REVIEW ARTICLE

Management of pennycress as a winter annual cash cover crop. A review

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Abstract

Agriculture in the Upper Midwest of the USA is characterized by a short growing season and unsustainable farming practices including low-diversity cropping systems and high fertilizer inputs. One method to reduce the magnitude of these problems is by integrating a winter annual into the summer-annual-dominant cropping system. For this reason, pennycress (*Thlaspi arvense*) has garnered interest in the agricultural community due to its winter annual growth habit and potential for industrial oil production, making it an ecologically and economically desirable crop. Despite decades of research focusing on pennycress as an agricultural weed, little is known about its best management practices as an intentionally cultivated crop. The majority of agronomic research has occurred within the past 10 years, and there are major gaps in knowledge that need to be addressed prior to the widespread integration of pennycress on the landscape. Here we review relevant agronomic research on pennycress as a winter annual crop in the areas of sowing requirements, harvest, seed oil content, seed oil quality, cropping strategies, ecosystem services, and germplasm development. The major points are as follows: (1) there is little consensus regarding basic agronomic practices (i.e., seeding rate, row spacing, nutrient requirements, and harvest strategy); (2) pennycress can be integrated into a corn (*Zea mays*)– soybean (*Glycine max*) rotation, but further research on system management is required to maximize crop productivity and oilseed yields; (3) pennycress provides essential ecosystem services to the landscape in early spring when vegetation is scarce; (4) breeding efforts are required to remove detrimental weedy characteristics, such as silicle shatter and high sinigrin content, from the germplasm. We conclude that pennycress shows great promise as an emergent crop; however, current adoption is limited by a lack of conclusive knowledge regarding management practices and future research is required over a multitude of topics.

Keywords Alternative cropping systems · Agronomic management · Corn-soybean rotation · Ecosystem services · Germplasm development · Pennycress · Industrial oilseeds

Contents

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1 Introduction

Pennycress (*Thlaspi arvense*), also known as field pennycress, fanweed, French-weed, and stinkweed, is an emerging *Brassicaceae* (mustard family) oilseed crop that was first identified for production in 1944 (Clopton and Triebold 1944). Despite its point of origin in Eurasia, naturalized accessions of pennycress have been found throughout temperate regions of the USA and Canada indicating regional adaptation (Holm et al. 1997; Warwick et al. 2002; Phippen and Phippen 2013)

Fig. 1 Pennycress overwinters as a rosette providing late fall and early spring ground cover when summer annuals are not on the landscape. Ecological benefits of winter cover include suppression of early spring weeds and a reduction in nutrient runoff due to early spring precipitation and snowmelt. Photo by Julija A. Cubins

and winter survivability (Saarinen et al. 2011). Interest in pennycress as an agricultural crop (Figs. 1 and 2) has been spurred by the demand for alternative land use to mitigate prominent, but unsustainable, farming practices in the Upper Midwestern USA (Heaton et al. 2013; Sindelar et al. 2017). Unlike many winter annual crops grown in the Upper Midwest, pennycress seed can be pressed for oil and provide near-term economic benefits to growers (Moser et al. 2009a, b; Moser 2012). While research has been conducted on pennycress as a persistent weed in canola (*Brassica napus*) and wheat (*Triticum aestivum*) for decades (Best and McIntyre 1975; Warwick et al. 2002), earnest development of agronomic management practices for pennycress as a cultivated crop did not begin until its oil was evaluated as a potential biodiesel feedstock in 2009 (Moser et al. 2009a, b) followed by the sequencing of the genome in 2015 (Dorn et al. 2015). More research is necessary to determine the agronomic best management practices given the recent emergence of pennycress as a crop. The objective of this review was to compile and summarize current agronomic research on pennycress and identify gaps in knowledge for future research.

2 Sowing requirements

Optimum planting date for pennycress varies significantly between regions. The majority of research related to pennycress planting date has occurred in the Upper Midwest, and there is evidence across growing locations in this region that early September sowing dates correspond to better establishment than late fall or early spring planting dates (Phippen et al. 2010b; Gesch et al. 2016; Dose et al. 2017). However, in the Mediterranean climates, pennycress is not sown until early October, and, in some cases, may not be planted until early November (Royo-Esnal et al. 2015, 2017; Gesch et al. 2016; Zanetti et al. 2018). In the Upper Midwest, early fall sowing dates correspond to higher soil temperatures, which favors

better germination and a longer vegetative growth period prior to winter frost (Phippen et al. 2010b; Royo-Esnal et al. 2017). In comparison to late fall planting dates, early September planting dates also resulted in higher yields and earlier harvest dates (Dose et al. 2017), which is favorable for double-

Fig. 2 Pennycress line used to assess agronomic properties in field production. Prior to ripening, silicles and seeds have reached their full size but have not begun to mature. Photo by Rebekah J. Carlson

cropping (Phippen et al. 2010b). In extreme cases, late planting dates can decrease the chance of flowering and, thus, reduce or eliminate seed production in a given year (Milberg and Andersson 1994).

