Willows (*Salix* spp.) as pollen and nectar sources for sustaining fruit and berry pollinating insects

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Ostaff, D. P., Mosseler, A., Johns, R. C., Javorek, S., Klymko, J. and Ascher, J. S. 2015. **Willows (*Salix* spp.) as pollen and nectar sources for sustaining fruit and berry pollinating insects**. Can. J. Plant Sci. **95**: 505–516. Willows (*Salix* spp.) are ubiquitous in the northern hemisphere, serving as an important pollen and nectar resource for insect pollinators and for the enhancement of insect-pollinated agricultural crops such as fruits and berries. We used a common-garden field test containing seven native North American willow species to assess attractiveness of male and female flower catkins by documenting visits of *Andrena* spp. (Apoidea: Anthophila), other wild bees (all native), and flower flies (Syrphidae). Most willows in Canada's Maritimes begin flowering very early in spring, as the first wild pollinators become active following winter, and stop flowering by mid-May. A later-flowering group normally begins flowering in mid-May and stops flowering by mid-June. Pollinator species were largely opportunistic, visiting whatever species of willow flowers were available during foraging, but *Andrena dunningi* appeared to prefer flowers of *S. nigra* and *S. interior*. There was a general preference for male flower catkins, with 72% of *Andrena* spp. and 82% of all flower flies collecting pollen and/or nectar from male flowers, because pollen is the major component of nest provisioning for most solitary bees and the major source of protein used to develop reproductive tissues in most flower flies. Most andrenids and flower flies were collected within the April–June flowering period of six of the seven willow species studied, indicating that these willows could be used to support the pollinator community before the flowering period of commercially valuable flower-pollinated crops such as lowbush blueberry, cranberry, and apple.

Key words: *Andrena*, crop pollination, flower flies, *Salix* spp., wild insect pollinators, willow flowering phenology

Ostaff, D. P., Mosseler, A., Johns, R. C., Javorek, S., Klymko, J. et Ascher, J. S. 2015. **Le saule (*Salix* spp.), source de pollen et de nectar pour les insectes qui fécondent les espèces fruitières**. Can. J. Plant Sci. **95**: 505–516. Le saule (*Salix* spp.) pousse partout dans l'hémisphère nord. Il constitue donc une importante source de pollen et de nectar pour les insectes pollinisateurs et concourt à l'amélioration des cultures fécondées par les insectes, notamment celles qui produisent des fruits. Les auteurs ont recouru à une parcelle expérimentale aménagée en jardin réunissant sept espèces de saule indigènes à l'Amérique du Nord pour évaluer l'attrait des chatons de fleurs mâles et femelles pour *Andrena* spp. (Apoidea : Anthophila), d'autres abeilles sauvages (toutes indigènes) et des mouches à fleurs (Syrphidae) en fonction du nombre de visites recensées. Dans les provinces maritimes du Canada, la plupart des saules fleurissent très tôt au printemps, lorsque les insectes sauvages pollinisateurs commencent à s'activer au sortir de l'hiver. Leur floraison prend fin à la mi-mai. Un groupe plus tardif commence habituellement à fleurir à la mi-mai et la floraison se poursuit jusqu'au milieu de juin. Les espèces pollinisatrices sont très opportunistes et visitent toutes les fleurs de saule disponibles lorsqu'elles butinent, mais *Andrena dunningi* semble privilégier celles de *S. nigra* et de *S. interior*. En règle générale, les insectes préfèrent les chatons de fleurs mâles, puisque 72 % des *Andrena* spp. et 82 % des mouches à fleurs en recueillent le pollen et le nectar. Le pollen constitue le gros des réserves du nid pour la plupart des abeilles solitaires et est la principale source de protéines servant au développement des tissus reproducteurs chez la plupart des mouches à fleurs. La majorité des andrénides et des mouches à fleurs ont été capturées entre avril et juin, soit durant la période de floraison de six des sept espèces de saule étudiées, signe que ces dernières pourraient servir à soutenir la population d'insectes pollinisateurs avant la floraison des cultures d'importance commerciale dont les fleurs doivent être fécondées, tels le bleuet nain, la canneberge et la pomme.

Mots clés: *Andrena*, pollinisation des cultures, mouches à fleurs, *Salix* spp., insectes sauvages pollinisateurs, phénologie de la floraison du saule

Many commercially grown fruits and vegetables rely on pollination by honey bees (*Apis mellifera* L.), native bees (Apoidea: Anthophila), and flies (Diptera), particularly flower fly (Syrphidae) pollinators (Ssymank et al. 2008; Potts et al. 2010; Calderone 2012; Garibaldi et al. 2013).

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However, managed honey bee populations have been threatened due to a combination of factors, including mites, bacteria, and the use of miticides and agrochemicals (Winston 1992; Hansen and Brodsgaard 1999; Sammataro et al. 2000; Spivak and Reuter 2001; Johnson et al. 2010; Mullin et al. 2010; Henry et al. 2012). Similarly, wild native bee populations have also been declining due to loss and degradation of nesting sites and floral resources, landscape fragmentation, intensive agronomic and monoculture practice, displacement of native floral hosts by exotic plants, use of pesticides, decimation of host plants by high deer populations, and loss of open habitats due to suppression of fires and other checks to forest succession (Kearns et al. 1998; Larsson and Franzén 2007; Grundel et al. 2010; Pendleton et al. 2011; Williams 2011; Brousseau et al. 2013). The status of flower flies as pollinators has received relatively little attention (Ssymank et al. 2008). There is evidence that, at the site level, flower fly diversity has decreased in England but increased in the Netherlands, and that in both countries a smaller number of species dominate pollinator communities when comparing pre- and post-1980 data sets (Biesmeijer et al. 2006). Maintaining or supporting diverse wild pollinator populations is particularly important to a broad range of agricultural crops for which honey bees alone are insufficient to maximize pollination and associated fruit and seed set (Garibaldi et al. 2013).

