

**Entomological considerations for domestication of pennycress,
Thlaspi arvense, as a cash cover crop**

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BY

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Dedication

To my parents,

Dad and Mom, your unwavering support, endless encouragement, and boundless love have been the foundation of my journey. Your sacrifices, wisdom, and belief in me have been my guiding light. This thesis is a testament to your enduring faith in my dreams and aspirations. Thank you for being my pillars of strength and my greatest inspirations.

Abstract

Pennycress (*Thlaspi arvense* L.), a common annual weed in temperate regions, is being domesticated as a winter cover crop and oilseed crop for the Midwest U.S. corn-soybean rotation. This domestication presents significant agricultural and environmental benefits; however, understanding of the interactions between pennycress and insect herbivore communities and agroecosystems remains limited. This research aimed to fill these knowledge gaps and support the development of integrated pest management (IPM) programs for this emerging crop.

First, a comprehensive review was conducted to compile available information on the insect herbivores, natural enemies, and pollinators associated with pennycress, as well as its response to stressors such as defoliation, stem injury, and stand loss. The review highlighted the need for further research to develop effective IPM strategies.

Second, field experiments were conducted over two years to assess the impact of artificial defoliation on pennycress biomass, yield components, and oil and protein content. The experiments, which tested various defoliation levels and timings, revealed that significant reductions in biomass, yield and protein content occurred, particularly during critical growth stages such as the rosette and flowering periods. These findings emphasize the importance of timing in managing defoliation to minimize crop loss. Finally, field experiments were

performed to evaluate the impact of relay-cropping soybean with pennycress on soybean aphid populations. Across four site-years in Minnesota with relatively low levels of soybean aphid infestation, relay-cropping soybean with pennycress generally reduced soybean aphid densities compared to soybean without pennycress. This suggests that pennycress could serve as a sustainable pest management tool in soybean production, while also enhancing other aspects of economic and environmental sustainability of the corn-soybean rotation system.

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Chapter 1: Potential insect threats to pennycress, *Thlaspi arvense* (Brassicales: Brassicaceae), an emerging oilseed cover crop

Abstract

Pennycress (*Thlaspi arvense* L.) is an annual plant in temperate regions that often grows as a weed. Pennycress is being domesticated as a new winter cover crop and oilseed crop for incorporation in the Midwest U.S. corn-soybean rotation, where it could offer economic and environmental benefits. While pennycress is gaining attention as a promising new crop, there remains a significant gap in understanding its interaction with insect communities and agroecosystems. This review compiles available information on insect herbivores (potential pests), and beneficial insects associated with pennycress growing in the wild (natural areas) or as a weed in agricultural areas. The limited knowledge on the response of pennycress to stressors (defoliation, stem injury and stand loss) similar to injury that could be caused by insects is also compiled here. By shedding light on the insects associated with pennycress and how pennycress might respond to injury from insect pests, this review sets the stage for further research and development of integrated pest management (IPM) programs for insect pests of this new crop.

Introduction

Pennycress (*Thlaspi arvense* L. (Brassicales: Brassicaceae)) is native to Eurasia and is now found in Europe, Asia, North America, South America, Africa and Australia (Best and McIntyre 1975, Warwick et al. 2002). In the United States (US), pennycress was first documented in 1818 (Mitich 1996) and it has been problematic weed for multiple crops (Warwick et al. 2002).

Pennycress is being considered as a new oil seed crop and winter cover crop (Sedbrook et al. 2014). The oil content in pennycress varies between 26 to 39% of the seed weight (Cubins et al. 2019). Pennycress meal is a beneficial source of protein as seeds of pennycress have protein content ranging between 20–27% of the seed weight (Hojilla-Evangelista et al. 2013, Selling et al. 2013). Furthermore, pennycress is a desirable low-input winter cover crop with the potential to reduce soil erosion, take up excess nitrogen from the soil, and contribute to weed suppression (Evangelista et al. 2017, Cubins et al. 2019, Moore et al. 2020). In the Midwest US, pennycress would likely be incorporated into the cropping systems (e.g., corn-soybean rotations) through double- or relay-cropping. For example, pennycress would be planted after the harvest of corn or possibly interseeded with the corn prior to the harvest of the corn (Cubins et al. 2019, Mohammed et al. 2020, Moore et al. 2020). The pennycress crop would overwinter, and soybean would be relay cropped into the pennycress prior to pennycress harvest or double cropped after pennycress harvest (Johnson et al. 2017, Cubins et al. 2019, Cecchin et al. 2021).

Domestication of pennycress is advancing rapidly due to the availability of a diversity of pennycress genotypes and the sequenced genome and transcriptome of this plant (Sedbrook et al. 2014, Basnet and Ellison 2024). Pennycress seeds contain glucosinolates, primarily sinigrin, which provide protection against herbivores, but can adversely affect some end uses for pennycress meal. Therefore, efforts are underway to lower the glucosinolate levels in pennycress seeds (Vaughn et al. 2005, Chopra et al. 2019). Domestication of crops in the past has led to increased vulnerability to insect pests (Chen and Welter 2005). The domestication of pennycress is changing its chemical defenses, which may impact its vulnerability to insect herbivores (e.g., Chen et al. 2018). The effects of pennycress domestication on insect herbivores remains unknown.

While there have been significant efforts to improve the agronomics (e.g., planting, fertilizing and harvesting) of pennycress as a new crop (Cubins et al. 2019), there has been little focus on studying the potential insect pests that could affect this crop. Experience with related crops, such as canola and rapeseed (*Brassica napus* L. (Brassicales: Brassicaceae)) suggests that insect pests could pose considerable threats to pennycress production. A diverse community of insect pests can attack various parts of canola and rapeseed plants, including the roots, stems, leaves, flowers, seed pods and (Lamb 1989, Alford 2003, Williams 2010, Zheng et al. 2020). From a worldwide perspective, insect pests that are problematic to these crops on multiple continents include diamondback moth

(*Plutella xylostella* (L.) (Lepidoptera: Plutellidae)), aphids (Hemiptera: Aphididae), flea beetles (*Phyllotreta* spp. (Coleoptera: Chrysomelidae)), cabbage root fly (*Delia radicum* (L.) (Diptera: Anthomyiidae)), cabbage seedpod weevil (*Ceutorhynchus obstrictus* (Marsham) (Coleoptera: Curculionidae), cutworms (Lepidoptera: Noctuidae), wireworms (Coleoptera: Elateridae), pollen beetle (*Brassicogethes aeneus* (F.) (Coleoptera: Nitidulidae)), and brassica pod midge (Zheng et al. 2020). Chemical control remains the predominant tactic for management of insect pests on these crops (Lamb 1989, Alford et al. 2003, Williams 2010, Zheng et al. 2020), though advances are being made in biological control, cultural control and host-plant resistance (Lamb 1989, Alford et al. 2003, Williams 2010, Zheng et al. 2020).

Here, we provide a review of insects that have been reported in association with pennycress and how pennycress responds to stressors similar to the feeding injury that could be caused by some insects. This information will help to provide a foundation for development of integrated pest management programs for this new crop. Current species names, as determined by searching the Integrated Taxonomic Information System and National Center for Biotechnology Information (NCBI) Taxonomy Database, are listed in parentheses following the species names used in the literature.

Herbivorous Insects Associated with Pennycress

A comprehensive review of the literature found reports of herbivorous insects from 9 countries associated with pennycress (Table 1). A total of 119 species of herbivorous insects across 6 insect orders were reported in association with above- and below-ground parts of pennycress plants (Table 1). Various life stages of these species have been reported with pennycress (Table 1). For the insects that have been studied more thoroughly, a review of their interactions with pennycress is provided below. In addition to insects, two-spotted spider mite (*Tetranychus urticae* (Koch) (Trombidiformes: Tetranychidae)), which is known as a pest of many crops, was also found on pennycress (Lipa et al. 1977).

Coleoptera

Flea beetles (*Phyllotreta* spp. (Coleoptera: Chrysomelidae)) are major pests of Brassicaceae crops (Warwick et al. 2002) and they have been reported feeding on leaves and flowers of pennycress in the field and in the laboratory (Lamb and Palaniswamy 1990, Soroka and Grenkow 2013). Plant death was observed in the Czech Republic for pennycress growing in the field and being attacked from emergence onward by adults of flea beetles (Štolcová 2005). Several studies have more closely examined flea beetle preferences for and performance on pennycress compared to other plants. In laboratory choice tests with adults of *Phyllotreta Cruciferae* (Goeze), feeding on *B. napus*, *Sinapis alba* L. (Brassicales: Brassicaceae), *Sinapis pubescens* L. (Brassicales:

Brassicaceae) and *Crambe glabrata* DC. (Brassicales: Brassicaceae) was higher than on pennycress (Soroka and Grenkow 2013). Non-preference resistance (i.e., antixenosis) of pennycress and *S. alba* has been observed for *P. cruciferae* (Gavloski et al. 2000). Choice tests done using leaf discs indicate that *Phyllotreta armoraciae* (Koch) prefers black mustard (*Brassica nigra* (L.) Koch (Brassicales: Brassicaceae)) and *S. alba* over pennycress (Nielsen et al. 1979), and that *Phyllotreta nemorum* (L.) and *P. cruciferae* prefer black mustard, radish (*Raphanus sativus* L. (Brassicales: Brassicaceae)), *S. alba*, and *B. napus* over pennycress (Nielsen et al. 2001). Similarly, *P. cruciferae* adults were found to exhibit a strong non-preference response to pennycress compared to *Brassica juncea* (L.) Czernajew (Brassicales: Brassicaceae), *Brassica carinata* A. Braun (Brassicales: Brassicaceae), *B. napus*, *B. rapa*, and *S. alba* in Manitoba, Canada (Palaniswamy et al. 1997); and pennycress was only marginally acceptable to *Phyllotreta striolata* (F.) in Alberta, Canada (Meisner and Mitchell 1983). In no-choice conditions, survival of *P. cruciferae* adults on intact leaves of pennycress was as low as 9%, and adults that did survive on pennycress lost weight (Palaniswamy et al. 1997). In contrast, based on feeding experiments performed in the Czech Republic, Štolcová (2009) concluded that *Phyllotreta nigripes* (F.) and *Phyllotreta atra* (F.) do not show clear preferences among pennycress, wild mustard and *B. napus*. Overall, glucosinolates have been suggested as important factors for flea beetle host selection, and reducing the expression of

glucosinolates in plants may change their susceptibility to being attacked by flea beetles (Soroka and Grenkow 2013).

Adults of cabbage seedpod weevil (*Ceutorhynchus obstrictus* (Marsham) (Coleoptera: Curculionidae)) were found on pennycress and other Brassicaceae weeds in Alberta, Canada (Doddall and Moisey 2004). In a mixed stand of pennycress, wild mustard (*Sinapis arvensis* L. (Brassicales: Brassicaceae)) and flixweed (*Descurainia sophia* (L.) Webb ex Prantl (Brassicales: Brassicaceae)), *C. obstrictus* adults were found more frequently on wild mustard, and more on buds than stems or leaves independently of plant species (Doddall and Moisey 2004). Pennycress did not appear to support *C. obstrictus* larval development as none of the pennycress seed pods had larval exit holes (Doddall and Moisey 2004). Thus, pennycress may serve as an alternative food source for *C. obstrictus* adults in early spring until canola crops develop inflorescences that attract adults for feeding and reproduction.

Alfalfa weevil (*Hypera postica* (Gyllenhal) (Coleoptera: Curculionidae)) was found to oviposit on pennycress growing as a weed in alfalfa (*Medicago sativa* L. (Fabales: Fabaceae) fields in Idaho, US (Saad and Bishop 1969). After rearing the alfalfa plants in the laboratory, eggs of *H. postica* were observed to hatch, but larvae did not feed on pennycress, suggesting that *H. postica* larvae may migrate from pennycress to alfalfa in the field (Saad and Bishop 1969).

The sap beetles (*Meligethes aeneus* F. (currently *Brassicogethes aeneus* (F.)) and *M. viridescens* F. (currently *Brassicogethes viridescens* (F.)) (Coleoptera: Nitidulidae)) are pests of Brassicaceae crops in Europe (Williams 2010), and have been reported from pennycress (Lipa et al. 1977). However, *M. aeneus* and *M. viridescens* were not found on pennycress in a field study looking at the temporal distribution and dynamics of these species across a variety of Brassicaceae crops and weeds in May–July in Estonia (Metspalu et al. 2011). Metspalu et al. (2011) suggested that the apparent unsuitability of pennycress to *M. aeneus* and *M. viridescens* may be due to plant chemistry (e.g., glucosinolates or other secondary metabolites).

Diptera

The serpentine leaf miner (*Liriomyza brassicae* (Riley) (Diptera: Agromyzidae)) was found to create mines on leaves of pennycress, yellow rocket (*Barbarea vulgaris* W.T. Aiton (Brassicales: Brassicaceae)) and black mustard growing in the wild in Wisconsin, US, and in the laboratory with multiple lineages of *L. brassicae* (Tavormina 1982). The development time of multiple lineages of *L. brassicae* from oviposition to adults on pennycress was, on average, between 21.3 and 21.6 days (Tavormina 1982).

Some root maggot flies (Diptera: Anthomyiidae) are pests of germinating seeds and seedlings of crops. Cabbage root fly (*Erioischia brassicae* (Bouche) (currently *Delia radicum* (L.)) (Diptera: Anthomyiidae)) pupae were found in the

soil near pennycress (up to an average of 0.9 pupae per plant) in a field survey of Brassicaceae weeds in the United Kingdom (Finch and Ackley 1977). However, when pennycress plants were inoculated with *E. brassicae* eggs in a greenhouse experiment, only 2% of the eggs produced pupae, the resulting pupae were smaller than those reared from other plants, and pennycress roots appeared healthy (i.e., not damaged by larval feeding) (Finch and Ackley 1977). In addition, pennycress is a reported host for *Delia floralis* (Fallén) (Diptera: Anthomyiidae) (Strickland 1938, Savage et al. 2016). Furthermore, adults of seed corn maggot (*Delia platura* (Meigen) (Diptera: Anthomyiidae)) have been found to be abundant on pennycress flowers (Forcella et al. 2023a). However, potential impacts of the feeding of *D. platura* larvae on pennycress seeds or seedlings remain to be evaluated.