There is little cohesion in regard to planting strategy (Table 1). In Minnesota alone, planting rates ranged from 5.5 to 16.8 kg ha^{-1} (Eberle et al. 2015; Johnson et al. 2015, 2017; Gesch et al. 2016; Dose et al. 2017) with little consistency across research studies. A study conducted in western Illinois directly compared three different seeding rates, 1.1, 2.2, and 4.9 kg ha^{-1}, but researchers were not able to draw conclusions regarding optimal planting rate (Phippen et al. 2010a).Seeding method was also evaluated, and it was determined that drilled plots had better stand establishment and higher yields than broadcasted plots regardless of seeding rate (Phippen et al. 2010a). Pennycress is positively photoblastic (Hazebroek and Metzger 1990a), and a single study concluded that broadcast seeding enhanced pennycress germination due to the increased exposure of seed to light (Carr 1993). Despite

this finding, the majority of recent studies are consistent with the results of Phippen et al. (2010a) and have sowed pennycress around a depth of 1 cm using a seed drill (Table 1).

Pennycress is very susceptible to environmental influences, and water availability is the major limiting factor to germination and development (Royo-Esnal et al. 2015; Gesch et al. 2016). Germination occurs most readily in cool, wet conditions (Hazebroek and Metzger 1990a, b; Johnson et al. 2015; Royo-Esnal et al. 2015, 2017), and pennycress requires between 25 and 40 mm of water to germinate (Royo-Esnal et al. 2015; Johnson et al. 2017). Royo-Esnal et al. (2015) noted that only 5% of seedlings emerged when soil moisture levels were low at planting compared with 18% emergence in years with adequate soil moisture. What is unclear is the amount of moisture that is considered appropriate for pennycress production. It is well established that pennycress is susceptible to moisture stress (Anderson and Best 1965; Hazebroek and Metzger 1990a; Royo-Esnal et al. 2015); however, prior studies have merely used "adequate" to quantify the amount of moisture

Table 1 Outline of study planting information

Study	Location (USA unless noted)	Treatment investigated	Seeding rate kg ha^{-1}	Planting method	Spacing cm	Seeding depth cm	Fertilization kg ha^{-1} N-P-K
Dose et al. 2017	Swan Lake, MN	Planting date	6.7	Drilled	20	0.6	90-34-34
Eberle et al. 2015	• Swan Lake, MN • Elkton, SD	Pollinator preference	6.7	• Drilled • Frost seeded	19	• 1.3 • ---	90-34-34
Gesch et al. 2016	Swan Lake, MN; Teruel, Spain	Effect of seed position	11.6*	Not reported	25	1.0	Not reported
Groeneveld and Klein 2014	Dundenheim, Germany	Pollinator preference	3.0–5.0	Broadcasted	---	---	Not fertilized
Carr 1993	Guptill, ND	Yield	Not reported	Broadcasted	---	---	Not reported
Johnson et al. 2015 Experiment 1	Lamberton, MN; Rosemount, MN; Waseca, MN	Companion crop, location, seeding rate	5.5, 11.0	Drilled	25	Not reported	Not reported
Johnson et al. 2015 Experiment 2	Lamberton, MN; Rosemount, MN; Wasecea, MN	Companion crop, location, seeding date, seeding rate, variety	5.5, 11.0	Drilled	25	Not reported	Not reported
Johnson et al. 2017	Rosemount, MN; Saint Paul, MN; Waseca, MN	Cropping system, harvest time	16.8	Drilled	10	Not reported	Not reported
Phippen et al. 2010a	Macomb, IL	Planting method, seeding rate	1.1, 2.2, 4.9	• Broadcasted • Drilled	• --- • 7.5	• --- • 1.0	Not reported
Phippen et al. 2010b	Macomb, IL	Herbicide, planting date	Not reported	Drilled	7.5	Not reported	Not reported
Phippen and Phippen 2012	Macomb, IL	Double-crop	6.7	Drilled	19	Not reported	Not fertilized
Rukavina et al. 2011	Macomb, IL	Fertilization	4.5	Not reported	---	---	0, 28, 56, 84, 112 N; 11 S
Groeneveld and Klein 2015	Oβweil, Germany	Insect diversity	22	Not reported	---	---	Cattle manure, unknown
Groeneveld et al. 2015	Oβweil, Germany	Insect diversity	22	Not reported	---	---	Cattle manure, unknown