Strategies must be developed to maintain and enhance the availability and effectiveness of wild pollinators to pollinate fruit and vegetable crops. Planting or cultivating native willows (*Salix* spp.) in areas surrounding crop fields could provide a consistent source of pollen and nectar to support pollinator populations early in the growing season when crops and most alternative native floral hosts are not yet flowering. Willows are largely entomophilous, i.e., insect pollinated (Sacchi and Price 1988; Mosseler and Papadopol 1989; Reddersen 2001; Karrenberg et al. 2002). Canada has 76 native willow species (Argus 2010) that are adapted to a wide range of site types and moisture regimes (Mosseler et al. 2014a). Some eastern North American bee species use willows as their main source of pollen (Lanham 1965; Tamura and Kudi 2000; Exeler et al. 2008), notably several oligolectic *Andrena* species. The latter include very early emerging species of subgenus *Andrena*, notably *A. clarkella* Kirby, which has been well-studied in its European range (Chambers 1968; Gebhardt and Röhr 1987; Haß et al. 2012; LeFréon et al. 2013), and also *A. frigida* Smith (LaBerge 1980). Other later-emerging, willow-specialist *Andrena* species of the subgenera *Micrandrena* (e.g., *A. salictaria* Robertson), *Parandrena* (spp.), *Trachandrena* (*A. mariae* Robertson and *A. sigmundi* Cockerell), and *Tylandrena* [*A. erythrogastra* (Ashmead)] (Ribble 1968; LaBerge and Bouseman 1970; LaBerge and Ribble 1972; LaBerge 1973; Miliczky 1988) use willow as a main pollen source. Many other less specialized *Andrena* species, such as *A. carlini* Cockerell, and other *Melandrena* species are important pollinators of crops, such as blueberries (*Vaccinium* spp.) and apples (*Malus* spp.), and regularly visit and collect pollen from willows in large numbers, relying upon them as an essential food source (Schrader and LaBerge 1978; Miliczky and Osgood 1995). Even oligoleges of other plants, e.g., *Andrena* (*A. erythronii* Robertson), which prefers pollen of the trout lily [*Erythronium americanum* Ker-Gawl (Liliaceae)], use willows as an important nectar source prior to bloom of their favored pollen sources (LaBerge 1986).

Andrena and other pollinators are important not only to the dispersal and colonization of flowering plants but are also critical to agricultural fruit and berry crops. Of particular significance to pollinators, willows exhibit a broad range of flowering phenology, with many of the precocious willows (e.g., *Salix bebbiana* Sarg., *S. discolor* Muhl., and *S. eriocephala* Michx.) flowering very early in the growing season (Mosseler and Papadopol 1989). Others do not begin flowering until mid-May to early June in eastern Canada (e.g., *S. amygdaloides* Andersson and *S. nigra* Marsh.), whereas *S. interior* Rowlee begins flowering early in the season and then continues to flower sporadically throughout the growing season (Mosseler and Papadopol 1989). Many willows can be relatively easily propagated from dormant, rootless stem cuttings, which readily produce roots when placed in moist soil. Thus, willows are amenable to large-scale, cost-effective artificial establishment for purposes such as site reclamation activities (Mosseler et al. 2014b). Dioecy (the separation of males and females on separate plants) ensures that planting practices favoring only male or female plants could be used to mitigate unwanted seed dispersal into crop fields. For these reasons, planting the appropriate willow species with a flowering phenology complementary (i.e., non-overlapping) to cultivated crops could be an effective and efficient strategy for enhancing local populations of wild pollinators.

In the present study, we established a common-garden field study to determine: (1) the seasonal flowering phenology of seven common willow species (Table 1) native to eastern Canada, and (2) the composition, phenology and relative abundance of the most common pollinator insects visiting male and female willow flower catkins. This is baseline information needed for selection of willow species with a flowering phenology complementary to crops relying primarily on insect-pollination by providing alternative floral hosts, especially at the beginning of the growing season.

MATERIALS AND METHODS

In 2008, a common-garden field test was established at the Atlantic Forestry Centre experimental tree nursery (AFC) in Fredericton (lat. 45°56′03.97″N, long. 66°39′20.45″W) with seven different willow species native to eastern North America (Table 1) that were collected from natural populations located in southern and eastern Ontario and adjacent areas of the Ottawa River Valley in Quebec [see Mosseler et al. (2014b)

Table 1. Native North American willow (*Salix*) species used in a common-garden study of flowering phenology and insect pollinator diversity and abundance in Fredericton, New Brunswick, Canada

Salix species	Height and habit	Natural habitat
S. amygdaloides (AMY)	8–15 m, tree	poorly drained, standing wetlands
S. bebbiana (BEB)	4–6 m, shrub	seepage slopes, ditches, upland sites
S. discolor (DIS)	4–10 m, shrub/small tree	wetlands, ditches, upland sites
S. eriocephala (ERI)	4–6 m, shrub	fast-flowing stream banks
S. interior (INT)	4–6 m, shrub	river banks, sandbars, floodplains
S. humilis (HUM)	2–3 m, shrub	well-drained upland sites, forest openings
S. nigra (NIG)	10–12 m, tree	river banks and floodplains

for population origins]. These seven willows were initially selected for their growth potential and as promising species for biomass production for emerging energy, chemicals, and materials industries (Mosseler et al. 1988, 2014b). The common garden was established with stem cuttings collected during winter from vigorous 1- and/or 2-yr-old stem sections (Densmore and Zazada 1978). *Salix amygdaloides* (AMY), *S. bebbiana* (BEB), *S. discolor* (DIS), *S. eriocephala* (ERI), *S. humilis* (HUM), *S. interior* (INT), and *S. nigra* (NIG) were represented by collecting five clones from each of four natural populations (20 clones per species, resulting in a total of 140 clones). Each clone was represented as a three-ramet (clonal plant) linear row plot spaced at 1 m × 1 m, within and between rows, in each of three replications (for a total of nine ramets per clone). The AFC site has a well-drained, sandy loam soil (Mosseler et al. 2014a) and a temperate climate with an average annual temperature of 5.6°C and an annual precipitation of 1124 mm (Environment Canada 2013).

