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Camelina uses, genetics, genomics, production, and management

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ABSTRACT

Camelina [*Camelina sativa* L. Crantz] is an annual oilseed crop in the Brassicaceae family that has been cultivated since 4000 BCE. Recently, interest in its oil, meal and the developed products has increased research in this crop. This renewed interest is evidenced by the tremendous increase in peer-reviewed publications containing the word 'camelina'. Databases report 335 publications between 2013 and 2016, with 149 of those published since 2015. The objective of this review was to compile and summarize new and existing information in order to identify gaps in knowledge and areas for future research. This review includes the most recent publications in camelina description and origin, uses, genetics, genomics, breeding, molecular genetics, physiology, agronomic management, and ecosystem services. Although the breadth of research in camelina over the last few years is impressive, several areas that would benefit from further research were identified. The development of new uses and the refinement of existing uses from camelina oil and meal will continue to add value to this crop. Advances in genetics, breeding, and genomics will speed up the development of high yielding camelina cultivars, with improved seed quality as well as disease and insect resistance. Understanding and improving freezing tolerance in camelina will advance the use of winter camelina as a cover crop or cash cover crop in double and relay cropping systems. Better management practices and weed control alternatives will be needed to increase camelina production worldwide. Lastly, commercial development of camelina will add one more crop to the already low agricultural diversity in many parts of the world.

Contents

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1. Introduction

Camelina [*Camelina sativa* (L.) Crantz], also called false flax, linseed dodder, or gold-of-pleasure is an oilseed crop in the Brassicaceae family. Camelina's adaptation to vast areas of the world, combined with its unique oil composition and properties useful for the production of biofuels, jet fuel, biobased-products, feed, and food has resurfaced interest in this ancient crop. This renewed interest is evidenced by the exponential increase in peer-reviewed publications containing the word 'camelina'; databases report 335 publications between 2013 and 2016, with 149 of those published since 2015. These publications and data reported within indicate the great potential of this new old crop. New uses for or products from camelina oil and meal, altered camelina oil composition through genetic transformation, and camelina physiology and agronomic management are among the most common themes in research. Current uses for camelina oil and meal are numerous and are summarized in Table 1; new research on agronomic adaptation and physiology of camelina are summarized in Table 2. The objective of this review was to compile and summarize new and existing information in order to identify gaps in knowledge and areas for future research.

2. Description and origin

Camelina originated in regions of southeast Europe and southwest Asia (Radatz and Hondelmann, 1981; Larsson, 2013). Findings at archaeological sites suggest camelina was cultivated and its seeds were used as food as well as oil in Scandinavia and Eastern Turkey. Archeological findings indicate it was cultivated as early as 4000 BCE in central Europe. The first findings of camelina in Scandinavia are from the Early Bronze Age (1800 BCE) (Karg, 2012), becoming more common from the Late Bronze and pre-Roman Iron Age (100 CE–250 BCE) (Larsson, 2013). Also, camelina seeds were found in a storage vessel in Eastern Turkey dating from 700 to 900 BCE (Dönmez and Belli, 2007) and in Romania in the transition from the Eneolithic to Bronze Age (Toncea, 2014), indicating that camelina was likely cultivated for its oil. Although its importance decreased in the Medieval Age (Karg, 2012), its cultivation continued sporadically over the years.

A striking feature of camelina is its ability to adapt to a wide range of environments. In the USA, camelina has been successfully grown from the arid Southwest (irrigated) (Hunsaker et al., 2011), to the Pacific Northwest (Schillinger et al., 2012), across the North and Central Plains (Berti et al., 2015; Aiken et al., 2015) and into the Corn Belt region (Gesch, 2014). Across Canada, camelina has been successfully produced from the western Prairie Provinces (Gugel and Falk, 2006; Blackshaw et al., 2011) to the eastern Maritime Provinces (Urbaniak et al., 2008).

Both spring and winter annual biotypes of camelina have been identified (Mirek, 1980). Winter annual types have proven to be extremely winter hardy (Gesch and Cermak, 2011). The existence of both, spring and winter types allows camelina to be integrated as a rotational crop in common cropping systems including those presently dominated by small grain cereals (Chen et al., 2015), corn (*Zea mays* L.), and soybean [*Glycine max* (L.) Merr.] (Gesch et al., 2014).

Like other members of the Brassicaceae family, camelina is a dicotyledonous species characterized by a high level of morphological plasticity. Plant height generally ranges from about 65 to 110 cm (Berti et al., 2011). Stems are either smooth or hairy, branched, and become woody at maturity. Leaves are arrow-shaped, sharp-pointed, 5- to 8-cm long with smooth to undulated edges. Its flowers, which are about 5- to 7-mm in diameter, (Fig. 1) are predominantly autogamous (Francis and Warwick, 2009). The silicles, commonly called seed capsules or pods, are 5- to 14-mm long, pear-shaped, slightly flattened, and contain 8 to 15 seeds golden to brown in color at maturity. Seeds are very small (0.7 mm × 1.5 mm), with a 1000-seed weight ranging between 0.8 and 1.8 g, depending on cultivar and growing conditions during seed development (Mirek 1981; Angelini et al., 1997; Zubr, 2003, 1997; Vollmann et al., 2007).

Fig. 1. Camelina flowers, silicles and fields of camelina near maturity and at swathing (Photos: Christina Eynck).

Table 1
Camelina oil and meal new uses and research reported between 2013 and 2016.

Product	References
Fuels	
Biodiesel	Moser (2016), Yang et al. (2016), Özçelik et al. (2015), Sáez-Bastante et al. (2015), Sun et al. (2015), Dangol (2014), Drenth et al. (2014), Li and Mupondwa (2014), Karcauskiene et al. (2014), Miller and Kumar (2014), Sun et al. (2014), Bernardo et al. (2003), Ciubota-Rosie et al. (2013), Keske et al. (2013)
Jet fuel	Zhao et al. (2015a), Drenth et al. (2015), Lokesh et al. (2015), Natelson et al. (2015), Oldani et al. (2015), Sivakumar et al. (2015a,b), Zhao et al. (2015a,b), Li and Mupondwa (2014)
Chemicals	
Hydrophylic monomers	Balanuca et al. (2015)
Adhesives	Li et al. (2015), Li and Sun (2015), Kim et al. (2015b)
Resins	Nosal et al. (2015)
Others	Goímez-Monedero, et al. (2015)
Animal feed	
Cows	Bayat et al. (2015), Khan et al. (2015), Colombini et al. (2014), Peng et al. (2014a,b)
Chicken-broilers and laying- hens	Ciurescu et al. (2016), Pekel et al. (2015), Nain et al. (2015), Aziza et al. (2014), Jaśkiewicz et al. (2014), Aziza et al. (2013), Pietras and Orczewska-Dudek (2013)
Swine	Adhikari et al. (2016), Taranu et al. (2014), Meadus et al. (2014), Kahindi et al. (2014)
Sheep	Mierlita and Vicas (2015), Steppa et al. (2014), Cieslak et al. (2013)
Fish	
Salmon	Hixson et al. (2016), Ye et al. (2016), Hixson et al. (2015b), Betancor et al. (2015), Xue et al. (2015), Hixson et al. (2014)
Trout	Bullerwell et al. (2016)
Other fish (cod, tilapia)	Hixson et al. (2015a), Booman et al. (2014), Hixson et al. (2014), Hixson et al. (2013)
Food and supplements	Ibrahim and El Habbasha (2015)

3. Fatty acid profile and synthesis

Seed oil content has been reported to range from 300 to 490 g kg^{-1} (Vollmann et al., 1996, 2007; Zubr, 2003; Blackshaw et al., 2011; Mupondwa et al., 2016). Camelina oil (Table 3) is rich in oleic, (18:1, 14–16%), linoleic (LA), (18:2, 15–23%), α-linolenic (ALA), (18:3, 31–40%), and eicosenoic (20:1, 12–15%) acid. Other minor fatty acids include palmitic (16:0), stearic (18:0), and erucic (22:1) acid (Putnam et al., 1993; Zubr, 1997; Singh et al., 2014). Camelina seed oil composition varies with cultivar, location, environment, and extraction method (Table 3). Triacylglyceride (TAG) biosynthesis in camelina is similar to that of all other plants (Voelker and Kinney, 2001) where fatty acids synthesis occurs in the plastids by a Type II fatty acid synthase complex. In most temperate climate oilseeds, the fatty acid chain elongates to 16 or 18 carbons in length. Oleic acid (18:1) is synthesized in plastids by a Δ^9-desaturase. After elongation, specific thioesterases cleave off the acyl carrier protein (ACP) from the fatty acid chain. Then, acyltransferases move the fatty acid chains to the cytosol or endoplasmic reticulum for further elongation or desaturation. Once desaturation has stopped, newly synthesized fatty acids are incorporated into TAGs (Voelker and Kinney, 2001).

In oilseeds, the linolenic acid content varies with temperature during seed development. At higher temperatures, ALA synthesis decreases causing an increase in the two other major constituents, oleic and linoleic acid (Berti et al., 2002; Gilbertson et al., 2014). The Δ^{15} desaturase (FAD3) that converts LA to ALA decreases its activity at temperatures greater than 25 °C. Similarly, Pavlista et al. (2016), observed a decrease in ALA in non-irrigated versus irrigated camelina, which was likely due to an increased temperature in non-irrigated plants.

4. Seed oil extraction

Camelina oil has been extracted from seeds using the following methods or combinations thereof: mechanical warm or cold pressing (Shukla et al., 2002; Zhao et al., 2014; Raczyk et al., 2015), solvent extraction (Stroescu et al., 2015), or supercritical SC—CO_2 (Moslavac et al., 2014; Belayneh et al., 2015). There are advantages and disadvantages for each particular method (Matthäus, 2012).

Belayneh et al. (2015) reported on the three most common oil extraction methods for camelina as well as the fatty acid profiles obtained for each method (Table 3). While the relative amounts of the individual fatty acids were as expected, about the same for

Table 2
Camelina adaptation, physiology, and agronomic research reported between 2013 and 2016.

Topic	References
Cultivar trials and adaptation	Sintim et al. (2016), Gesch et al. (2015), Gesch (2014), Toncea et al. (2013), Toncea (2014), Waraich et al. (2013)
Camelina physiology	
Germination and emergence	Allen et al. (2014)
Plant growth and development	Cendero-Mateo et al. (2015), Dalal et al. (2015), Schulte et al. (2013), Fujita et al. (2014)
Water use/irrigation	Pavlista et al. (2016), Gesch and Johnson (2015), Hunsaker et al. (2013)
Abiotic stresses	Khalid et al. (2015), Sharratt et al. (2015)
Camelina management	
Sowing date, rate and depth, plant density, sowing methods	Sintim et al. (2016), Aiken et al. (2015), Gesch (2014), Masella et al. (2014), Zanetti et al., 2013
Fertilization	Jiang and Caldwell (2016), Sintim et al. (2015), Allen et al. (2014), Jiang et al. (2014), Jiang et al. (2013), Johnson and Gesch (2013), Solis et al. (2013), Wysocki et al. (2013)
Weeds, insects, and diseases	Ghaouti et al. (2016), Thom et al. (2016), Chesnais et al. (2015), Eberle et al. (2015), Soroka et al. (2015), Davis et al. (2013), Jha and Stougaard (2013)
Harvest	Gesch et al. (2014)
Crop rotations, double and relay-cropping	Berti et al. (2015), Sharratt et al. (2015), Chen et al. (2015), Dobre et al. (2014), Gesch et al. (2014)

Table 3
Oil content and fatty acid profile of camelina seed oil extracted by various methods.