Swede midge (*Contarinia nasturtii* (Kieffer) (Diptera: Cecidomyiidae)) has been observed to feed on various Brassicaceae weeds including pennycress (Stokes 1953a, 1953b), but it was not found on pennycress growing in and near Brassicaceae vegetable fields in New York, US (Chen et al. 2009). In a no-choice experiment, *C. nasturtii* oviposited on pennycress, but the number of larvae produced on pennycress was about four times lower than on cauliflower (Chen et al. 2009). In an ovipositional choice test experiment with pennycress, cauliflower and five other Brassicaceae weeds, no *C. nasturtii* larvae were found on pennycress (Chen et al. 2009).

Hemiptera

Aphids have been observed infesting pennycress in Wisconsin and Missouri, US, and concern raised about their pest status for this new crop (Basnet and Ellison 2024). Cabbage aphid (*Brevicoryne brassicae* (L.) (Hemiptera: Aphididae)) was found to feed on pennycress in a laboratory experiment in Poland (Gabryś and Pawluk 1999). Results of tests using an electrical penetration graph showed that pennycress is an acceptable host for *B. brassicae*, but that the phloem elements of pennycress may contain a deterrent factor (Gabryś and Pawluk 1999).

Turnip aphid (*Hyadaphis pseudobrassicae* (Davis) (currently *Lipaphis pseudobrassicae* (Davis)) (Hemiptera: Aphididae)) colonized and fed on pennycress in a series of greenhouse experiments in Iowa, US (Jarvis 1970). Survival of pennycress plants 3–4 weeks after infestation with *H. pseudobrassicae* was 66% with no individual plants of pennycress showing resistance to this aphid (Jarvis 1970). In a second experiment, colonization of pennycress seedlings by alate *H. pseudobrassicae* was about 1/5 that of the average colonization on several susceptible genotypes of *B. napus*. In a third experiment, population growth of *H. pseudobrassicae* on pennycress was about 1/4 that of the average population growth on several susceptible genotypes of *B. napus* (Jarvis 1970).

The plant bugs (*Lygus lineolaris* (Palisot), *Lygus elisus* Van Duzee, and *Lygus borealis* (Kelton) (Hemiptera: Miridae)) were found on pennycress growing in the wild in Manitoba, Canada (Gerber and Wise 1995). Overwintered adults of *L. lineolaris* appeared on pennycress during the second and third weeks of May, followed by nymphs in the third and fourth weeks of May (Gerber and Wise 1995). *Lygus* spp. nymphs remained abundant on pennycress from late May to late June, and likely consisted mainly of *L. lineolaris* (Gerber and Wise 1995). However, by the time pennycress ripened at the end of June, few *Lygus* spp. remained on the plants, suggesting that this plant stage is unsuitable for *Lygus* spp. (Gerber and Wise 1995).

Two stink bugs (*Dolycoris baccarum* (L.) and *Carpocoris fuscipinus* (Boheman) (Hemiptera: Pentatomidae)) fed on and oviposited on pennycress in a laboratory study in Poland (Modnicki et al. 2019). Compared to three other Brassicaceae species (i.e., *Berteroa incana* (L.), *Diplotaxis tenuifolia* (L.), and flixweed), pennycress had the most feeding sites (i.e., punctures) from *C. fuscipinus* adults and the fewest from *D. baccarum* adults (Modnicki et al. 2019). Over a period of three days, *D. baccarum* oviposited, on average, the fewest eggs on pennycress (6.8 eggs), while *C. fuscipinus* oviposited an intermediate number of eggs on pennycress (13.8 eggs) compared to the other plants. The duration of egg development and rate of egg hatching for *D. baccarum* and *C. fuscipinus* did not differ significantly among host plants (Modnicki et al. 2019). On average, the duration of egg development of *D. baccarum* and *C. fuscipinus* on

pennycress was 10.2 and 11.4 days, respectively (Modnicki et al. 2019). The average rate of egg hatching on pennycress for *D. baccarum* and *C. fuscipinus* was 60.3 and 58.6%, respectively (Modnicki et al. 2019).

Lepidoptera

Bertha armyworm (*Mamestra configurata* Walker (Lepidoptera: Noctuidae)) survival and development was examined in a laboratory experiment in Canada with neonate first instars placed on excised leaf tissue of ten plant species from five families, but *M. configurata* did not survive on pennycress (Dosdall and Ulmer 2004).

Southern armyworm (*Prodenia eridania* (Cramer) (currently *Spodoptera eridania* (Stoll)) (Lepidoptera: Noctuidae)) larvae were evaluated in the laboratory for feeding and growth on 74 plant species from multiple families in Illinois, US (Soo Hoo and Fraenkel 1966). Larvae fed on pennycress but pennycress did not support growth of *S. eridania* (Soo Hoo and Fraenkel 1966).

Cabbage looper (*Trichoplusia ni* (Hübner) (Lepidoptera: Noctuidae)) was found to feed on pennycress, broccoli and other seven agricultural weeds in a series of experiments with greenhouse-grown plants in British Columbia, Canada (Cameron et al. 2007). In a choice-test experiment, adults of *T. ni* showed a preference to oviposit and feed on pennycress compared to broccoli (Cameron et al. 2007). However, in no-choice experiments, first instar *T. ni* consumed relatively little leaf tissue of pennycress and less than 2% of those larvae

survived after 7 days, whereas survival was greater than 60% on the other plant species (Cameron et al. 2007). Thus, Cameron et al. (2007) suggested that pennycress could be explored as a dead-end trap crop for *T. ni* management.

Pieris butterflies (Lepidoptera: Pieridae) have shown variable responses to pennycress. Multiple species, including *Pieris napi macdonnoughii* Remington (currently *Pieris macdunnoughi* Remington), *Pieris occidentalis* (Reakirt), *Pieris rapae* (L.), and *Pieris napi* (L.), were observed to oviposit on pennycress in natural plant communities or under laboratory conditions (Chew 1975, 1977, 1980, Slansky and Feeny 1977, Nakajima et al. 2013, Okamura et al. 2016). However, the larvae of *P. macdunnoughi* and *P. occidentalis* seem incapable of surviving when fed exclusively on pennycress (Chew 1975, 1980, Nakajima et al. 2013). Furthermore, the population fitness cost associated with oviposition of *P. macdunnoughi* on pennycress was estimated as 3% in natural landscapes, but no significant differences in population dynamics was observed over a 40-year period (Nakajima et al. 2013).

The larval growth of *P. rapae* when reared on pennycress was intermediate among multiple Brassicaceae plants in laboratory studies (Slansky and Feeny 1977, Okamura et al. 2016). Females of *P. napi* were found to lay eggs on pennycress plants of all sizes in Sweden, but more eggs were laid on smaller (e.g., 5 cm) compared to larger (e.g., 20 cm) plants, and smaller plants seemed to be more advantageous to survival and development of *P. napi* (Forsberg 1987).

Diamondback moth (*Plutella maculipennis* (Curt.) (currently *Plutella xylostella* (L.)) (Lepidoptera: Plutellidae)), which migrates to northern areas each spring, is found on pennycress in early spring in Ontario, Canada and North Dakota, US (Harcourt 1957, Kmec and Weiss 1997). Pennycress is a host for the first generation of *P. xylostella* prior to emergence of cultivated Brassicaceae plants (Harcourt 1957, Kmec and Weiss 1997). Adult *P. xylostella* in North Dakota were present from May to June in pennycress adjacent to field crops (Kmec and Weiss 1997). The density of *P. xylostella* eggs on leaves of pennycress varied from about 10–60 eggs m⁻² and egg density was correlated with counts of adult *P. xylostella* in the field (Kmec and Weiss 1997). In Michigan, Idris and Grafius (1996) found intermediate levels of oviposition, development and survival of *P. xylostella* on pennycress compared to several Brassicaceae plants, but similar egg hatches were observed. The average number of eggs per female *P. xylostella* on pennycress was lower than broccoli but similar to canola and three other weeds in a choice test, and similar to broccoli, cauliflower, canola and six other weeds in a no-choice test (Idris and Grafius 1996). Developmental time (from egg hatch to pupation) on pennycress (~13–14 days) was similar to red cabbage and several weeds (Idris and Grafius 1996). Furthermore, survival of *P. xylostella* larvae from hatching through the second instar was ~40% on pennycress, which was similar to red cabbage, but lower than broccoli, kale, cauliflower, green cabbage and canola (Idris and Grafius 1996). Survival of *P. xylostella* larvae from third through fourth instar was high on pennycress (~85%)

and similar to broccoli, kale, cauliflower, canola and two weeds (Idris and Grafius 1996). The suitability of pennycress and seven other Brassicaceae weeds as hosts for *P. xylostella* was examined in China using clip cages on intact leaves (Niu et al. 2014). Development time from egg to adult emergence (20.1 days) was the longest, the pupal weight (females: 4.3 mg; males: 3.1 mg) and survival from egg to adult (48.8%) were the lowest, and female adult longevity (15.1 days) and fecundity (192.4 eggs per female) were intermediate on pennycress compared to the other plants (Niu et al. 2014). Overall, *P. xylostella* raised on pennycress had the lowest intrinsic and finite rates of increase, longest generation time, and lowest net reproductive rate compared to the other plants (Niu et al. 2014).

Furthermore, pennycress and three other flowering plants were evaluated as nectar sources for adult *P. xylostella* in a laboratory experiment in Alberta, Canada (Munir et al. 2018). The longevity of adult *P. xylostella* (~25 days) on floral resources of pennycress was similar to that of *S. arvensis* and *B. napus*, and higher than *Lobularia maritima* (L.) Desvaux (Brassicales: Brassicaceae), 10% honey solution, or water; however, the weight of *P. xylostella* adults was lower on floral resources of pennycress compared to *L. maritima*, 10% honey solution, or water (Munir et al. 2018).

Eri silkmoth (*Samia cynthia ricini* Boisduval (currently *Samia ricini* Anderson) (Lepidoptera: Saturniidae)) larval growth was examined in a greenhouse experiment in Japan using 12 Brassicaceae species varying in

defensive traits, but first instar *S. cynthia ricini* fed on pennycress did not gain as much weight as those feeding on other species such as *Capsella bursa-pastoris* (L.) Medikus (Brassicales: Brassicaceae) or *Cardamine scutata* Thunberg (Brassicales: Brassicaceae) (Okamura et al. 2016).

Thysanoptera

The onion thrips (*Thrips tabaci* Lindeman (Thysanoptera: Thripidae)) was found on pennycress in a field survey of 69 weed species near onion (*Allium cepa* L. (Asparagales: Amaryllidaceae)) fields in New York, US (Smith et al. 2011). *Thrips tabaci* was found to reproduce on pennycress, and the highest *T. tabaci* abundance was observed on pennycress along with *B. vulgaris*, *S. arvensis*, and *Raphanus raphanistrum* L. (Brassicales: Brassicaceae) (Smith et al. 2011).

Pennycress Response to Stresses Similar to Insect Injury

The response of pennycress to insect feeding is poorly understood. Some insight into how pennycress might respond could be inferred from how related crops (e.g., rapeseed and canola) respond to insect pests (e.g., Lamb 1989). Furthermore, a more specific understanding about how pennycress responds to insect feeding may be gained by examining the limited research on the response of pennycress to simulated injury (e.g., stand loss, defoliation and apical stem injury).

Reductions in plant density due to insect feeding can have varying effects on crop yield, depending on plasticity of the plant's growth (Bardner and Fletcher 1974). A greenhouse experiment was performed in the United Kingdom to examine the response of pennycress to varying initial plant density and subsequent removal of neighboring plants at different timings (Matthies 1990). Pennycress seed was sown in pots and thinned after germination to targeted densities ranging from 1 to 64 seedlings per 12×12-cm pot (Matthies 1990). Then, for the thinning treatments, all neighboring plants were removed from around a central focal plant in each pot during the vegetative, flowering and seed pod stages of pennycress (Matthies 1990). In this study, pennycress showed plasticity in response to plant density by producing more seed per plant and larger seed as plant density decreased (Matthies 1990). In addition, pennycress showed greater ability to compensate when removal of neighboring plants occurred at earlier growth stages (Matthies 1990).

Defoliation can have diverse physiological and morphological consequences on plants that can take place across a broad spectrum of timeframes (Clement et al. 1978, Hammond and Pedigo 1982, Aldea et al. 2005, van Klink et al. 2015). In a greenhouse experiment carried out in the United Kingdom, the effects of defoliation during two stages of pennycress flower development were investigated (Pyke 1989). For the defoliation treatments, all leaves on the primary stems of plants were removed when the first flower opened ("early defoliation") or when 50% of flowers had lost their corolla and began

enlarging (“mid-defoliation”) (Pyke 1989). Early defoliation caused fewer pods on defoliated plants compared to undefoliated plants (Pyke 1989). In contrast, mid-defoliation had no effect on the number of pods but resulted in a greater number of aborted seeds per pod on defoliated plants compared to control plants (Pyke 1989). Pyke (1989) noted that pods with aborted seeds were smaller but remained green on the plants and therefore may act as a photosynthetic source for seeds developing in other pods.