At the time of flowering in 2010, the propagated willows had been growing for two full growing seasons following the placement of unrooted, dormant cuttings in the AFC common garden. These willows were approximately 1–2 m in height, depending on species, and were entering their third growing season. During the dormant season of 2010–2011, the common garden was partially harvested for biomass measurements. Therefore, the observations on the flowering phenology made in 2012 were based on a mixture of 1-yr-old coppice growth as well as 4-yr-old plants originating from stem cuttings. Observations on the beginning and ending dates of flowering were made on each clone in the common garden at 2-d intervals from the beginning of the flowering seasons of 2010 and 2012 and ending in mid-June, and then periodically throughout the summer and autumn until late November according to protocols described in Mosseler and Papadopol (1989) for identifying male and female flower receptivity.

Every 2–3 d, from April 07 to June 11, during warm, dry weather, collections of insects visiting male and female willow catkins were made by passing between rows of willow in the AFC common garden and collecting insects present on willow flower catkins. Collections were made using a heavy-duty hand-held, battery-powered vacuum/aspirator (product 2820GA, BioQuip Products Inc., http://www.bioquip.com/). Specimens were transferred to plastic collection vials, labeled by collection date, willow species, specific clone, and sex of flower visited, and placed in a freezer until they could be pinned, labeled and identified. No collections were made after June 11, the date when six of the seven species of willow had ceased flowering.

RESULTS

The flowering periods for most willow species are short (Fig. 1), and flowering was normally completed within a period of 2–3 wk for each willow species. However, following an initial heavy flowering in May, INT, which has distinctive specialist andrenid bee visitors (e.g., *Andrena amphibola* Viereck, *A. andrenoides* Cresson, *A. bisalicis* Viereck, *A. crataegi* Robertson, *A. nida* Muller) (LaBerge 1969, 1973, 1977; LaBerge and Ribble 1972), produced receptive flowers sporadically throughout the growing season until approximately mid-September. There was some yearly variation in flowering period for these seven willows but relative to each other, the flowering periods for each species were similar from year to year. Most of the precocious flowering shrub willows (e.g., BEB, DIS, ERI, and HUM) normally began flowering at the beginning of their second growing season; however, some clones of the tree willows AMY and NIG, were still not flowering as they entered their fourth growing season in 2011 and may require more time to attain reproductive maturity.

A total of 298 bees (Apoidae: Anthophila) and 84 flower flies (Diptera: Syrphidae) were collected. Thirty species of bees belonging to four families and seven genera were collected: Andrenidae: *Andrena*; Halictidae: *Lasioglossum*, *Halictus*, *Augochlora*, *Augochlorella*; Apidae: *Bombus*; Colletidae: *Colletes* (Table 2). In addition, 23 species of flower flies belonging to two subfamilies were also collected (Table 2): Syrphinae represented by 11 genera (*Syrphus*, *Parasyrphus*, *Sphaerophoria*, *Dasysyrphus*, *Allograpta*, *Melanostoma*, *Melangyna*, *Didea*, *Epistrophe*, *Lapposyrphus*, *Platycheirus*) and Eristalinae represented by seven genera (*Orthonevra*, *Eristalis*, *Syritta*, *Heliophilus*, *Xylota*, *Chalcosyrphus*, and *Heringia*) (Table 2).

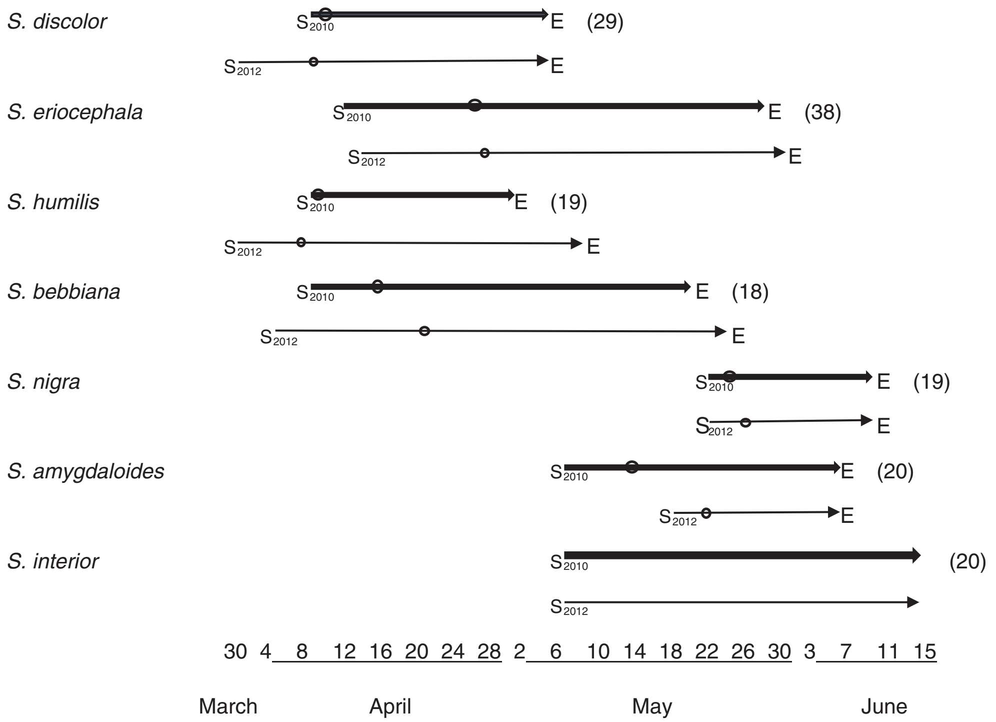

Fig. 1. Start (S) and end (E) of flowering of seven native North American willow species observed in 2010 and 2012 on plants in a common-garden field study established in Fredericton, New Brunswick. Circles on lines representing the flowering period indicate peak flowering periods and the number in parentheses represents the number of willow clones observed.