		Fatty acid profile (% area)[a]		
Fatty acid	Common name	Soxhlet	Cold press	SC[b]-CO_2
C16:0	Palmitic	7 + 0.1	5.7 + 0.0	5.8 + 0.0
C18:0	Stearic	2.4 + 0.0	2.4 + 0.0	2.4 + 0.0
C18:1	Oleic	15.8 + 0.1	15.7 + 0.1	15.9 + 0.1
C18:2	Linoleic	18.4 + 0.1	18.5 + 0.1	18.3 + 0.2
C18:3	Linolenic	33.0 + 0.1	32.8 + 0.2	33.0 + 0.3
C20:0	Eicosanoic	1.7 + 0.0	1.7 + 0.0	1.7 + 0.0
C20:1	Eicosenoic	15.0 + 0.1	15.1 + 0.0	14.9 + 0.1
C20:2	Eicosadienoic	1.8 + 0.0	1.8 + 0.0	1.8 + 0.0
C20:3	Dihomo-gamma linolenic	1.3 + 0.0	1.3 + 0.0	1.2 + 0.0
C22:0	Docosaenoic	0.4 + 0.0	0.4 + 0.0	0.3 + 0.0
C22:1	Erucic	3.4 + 0.0	3.5 + 0.0	3.3 + 0.1
C22:2	Docosadienoic	0.5 + 0.0	0.5 + 0.0	0.5 + 0.0
C24:1	Nervonic	0.6 + 0.0	0.7 + 0.0	0.6 + 0.0
Fatty acid groups, %				
SFA[c]		10.2 + 0.1	10.2 + 0.1	10.2 + 0.1
MUFA[c]		34.8 + 0.2	34.9 + 0.1	34.7 + 0.3
PUFA[c]		55.0 + 0.1	54.9 + 0.0	54.8 + 0.5
n-6/*n*-3		0.6 + 0.5	0.6 + 0.1	0.6 + 0.8
Oil content, %		35.9 + 1.3	29.9 + 1.0	31.6 + 3.1
Extraction rate, %		100[d]	83.0[d]	88.0[d]

[a] Table adapted from Belayneh et al. (2015).
[b] Supercritical.
[c] SFA – saturated fatty acid; MFA – monounsaturated fatty acid; PUFA – polyunsaturated fatty acid.
[d] Assuming complete extraction.

each method, significant differences were found in oil content. Total oil yield obtained with the Soxhlet (hexane) or solvent extraction for 6 h was 35.9%, whereas it was 31.6% and 29.9% with the SC—CO_2 extraction and after cold pressing, respectively (Table 3). The SC—CO_2 method was found to be very efficient in recovering most of the oil, even though the extraction rate was slow. The recovery of the oil was 88 and 83% with SC—CO_2 extraction and mechanical pressing, respectively, relative to extraction with hexane (100%).

In general, crude camelina oil has a clear yellow color with the typical broccoli-like aroma and flavor, whereas chemically refined camelina oils produce a colorless to pale yellow refined, bleached, and deodorized (RBD) oil (Crowley and Fröhlich, 1998). The shelf life of unrefined camelina oil is 12–24 months. In contrast, RBD oil has a shelf life of 6–9 months. These differences in shelf life are likely a result of unrefined oils containing natural tocopherols (anti-oxidants), with an average content of 806 mg kg^{-1} (Waraich et al., 2013).

5. Uses

5.1. Biodiesel

Fatty acid composition of camelina seed oil can differ with environment, which can lead to differences in the physical properties of the produced biodiesel (Pinzi et al., 2009; Moser, 2012, 2016; Ciubota-Rosie et al., 2013; Drenth et al., 2015; Yang et al., 2016). Table 4 shows a series of different biodiesel properties of camelina methyl esters with the standards specified for the ASTM D6751 and EN 14214 with values reported in the literature (ASTM, 2015; EN, 2012).

The three main properties used to evaluate biodiesel are: cloud point (CP) to assess cold flow, cetane number (CN), and oxidative stability. Unformulated camelina B100 meets the standards for CN and comes close, but fails to meet the standards for CP and oxidative stability (Yang et al., 2016). However, unformulated camelina B100 material can be easily modified to help meet current standards while keeping production costs low. Biodiesel from camelina has similar properties to that made from canola (*Brassica napus* L.) oil (Fröhlich and Rice, 2005).

5.2. Hydroprocessed renewable jet (HRJ) fuel

The production of renewable jet (RJ) fuel from camelina oil can simply be considered a two-step process (Fig. 2) – initial hydrodeoxygenation (HDO) or hydrotreatment, then selective

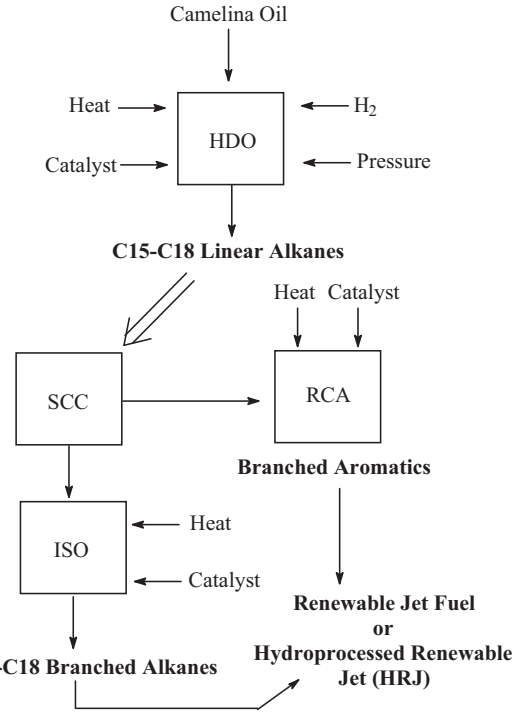

Fig. 2. Industrial production of renewable jet fuel from camelina oil. HDO = hydrodeoxygenation; ISO = isomerization; SCC = selective catalytic cracking; RCA = ring-closing aromatization. Renewable jet fuel = mixture of branched aromatics and C7–C9 branched alkanes.

Table 4
Biodiesel properties of camelina methyl esters reported in the literature.

Properties	ASTM[a] D6751	EN[a] 14214	Yang et al. (2016)	Ciubota-Rosie et al. (2013)	Soriano and Narani (2012)	Moser and Vaughn (2010)	Fröhlich and Rice (2005)
Density at 15 °C, kg m^{-3}	–[a]	860–900	887	888	–	–	–
Kinematic vis at 40 °C, mm^2 s^{-1}	1.9–6.0	3.5–5.0	3.9	4.3	4.3	4.2	6.4
Cetane number	>47	>51	50	42	–	53	–
Acid value, mg KOH g^{-1}	<0.50	<0.50	0.25	0.15	–	0.31	0.33
Iodine number, g I_2 g^{-1}	–	<120	166	152	–	151	153
Flash point, °C	>93	>101	152	152	172	–	–
Cloud point, °C	–[b]	–	−1.6	0.0	2.7	3.0	3.0
Cold filter plugging point, °C	–	–	–	−4.0	1.1	−3.0	−3.0
Oxidative stability @ 110 °C, h	>3.0	>8.0	1.9	1.3	0.6	2.5	–
Sulphur content, mg kg^{-1}	<15.0	<10.0	3.6	5.6	5.5	3.0	–
Phosphorus content, mg kg^{-1}	<10.0	<4.0	<2.0	<0.1	–	0.0	–
Methyl ester content, wt%	–	>96.5	98.5	97.5	–	–	98.4
Free glycerol, wt%	<0.02	<0.02	<0.001	0.006	–	–	<0.1

[a] ASTM – American Society and Testing Methods (ASTM, 2015); EN – European Standards (EN, 2012), and – no data collected.
[b] According to climate zone.

catalytic cracking (SCC) or hydrocracking (HC) and isomerization (ISO), followed by product separation and formulation (Moser and Vaughn, 2010, 2015; Zhao et al., 2015a,b,c). After the first step, HDO, the compounds produced, linear alkanes, can be used in a renewable diesel mixture (Moser and Vaughn, 2010). The linear alkane fraction has physical properties that cause these materials to freeze or solidify at temperatures encountered at high altitudes. Consequently, ASTM D1655 requires that aviation turbine (jet) fuels have freezing points no higher than −40 °C. Selective catalytic cracking and isomerization of the linear alkanes to shorter-branched hydrocarbons (C7–C18) is standard practice. Branched aromatics can be produced as a side product of the SCC step. The hydroprocessed renewable jet (HRJ) fuel is a mixture of the branched aromatics and the C7–C18 branched alkanes (Fig. 2).

Corporan et al. (2011) compared JP-8 (typical jet fuel) and camelina HRJ fuel as shown in Table 5. The camelina HRJ fuel demonstrated superior thermal oxidative stability compared to JP-8 (Corporan et al., 2011). Engine tests with the camelina fuel demonstrated no anomalies with regard to engine operation, producing significantly lower soot and carbon monoxide emissions compared with baseline JP-8 fuel. The material compatibility tests revealed that the camelina fuel possesses elastomer seal swelling capability in conditioned nitrile O-rings. However, its elastomer swelling was significantly lower than for JP-8, which could result in fuel leaks in an aircraft system. In general, Corporan et al. (2011) as well as others (Sivakumar et al., 2015a,b) have demonstrated that camelina HRJ fuels have comparable properties to conventional fuels used in turbine engines. Additionally, camelina has successfully passed techno-economic and life cycle analyzes as a second generation biofuel (Lokesh et al., 2015; Natelson et al., 2015).

Camelina HRJ fuels are considered as viable drop-in replacement jet fuels and have been initially tested by the US Air Force (USAF) back in 2009. Since the initial test flights, numerous fighter jets (Thunderbirds), and jets (KLM Royal Dutch and Japan Airlines) have been successfully tested on a blend of JP-8 and camelina-derived jet fuel.

5.3. Chemical derivatives

Chemical derivation of camelina oil has been mainly limited to biofuel formation, especially biodiesel. Additional work has led to the development of additional products such as: nanocomposite materials (Balanuca et al., 2014), monomers (Balanuca et al., 2015; Li et al., 2015), alkyd resins (Nosal et al., 2015), and pressure sensitive adhesives (Kim et al., 2015b). Li and Sun (2015) developed ultraviolet polymers for pressure-sensitive adhesive applications from camelina oil.

Epoxidized camelina oil (Kim et al., 2015b) has been used as the starting material for a host of additional chemical derivatives. Epoxidized camelina oil (Fig. 3) can be converted to partially acrylated epoxidized camelina oil, and then to di-hydroxyl acrylated epoxidized camelina oil (acrylic polyol). The acrylic polyol is then copolymerized with 2-ethylhexyl acrylate to form tacky viscoelastic polymers.

Balanuca et al. (2015) extended the work on epoxidized camelina oil with the synthesis of several types of hydrophilic camelina oil based monomers (Fig. 3). Additionally, Balanuca et al. (2014) investigated the PEG methacrylated camelina oil with different PEG copolymer systems reinforced with polyhedral oligomeric silsesquioxanes (POSS) compounds (Fig. 3).

Nosal et al. (2015) reported the synthesis of alkyd (synthetic polyester) resins or drying oils based on camelina oil. The alkyd resins derived from diglycerol and polyglycerols had flexibility and drying time similar to products manufactured on the basis of pentaerythritol.