*Average 1000-seed weight for seeds at harvest maturity from Cubins (2019), unpublished, used to extrapolate planting rate

available (Zanetti et al. 2013; Royo-Esnal et al. 2015). Determining the threshold of adequate versus inadequate moisture for pennycress development may warrant further research. In comparison to sympatric species such as wild oat (*Avena fatua*) and wheat, pennycress has low water use efficiency (Anderson and Best 1965), requiring 405 kg of water to produce 0.45 kg of dry matter (Hazebroek and Metzger 1990a). Depressed yields are directly associated with limited water availability as low moisture levels can decrease the likelihood of branching, which allows pennycress to compensate for low stand density (Matthies 1990), and may reduce pennycress vertical growth to only 1.25% of its potential height (Best and McIntyre 1975). In general, pennycress is not well adapted for arid environments where natural precipitation is the only form of moisture (Royo-Esnal et al. 2017). Johnson et al. (2017) remedied issues associated with limited moisture by watering pennycress plots with 25 mm of water to promote germination. Another study conducted in Montana showed that, when supplemental irrigation was provided, pennycress yielded 1684 kg ha^{-1} (Clopton and Triebold 1944). Alternatively, higher planting rates can be used to compensate for potentially lower germination rates during dry conditions (Johnson et al. 2015; Zanetti et al. 2018), but may not be a reliable way to meet yield goals. In the future, breeding efforts will be necessary to develop pennycress varieties suitable for dryland regions. While pennycress seeding method and seeding depth has been established, optimal seeding rate over a variety of climatic conditions has not been well developed and requires future research.

2.1 Fertilization requirements

Few studies have been conducted concerning the direct fertilization needs of pennycress. Ongoing experiments with pennycress within the corn-soybean rotation suggest that no fertilizer application may be necessary for successful production due to residual nutrients applied during the summer annual portion of the system. Yield response due to the application of nitrogen and sulfur fertilizers on pennycress seed yield and oil content was quantified by Rukavina et al. (2011). This study, conducted in western Illinois, indicated that a fall application of 112 kg ha^{-1} N produced the maximum seed yield of 995 kg ha^{-1}, but did not significantly outperform treatments with lower fertilizer rates. This indicates that maximum yields may be achieved with fewer resources. The lowest N application rate that maintained top pennycress yield required a split application of 28 kg ha^{-1} applied in both the fall and spring (Rukavina et al. 2011). Recent studies in Minnesota have utilized a spring application of 90, 34, and 34 kg ha^{-1} of N, P, and K, respectively, following spring thaw before pennycress reproductive development began (Eberle et al. 2015; Dose et al. 2017). However, the benefits of fertilization were not quantified. There is also a risk of plant lodging due to over-

fertilization when pennycress is exposed to extreme weather events (i.e., heavy winds or excessive precipitation) after plants have elongated during reproductive development (personal observation). Overall, there is no clear fertilization strategy to optimize pennycress production and more research is needed on this component of the pennycress production system.

3 Harvest

Current pennycress lines are prone to shatter, which increases susceptibility to seed loss at harvest when plants are at low moisture content (Best and McIntyre 1975; Sedbrook et al. 2014; Dorn et al. 2015). This loss can be caused by environmental disturbances, such as high wind or precipitation, or by cultural disturbances, such as equipment for harvest or the planting of a subsequent relay crop, and has been noted in related *Brassicaceae* species (Vera et al. 2007; Sintim et al. 2016). Loss due to shattering directly corresponds to pennycress yield reduction at harvest and can significantly contribute to the weed seed bank as a single plant can shed between 1600 and 15000 seeds (Best and McIntyre 1975). Carlson (2018) found that seed loss due to shattering was equivalent to 300 times the initial seeding rate. While silicle shatter is an undesirable trait for agricultural production, it is important to remember that the studies reviewed in this paper largely utilize wild accessions of pennycress (Phippen and Phippen 2013; Johnson et al. 2015, 2017; Royo-Esnal et al. 2017; Carlson 2018; Ott 2018; Zanetti et al. 2018; Cubins 2019; Ott et al. 2019), which retain many weedy characteristics (Frels et al. 2017; Zanetti et al. 2018; Altendorf et al. 2019) that are beneficial for natural propagation (Warwick et al. 2002). Pennycress seed is viable as early as 6 days after anthesis (Hume 1984), may not experience any dormancy when produced under warm conditions (Hume 1994), and can persist in the weed seed bank for decades (Croker 1938; Kjaer 1948). As shattered seed germinates, pennycress seedlings may directly compete with crops that follow, such as canola, wheat, and safflower (*Carthamus tinctorius*) (Warwick et al. 2002). However, pennycress susceptibility to herbicide chemistries (Andersson 1994) such as glyphosate and glufosinate (Sedbrook et al. 2014) as well as suspected susceptibility to 2,4-dichlorophenoxyacetic acid, imazethapyr, and acifluorfen will likely decrease its competitive ability if a pre-emergent herbicide is used (Sindelar et al. 2017).

