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Weather and landscape influences on pollinator visitation of flowering winter oilseeds (field pennycress and winter camelina)

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Keywords

Camelina sativa, early-season forage, nectar, pollen, Thlaspi arvense

Disciplines

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Weather and landscape influences on pollinator visitation of flowering winter oilseeds (field pennycress and winter camelina)

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Abstract
Flowers of field pennycress (*Thlaspi arvsense* L.) and winter camelina (*Camelina sativa* (L.) Crantz.) produce abundant pollen and nectar in early spring and thereby may be valuable for pollinators. Insects observed in field plots of these flowers were classified into seven easily identifiable groups (bumblebee, honeybee, solitary bee, butterfly/moth, beetle, fly and other) and monitored for 2 years at three sites in the Upper Midwest region of the USA. Average seasonal observations across years and sites varied from 1.6 to 5.3 total insects/min for field pennycress and 1.4 to 4.5 insects/min for winter camelina. Lowest visitation rates occurred in central Iowa and highest rates in south-eastern Minnesota for both crops. Multiple regressions showed that visitation rates for specific insect groups were correlated poorly but significantly ($p < .10$) with select variables. For example, in field pennycress, visitation by combined bumblebees and honeybees (Apidae) increased with greater air temperature at sampling time and annual site precipitation, whereas fly (Diptera) visitation was related to sampling date and flower cover. Similarly, in winter camelina, solitary bees were linked to increasing air temperature at sampling time and annual site precipitation, whereas flies were correlated with wind speed and flower cover at sampling. Field pennycress and winter camelina are reliably attractive to beneficial pollinating insects across a wide geographic region, but visitation rates and proportional representation of various insect groups depended on a range of site and weather characteristics.

KEYWORDS
Camelina sativa, early-season forage, nectar, pollen, *Thlaspi arvense*

1 | INTRODUCTION

Forage availability and quality are important factors within landscapes that determine the health and abundance of pollinating insects (Hellerstein et al., 2017; Roulston & Goodell, 2010; Smart et al., 2019). Moreover, land use is associated with forage availability and quality, and it thereby determines the suitability of landscapes for pollinators (Hellerstein et al., 2017; Stanley & Stout, 2013). Nowhere in the USA has landscape suitability for pollinators declined more in recent years than in the Upper Midwest and Northern Great Plains (Hellerstein et al., 2017) which, ironically, are major sources in the nation for honey production and transient honeybees (*Apis mellifera* L.) used for pollination of high-value crops in California and elsewhere (Smart et al., 2019). In this region, crops such as soybean (*Glycine max* (L.) Merr.) and maize (*Zea mays* L.) have increased in spatial extent replacing more diverse perennial vegetation previously grown in the Conservation Reserve Program as well as in pasture and rangeland (Hellerstein et al., 2017).

Soybean, corn and spring wheat (*Triticum aestivum* L.) are the staple crops of the Upper Midwest and Northern Great Plains, and none of them is considered a desirable forage for pollinators. Farmers are unlikely to replace these summer-growing crops willingly with alternative and pollinator-friendly crops such as spring canola (*Brassica napus* L.) and sunflower (*Helianthus annuus* L.). Understandably, reticence likely is due to differential profitability of the staple crops compared with the alternatives. Accordingly, enabling farmers to sow crops valuable both to pollinators and farm economics while simultaneously retaining acreages of their staple crops may result in mutually beneficial outcomes for pollinators and farmers, as well as generally for the agroecosystems of the Upper Midwest and Northern Great Plains. Winter-hardy cover crops, which can be double-cropped with traditional summer crops, and whose flowers appear in early spring and produce seeds enriched with beneficial oils in late spring, may be valuable new resources for both farmers and pollinators.

Field pennycress and winter camelina (hereafter simply pennycress and camelina) are potential autumn-sown winter annual crops for the Upper Midwest, a region where only summer crops traditionally are grown. The oil-rich seeds of these mustard-type plants (Brassicaceae) can be harvested in June, and short-season summer crops can be sown immediately after cover crop harvest (i.e. sequential double-cropping) (Gesch & Archer, 2013). Alternatively, longer-season summer crops can be relay-sown into the cover crops as they begin bolting in April and May (i.e. relay double-cropping) (Berti et al., 2015; Gesch et al., 2014; Johnson et al., 2017). Sequential- and relay-cropping systems can lead to greater net returns for growers as well as enhanced ecosystem services (Berti et al., 2017). One such ecosystem service is early-season forage availability for pollinating insects.