5.4. Non-food based products from meal

Cold-pressed meal (press cake) of camelina after oil extraction contains 100–150 g kg^{-1} of oil and 400 g kg^{-1} of protein with a relatively low glucosinolate and fiber content, making it a desirable animal feed (Zubr, 2003; Singh et al., 2014). Camelina meal contains up to 23–44 μmoles g^{-1} glucosinolates (Eeva-Liisa et al., 2007; Singh et al., 2014), 100–150 g kg^{-1} crude fiber (Kakani et al., 2012; Singh et al., 2014), and 1–6% phytate (Singh et al., 2014; Adhikari et al., 2016). Camelina meal is valued at about $100 Mg^{-1} as an animal feed, while for other industrial uses the meal values are often lower (about $20 Mg^{-1}) (Agusdinata et al., 2011). The price disparity has led to research more heavily focused on food or feed-based products versus nonfood based products. Although the number of reports on nonfood type uses for camelina meal is limited, a range of applications has been explored. Some of the most unique applications include bio-herbicides (Cao et al., 2015), soil fungicides (Ma et al., 2015), adhesives (Li et al., 2015), and bio-oils (Boateng et al., 2010).

Cao et al. (2015) used an economically viable and environmentally friendly membrane separation technique to extract glucosinolates from the meal. Glucosinolates can produce ionic thiocyanates (SCN), which can act as a bio-herbicide against redroot pigweed (*Amaranthus retroflexus* L.) and wild oat (*Avena fatua* L.) (Cao et al., 2015). Additionally, being able to extract and purify glucosinolates will allow for the needed quantification of their effects on various animals.

Table 5
American Society and Testing Methods (ASTM) specifications test on standard (petroleum based), JP-8, and camelina HRJ jet fuels.

ASTM tests	Standards	JP-8[a]	Camelina HRJ
Total acid number, mg KOH g^{-1} (D3242)	max 0.015	0.005	0.002
Aromatics, % vol (D1319)	max 25.0	17.2	0.0
Total sulfur, % wt (D4294 or D2622)	max 0.300	0.064	0.0018
Distillation, initial boiling point (IBP), °C (D86)	report	152	151
10% recovered, °C (D86)	max 205	173	161
Final boiling point, °C (D86)	max 300	260	259
Loss, % vol (D86)	max 1.5	0.2	0.9
Freeze point, °C (D5972)	max −47	−49	<−77
Existent gum, mg 100 mL^{-1} (D381)	max 7.0	0.4	<1
Viscosity @ −20 °C, cSt (D445)	max 8.0	4.1	3.3
Lubricity test (BOCLE) (D5001) wear scar, mm	report	0.54	0.76
Specific gravity (D4052)	0.775–0.840	0.799	0.751
Smoke point, mm (D1322)	min 19.0	25	50
Flash point, °C (D93)	min 38	48	43
Heat of combustion, MJ kg^{-1} (D3338)	min 42.8	43	44.1
Thermal Oxidative Stability[b], μg/cm^2	–	3.0	0.2–0.7

[a] JP-8, Jet Propellant 8; HRJ, Hydroprocessed Renewable Jet Fuel.
[b] Corporan et al. (2011).

Li et al. (2015) observed that the protein composition of camelina meal is similar to that of canola meal which has shown potential as an alternative to conventional petroleum-based adhesives. They found that three protein fractions are extractable from camelina meal: albumin, globulin, and glutelin. Overall, globulins showed better adhesion performance than glutelins.

In order to meet the increasing biofuel demands, Boateng et al. (2010) investigated the thermochemical conversion (pyrolysis) of camelina meal to high-energy liquid fuels. It was concluded that camelina meal was ideal for their fast pyrolysis process. High yields (up to 70% by wt.) and energy-dense liquid fuel intermediates were produced. The liquid materials produced were unusually and surprisingly stable with low oxygen content (<30% by wt.). The liquid fuel quality was also high, with a gross calorific value ranging between 29.0 and 34.7 MJ kg^{-1}. Additionally, other parts of the camelina plant besides the meal have been subjected to pyrolysis to obtain potentially useful bio-oils (Goímez-Monedero et al., 2015), which could provide additional quantities of renewable biofuels.

5.5. Animal feed

Both camelina oil and meal can be used for animal feed. The oil is mainly used as *n*-3 rich oil source and the meal as high quality protein-rich ingredient. Many studies indicate that fish (Ye et al.,

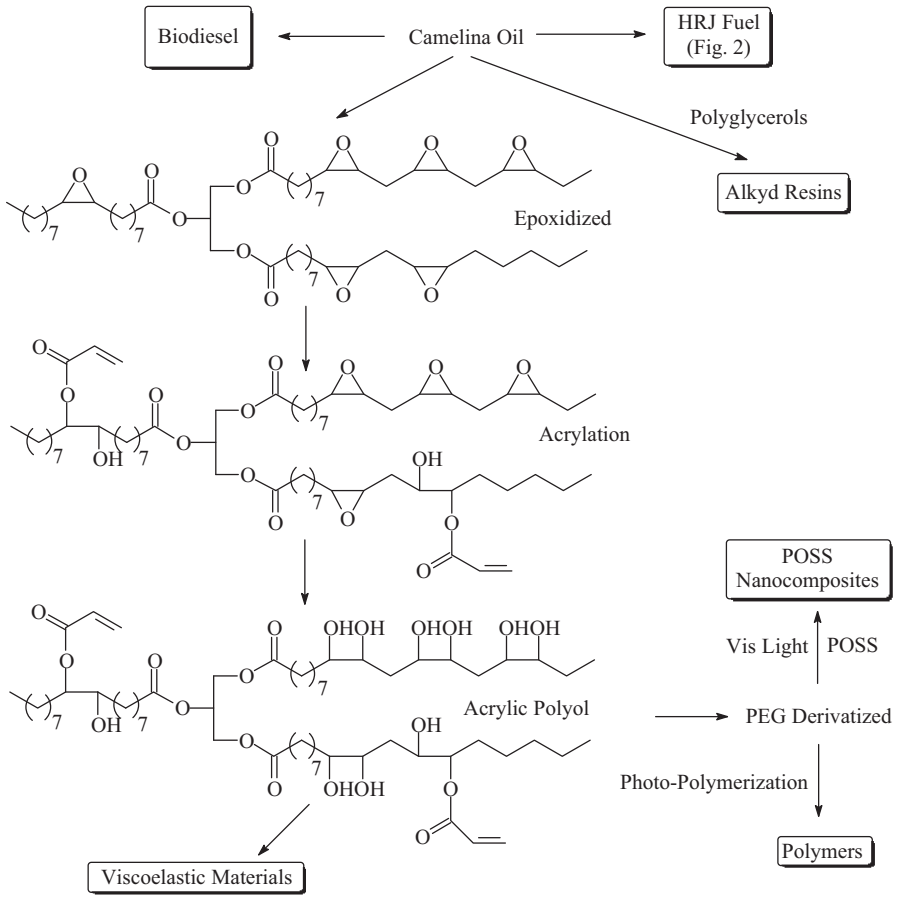

Fig. 3. Chemical derivatives of camelina oil.

2016; Hixson et al., 2013, 2014, 2015a,b), chicken (Jaśkiewicz et al., 2014; Pietras and Orczewska-Dudek, 2013), swine (Kahindi et al., 2014; Meadus et al., 2014), cattle (Halmemies-Beauchet-Filleau et al., 2011; Szumacher-Strabel et al., 2011), and sheep (Cieslak et al., 2013) fed with camelina oil or meal have lower blood plasma cholesterol and higher contents of ALA, or eicosapentaenoic acid (EPA), and docosahexaenoic (DHA) fatty acids.

Fish is a significant source of polyunsaturated fatty acids (PUFAs), particularly EPA and DHA in human diets. Nearly half of the world's fish for human consumption is produced on fish farms (Rose et al., 2001). The expansion of farming of carnivorous fish species has increased the demand for both fish meal and oil (Naylor et al., 2000). As a consequence, the demand for fish oil and meal often exceeds the supply, increasing the demand for seed oils as fish oil replacement in feed rations. Many studies have shown that seed oils can replace, in part, the lipids from fish oil. However, most oilseeds have low content of *n-3* PUFAs, resulting in lower levels of EPA and DHA in fish tissues (Bell et al., 2010; Jobling et al., 2008).

Similar to other oilseed crops, camelina oil and meal are potential replacements for fish oil and meal in fish feed. Several studies indicate that camelina oil and meal can increase total lipid content in salmon (*Salmo salar* L.) and Atlantic cod (*Gadus morhua* L.) without affecting sensory quality of fish fillets (Hixson et al., 2014). But replacing fish oil with a high percentage of camelina oil (80%) can actually decrease the content of PUFAs in Atlantic cod (Hixson et al., 2013). In general, fish fed diets containing camelina oil are lower in saturated fatty acids and higher in mono- and polyunsaturated fatty acids (MUFAs and PUFAs) (mainly ALA and LA) than those fed fish oil (Hixson et al., 2013, 2014). However, most studies show a decrease in EPA and DHA in fish fed camelina oil compared with those fed fish oil (Hixson et al., 2013, 2014, 2015a,b; Betancor et al., 2015). Camelina meal is a potential high protein source for fish feed. But some studies have shown that inclusion of high contents of camelina meal in fish diets decreases fish weight, probably due to some antinutritional compounds in the meal (Ye et al., 2016; Hixson et al., 2015a,b; Bullerwell and Anderson, 2012).

The addition of 6% camelina oil to feed rations for broiler chickens decreased the cholesterol content in the blood plasma and enriched the *n-3* PUFAs in the breast, mainly ALA without impairing the flavor of the cooked meat (Jaśkiewicz et al., 2014; Pietras and Orczewska-Dudek, 2013). Likewise, including camelina in the feed rations of laying hens increased egg production and the content of ALA in egg yolks (Aziza et al., 2013). However, replacing corn-soybean meal with more than 100 g kg^{-1} of camelina meal in broiler diets had negative effects on growth and development (Pekel et al., 2015).

Camelina meal is a potential energy source for swine diets because, after cold or expeller-pressing, a relatively high percentage of the oil (100–150 g kg^{-1}) remains in the meal. Camelina meal also has potential as a high quality protein source for ruminant rations because its protein content is higher than that of canola meal and similar to soybean meal. The relatively high histidine content in camelina meal makes it interesting as a supplement for silage- and grain-fed lactating cows (Colombini et al., 2014). Camelina meal or oil inclusion in animal diets increased milk yield and changed milk composition in dairy cattle (Halmemies-Beauchet-Filleau et al., 2011; Szumacher-Strabel et al., 2011). Butter and other dairy products made from milk of cows fed camelina oil also had a different fatty acid composition, such as an increased content of conjugated LA, and increased spreadability (Hurtaud and Peyraud, 2007; Ionescu et al., 2015). Diets containing camelina meal also led to higher contents of either C18:2 c9t11 or C18:2 t10c12 isomers in lamb muscle as well as an increase in vaccenic acid (VA), arachidonic acid (AA), EPA, DPA, LA, oleic, and ALA acid (Cieslak et al., 2013).