Apical injury to stems of plants that produce terminal flowers may result in increased branching from axillary buds and thereby increase the number of flowers, but also results in loss of resources in the removed tissue, loss of photosynthetic area, and delays in seed production (Trumble et al. 1993, Fay et al. 1996). In a greenhouse study carried out in Indiana, US, the impact of apical stem removal and fertilization on the branching and seed production of pennycress was assessed (Benner 1988). Early stem removal was performed when plants started to show internode elongation, and late stem removal was performed when most plants had formed flower buds or open flowers (Benner 1988). When the plants started to show internode elongation, 20 days after being transplanted, early treatments involving apex removal and nutrient addition were conducted (Benner 1988). Late treatments, which also involved apex removal and nutrient addition, were performed 30 days after transplanting, when most plants had formed flower buds or open flowers, which could potentially affect their response differently from plants that had not yet produced flowering

structures (Benner 1988). Removal of the plant apex led to a decrease in the number of primary branches and an increase in the number of secondary and tertiary branches (Benner 1988). These effects were generally more pronounced when the apex was removed earlier than later (Benner 1988). Moreover, the number of fruits produced on all types of branches was higher in the plants where the apex was removed, regardless of the timing, with the early-removed plants producing more fruits on these branches than the late-removal ones (Benner 1988). The total weight of seeds per plant was greater for early-removal plants compared to late-removal plants, and the total weight of seeds for the control plants was generally greater than that of plants with either removal timing (Benner 1988). Benner (1988) observed that pennycress had some ability to compensate for apical removal by increasing the number of seeds produced, but not the size of the seeds.

Beneficial Insects Associated with Pennycress

Natural enemies such as parasitoids and predators could be affected by incorporation of pennycress into cropping systems. Conflicting results have been observed for the effects of pennycress on *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae), a parasitoid of *P. xylostella*. In a field study in Michigan, US, the longevity and fecundity of adult *D. insulare* females provided floral resources of pennycress was similar to (or slightly higher) than those provided only water, and lower than those provided floral resources of *B. vulgaris* or *C. bursa-pastoris*, or a honey-water solution (Idris and Grafius 1995). In

contrast, in a laboratory experiment in Alberta, Canada, the longevity of adult *D. insulare* on floral resources of pennycress (~25 days) was higher than on floral resources of *S. arvensis*, *B. napus*, or *L. maritima*, a honey-water solution, or water; however, the weight of *D. insulare* adults was lower on pennycress compared to *S. arvensis*, but higher than on water (Munir et al. 2018). In addition, indirect host-mediated effects of pennycress on *D. insulare* have also been examined. In a laboratory experiment in Michigan, US, parasitism rates were lower and development times were longer for *D. insulare* when their host (i.e., *P. xylostella*) was reared on pennycress compared to several cultivated *Brassica* spp. (Idris and Grafius 1996).

Lipa et al. (1977) documented nine species of predators associated with pennycress in Europe, including *Adonia variegata* (Goeze) (currently *Hippodamia variegata* (Goeze)), *Coccinella quatuordecimpustulata* (L.), *Coccinella quinquepunctata* (L.), *Coccinella septempunctata* L., *Coccinella undecimpunctata* (L.), *Propylaea quatuordecimpunctata* (L.) (Coleoptera: Coccinellidae), *Tachyporus hypnorum* F. (Coleoptera: Staphylinidae), *Nabis pseudoferus* Rem. (Hemiptera: Nabidae), and *Aeolothrips intermedius* Bagn. (Thysanoptera: Aeolothripidae). In the Midwest US, Forcella et al. (2023a) found that adult Syrphidae were common visitors to pennycress flowers, however, the abundance of the predatory larvae of Syrphidae on pennycress was not quantified. In addition, the incorporation of pennycress into crop rotations may favor predatory insects. In a field experiment in Germany, a double-cropping system of pennycress and corn resulted in higher

species richness and abundance of predatory ground beetles and higher species richness and diversity of spiders compared to two or three other common cropping systems (Groeneveld and Klein 2015a, Groeneveld and Klein 2015b).

The early flowering time of pennycress can provide a source of early season floral resources to pollinators when most plants have not yet bloomed (Evangelista et al. 2017). The communities of pollinating insects associated with pennycress have received considerable attention (Mulligan and Kevan 1973, Groeneveld and Klein 2014, Eberle et al. 2015, Hassall et al. 2017, Stavert et al. 2018, Thom et al. 2018, Forcella et al. 2021, 2023a, 2023b).

Conclusions

Pennycress has the potential to provide multiple benefits as a cover and oilseed crop in corn-soybean rotations of the Midwest US. Significant advances have been made with genetic improvements and agronomic practices for this crop. However, as this crop begins to be adopted by farmers, there is an urgent need for guidance on potential pests, impacts of those pests, and management strategies.

To our knowledge, insect herbivore communities associated with pennycress grown as a crop or cover crop, have not been fully documented. To provide a foundation for understanding potential insect pest threats, the scattered knowledge about insects associated with pennycress was compiled in this review. Among the taxa found associated with pennycress, several taxa,

including *Phyllotreta* spp., Aphididae, *Lygus* spp. and *P. xylostella*, may pose the greatest pest threats to pennycress. However, because the primary focus of those studies was on pennycress growing in the wild (natural systems) or as a weed in agricultural systems, further work is needed to characterize the insect herbivore communities associated with pennycress growing under monoculture or intercropping scenarios representing how this crop will be deployed on the agricultural landscape. For example, seed maggots (Diptera: Anthomyiidae) are attracted to the flowers of pennycress (Forcella et al. 2023a), but it remains unknown if this might lead to increased abundance of such pests attacking seed of crops relay cropped into pennycress. Furthermore, as domestication of pennycress continues, the susceptibility of new pennycress genotypes to insect pests will need to be evaluated.

Finally, we are not aware of any published reports regarding how pennycress responds to injury from insects. However, limited studies showing responses of pennycress (including yield loss or compensation) to reduction in plant density, and artificial defoliation and stem injury provide some insight as to how it might respond to insect pests. Further work is needed to examine the response to pennycress to actual and simulated insect injury. Such information will provide a foundation for development of management guidelines such as economic injury levels and economic thresholds.

Table 1. 1: Insect herbivores reported in association with pennycress (*Thlaspi arvense*)

Order	Family	Species ¹	Country ²	Life stage ³	Plant part ⁴	Reference
Coleoptera	Cantharidae	<i>Cantharis lateralis</i>	Poland	A	S, L	Lipa et al. 1977
	Chysomelidae	<i>Chaetocnema concinna</i>	Poland	A	S, L	Lipa et al. 1977
		<i>Gastroidea polygoni</i>	Poland	A	S	Lipa et al. 1977
		<i>Haltica palustris</i>	Poland	A	S	Lipa et al. 1977
		<i>Phyllotreta armoraciae</i>	Denmark	-	L	Nielsen et al. 1979
		<i>Phyllotreta atra</i>	Poland & Czech Republic	A	S, L	Lipa et al. 1977, Štolcová 2009

<i>Phyllotreta cruciferae</i>	Poland Denmark & Canada	A	S, L	Lipa et al. 1977, Gavloski et al. 2000, Palaniswamy et al. 1997, Nielsen et al. 2001
<i>Phyllotreta flexuosa</i>	Poland	A	S, L	Lipa et al. 1977, Nielsen et al. 2001
<i>Phyllotreta nemorum</i>	Poland & Denmark	A	S, L	Lipa et al. 1977, Nielsen et al. 2001

	<i>Phyllotreta nigripes</i>	Czech Republic	-	L	Štolcová 2009
	<i>Phyllotreta striolata</i>	Canada	-	-	Meisner and Mitchell 1983
	<i>Phyllotreta undulata</i>	Poland	A	S, L	Lipa et al. 1977
	<i>Phyllotreta vittula</i>	Poland	A	S, L	Lipa et al. 1977
	<i>Psylliodes napi</i>	Poland	A	S, L	Lipa et al. 1977
Curculionidae	<i>Ceutorhynchus assimilis</i>	Poland	A	S, L	Lipa et al. 1977
	<i>Ceutorhynchus chalybaeus</i>	Poland	A	S, R	Lipa et al. 1977
	<i>Ceutorhynchus contractus</i>	Poland	A	L	Lipa et al. 1977

<i>Ceutorhynchus erysimi</i>	Poland	A	S, R	Lipa et al. 1977
<i>Ceutorhynchus floralis</i>	Poland	A	S, L, SPL	Lipa et al. 1977
<i>Ceutorhynchus granulicollis</i>	Poland	A	S, L	Lipa et al. 1977
<i>Ceutorhynchus napi</i>	Poland	A	S, L	Lipa et al. 1977
<i>Ceutorhynchus obstrictus</i>	Canada	A	L	Dosdall and Moisey 2004
<i>Ceutorhynchus pleurostigma</i>	Poland	A	S, L	Lipa et al. 1977
<i>Ceutorhynchus pulvinatus</i>	Poland	A	S, L, SPL	Lipa et al. 1977
<i>Ceutorhynchus quadridens</i>	Poland	A	S, R	Lipa et al. 1977

	<i>Ceutorhynchus roberti</i>	Poland	A	S, L	Lipa et al. 1977
	<i>Hypera postica</i>	United States	A, E	S	Saad and Bishop 1969
	<i>Trachyphloeus bifoveolatus (Romualdius bifoveolatus)</i>	Poland	A	O	Lipa et al. 1977
Dermestidae	<i>Anthrenus pimpinellae</i>	Poland	A	O	Lipa et al. 1977
Elateridae	<i>Agriotes lineatus</i>	Poland	A	O	Lipa et al. 1977
	<i>Athous niger</i>	Poland	L	R	Lipa et al. 1977
Melyridae	<i>Malachius marginellus</i>	Poland	A	S	Lipa et al. 1977

Nitidulidae	<i>Meligethes aeneus</i>	Poland	A	F	Lipa et al. 1977
	<i>(Brassicogethes aeneus)</i>				
	<i>Meligethes lugubris</i>	Poland	A	O	Lipa et al. 1977
	<i>(Thymogethes lugubris)</i>				
	<i>Meligethes picipes</i>	Poland	A	O	Lipa et al. 1977
Phalacridae	<i>Meligethes planiusculus</i>	Poland	A	O	Lipa et al. 1977
	<i>Olibrus aeneus</i>	Poland	A	O	Lipa et al. 1977
	<i>Olibrus corticalis</i>	Poland	A	O	Lipa et al. 1977
Diptera	<i>Stilbus testaceus</i>	Poland	A	O	Lipa et al. 1977
	Agromyzidae <i>Liriomyza brassicae</i>	United States	A, E, L	L	Tavormina 1982

	<i>Liriomyza strigata</i>	Poland	A	L	Lipa et al. 1977
	<i>Phytomyza horticola</i>	Poland	A	L	Lipa et al. 1977
	<i>Phytomyza rufipes</i>	Poland	A	L	Lipa et al. 1977
	<i>Delia floralis</i>	Canada	-	-	Strickland 1938 Savage et al. 2016
	<i>Delia platura</i>	United States	A	F	Forcella et al. 2023a
	<i>Erioschia brassicae</i> (<i>Delia radicum</i>)	United Kingdom	A, E, L	-	Finch and Ackley 1977
Cecidomyiidae	<i>Contarinia nasturtii</i>	Poland & United States	A, E, L	SP, L	Lipa et al. 1977

						Chen et al. 2009
	Drosophilidae	<i>Scaptomyza flavoela</i>	Poland	A, L, P	L	Lipa et al. 1977
Hemiptera	Aphididae	<i>Acyrtosiphon pisum</i>	Poland	N ⁵ , A	S, L	Lipa et al. 1977
		<i>Aphis craccivora</i>	Poland	A, N ⁵	S, L	Lipa et al. 1977
		<i>Aphis fabae</i>	Poland	A, N ⁵	S, L	Lipa et al. 1977
		<i>Aphis nasturtii</i>	Poland	A, N ⁵	S, L	Lipa et al. 1977
		<i>Aulacorthum solani</i>	Poland	N ⁵	S, L	Lipa et al. 1977
		<i>Brevicoryne brassicae</i>	Poland	A, N	S, L	Gabryś and Pawluk 1999

<i>Cavariella aegopodii</i>	Poland	A, N ⁵	O	Lipa et al. 1977
<i>Hyadaphis pseudobrassicae (Lipaphis pseudobrassicae)</i>	United States	A	-	Jarvis 1970
<i>Lipaphis erysimi</i>	Poland	A, N ⁵	S, L	Lipa et al. 1977
<i>Lipaphis</i> sp.	Poland	N ⁵	S, L	Lipa et al. 1977
<i>Myzus cerasi</i>	Poland	A, N ⁵	O	Lipa et al. 1977
<i>Myzodes persicae (Myzus persicae)</i>	Poland	A, N	S, L	Lipa et al. 1977
<i>Rhopalosiphum padi</i>	Poland	A	O	Lipa et al. 1977

	<i>Sitobion</i> sp.	Poland	N ⁵	O	Lipa et al. 1977
Aphrophoridae	<i>Philaenus spumarius</i>	Poland	A, L	O	Lipa et al. 1977
Cicadellidae	<i>Athysanus quadrum</i>	Poland	A	O	Lipa et al. 1977
	<i>Eupteryx atropunctata</i>	Poland	A	O	Lipa et al. 1977
	<i>Euscelidius schenckii</i>	Poland	A, N ⁵	O	Lipa et al. 1977
	<i>Macrosteles cristatus</i>	Poland	A	O	Lipa et al. 1977
	<i>Macrosteles laevis</i>	Poland	A	O	Lipa et al. 1977
	<i>Macrosteles sexnotatus</i>	Poland	A	O	Lipa et al. 1977

