination of this bee, coupled with the extraordinary floral mechanism of alfalfa suggest strongly that some degree of mutual evolution has occurred.

The alfalfa leafcutter bee's relatively narrow host preferences (oligolecty) and stereotyped behavior on alfalfa and perhaps other flowers contrast with the wide range of hosts (polylecty) and dependence on learned behavior of the honeybee. Honeybees working alfalfa for the first time usually trip blossoms but quickly learn to bypass the tripping mechanism and rob the flowers (Weaver 1965). Similarly, inexperienced honeybees on white clover blossoms make a variety of disorganized probes and orient in various awkward ways that are very

inefficient for collecting nectar and pollen, while experienced honeybees have learned to orient properly and efficiently (Weaver 1965). As noted earlier (Part B), honeybees completely monopolized a white clover population in Ottawa, demonstrating their opportunism. Clearly, honeybees depend much more than alfalfa leafcutter bees on modifying their behavior by learning, which is crucial to their generalist life style. This makes sense, since honeybee colonies must survive on a variety of different flowers that become available throughout the summer. On the other hand, solitary bees such as the alfalfa leafcutter bee frequently have a very short life span, which coincides with the flowering of a limited number of plants (Westerkamp 1991).

While it would seem logical that specialist bees might have instinctive behavior to use their host flowers in an efficient manner in comparison to generalist bees, "there is little comparative information on acquisition of foraging methods by generalists and specialists" beyond that of Lavery and Plowright (1988). They studied the bumblebee Bombus consobrinus, which specializes on the monkshood (Aconitum) flower, in comparison with several related generalist species on the same flowers. Naive workers of the specialist proved to have innate foraging skills, immediately probing in the vicinity of the nectary and quickly locating the nectar. The generalists showed no such predisposition, probed in the wrong places, and often simply gave up. Strickler (1979), in another study of the comparative efficiency of generalists and specialists, hypothesized that the

motor patterns used by a specialist when foraging on its preferred host work comparatively inefficiently on flowers with different morphologies. The present findings that alfalfa leafcutter bees seem behaviorally programmed to work alfalfa flowers while such generalists as the honeybee are relatively inefficient seems to be in agreement with these observations.

CONCLUSIONS

Literature analysis revealed a total of 14 species of bees recorded on alfalfa flowers. Bee families and genera were found to differ in their frequency on alfalfa flowers. In North America, over 30% of the social Apidae occurred on alfalfa, but since these are known to visit a wide variety of flowers this does not reflect a preference for this legume. Of the predominantly solitary bee families, the Megachilidae were most frequently observed on alfalfa; of genera of bees, Megachile was the most frequent.

Six hundred and four collections of Hymenoptera were made from alfalfa in eastern and western Canada, and were identified. Of these, 545 were pollinating bees, belonging to 13 genera. Interestingly, the first, second and third most frequent genera (Megachile, Bombus, and Halictus) represented the same order of importance of these bees as pollinators of alfalfa, as compiled from the literature reviewed.

The success of alfalfa in attracting wild pollinators away from surrounding native vegetation depends strongly on spatial relationships. For purposes of analysis, the following five situations were recognized.

(i) Large alfalfa monocultures characteristically attracted virtually no pollinators in the centre of the plantation. In some cases this is likely due to the limited flight range of some of the smaller bees; in other cases, the bees simply do not find the large expanse of alfalfa flowers attractive in comparison to

the surrounding native flowers.

(ii) Small monocultures surrounded by wild vegetation were only slightly more attractive to pollinators than the central areas of large plantations. Apparently only a small amount of spill-over from adjacent competing wildflowers to the alfalfa occurred.

(iii) The periphery of large alfalfa monocultures attracted more pollinators from the surrounding wild vegetation than either of the above situations. This greater attractiveness in comparison to small monocultures may be explained by the ease with which bees may simply fly over the small monocultures, in comparison to their encountering only alfalfa once they venture within the periphery of the plantation.

(iv) A spatial arrangement still more attractive was an intermixture of alfalfa and wild vegetation. This seemed to provide a high density of pollinators near alfalfa flowers, albeit also near competing wildflowers.

(v) The spatial situation apparently attracting the most bees to alfalfa was a small monoculture of alfalfa isolated (at least seasonally) by a considerable distance from competing flowers, but with habitats providing nesting sites for bees. In this situation, bees occupying a considerable area had little choice other than alfalfa within their normal flight distance.

Alfalfa was less attractive to native pollinators than a number of other plant species examined. Virginia creeper (Parthenocissus quinquifolia (L.) Planch.), narrow-leaved

meadowsweet (Spiraea alba Du Roi), and white clover (Trifolium repens L.) all were found to exceed alfalfa in terms of pollinator density.

In common with some previous studies of the comparative attractiveness of purple-flowered alfalfa (M. sativa subsp. sativa) and yellow-flowered alfalfa (M. sativa subsp. falcata (L.) Arcangeli), it was found that the purple-flowered subspecies exceeded the yellow-flowered subspecies in attractiveness, but mostly with respect to the genus Megachile.

A comparison of the alfalfa seed yield produced by commercial pollination by alfalfa leafcutter bees, and the alfalfa seed yield resulting from pollination by the native pool of pollinators at a site in Ottawa, showed that the latter produced moderate seed yield, approaching the lower range of yields in Ontario using managed alfalfa leafcutter bees.

Examining bees attracted to floral bouquets placed near an alfalfa leafcutter bee colony proved to be a simple way of assessing comparative attractiveness of different flowers to bees. Substantial differences in attractiveness were found among purple-flowered, yellow-flowered, white-flowered alfalfa, and 15 other species. Also, differences were found between leafcutter bees and honeybees. White sweetclover (Melilotus alba Desr.) and yellow sweetclover (M. officinalis (L.) Lam.) were the most attractive to the leafcutter bees, while the former was the only species attractive to honeybees. Next in attractiveness to leafcutter bees were, respectively, the three colour variants of

alfalfa and canola (Brassica campestris L.), several other legume species, and species of several other families. Flies were also attracted, but only to the flowers of species of Compositae that were tested.

Several legume forages planted in adjacent rows were examined for their attractiveness to a nearby colony of leafcutter bees. Results similar to the above were found, verifying the relative attractiveness of the forages.