Despite these production challenges, it is largely agreed that pennycress is a good candidate for mechanical harvest (Clopton and Triebold 1944; Eberle et al. 2015; Dose et al. 2017) even though mechanical harvest is the most efficient when seeds are dry and silicles are prone to shatter. One strategy for reducing shattering loss is to harvest pennycress at physiological maturity. Pennycress physiological maturity

occurred nearly 2 weeks prior to typical harvest periods, i.e., harvest maturity (Fig. 3), when seed moisture was low enough for effective mechanical harvest (Cubins 2019). Delaying harvest until typical harvest periods resulted in a 70% loss in seed yield compared with harvesting at physiological maturity, i.e., maximum yield potential. Consequently, Cubins (2019) proposed the use of a harvest aid at physiological maturity to dry pennycress to a point that facilitates efficient mechanical harvest. The majority of agronomic studies reviewed were harvested by hand (Table 1), which does not require seeds to have reached full maturity by the time of harvest. In some studies, however, paraquat dichloride (1′dimethyl-4,4′-bipyridinium dichloride) was applied to assist plant drying prior to combining (Eberle et al. 2015; Dose et al. 2017) and may be used as a desiccant in the future to decrease the time between physiological maturity and harvest maturity. Harvest timing spanned mid-May through mid-July at all reviewed study locations. Studies that were conducted in Illinois were more likely to be harvested in late May or early June (Phippen et al. 2010b; Rukavina et al. 2011; Phippen and Phippen 2012) as opposed to studies in western Minnesota and North Dakota, which were harvested between late June and early July (Carr 1993; Eberle et al. 2015; Gesch et al. 2016; Dose et al. 2017; Cubins 2019). Different growing conditions (e.g., length of winter

Fig. 3 Pennycress at harvest maturity when plant and seed moisture have reached adequate levels (12–15%) for effective mechanical harvest. Photo by Sarah Moore

and amount of precipitation) are highly influential in determining when pennycress reaches maturity and can be harvested. Loss of seed at low moisture content in pennycress has been well documented, and strategies to reduce moisture content using a harvest aid when seed reaches physiological maturity should be the focus of future research.

3.1 Seed yield

The primary product of pennycress production is oil (Moser et al. 2009a; Moser 2012), and oil production can be optimized by simultaneously maximizing seed yield and seed oil content. One estimate suggests that pennycress yields need to reach 1684 kg ha^{-1} to offset production costs (J. Sedbrook, personal communication, 8 May 2018). While pennycress has the potential for prolific yields, studies of natural accessions have demonstrated a high degree of yield variability. It should be noted that there is a lack of published material pertaining to pennycress yield outside the Upper Midwest, so yield information is restricted to the USA. Of the studies considered in this review (Table 2), only two had yields that exceeded the proposed threshold of profitability and each had treatments that yielded far lower values (Carr 1993; Johnson et al. 2017). Average yields of the studies reviewed were greatest in Illinois, the southern-most state, followed by Minnesota and South Dakota (Fig. 4). Yields in Illinois had a greater standard deviation than those in Minnesota, which may be partially due to that fact that fewer field studies have been conducted in Illinois as opposed to Minnesota (Fig. 4; Table 2). While there are many factors that contribute to variability in pennycress seed yield, stand density and environment are the primary constraints. A high degree of phenotypic plasticity (Susko and Cavers 2008) in pennycress can partially compensate for low stand density by increasing the seed yield of individual plants in response to decreased population density (Matthies 1990). Due to the branching morphology of pennycress, yields across planting rates were similar to each other even at half or a quarter of the maximum seeding rate of 4.9 kg ha^{-1} (Phippen et al. 2010a). Another example this plasticity occurs with spring versus fall germinated seed. Seedlings that germinate in the spring are more likely to grow taller, branch more, and produce a greater amount of small seed than fall-germinated pennycress (Hume 1990). While relying on natural branching may be a good strategy in years with unexpected stand loss, planting at a higher seeding rate is considered a more reliable method of increasing stand uniformity and reducing the risk of low yield due to poor germination (Johnson et al. 2015). Overall, there is consensus that pennycress yield is highly dependent on in-season environmental factors (Johnson et al. 2017), which further complicates the design of pennycress best management practices. Yields in one study reflected rainfall patterns because germination was highly dependent on soil moisture (Johnson et al.