	<i>Macrosteles</i> sp.	Poland	A	O	Lipa et al. 1977
	<i>Psammotettix alienus</i>	Poland	A	O	Lipa et al. 1977
	<i>Psammotettix</i> sp.	Poland	A	O	Lipa et al. 1977
Delphacidae	<i>Javesella pellucida</i>	Poland	A	O	Lipa et al. 1977
	<i>Javesella</i> sp.	Poland	A	O	Lipa et al. 1977
	<i>Laodelphax striatella</i> (<i>Laodelphax striatellus</i>)	Poland	A	O	Lipa et al. 1977
Lygaeidae	<i>Cymus clavicolus</i>	Poland	A	O	Lipa et al. 1977
	<i>Nysius ericae</i>	Poland	A	O	Lipa et al. 1977

	<i>Nysius senecionis</i>	Poland	A	O	Lipa et al. 1977
Miridae	<i>Adelphocoris lineolatus</i>	Poland	A	O	Lipa et al. 1977
	<i>Apolygus limbatus</i>	Poland	A	O	Lipa et al. 1977
	<i>Calocoris norvegicus</i>	Poland	A	O	Lipa et al. 1977
	<i>Lygus borealis</i>	Canada	A	-	Gerber and Wise 1995
	<i>Lygus elisus</i>	Canada	A		Gerber and Wise 1995
	<i>Lygus gemellatus</i>	Poland	A	S, L	Lipa et al. 1977
	<i>Lygus lineolaris</i>	Canada	A, N	-	Gerber and Wise 1995

	<i>Lygus pratensis</i>	Poland	A	S, L	Lipa et al. 1977
	<i>Lygus rugulipennis</i>	Poland	A	S, L	Lipa et al. 1977
	<i>Lygus</i> sp.	Poland	N ⁵	S, L	Lipa et al. 1977
	<i>Orthotylus flavosparsus</i>	Poland	A	R	Lipa et al. 1977
	<i>Polymerus vulneratus</i>	Poland	A	S, L	Lipa et al. 1977
Pentatomidae	<i>Carpocoris fuscispinus</i>	Poland	A, E	-	Modnicki et al. 2019
	<i>Dolycoris baccarum</i>	Poland	A, E	-	Modnicki et al. 2019
	<i>Eurydema oleracea</i>	Poland	A, N	S, L	Lipa et al. 1977

		<i>Eurydema ornata</i>	Poland	A	S, L	Lipa et al. 1977
	Trioziidae	<i>Bactericera nigricornis</i>	Poland	A, N	S, L	Lipa et al. 1977
Hymenoptera	Tenthredinidae	<i>Athalia colibri</i>	Poland	A	O	Lipa et al. 1977
Lepidoptera	Noctuidae	<i>Prodenia eridania</i> (<i>Spodoptera eridania</i>)	United States	L	L	Soo Hoo and Fraenkel 1966
		<i>Trichoplusia ni</i>	Canada	L	L	Cameron et al. 2007
	Pieridae	<i>Leptidea sinapis</i>	Poland	P	S, L	Lipa et al. 1977
		<i>Pieris brassicae</i>	Poland	A, L	S, L	Lipa et al. 1977
		<i>Pieris napi</i>	Poland, United States,	A, E, L	S, L	Lipa et al. 1977,

		Sweden & Japan			Forsberg 1987
	<i>Pieris napi</i>	Poland,	A, E, L	S, L	Chew 1975,
	<i>macdunnoughii</i>	United States			1977, 1980,
	<i>(Pieris macdunnoughi)</i>	& Sweden			Lipa et al. 1977,
					Nakajima et al. 2013
	<i>Pieris occidentalis</i>	United States	A, L	L	Chew 1975, 1980, 1977
	<i>Pieris rapae</i>	Poland,	E, L, P	S, L	Okamura et al. 2016,
		United States & Japan			Chew 1975, Slansky and Feeny 1977
Plutellidae	<i>Plutella maculipennis</i>	China,	A, E, L, PS, L		Niu et al. 2014,
	<i>(Plutella xylostella)</i>				

			United States & Poland			Idris and Grafius 1996, Kmec and Weiss 1997, Munir et al. 2018, Lipa et al. 1977
	Saturniidae	<i>Samia cynthia ricini</i> (<i>Samia ricini</i>)	Japan	L	-	Okamura et al. 2016
Lepidoptera	Tortricidae	<i>Cnephasia virgaureana</i>	Poland	A, L	F, S, L	Lipa et al. 1977
Thysanoptera	Aeolothripidae	<i>Melanthrips fuscus</i>	Poland	A	F	Lipa et al. 1977
	Phlaeothripidae	<i>Haplothrips aculeatus</i>	Poland	A	O	Lipa et al. 1977

	<i>Haplothrips setiger</i>	Poland	A	F	Lipa et al. 1977
Thripidae	<i>Dictyothrips betae</i>	Poland	A	O	Lipa et al. 1977
	<i>Frankliniella intonsa</i>	Poland	A	F	Lipa et al. 1977
	<i>Limothrips denticornis</i>	Poland	A	O	Lipa et al. 1977
	<i>Taeniothrips atratus</i>	Poland	A	F	Lipa et al. 1977
	<i>Taeniothrips vulgatissimus</i>	Poland	A	O	Lipa et al. 1977
	<i>Thrips angusticeps</i>	Poland	A, L	F, S, L	Lipa et al. 1977
	<i>Thrips fuscipennis</i>	Poland	A	F, S, L	Lipa et al. 1977

<i>Thrips major</i>	Poland	A	F, S, L	Lipa et al. 1977
<i>Thrips tabaci</i>	Poland & United States	A, L	F, S, L	Lipa et al. 1977, Smith et al. 2011

This table is updated and modified from Lipa et al. (1977)

¹Current scientific names in parenthesis

²Collections by Lipa et al. (1977) were made primarily from Poland, but may also represent observations from Czechoslovakia, Germany and Hungary

³Life stages: A=adults, E=eggs, L=larvae, N=nymphs, P=pupae

⁴Plant parts: S=stem, L=leaves, R=root, F=flower, O=occasional, SP=seedpod

⁵Lipa et al. (1977) listed larva instead of nymph for the immature stage of these hemimetabolous insects

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Chapter 2: Effects of artificial defoliation on the biomass and yield of pennycress, *Thlaspi arvense* (Brassicales: Brassicaceae), a new oilseed producing cover crop

Abstract

Pennycress (*Thlaspi arvense*) is a winter annual species found in temperate regions and in disturbed agricultural lands is being domesticated as a new winter cash cover crop in the Midwest of the United States. However, the response of pennycress to various stressors, including insect pests, remains poorly understood. Artificial defoliation has been effectively used to assess potential impacts of insect pests on several crop species. Over two years, we evaluated the impacts of artificial defoliation on pennycress biomass and yield. Field-planted pennycress was assessed in randomized complete block design experiments, with six replications of several treatments comprised of combinations of defoliation levels (25%, 50% and 100%) and timings. The timings included rosette (vegetative rosette), flowering (early flowering) and pod (early pod development), and a non-defoliated control. Our results demonstrated significant reduction in biomass and yield, particularly with defoliation of 100% at all stages. Rosette and flowering defoliation stages were particularly detrimental, highlighting the critical growth periods for pennycress. These findings enhance our understanding of pennycress's response to defoliation and can inform the

development of integrated pest management (IPM) programs for this emerging crop.

Introduction

Thlaspi arvense L. (Brassicales: Brassicaceae), commonly referred to as field pennycress or pennycress, is native to Eurasia and has invaded temperate regions of North America and Europe (Best and McIntyre 1975; Warwick et al. 2002; Phippen and Phippen, 2012). Despite its designation as a weed in some areas (Geng et al., 2021), pennycress has garnered interest in its utilization for sustainable agriculture, biofuel production, and ecological restoration (Phippen and Phippen, 2012).

Pennycress grows as both a summer and winter annual (Sedbrook et al., 2014). As a winter annual, it initiates germination in the fall, forming a cluster of leaves that persist over the winter as a low-growth rosette (Best and McIntyre, 1975). The subsequent spring heralds renewed growth, allowing pennycress to achieve a height of approximately 80 cm (Best and McIntyre, 1975). Initially, the stems that arise from the rosettes are unbranched, but they may exhibit branching as development proceeds (Anderson et al., 2016). As spring progresses, pennycress undergoes flowering and development of seed pods (i.e., silicles) (Cubins et al., 2019). Pennycress plants have the capacity to produce as many as 15,000 seeds per plant (Moser et al., 2009).

Pennycress is being domesticated as a new oilseed producing cover crop for temperate regions (Sedbrook et al., 2014). Pennycress serves as a valuable

oilseed crop with seeds rich in oil content (Sedbrook et al. 2014; Geng et al. 2021; Ma et al. 2023). Researchers are actively exploring its potential as a sustainable energy source for biofuel production. As a cover crop, pennycress contributes to soil health by preventing erosion, suppressing weeds, and enhancing nutrient cycling (Basnet and Ellison, 2024; Cubins et al., 2019; Ma et al., 2023; Muturi et al., 2024). Its deep root system helps break up compacted soil, improving water infiltration and nutrient absorption. Additionally, pennycress provides habitat and food for various wildlife species, with its flowers attracting pollinators and its seeds serving as a valuable food source during winter months (Sedbrook et al., 2014; Geng et al., 2021; Ma et al., 2023).

Advances in pennycress genetics and genomics have paved the way for rapid genetic improvement of various traits and ultimately the domestication of pennycress (Chopra et al., 2020; Ma et al., 2023). Furthermore, the agronomic practices for production of pennycress are being developed, including recommendations for sowing, fertilizing, and harvesting the crop (Cubins et al., 2019). Nevertheless, the response of pennycress to various stressors, such as insect pests, remains poorly understood. Pyke (1989) discovered that leaf removal in pennycress can lead to a reproductive shutdown if it happens early in the reproductive phase. However, if leaf removal occurs later during inflorescence development, it triggers a switch from reproductive to vegetative growth. This switch enables the plant to continue producing metamers, but when

resources are constrained, it results in the production of vegetative metamers (Pyke, 1989).

Insect pests pose a persistent and significant threat to global agriculture, impacting crop production and food security (Riegler, 2018). Insect defoliation reduces the plant's ability to photosynthesize effectively, which often results in reduced crop yields (Macedo et al., 2003). Yield losses due to defoliation can vary widely depending on the crop, insect species, and the timing and severity of defoliation (Macedo et al., 2003). Insect defoliators, including caterpillars (Lepidoptera), beetles (Coleoptera), and others have been found to feed on pennycress leaves (Idris and Grafius, 1996; Dossall and Moisey, 2004; Štolcová 2005; Cameron et al., 2007).

Artificial defoliation has been used successfully to assess potential impacts of insect pests on various crops (Burkness et al., 1999; Eskandarlee et al., 2024; Jetton and Robison, 2014; Pedigo et al., 2021; Poston et al., 1976; Syrový et al., 2016; Thrash et al., 2021; Tong et al., 2003), including another brassica species, cabbage, canola, rapeseed, sunflower, soybean (Burkness et al., 2005; Eskandarlee et al., 2024; Poston et al., 1976; Syrový et al., 2016; Thrash et al., 2021). Artificial defoliation is a controlled and deliberate process involving the removal of part or all leaf tissue from plants. This experimental technique allows one to quantify the impact of leaf removal on plant growth, development, and yield (Jetton and Robison, 2014; Tong et al., 2003).

In this two-year study, we assessed the effects of defoliation timing and intensity on the value of pennycress as a cover crop as measured by aboveground biomass, and as an oilseed crop as measured by total yield, yield components, and oil and protein contents. These results will provide a foundation for the development of pest management strategies for pennycress production and recommendation to growers and researchers.

Material and Methods

2020-2021 Experiment

Pennycress genotype MN106 (wild type) was fall-planted on 9 September 2020 in St. Paul, MN, United States. Seeds were sown at a depth of 0.64 cm and a seeding rate of 2.7 kg/ha with 1.54 m spacing between adjacent rows. Individual plots were one row wide and 0.61 m long with 0.61 m spacing between plots. No fertilizer was applied.

The experiment was performed as a randomized complete block design with six replications of four defoliation treatments and an undefoliated control. The defoliation treatments involved combinations of defoliation intensity and defoliation timing: 50% and 100% defoliation were applied at the rosette stage (stage 48: basal rosette with no signs of floral initiation) and at the flowering stage (stage 65: 50% of flowers open) (Altendorf et al., 2017).

Defoliation was carried out across the entire canopy of each plot using small scissors to remove leaf blade tissue. Rosette stage defoliation was

performed on 8 April 2021 to all leaves greater than 1.25 cm in length. The 50% level of defoliation involved removing the distal half of the leaf blade area (not including petiole) by cutting perpendicular to the leaf midvein. The 100% level of defoliation involved removing the entire leaf blade where it meets the petiole. Flowering stage defoliation was performed on 5 May 2021 to all leaves greater than 1.25 cm in length, with the same methods used at the rosette stage, for remaining basal and stem leaves, except when leaves had already died.

To validate the accuracy of the 50% defoliation treatment for each defoliation timing, 20 leaves were collected from outside the experimental plots, cut as described above, and imaged. Then, the ImageJ software version 1.54j (Schindelin et al., 2012) was used to calculate the actual mean defoliation percentage. The accuracy of the 100% defoliation treatment was not validated because the decision of where to cut on the leaf was much less subjective.

Pennycress was harvested on 16 June 2021 at the maturity stage (stage 97: plant dead or dry) (Altendorf et al., 2017) using a rice knife or pruning shears. All plants within each plot were cut at ground level and placed in a paper lawn-and-leaf bag (one bag per plot). Extra care was taken during the cutting and bagging process to prevent loss of seed. The harvested plants were then placed in a drying oven at 60°C for 7 days. The aboveground biomass was measured by weighing the dried plants from each plot. Plants were threshed using a threshing machine to ensure all seed pods were opened and all seeds were removed from pods. Seeds were separated from plant residue, first by manual removal of large

plant debris, and then using a seed blower (model B South Dakota Blower, Ames Powercount Co.) to remove fine plant debris.