On most of several tested forages, leafcutter bees spent more time working the flowers than did honeybees. In all instances of honeybees foraging on alfalfa flowers, the bees robbed nectar through the side of the flower, which remained untripped. Leafcutter bees spent more time on purple-flowered alfalfa flowers than on yellow-flowered alfalfa flowers, and showed a tendency to spend more time on larger flowers.

The behavior of leafcutter bees on several types of flowers differed, and provided evidence of different stereotypical behavior patterns in response to the different floral morphology. A previously unrecorded stereotypical behavior was recorded on alfalfa flowers. Adults that had just emerged from their cells were placed near alfalfa flowers, and exhibited this same sequence of behavior, showing that the behavior is instinctive. This almost certainly indicates that the bee's behavior is an adaptation that evolved to accommodate the rather rare mechanism of the alfalfa flower.

Scientific and practical importance of the thesis

a. Scientific

1. This study provides the first demonstration of a stereotyped pollination behavior of the alfalfa leafcutter bee specific to the alfalfa flower. Coupled with the highly evolved floral pollination mechanism, this is the best evidence available for some sort of co-evolutionary relationship of the bee and the plant.
2. The methodology of testing the relative attractiveness of flowers by presenting a colony of bees with a choice of bouquets of cut flowers has apparently not been reported in the literature. The method proved to be simple, effective, and efficient, and may well be taken up by pollination researchers.
3. Several generalizations in the literature about alfalfa pollination were confirmed: the importance of the Megachilidae for pollinating alfalfa; the preference of alfalfa leafcutter bees for purple-flowered alfalfa over yellow-flowered; the preference of alfalfa leafcutter bees for alfalfa flowers over the flowers of most other plant species.

b. Practical

1. It was demonstrated that spatial arrangements of alfalfa plantations and wildflowers greatly affect the attractiveness of the alfalfa to wild pollinators. The arrangement most highly attractive to wild pollinators is a small plantation of alfalfa isolated from competing wildflowers, but with the surrounding area providing nesting sites. It was shown that seed set

approaching commercial yields could be obtained, without the expense and effort of managed bees. This information should be of value to those wishing to produce alfalfa seed without the use of managed pollinators.

2. It was found that foraging behavior of the alfalfa leafcutter bee adapts it to pollinating alfalfa. While a variety of morphological, distributional, and ecological features of pollinators are important to their suitability for given crops, behavior may often be the most critical factor.

3. The most comprehensive literature survey of bee species foraging on alfalfa was compiled. This will be useful for agronomists wishing to consider alternative species of bees as possible managed pollinators of alfalfa. It was determined from an analysis of alfalfa pollinators recorded in hundreds of research papers, and confirmed by collecting hundreds of bees on alfalfa, that the three genera of pollinating bees most attracted to alfalfa are, respectively, Megachile, Bombus, and Halictus. From a practical viewpoint, the first two genera are the most promising as pollinators.

Literature cited

- Abrol, D.P. 1988a. Effect of climatic factors on pollination activity of alfalfa-pollinating subtropical bees Megachile nana Bingh. and Megachile flavipes Spinola (Hymenoptera: Megachilidae) Acta Ecologica/Ecol. Gener. 9: 371-377.
- Abrol, D.P. 1988b. Foraging range of alfalfa pollinating Megachile flavipes Spinola and Megachile nana Bingh (Megachilidae: Hymenoptera), J. Anim. Morphol. Physiol. 35: 11-16.
- Akerberg, E. and Lesins, K. 1949. Insects pollinating alfalfa in Central Sweden. Ann. Roy. Agr. Coll. Swed. 16: 630-643.
- Anasiewicz, A. 1975. The bees (Apoidea, Hymenoptera) on alfalfa (Medicago media Pers.) plantations. II. Trophic relationship to vegetation. Ecol. Pol. 23: 147-162.
- Ayers, G.S., Hoopingarner, R.A., and Howitt, A.J. 1987. Testing potential bee forage for attractiveness to bees. Amer. Bee J. 127: 91-98.
- Baker, H.G. 1983. An outline of the history of anthecology, or pollination biology. In L. Real (ed.), Pollination biology. Academic Press, Toronto. pp. 7-28.
- Banaszak, J. 1983. Ecology of bees (Apoidea) of agricultural landscape. Pol. Ecol. Stud. 9: 421-505.
- Banaszak, J. and Manole, T. 1987. Diversity and density of pollinating insects (Apoidea) in the agricultural landscape of Rumania. Bull. Entomol. Pol. 57: 747-756.

- Barnes, D.K., Goplen, B.P., and Baylor, J.E. 1988. Highlights in the U.S.A. and Canada. In A.A. Hanson, D.K. Barnes and R.R. Hill (eds.), Alfalfa and alfalfa improvement. American Society of Agronomy, Crop Science Society of America, Soil Science Society of America, Madison, Wisc. pp. 1-24.
- Batra, S.W.T. 1976. Comparative efficiency of alfalfa pollination by Nomia melanderi, Megachile rotundata, Anthidium florentinum and Pithitis smaragdula (Hymenoptera: Apoidea). J. Kansas Entomol. Soc. 49: 18-22.
- Batra, S.W.T. 1979. Osmia cornifrons and Pithitis smaragdula, two Asian bees introduced into the United States for crop pollination. Proc. IVth Inter. Symp. Poll., Maryland Exp. Stat., Special Misc. Publ. 1. pp. 307-312
- Benedek, P. 1972. The role of honeybees in the pollination of lucerne in relation to the activity of wild bees. Z. ang. Ent. 70: 174-179.
- Bohart, G.E. 1955. Notes on the habits of Osmia (Nothosmia) seclusa Sandhouse (Hymenoptera, Megachilidae) Proc. Ent. Soc. Wash. 57: 235-236.
- Bohart, G.E. 1957. Pollination of alfalfa and red clover. Ann. Rev. Entomol. 2: 355-380.
- Bohart, G.E. 1958. Alfalfa pollinators with special reference to species other than honeybees. 10th International Cong. Ent. Proc., Montreal 4: 929-937.
- Bohart, G.D. 1972. Management of wild bees for the pollination of crops. Ann. Rev. Entomol. 17: 287-312.