5.6. Food and supplements

Camelina oil has many potential benefits for human health and can be used as salad or cooking oil, although it is not suitable for high temperature frying. Camelina's high content of PUFAs and omega-3 fatty acids makes it suitable for nutritional supplements. Several reports indicate that intake of camelina oil decreased cholesterol in blood serum (Karvonen et al., 2002). Additionally, the high content of natural antioxidants (e.g., vitamin E at approximately 1.10 mg g^{-1}) in the oil protects it from oxidation (Ibrahim and El Habbasha, 2015).

6. Current and potential markets

Commercial development of camelina as a crop in the USA did not happen until recently, mainly in the state of Montana, where it expanded rapidly from no commercial production in 2004–9150 ha in 2007 (Pilgeram et al., 2007; NASS, 2015). Unfortunately, low seed yield and price contributed to the reduction in camelina contracts reducing the acreage in 2014 to only about 360 ha (NASS, 2015).

Other states have ventured to produce camelina with government incentives for biodiesel production under the Biomass Crop Assistance Program (BCAP), which was launched in 2011 in Montana, California, Washington, and Oregon with the purpose of increasing camelina cultivation (WAPMC, 2012). The BCAP incentive increased camelina contracts to about 4800 ha (USDA-FSA, 2011). Camelina is grown under contract in Canada and it was estimated that 9100 ha were grown between 2007 and 2009, with about half in the province of Saskatchewan (Li and Mupondwa, 2014). Currently, acreage is between 2000 and 4000 ha in Western Canada (mainly Alberta and Saskatchewan) (C. Eynck, personal communication, 30 April 2016).

Because there is not an established market for camelina many economic studies have used canola prices for economic feasibility evaluations (Keske et al., 2013; Gesch et al., 2014). In Montana, Hess et al. (2011) developed a camelina cost calculator. The camelina price used for budget enterprises was \$0.20 kg^{-1} and the total operating cost was about \$118 ha^{-1}. Gesch et al. (2014), determined that winter camelina breakeven price in double or relay cropping with soybean in Minnesota was \$0.65 kg^{-1}–\$1.14 kg^{-1}. Camelina production costs and profitability vary depending on the region of production. For instance, in Canada oil production costs range from \$0.39 to \$1.88 L^{-1} when camelina meal has a market value of \$0.30 kg^{-1} (Mupondwa et al., 2016). Also, values of \$50 ha^{-1} cost and a profit of \$50 ha^{-1} are advertised by camelina seed contractors in Canada. Further, a camelina breakeven price has been calculated in comparison with the price of diesel. This model resulted in a breakeven price of \$0.83 L^{-1} diesel for an experienced producer of camelina (Keske et al., 2013). Barriers to wide-scale adoption of this crop as feed or feedstock for biofuels include: lack of an open market, low seed yield, low price for the seed, perceived as a weed by farmers (Jewett, 2015), and antinutritional factors in both the meal and oil.

7. Camelina genetics, breeding, and improvement

7.1. Camelina breeding procedures and objectives

Camelina sativa is a predominantly autogamous species (Plessers et al., 1962; Zubr, 1997; Mulligan, 2002) with very low levels of intraspecific outcrossing: rates range from 0.01 to 0.28% at 20 to 60 cm distance (Walsh et al., 2012). Based on this, pure line selection is the breeding method of choice for camelina cultivar development; after artificial hybridization, segregating generations are handled using either the pedigree or bulk breeding method

(Vollmann and Eynck, 2015). The single-seed descent method as an approach to reach homozygosity in a short time has been used in breeding (Seehuber et al., 1987) and for development of recombinant inbred line (RIL) mapping populations (Gehringer et al., 2006) (S. Hulbert, personal communication, 30 April 2016), the latter being an immediate consequence of a lack of an efficient double-haploid protocol for camelina (Ferrie and Bethune, 2011). Next to hybridization, mutagenesis has been applied to create novel genetic variation in camelina. While EMS seed treatment was used to induce ALS-herbicide resistance in *C. sativa* (Walsh et al., 2012) (C. Eynck, personal communication 15 May 2016), seed treatment with both EMS and gamma irradiation was successfully utilized to modify the fatty acid profile of the seed oil (Vollmann et al., 1996; Büchsenschütz-Nothdurft et al., 1998) (R. Gugel, personal communication, 15 April 2016).

The major breeding objectives for camelina include, but are not limited to, developing adapted early-maturing strains with superior seed yield, high seed oil and meal protein contents, increased seed size, resistance to biotic stresses such as disease and insect pests as well as broadleaf herbicide tolerance. A breeding objective that deserves special attention is the improvement of seed size. As mentioned earlier, *C. sativa* is relatively small seeded when compared with other oilseeds such as canola or flax (*Linum usitatisimum* L.). Camelina's current seed size may in fact hamper its adoption in modern agriculture since small-seeded crops are generally more difficult to manage with large farm equipment. Larger seeded forms may exhibit better seedling emergence and establishment of the crop under dry seeding conditions (Eynck and Falk, 2013). Also, post-harvest processes may benefit from a larger seed since oil extraction is generally more efficient with large-seeded cultivars (Vollmann et al., 1996). However, Vollmann et al. (1996, 2007) concluded from their observations that an improvement of the 1000-seed weight of camelina above 1.5 g may be of low immediate value due to concomitant reductions of both oil content and seed yield. Conversely, our own work has shown that certain populations derived from crosses of large-seeded lines and lines with high oil content in fact bear individuals that combine both features.

Few studies have addressed the outcrossing nature of *C. sativa* with related crucifers of lineages 1 (*Camelineae*, *Cardamineae*) and 2 (*Brassicaceae*). Hybridization attempts between *C. sativa* and different Brassica crop species, such as *B. napus* and *B. rapa* (Argentine and Polish canola, respectively), *B. juncea* (oriental and brown mustard) and *B. nigra* were unsuccessful (Salisbury, 1991; Séguin-Swartz et al., 2011). *Camelina. sativa* also did not cross-fertilize *Arabidopsis. thaliana* and the small number of seeds produced from crosses with *Cardamine hirsuta* contained embryos that aborted at an early stage of development (Julié-Galau et al., 2014). Hybridization between *C. sativa* and *Capsella bursa-pastoris* resulted in few hybrids exhibiting female sterility and very low to no male fertility (Julié-Galau et al., 2014; Martin et al., 2015). Conversely, crosses between *C. sativa* and some of its wild relatives revealed a high level of interfertililty with *C. alyssum*, intermediate outcrossing rates between *C. sativa* and *C. microcarpa* and the development of only few, mainly sterile hybrids after crossing *C. sativa* and *C. rumelica* (Séguin-Swartz et al., 2013). While a hexaploid genome structure has been suggested for *C. alyssum* and *C. microcarpa* in one study (Hutcheon et al., 2010), the genome status of *C. microcarpa* was found to be more complicated, with reports of hexaploid, tetraploid, and even diploid populations (S.L. Martin, personal communication, 15 April 2016). The close relationship and interfertililty between *C. sativa* and *C. alyssum* and hexaploid *C. microcarpa* can be harnessed for the introgression of traits of interest and the general enhancement of genetic variation in camelina breeding.

7.2. Genomic applications: Genetic diversity, mapping and marker-assisted selection

Genetic diversity is a key factor to develop new genetic material and improved cultivars. Germplasm collections of *C. sativa* and its wild relatives are maintained by several institutions; however, the number of available accessions is comparatively low reflecting the minor role camelina has played as a crop in the past (Vollmann and Eynck, 2015). Thus, a total of 801*C. sativa* accessions are listed in the European catalogue of plant germplasm collections (EURISCO, http://www.eurisco.ecpgr.org), 137 accessions are held at Plant Gene Resources of Canada (PGRC, http://pgrc3.agr.gc.ca/) and 44 are listed in the USDA National Plant Germplasm System (http://www.ars-grin.gov/npgs/) as of May 2016.

Using a set of 15 RAPD markers, Vollmann et al. (2005) observed little genetic diversity among 41*C. sativa* accessions from a range of geographies, a finding that was confirmed for other *C. sativa* populations by Manca et al. (2013) and Singh et al. (2015) using SSR and SNP markers, respectively. However, Vollmann et al. (2005) in the same material, found considerable phenotypic variation for agronomic and seed quality traits. This observation is in agreement with earlier findings (Seehuber 1984; Budin et al., 1995; Schuster and Friedt, 1998; Zubr and Matthäus, 2002; Zubr, 2003) and suggests that despite a low level of genetic diversity sufficient phenotypic variation is present in current camelina germplasm to allow good progress toward agronomic improvement. The fact that seed oil content, a highly heritable trait in camelina (Vollmann et al., 1996), and seed yield appear to be positively correlated (Seehuber, 1984; Vollmann et al., 1996, 2007; Gehringer et al., 2006) may help in the selection of desirable genotypes. Interestingly, a high degree of genetic diversity was revealed through the use of AFLP fingerprinting in a previously not accessible set of *C. sativa* accessions from the Russian-Ukrainian area (Ghamkhar et al., 2010). In concert with archaeological records, this region was identified as a genetic diversity hotspot and potential centre of origin.

Little work has been done on creating a genetic map and the identification of quantitative trait loci (QTLs) associated with agronomic or seed quality traits in *C. sativa*. A RIL population was used to construct a linkage map from 157 AFLP and three Brassica SSR markers on a total of 20 linkage groups. QTLs for oil content, seed yield, plant height, 1000-seed weight, oleic, linoleic, linolenic, eicosenoic (gondoic), and erucic acid were identified. In accordance with the correlation repeatedly found in field studies, the major QTL for oil content co-localized with a QTL for seed yield (Gehringer et al., 2006). The mapping population developed by Gehringer et al. (2006) was subsequently utilized to develop a more detailed genetic map using an Illumina GoldenGate SNP array (768 SNPs), developed through capture of 3′ cDNA tags and genomic reduction libraries, as well as 46 EST-SSR markers (Singh et al., 2015).

8. Molecular genetics and resources

8.1. Reference genome

Chromosome counts in *C. sativa* have been reported as $n = 6$ or 14, or $2n = 12$, 26 or 40 with $2n = 40$ being most commonly reported (Warwick et al., 1999; Mulligan, 2002; Gehringer et al., 2006), a number highly suggestive of polyploidy (Warwick et al., 1999).

Camelina sativa was originally reported as a diploid but amplification of more than 1 locus by 31 of 55 homoeologous SSR primers, and 21% of AFLP markers that produced skewed segregation suggested a polyploid nature or a duplicated genome structure (Ghamkhar et al., 2010). Likewise, based on a large chromosome number, a three-fold larger genome than that of other *Camelina* relatives, and existence of three functional copies of *FAD2* and *FAE1*,

Hutcheon et al. (2010) proposed an allohexaploid makeup. The more recent release of a reference genome for *C. sativa* ($n = 20$) with an estimated genome size of ~782 Mb confirmed its hexaploid nature, which is relatively conserved across the three sub-genomes (Kagale et al., 2014). The same authors hypothesized that the *C. sativa* genome originated from an allotetraploid sub-genome (Cs-G2 and Cs-G3) with seven chromosomes each and a diploid sub-genome (Cs-G1) with six chromosomes, with sub-genomes Cs-G1, Cs-G2, and Cs-G3 predicated to encode 28,274, 27,218, and 29,207 genes, respectively (Kagale et al., 2014).