Total seed weight from each plot was measured using a precision scale (Entris, Sartorius). To estimate seed size (i.e., 100-seed weight) for each plot, eight sets of 100 seeds were randomly selected for each plot, each set of 100 seeds was weighed using the precision scale, and the eight sets of weights were then averaged. The total number of seeds (SN) from each plot was estimated from the measured total seed weight (TW) and the estimated 100-seed weight (SS) as $SN=(TW/SS) \times 100$. Furthermore, the oil and protein content of the seed from each plot was measured using a NIR spectrometer (DA 7250, Perten Instruments) (Chopra et al., 2019).

2021-2022 Experiment

Pennycress genotype MN106 (wild type) was fall-planted on 15 September 2022, in St. Paul, MN, United States. Seeds were sown at a depth of 0.1 cm and a seeding rate of 2.7 kg/ha with 1.52 m spacing between adjacent rows. Individual plots were one row wide and 0.61 m long with 0.61 m spacing between plots. Nitrogen (22.68 kg/ha) was applied on 10 May 2022 on plots.

The experiment was performed as a randomized complete block design with six replications of seven defoliation treatments and an undefoliated control. The defoliation treatments involved combinations of defoliation intensity and defoliation timing: 50% defoliation was applied at the rosette stage (stage 48:

basal rosette with no signs of floral initiation); and 25%, 50% and 100% defoliation were applied at both the flowering stage (stage 65: 50% of flowers open, i.e., full flowering) and seedpod development stage (stage 69: 90% of flowers open, first pods reaching final size) (Altendorf et al., 2017).

Defoliation was carried out across the entire canopy of each plot using small scissors to remove leaf blade tissue with the same methods described for the 2020–2021 experiment. Defoliation at the rosette, flowering, and seedpod development stages were performed on 19 April, 16 May, and 01 June 2022, respectively.

To validate the accuracy of the 50% defoliation, the methods described from the 2020–2021 experiment were used on 14 leaves. Again, the accuracy of the 100% defoliation treatment was not validated, because the decision of where to cut the leaf was much less subjective.

On 21 June 2022, the pennycress was harvested at the maturity stage (stage 97: plant dead or dry) (Altendorf et al., 2017). Harvesting and processing were performed, and total seed weight, seed size, seed oil and protein contents were estimated with the same methods used for the 2020–2021 experiment.

Statistical Analysis

Defoliation data were analyzed using R version 4.2.0 (R Core Team, 2022) in Rstudio (RStudio Team, 2022). A separate analysis was conducted for each year for each response variable (i.e., biomass, yield, seed number, weight of 100

seeds, oil content and protein content). A linear regression model (package: stat, code: lm) was used to test the effects of the defoliation treatments and blocks on each response variable. The significance of defoliation treatments and blocks in each model was checked with a type II analysis of variance (package: car, code: Anova), and pairwise comparisons among the levels of treatment were conducted with estimated marginal means with p-values adjusted with the Tukey's method (package: emmeans; code: emmeans). Global validation of linear model assumptions (package: gvlma, code: gvlma) was used to conduct a test of the assumptions of the linear model for each response variable. All datasets met the assumptions.

Results

2020-2021 Experiment

The biomass of pennycress differed significantly among treatments ($F=49.98$; $df=4, 20$; $P<0.001$) and block ($F=4.34$; $df=5, 20$; $P<0.001$). Defoliation of 50% or 100% at the rosette or flowering stages had lower biomass compared to the control (Figure 1.1A). The biomass of pennycress was lower for 100% defoliation compared to 50% defoliation at either timing (Figure 1.1A).

Similarly, total yield differed significantly among treatments ($F=23.20$; $df=4, 20$; $P<0.001$) and was not significant for blocks ($F=1.07$; $df=5, 20$; $P=0.406$). Defoliation of 100% at the rosette or flowering stages had lower total yields

compared to the control (Figure 1.1B). Total yield was lower for 100% defoliation compared to 50% defoliation at either timing (Figure 1.1B).

The weight of 100 seeds differed significantly among treatments ($F=12.17$; $df=4, 20$; $P<0.001$) and was not significant for blocks ($F=2.65$; $df=5, 20$; $P=0.054$). Defoliation of 100% at the rosette or flower stages had lower weight of 100 seeds compared to the control. The weight of 100 seeds was lower for 100% defoliation at the rosette stage compared to the other defoliation treatments (Figure 1.1C).

The seed number differed significantly among treatments ($F=17.07$; $df=4, 20$; $F<0.001$) and was not significant for blocks ($F=1.42$; $df=5, 20$; $P=0.258$). The defoliation of 100% at the rosette or flowering stages had lower seed numbers compared to the control (Figure 1.1D). Seed number was lower for 100% defoliation at the flowering stage compared to 50% defoliation at the rosette stage (Figure 1.1D).

The oil content differed significantly among treatments ($F=24.86$; $df=4, 20$; $P<0.001$) and was not significant for blocks ($F=1.34$; $df=5, 20$; $P=0.285$). The oil content was higher for all defoliation treatments compared to the control (Figure 1.1E). Defoliation of 50% at the flowering stage had higher oil content compared to 100% defoliation at the rosette and flowering stages (Figure 1.1E).

The protein content differed significantly among treatments ($F=5.77$; $df=4, 20$; $P=0.002$) and was not significant for blocks ($F=1.32$; $df=5, 20$; $P=0.295$).

Defoliation of 100% at the rosette or flowering stages, or 50% at the flowering stage had lower protein contents compared to the control (Figure 1.1F).

2021-2022 Experiment

The biomass of pennycress differed significantly among treatments ($F=4.91$; $df=7, 35$; $P<0.001$) and was not significant for blocks ($F=0.52$; $df=5, 35$; $P=0.763$). Defoliation of 100% at the flowering stage had lower biomass compared to the control (Figure 2.1A). Defoliation of 100% at the flowering stage had lower biomass compared to defoliation of 25% at the flower and pod stages, defoliation of 50% at the rosette stage and defoliation of 100% at the pod stage.

The total yield differed significantly among treatments ($F=6.68$; $df=7,35$; $P<0.001$) and was not significant for blocks ($F=0.75$; $df=5, 35$; $P=0.591$). Defoliation of 100% at the flowering stage had lower total yields compared to the control (Figure 2.1B). Defoliation of 100% at the flowering stage had lower total yield compared to the other defoliation treatments, except defoliation of 100% at the pod stage.

The weight of 100 seeds differed significantly among treatments ($F=3.55$; $df=7,35$; $P<0.001$) and blocks ($F=2.50$; $df=5, 35$; $P<0.001$). Defoliation of 100% at the pod stage had a lower weight of 100 seeds compared to the control (Figure 2.1C). Defoliation of 100% at pod stage had lower weight of 100 seeds compared to 25% and 50% defoliation at flowering and rosette stages respectively.

Furthermore, defoliation of 100% at the pod stage did not differ from defoliation of 50% and 100% at the flowering stage, and 25% and 50% at pod stage.

The seed number differed significantly among treatments ($F=5.90$; $df=7,35$; $P<0.001$) and was not significant for blocks ($F=0.65$; $df=5, 35$; $P=0.662$). Defoliation of 100% at the flowering stage had lower seed numbers compared to the control (Figure 2.1D). Furthermore, defoliation of 100% at the flowering stage had lower seed numbers compared to defoliation of 25% at the flowering and pod stages, and 50% at the rosette, flower, and pod stages.

The pennycress oil content did not differ among treatments ($F=0.69$; $df=7,35$; $P=0.683$) (Figure 2.1E) and blocks ($F=0.89$; $df=5, 35$; $P=0.828$).

The protein content differed significantly among treatments ($F=3.64$; $df=7,35$; $P<0.001$) and was not significant for blocks ($F=0.75$; $df=5, 35$; $P=0.498$). Defoliation of 50% and 100% at the pod stages had lower protein contents compared to the control (Figure 2.1F). Furthermore, defoliation of 100% at the pod stage did differ from the defoliation of 25% at the flowering stage (Figure 2.1F).

Discussion

Pennycress is being considered as a major winter oilseed crop, offering environmental benefits such as erosion control, and serving as a food source for pollinators (Basnet and Ellison, 2024; Cubins et al., 2019; Ma et al., 2023). The present study provides the most thorough assessment of the impacts of

defoliation on pennycress. Intensity and timing of defoliation significantly affected pennycress aboveground biomass, total yield, seed size, seed number and protein and oil content.

Biomass consistently decreased in both years when 100% defoliation occurred during the flowering stage, whereas susceptibility to 50% or less defoliation at various growth stages varied between years. These finds are consistent with prior research in canola/rapeseed *Brassica napus* L. (Brassicales: Brassicaceae), and sunflower *Helianthus annuus* L. (Asterales: Asteraceae), where defoliation has been shown to reduce biomass accumulation (Alimohammadi and Azizov, 2019; Ghafoor et al., 2023; McCormick et al., 2013). Cover crops are commonly used to suppress weeds by outcompeting them for resources such as light, nutrients, and space (Kunz et al., 2016; Price and Norsworthy, 2013; Teasdale, 1996). Higher biomass in cover crops leads to more effective competition for these resources, resulting in improved weed suppression and enhanced ecosystem services (Kunz et al., 2016; Price and Norsworthy, 2013; Teasdale, 1996).

Defoliation can negatively affect root growth and function by reducing the supply of photosynthates, which limits the energy available for root development and impairs water and nutrient uptake, further reducing biomass (Farooq et al., 2009; Mohammadi Alagoz et al., 2023). Additionally, defoliation can disrupt root-shoot signaling, leading to altered growth patterns and reduced overall plant vigor (Farooq et al., 2009; Mohammadi Alagoz et al., 2023). The removal of

leaves also decreases transpiration rates, impacting the plant's water regulation and altering water uptake and distribution (Farooq et al., 2009; Mohammadi Alagoz et al., 2023). Changes in water movement and hydraulic conductivity due to defoliation can lead to water stress and further reduce growth (Farooq et al., 2009; Mohammadi Alagoz et al., 2023).

Pennycress seeds, rich in oil content (>30%), are emerging as a valuable resource in bio-industry (Esfahanian et al., 2021). Similar to biomass, susceptibility of pennycress to yield impacts from 50% or less defoliation at different growth stages varied between years, but 100% defoliation during the flowering stage decreased total yield and seed number in both years. Similarly, Pyke (1989) found that intensity and timing of defoliation are crucial in determining the extent of impact on pennycress yield. Furthermore, multiple studies have indicated that defoliation can reduce yield of canola (Alimohammadi and Azizov, 2019; Barimavandi et al., 2010; Ghafoor et al., 2023). Syrový et al. (2016) reported that defoliation of 100% reduced canola yield more than defoliation of 50%. Clarke (1978) found 24% yield reduction in canola when defoliated completely at the flowering stage. Lastly, Baldwin et al. (2021) observed that defoliation over 50% at both vegetative and flowering stages reduced yield in *Brassica carinata* A. Braun (Brassicales: Brassicaceae).

Defoliation primarily impacts a plant's ability to photosynthesize by reducing leaf area (Baslam et al., 2020; Iqbal et al., 2012; Lin et al., 2012; Tanaka and Makino, 2009). Reduced leaf area limits carbon dioxide (CO₂)

absorption by the plants and, consequently, carbon assimilation during photosynthesis (Briske and Richards, 1995; Iqbal et al., 2012). During photosynthesis, there is accumulation of carbohydrates that are used by the plants for growth of seeds (Diepenbrock, 2000; Ghafoor et al., 2023; Raza et al., 2022). Defoliation of 100% halts plant's carbohydrate production, severely limiting the supply of sugars that are essential for seed development. This can cause the plant to redirect more resources toward vegetative growth, a compensatory mechanism also observed in canola plants (McCormick et al., 2013; Ramachandran et al., 2000). The energy and time required to regrow leaves can delay the plant's overall development (Kirkegaard et al., 2018). This delay can affect the timing of flowering and subsequently the seed development phase.

In addition, defoliation induces stress responses in plants, activating hormones like abscisic acid (ABA) (Kaur et al., 2021; Pan et al., 2023) and jasmonic acid (JA), which trigger various physiological changes (Pan et al., 2023; Singh and Roychoudhury, 2023). ABA and JA can modify gene expression patterns, influencing seed dormancy, enhance flower development by modulating stamen and petal growth, and influence the timing of flowering through interactions with other plant hormones (Kaur et al., 2021; Pan et al., 2023, 2020; Peng et al., 2021). These responses can indirectly influence seed development, flowering, and other vital processes (Kaur et al., 2021; Pan et al., 2023, 2020; Peng et al., 2021; Singh and Roychoudhury, 2023).

Plants in their early growth stages are generally more resilient to defoliation. They can often compensate for the effects of defoliation by delaying maturation and extending the vegetative phase, which allows them to regenerate lost leaf area and recover in terms of biomass (Jamshidi Zinab et al., 2023; McCormick et al., 2013). In contrast, the effects of defoliation become more critical during the flowering and reproduction stages because the plant has less flexibility to alter its developmental timeline, resulting in the production of fewer seeds. This underscores the sensitivity of these two growth stages (Clarke, 1978; Kirkegaard et al., 2012; McCormick et al., 2013; Syrový et al., 2016; Ulas et al., 2015).

Increased oil content in pennycress is beneficial for enhanced biofuel production, economic profitability and versatility in industrial applications (Ma et al., 2023). All defoliation treatments resulted in increased oil content of pennycress seed in year 1, but no effects of defoliation on oil content were observed in year 2. Fortescue and Turner, (2007) noted that defoliation of canola had minimal effect on oil content, even though it significantly reduced seed number. In contrast, Kirkegaard et al., (2018) and Ghafoor et al., (2023) reported that defoliation in canola and rapeseed lowered oil content, likely due to a reduced supply of assimilates to the flower buds.