- Brookes, B.S. and Small, E. 1988. Enhanced floral analysis by low temperature scanning electron microscopy. *Scanning Microscopy* 2: 247-256.
- Butler, G.D., Jr. and Wargo, M.J. 1963. Biological notes on Megachile concinna Smith in Arizona (Hymenoptera: Megachilidae). *Pan-Pac. Entomol.* 39: 201-206.
- Clement, W.M. 1965. Flower color, a factor in attractiveness of alfalfa clones for honeybees. *Crop. Sci.* 5: 267-268.
- D'Albore, G.C. Ricciardelli. 1984. Osservazioni sugli insetti pronubi di alcune leguminosae (Onobrychis viciifolia Scop., Lotus corniculatus L., Medicago arborea L., Medicago sativa L.) in un areale specializzato. *Redia* 67: 145-156.
- de la Sierra, E. Asensio 1979. Report on alfalfa pollination studies in Spain. *Proc. IVth Int. Symp. Pollination Md. Agric. Exp. Sta. Spec. Misc. Publ.* 1: 103-107.
- de la Sierra, E. Asensio and Ibáñez, J.A.R. 1980. Selección de abejas solitarias para polinización de alfalfa en España. *An. INIA/ ser. Agric.* 13: 33-34.
- Delaude, A. and Tasei, J-N. 1972. Premières observations sur la pollinisation et la coulure des fleurs de luzerne en Charentes (Medicago sativa L.). *Apid.* 3: 79-97.
- Dimitrov, P., Dimitrov, Z., Atanasov, N. and Vasileva, E. 1987. Specific body and number of bees (Hymenoptera, Apoidea) pollinating alfalfa in the region of Rousse district. *Rastenievd Nauki.* 24: 58-62.

- Dochkova, B.K.; Atanasov, N. and Vasileva, E.I. 1987. Species composition and number of the wild bees (Hymenoptera, Apoidea) - pollinating on the forage plants from the region of Pleven. *Acta Zoologica Bulgaria* 35: 34-43.
- Duncan, D.B. 1955. Multiple range and multiple F test. *Biometrics* 11: 1-41.
- Fairey, D.T. and Lefkovitch, L.P. 1989. Alternative floral sources for leafcutting bees. Canadian Alfalfa Seed Council, 8th Annual Alfalfa Seed School, Winnipeg. pp. 9-12
- Fairey, D.T., Levkovitch, L.P., and Lieverse, J.A.C. 1989. The leafcutting bee, Megachile rotundata (F.): a potential pollinator for red clover. *J. Appl. Ent.* 107: 52-57.
- Fairey, D.T., Lieverse, J.A.C. and Siemans, B. 1984. Management of the alfalfa leafcutting bee in northwestern Canada. Publ. No. NRG 84-21, Agriculture Canada, Beaverlodge Alberta
- Free, J.B. 1970. Insect pollination of crops. Academic Press, New York.
- Goplen, B.P. 1970. Alfalfa flower color preference shown by leafcutters. *Forage Notes* 16: 16-17.
- Goplen, B.P. and Brandt, S.A. 1975. Alfalfa flower color associated with differential seed set by leaf-cutter bees. *Agron. J.* 67: 804-807.
- Goplen, B.P. et al. 1980. Growing and managing alfalfa in Canada. Publication 1705. Agriculture Canada, Ottawa.

- Goyal, N.P. and Atwal, A.S. 1975. Studies on the relation of the population of insect pollinators with seed production in lucerne (Medicago Sativa) Indian. J. Ecol. 2: 58-61.
- Hanson, C.H. et al. 1964. Performance of two-clone crosses in alfalfa and an unanticipated self-pollination problem. USDA Agr. Res. Ser. Tech. Bull. 1300.
- Hely, F.W., and Zorin, M. 1977. Influence of temperature and humidity on tripping of lucerne flowers. Aust. J. Agric. Res. 28: 1015-1027.
- Hintz, H.F. 1983. Horse nutrition, a practical guide. Arco Publishing Inc., New York.
- Hobbs, G.A. and Lilly, C.E. 1954. Ecology of species of Megachile Latreille in the mixed prairie region of southern Alberta with special reference to pollination of alfalfa. Ecology 35: 453-462.
- Hobbs, G.A.; Nummi, W.O. and Virostek, J.F. 1961. Food-gathering behavior of honey, bumble, and leaf-cutter bees (Hymenoptera: Apoidea) in Alberta. Can. Ent. 93: 409-419.
- Holm, S.N. 1966. The utilization and management of bumble bees for red clover and alfalfa seed production. Ann. Rev. Entomol. 11: 155-182.
- Holm, S.N. 1973. Osmia rufa L. (Hym. Megachilidae) as pollinator of plants in greenhouses. Ent. Scand. 4: 217-224.

- Hurd, P.D., Jr. 1979. Superfamily Apoidea. In K.V. Krombein, P.D. Hurd, Jr., D.R. Smith, and B.D. Burks (eds.) Catalog of Hymenoptera in America north of Mexico, Vol. 2. Smithsonian Institution Press, Washington. pp. 1741-1782.
- Ivanochko, M. 1979. Taxonomy, biology, and alfalfa pollinating potential of Canadian leaf-cutter bees (Hymenoptera: Megachile). M.Sc. thesis, Macdonald College of McGill University, Montreal.
- Johansen, C., and Mayer, D. 1976. Alkali bees: their biology and management for alfalfa seed production in the Pacific Northwest. PNW (Coop. Ext. Serv.) 155.
- Kapil, R.P and Jain, K.L. 1980. Biology and utilization of insect pollinators for crop production. Haryana Agric. Univ. Hissar, India. pp. 13-24.
- Kapil, R.P. and Jain, K.L. 1986. Management of megachilid bees for the pollination of alfalfa. In Pollination biology - An analysis. (ed.) Kapil, R.P. Inter-India Publications, India. pp 103-114.
- Kapil, R.P.; Grewal, G.S.; Kumar, S. and Atwal, A.S. 1974. Insect pollinators of alfalfa, Medicago sativa L. Indian J. Ent. 36: 214-220.
- Kauffeld, N.M. and Sorensen, E.L. 1971. Interrelationships of honeybee preference of alfalfa clones and flower color, aroma, nectar volume, and sugar concentration. Kansas Agric. Expt. Stn. Res. Publ. 163.