Although pennycress and camelina are primarily self-pollinated (Walsh et al., 2012; Sedbrook et al., 2014; Vollmann and Eynck, 2015), flowers of both species are visited frequently by insects (Eberle et al., 2015; Groeneveld & Klein, 2013; Rizzitello, 2016). Anthesis of autumn-sown pennycress and camelina is as early as late April in the Upper Midwest (Walia et al., 2018). Flowering of no other crops in this region is so early; even winter canola (*Brassica napus* L.), which lacks sufficient hardiness to be grown commercially in the region, begins flowering much later than pennycress and camelina (Eberle et al., 2015). Consequently, native and domesticated insects that emerge from over-winter nests or commercial beehives in April through June near fields of pennycress or camelina have access to copious supplies of nectar (sugar equivalent of 50–100 kg/ha) and pollen (protein equivalent of about 10 kg/ha) from these mass-flowering crops (Eberle et al., 2015; Thom et al., 2018).

The studies by Eberle et al. (2015) and Thom et al. (2018) were performed in eastern South Dakota and adjacent western Minnesota. No other information is available about pollinators on camelina and pennycress from the Upper Midwest and Northern Great Plains, including relationships between pollinator visitation and site-specific landscape, weather, and climatic variables. Thus, the objectives of our study were to (a) monitor pollinator insect visitation to field pennycress and winter camelina across a range of environments in the Upper Midwest, and (b) to explore whether climatic and/or landscape variables affect visitation through multiple regression of visitation with these variables.

2 | METHODS AND MATERIALS

2.1 | Study locations

Three experimental sites were chosen to represent geographic (north to south) and environmental (cold-dry to warm-wet) gradients within the Upper Midwestern portion of the U.S. Corn Belt. These sites (latitude and longitude) were Morris, MN (45.68, −95.80) in both 2017 and 2018; Waseca, MN (44.07, −93.52) in 2017; Rosemount, MN (44.71, −93.07) in 2018; and Ames, IA (42.00, −93.73) in both 2017 and 2018. The sites chosen for the study differ for mean annual temperature and precipitation. Average annual air temperatures and total precipitation for these sites are as follows: 5.8°C and 673 mm (Morris), 7.1°C and 908 mm (Waseca), 6.9°C and 887 mm (Rosemount), and 9.7°C and 910 mm (Ames). All sites were within established research farms belonging to Iowa State University (Ames), the University of Minnesota (Rosemount and Waseca) or USDA-ARS (Morris).

Soils at all sites were loams, and in these soils, both pennycress (variety 'MN106') and camelina (variety 'Joelle') were sown at 12 kg seed/ha in September of 2016 and/or 2017. Seeds were drilled 1-cm deep in 15-cm rows in Minnesota but broadcasted and incorporated to 1-cm depth in Iowa. Plots were 3.1 by 10.0 m and distributed in a randomized complete block design with four replications for each crop. Plots were fertilized in spring with the equivalent of 70-30-30-6 kg/ha of N-P-K-S. Although the entire experiment at each site was contained within an area of about 0.1 ha, these areas at all sites were within larger fields (>10 ha) and at least 100 m from the nearest woodland, grassland, or pasture. However, all plots were within 25 m of narrow and unpaved road verges in which perennial grass-dominated vegetation was mown regularly. Road verges can be used as nesting sites for some pollinating insects (Phillips et al., 2020).

2.2 | Sampling

Once anthesis commenced, plots were scouted every 1 to 5 days at times amenable to insect visitation. Methodology followed that of Eberle et al. (2015) and Thom et al. (2018). Scouting criteria typically involved air temperatures >15°C, wind speeds <20 km/h, and time periods between 10:00 and 16:00 hr. Cover of open flowers was estimated visually in each plot as a percentage of the ground surface area. While walking slowly along the borders of each plot, observers counted the number of bumblebees (*Bombus* spp.), honeybees, small bees (solitary bees, primarily Andrenidae and Halictidae), butterflies/moths (Lepidoptera), beetles (Coleoptera), flies and 'other' insects visiting flowers over a one-minute period. Each plot was examined 3 to 9 times over the course of anthesis. During each examination, time of day, wind speed and air temperature were recorded, and sky clarity was assessed as one of four broad categories: overcast, mostly cloudy, partly cloudy and clear (ca. 0%–15%, 16%–50%, 51%–85% and 90%–100% sky clarity, respectively).