Protein content can affect the utility of pennycress in applications like animal feed or in industries that require high-protein biomass (Sun et al., 2023). Some defoliation treatments resulted in decreased protein content of pennycress,

but the effects of intensity and timing of the defoliation were inconsistent between years. Similarly, Proulx and Naeve, (2009) found that defoliation decreased protein content in soybean. In contrast to our study, defoliation was found to increase protein content in rapeseed and canola (Ghafoor et al., 2023; Kirkegaard et al., 2018).

Defoliation can induce the expression of genes involved in lipid (oil) biosynthesis (Vanhercke et al., 2019; Yao et al., 2024; Zhang et al., 2016). This response entails the upregulation of genes encoding enzymes crucial for fatty acid synthesis, leading to a reallocation of resources that enhances oil production and increases oil content within the plant (Vanhercke et al., 2019; Yao et al., 2024; Zhang et al., 2016). This response to defoliation could be attributed to possible shift in metabolic activity towards oil production (Iqbal et al., 2012).

Defoliation can disrupt nitrogen uptake and assimilation, reducing the availability of nitrogen for protein synthesis (Schjoerring et al., 1995). Schjoerring et al., (1995) found that 50% of the total nitrogen in winter *Brassica napus* L. (Brassicales: Brassicaceae) is in the rosette leaves before flowering. As the plant progresses, this nitrogen is transferred from the leaves to the stems, pods, and eventually the developing seeds. As the plants grow, senescence of the leaves can lead to a loss of about 10% of the absorbed nitrogen, but defoliation can remove up to 50% of the nitrogen, depending on the growth stage of the plant when defoliation occurs (Schjoerring et al., 1995).

Conclusion

Our results indicated that defoliation reduced pennycress biomass, yield and yield components, and protein content. Such reductions could compromise the overall productivity and profitability of pennycress. Interestingly, our findings also revealed an increase in oil content in seeds following defoliation. This increase, while potentially beneficial for biofuel production, may not offset the overall negative effects of defoliation on crop yield and seed quality. Thus, our study underscores the need for effective management strategies to mitigate defoliation and optimize pennycress production for both agricultural and industrial uses. Further research should evaluate how different environmental factors influence the response of pennycress to defoliation and identify traits associated with enhanced biomass and yield under stress.

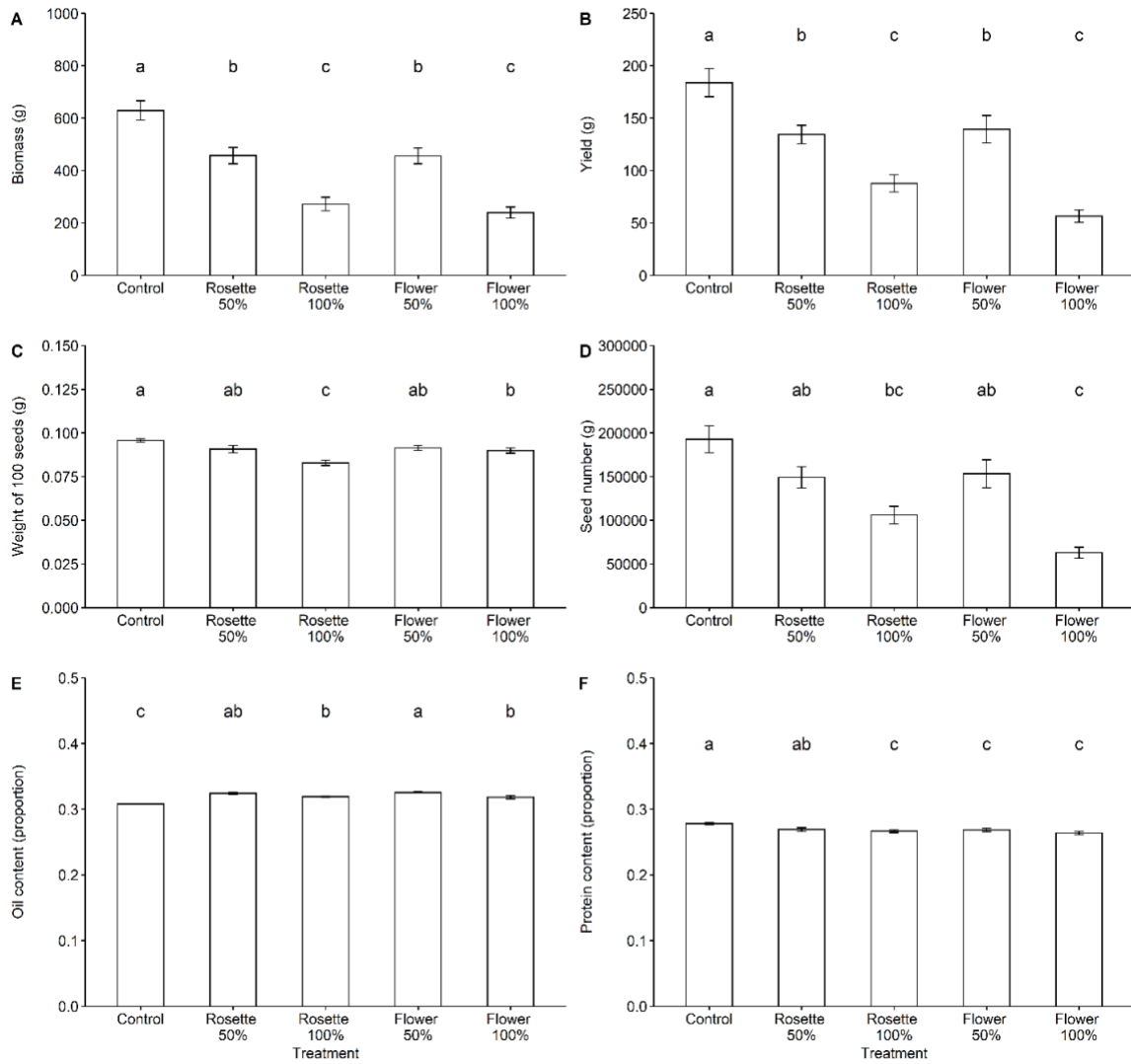


Figure 1. 1: Mean (\pm SE) biomass (A), yield (B), weight of 100 seeds (C), seed number (D), oil content (E) and protein content (F) per plot for pennycress that underwent artificial defoliation at levels of 50% or 100% at rosette or flower growth stages in a field experiment in Minnesota, US in 2020-2021. Means with different letters differ significantly ($p < 0.05$), ANOVA and Tukey's HSD test.

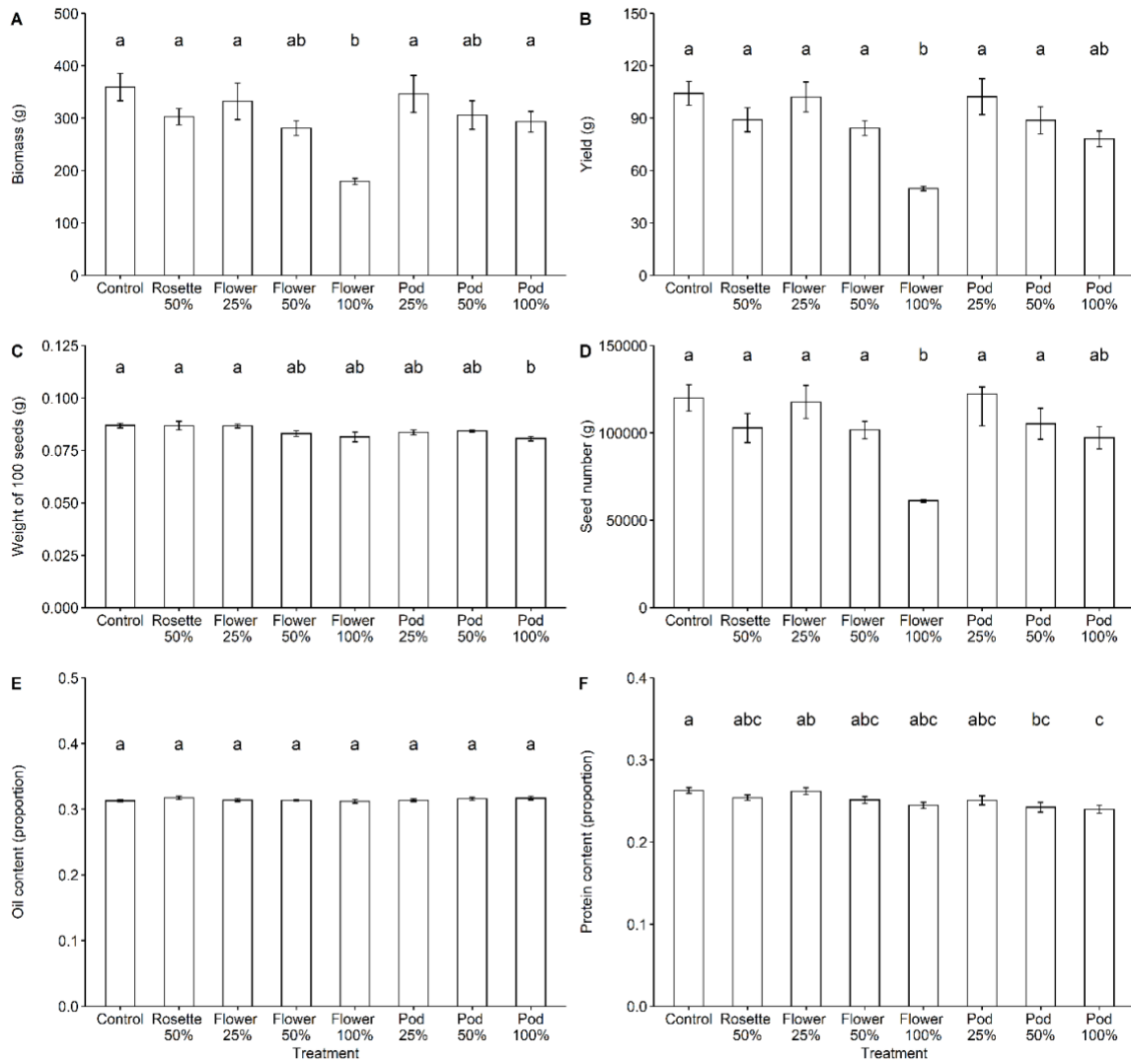


Figure 1. 2: Means (\pm SE) biomass (A), yield (B), weight of 100 seeds (C), seed number (D), oil content (E) and protein content (F) per plot for pennycress that underwent artificial defoliation at levels of 25%, 50% and 100% at rosette, flower, or pod growth stages in a field experiment in Minnesota, US in 2021-2022. Means with different letters differ significantly ($p < 0.05$), ANOVA and Tukey's HSD test.

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Chapter 3: Potential of relay-cropping soybean with a pennycress (*Thlaspi arvense*) cover crop to suppress soybean aphid (*Aphis glycines*) populations

Abstract

The soybean aphid *Aphis glycines* (Matsumura), remains a major pest for soybean growers in the Midwest, leading to yield losses of up to 40% and developing resistance to some insecticides. This underscores the necessity for more sustainable pest management approaches, such as cultural control methods. Relay-cropping soybean with a winter cover crop has shown potential in reducing soybean pest populations. Field pennycress or pennycress (*Thlaspi arvense*) is currently being domesticated as a new cover crop and oilseed crop and in this study, we evaluated the impact of relay-cropping soybean with pennycress as a cover crop on soybean aphid populations across four site-years in Minnesota. The experimental design included combinations of two soybean varieties planted with and without pennycress. Aphid populations were monitored weekly by counting aphids on ten randomly selected soybean plants per plot. Though aphid infestations were relatively low across the site-years, the results demonstrated that soybean relay-cropped with pennycress had lower densities compared to soybean without the cover crop. These findings indicate that pennycress cover crops hold promise as a cultural control tactic to reduce soybean aphid populations, providing a more sustainable pest management

option for growers. Additionally, the use of pennycress as a winter cover crop could incentivize its adoption in corn-soybean rotations, enhancing both pest control and crop diversification.

Introduction

In the upper Midwest of the United States, corn (*Zea mays* L. (Poales: Poaceae)) and soybean (*Glycine max* (L.) Merr. (Fabeles: Fabaceae)) are frequently rotated year-to-year in cropping systems (Edwards et al. 1988, Mourtzinis et al. 2017, Rusch et al. 2020). Such systems heavily rely on external inputs and have a prolonged fallow period between planting seasons (Rusch et al. 2020). During this fallow time, the soil is at risk of erosion and valuable nutrients may leach into nearby water bodies (Rusch et al. 2020). Introducing winter cover crops into such rotations can help mitigate these issues and enhance the sustainability of the farming system (Cubins et al. 2019, Rusch et al. 2020).

Cover crops play a pivotal role in sustainable agriculture, benefiting both the environment and farmers. These crops contribute to soil health by reducing erosion, stabilizing soil and reducing nutrient runoff (Fageria et al. 2005, Snapp et al. 2005, Plastina et al. 2020). *Thlaspi arvense* L. (Brassicales: Brassicaceae) commonly known as pennycress or field pennycress is being developed as a new crop (Mitich 1996, Moser et al. 2009, Sedbrook et al. 2014, Cubins et al. 2019). Originally from Eurasia, pennycress grows as a weed across temperate

regions of North America ((Mitich 1996, Moser et al. 2009, Sedbrook et al. 2014, Cubins et al. 2019). However, pennycress caught the attention of the agricultural sector in the upper Midwest due to its potential for economic value and ecosystem services (Phippen and Phippen 2012, Bishop and Nelson 2019, Cubins et al. 2019). Pennycress can be integrated into rotations, such corn-soybean or wheat-soybean, as a winter cover crop (Phippen and Phippen 2012, Cubins et al. 2019a, 2019b, Ott et al. 2019). After the harvest of wheat or corn in the summer or fall, respectively, pennycress is planted. The pennycress germinates and establishes itself before winter, providing ground cover during fall, winter and spring. Soybeans are then double cropped or relay-planted with the pennycress in late spring before pennycress harvest (Phippen and Phippen 2012, Cubins et al. 2019a, 2019b, Ott et al. 2019).