Table 2 Outline of study harvest information

Study	Location (USA unless noted)	Treatment investigated	Harvest method	Minimum yield kg ha^{-1}	Maximum yield kg ha^{-1}	Minimum oil content %	Maximum oil content %
Dose et al. 2017	Swan Lake, MN	Planting date	Plot combine	200	1100	34	36
Eberle et al. 2015	• Swan Lake, MN • Elkton, SD	Pollinator preference	• Plot combine • Hand harvest	• 230 • 0	• 1110 • 520	Not reported	Not reported
Gesch et al. 2016	• Swan Lake, MN • Teruel, Spain	Effect of seed position	Hand harvest	Not reported	Not reported	• 32 • 26	• 33 • 31
Carr 1993	Guptill, ND	Yield	Hand harvest	119	1628	26	26
Johnson et al. 2015 Experiment 1	• Lamberton, MN • Rosemount, MN • Waseca, MN	• Companion crop • Seeding rate • Companion crop, seeding rate • Companion crop • Seeding rate	Hand harvest	• 104 • 161 • 477 • 390 • 672	• 113 • 168 • 1387 • 513 • 694	Not reported	Not reported
Johnson et al. 2015 Experiment 2	• Rosemount, MN (2010/2011) • Rosemount, MN (2012)	• Companion crop • Seeding date • Companion crop • Seeding date • Variety	Hand harvest	• 133 • 116 • 441 • 441 • 796	• 270 • 204 • 1129 • 1245 • 1245	Not reported	Not reported
Johnson et al. 2017	• Rosemount, MN • Saint Paul, MN • Waseca, MN	Cropping system, harvest time	Hand harvest	• 500 • 1450 • 75	• 1000 • 2400 • 1200	Not reported	Not reported
Phippen et al. 2010a	Macomb, IL	Planting method, seeding rate	Hand harvest	345	535	28	29
Phippen et al. 2010b	Macomb, IL	• Herbicide • Planting date	Hand harvest	• 150 • Not reported	• 1120 • Not reported	• 30 • 30	• 34 • 36
Phippen and Phippen 2012	Macomb, IL	Double-crop	Not reported	672	896	Not reported	Not reported
Rukavina et al. 2011	Macomb, IL	Fertilization	Hand harvest	351	1117	34	36

2015). Dose et al. (2017) presented contrary evidence to this finding, suggesting that pennycress yield was not correlated to seasonal variables such as precipitation, soil temperature at planting, or cumulative photohydrothermal time, but was most reflective of air temperature at planting in which earlier planting dates corresponded with higher yields. There is a high degree of yield variability in current lines of pennycress. Much of this corresponds to environmental influence but may be reduced by planting at higher seeding rates to increase stand uniformity.
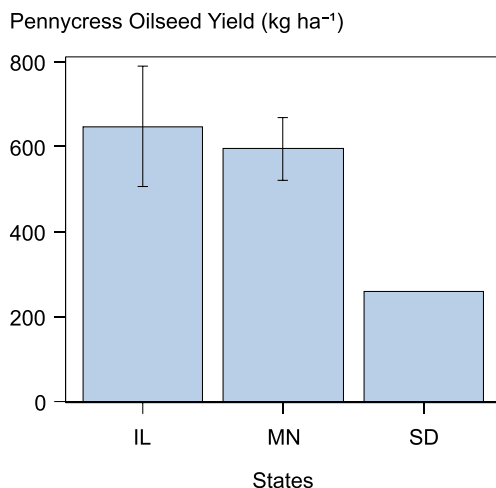

Fig. 4 Differences between pennycress oilseed yield (kg ha^{-1}) by state in the Upper Midwest