The reference genome shares close similarity to the Arabidopsis genome, both members of the Brassicaceae lineage I Camelineae tribe (Kagale et al., 2014). The similar functionality and expected phenotypes of transgenic *C. sativa* expressing homologous *Arabidopsis* genes (An and Suh, 2015; Choudhury et al., 2014; Lee et al., 2014; Nguyen et al., 2013) and the high degree of syntelogs (62,278) reported between the reference genome of *C. sativa* and *A. thaliana* (Kagale et al., 2014) suggest they likely have conserved functional characteristics. Although, many of the *C. sativa* genes annotated to *Arabidopsis* genes are expected to retain similarly functional characteristics, the allohexaploid nature of camelina with three copies of homologous genes make studies less straight forward (Bansal and Durrett, 2016).

8.2. Reference transcriptomes

The leaf transcriptome of greenhouse grown *C. sativa* (ecotype MT-5) has been investigated using Illumina paired-end RNAseq technology (Liang et al., 2013). *De novo* assembly of the reads identified 83,493 unigenes within the leaf transcriptome of which 67,791 were annotated, with 25,329 representing non-redundant protein sequences. Although a high degree of sequence identity was also noted between annotated unigenes of *C. sativa* compared with coding sequences of *A. thaliana*, some of the annotated unigenes associated with disease-resistance were reported to be more similar to those of *B. rapa* (Liang et al., 2013). Also, RNAseq has been used to profile the drought responsive transcriptome of *C. sativa* (BN14) leaf, stem, root, and young inflorescence tissue, which resulted in annotation of 60,171 transcripts and identification of 10,286 SSRs (Kanth et al., 2015). To date, Illumina next-generation RNAseq reads have also been generated from pre- and post-vernalized rosettes of both winter (cv. Joelle) and spring (cv. CO46) types of *C. sativa*. Of the 89,416 predicted genes in the *C. sativa* reference genome (Kagale et al., 2014), over 74,000 genes were expressed (RPKM > 0) in rosettes, with 22,157 showing high expression (RPKM ≥ 5) depending on the treatment and cultivar (J. Anderson, personal communication, 30 April 2016).

The seed transcriptome of field grown *C. sativa* 10 and 20 day after flowering (DAF) was investigated using 454 pyrosequencing technology (Wang et al., 2015). Of the 32,759 *de novo* assembled unigenes identified, 220 annotated as being involved in fatty acid synthesis had increased abundance at 20 DAF; of which, 47 were involved in polyunsaturated fatty acid biosynthesis. Nguyen et al. (2013) also used 454 pyrosequencing technology to sequence the seed transcriptome of *C. sativa* (cv. Suneson) 10 to 20 days after pollination to identify targets of meal and oil improvement. Along with the 2047 ESTs included in the previous study, assembly identified greater than 60,000 transcripts resulting from 22,597 putative genes.

8.3. Genetic transformation

Transformation of *C. sativa* can be accomplished using the *Agrobacterium*-mediated floral dip approach under vacuum (Lu and Kang, 2008). Further, transgenic lines can be generated in as little as 6 to 8 weeks and transgenic seeds can be identified using selectable markers for seed fluorescence and resistance to specific herbicides or antibiotics. *Camelina sativa* has been successfully transformed to produce several unusual fatty acids, such as long chain *n*-3 fatty acids [EPA and ecoisatetraenoic acid (ETA)], mono and sesquiterpenes, nervonic acid (NVA, C 24:1), poly-3-hydroxybutyrate (PHB), high oleic, hydroxyl fatty acids, omega-7 fatty acids, and medium chain saturated fatty acids (C 12:0 and C14:0) (Huai et al., 2015; Kim et al., 2015a; Liu et al., 2015; Malik et al., 2015; Ruiz-Lopez et al., 2015; Usher et al., 2015; Bansal and Durret, 2016).

The recent transformation of *C. sativa* with constructs containing heterologous genes from multiple species resulted in seeds containing up to 31% EPA and or 12% EPA and 14% DHA, which are reported to be equivalent to the heart-healthy levels of omega-3 (LC-PUFAs) found in fish oil – making it a terrestrial source for these fatty acids (Ruiz-Lopez et al., 2015). Transformation studies have also shown that overexpression of the *Arabidopsis* EP2/EREBP-type transcription factor WRINKLED1 (*AtWRI1*) in *C. sativa* enhanced seed mass and oil content (An and Suh, 2015), while expression of Cecropin P1 increased resistance to microbial phytopathogens (Zakharchenko et al., 2013). Transformation studies have also demonstrated the ability to bioengineer *C. sativa* to accumulate mono- and sesquiterpenes in seeds that are normally devoid of such products (Augustin et al., 2015).

In *C. sativa* transformed with β-ketoacyl-CoA synthase (considered the rate limiting step in fatty acid elongation) from *Lunaria annua*, NVA content in seed oil was 6–12% compared with little, if any, in wild-type seed (Huai et al., 2015). Very long chain fatty acids, such as NVA, are considered prime feedstocks for various medical and industrial products (Taylor et al., 2009). Seed oil composed of wax esters is also valued by industry and in *C. sativa* transformed with fatty alcohol-forming acyl-CoA reductase from *Mus musculus* (*MmFAR1*) and wax ester synthase from *Simmondsia chinensis* (*ScWS*) up to 21% of the seed oil triacylglycerol was replaced by wax esters (Iven et al., 2016). Because expression of these same genes in *Arabidopsis* resulted in 59% of seed oil TAG being replaced by wax esters, it was suggested that the competing loci of camelina's hexaploid genome may play a factor in the overall wax ester content.

Poly-3-hydroxybutyrate is a renewable and biodegradable polymer for replacement of some petroleum derived plastics (Snell and Peoples, 2009; Tsui et al., 2013). Transformation of *C. sativa* using vectors for seed-specific expression of genes encoding plastid targeted PHB enzymes resulted in a nearly twofold increase in PHB levels in seed (Malik et al., 2015). However, transgenic lines with increased levels of PHB had reduced seedling vigor, lower total oil content with increased levels of saturated fatty acids, but normal levels of seed protein. Competition for the common precursor acetyl-CoA between PHB production and fatty acid biosynthesis in seed plastids was suggested as the likely cause for reduced oil content and altered fatty acid profiles observed in transgenic seeds producing increased levels of PHB.

Nguyen et al. (2013) used RNAi technology to develop seeds deficient in napins by targeting 2S Seed Storage Protein genes, and to develop seed lines with high oleic acid by targeting *FAD2* and *FAE1*. In fact, in a double *FAD2*/*FAE1* RNAi seed line, they obtained 70 wt% oleic acid, with as little as 4 wt% LA and ALA, and reduced C20 and C22 fatty acids from 17 wt% in wild type to approximately 4 wt% in double RNAi seed lines. Interestingly, Nguyen et al. (2013) also demonstrated nearly identical high oleic acid phenotypes from *C. sativa* transformed with RNAi constructs containing *AtFAD2* and *AtFAE1*, which further confirmed the close genetic relationship between *C. sativa* and *A. thaliana*. Because polyunsaturated fatty acids such as LA and ALA are more prone to oxidation, which is undesirable for biodiesel blends (Durrett et al., 2008), these findings hold significance for biofuel and lubricant production. *FAD2* catalyzes the desaturation of oleic acid to linoleic acid, and *FAE1*

initiates addition of 2C units to 18C fatty acyl-CoAs, resulting in very long-chain fatty acids. These results are somewhat consistent with earlier work by Kang et al. (2011) where suppression of *FAD2* in camelina increased oleic acid content to 50 wt% and reduced LA and ALA content to 6 and 11 wt%, respectively, but it did not reduce C20 and C22 fatty acid contents.

A high-oleic *C. sativa* line transformed with diacylglycerol acetyltransferase from *Euonymus alatus* (*EaDAcT*) produced *sn-3* acetyl triacylglycerol (acetyl-TAG) oils with fatty acid compositions and physiochemical properties similar to acetyl-TAG from wild-type seed (Liu et al., 2015). Because acetyl-TAGs have reduced viscosity and improved cold temperature properties, they have desirable properties as biodegradable lubricants, food emulsifiers, plasticizers, and as a biodiesel feedstock. High oleic transgenic lines accumulating acetyl-TAGs (predominantly acetyl-dioleoyl-glycerol) were also reported to have little effect on seed weight, oil content, harvest index, and seed yield (Liu et al., 2015). Finally, transgenic lines of *C. sativa* overexpressing Heavy-Metal P1B-ATPase 3 (*CsHMA3*) have also shown promise for phytoremediation of metal contaminated soils (Park et al., 2014). Under heavy metal stress, seeds of these transgenic lines had increased content of unsaturated fatty acids compared with wild-type seed, and leaves and roots of wild-type plants had increased reactive oxygen species (ROS) compared with the *CsHMA3* transgenic plants.

8.4. *Toolbox ripe for developing* C. sativa *as a model system for future research*

The ability to easily transform, quickly regenerate, functionally test germplasm, in combination with next-generation sequencing and software for identifying markers makes *C. sativa* an attractive platform for manipulating germplasm with the desired agronomic traits discussed within this review. Some drawbacks do include the polyploid nature of *C. sativa* and low efficiency of producing double haploids. So far, most of the molecular and genetic studies described have related to spring-types of *C. sativa*, highlighting the gap in our knowledge related to the utility and economic value of winter-types. Because some winter ecotypes of *C. sativa* have proven tolerance to harsh freezing environments of the northern USA (Gesch and Cermak, 2011), breeding programs aimed at identifying the underlying mechanism of freezing tolerance should provide important clues for enhancing winter hardiness in other agronomically important Brassicaceae species such as winter canola. As cover crops, winter-hardy Brassicaceae species provide important ecosystem services beneficial to the development of climate-smart agricultural cropping systems, including suppression of spring-time weed establishment (R. Gesch and F. Forcella, personal communication, 15 May 2016), that contribute to the overall economic output in double cropping systems (Gesch and Archer, 2013).

8.5. *Molecular genetics of spring vs. winter ecotypes*

Both *C. sativa* and *A. thaliana* have a monocarpic life cycle where plants flower only once and then die. So far, the molecular basis for spring and winter flowering phenotypes in *C. sativa* is not known. In *A. thaliana*, cold induces a stable epigenetic silencing of the MADS-box transcription factor *FLOWERING LOCUS C (FLC)* (Michaels and Amasino, 1999). In turn, the vernalization-induced silencing of FLC inhibits its ability to repress the down-stream floral regulators *FLOWERING LOCUS T (FT)* and *SUPPRESSOR OF OVEREXPRESSION OF CO1 (SOC1)* (Helliwell et al., 2006). In closely related Brassicaceae species that have a polycarpic and perennial life cycle, such as *A. halleri*, *A. lyrata,* and *Arabis alpine*, orthologues of *FLC* are also repressed by vernalization. However, repression is not stable upon return to warm temperatures and cyclic fluctuation in expression of *FLC*, based on seasonal environments, also has an influence on the vegetative to floral states (Aikawa et al., 2010; Irish, 2010; Wang et al., 2009).

Winter varieties of camelina, often referred to as *C. sativa* ssp. *pilosa* (Martinelli and Galasso, 2011), and varieties of *A. thaliana* with intact *FLC* and *FRIDGIDA (FRI)* display similar prolonged rosette phases of growth, while vernalization induces a vegetative to reproductive transition (Song et al., 2014, 2015). In the reference genome of *C. sativa* the three copies of FLC (Csa08g054450; Csa13g011890; Csa20g015400) do not appear to have obvious mutations. Thus, exploring differences between the genotypic and phenotypic characteristics of the spring and winter flowering habits in *C. sativa* has potential to identify as of yet unresolved regulation of flowering in winter and spring types. Preliminary analysis of the transcriptomes (NCBI BioProject ID = PRJNA292793) of spring (CO46) and winter (Joelle) types of *C. sativa* indicates significant differences in *FLC* transcript abundance prior to vernalization and the potential for antisense regulation of *FLC* involving *COOLAIR* (Li et al., 2015) is being explored (J. Anderson, personal communication, 15 May2016).