2.3 | Statistical evaluation

Multiple regression was used to examine visitation by each of the seven categories of insects, as well as groups of insects. These groups were named Apidae (=honeybees + bumblebees), Hymenoptera (=Apidae + solitary bees) and total insects. Of the many factors that possibly influenced visitation at the time observations were made, seven were analysed: sampling date (days after 31 December each year), sampling time (hours after midnight each day), sky clarity (0%, 33%, 66% and 100% for overcast, partly cloudy, mostly cloudy and clear, respectively), wind speed (km/h), air temperature (°C), flower cover (%) and year (2017 or 2018). Statistix 9.0 software was employed for these analyses. Probability levels >.10 were considered non-significant; this level was chosen because of the inherent variability of pollinator populations in early spring.

Lastly, aerial images of all sites were accessed from the Google Earth website in late 2018. Such images also were accessed for pollinator study sites of camelina in the eastern USA (Storrs, Connecticut; Rizzitello, 2016) and of camelina and pennycress in Western Europe (Neureid, Germany; Groeneveld & Klein, 2013). The landscape within a 1 km radius of each site was categorized broadly as water bodies, buildings, roads, woodland and farmland (crop + pasture). Greater specificity was not possible. Category proportions were calculated using ArcGIS 10.6 (Environmental Systems Research Institute) software. Finally, proportional landscape categories were regressed against proportional insect categories to ascertain possible relationships among landscape types and insect visitors. The 1 km radius represented the foraging limit of many solitary bees (Gathmann & Tscharntke, 2002).

3 | RESULTS

3.1 | Flower cover and insect visitation

Pennycress flowered slightly earlier than camelina during most site-years (Figure 1a,b), and accordingly, it attracted insects earlier than camelina (Figure 1c,d). Similarly, flowering commenced earliest in Ames, then in Waseca/Rosemount, and last in Morris, which followed the expected climatic gradient among the sites.