The use of cover crops, particularly in reduced tillage systems, can impact arthropod populations through various mechanisms (Tillman et al. 2004, Schmidt et al. 2018, Scavo et al. 2022). The temporal overlap of the two crops (e.g., pennycress and soybean) in relay-planting creates a polyculture, as opposed to the typical monoculture (e.g., soybean alone). Polycultures can reduce herbivore densities by decreasing the concentration of resources available to pests (i.e., resource concentration hypothesis) (Root 1973). Polycultures can also enhance the presence and effectiveness of natural enemies of pests, thereby reducing pest populations (i.e., natural enemies hypothesis) (Root 1973). In addition, polycultures can also alter the quality of host plants through interspecific plant

competition, leading to reduced herbivore densities (Altieri and Letourneau 1982). Furthermore, tillage practices and the presence of cover crop residue in the soil can either increase or decrease insect populations (Stinner and House 1990). The mechanical disturbance of soil through tillage exposes soil-dwelling pests to predators and parasitoids, or potentially causes physical harm to or traps the pests (Williams, 2010; Rivers et al., 2017; Skidmore et al., 2019).

In the upper Midwest of the United States, soybean continues to face significant challenges from soybean aphid (*Aphis glycines* Matsumura) (Ragsdale et al. 2007, Koch et al. 2015, 2018, Hanson et al. 2017). This pest can cause up to 40% yield loss causing significant economic loss to soybean growers (Ragsdale et al. 2007). Native to Asia, soybean aphid was first detected in North America in Wisconsin in 2000 and quickly spread across most of the soybean growing areas (Ragsdale et al. 2007, Tilmon et al. 2011, Koch et al. 2015, 2018, Hanson et al., 2017). Feeding by the soybean aphid is linked to decreased plant height, fewer pods, smaller seed size and quality, and lower crop yields (Ragsdale et al. 2007). This pest is also known to transmit various plant diseases and the honeydew it secretes encourages the development of sooty mold on the leaves of soybean plants (Tilmon et al. 2011).

Since 2000, the soybean aphid has been intensively managed due to its potential for significant economic damage (Song and Swinton 2009). While various pest management strategies exist, including host-plant resistance and biological control, the predominant method remains the use of foliar insecticides

(Hodgson et al. 2012, Koch et al. 2015, 2018). However, aside from these known control methods, another management strategy that has garnered interest is the employment of cover crops as a cultural control to reduce soybean aphid populations (Heimpel et al. 2005, Koch et al. 2012). Research has shown that the population of soybean aphids can be suppressed when soybeans are relay-cropped with a rye (*Secale cereal* L.) cover crop (Koch et al. 2012, 2018).

Despite the recognized benefits of cover crops for soil health and pest management, their adoption by farmers has been minimal in northern states like Minnesota (Dunn et al. 2016, Burnett et al. 2018, Cubins et al. 2019, Scavo et al. 2022). However, there is a growing interest in and a higher potential for the adoption of pennycress as a cover crop due to its combined benefits as a cover crop and oilseed crop (Dunn et al. 2016, Burnett et al. 2018, Cubins et al. 2019, Scavo et al. 2022). Given this increasing interest, the objective of this study was to evaluate the potential effects of relay-cropping soybean with a pennycress cover crop on soybean aphid populations across multiple site-years in Minnesota.

Materials and Methods

This study was conducted at the University of Minnesota Rosemount Research and Outreach Center, Rosemount, MN (44° 43'N, 93°04'W; 294 m above sea level) in 2022 and 2023, the USDA-ARS Swan Lake Research Farm, Morris, MN (45°40'N, 95°48'W; 345 m above sea level) in 2022, and the

University of Minnesota Experiment Station at St. Paul, MN (44° 59'N, 93°10'W; 294 m above sea level) in 2023. The soil at Rosemount, Morris and St. Paul were Waukegan silt loam (i.e., fine-silty over sandy, mixed, superactive, mesic Typic Hapludoll), Aazdahl-Formdale-Balaton clay loam (i.e., fine-loamy, mixed, superactive, frigid Aquic Hapludoll) and Waukegan silt loam (i.e., fine-silty over sandy or sandy-skeletal, mixed, superactive, mesic Typic Hapludoll), respectively (Web Soil Survey USDA-NRCS, 2024). In 2022, the annual average temperature and liquid precipitation for Rosemount and Morris were 6.1°C and 5.4°C, and 75.8 cm and 56.1 cm, respectively (USDA-ARS, 2023). In 2023, the annual average temperature and liquid precipitation for Rosemount and St. Paul were 8.2°C and 8.3°C, and 96.0 cm and 96.6 cm, respectively (USDA-ARS, 2023). The plant hardiness zones for Rosemount, Morris and St. Paul are 5a, 4b, and 5a, respectively (USDA-ARS, 2023).

The treatments evaluated for this study were a subset of a larger experiment that was conducted using a split-plot design with the presence or absence of pennycress as a whole-plot factor and soybean variety as the split-plot factor at four site-years (Roberts and Lorenz, unpublished). Pennycress genotype MN-106NS, a black-seeded variety originally collected in Coates, MN, with minimal silicle shattering (Dorn et al. 2013, 2015), was used as the cover crop treatment across all site years. Pennycress was planted after harvest of spring wheat at 11.21 kg/ha on 13 and 17 September 2021 at Rosemount and Morris, respectively, and on 26 and 30 September 2022 at Rosemount and St.

Paul, respectively. At Rosemount 2022, Morris 2022 and Rosemount 2023, pennycress was planted 0.3 cm deep in multiple passes of the planter with 3 rows of pennycress planted 19 cm apart and a skip row where soybean would be planted between each set of three rows of pennycress, so that three rows of pennycress would separate each row of soybean. At St. Paul 2023, pennycress was broadcast seeded with an alfalfa seeder. In early spring when pennycress growth resumed, 56.04 kg/ha of nitrogen in the form of urea was applied.

In years 1 and 2 of the larger experiment, 40 and 8 soybean genotypes, respectively, were used as the split-plot factor at each site. For the present study, two commercial soybean genotypes BS1146 and AgriGold G1502RX (referred to here as AgriGold) were chosen sampling. BS1146, developed by Brushvale Seed, is a conventional food-type soybean, with large seeds and high protein, developed for organic systems. AgriGold, developed by AgReliant Genetics, is tolerant of glyphosate and dicamba herbicides. Both varieties have tolerance to soybean cyst nematodes and similar maturities (1.1 vs 1.5 maturity group). Soybean was planted 3.8 cm deep with 0.76 m row spacing and a seeding rate of 70,512 seed per hectare on 10 and 26 May 2022 at Rosemount and Morris, respectively, and on 5 June and 31 May 2023 at Rosemount and St. Paul, respectively. Soybean plots were 11.15 m long and 4 rows (3.66 m wide). Soybean was planted into whole-plots with a standing pennycress crop after the start of flowering, and prior to silicle formation and canopy closure of the pennycress, or into whole plots without a cover crop. After the emergence of

soybean, pennycress was harvested on 23 and 28 June 2022 at Rosemount and Morris, respectively, and on 11 July 2023 in St. Paul. However, pennycress was not harvested at Rosemount 2022, due short pennycress plant height caused by drought.

To determine the abundance of soybean aphids in the research plots, each plot was sampled weekly during the growing season for soybean. On each sample date, ten soybean plants were randomly selected from the middle two row of each plot, and nondestructive visual whole-plant inspections were performed to quantify soybean aphids. Counts of soybean aphid from each plant included nymphs and winged and wingless adults. Aphid counts were then summarized as cumulative aphid-days (CAD) (Hanafi et al. 1989) using the formula:

$$CAD = \sum_{i=1}^n \left[\frac{(x_i + x_{i+1})}{2} \right] \times t_i, \text{ where } x_i \text{ is the mean number of aphids per plant on a}$$

given sample date is the mean number of aphids per plant on the subsequent sample date, and t_i is the number of days between two consecutive sample dates.

Statistics

Analyses were performed using R version 4.2.0 (R Core Team 2022) in Rstudio (RStudio Team 2022). Separate analyses were conducted for each site-year using linear regression models (package: `stat i, x_{i+1}`, code: `lm`) with CAD as the response variable and cover crop (presence or absence), soybean variety

(BS1146 or AgriGold), and their interaction as predictors. Because of the spatial configuration of the plots of the two soybean varieties examined for this study, the analyses were performed as if the experimental design was a randomized complete block. The significance of cover crop and variety in each model was assessed with analysis of variance (package: car, code: Anova), and pairwise mean comparisons were performed with the p-value adjusted with the Tukey's method (package: emmeans; code: emmeans).

Results

Year 1

At Rosemount 2022, mean aphid densities ranged from 0 to 17.4 aphids per plant per date across treatments and sample dates, with the peak density occurring on 25 August. Soybean varieties relay-cropped with the pennycress cover crop had lower CAD compared to soybean varieties without the pennycress cover crop ($F=17.4$; $df=1,4$; $P<0.001$) (Figure 1). The effects of soybean variety ($F=2.2$; $df=1,4$; $P=0.18$) and the interaction between soybean variety and cover crop ($F=3.2$; $df=1,4$; $P=0.11$) were not significant.

At Morris 2022, mean aphid densities ranged from 0 to 123.0 aphids per plant per date across treatments and sample dates, with the peak density occurring on 23 August. Soybean varieties relay-cropped with the pennycress cover crop had marginally lower CAD compared to soybean varieties without the pennycress cover crop ($F=4.42$; $df=1,4$; $P=0.07$) (Figure 2). The effects of

soybean variety ($F=0.70$; $df=1,4$; $P=0.43$) and interaction ($F=0.00$; $df=1,4$; $P=0.10$) were not significant.

Year 2

At Rosemount 2023, mean aphid densities ranged from 0.3 to 34.3 aphids per plant per date across treatments and sample dates, with the peak density occurring on 8 August. Soybean varieties relay-cropped with the pennycress cover crop had lower CAD compared to soybean varieties without pennycress cover crop ($F=1.8$; $df=1,8$; $P<0.001$) (Figure 3). The effects of soybean variety ($F=0.00$; $df=1,8$; $P=0.97$) and the interaction between soybean variety and cover crop ($F=1.14$; $df=1,8$; $P=0.30$) were not significant.

At St. Paul 2023, mean aphid densities ranged from 0.9 to 45.7 aphids per plant per date across treatments and sample dates, with the peak density occurring on 24 July. Soybean varieties relay-cropped with the pennycress cover crop had lower CAD compared to soybean varieties without pennycress cover crop ($F=113.8$; $df=1,8$; $P<0.001$) (Figure 4). The effects of soybean variety ($F=2.95$; $df=1,8$; $P=0.11$) and the interaction between soybean variety and cover crop ($F=0.11$; $df=1,8$; $P=0.74$) were not significant.

Discussion

In this study, soybean varieties relay-cropped with pennycress generally exhibited lower CAD for soybean aphid compared to soybean varieties without pennycress. Across the four site-years, there were no significant effects of

soybean variety or interaction between soybean variety and cover crop. Similarly, Koch et al. (2012) found that relay-cropping soybean with rye with led to reductions in soybean aphid densities. Schmidt et al. (2007) documented reductions in soybean aphid numbers when soybean was planted into alfalfa as a living mulch and attributed this to enhance the presence of natural enemies. Using a spring-seeded oat (*Avena sativa* L.) or rye cover crops, Lundgren et al. (2013) found that soybean aphid populations were lower compared to systems without the use of cover crops. Overall, the results presented here, and supported by similar research, highlight the potential for relay-cropping soybean into pennycress as a potential sustainable pest management strategy.

Though it remains unknown how pennycress affected soybean aphid populations on soybean, various mechanisms have been proposed to explain the differences in herbivore populations between polycultures and monocultures (Bröcher et al., 2023). According to the resource-concentration hypothesis, herbivores are more likely to locate and stay on a host plant in monocultures than in polycultures, leading to higher population densities in monocultures (Root 1973). Volatiles produced by pennycress may influence soybean aphid populations by either deterring the aphids or attracting their natural enemies, potentially reducing aphid infestations in soybean field (Hodgson et al. 2012). Additionally, the polyculture created by planting soybean into the cover crop can support a diverse community of natural enemies, such as predators and parasitoids, that help control aphid populations (Tillman et al. 2004, Schmidt et al.

2018, Scavo et al. 2022, Adjeiwaa et al. 2024). Numerous studies have shown that generalist natural enemies play a crucial role in managing soybean aphid population in North America (Costamagna and Landis 2006, Ragsdale et al. 2011). Our results suggests that relay-cropping with pennycress offers a promising strategy for managing soybean aphid populations. If pennycress is implemented in a double-cropping system, we expect to potentially see more or less impact on soybean pests, because there would no longer be co-occurrence (i.e., a polyculture) of both species. However, further research is needed to understand the dynamics of pest populations in such a system.

To maximize the benefits of relay-cropping soybean with pennycress, it is essential to optimize the agronomics of the system to reduce competition between the two crops. This includes fine-tuning planting densities, adjusting sowing and harvest timings, and managing nutrients effectively to ensure both crops thrive without compromising each other's yields (Johnson et al. 2015, Cubins et al. 2019, Ott et al. 2019, Basnet and Ellison 2024). Additionally, the economic feasibility of this approach must be evaluated, considering the costs of implementation, potential yield impacts, and market demand for pennycress as an oilseed crop (Johnson et al. 2015, Cubins et al. 2019, Ott et al. 2019, Basnet and Ellison 2024). A thorough cost-benefit analysis will be crucial in determining whether this integrated cropping system is a profitable and sustainable option for corn-soybean growers.