The most common bee genus was *Andrena*, representing 63% of all bee species ($N = 19$) collected. For eight of nine predominant *Andrena* species (*A. frigida*, *A. clarkella*, *A. hippotes* Robertson, *A. vicina* Smith, *A. algida* Smith, *A. carlini*, *A. crataegi*, *A. cressonii* Robertson), more than half of individuals were collected from two species of willow, ERI and INT; for the other (*A. dunningi* Cockerell), 72% were collected from NIG and INT. Sixty-five percent of the most common flower fly species were collected from three willow species: INT, AMY, and ERI. The order of abundance of collection on the different willow species by *Andrena* was ERI > INT > NIG > DIS > AMY > BEB > HUM; by flower flies INT > AMY > ERI > DIS > NIG > HUM > BEB (Table 3).

The earliest collections of *Andrena* and flower flies were on April 07 (*A. frigida*, *A. clarkella*, *A. hippotes*) and April 11 [*Dasysyrphus laticaudus* (Williston)], respectively. The last collection of both andrenids (*A. crataegi*, *A. carlini*, *A. hippotes*) and flower flies (*Syrphus ribesii* (L.), *Lapposyrphus lapponicus* (Zetterstedt), *Orthonevra anniae* (Sedman), *O. nitidus* (Wiedemann), *Eristalis dimidiata* Wiedemann, *Heliophilus fasciatus* Walker, and *Xylota quadrimaculata* Loew) occurred on June 11 (Fig. 2a, b). The period during which an individual species was collected was 52 d for the Andrenidae (range 37 d for *A. carlini* to 65 d for *A. hippotes*) and 36 d for Syrphidae [range 18 d for *Parasyrphus genualis* (Williston) to 53 d for *S. ribesii*] (Table 3). Ninety-six percent and 65%, respectively, of all andrenids and flower flies collected were female. Males were collected for only three of 19 species of *Andrena* (*A. dunningi*, *A. hippotes* and *A. vicina*), with *A. hippotes* having the greatest percentage of males collected (20%) (Table 2). *Eristalis dimidiata* was the only flower fly where more males than females were collected (males = 65%).

Six of the nine predominant *Andrena* species (*A. frigida*, *A. clarkella*, *A. dunningi*, *A. hippotes, A. algida* and *A. vicina*) were collected when all species of willow were in flower, two species (*A. carlini* and *A. cressonii*) were collected after HUM or DIS had ceased flowering, and one species (*A. crataegi*) was collected when only the late-flowering willow species (INT, AMY, and NIG) were in bloom (Figs. 1 and 2a). Three of the five most common flower fly genera (*Syrphus*, *Dasysyrphus*, and *Sphaerophoria*) were collected during the flowering period of all willow species, whereas the other two genera (*Eristalis* and *Parasyrphus*) were collected when two early flowering willow species (DIS and HUM) were not in flower (Figs. 1 and 2b).

Generally, *Andrena* and flower flies preferred male flowers (Table 4). Seventy-two percent of *Andrena* and 82% of flower flies were collected on male flowers. For the four most commonly collected *Andrena* (*A. frigida*,

Table 2. Bees (Apoidea: Anthophila) and flower flies (Syrphidae) collected from male and female flowers of seven native North American willow species established in a common garden in Fredericton, New Brunswick, Canada