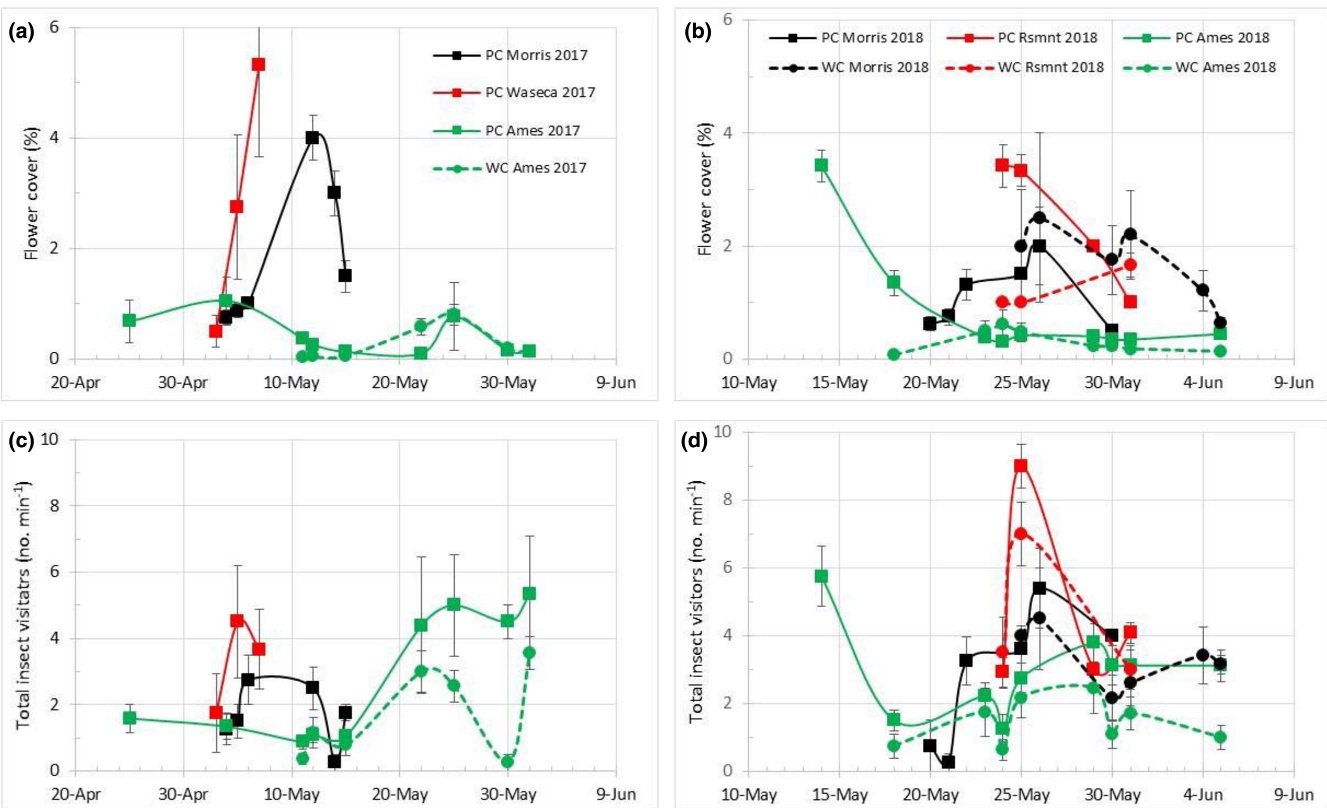

FIGURE 1 Flower cover for 2017 (A) and 2018 (B) and total insect visitation for 2017 (C) and 2018 (D) of pennycress (PC; squares, solid lines) and winter camelina (WC; circles, broken lines) at three sites in 2017 (Morris MN, Waseca MN and Ames IA) and 2018 (Morris MN, Rosemount MN and Ames IA). Standard errors represented by vertical bars

Over the course of anthesis, estimated per cent ground cover by open flowers of pennycress was as high as 5–6% in Morris and Waseca in 2017, but only 1% in Ames. However, flowering in Ames persisted for longer than at the more northern sites. Persistence of pennycress flowering in Ames during 2017 probably reflected autumn germination plus delayed germination in spring of previously dormant seeds and, hence, an extended and bimodal flowering pattern. Pennycress seed dormancy represents a wild trait in this new crop (Dorn et al., 2015). In both Morris and Waseca, camelina failed to form stands in 2017 that were sufficiently dense to record data on flower cover and insect visitation.

High levels of insect visitation tended to occur when flower cover reached its maximum in 2017 (Figure 1), but the relationship was not absolute. Maximum visitation rates ranged from 3 to 5 total insects/min (per 31 m^2 plot area) across sites. In Ames, appreciably more insects visited pennycress flowers in late May than earlier despite low coverage of flowers on some of these later dates, which probably reflected abundant emergence of insects in late May compared with earlier time periods.

Proportional representations of the different insect groups are shown in Table 1. Beetles, flies and solitary bees were the most common groups observed. These three taxa, plus the Apidae (=bumblebees + honeybees), are emphasized below. The percentage of total observed insects represented by beetles, flies, solitary bees and Apidae on pennycress in 2017 was 23%, 32%, 32% and 0%, respectively in Morris; 8%, 83%, 0% and 8% in Waseca; and 15%, 61%, 21% and 0% in Ames. For camelina in Ames, these values were 9%, 36%, 50% and 1%.

In 2018, flowering of pennycress commenced two to three weeks later than in 2017 (Figure 1a,b). Flower cover of pennycress reached 2.0%–3.5% at all sites. Camelina established and flowered successfully at all sites in 2018, reaching about 2% cover in Morris and Rosemount, but <1% cover in Ames. Anthesis of camelina typically commenced 1–2 weeks later than that of pennycress in both 2017 and 2018, as was observed by Eberle et al. (2015).

Insect visitation to flowers of pennycress and camelina in 2018 was similar to that in 2017, with highest rates for pennycress between 5 and 9 insects/min (per 31 m^2 plot area) and that for camelina between 3 and 7 min^{-1} (Figure 1). Beetles, flies, solitary bees and Apidae (Table 2) represented 18, 45, 15 and 0% (Morris); 5%, 65%, 11% and 3% (Rosemount); and 10%, 54%, 26% and <1% (Ames) of total insect visitors in pennycress. Analogous values for camelina were 1%, 29%, 11% and 7% (Morris); 5%, 37%, 0% and 4% (Rosemount); and 3%, 40%, 41% and 4% (Ames). As in 2017 beetles were observed frequently, flies (especially Syrphidae) were common pollinators for both crops; solitary bees usually had significant representation; and Apidae were scarce, especially for pennycress (i.e. transient honeybees had not yet returned to the region).