4 Seed oil content and quality

Pennycress seed oil content ranges between 26 and 39% (Carr 1993; Phippen et al. 2010a; Rukavina et al. 2011; Gesch et al. 2016; Dose et al. 2017), and this high oil content makes it a good candidate for biodiesel production (Clopton and Triebold 1944; Phippen and Phippen 2013; Isbell et al. 2015b; Royo-Esnal et al. 2017). A range of seed oil content from recent agronomic studies can be found in Table 2. Similar to seed yield, environmental factors, such as soil temperature and precipitation, can significantly influence seed oil content. Dose et al. (2017) found that low soil temperatures accounted for 63% of the variation in seed oil

content of fall-planted pennycress. When pennycress was planted at soil temperatures below 5 °C (i.e., November planting date), seed oil content ranged between 26 and 30%, whereas when pennycress was planted at soil temperatures of 30 °C (i.e., late August planting date), seed contained around 36% oil. By planting earlier, pennycress had a longer maturation period, which favored high oil content (Dose et al., 2017); however, lower erucic acid levels were associated with later planting dates (Phippen et al. 2010b), which may be due to a shorter growth period. Precipitation also has significant influence on seed oil content. A year with 253 mm versus 406 mm of precipitation yielded seed with 26% and 36% oil, respectively, and variation in precipitation accounted for 86% of the variation in oil content (Dose et al. 2017). Overall, seed oil content was stable across drilled and broadcasted planting methods and was not shown to be as variable as yield over planting method and varying seeding rates (Phippen et al. 2010a). Seed oil content has been relatively stable across research studies and methods but still experiences variation due to environmental factors.

Pennycress oil is mainly comprised of components of the oleic acid (18:1) biosynthetic pathway: linoleic (18:2), linolenic (18:3), eicosenoic (20:1), and erucic (22:1) acids (Sedbrook et al. 2014). Of these products, erucic acid accounts for the majority of seed oil content and reported values have consistently ranged between 29 and 36% (Isbell 2009; Moser et al. 2009b; Cermak et al. 2013; Phippen and Phippen 2013; Zanetti et al. 2018). The remaining fatty acids have yielded similarly across accessions and study locations with oleic, linoleic, linolenic, and eicosenoic acids comprising around 11%, 20%, 13%, and 10%, respectively, of the total fatty acid content (Evangelista et al. 2017; Zanetti et al. 2018; Altendorf et al. 2019; Cubins 2019). Due to this composition, pennycress oil is a candidate to be used as an industrial lubricant (Cermak et al. 2015) due to its high viscosity and cold flow properties (Fan et al. 2013; Cermak et al. 2015; Evangelista et al. 2017). For these reasons, pennycress is also a candidate to increase domestic fuel production for the aviation industry (Sindelar et al. 2017). When compared with other oilseed crops, pennycress would need to produce between 561 and 1123 kg ha^{-1} of oil to directly compete with markets for rapeseed oil due to similar oil properties (Clopton and Triebold 1944). More recently, established extrusion procedures have yielded 600 to 1200 L of pennycress oil per hectare (Moser et al. 2009a), which is equivalent to 540 to 1080 kg ha^{-1} (Noureddini et al. 1992).

1993; Heaton et al. 2013; Sindelar et al. 2017; Bishop and Nelson 2019). Due to its early summer harvest, pennycress can be double-cropped with soybean and other summer annuals without jeopardizing yield (Isbell 2009; Moser 2012; Phippen and Phippen 2012; Johnson et al. 2017). There were no differences in oil content or protein of soybeans double-cropped with pennycress when compared with soybeans grown without a fall-seeded crop (Johnson et al. 2015). Despite a slightly shorter growing season, double-cropped soybean had ample time to reach maturity before the first fall frost (Johnson et al. 2015) and soybean yields were maintained even with the addition of pennycress (Johnson et al. 2015; Bishop and Nelson 2019). Phippen and Phippen (2012) demonstrated that, when double-cropped with soybean, pennycress had a positive effect on soybean yield in both years of the study but was only significant in the second year, further indicating the importance of annual environmental fluctuation. Only one study found that pennycress reduced soybean grain yield by 18–30% when double- or relay cropped (Johnson et al. 2017). Although there was a reduction in soybean yield, total annual grain yield was increased by 48–102% depending on location and environment after oilseed yields (i.e., pennycress and soybean) were combined (Johnson et al. 2017). Similarly, in a relay cropping study where a full season soybean was no-till planted into standing pennycress, total annual seed yield was 79% greater than a conventionally managed soybean planted without a relay crop (Ott et al. 2019).

Despite the potential economic benefit of incorporating pennycress into a cropping rotation, risks may be incurred. Integrated systems will be most successful in areas with ample precipitation as pennycress yields may be negatively affected if competition for water is present (Clopton and Triebold 1944; Johnson et al. 2015; Royo-Esnal et al. 2017). This has the potential to negate economic benefits if oil yield is not great enough to match input costs. Due to its small seed size, pennycress had trouble germinating in high residue environments (Eberle et al. 2015; Johnson et al. 2017) indicating that planting pennycress into annual crops with a large amount of stubble or leaf litter following harvest may be unsuitable for pennycress production unless residue is removed prior to planting (personal observation). In short, pennycress can be integrated into a summer annual cropping system while increasing total annual oilseed yield; however, it is not without challenges and, in some years, the risks incurred may be greater than the profit contributed by the additional crop.

