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Camelina Seed Yield and Fatty Acids as Influenced by Genotype and Environment

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ABSTRACT

Camelina (*Camelina sativa* L. Crantz) is an alternative oilseed crop with potential for fallow replacement in dryland cereal-based crop production systems in the semiarid Great Plains. The interaction between genotype and environment was investigated on camelina seed yield, oil content, and fatty acid composition across two locations in the U.S. Great Plains. Treatments were three spring camelina genotypes (cultivars Blaine Creek, Pronghorn, and Shoshone), three growing seasons (2013, 2014, and 2015) and two locations (at Hays, KS, and Moccasin, MT). Results showed camelina grown at Hays yielded 54% less than that at Moccasin. Blaine Creek yielded 17 and 42% more than Pronghorn and Shoshone at Hays but yields were not different among genotypes at Moccasin. Oil content ranged from 262 g kg^{-1} at Hays to 359 g kg^{-1} at Moccasin. The proportion of polyunsaturated fatty acids (PUFAs) ranged from 51% at Hays to 55% at Moccasin, whereas monounsaturated fatty acid (MUFA) and saturated fatty acid (SFA) contents were greater at Hays. The linolenic acid content ranged from 26% when Pronghorn was planted at Hays to 35% when planted at Moccasin. In general, the variations in seed yield and fatty acid profile corresponded well with growing season precipitation and temperatures at each environment.

Core Ideas

- Genotype × environment affected camelina seed yield, oil and constituent fatty acids.
- Blaine Creek produced the greatest seed among the camelina genotypes studied.
- Camelina grown at Hays, KS, had less yields and oil content compared to Moccasin, MT.
- Camelina at Moccasin, MT had greater linolenic acid content compared to Hays, KS.

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Camelina is an alternative crop with potential for dryland crop production in the Great Plains region. Camelina is cold and drought tolerant (Budin et al., 1995; Gugel and Falk, 2006) and requires relatively low fertilizer inputs (Putnam et al., 1993). It is well adapted to the water-limited environments in the Great Plains compared to other oilseed crops such as canola *(Brassica napus* L.) or sunflower (*Helianthus annuus* L.) (Obour et al., 2015). It has a short growth cycle and depending on production environment and planting date, camelina will mature within 75 to 112 d after planting (McVay and Lamb, 2008; Sintim et al., 2016). Thus camelina could be planted in rotation with winter wheat (*Triticum aestivum* L.), seeded in early spring and harvested in the summer with adequate time for soil water recharge. These attributes make camelina a crop of choice for replacing portions of the fallow period in the predominantly dryland wheat–fallow or wheat–summer crop–fallow cropping system in the Great Plains region.

Seed produced from camelina in the Great Plains contains on average from 30 to 40% oil content (Pavlista et al., 2012; Jiang et al., 2014; Sintim et al., 2016) but values as high as 48% have been reported elsewhere (Vollmann et al., 2007). The oil contains approximately 60% PUFAs, mainly linoleic acid (18:2n-6; about 15%) and a-linolenic acid (18:3n-6; about 35–45%), 30% MUFAs, and 6 to 10% SFAs (Zubr and Matthaus, 2002; McVay and Lamb, 2008; Kirkhus et al., 2013; Jiang et al., 2014). Greater unsaturated fatty acid content (~90%) makes camelina oil unique with several industrial applications. Both biodiesel and renewable jet fuels have been successfully produced from camelina oil (Fröhlich and Rice, 2005; Moser, 2010; Shonnard et al., 2010; Soriano and Narani, 2012). Besides biofuel production, camelina oil and meal has high potential in the biopolymer industry for making adhesives, coatings, resins, and gums (Zaleckas et al., 2012; Kim et al., 2015; Zhu et al., 2017). The ability to genetically modify camelina using a simple transformation method

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Abbreviations: MUFA, monounsaturated fatty acid; PUFA, polyunsaturated fatty acid; SFA, saturated fatty acid.

that involves vacuum infiltrating young inflorescences with an *Agrobacterium* suspension (floral dip transformation) also offers additional opportunities to create novel oil compositions useful for fuel and industrial applications (Bansal and Durrett, 2016).