- Kauffeld, N.M. and Sorensen, E.L. 1980. Foraging behavior of honeybees on two-clone alfalfa combinations differing in bee attractiveness. *J. Econ. Entomol.* 73: 434-435.
- Kevan, P. 1987. Alfalfa leafcutter bees and the Ontario alfalfa growers. *Can. Beek.* 13: 81.
- Klostermeyer, E.C. 1982. Biology of the leafcutting bee. In G.H. Rank (ed.), *Proceedings of the first international symposium on alfalfa leafcutting bee management.* University of Saskatchewan Printing Services, Saskatoon. pp. 10-19.
- Krombein, K.V. 1967. *Trap-nesting wasps and bees: life histories, nests, and associates.* Smithsonian Press, Washington
- Laberge, W.E. and Ribble, D.W. 1966. Biology of Florilegus condignus (Hymenoptera: Anthophoridae), with a description of its larva, and remarks on its importance in alfalfa pollination. *Ann. Ent. Soc. Amer.* 59: 944-950.
- LaPlaca Reese, C.S. and Barrows, E.M. 1980. Co-evolution of Claytonia virginica (Portulacaceae) and its main native pollinator, Andrena erigeniae (Andrenidae). *Proc. Entomol. Soc. Wash.* 82: 685-694.
- Larkin, R.A. and Graumann, H.O. 1954. Anatomical structure of the alfalfa flower and an explanation of the tripping mechanism. *Bot. Gaz.* 116: 40-52.
- Laverty, T.M. and Plowright, R.C. 1988. Flower handling by bumblebees: a comparison of specialists and generalists. *Anim. Behav.* 36: 733-740.

- Levin , M.D. 1987. Value of bee pollination to United States agriculture. Amer. Bee J. 124: 184-186.
- Linsley, E.G. 1946. Insect pollinators of alfalfa in California. J. Econ. Ent. 39: 18-29.
- Linsley, E.G. 1958. The ecology of solitary bees. Hilgardia 27: 543-599.
- Lupo, A. 1984. Osmia latreillei iberoafricana Pet. (Megachilidae; Hymenoptera) as a potential pollinator. Proc. Vth Inter. Symp. Poll. Les colloques de l'INRA, No. 21 pp.467-476.
- Marletto, F., Manino, A., and Saglia, A. 1988. Insetti impollinatori di erba medica in Valle di Susa. Apicolt. mod. 79: 153-158.
- Martin, J.E.H. 1977. The insects and arachnids of Canada. Part 1, collecting, preparing and preserving insects, mites, and spiders. Canada Department Agriculture Public. 1643.
- Masner, L., and seven others. 1979. Hymenoptera. In H.V. Danks (ed.), Canada and its insect fauna. Memoirs of the Entomological Society of Canada, No. 108. pp. 485-508.
- McGregor, S.E. 1976. Insect pollination of cultivated crop plants. Agric. Res. Service, U.S. Dept. Agric. Handbook No. 496. Washington, D.C.
- Medler, J.T. and Koerber, T.W. 1958. Biology of Megachile relativa Cresson (Hymenoptera, Megachile) om trap-nests in Wisconsin. Ann. Ent. Soc. Amer. 51: 337-344.
- Menke, H.F. 1952. A six million dollar native bee in Washington state. Amer. Bee J. 92. 334-335.

- Michaud, R., Lehman, W.F., and Rumbaugh, M.D. 1988. World distribution and historical development. In A.A. Hanson, D.K. Barnes and R.R. Hill (eds.), Alfalfa and alfalfa improvement. American Society of Agronomy, Crop Science Society of America, Soil Science Society of America, Madison, Wisc. pp. 25-91.
- Michener, C.D. 1936. Some North American Osmiinae (Hymenoptera, Apoidea) Amer. Mus. Nov. No. 875.
- Michener, C.D. 1953. The biology of the leafcutter bee (Megachile brevis) and its associates. Univ. Kansas Sci. Bull. 35: 1659-1748.
- Mitchell, T.B. 1962. Bees of the eastern United States Vol. I, Tech. Bull. 152, North Carolina St. Univ.
- Mitchell, T.B. 1962. Bees of the eastern United States Vol. II, Tech. Bull. 152, North Carolina St. Univ.
- Móczár, L. 1959. The activity of the wild bees, (Hym., Apoidea) in Hungarian lucerne fields. Acta Agron. 9: 237-289.
- Nye, W.P. 1980. Notes on the biology of Halictus (Halictus) farinosus Smith (Hymenoptera: Halictidae). U.S. Department of Agriculture, Science and Education Administration Agricultural Research Results, Oakland, Calif. pp. 1-20.
- Nye, W.P. and Mackensen, O. 1968. Breeding bees to the crop. Utah Science (Utah State Univ. Agric. Expt. Sta.) 29: 46-48, 60.
- Özbek, H. 1976. Pollinator bees on alfalfa in the Erzurum region of Turkey. J. Apic. Res. 15: 145-148.

- Packer, J.S. 1970. The flight and foraging behavior of the alkali bee Nomia melanderi (Ckll.) and the alfalfa leafcutter bee Megachile rotundata (F.). Unpublished Ph.D. thesis, Utah State University, Logan, Utah.
- Parker, F.D. 1989. Nest clustering as a means of managing Osmia sar afaelae (Hymenoptera: Megachilidae). J. Econ. Entomol. 82: 401-403.
- Parker, F.D., Batra, S.W.T., and Tepedino, V.J. 1987. New pollinators for our crops. Agricultural Review 2: 279-304.
- Parker, F.D., Torchio, P.F., Nye, W.P. and Pedersen, M. 1976. Utilization of additional species and populations of leafcutter bees for alfalfa pollination. J. Api. Res. 15: 89-92.
- Pedersen, M.W. 1967. Cross-pollination studies involving three purple-flowered alfalfas, one white-flowered line, and two pollinator species. Crop Sci. 7: 59-62.
- Pedersen, M.W., Bohart, G.E., Marble, V.L., Klostermeyer, E.C. 1972. In C.H. Hanson, (ed) Alfalfa science and technology. American Society of Agronomy, Madison, Wisc. pp. 689-720.
- Pengelly, D.H. 1953. Alfalfa pollination in southern Ontario Ent. Soc. Ont. Ann. Rep. pp. 101-118.
- Pesenko, Yu.A. 1976. On the formation of solitary bee populations (Hymenoptera, Apoidea) in the alfalfa fields. Zool. Inst. USSR Acad. Sci. (Leningrad) 55: 856-859.