		No. of specimens	
Family	Species	Female	Male
Andrenidae	*Andrena* (*Andrena*) *frigida* (Smith 1853)[z]	60	0
	Andrena (*Andrena*) *clarkella* (Kirby 1802)[z]	47	0
	Andrena (*Melandrena*) *dunningi* (Cockerell 1898)	38	1
	Andrena (*Trachandrena*) *hippotes* (Robertson 1895)	24	6
	Andrena (*Melandrena*) *vicina* (Smith 1853)	11	2
	Andrena (*Melandrena*) *carlini* (Cockerell 1901)	10	0
	Andrena (*Euandrena*) *algida* (Smith 1853)[z]	7	0
	Andrena (*Plastandrena*) *crataegi* (Robertson 1893)	5	0
	Andrena (*Holandrena*) *cressonii* (Robertson 1891)	4	0
	Andrena (*Gonandrena*) *persimulata* (Viereck 1917)	2	0
	Andrena (*Micrandrena*) *salictaria* (Robertson 1905)[z]	2	0
	Andrena (*Thysandrena*) *bisalicis* (Viereck 1908)[z]	1	0
	Andrena (*Conandrena*) *bradleyi* (Viereck 1907)[y]	1	0
	Andrena (*Andrena*) *milwaukeensis* (Graenicher 1903)	1	0
	Andrena (*Larandrena*) *miserabilis* (Cresson 1872)	1	0
	Andrena (*Trachandrena*) *rugosa* (Robertson 1891)	1	0
	Andrena (*Andrena*) *rufosignata* (Cockerell 1902)	1	0
	Andrena (*Trachandrena*) *sigmundi* (Cockerell 1902)[z]	1	0
	Andrena (*Simandrena*) *wheeleri* (Graenicher 1904)	1	0
Apidae	*Bombus* (*Pyrobombus*) *impatiens* (Cresson 1863)	3	0
	Bombus (*Pyrobombus*) *ternarius* (Say 1837)	3	0
	Bombus (*Bombus*) *terricola* (Kirby 1837)	1	0
	Bombus (*Pyrobombus*) *vagans* (Smith 1854)	2	0
Colletidae	*Colletes inaequalis* (Say 1837)	0	1
Halictidae	*Lasioglossum* (*Evylaeus*) *cinctipes* (Provancher 1888)	1	0
	Lasioglossum (*Lasioglossum*) *athabascense* (Sandhouse 1933)	1	0
	Lasioglossum (*Sphecodogastra*) *comagenense* (Knerer and Atwood 1964)	1	0
	Lasioglossum (*Dialictus*) spp.[x]	50	0
	Halictus (*Protohalictus*) *rubicundus* (Christ 1791)	6	0
	Augochlora (*Augochlora*) *pura* (Say 1837)	1	0
	Augochlorella aurata (Smith 1853)	1	0
Syrphidae (Syrphinae)	*Syrphus vitripennis* (Meigen 1822)	4	5
	Syrphus ribesii (Linnaeus 1758)	3	1
	Syrphus torvus (Osten Sacken 1875)	1	1
	Dasysyrphus laticaudus (Williston 1887)	6	2
	Parasyrphus genualis (Williston 1887)	3	3
	Parasyrphus nigritarsis (Zetterstedt 1843)	1	0
	Sphaerophoria contigua Macquart 1847	2	3
	Sphaerophoria scripta (Linnaeus 1758)	3	1
	Platycheirus obscurus (Say 1824)	0	1
	Platycheirus sp.	4	0
	Allograpta obliqua (Say 1823)	4	0
	Melanostoma mellinum (Linnaeus 1758)	2	1
	Melangyna lasiophthalma (Zetterstedt 1843)	2	0
	Didea alneti (Fallen 1817)	0	1
	Epistrophe nitidicollis (Meigen 1822)	0	1
	Lapposyrphus lapponica (Zetterstedt 1838)	1	0
Syrphidae (Eristalinae)	*Eristalis dimidiata* (Wiedemann 1830)	3	6
	Eristalis flavipes (Walker 1849)	4	0
	Orthonevra anniae (Sedman 1966)	2	0
	Orthonevra nitidus (Wiedemann 1830)	1	0
	Orthonevra pulchella (Williston 1887)	0	1
	Heringia sp.	4	0
	Syritta pipiens (Linnaeus 1758)	1	2
	Helophilus fasciatus (Walker 1849)	2	0
	Chalcosyrphus nemorum (Fabricius 1805)	1	0
	Xylota quadrimaculata (Loew 1866)	0	1

[z] Willow specialist.
[y] Blueberry specialist.
[x] Under taxonomic revision.

Table 3. Percentage of the most common specimens of Andrenidae and Syrphidae collected in 2010 from 2-yr-old plants of seven native North American willow species established in a common garden in Fredericton, New Brunswick, Canada

	No. of	Collection	Range			Salix	Species			
Insect	specimens	Earliest	Latest	*discolor*	*eriocephala*	*humilis*	*bebbiana*	*nigra*	*amygdaloides*	*interior*
Andrenidae										
Andrena frigida	60	Apr. 07	May 31	20	53	5	5	3	2	12
A. clarkella	46	Apr. 07	May 31	7	46	4	4	0	22	17
A. dunningi	39	Apr. 24	Jun. 07	3	10	3	3	46	10	26
A. hippotes	29	Apr. 07	Jun. 11	10	24	3	10	17	3	28
A. vicina	12	Apr. 11	Jun. 07	0	17	0	17	25	8	33
A. carlini	10	May 05	Jun. 11	20	20	0	0	10	10	40
A. algida	7	Apr. 12	May 19	14	43	14	14	0	14	0
A. crataegi	5	May 31	Jun. 11	0	0	0	0	60	0	40
A. cressonii	4	May 05	May 31	0	25	0	0	0	0	75
Syphridae										
Syrphus ribesii	4	Apr. 27	Jun. 11	0	0	25	0	25	0	50
S. vitripennis	9	Apr. 20	May 17	1	22	11	11	0	22	22
S. torvus	2	May 14	May 19	0	0	0	0	0	50	50
Eristalis dimidiata	9	May 14	Jun. 11	0	11	0	0	0	11	78
E. flavipes	4	May 05	May 19	0	0	0	25	0	75	0
Dasysyrphus laticaudus	8	May 05	May 31	0	38	0	12	0	0	50
Sphaerophoria scripta	4	May 10	May 19	50	0	0	0	0	50	0
S. contigua	5	Apr. 11	May 10	60	20	20	0	0	0	0
Parasyrphus genualis	6	May 14	May 31	0	0	0	0	17	0	83
P. semiinterruptus	2	May 05	May 14	0	0	0	0	0	0	100
P. nigritarsus	1	May 14	–	0	0	0	0	0	0	100

A. clarkella, *A. dunningi*, *A.hippotes*), 67, 61, 90, and 67%, respectively, of the individuals collected were from male flowers. Within individual willow species, all flower flies collected from AMY were from male flowers, whereas 93, 82, 67 and 50%, respectively, collected from of INT, ERI, NIG, and DIS were from male flowers. The opposite was true for HUM and BEB; 100 and 67% of flower flies taken from HUM and BEB, respectively, were from female flowers. *Eristalis* spp., *P. genualis*, *Syrphus* spp., and *D. laticaudus* showed the highest preference for male flowers, with 83, 83, 82, and 78% of individuals taken from male flowers, respectively. *Sphaerophoria* spp. showed a similar but less pronounced preference: 57% of individuals were taken from male flowers.