By leveraging the ecological benefits of cover crops, farmers may be able to reduce reliance on insecticides, promote biodiversity, and enhance the sustainability of their cropping systems (Huss et al. 2022, Quintarelli et al. 2022, Scavo et al. 2022). This shift away from chemical control would not only lower costs associated with purchasing and applying insecticides but also decrease the associated environmental and human health risks (Huss et al. 2022). These findings support the integration of cover crops into IPM programs. Such cultural practices could be combined with other IPM strategies such as biological controls and resistant soybean varieties, so that farmers can develop more robust sustainable pest management systems (Philips et al. 2014, Riyaz and Kathiravan 2019, Deguine et al. 2021).

Conclusion

Our study demonstrates that relay-cropping soybean with a pennycress cover crop can significantly reduce soybean aphid populations compared to soybean grown without pennycress. The consistent reduction in aphid populations observed across different years and locations underscores the potential effectiveness of pennycress as a component of integrated pest management strategies in soybean production. However, across these site years, soybean aphid populations were low compared to the economic threshold of 250 aphids per plant (Ragsdale et al. 2007); therefore, further research is needed to evaluate the pest suppressive effects under higher levels of aphid infestation. In addition, future research should explore the long-term impacts of

cover crops on pest dynamics and crop yields across a diverse agroecological region, as well as the economic feasibility of such practices for farmers. By integrating cover crops like pennycress into their soybean production system, farmers may improve insect pest control, in addition to the other documented ecological services of this new cover crop (e.g., enhanced soil health, nutrient management, weed suppression and pollinator resources).

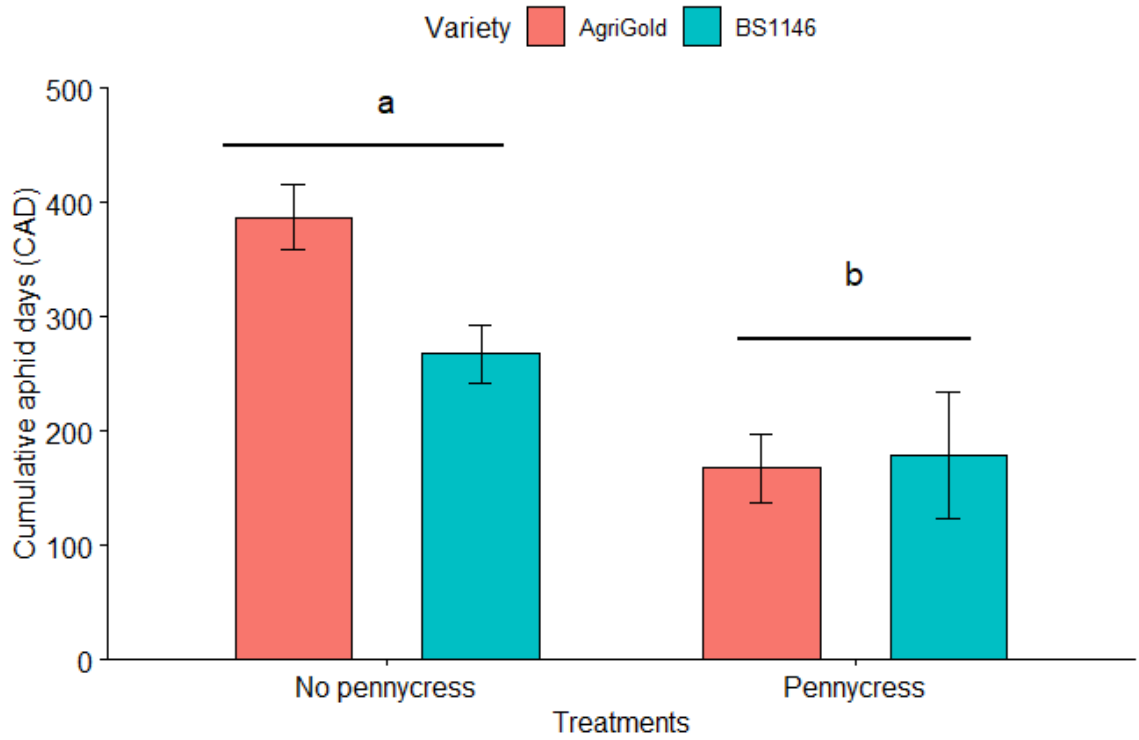


Figure 2. 1: Mean (\pm SE) cumulative aphid days (CAD) for soybean aphid on two soybean varieties (AgriGold and BS1146) relay-cropped with pennycress and no pennycress at Rosemount, Minnesota in 2022. Means with different letters differ significantly ($p < 0.05$), ANOVA.

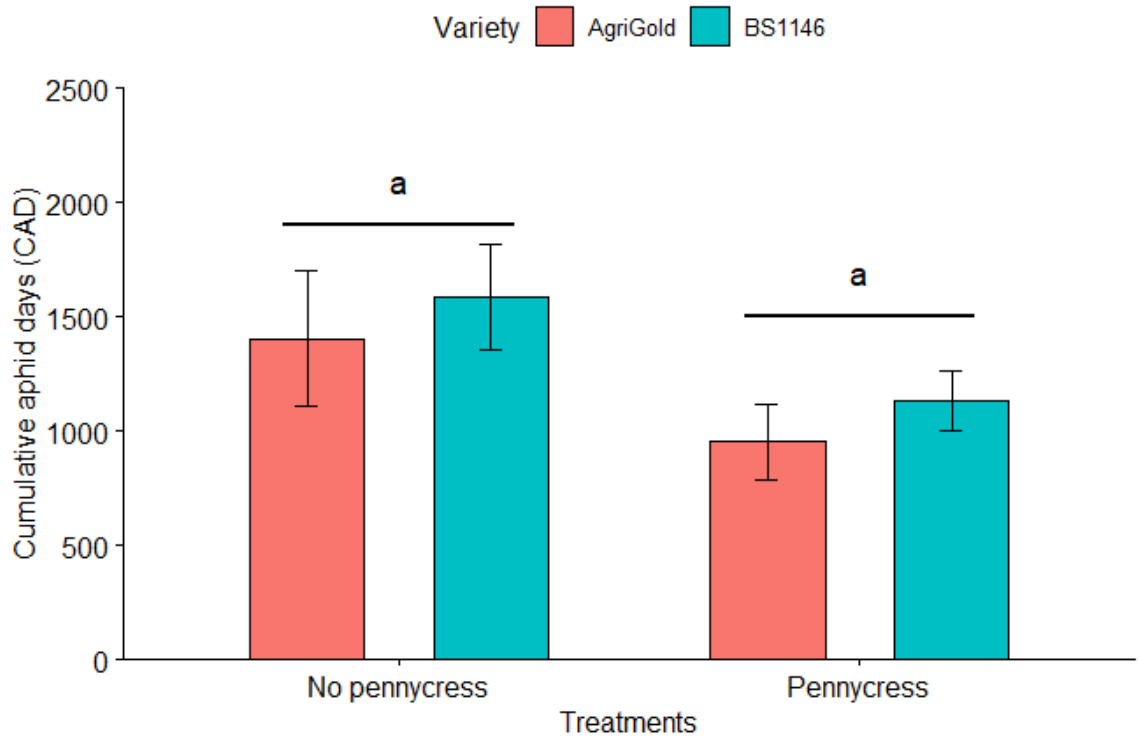


Figure 2. 2: Mean (\pm SE) cumulative aphid days (CAD) for soybean aphid on two soybean varieties (AgriGold and BS1146) relay-cropped with pennycress and no pennycress at Morris, Minnesota in 2022. Means with different letters differ significantly ($p < 0.05$), ANOVA.

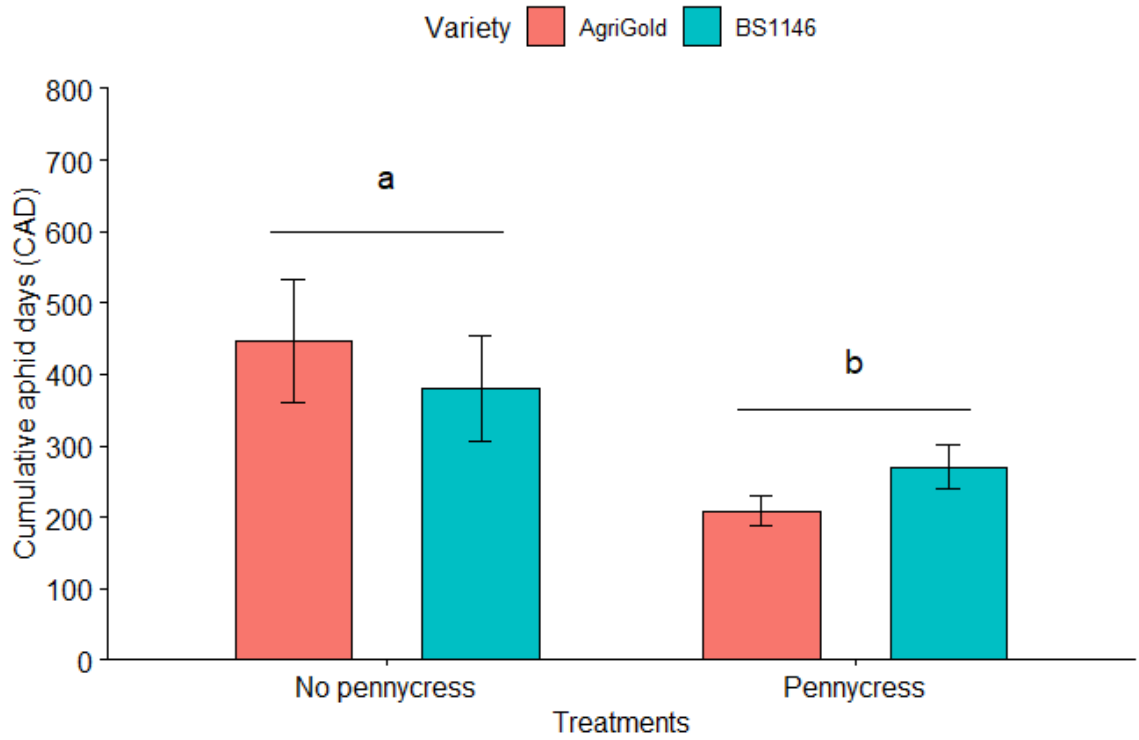


Figure 2. 3: Mean (\pm SE) cumulative aphid days (CAD) for soybean aphid on two soybean varieties (AgriGold and BS1146) relay-cropped with pennycress and no pennycress at Rosemount, Minnesota in 2023. Means with different letters differ significantly ($p < 0.05$), ANOVA ($P < 0.05$).

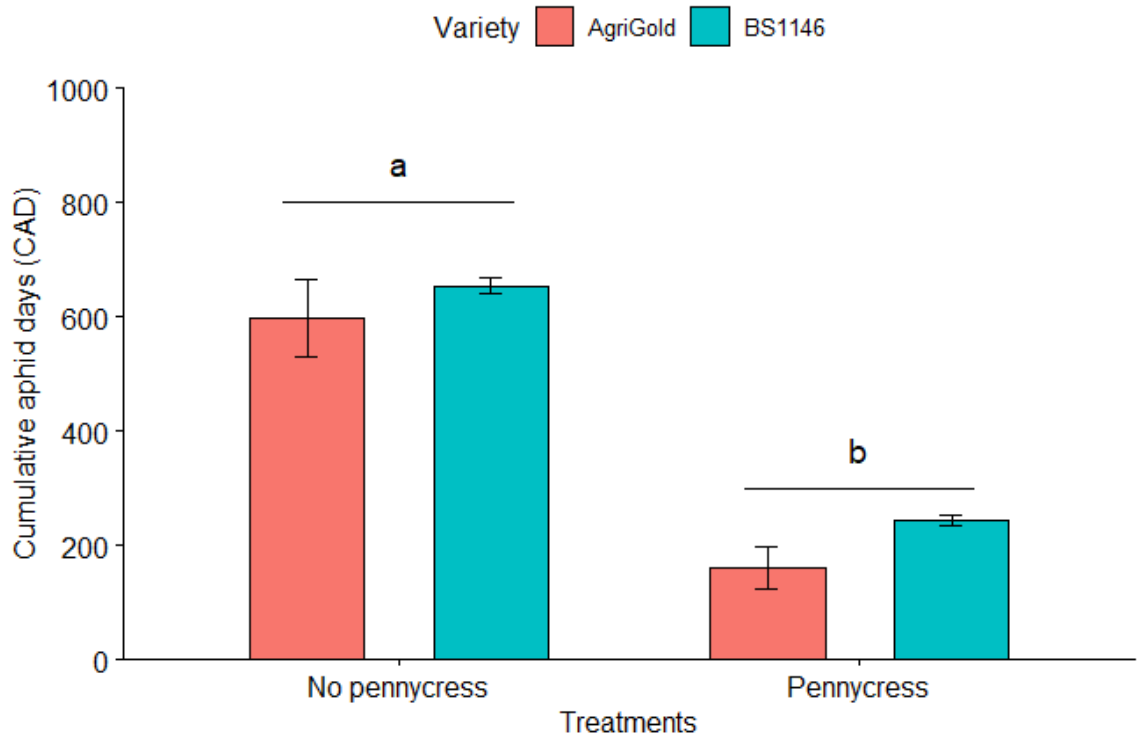


Figure 2. 4: Mean (\pm SE) cumulative aphid days (CAD) for soybean aphid on two soybean varieties (AgriGold and BS1146) relay-cropped with pennycress and no pennycress at St. Paul, Minnesota in 2023. Means with different letters differ significantly ($p < 0.05$), ANOVA.

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