- Popov, V.V. 1956. Bees, their relationship to flowering plants and the problem of alfalfa pollination. Entomol. oboz. 35: 528-596.
- Randhawa, A.G. and Yunus, M. 1974. Insect visitors of lucerne flowers and their foraging behaviour. Proc. 25th Pakistan Sci. Conf. Abstr. Sect. Biol. 25: 22-23.
- Richards, K.W. 1983. Leafcutter bees revive alfalfa seed production. Can. Agr. 29: 31-34.
- Richards, K.W. 1984. Alfalfa leafcutter bee management in Western Canada. Publication 1495/E. Agriculture Canada, Ottawa.
- Richards, K.W. 1989. Effectiveness of the alfalfa leafcutter bee as a pollinator of forage legumes with special reference to cicer milkvetch and sainfoin. Eighth Annual Canadian Alfalfa Seed School, Canadian Alfalfa Seed Council, Winnipeg.
- Richards, K.W. and Krunic, M.D. 1990. Introduction of alfalfa leafcutter bees to pollinate alfalfa in Yugoslavia. The Entomologist 109: 130-135.
- Robinson, W.S., Nowogrodzki, R., and Morse, R.A. 1989. The value of honeybees as pollinators of U.S. crops. Amer. Bee J. 129: 411-423, 477-487.
- Roberts, R.B. 1978. Megachile rotundata (Fabricius), not Megachile pacifica (Panzer), is the name of the alfalfa leafcutting bee (Hymenoptera; Megachilidae). Bull. Ent. Soc. Amer. 24: 392.

- Rumbaugh, M.D. 1991. Plant introductions: the foundation of North American forage legume cultivar development. In Shands, H.L., Wiesner, L.E. (eds.), Use of plant introductions in cultivar development, part 1. CSSA Special Publication No. 17, Crop Science Society of America, Madison. pp. 103-114.
- Rust, R.W. 1974. The systematics and biology of the genus Osmia, subgenera Osmia, Chalcosmia, and Cephalosmia (Hymenoptera: Megachilidae). Wasmann J. Biol. 32: 1-93.
- Rust, R.W., Thorp, R.W. and Torchio, P.F. 1974. The ecology of Osmia nigrifrons with a comparison to other Acanthosmioides. J. Nat. Hist. 8: 29-47.
- Ruszkowski, A., Bilinski, M., Gosek, J., Kuna, K., Kaczmarska, K., Jablonski, B., and Kosior, A. 1980. The plants used by leaf-cutting-bees (Megachile Latr.) [In Polish]. Pszczelnicze Zeszyty Naukowe 24: 97-112.
- Skepasts, A.V. and Taylor, D.W. 1984. Alfalfa seed production in northern Ontario. Highlights of agriculture in Ontario 7: 15-17.
- Smith, M.V. 1960. Legume pollination in Ontario. Ontario Dept. Agriculture publication 139.
- Southwick, E.E. 1988. Bee research digest: some notes on solitary bees. American Bee J. 128: 421-422.
- Steiner, J.J., Beuselinck, P.R., Peaden, R.N., Kojis, W.P., and Bingham, E.T. 1992. Pollinator effects on crossing and genetic shift in a three-flower-color alfalfa population. Crop Sci: 32: 73-77.

- Steiner, K.E. and Whitehead, V.B. 1990. Pollinator adaptation to oil-secreting flowers - Rediviva and Diascia. *Evolution* 44: 1701-1707.
- Stephen, W.P. 1987. Megachile (Eutricharea) apicalis Spinola, an introduced bee with potential as a domesticatable alfalfa pollinator. *J. Kansas Ent. Soc.* 60: 583-584.
- Stephen, W.P. and Torchio, P.F. 1961. Biological notes on the leafcutting bee, Megachile (Eutrichraea) rotundata. *Pan-Pac. Entomol.* 37: 85-93.
- Strickler, K. 1979. Specialization and foraging efficiency of solitary bees. *Ecology* 60: 998-1009.
- Tasei, J-N. 1972. Observations préliminaires sur la biologie d' Osmia (Chalcosmia) coerulescens L., (Hymenoptera: Megachilidae), pollinisatrice de la luzerne (Medicago sativa L.). *Apidologie* 3: 149-165.
- Tirgari, S. 1971. Preliminary attempt and prospects for the establishment of nesting site of Melitta leporina (Panz) and other ground-nesting solitary wild-bees. *Int. Congress Entom.* 8: 325-326.
- Torchio, P.F. 1990. Diversification of pollination strategies for U.S. crops. *Environ. Entomol.* 19: 1649-1656.
- Torchio, P.F. and Asensio, E. 1985. The introduction of the European bee, Osmia cornuta Latr., into the U.S. as a potential pollinator of orchard crops, and a comparison of its manageability with Osmia lignaria propinqua Cresson (Hymenoptera: Megachilidae). *J. Kans. Ent. Soc.* 58: 42-52.

- Torchio, P.F. and Parker, F.D. 1975. First get the seeds. Utah Sci., Utah Agric. Exp. Stn. 36: 26-30.
- Torchio, P.F. and Tepedino, V.J. 1980. Sex ratio, body size and seasonality in solitary bee, Osmia lignaria propinqua Cress. (Hymenoptera: Megachilidae). Evolution 34: 993-1004.
- Wafa, A.K.; Ibrahim, S.H. and Eweis, M.A. 1975. Insect pollinators of alfalfa, Medicago sativa L. Agric. Res. Rev. Cairo 53: 199-207.
- Weaver, N. 1965. Foraging behavior of honeybees on White clover. Insectes Sociaux, Paris No. 3, pp. 231-240.
- Westerkamp, C. 1991. Honeybees are poor pollinators - why? Pl. Syst. Evol. 177: 71-75.
- Youssef, N.N. and Bohart, G.E. 1968. The nesting habits and immature stages of Andrena (Thysandrena) candida Smith (Hymenoptera, Apoidea) J. Kansas Entomol. Soc. 41: 442-455.