DISCUSSION

Our study provides evidence of a diverse assemblage of pollinator species associated with seven common native North American willow species with various attributes, including prolific flowering (ERI and INT), both tree forms (AMY and NIG) and shrub forms (BEB, DIS, ERI, HUM and INT), and species adapted to both wet, lowland sites (AMY, DIS, ERI and INT) as well as drier, upland sites (BEB, DIS, and HUM). This variation in plant form, site adaptability, and flowering phenology provides an array of plant choices for pollinating insects throughout the foraging season (e.g., *A. frigida* and *A. clarkella* foraged over the full period when all seven willows were in flower).

For six of the seven willows studied here, flowering phenology was similar to that described by Mosseler and Papadopol (1989) in a common-garden experiment established near Toronto, Ontario. Although HUM was not part of these earlier phenological observations, it proved to be a prolific, precocious flowering species, similar to BEB, DIS, and ERI. Unfortunately, several of the precocious flowering willows (BEB, DIS, and HUM) do not develop roots from dormant, rootless stem cuttings as readily as riparian species such as AMY, ERI, INT, and NIG, and therefore, survival rates were somewhat lower in some of these precocious willows (Mosseler et al. 2014b). Although HUM may not be reproductively isolated from the other precocious willows through flowering phenology, it is often ecologically or spatially isolated from these other shrub willows through its adaptation to drier site types associated with small openings in forest cover. Thus, under natural conditions, HUM maintains some degree of reproductive isolation from these other shrub willows. Differences in site adaptations among these willows will become important when matching willow species to the soil, moisture, or other site requirements of crop species to be pollinated.

Flower flies and bees of the genus *Andrena* are common visitors to flowering plants and were well represented in our study. *Andrena* species are important pollinators for berry and fruit crops. They typically pupate in late summer and overwinter as adults, allowing early emerging *Andrena* species to begin nesting activities on the first warm days in the spring (e.g., Batra 1999a, b). By emerging early, *Andrena* can forage when tree fruits

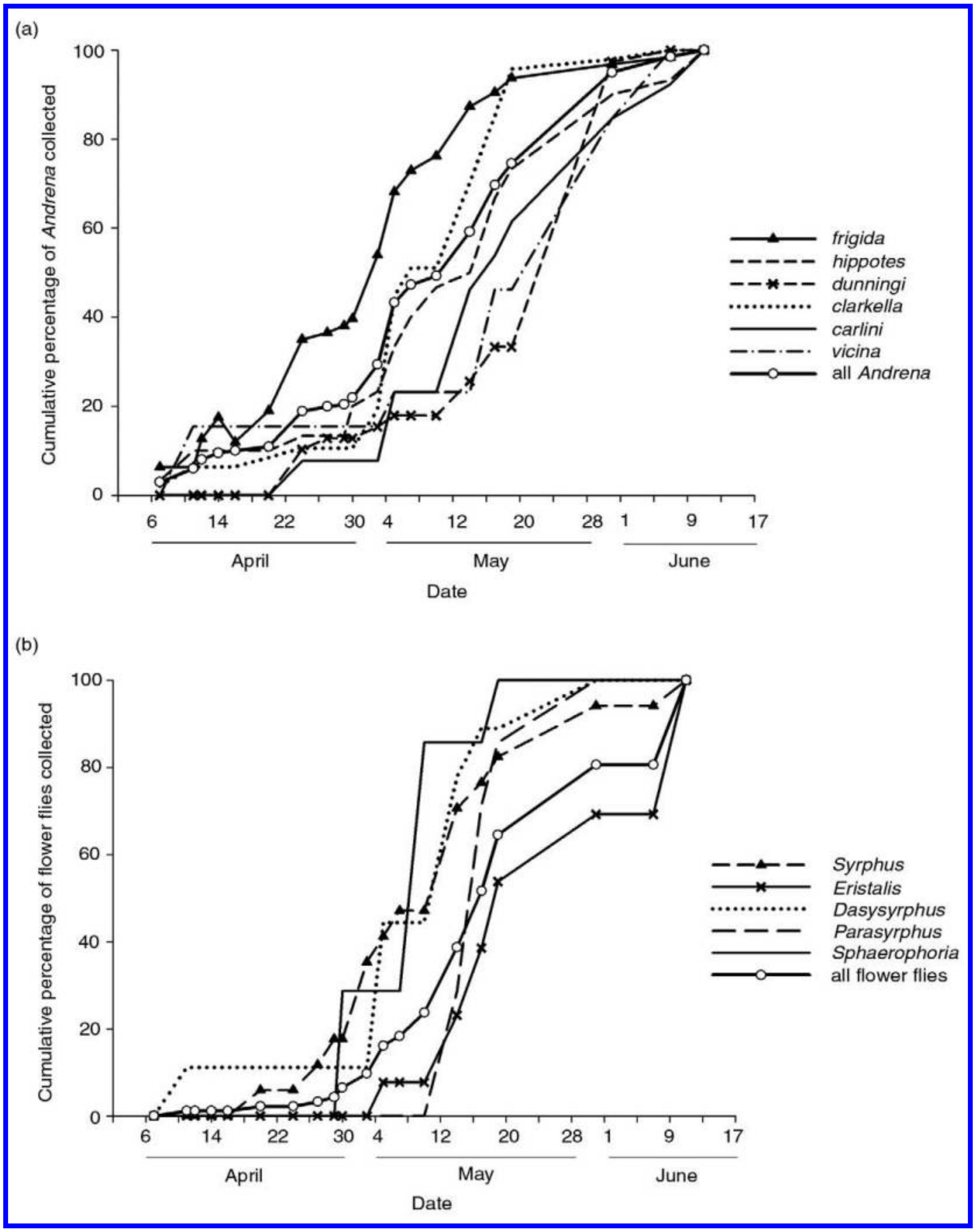

Fig. 2. Cumulative percentage of andrenids (a) and flower flies (b) collected in 2010 from seven native North American willow species in a common garden established in Fredericton, New Brunswick, Canada.