When averaged across seasons visitation rates for total insects were highest for south-eastern Minnesota (Waseca and Rosemount) and approximately equal in Iowa (Ames) and western Minnesota (Morris) in both years for pennycress, but higher in Morris than Ames for camelina (Tables 1 and 2). Air temperatures and wind speeds during observations of visitation were relatively uniform across sites.

3.2 | Variables associated with insect visitation in the Upper Midwest

Multiple regressions of insect visitation with nine site and sampling variables revealed relatively few significant associations (Table 3). Only significant regressions will be discussed. For pennycress,

TABLE 1 Average seasonal flower cover, flower-visiting insect abundances (in 31 m^2 plots) of eight insect categories, and air temperature and wind speed over the course of anthesis of field pennycress at three sites and winter camelina at one site in 2017

	Pennycress			Camelina
Variable	Morris MN	Waseca MN	Ames IA	Ames IA
% ground surface area				
Flower cover	1.85 (0.27)	2.64 (0.85)	0.41 (0.08)	0.19 (0.04)
No. observed min^{-1}				
Honeybees	0.00	0.27 (0.14)	0.00	0.02 (0.01)
Bumblebees	0.00	0.00	0.00	0.00
Solitary bees	0.54 (0.16)	0.00	0.32 (0.06)	0.69 (0.12)
Flies	0.54 (0.12)	2.73 (0.68)	0.95 (0.15)	0.50 (0.09)
Butterflies	0.00	0.00	0.00	0.00
Beetles	0.39 (0.13)	0.27 (0.20)	0.23 (0.04)	0.13 (0.04)
Other insects	0.21 (0.10)	0.00	0.05 (0.02)	0.04 (0.02)
Total insects	1.67 (0.25)	3.27 (0.83)	1.55 (0.18)	1.39 (0.19)
°C				
Air temperature	21.1 (0.33)	21.2 (0.68)	21.3 (0.27)	21.6 (0.23)
km/h				
Wind speed	25.0 (1.53)	20.1 (2.31)	15.5 (0.05)	15.9 (0.50)

Note: Values in parentheses are standard errors of the means.

TABLE 2 Average seasonal flower cover, flower-visiting insect abundances (in 31 m^2 plots) of eight insect categories, and air temperature and wind speed over the course of anthesis of field pennycress and winter camelina at three sites in 2018

	Pennycress			Camelina		
Variable	Morris MN	Rosemount	Ames IA	Morris MN	Rosemount	Ames IA
% ground surface area						
Flower cover	1.26 (0.19)	2.57 (0.24)	0.68 (0.06)	1.50 (0.24)	1.22 (0.10)	0.30 (0.05)
No. observed/min						
Honeybees	0.00	0.11 (0.05)	0.01 (0.01)	0.17 (0.09)	0.11 (0.08)	0.06 (0.02)
Bumblebees	0.00	0.03 (0.03)	0.00	0.03 (0.03)	0.06 (0.06)	0.00
Solitary bees	0.44 (0.15)	0.57 (0.13)	0.73 (0.07)	0.34 (0.11)	0.00	0.60 (0.09)
Flies	1.23 (0.25)	3.41 (0.49)	1.52 (0.13)	0.90 (0.17)	1.67 (0.28)	0.59 (0.09)
Butterflies	0.00	0.03 (0.03)	0.03 (0.01)	0.03 (0.03)	0.00	0.02 (0.01)
Beetles	0.52 (0.22)	0.27 (0.09)	0.28 (0.04)	0.03 (0.03)	0.22 (0.13)	0.05 (0.02)
Other insects	0.63 (0.16)	0.86 (0.18)	0.32 (0.04)	1.55 (0.22)	2.44 (0.54)	0.15 (0.03)
Total insects	2.93 (0.47)	5.27 (0.51)	2.84 (0.18)	3.07 (0.30)	4.50 (0.64)	1.47 (0.19)
°C						
Air temperature	21.4 (0.76)	24.8 (0.22)	27.7 (0.17)	24.0 (0.51)	24.8 (0.32)	27.8 (0.18)
km/h						
Wind speed	17.7 (0.84)	8.2 (0)	17.3 (0.33)	15.3 (1.06)	8.2 (0)	17.4 (0.36)

Note: Values in parentheses are standard errors of the means.

significant regressions occurred for visitation by total, Apidae, fly and 'other' insect categories. Total visitation was affected positively by sampling date and flower cover. Apidae visitations were associated negatively with air temperatures during observation periods and positively associated with annual site precipitation. Fly visitation was related positively to time of day and flower cover. Lastly, visitation by the 'other' insect category was influenced only by year, with more of these insects observed in 2018 than 2017.