9. Physiology

9.1. *Seed germination and development*

Based on the few studies that have addressed seed germination and emergence, despite camelina's small seed size, it tends to be quite vigorous. When measured under controlled environment conditions at 4, 10, 16, 21, 27, and 32 °C, Russo et al. (2010) reported that cultivar NEB C-1 germinated 100% of its seed at all temperatures except 32 °C. Also, 100% germination occurred within 9, 5, and 2 days at 4, 10, and 16 °C, respectively. Allen et al. (2014) exposed seeds of five different spring camelina cultivars to 0, 2, 4, and 16 °C, at soil depths of 3 and 6 mm under controlled environment conditions. In this study, the calculated base temperature for camelina growth was −0.7 °C, requiring an average of 1150 growing degree hours for emergence. They further demonstrated that the base temperature was 19% lower at the 6-mm sowing depth and that emergence was 11% quicker at the 3-mm sowing depth. Moreover, by 68 days, emergence was nearly 100% at 0 °C.

Few studies have addressed the physiological development of camelina seed. Maximum dry matter accumulation of developing seeds, and hence physiological maturity, occurred at around 30 days after anthesis in camelina grown under environment controlled conditions (Pollard et al., 2015). Maximum oil accumulation occurred a few days earlier at about 27 days after anthesis. In a similar study, Rodríguez-Rodríguez et al. (2013) demonstrated that maximum protein and oil accumulation in developing camelina seeds occurred at about 35 days after anthesis and the maximum rate of oil accumulation of 15 $\mu g\,day^{-1}$ occurred between about 12 to 27 days after anthesis. Whereas in the Pollard et al. (2015) study it was found to be 26 $\mu g\,day^{-1}$ between 14 and 20 days after anthesis.

9.2. *Plant growth and development*

The extended BBCH (Biologische Bundesantalt, Bundessortenamt und Chemische Industrie) scale has been used by Martinelli and Galasso (2011) to accurately describe the phenological growth stages of camelina. These authors have used the BBCH scale to describe the ten principal growth stages using both a two- and three-digit code and included corresponding illustrations, which has become an important tool in agronomic and physiological studies.

The life cycle of camelina is relatively short, which again is another reason it fits well in small grain cropping systems in the western USA and Canada. For 19 camelina accessions grown in western Canada, Gugel and Falk (2006) reported a range in days from sowing to 20% flowering of about 38 to 52 days, and a range in days to maturity of 72 to 106 with an overall average of 92 days. Gesch (2014) studied 10 different spring cultivars and nine sowing dates across three years in west central Minnesota. Averaged across cultivars, days from planting to 50% flowering ranged from about 36 to 59 days, decreasing with later sowing and associated with higher temperatures. This corresponded to a range of growing degree days (GDD; 5 °C base temperature) of 469 to 578 °C d. In the same study, the days from sowing to harvest ranged from 75 to 100, corresponding to a range in GDD of 1101 to 1216 °C d. For two different winter camelina cultivars (BSX-WG1 and Joelle) sown between mid-September and mid-October in west central Minnesota, the accumulated GDD required to reach 50% flowering ranged from 466 to 914 °C d (Gesch and Cermak, 2011). The large range in GDD to 50% flowering was mainly due to warm autumn temperatures in one of the years of the study. Despite this, however, across both years of the study, most plants began flowering in a relatively narrow window of time between late May and early June.

Root growth of camelina has not been extensively studied, and published information in this regard is scarce. What information does exist tends to indicate that camelina may not have an extensive root system. In a controlled environment study, Pan et al. (2011) reported a range in root:shoot ratio at maturity of 0.41–0.73 for well-watered plants. An increase in root:shoot ratio with increased soil water depletion was detected indicating an allocation of C to roots under drought stress. In another controlled environment study, a root:shoot of 0.10–0.12 for spring camelina at maturity was reported (Johnson and Gesch, 2013). This is similar to the 0.10 root:shoot ratio of camelina at 61 days after planting reported by Pavlista et al. (2012) for field grown plants in Nebraska. These root:shoot ratios are lower than those reported for other oilseed species (Gan et al., 2009) and annual grain crops (Johnson et al., 2006).

Gesch and Johnson (2015) studied the seasonal water use and root density distribution of winter camelina (Joelle) in west central Minnesota and reported that over 80% of camelina's root density was found within the 0 to 0.3 m soil profile, with only about 6% in the 0.6- to 1.0-m depth. In that study, the root:shoot ratio ranged from 0.14–0.53 over a two-year period. The higher root:shoot ratio for winter camelina than previously reported for spring camelina might have been due to an extended period in autumn for roots to become established before overwintering and resuming growth the following spring, which may have resulted in greater root growth.

9.3. Abiotic stress tolerance

Several lines of evidence indicate that camelina has a relatively high level of tolerance to drought and low temperature stress. Under cool semi-dry environments, camelina productivity has been shown to be competitive with that of *B. napus* and other mustard species. In six out of nine site-years across growing locations in Alberta, Saskatchewan, and Manitoba Canada, camelina produced seed yields as high as or higher than canola (Blackshaw et al., 2011). Others from the USA (Pavlista et al., 2011) and Canada (Gugel and Falk, 2006) have also shown that camelina is competitive with other more genetically refined Brassica species such as *B. napus* and *B. juncea* under certain environments.

Total season water use of camelina grown during the winter months in Arizona was found to range from 332 to 371 mm, a little more than half the amount of water required to produce vegetable crops during a similar timeframe in the same area (French et al., 2009; Hunsaker et al., 2011). However, this study was conducted with supplemental irrigation. The same study demonstrated that there was no difference in seed yield among treatments with 40–75% available soil water depleted. Only under the highest water stress treatment (85% depletion of available water) was there a significant reduction in yield, although this was only 13% lower than the average of 1142 kg ha^{-1} for the other treatments.

Generally, these studies demonstrate that camelina has a relatively low water use requirement and high tolerance to drought. As suggested by Hunsaker et al. (2011), camelina's resiliency to drought might in part be related to the ability to extract water from deep in the soil profile. However, camelina's short lifecycle is another factor that probably plays an important role in its low water use and may help to avoid severe drought stress.

Gesch and Johnson (2015) measured water use of autumn-sown winter camelina in Minnesota between spring regrowth while seedlings were still in the rosette stage (early to mid-April) until harvest in late June to early July. Over both years of the study, camelina's water use ranged from only 96 to 185 mm. These values were much lower than those determined by Hunsaker et al. (2011), due to the rainfall differences. Gesch and Johnson (2015) observed that not only is camelina a low water user, but the majority of its water use occurred during a time when excess soil moisture often exists in the upper Midwest due to lack of vegetation on the agricultural landscape. Conversely, for camelina grown in a semi-arid environment, seed yield increased significantly when irrigated (Pavlista et al., 2016).

Both spring and winter genotypes of camelina have exceptional low temperature tolerance. Spring camelina seedlings (cv. Calena) at the two-leaf stage exposed to air temperatures of −23 °C for 8 h without snow cover sustained a 70% survival rate (Schillinger et al., 2012). In addition to low temperature tolerance, winter cultivars demonstrate exceptional freeze hardiness (Gesch and Cermak, 2011) that surpasses that of spring-types. In growing areas where snow cover can often be minimal, despite extremely low air temperatures that average below 0 °C from December until early March, the survival of winter camelina even rivals that of winter rye (*Secale cereale* L.) and far surpasses winter annual oilseed rape (Gesch, personal communication, 1 May 2016).

There are several reports that indicate camelina possesses good tolerance to lodging over a wide range of environments (Robinson, 1987; Putnam et al., 1993; Gugel and Falk, 2006; Gesch, 2014). Robinson (1987) reported that compared with other Brassica oilseed species such as canola and crambe (*Crambe abyssinica* Hochst.), camelina tended to show better lodging resistance. Gesch (2014) reported that lodging was minimal for 10 cultivars of spring camelina at different growth stages of development (due to different sowing dates) when exposed to two extreme wind events associated with strong mid-summer thunderstorms.

Although there is little doubt that camelina can be successfully produced under semi-arid environments (Guy et al., 2014) there are reports indicating that heat stress may be problematic, especially during the reproductive phase. Over three years and nine different sowing dates, Gesch (2014) found that camelina seed yields and oil content significantly declined when high temperatures coincided with the reproductive phase, even when water was not limiting. Others have also reported that high temperatures may hinder camelina seed yields (Berti et al., 2011; Schillinger et al., 2012).

With respect to other abiotic stresses, camelina has been reported to be highly susceptible to waterlogging in the field (Gesch and Cermak, 2011). There is also evidence, albeit through *in vitro* assays, that camelina may be susceptible to salinity stress (Khalid et al., 2015).

10. Agronomic management

10.1. Sowing requirements

Optimum sowing date for spring camelina will vary with location and environment. All reports of spring camelina seeding in the USA, indicate that sowing early in the spring (April-May) compared with a later sowing date in mid-summer results in higher seed yield (Sintim et al., 2016; Gesch, 2014). The best time to sow spring camelina in west central Minnesota is from about mid-April to mid-May (Gesch, 2014) and in Wyoming in early May (Sintim et al., 2016). In regions such as the Pacific Northwest and Northern Great Plains that are prone to high temperatures in mid- to late summer, there is a consistency between early spring sowing dates and optimum seed yields (Schillinger et al., 2012; Gesch, 2014). This is likely because the reproductive phase of early spring-sown camelina coincides with mild summer temperatures. In Mediterranean climates, with mild winters, fall sowing is optimal (Berti et al., 2011; Masella et al., 2014). Seed yield decreases as sowing date is delayed, which is explained by the formation of fewer silicles plant^{-1}, decreased seed weight (Berti et al., 2011), and reduced branching (Masella et al., 2014). The optimum sowing date for winter camelina in the northern USA is early autumn, typically early September to early October (Gesch and Cermak, 2011; Gesch and Archer, 2013; Berti et al., 2015).

Camelina seeding rate commonly varies between 4 and 6 kg ha^{-1}. Although the number of plants needed would be enough with about 2 kg ha^{-1} of seed, higher rates are usually recommended to account for losses due to soil preparation and planting, lack of moisture, and competition with weeds. Seeding rates lower than 4 kg ha^{-1} have resulted in reduced yield in some years and locations, whereas seeding rates greater than 6 kg ha^{-1} have not shown seed yield increase (Dobre et al., 2014).

Camelina's outstanding compensating ability to maintain seed yield was demonstrated by McVay and Khan (2011) performing stand reduction on field-grown plants in Montana. McVay and Khan (2011) started with a control population of 193 plants m^{-2}, and reduced stands by 25, 50, 75, and 90% at both rosette and bolting stages. They reported that reductions in plant stands of up to 75% at rosette and up to 50% at bolting had no significant effect on seed yields. Thus, plasticity of plants and ability to compensate yield was greater at the rosette rather than the bolting stage. When plant stands were reduced by 75% at bolting, seed yield declined by 50%. This high level of yield compensation is due to increased branching, producing more silicles and seed per plant, and increased individual seed weight (Urbaniak et al., 2008; Berti et al., 2011).