While the focus of camelina in the United States has been for biofuel production, camelina oil also possesses good nutritional qualities. For example, it is a very good source of a-linolenic acid (>35% of the fatty acid in the oil), a precursor for other omega-3 fatty acids essential in human and animal health (Zubr and Matthaus, 2002). Clinical trials showed consumption of camelina oil increased the proportion of linolenic acid and associated metabolites (eicosapentaenoic and docosahexanoic acids) in the serum of hypercholesterolemic human subjects (Karvonen et al., 2002). Camelina therefore possesses great potential in the health food market for individuals interested in utilizing dietary changes to manage high blood cholesterol and related cardiovascular diseases. Furthermore, camelina seed contains on average from 29 to 34% protein (Campbell et al., 2013; Sintim et al., 2016); the high protein meal after oil extraction has been used as a component in livestock feed rations (Moriel et al., 2011; Colombini et al., 2014).

Despite good oil quality and the potential of camelina as a short-season crop for rotation in semiarid crop production systems, there is limited agronomic information on camelina. Multi-state research efforts comparing the performance of camelina genotypes on seed and oil yields across the central and northern Great Plains are limited. Most of the production and research on camelina in the United States has been conducted in the northern Great Plains (Robinson, 1987; Putnam et al., 1993; Budin et al., 1995; Gesch and Cermak, 2011; McVay and Khan, 2011; Chen et al., 2015; Sintim et al., 2016). However, recent studies showed camelina could be grown successfully in the central Great Plains region of western Nebraska (Pavlista et al., 2012; Pavlista et al., 2016) and western Kansas (Aiken et al., 2015) with seed yields (900–1000 kg ha^{-1}) comparable to that reported under dryland in the northern Great Plains. A maximum yield of 2500 kg ha^{-1} was achieved under irrigation in western Nebraska (Pavlista et al., 2016). Depending on the climate, camelina yields have been documented to range from 500 to 2880 kg ha^{-1} (McVay and Lamb, 2008; Vollmann et al., 2007; Moser, 2010). Climatic variables, seasonal precipitation and temperature, camelina genotypes, and genotype ′ environment interaction can influence camelina seed yield and oil quality. Air temperatures and precipitation are reported to influence seed yield and fatty acid composition in oilseed crops (Canvin, 1965; Berti and Johnson, 2008; Kirkhus et al., 2013). Increased air temperature during seed development decreased seed oil content and the proportion of unsaturated fatty acids (Canvin, 1965; Schulte et al., 2013). Higher temperatures at flowering and seed formation reduced oil content in camelina but had no significant effect on fatty acid composition (Jiang et al., 2014).

Understanding the effects of genotype and environment on camelina oil content and fatty acid composition will be useful in the efforts of developing agronomic recommendations for potential incorporation of camelina into dryland agriculture in the Great Plains. We hypothesize that camelina grown in the central Great Plains will produce camelina seeds with similar oil content and quality as that grown in the northern Great Plains. Our objective was to determine camelina performance, oil content, and fatty acid profile as affected by genotype and growing environment under dryland conditions in the semiarid Great Plains region.

MATERIALS AND METHODS

Site Description

Field experiments were conducted at Kansas State University Agricultural Research Center near Hays, KS (38°86′ N, 99°27′ W, and 609 m above sea level) and at Montana State University Central Agricultural Research Center near Moccasin, MT (47° 03′ N, 109° 57′ W, 1400 m above sea level) from 2013 through 2015 growing season. The soil at Hays is Crete silt loam (fine, smectitic, mesic Pachic Udertic Argiustoll), which consists of deep, moderately well-drained soils formed from loess material. The soil at Moccasin is classified as a Judith clay loam (fine-loamy, carbonatic, frigid Typic Calciustoll), generally shallow not more than 60-cm deep with gravel underneath (Chen et al., 2012). Before planting in each year, composite soil samples were taken at 0- to 15-cm depth from all sites. The soil samples were air-dried and ground to pass through a 2-mm mesh sieve and analyzed for soil chemical properties following standard soil test procedures. Briefly, pH was determined potentiometrically by an electrode (Thomas, 1996). Soil nitrate-nitrogen (NO_3–N) concentration was determined colorimetrically after soil samples were extracted with 2 M KCl (Keeney and Nelson, 1982). Soil test P was determined by Mehlich-3 extraction method (Mehlich, 1984) at Hays and by the sodium bicarbonate extraction procedure (Olsen and Sommers, 1982) at Moccasin. Exchangeable Ca, Mg, and K concentration were determined by NH_4OAc extraction (Knudsen et al., 1982). Soil organic C was determined by combustion using a Leco CN analyzer (LECO Corporation, St. Joseph, MI).