For camelina flowers, significant regressions occurred for visitation by total, solitary bee, fly and 'other' categories of insects. Total insect visitors were affected by wind speed, with fewer insects on windier days. Solitary bees were influenced positively by both temperature during observations and flower cover, and negatively by annual site precipitation. Flies were affected negatively by wind speed and positively by flower cover. The 'other' insect category was influenced negatively by temperature during observations and positively by annual site precipitation.

3.3 | Landscape features and proportional representation of pollinators

Landscape variables (Table 4), including their combinations, had limited effects on the proportions of total insects visiting flowers. For pennycress, no single variable was correlated significantly with the proportions of any insect group. For camelina, however, the proportion of solitary bee visitors increased as the proportion of the landscape occupied by roads increased ($r^2 = .44$, $p < .1$). Apidae on camelina increased as land area occupied by buildings increased ($r^2 = .59$, $p < .1$). The former correlation likely reflects the extent of road verges with open but undisturbed land amenable to ground-nesting solitary bees. The latter correlation may be associated with farm habitation, including gardens and flowerbeds (i.e. nesting sites), and possibly proximity to apiaries.

4 | DISCUSSION

Eberle et al. (2015) studied pollinator visitation to pennycress and camelina during anthesis at two locations (western Minnesota and eastern South Dakota) that have similar climates, with mean annual air temperatures and precipitation levels of 5.8 and 6.2°C, and 673 and 617 mm, respectively. Displays of pennycress flowers attracted, on average, 49 insects during one-minute plot (112 m^2) surveys, whereas camelina flowers attracted 37 insects/min. Pennycress flowering occurred somewhat earlier than that of camelina, and therefore, most of its pollinators (73%) were early-emerging flies, including abundant Syrphidae (hoverflies), whereas only 7% were solitary bees, 2% beetles and 1% Apidae (honeybees plus bumblebees). In contrast, 38% of the insects attracted to camelina flowers were flies, 28% solitary bees, 1% beetles and 4% Apidae. For comparison, 41% of insects visiting winter canola flowers were flies, 29% solitary bees and 6% Apidae.

The only other surveys of pollinator visitation to pennycress and/or camelina are from sites near Neureid in southern Germany (Groeneveld & Klein, 2013) and Storrs, Connecticut, in the eastern USA (Rizzitello, 2016). However, at both sites, the crops were sown in spring rather than autumn. In Germany, both crops flowered in August, whereas in Connecticut camelina flowered in mid-June. At these sites, the mean annual air temperatures and

TABLE 3 Attributable variability (r^2) and statistical probability (p) of significant effects on insect visitation to flowers of pennycress and winter camelina of nine predictor variables in multiple regressions

	Honeybee	Bumblebee	Apidae	Solitary bee	Fly	Butterfly	Beetle	Other	Total
Pennycress	r^2, *p* and direction (+ or −)								
r^2	.37	.26	**.40**	.38	**.43**	.31	.29	**.61**	**.43**
Overall	.12	.43	**.08**	.11	**.05**	.25	.32	**.01**	**.05**
Year	.95	.61	.98	.67	.41	.21	.52	**.02+**	.54
Date	.84	.55	.81	.49	**.01+**	.44	.11	.44	**.01+**
Time of day	.97	.62	.99	.42	.74	.18	.37	.22	.69
Sky clarity	.20	.40	.17	.99	.87	.96	.95	.58	.69
Wind speed	.79	.32	.85	.32	.88	.76	.96	.19	.75
Temperature	**.01−**	**.03−**	**.01−**	**.01+**	.93	.30	.58	.74	.79
T yearly	.92	.59	.89	.46	.14	.58	**.10+**	.48	.52
PPT yearly	**.01+**	**.02+**	**.01+**	**.02−**	.20	.85	.30	.93	.31
Flower cover	.41	.14	.35	.14	**.02+**	.63	.38	.34	**.05+**
Camelina									
r^2	.39	.47	.36	**.67**	**.63**	.37	.32	**.78**	**.67**
Overall	.46	.28	.56	**.03**	**.05**	.55	.67	**.01**	**.03**
Year	.98	.49	.81	.21	.46	.23	.44	.99	.86
Date	**.05+**	.37	**.08+**	.61	.47	.23	.82	.47	.75
Time of day	.79	.49	.67	.76	.73	.59	.60	.61	.82
Sky clarity	.73	.55	.65	.80	.71	.32	.42	.70	.49
Wind speed	.67	.24	.95	.14	**.01−**	.83	.17	.85	**.06−**
Temperature	.61	.16	.40	**.01+**	.51	.89	.78	**.01−**	.45
T yearly	.81	.63	.98	.52	.28	.18	.76	.78	.88
PPT yearly	.90	**.06+**	.46	**.03−**	.63	.48	.87	**.03+**	.35
Flower cover	.58	.17	.97	**.01+**	**.04+**	.25	.36	.13	.19