Good seed to soil contact during sowing is vital for stand establishment. Only a few studies have addressed sowing methods for camelina, which has included evaluating broadcast and shallow drill seeding (Robinson, 1987; Urbaniak et al., 2008; Schillinger et al., 2012; Aiken et al., 2015). Generally, both methods have resulted in sufficient stands with little or no difference in seed yield (Urbaniak et al., 2008; Schillinger et al., 2012). However, Aiken et al. (2015) demonstrated that sowing with a no-till drill at 20-mm depth resulted in better emergence and earlier flowering than with broadcast sowing.

Most current recommendations suggest sowing seed at soil depths between 6- and 13-mm (McVay and Lamb, 2008). Some evidences indicates that because of camelina's high seed vigor, it may be able to be sown deeper than most current recommendations suggest. After observing a significant amount of emergence at a sowing depth of 50 mm in a tilled silt-loam soil, Robinson (1987) commented that camelina may be sown deeper than expected based on its seed size, which is another testament to its resiliency and vigor. Recently, it was demonstrated that sowing at 20 mm deep, in a fine-loamy soil did not sacrifice stands or yields compared to shallower depths, although sowing at 40 mm did reduce stands by 67% and yields by 23% (Gesch, 2015). Furthermore, stand establishment for deep sowing was also shown to be compensated for, by increasing seeding rate.

10.2. Fertilization requirements

Numerous studies on camelina fertilization have been conducted. Most studies report camelina response to nitrogen and sulfur and only a few report the response to phosphorus. Positive seed yield response to nitrogen fertilization has been reported by several authors, but the nitrogen rate to achieve maximum seed yield varies (Zubr, 1997; Urbaniak et al., 2008; Gesch and Johnson, 2013; Solis et al., 2013; Wysocki et al., 2013; Mahli et al., 2007; Sintim et al., 2015; Jiang and Caldwell, 2016). Location, soil type, and genotype are the most common factors influencing nitrogen response. Although camelina has been categorized as a low input crop, research shows that given optimum growth conditions, camelina can increase its seed yield at rates up to 200 kg N ha^{-1} (Jiang and Caldwell, 2016; Solis et al., 2013). If fertilized with those high rates, camelina would no longer be a low input crop. Camelina's positive seed yield response to nitrogen in these studies mainly resulted from increased branching and number of silicles m^{-2} (Solis et al., 2013; Jiang et al., 2014; Jiang and Caldwell, 2016). Moreover, nitrogen uptake into biomass and seed increased with increasing nitrogen rates. Conversely, nitrogen fertilizer use efficiency and the percent recovery of applied nitrogen decreased with increasing nitrogen rates (Solis et al., 2013; Wysocki et al., 2013; Malhi et al., 2014). Under certain environments such as eastern Canada and the Pacific Northwest, although camelina yields have been reported to increase with applied nitrogen, the yield increase above about 60–80 kg N ha^{-1} is often not enough to warrant applying additional nitrogen (Urbaniak et al., 2008; Wysocki et al., 2013).

Nitrogen fertilizer rate has been shown to be positively correlated with seed protein content and negatively correlated with seed oil content in camelina in several studies (Solis et al., 2013; Jiang et al., 2014, 2013; Sintim et al., 2015). Oil composition and protein content appear to be largely genotype-dependent. Additionally, increased nitrogen rates can increase the risk of lodging (Solis et al., 2013) and disease susceptibility (Jiang and Caldwell, 2016).

Although response to phosphorus has not been studied as extensively as to nitrogen, in a study conducted in Chile, seed yield did not respond to phosphorus, but interestingly there was significant interaction between phosphorus and nitrogen (Solis et al., 2013). Thus, seed yield response to nitrogen was maximized in the absence of phosphorus fertilizer application.

Plants in the Brassicaceae family are usually very S-demanding and response to S has been observed in canola (Mahli et al., 2007). Conversely, most studies for camelina have not reported a response of camelina seed yield to sulfur (Solis et al., 2013; Wysocki et al., 2013; Sintim et al., 2015). Jiang et al. (2014) did observe increased seed yield, seed protein content, and proportion of PUFAs in camelina oil when 25 kg S ha^{-1} was applied.

10.3. Weeds, diseases, and insects

Weed control is currently one of the major challenges in camelina production (Lenssen et al., 2012). The best weed control approach is to plant early into relatively weed-free fields. Early planting and good stand establishment allows camelina to compete with weeds. Although it has been claimed that camelina is very competitive and will suppress weeds, in some instance this has not been the case. Cool-season weeds such as *Bromus tectorum* can outcompete camelina (Davis et al., 2013). Green foxtail [*Setaria viridis* (L.) Beauv.], and Russian thistle (*Salsola kali* L.) at densities

of 40 and 39 plants m^{-2}, respectively presented serious competition for camelina (Lenssen et al., 2012). Camelina seed yield has been reported to decrease by 50% when grown a in mixture with faba beans (*Vicia faba* L.) (Ghaouti et al., 2016). Perennial broadleaf weeds such as field bindweed (*Convolvulus arvensis* L.), Canada thistle [*Cirsium arvense* (L.) Scop.], and skeleton weed (*Chondrilla juncea* L.) are also problematic for camelina (WAPMC, 2012). In Chile, camelina showed very high susceptibility to dodder (*Cuscuta* spp.), a parasitic weed of many crops (M.T. Berti, personal communication, 15 May 2016).

Sethoxydim, a grass herbicide, is the only herbicide currently registered for use in camelina, at rates between 0.21 and 0.54 kg ai ha^{-1} in the USA (Enjalbert and Johnson, 2011; WAPMC, 2012). Additionally, in Canada, quizalofop is registered, at rates between 0.37 to 0.74 kg ai ha^{-1}. Camelina tolerates only a few broadleaf herbicides. Dinitroaniline herbicides, in general, provide adequate safety and early season weed control. Unfortunately, many weeds are not controlled by these herbicides. Other pre-emergence herbicides evaluated in camelina include pendimethalin, quinclorac, S-metolachlor, and dimethenamid-P. Pendimethalin at the 1.06 or 2.14 kg ai ha^{-1} rate did not reduce seed yield although some injury was observed. Pre-emergence applications of 0.28 and 0.84 kg ai ha^{-1} of quinclorac did not significantly injure camelina. S-metolachlor at 1.06 to 2.14 kg ai ha^{-1} did not reduce seed yield but caused 20% injury to camelina. Dimethenamid-P applied at 0.63 kg ai ha^{-1} did not affect camelina density, and seed yield; however, at the 1.26 kg ha^{-1} rate, injury was as high as 60% and seed yield was reduced by 31% (Jha and Stougaard, 2013).

Camelina mutants resistant to acetolactate synthase inhibitor herbicides were developed by Walsh et al. (2012). Thus, camelina cultivars with resistance to imazethapyr, sulfosulfuron, and flucarbazone might be available in the near future.

Camelina is susceptible to some diseases common to crops in the Brassicacea family including damping-off caused by *Rhizoctonia solani* Kühn, and *Pythium debaranium* Auct non R. Hesse, clubroot (*Plasmodiophora brassicae* Woronin), white rust [*Albugo candida* (Pers.) Kuntze] (Séguin-Swartz et al., 2009), and aster yellows disease caused by a phytoplasm (Soroka et al., 2015). Some genotypes are also susceptible to downy mildew (*Hyaloperonospora camelinae* Gäum) (Putnam et al., 2009), especially under hot humid conditions (Gesch, 2014). Fortunately, camelina is highly resistant to two of the most important diseases in canola and other brassicas, alternaria black spot [*Alternaria brassicae* (Berk.) Sacc. and *A. brassicicola* (Schw.) Wiltsh] and blackleg [*Leptosphaeria maculans* (Desmaz.) Ces. & De Not. [anamorph *Phoma lignam* (Tode/Fr.) Desmaz.]. Additionally, many genotypes exhibit resistance to sclerotinia stem rot [*Sclerotinia sclerotiorum* (Lib.) de Bary], brown girdling root rot (*Fusarium* spp and *R. solani*), and downy mildew (Séguin-Swartz et al., 2009).

Camelina is not susceptible to three of the common insects of canola; flea beetles (*Phyllotreta* spp.), root maggots (*Delia* spp.), and diamondback moth (*Plutella xylostella* L.). Feeding damage from Bertha armyworm (*Mamestra configurata* Walker) was similar in camelina compared with canola. Although camelina is not directly damaged by the feeding of the leafhopper *Macrosteles quadrilineatus* (Forbes), this insect transmits the aster yellows phytoplasm which camelina is highly susceptible to. Other insects, such as aphids have been reported on camelina but without causing economic damage. However, the colonization ability of camelina by different aphid species could constitute a reservoir for aphids threatening other crops in the rotation (Chesnais et al., 2015). Winter camelina stand failures in Colorado, USA, have been related to the presence of *Ceutorhynchus cyanipennis* and *C. americanus*. The larvae of these insects feed on stems below the soil line reducing winter camelina stands in the falls (Jewett, 2015).

10.4. Harvest, drying, and processing

Camelina can be direct combined or swathed and then combined, both methods result in similar seed yields (Gesch et al., 2014). However, to direct-combine camelina settings should be adapted to camelina; e.g. combine speed, wind flow (fan speed), small opening screens, leak sealing, distance between the threshing cylinder and the concave, and others, in order to prevent seed loss. Although seed shattering may occur in camelina, it usually does not shatter heavily. Total seed loss with direct combining was 11.7% according to Sintim et al. (2016). Early harvest (50% ripe silicles) resulted in 9.5 and 23.6% greater seed yield than the mid-harvest (70–80% ripe silicles) and late harvest (>90% ripe silicles).

Sintim et al. (2016) suggested that in order to achieve a balance between seed yield, seed oil content, and acceptable loss due to shattering, camelina should be harvested when 75% of silicles are mature. However, for proper storage, camelina seed should be dried to about 80–100 g kg^{-1} moisture (McVay and Lamb, 2008). Therefore, unless a farmer has the capacity to mechanically dry seed, it is best to harvest when silicles are >90% mature, when the moisture content of the seed is 150 g kg^{-1} or less from the field and quickly air dries upon handling (R. Gesch, personal communication, 15 May 2016). Post-harvest seed cleaning and conditioning is necessary after harvest to obtain a high quality seed.

10.5. Crop rotations and intercropping

Interestingly, camelina in rotation with other crops or in intercropping systems was a common practice in the Iron Age. Archeological records indicate it is likely camelina and flax were grown and harvested together. This mixed intercropping would allow early Scandinavian settlers to have a mixed oil or take advantage of the different nutrient demands of both crops (Larsson, 2013).

In the past ten years, several studies of camelina in rotation with cereals as well as common upper Midwest crops including corn and soybean have been reported (Lenssen et al., 2012; Dobre et al., 2014; Gesch et al., 2014; Berti et al., 2015; Chen et al., 2015). Camelina as a rotational crop usually does not affect the subsequent crop's seed yield (Shonnard et al., 2010) and has been shown to even enhance the yield of certain crops like corn, soybean, and wheat (*Triticum aestivum* L.) (Gesch et al., 2015). However, in dryer areas such eastern Montana where a common rotation is fallow-winter wheat, substituting camelina in the fallow year reduced winter wheat grain yield in comparison with the fallow-wheat sequence. Also, economic returns were greater for the fallow-wheat system (Chen et al., 2015). Using winter camelina for double cropping in west central Minnesota, yields of soybean and sunflower (*Helianthus annuus* L.) immediately following camelina were 82% and 72%, respectively of their monocropped counterparts. However, the net economic returns for the double-cropped camelina and soybean were higher than for monocropped soybean (Gesch and Archer, 2013).