5 Cropping strategies

The aforementioned oil characteristics can be leveraged by including pennycress in an integrated cropping system such as a double- or relay crop (Clopton and Triebold 1944; Carr

6 Ecosystem services

An ability to scavenge nutrients has made pennycress an attractive option as a low-input winter annual. Between 73 and 77% of annual nitrate loss in the corn-soybean rotation occurs

between April and June (Randall and Vetsch 2005), which suggests excess soil nitrogen availability to support a winter annual crop. Pennycress had 18 to 19% less nitrogen in the soil profile down to 60 cm in the fall compared with a fallow plot and 53 to 72% less nitrogen in the spring after oilseed harvest and before soybean planting (Johnson et al. 2017). Similarly, soybean relay cropped with pennycress sequestered between 35 and 40 kg ha^{-1} of nitrogen by mid-spring, which was comparable to a crop of winter rye (*Secale cereale*) (Ott et al. 2019). This corresponded to a 20 kg ha^{-1} reduction in soil nitrate levels when directly compared with a fallow tilled control (Ott 2018) and indicates that pennycress is efficiently able to remove nitrogen from the soil profile.

Pennycress can be utilized as part of a comprehensive integrated weed management strategy (Vaughn et al. 2005; Johnson et al. 2015). Fall establishment can provide early spring ground cover and suppress aggressive spring-germinating weeds such as common lambsquarters (*Chenopodium album*), giant ragweed (*Ambrosia trifida*), and tall waterhemp (*Amaranthus tuberculatus*) (Johnson et al. 2015). Johnson et al. (2015) speculated that weed suppression may have been caused by allelopathic compounds rather than ground cover when pennycress seeding rates and companion crops were taken into account. The majority of weed suppression research has focused on the use of the sinigrin components allyl isothiocyanate and allyl thiocyanate in pennycress seed meal to suppress weed seed germination (Vaughn et al. 2005, 2006; Isbell 2009). Pennycress seed meal can provide 100% suppression of weed seeds when incorporated into the soil at 1% (wt/wt) (Isbell 2009). Similarly, pennycress seed meal was able to suppress the germination of both sicklepod (*Senna obtusifolia*) and velvetleaf (*Abutilon theophrasti*) at allyl isothiocyanate and allyl thiocyanate concentrations of 5 ppm, and provided over 90% control of weeds in both tarped and untarped field conditions (Vaughn et al. 2005). While acting as an effective weed control, what remains unclear is whether these compounds stay active in the soil and pose risks to intentionally seeded crops if they are planted too soon after pennycress harvest or residue incorporation. Allyl isothiocyanate and allyl thiocyanate were found to suppress the germination of wheat, annual ryegrass (*Lolium multiflorum*), and arugula (*Eruca vesicaria* ssp. *sativa*) at 1, 1, and 5 ppm, respectively (Vaughn et al. 2005). It is interesting to note that the germination of arugula, a fellow *Brassicaceae*, was less affected by pennycress seed meal application than wheat and annual ryegrass (Vaughn et al. 2005), indicating that pennycress volatiles may not be as effective at controlling the germination of other *Brassicaceae* crops. Another study found that wheat germination was inhibited by pennycress seed meal at levels as low as 0.1% (Vaughn et al. 2006).

There is also potential for pennycress to be an integral part of an effective and sustainable integrated pest management strategy. Pennycress increased biocontrol potential and provided habitat for spiders, a generalist predator (Groeneveld et al. 2015). Spider abundance was not affected by pennycress growth in a corn-pennycress system, and spider species richness and diversity increased when compared with three common corn crop rotations, as characterized by the Shannon index (Groeneveld et al. 2015). The addition of pennycress to a corn rotation also increased and stabilized ground beetle diversity more effectively than a mustard (*Sinapis alba*)–corn rotation, a green fallow–corn rotation, or a bare fallow–corn rotation (Groeneveld and Klein 2015). This was mainly due to the evenness of plant cover throughout the growing season.