Appendix 1: List of study sites**A. Alfalfa Populations in Ottawa region**

- SITE 1:** Large alfalfa monoculture grown for forage on the northeast corner of the intersection of Fallowfield Rd. and Woodroffe Ave.
- SITE 2:** Large alfalfa monoculture grown for forage on the southwest corner of the intersection of Eagleson Rd. and Fallowfield Rd.
- SITE 3:** Large alfalfa monoculture grown for forage to the west of Eagleson Rd. about 1 km. north of intersection of Site 2.
- SITE 4:** Large alfalfa monoculture grown for forage on the north side of Fallowfield Rd. about 0.50 km east of the intersection in Site 1.
- SITE 5:** Large alfalfa monoculture grown for forage on the north side of Fallowfield Rd. about 0.25 km east of the intersection in Site 1.
- SITE 6:** Central Experimental Farm alfalfa monoculture grown for forage west of Fisher Ave., north of Baseline Rd. on the south side of access road.
- SITE 7:** Large alfalfa field grown for forage in Osgoode, northeast corner of the intersection of Main St. and Nixon Dr.
- SITE 8:** Animal Diseases Research Centre, Woodroffe Ave. complex, a large alfalfa monoculture grown for forage 0.50 km east of Greenbank Rd. and 0.50 km south of

Knoxdale Rd. on farm road.

SITE 9: Animal Diseases Research Centre, Woodroffe Ave.

complex, a large alfalfa monoculture grown for forage
0.25 km east of Greenbank Rd. and 0.50 km south of
Knoxdale Rd. on farm road.

SITE 10: Central Experimental Farm, small alfalfa monoculture,

30 m x 30 m, grown for forage west of Fisher Ave., north
of Baseline Rd. on the north side of access road.

SITE 11: Central Experimental Farm, small alfalfa monoculture,

10 m x 20 m, opposite the southwest corner of K.W.
Neatby Bldg. parking lot, surrounded by a variety of
grasses and weeds.

SITE 12: Central Experimental Farm, volunteer alfalfa plants

and mixed weedy vegetation on southeast corner of
intersection of Carling Ave. and Driveway about 100 east
of the Driveway.

SITE 13: Central Experimental Farm, volunteer alfalfa plants

and mixed weedy vegetation on northwest corner of
intersection of Driveway and Ash Lane.

SITE 14: Central Experimental Farm, volunteer alfalfa plants

and mixed weedy vegetation in centre of field half way
between Carling Ave. and the Driveway, west of Ash Lane.

SITE 15: Central Experimental Farm, breeder isolation plot of

alfalfa cultivar 'ComSel', 27 m x 120 m + 20 m X 20 m
(total 0.364 ha), south of Carling Ave. and north of
Winding Lane, west of the K.W. Neatby Building, just east

of the Parkdale intersection. It is isolated from other alfalfa plants by at least 600 m.

SITE 16: Central Experimental Farm, volunteer alfalfa plants, yellow- and purple-flowered, mixed with a variety of other weedy species just south of the traffic lights intersecting the Driveway and the cut off of Fisher Ave to Holland Ave.

B. Alfalfa Populations in the Peace River region

SITE 17: Forage demonstration plot planted about 1987, in north part of Beaverlodge Research Station. Forages were planted in 7 m rows in a north-south direction, each occupying about 20 square metres and about 1 metre apart. From west to east forages were respectively: alfalfa 'Anik', alfalfa 'Peace', red clover 'Altaswede', white clover 'Nora', Alsike clover 'Aurora', birdsfoot trefoil 'Leo', crownvetch 'Kompolti', cicer milkvetch 'Oxley', and sainfoin 'Melrose'. This site was about 50 m northwest of Site 18. The alfalfas, white and Alsike clover and birdsfoot trefoil were in full flower; the remaining forages were in partial flower.

SITE 18: Experimental forage trial at Beaverlodge Research Station about 50 m southeast of Site 17. Total plot was about 25 m x 10 m with about 20 varieties of purple-flowered alfalfa, the yellow-flowered alfalfa 'Anik', sainfoin, a few volunteer yellow sweet clover, and to the south volunteer white clover and a leafcutter bee

shelter with about 20,000 bees.

SITE 19: Experimental variety trial site, ca. 25 m x 25 m, with purple-flowered alfalfa, birdsfoot trefoil, Alsike clover, and contaminant white and yellow sweet clover. The plot was about 1 km south of the main Beaverlodge Research Station building just north of the Saskatoon plantings.

SITE 20: A managed alfalfa field, 1 km by 1 km, at Three Creeks, Alberta near the Peace River area. The field was serviced by alfalfa leafcutter bees and was in full bloom at the time. Collected on the periphery of the field which was surrounded by bush and farmland.

SITE 21: A managed alfalfa field, one km by one km, at Eaglesham, Alberta. The field was serviced by leafcutter bees and was in moderate bloom at the time. It was next to a large planting of canola and was also badly contaminated with canola, dandelion, thistle, Alsike clover, red clover and other weeds. Collections were from the periphery of the field which was adjacent to some bushland.

SITE 22: A managed alfalfa field, approximately one km by one km, at Taylor Flats, B.C. The field was serviced by alfalfa leafcutter bees and was in full bloom at the time. It was surrounded by cultivated fields and a thin strip of bush on one edge. Collections were from the periphery of the field near the bush.

SITE 23: A managed alfalfa field, about 40 ha, at Dawson Creek, B.C. The field was serviced by alfalfa leafcutter bees and was in full bloom at the time. It was a young stand with very few weeds and was surrounded by some bush but mostly farmland. Collections were from the periphery of the field near the bush.

C. White Clover Population in Ottawa region

SITE 24: Central Experimental Farm, very abundant weedy white clover on mown roadside, Ash Lane, about 100 m south of Driveway, with no competing flowers for 100 m.

Appendix 2: List of Hymenoptera collected at the 20 alfalfa sites.