Note: Predictor variables are as follows: year of study; sampling date; time of day, sky clarity, wind speed, and air temperature during observations (Temperature); yearly average site temperature (T yearly); yearly average site precipitation (PPT yearly); and flower cover. Direction refers to positive (+) or negative (−) effects of predictor variables with *p* values ≤.10, all of which are in bold typeface.

precipitation levels are 8.0°C and 944 mm in Germany and 9.4°C and 1,264 mm in Connecticut. Thus, compared with Minnesota and South Dakota, both the German and Connecticut sites were much warmer and wetter, but similar to the Iowa site in the current study.

Average numbers of observed pollinators/min at the German site were 0.6 for pennycress and 0.8 for camelina. These values are only a small percentage of what was observed in Minnesota and South Dakota by Eberle et al. (2015), about 20% of what was observed at the Minnesota sites examined in this study, but about 50% of the values at the Iowa site (Tables 1 and 2). (Visitation frequency was not measured at the site in Connecticut.) Interestingly, the colder and drier sites appear to support more intense visitation for pennycress and camelina than the warmer and wetter sites.

Proportionally, beetles, flies, solitary bees and Apidae at the German site represented 3%, 18%, 65% and 0% of pennycress insects; and 1%, 11%, 25% and 45% of camelina insects, respectively. Thus, appreciable differences existed between the two crops in Germany in terms of insect taxa, as well as between the German and North American sites in terms of visitation frequencies. Although visitation frequency was not measured at the Connecticut site, proportional representation of insect groups could be calculated, where beetles, flies, solitary bees and Apidae represented 0–1, 45%–51%, 12%–22% and 32%–36%, respectively, of the pollinator fauna on camelina. Representation by flies in Connecticut was similar to that in the Midwestern states, but much higher than that in Germany. The proportion of solitary bees was similar among all sites, as was the proportion of beetles. However, the contributions of Apidae to the pollinator fauna were considerably greater in Germany and Connecticut than in the Midwest, including Iowa. Absence of honeybees in the Midwest could have resulted from their transient lifestyle: that is, commercial beehives reside on the Gulf and West Coasts during autumn through late spring, and only return to the Upper Midwest in late spring and summer. (Feral honeybees are rare in this region.)

Despite flowering in August when Apidae are expected to be abundant, pennycress in Germany attracted none of these insects, whereas 45% of insect visitors to flowers of camelina were

TABLE 4 Percentage of landscape types at each of seven research sites where insect visitors to flowers of winter pennycress and/or camelina were recorded

Research site	Water bodies	Buildings	Roads	Woodland	Farmland
% of landscape type					
Ames, IA	0.0	0.7	1.7	0.8	96.2
Brookings, *SD*	0.2	2.0	1.8	3.5	92.5
Dundenheim, Germany	0.0	13.8	1.9	1.8	82.5
Morris, MN	24.2	5.0	0.8	5.0	70.0
Rosemount, MN	0.0	1.5	0.3	17.5	80.7
Storrs, CT	0.4	6.2	1.9	81.0	10.6
Waseca, MN	2.4	3.9	1.6	0.0	92.1

Abbreviations: CT, Connecticut; IA, Iowa; MN, Minnesota; *SD*, South Dakota.