Pollinators can also benefit from pennycress's early flowering time. Forage is scarce in the early spring when most plants on the landscape have not germinated or bloomed, but pennycress can help to fill this gap (Evangelista et al. 2017). In 1 year of study, pennycress produced only 13 kg ha^{-1} of nectar in comparison with camelina and canola, which produced 100 and 83 kg ha^{-1} of nectar, respectively (Eberle et al. 2015). While pennycress produces less nectar than other angiosperms, as many as 68 insects per minute visited its flowers, indicating that pennycress may provide other resources to pollinators such as pollen. Indeed, pennycress produced 38 kg ha^{-1} of pollen compared with 58 and 109 kg ha^{-1} by camelina and canola (Thom et al. 2018). Recorded visitors mainly consisted of flies, but an earlier flowering period over 1 year of the study lead to a 200% increase in the number of small bees visiting, potentially due to a lack of other flowering resources on the landscape. Research conducted in Germany concluded similarly that the majority of flower visitors were flies, but also noted a number of bee visitors (Groeneveld and Klein 2014). Pennycress provides services that are imperative to a sustainable ecosystem, and the integration of this crop can reduce nutrient leaching, decrease pest pressure, and increase the population of beneficial organisms.

7 Germplasm development

Pennycress has excellent potential for rapid domestication and genetic improvement (DeHaan et al. 2016). The advantages of pennycress include a small diploid genome, self-fertility, a rapid lifecycle, and a close genetic relationship with the well-studied *Brassicaceae* species *Arabidopsis thaliana* and canola (Sharma et al. 2007; Sedbrook et al. 2014; Dorn et al. 2015). The small genome size allowed rapid development of a pennycress transcriptome and draft genome that are being used to identify key genes for domestication (Dorn et al. 2013, 2015). Wild collections (accessions) of pennycress have been made throughout the USA, Canada, and Europe for the purpose of developing breeding programs. Some of these accessions are maintained at the USDA North Central Regional Plant Introduction Station in Ames, IA. Accessions are also

maintained at Western Illinois University and at the University of Minnesota, and have been screened for agronomic and oil-quality/end use traits (Sedbrook et al. 2014; Altendorf et al. 2019). Phenotypic variation for maturity, yield components, and seed dormancy have been identified in wild pennycress accessions (Isbell et al. 2015a, 2017; Altendorf et al. 2019); however, significant variations for traits such as silicle shatter, erucic acid content, and sinigrin content were not identified. A recent evaluation of genetic diversity showed that the genetic variation present in North American pennycress accessions was limited (Frels et al. 2017). Therefore, alternative tools such as chemical mutagenesis and gene editing have been used to create genetic variation for key domestication traits (Chopra et al. 2018, 2019a; McGinn et al. 2018).

Wild pennycress carries three traits that limit commercialization for multiple end uses: silicle shatter at low moisture content, oil with high erucic acid content, and sinigrin content in the meal remaining after pressing (Sedbrook et al. 2014). In order to develop pennycress for profitable end uses, including human and animal food uses, the germplasm must be improved to reduce these undesirable traits. The reduction in erucic acid and sinigrin content has largely followed the steps laid out by researchers who developed canola from rapeseed (Bell 1982; Claver et al. 2017). Recently, pennycress lines with reduced erucic acid content and increased oleic, linoleic, and linolenic acid content were identified through the use of both chemical mutagenesis and CRISPR-Cas9 gene editing (McGinn et al. 2018; Chopra et al. 2019b). In addition, pennycress lines with reduced sinigrin and silicle shatter were identified (Chopra et al. 2019b). Stacking the reduced erucic content, sinigrin content, and silicle shatter traits together will result in pennycress lines with edible oil and meal and improved harvestability. Further combining these traits into elite breeding lines selected for improved germination, early maturity, and increased yield will ease the adoption of pennycress as a cash cover crop.

8 Conclusion

Few studies have tackled questions pertaining to pennycress best management practices, and many questions remain unanswered. Techniques used in pennycress agronomic research vary greatly among researchers and requires clarification. The time of seeding and seeding method are established parameters, but seeding rate and row spacing warrant further evaluation to optimize plant density in both arid and precipitous conditions. Nutrient recommendations are very preliminary, and pennycress baseline requirements must be quantified. Using this information, researchers will be able to determine whether pennycress requires nutrient input or if its scavenging ability is sufficient without additional fertilization. Techniques to reduce pennycress shatter loss at harvest will

also be necessary in ensuring maximum profitability, and breeding strategies have been implemented to develop non-shatter lines for future use (Dorn et al. 2015). Until more shatter-resistant cultivars are available for production, refined harvest management strategies are necessary to reduce pennycress moisture to facilitate the earliest harvest after physiological maturity occurs. This will allow pennycress to be mechanically harvested on a field scale and double-cropped with corn, soybean, or other summer annuals. Future studies outlining economically important pests (i.e., weeds, insects, nematodes, and diseases) also need to be conducted. Attention to pennycress as a cash cover crop is relatively recent, and additional research is required to determine best management practices before large-scale adoption can occur.

Compliance with ethical standards

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