<u>Voucher specimens</u>	<u>Identification</u>	<u>Site</u>
B. Brookes -		
12	<u>Lasioglossum coriaceum</u> (Smith)	4
19 ¹	<u>Gorytes</u> sp.	5
30	<u>Evylaeus divergens</u> (Lovell)	5
31-34	<u>Apis mellifera</u> L.	6
35-37	<u>Andrena wilkella</u> (Kirby)	6
39	<u>Hylaeus modestus</u> Say	7
49	<u>Bombus impatiens</u> Cress.	8
51 ¹	<u>Bombus terricola</u> Kirby	8
54	<u>Ichneumon</u> sp.	8
57	<u>Bombus affinis</u> Cress.	8
58	<u>Bombus terricola</u> Kirby	8
59 ¹	<u>Dolichivespula arctica</u> Rowher	8
63 ¹	<u>Podalonia luctuosa</u> (Smith)	8
65	<u>Bombus impatiens</u> Cress.	8
66-67	<u>Apis mellifera</u> L.	8
68	<u>Apis mellifera</u> L.	9
70	<u>Andrena wilkella</u> (Kirby)	9
72	<u>Bombus terricola</u> Kirby	9
73	<u>Apis mellifera</u> L.	9
74 ¹	<u>Ichneumon</u> sp.	9
76 ¹	<u>Ammophila urnaria</u> Dahlbom	9
81-82	<u>Bombus affinis</u> Cress.	10

83	<u>Bombus impatiens</u> Cress.	10
84	<u>Bombus terricola</u> Kirby	10
85	<u>Bombus impatiens</u> Cress.	10
86	<u>Bombus affinis</u> Cress.	10
87	<u>Bombus terricola</u> Kirby	10
88	<u>Bombus affinis</u> Cress.	10
89	<u>Bombus impatiens</u> Cress.	10
91-93	<u>Bombus terricola</u> Kirby	10
94	<u>Bombus affinis</u> Cress.	10
95	<u>Bombus terricola</u> Kirby	10
96 ¹	<u>Philanthus ventilabris</u> F.	10
97	<u>Bombus terricola</u> Kirby	10
98 ¹	<u>Philanthus ventilabris</u> F.	10
101-102	<u>Megachile</u> sp.	11
103-104	<u>Bombus</u> sp.	11
105	<u>Megachile</u> sp.	11
106	<u>Andrena</u> sp.	11
107	<u>Megachile</u> sp.	11
108-109	<u>Andrena</u> sp.	11
110	<u>Megachile</u> sp.	11
111	<u>Bombus</u> sp.	12
112	<u>Megachile</u> sp.	12
113	<u>Andrena</u> sp.	12
114	<u>Agapostemon</u> sp.	12
115	<u>Andrena</u> sp.	12
116	<u>Halictus</u> sp.	12

117-118	<u>Andrena</u> sp.	12
119	<u>Agapostemon</u> sp.	12
120	<u>Andrena</u> sp.	12
121-122	<u>Andrena</u> sp.	13
124	<u>Lasioglossum</u> sp.	13
126-127	<u>Andrena</u> sp.	14
130-145	<u>Megachile</u> sp.	12
146-149, 152-154	<u>Andrena</u> sp.	12
155	<u>Bombus</u> sp.	12
156-181	<u>Megachile</u> sp.	15
182-193	<u>Bombus</u> sp.	15
194	<u>Evyllaeus</u> sp.	15
195-198 ¹	<u>Polistes fuscatus</u> (Fab.)	15
199-201	<u>Andrena</u> sp.	15
202-203	<u>Halictus</u> sp.	15
204	<u>Andrena</u> sp.	15
205-206	<u>Halictus</u> sp.	15
207-233	<u>Megachile</u> sp.	15
234-240	<u>Bombus</u> sp.	15
243-249	<u>Megachile</u> sp.	15
250	<u>Halictus</u> sp.	15
251-252	<u>Andrena</u> sp.	15
253	<u>Halictus</u> sp.	15
254	<u>Andrena</u> sp.	15
255	<u>Halictus</u> sp.	15
256	<u>Andrena</u> sp.	15

257-268	<u>Halictus</u> sp.	15
269	<u>Agapostemon</u> sp.	15
270-282	<u>Megachile</u> sp.	15
283-290	<u>Bombus</u> sp.	15
292-296 ¹	<u>Polistes fuscatus</u> (Fab.)	15
297	<u>Andrena</u> sp.	15
298-300	<u>Halictus</u> sp.	15
301	<u>Andrena</u> sp.	15
302-303	<u>Halictus</u> sp.	15
304-305	<u>Andrena</u> sp.	15
306-338	<u>Megachile</u> sp.	15
339-355	<u>Bombus</u> sp.	15
356-361 ¹	<u>Polistes fuscatus</u> (Fab.)	15
362-370	<u>Megachile</u> sp.	15
372-379	<u>Halictus</u> sp.	15
380	<u>Andrena</u> sp.	15
381-407	<u>Halictus</u> sp.	15
410	<u>Dialictus</u> sp.	15
411	<u>Agapostemon</u> sp.	15
412	<u>Halictus</u> sp.	15
415-421	<u>Megachile</u> sp.	16
422-426 ¹	<u>Polistes fuscatus</u> (Fab.)	16
427-433	<u>Megachile</u> sp.	16
434-435	<u>Hoplitis</u> sp.	16
437	<u>Megachile</u> sp.	16
438 ¹	<u>Polistes fuscatus</u> (Fab.)	16

439-446	<u>Megachile</u> sp.	16
447-451	<u>Andrena</u> sp.	16
452	<u>Halictus</u> sp.	16
454 ²	<u>Coelioxys</u> sp.	16
455-462	<u>Megachile</u> sp.	16
463-469 ¹	<u>Polistes fuscatus</u> (Fab.)	16
470-472	<u>Andrena</u> sp.	16
473	<u>Melissodes</u> sp.	16
474-475	<u>Halictus</u> sp.	16
476-486	<u>Megachile</u> sp.	16
487	<u>Osmia</u> sp.	16
488-507	<u>Megachile</u> sp.	16
508	<u>Hoplitis</u> sp.	16
512	<u>Megachile</u> sp.	16
513-517 ¹	<u>Polistes fuscatus</u> (Fab.)	16
518-519 ²	<u>Coelioxys</u> sp.	16
520	<u>Melissodes</u> sp.	16
521-522	<u>Andrena</u> sp.	16
523	<u>Halictus</u> sp.	16
524	<u>Megachile</u> sp.	16
525	<u>Andrena</u> sp.	16
526-531	<u>Megachile</u> sp.	16
532	<u>Andrena</u> sp.	16
533-535	<u>Megachile</u> sp.	16
537-538	<u>Halictus</u> sp.	16
545, 546	<u>Dialictus</u> sp.	16