honeybees (no bumblebees were observed at the German site). This suggests that the cause of low values for Apidae (2%) on pennycress in Minnesota and Iowa may not be due solely to very early flowering in spring as initially suspected, but the inherent features of pennycress flowers instead. Camelina flowering in Connecticut had high proportions of Apidae, 32%–36% of insect visitors, which was similar to the situation in Germany. In contrast, for camelina in Minnesota and Iowa, which flowered in May, values of Apidae (4%) were four times higher than those for pennycress (1%), but still very modest compared with analogous values for Connecticut and Germany. Thus, honeybee transience may still be the most robust explanation for low values of Apidae on camelina in the Upper Midwest. Importantly, new breeding efforts for pennycress may result in larger, more nectar-rich, earlier blooming flowers and other traits, which may attract Apidae to new pennycress varieties in the future (Chopra et al., 2020; Thomas et al., 2017).

Solitary bees averaged 15% of total insect visitors to pennycress flowers in Minnesota and Iowa, but 65% in Germany. Values for camelina were 16% in Minnesota and Iowa, 25% in Germany, and 12%–22% in Connecticut. The warmest site of those examined in Minnesota and Iowa (i.e. Ames) had the greatest average values for solitary bees (24% for pennycress and 45% for camelina) and mimicked the warm German site in this regard.

On average, 60% of insects on pennycress in Minnesota and Iowa were flies, whereas the analogous value for flies on pennycress in Germany was 18%. For camelina flowers, 35% of insects were flies in Minnesota and Iowa, only 11% were flies in Germany, and 45%–51% were flies in Connecticut. In this latter case, the Upper Midwest was more similar to Connecticut than to Germany. Fly visitation is especially interesting because many of the flies were syrphids. Larvae of several syrphid species are predatory and can behave as biological control agents for pests such as soybean aphid (*Aphis glycines* Matsumara) (Costamagna & Landis, 2016; Eckberg et al., 2015). Control of aphids would be a valuable symbiotic outcome in a system where camelina or pennycress are double-cropped with soybean. In contrast, some syrphids are herbivorous and could be deleterious (Grosskoph, 2005), although none are known to be so on camelina or pennycress.

For beetles, average proportional visitation was 11% on pennycress and 4% for camelina in the Minnesota and Iowa sites. Comparable values for Germany were 15% for pennycress and <1% for camelina. Thus, beetles appeared to have a greater affinity for pennycress than camelina at all of the sites where both cover crops were examined. In Connecticut, beetles represented 1% or less of insect visitors to camelina flowers, which coincides with the very low value for the German site.

In summary, a range of insect pollinators visit the flowers of field pennycress and winter camelina, and the more flowers present usually resulted in increased visitation. Of the many factors that regulate pollinator abundance, forage resource availability is the most important (Roulston & Goodell, 2010), especially availability early in the spring (Malfi et al., 2019). Thus, extensive plantings of pennycress and camelina may have important consequences for pollinator populations in cold but extensively cropped regions such as the Upper Midwest. Variation in pollinator visits could be attributed to weather variability for flies on pennycress and camelina and solitary bees on camelina. However, climatic factors that were statistically significant in regressions, such as annual precipitation, had disparate influences on pollinator visitations, for example positive for Apidiae, but negative for solitary bees. Nevertheless, if pennycress and camelina become common and profitable winter crops in relay systems with soybean and other summer-growing crops in the Upper Midwest, their flowers will represent significant early-season forage resources for native and managed pollinators alike. Solitary bees and flies, such as Syrphidae, were common visitors to both crops across a latitudinal gradient >2.5° (i.e. 42.00°–45.68°N). Solitary bees are vulnerable to diminished forage and nesting resources (Spivak et al., 2011), and syrphid fly larvae can be predators of crop pests such as soybean aphid (Costamagna & Landis, 2016). Thus, the wide-scale planting of these crops across the Upper Midwest may provide both direct and indirect ecosystem services.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

FF, AWL, RWG, MSW and MTB conceived research. FF, SP, AWL, CH, RWG and MSW conducted experiments. FF and SP analysed data and conducted statistical analyses. FF wrote the manuscript. AWL, RWG, MSW and MTB secured funding. All authors edited and approved the manuscript.

DATA AVAILABILITY STATEMENT

All data are available from the University Digital Conservancy and are downloadable from http://hdl.handle.net/11299/214095.

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