Double or dual cropping is defined as two crops grown on the same field within a year (Crabtree et al., 1990; Kyei-Boahen and Zhang, 2006). Also, double cropping can be defined as the seeding of a second crop once the winter annual crop has been harvested. Relay cropping is a temporal crop intensification system (Heaton et al., 2013). It is defined as a method of multiple cropping, where a crop is planted into an already established crop whereby the life cycles of the two crops overlap each other during a certain period (Kline et al., 2003). Relay cropping allows earlier seeding of crops and increases the potential to harvest the small grain as a cash crop (Gesch et al., 2014).

Fig. 4. Relay cropping soybean with winter camelina. The picture on the left is in late May when camelina began flowering and soybean had just emerged (soybean was sown in early May). The picture on the right is in late June when camelina was harvested. Soybean was harvested later in early October. (Photo: Russ Gesch).

Winter camelina has been identified as an excellent crop for both double and relay cropping in the North Central USA (Fig. 4) (Berti et al., 2015; Gesch et al., 2014). Winter camelina matures early in the summer to allow producing a second crop, typically a short-season summer annual such as soybean (Gesch and Archer, 2013; Gesch et al., 2014). Double and relay cropping camelina with soybean can result in total seed oil yield (both crops combined) that is as much as 50% greater, and economic returns that are as high or higher, than producing a sole soybean crop (Gesch et al., 2014). Moreover, dual cropping of winter camelina with forage crops such as sorghum [*Sorghum bicolor* (L.) Moench.] and foxtail millet (*Setaria italica* L.) has also been proven to be agronomically viable for the upper Midwest (Gesch and Archer, 2013; Berti et al., 2015).

10.6. Camelina seed yield across environments

As camelina production management practices develop around the world numerous publication on camelina seed yield have been reported (Table 6). Seed yields vary with cultivar, climate, and the types of soil where camelina is cultivated (Vollmann et al., 1996, 2007; Zubr, 2003; Blackshaw et al., 2011; Berti et al., 2011; Masella et al., 2014; Mupondwa et al., 2016). Highest seed yields have been reported in Mediterranean climates (Berti et al., 2011; Masella et al., 2014).

In North America, spring camelina, is particularly being targeted for the western Prairie provinces of Canada, the North and Central Plains, and the Pacific Northwest in the USA, where it not only thrives, but also may be economically competitive with small grain commodity crops and other alternative oilseeds common to these areas (Blackshaw et al., 2011; Keske et al., 2013; Chen et al., 2015). Camelina as a standalone crop in the upper Midwest Corn Belt region may have challenges competing economically with corn and soybean. However, with the recent advent of dual cropping with winter camelina, this may be a way to integrate camelina into corn-soybean systems in an economically viable fashion as a cash cover crop, while also adding ecosystem services. Testing new cultivars in new areas will always be necessary to determine yield potential associated with genotype x phenotype x environment interactions ($G \times P \times E$).

11. Ecosystem services

Recently, winter camelina has been evaluated as a cash cover crop in corn-soybean or wheat soybean cropping systems. Camelina interseeded in standing corn and soybean before the cash crop matures, allows camelina to establish and provides soil cover in the fall. Because of camelina's winter-hardiness, it regrows in the spring protecting the soil from erosion before the next summer annual cash crop is established (Gesch et al., 2014). In the Midwest states in the USA, winter cereal rye is commonly used as a cover crop because it survives freezing even in climates where winter annual crops often succumb to winter-kill. Thus, in these areas, winter rye is one of the only cover crop options to minimize soil erosion and nutrient run-off early in the spring. Therefore, the development of winter camelina is vital to provide an additional cover crop option for cold temperate climates such as the northern USA Also, camelina might be grown in mixture with rye to benefit from the ecosystem services that both crops offer.

Although the effect of camelina on soil physical and chemical properties has not been studied, many plants in the Brassicaceae family are used as summer annual and cover crops and their benefits to soil structure and nutrient cycling are well known (Dean and Weil, 2009; White and Weil, 2011; Lounsbury and Weil, 2015).

Generally, camelina produces a relatively small amount of biomass compared to other common grain crops like wheat and corn. When used exclusively as an annual crop, following harvest, little residue is returned to the soil, somewhat similar to soybean. Therefore, when monocropped rather than used as a cash cover crop, camelina could potentially leave the soil vulnerable to erosion, although this has not been well studied. In the semi-arid Pacific Northwest, where wind erosion from agricultural systems has been cited as a major environmental and health issue, Sharratt et al. (2015) reported that a rotation of winter wheat-camelina-summer fallow under conventional tillage resulted in greater annual soil losses by wind erosion than a winter wheat-summer fallow rotation. This was even after correcting for length of rotation (i.e., 3-year versus 2-year rotation scheme).

Camelina's deep tap root system, depending on soil type and conditions, will likely enhance nutrient scavenging while the cover

Table 6
Camelina seed yields reported in different countries.[a]

Country/State	Seed yield (kg ha^{-1})	Cultivars reported	Main variation factor	References
Austria	1574–2248	Calena, Lindo, and breeding lines	Seed size and breeding lines	Vollmann et al. (2007)
Canada	500–1600	CS005, CS006	Sowing rate	Johnson et al. (2010)
Chile	420–2390	Blaine Creek, Gold of pleasure	Sowing date, N, P, S, fertilization	Berti et al. (2011), Solis et al. (2013)
Denmark	1270–2360			Zubr (1997)
Germany	1100–2650	Breeding lines	Breeding lines	Gehringer et al. (2006)
Italy	1200–3300	Calena, Ligena, Ukrajinskaja, Lindo, ZarjaSocialisa, Soledo, Morgesonne	Sowing date and genotypes	Masella et al. (2014)
Romania	1761–2892	Camelia, Calena, Lindo	Cultivars	Toncea (2014), Toncea et al. (2013)
Slovenia	400–800	n.a.		Rode (2002)
Turkey	572–997	Vinimik 17, accessions	Accessions and breeding lines	Katar et al. (2012)
USA/AZ	1178–1638	Robinson	Irrigation	Hunsaker et al. (2013)
USA/MN, ND	743–2300	Robinson, Blaine Creek, Suneson, CO54-97, Calena, Celine, Galena, CO46, Ligena, Gold of Pleasure, Joelle	Double cropping, relay cropping, cultivars, sowing date	Gesch et al. (2015, 2014), Berti et al. (2015)
USA/MT	912	Blaine Creek	Crop rotation	Pavlista et al. (2016), Chen et al. (2015)
USA/NE	620–2543	Cheyenne, Boa	Irrigation, planting methods	Pavlista et al. (2016), Aiken et al. (2015)
USA/WA	720–1068	Blaine Creek, Pronghorn, Shoshone	Sowing date, harvest	Sintim et al. (2016)

[a] References are mostly on spring camelina. Only Gesch et al. (2015, 2014) and Berti et al. (2015) include 'Joelle', a winter type cultivar.

provided will reduce nutrient run-off especially for winter annual biotypes. Other tap-rooted brassicas such as radish and turnip are known for reducing soil compaction, improving infiltration characteristics that are also likely to be provided by camelina.

Recent evidence also indicates that camelina can provide an important service to domestic and native pollinators by sustaining their abundance and health. Both winter and spring camelina provide nectar and pollen for honey bees and other pollinators early in the season, sometimes long before most common crops grown in the Midwest begin to flower. Flowering of winter camelina in the upper Midwest typically peaks in late May, and that of spring camelina in late June, both flower much earlier than soybean, canola, flax, and other minor oilseeds in the same area (Thom et al., 2016; Eberle et al., 2015). Total nectar sugar produced throughout anthesis was reported to be more for winter camelina (100 kg ha^{-1}) than for pennycress (*Thlaspi arvense* L.) (12 kg ha^{-1}) and canola (82 kg ha^{-1}) (Eberle et al., 2015). The nectar sugar produced by camelina flowers is a good food source for honey bees (*Apis mellifera* L.), which usually need 100–250 kg yr^{-1} colony^{-1} (Axel et al., 2011).

12. Identified gaps in knowledge and areas needing research

Although the breadth of research in camelina in the last few years is impressive, several areas that would benefit from further research were identified.

12.1. Uses and product development

Research on new uses and products from camelina oil has been hampered by the limited supply of refined oil. As the oil becomes more available, additional products will be developed. In order for these products to become commercialized a number of events need to occur: a consistent oil supply with a known price must be established, which includes dealing with logistical issues such as transport and storage of camelina seeds and oil. Camelina oil can initially be envisioned as drop-in vegetable oil for the HRJ fuel process, but again the exact feedstock specs must be developed and published for the different fuel cracking processes.

Research on substitution of fish oil in fish diets has been extensive. Nevertheless, new research will be needed to refine the levels of inclusion of camelina oil and meal in different fish species at different developmental stages, as well as in and other animal diets.

12.2. Breeding and molecular genetics

Rethinking of appropriate cropping systems and rotational options is needed as we move into an era of climate-smart agriculture. Winter-hardy oilseed cover crops show tremendous promise for providing needed ecosystem services, but currently low seed yield and other quality traits hamper the potential of winter camelina to be considered economically viable for double- or relay-cropping in the Great Plains or upper Midwest. Development of populations from crosses between winter and spring types of *C. sativa*, combined with leveraging next-generation sequencing technologies to identify genetic factors associated with, for example, freezing tolerance, flowering, yield, and seed oil quantity and quality are needed. Either through conventional breeding or transgenic approaches, increasing the seed size, seed yield and oil quality in winter types of camelina could enhance their economic value as cover crops in double and relay cropping systems of the upper Great Plains and Midwest. Using transgenic approaches such as RNAi and CRISPR/Cas 9 technology in this model system could be beneficial to elucidating genetic and molecular mechanism regulating flowering and tolerance to freezing in *C. sativa*.

12.3. Physiology and adaptation

Seed development studies have been done in growth chambers or controlled conditions. Research is needed on field-grown plants to compare seed developmental responses with those of growth chamber-grown plants.

Research is greatly needed to better understand the physiological and molecular mechanisms responsible for freeze and drought hardiness of camelina, which presumably could be used to improve these traits in other economically important oilseed crops such as canola. Also, research is needed to better understand camelina's response to high temperature stress, waterlogging, and salinity stress with the emphasis on using this information to improve its resistance to these abiotic stresses.

12.4. Agronomic management

Research in agronomic management of camelina has grown exponentially in the last decades. Sowing rates, plant density, and sowing date studies are numerous and there are not many questions unanswered, although in new regions studies on sowing dates might be warranted to evaluate potential adaptation. The few

studies published on sowing depth are somewhat conflicting, probably due to differences in soils. New research to pin point the soil factors interacting with sowing depth are needed.

Studies on nitrogen fertility are manifold and are somewhat conflicting and therefore it is not fully clear how camelina responds to nitrogen. Research on other nutrients, such as phosphorus, sulfur, and micronutrients are either inconclusive or nonexistent. Research and development of new herbicides for camelina is greatly needed to expand camelina commercial production. Also, the critical time for weed competition has not been researched.

Considerably more research is needed, concerning camelina's impact on soil chemical, physical, and biological properties. The use of winter camelina as a cover crop is very recent and additional research is needed to determine its management as a cover crop, including sowing dates, interseeding, fertilization, and termination.

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