547	<u>Hylaeus</u> sp.	16
548	<u>Dialictus</u> sp.	16
549-550	<u>Megachile</u> sp.	16
551	<u>Andrena</u> sp.	16
552-556	<u>Megachile</u> sp.	16
557	<u>Halictus</u> sp.	16
558	<u>Andrena</u> sp.	16
559 ¹	<u>Polistes fuscatus</u> (Fab.)	16
560	<u>Megachile</u> sp.	16
561-564	<u>Andrena</u> sp.	16
565	<u>Bombus borealis</u> Kirby	16
566-568 ¹	<u>Polistes fuscatus</u> (Fab.)	16
569-570	<u>Megachile</u> sp.	16
571-573	<u>Bombus</u> sp.	16
574-578	<u>Apis mellifera</u> L.	16
580-582	<u>Andrena</u> sp.	13
586-587 ¹	<u>Ichneumon</u> sp.	16
588-597	<u>Megachile</u> sp.	16
598-599 ¹	<u>Polistes fuscatus</u> (Fab.)	16
601-602	<u>Halictus</u> sp.	16
604-609	<u>Megachile</u> sp.	16
610-612	<u>Andrena</u> sp.	16
613	<u>Dialictus</u> sp.	16
614	<u>Megachile</u> sp.	16
615-619 ¹	<u>Polistes fuscatus</u> (Fab.)	16
620-626	<u>Megachile</u> sp.	16

627-630	<u>Dialictus</u> sp.	16
631	<u>Bombus</u> sp.	16
632	<u>Megachile</u> sp.	16
633-635 ¹	<u>Polistes fuscatus</u> (Fab.)	16
636-640	<u>Megachile</u> sp.	16
641	<u>Halictus</u> sp.	16
642-644	<u>Andrena</u> sp.	16
647	<u>Dialictus</u> sp.	16
648-649	<u>Apis mellifera</u> L.	16
650 ¹	<u>Polistes fuscatus</u> (Fab.)	16
651-653	<u>Heriades</u> sp.	16
654	<u>Dialictus</u> sp.	16
655	<u>Heriades</u> sp.	16
657	<u>Dialictus</u> sp.	16
658	<u>Evyllaesus</u> sp.	16
659-662	<u>Dialictus</u> sp.	16
663	<u>Bombus</u> sp.	16
664-676	<u>Megachile</u> sp.	16
677-693	<u>Heriades</u> sp.	16
694	<u>Evyllaesus</u> sp.	16
695	<u>Andrena</u> sp.	16
696	<u>Evyllaesus</u> sp.	16
697	<u>Lasioglossum</u> sp.	16
698-711	<u>Evyllaesus</u> sp.	16
712	<u>Dialictus</u> sp.	16
713	<u>Evyllaesus</u> sp.	16

714	<u>Halictus</u> sp.	16
715	<u>Evyllaesus</u> sp.	16
716	<u>Heriades</u> sp.	16
717	<u>Evyllaesus</u> sp.	16
718	<u>Dialictus</u> sp.	16
719	<u>Evyllaesus</u> sp.	16
720	<u>Andrena</u> sp.	16
721-724	<u>Dialictus</u> sp.	16
725-729	<u>Agapostemon</u> sp.	16
730	<u>Agapostemon virescens</u> (Fab.)	16
731-732	<u>Apis mellifera</u> L.	16
734-735	<u>Bombus</u> sp.	16
737	<u>Dialictus</u> sp.	16
738 ¹	<u>Perilampus</u> sp.	16
739	<u>Dialictus</u> sp.	16
740-743	<u>Megachile</u> sp.	16
744-753	<u>Apis mellifera</u> L.	16
754	<u>Megachile</u> sp.	16
755	<u>Lasioglossum</u> sp.	16
756	<u>Andrena</u> sp.	16
757	<u>Halictus</u> sp.	16
758-763	<u>Andrena</u> sp.	16
764-778	<u>Bombus</u> sp.	16
783-787, 789-795	<u>Dialictus</u> sp.	16
796-885	<u>Apis mellifera</u> L.	17
886	<u>Andrena</u> sp.	17

887-894	<u>Apis mellifera</u> L.	20
895-896	<u>Megachile</u> sp.	20
898 ¹	<u>Dolichovespula maculata</u> (L.)	20
901-908	<u>Megachile</u> sp.	21
909-910	<u>Andrena</u> sp.	21
911	<u>Megachile</u> sp.	21
914-915 ¹	<u>Banchus</u> sp.	
916-919	<u>Megachile</u> sp.	22
920 ¹	<u>Vespula vulgaris</u> (L.)	22
921-923	<u>Megachile</u> sp.	22
925 ¹	<u>Vespula vulgaris</u> (L.)	22
927	<u>Apis mellifera</u> L.	22
928 ¹	<u>Ichneumon</u> sp.	
929-930 ¹	<u>Banchus</u> sp.	
931-932 ¹	<u>Dusona</u> sp.	
933-935	<u>Apis mellifera</u> L.	23
937-939	<u>Megachile</u> sp.	23
940 ¹	<u>Banchus</u> sp.	
941-953	<u>Bombus terricola</u> Kirby	20
954	<u>Bombus rufocinctus</u> Cress.	20
955	<u>Bombus vagans</u> Smith	21
956-958	<u>Bombus rufocinctus</u> Cress.	22
959	<u>Bombus vagans</u> Smith	22
960-967	<u>Bombus rufocinctus</u> Cress.	22
968	<u>Bombus borealis</u> Kirby	22

967-973	<u>Bombus rufocinctus</u> Cress.	22
974	<u>Bombus borealis</u> Kirby	22
975	<u>Bombus rufocinctus</u> Cress.	22
976	<u>Bombus terricola</u> Kirby	23
977	<u>Bombus nevadensis</u> Cress.	23
978	<u>Bombus vagans</u> Smith	23

¹ Genera of Hymenoptera that are not included in the superfamily Apoidea and are not considered to have a significant pollinating role.

² Parasitic genus in the family Megachilidae that is not considered to have a pollinating role.

END

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FIN