bloom, in the absence of workers of eusocial Halictinae and *Bombus*, which are numerically dominant at floral resources during the summer and autumn (Ginsberg 1983). Large *Andrena* with a preference for Rosaceae, including species of the subgenera *Melandrena, Trachandrena, and Tylandrena*, are efficient and locally abundant pollinators of apples (Schrader and LaBerge 1978; Schreck and Schedl 1979), pears (e.g., Miura 1982), and other tree fruits, especially during periods of adverse weather when honey bee activity is reduced (Boyle-Makowski 1987; Jacob-Remacle 1989). *Andrena* species can be better pollinators than the honeybees as they carry more pollen and more fruit pollen and are present during peak blossom. Their range of activity is slightly narrower than that of the honeybees, but their numbers do not fluctuate with changing weather conditions, and they may suffer less from competition with honey bees than do bumble bee populations (Boyle-Makowski 1987).

Table 4. Andrenidae and Syrphidae collected from male and female flowers of seven native North American willow species observed as 2-yr-old (2010) plants established in a common garden in Fredericton, New Brunswick, Canada

	discolor		*eriocephala*		*humilis*		*Salix* spp. *bebbiana*		*nigra*		*amygdaloides*		*interior*	
Insect	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
Andrenidae														
Andrena frigida	6	6	7	25	1	2	3	0	1	1	0	1	1	6
A. clarkella	1	2	8	13	1	1	2	0	0	0	1	9	5	3
A. dunningi	0	1	1	3	1	0	0	1	1	17	0	4	1	9
A. hippotes	3	0	0	7	1	0	2	1	1	4	0	2	2	6
A. vicina	0	0	0	2	0	0	1	1	0	3	0	1	0	4
A. algida	1	0	1	2	0	1	0	1	0	0	0	1	0	0
A. carlini	1	1	0	2	0	0	0	0	0	1	0	1	1	3
A. crataegi	0	0	0	0	0	0	0	0	0	3	0	0	0	2
A. cressonii	0	0	1	0	0	0	0	0	0	0	0	0	2	1
Total	12	10	18	54	4	4	8	4	3	29	1	19	12	34
Syrphidae														
Syrphus ribesii	0	0	0	0	1	0	0	0	0	1	0	0	0	2
S. vitripennis	0	1	1	1	1	0	0	1	0	0	0	2	0	2
S. torvus	0	0	0	0	0	0	0	0	0	0	0	1	0	1
Eristalis dimidiata	0	0	0	1	0	0	0	0	0	0	0	1	1	5
E. flavipes	0	0	0	0	0	0	1	0	0	0	0	3	0	0
Dasysyrphus laticaudus	0	0	1	2	0	0	1	0	0	0	0	0	0	4
Sphaerophoria scripta	1	1	0	0	0	0	0	0	0	0	0	2	0	0
S. contigua	2	1	0	1	1	0	0	0	0	0	0	0	0	0
Parasyrphus genualis	0	0	0	0	0	0	0	0	0	1	0	0	1	3
P. semiinterruptus	0	0	0	0	0	0	0	0	0	0	0	0	0	2
P. nigritarsus	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Total	3	3	2	5	3	0	2	1	0	2	0	9	2	20

Our data on frequency of collecting *Andrena* species and flower flies suggest a preference for foraging on male vs. female willow flowers. Ultimately, this is likely because *Andrena*, like most bees, use pollen as the primary food for their offspring (Thorp 2000) and nearly all flower flies require protein-rich pollen to produce reproductive tissues and the carbohydrate-rich nectar to power flight and other activities (Holloway 1976; Gilbert 1981; Kevan and Baker 1983; Branquart and Hemptinne 2000; Larson et al. 2001). As both male and female willow flowers have nectaries (Argus, personal communication 2013), it is possible that male flowers supply the required nectar, and there may be no need to forage on female flowers. However, Williams and Tepedino (2003) found that all females of the solitary mason bee, *Osmia lignaria* Say (Megachilidae), divided their foraging effort between a rich nectar source, *Hydrophyllum capitatum* Douglas ex Benth (Hydrophyllaceae), and rich pollen sources such as *Salix exigua* Nutt., *S. lasiandra* Benth, and some *S. fragilis* L. Rezkova et al. (2012) confirmed the existence of distinctive pollen and nectar collecting days for *A. vaga* Panzer.

The proximate cues that *Andrena* spp. and flower flies use when foraging for pollen and nectar may be olfactory, visual, or both. Floral scents in several European willows have elicited a response in *Andrena*, with those of *Salix caprea* L., *S. cinerea* L., and *S. fragilis* shown to attract *Andrena vaga* (Dötterl et al. 2005; Füssel et al. 2007; Burger et al. 2013). Burger et al. (2013) identified an aromatic compound from willows that *A. vaga* could detect at even trace amounts and speculated that this compound could be used to locate plants from large distances. However, Tollsten and Knudsen (1992) and Füssel et al. (2007) found no difference in the scent between male and female flowers of *Salix*, suggesting that olfactory cues may not account for our observations of greater frequency of bees and flower flies on male vs. female flowers. Dobson (1987) suggested that experienced bees rely less on odors in general and more on visual cues than pollen or floral scents, whereas experienced males and females from the flower fly *Episyrphus balteatus* relied on olfactory rather than visual cues (Primante and Dötterl 2010). Kevan (1972) found pistillate catkins of *Salix arctica* Pall. were highly attractive to insects. In our study, ERI, one of the willow species most preferred by andrenids, also had the most prolific flower production and presented the strongest visual display of all the willows tested. Flower flies were more commonly found on two species of *Salix*, INT and ERI, with the most prolific flowering, suggesting a response to a visual rather than an olfactory cue.

Planting willows near fruit or berry crops may be an effective way to increase pollination and fruit production. The addition of *Salix*, with its rich source of pollen and nectar, could help build populations for pollination in subsequent years via increased fecundity. Kim (1997) found that progeny size of the leaf-cutter bee, *Megachile apicalis* was directly determined by food allocation by females, so that the larger the food mass the progeny received, the greater the eventual size of adults with larger females provisioning brood cells faster and attaining greater realized fecundity. However, the ability of females to influence offspring size through provisioning behavior may be disrupted by reduced resource availability, due to such factors as weather, or nesting habit and competition for nesting sites (Rouston and Cane 2000). In many pollinator-dependant agroecosystems, such as lowbush blueberry (*Vaccinium angustifolium* Aiton) and apple (*Malus domestica* Borkh.), early season foraging opportunities for bees are often limited (S. K. Javorek, unpublished data; Stubbs et al. 1992). The provision of *Salix* species in these landscapes not only provides an important vernal food source but encourages nest initiation proximal to crops, enhancing native pollinator availability when flowering commences. Over 70% of the 79 species recognized as pollinators of lowbush blueberry and/or apple in Atlantic Canada also visit willow, further emphasizing the value of willows as alternative forage in these agroecosystems (Boulanger et al. 1967; Stubbs et al. 1992; Javorek et al. 2002; Sheffield et al. 2003). Prolific, early flowering species, such as ERI, planted near crops may attract and keep early flying *Andrena* bees in the vicinity and provide the food resources necessary to enhance their populations. When flowering is complete, the andrenids would be able to switch their activity to nearby, later-blooming fruit crops of interest, e.g., lowbush blueberry or apples. Both oligolectic and polylectic *Andrena* use low-bush blueberry as a major pollen source and have been shown to have the highest average pollination percentage of pollen-harvesting bees (95%), along with *Bombus* spp., which are limited in number in spring when only queens are present (Javorek et al. 2002). *Andrena* spp. were the most effective bees in depositing pollen per single visit (Javorek et al. 2002). Of the 17 *Andrena* species collected, all but *A. dunningi*, *A. persimulata* Viereck, and *A. bisalicis*, are known to visit blueberry in Maine, Quebec, New Brunswick, and Nova Scotia (Boulanger et al. 1967; Sheffield et al. 2003; S. K. Javorek, unpublished data). The mean cessation of flowering of five (HUM, DIS, BEB, AMY and ERI) of the seven willow in our study (Fig. 1) would have occurred before the onset of bloom in lowbush blueberry, which begins flowering toward the end of May (Bell and Burchill 1955). Therefore, these willows would be attractive candidates for planting to attract native bee pollinators to improve pollinator numbers at blueberry operations, as the willows would not compete with the crop for pollinators. Studies showing the oligolectic habit of some *Andrena* (see references above) suggest that when there was an overlap of flowering of willow and lowbush blueberry, andrenids would prefer willow to lowbush blueberry. However it is not known what impact this would have on the behavior of andrenids and flower flies. *Salix eriocephala* was one of the most prolific flowering and preferred willows by the *Andrena* and flower flies collected in our study. Among the seven willows studied, only INT would be in direct competition with lowbush blueberry for pollinators due to extensive overlap in bloom periods. In addition to visiting lowbush blueberry, 10 of the *Andrena* species collected in our study (*A. vicina*, *A. carlini*, *A. crataegi*, *A. cressonii*, *A. bradleyi* Viereck, *A. milwaukeensis* Graenicher, *A. miserablis* Cresson, *A. rugosa* Robertson, *A. sigmundi* Cockerell and *A. rufosignata* Cockerell) have been shown to also visit apple (Sheffield et al. 2003). Even though the two most commonly collected *Andrena* species, *A. frigida* and *A. clarkella*, are known to be oligolectic on willows (LaBerge 1980), they will visit lowbush blueberry if willows are not available (Stubbs et al. 1992; Javorek et al. 2002). *Andrena bradleyi*, a specialist on blueberry, visits willow (LaBerge 1980). *Andrena carlini* and *A. vicina*, two of the dominant native bee species observed visiting blueberry flowers in a study by Tuell et al. (2009), and found foraging on willows in our study, are largely polylectic. Planting willow species that cease flowering near the onset of flowering of lowbush blueberry may force bee associates to shift foraging to the berry crop, thereby increasing pollination. Despite being one of the more common species collected and being an early emerging pollinator that foraged throughout the flowering period of all species of willow (April to June), *A. dunningi* is not known to visit lowbush blueberry but has been found on apple (Sheffield et al. 2003).

Our study indicates that willow species flowering before the start of flowering of local agricultural crops could be planted on adjacent land to promote and enhance wild pollinator populations. This strategy could provide a consistent source of pollen and nectar at the beginning of the growing season when bees are establishing their nests, but crops are not yet flowering. This approach can potentially support a broader, more diverse, and more numerous assemblage of insects to pollinate local crops. Willows may be ideal for this purpose as they have the advantage of being easily and cost-effectively propagated via unrooted stem cuttings. Moreover, willows have a dioecious breeding system that can be exploited to prevent unwanted expansion of willows into crop fields through preferential planting of only male (or female) plants. Given that male willows, which were generally preferred over female willows in our study, provide both pollen and nectar for foraging native bees and flower flies, the lack of female plants in the area may not adversely affect native bee pollinator assemblages. With the multitude of problems currently facing honey bees, native willows could be used to support the diversity and abundance of wild pollinator populations and enhance pollination and associated fruit and seed set in many agricultural crops.

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