Results of chemical composition over the 3 yr for each site are presented in Table 1. The two study sites Hays, KS, and Moccasin, MT, are located in the semiarid Great Plains with long-term annual average precipitation amounts of 550 and 325 mm, respectively.

Study Design and Treatment Structure

The study at Hays involved evaluating agronomic performance of spring camelina genotypes at three planting dates. The dates ranged from 15 March through the end of April, and three camelina cultivars, Blaine Creek, Pronghorn and Shoshone, were evaluated. All treatments were arranged in a randomized complete block design (RCBD) with four replications in a split-plot arrangement. Seeding date was the main plot and camelina cultivar was the subplot factor. The study design at Moccasin was a RCBD with four replications with the same three spring camelina cultivars (Blaine Creek, Pronghorn, and Shoshone) as the main factor evaluated in this study. Spring camelina planting time at Moccasin occurred in the first week in April for all seasons. The data collected from the second seeding date at Hays (which was planted the first week in April) was used to compare camelina genotype performance across the locations (Hays and Moccasin). The experimental design for the comparison was therefore a RCBD with three camelina genotypes planted over 3 yr at the two locations.

Table 1. Selected physical and chemical characterization of the soils at Hays, KS, and Moccasin, MT, for the different years.†

Environment	Soil type	Texture	pH	Organic C‡	P	K§	Ca	Mg	NO_3–N
				g kg^{-1}	mg kg^{-1}				
Hays 2013	Mollisol	Silty clay loam	6.7	19	62	704	3777	498	18
Hays 2014	Mollisol	Silty clay loam	7.1	18	20	502	3272	589	3.6
Hays 2015	Mollisol	Silty clay loam	6.4	23	21	632	3110	631	14.5
Moccasin 2013	Mollisol	Clay loam	6.9	20	25	356	nd¶	nd	6.4
Moccasin 2014	Mollisol	Clay loam	7.1	22	27	360	nd	nd	6.2
Moccasin 2015	Mollisol	Clay loam	7.0	18	24	386	nd	nd	6.5

† Soil was sampled from 0- to 15-cm depth and soil analysis performed using standard procedures.

‡ Organic C by dry combustion using Leco C/N analyzer; available P by Mehilich-3 extraction method (Mehlich, 1984) at Hays (KS) and Olsen-P extraction method (Olsen and Sommers, 1982) at Moccasin (MT), P concentration following extraction was determined using inductively coupled plasma–optical emission spectrometry (ICP–OES).

§ Exchangeable K, Ca, and Mg concentration were determined on an ICP–OES after NH_4OAc extraction (Knudsen et al., 1982); and NO_3–N by 2 M KCl extraction procedure and N concentration determined colorimetrically by Cd reduction (Keeney and Nelson. 1982).

¶ nd = not determined.

Plot Management and Data Collection

The study at Hays was planted in a no-till system into wheat stubble using a Great Plains 3P100GNT drill (Great Plains Manufacturing, Inc., Salina, KS) at seeding rate of 5.6 kg ha^{-1} and at a seeding depth of 1 to 2 cm. Individual plot size was 3.0 by 9.1 m long with 25 cm row spacing. Prior to planting, the entire plot area was sprayed with glyphosate [isopropylamine salt of *N*-(phosphonomethyl) glycine] at 728 mL ha^{-1} and 1060 mL ha^{-1} Prowl H_2O [N-(1-ethylpropyl)-3,4-dimethyl-2,6-dinitrobenzenamine] to provide pre-emergent weed control. Broadcast N fertilizer at 56 kg ha^{-1} was applied to all plots 2 wk after emergence. Phosphorus and K fertilizers were not applied because soil test levels for these nutrients were adequate (Table 1). The study at Moccasin was planted on a tilled field in rotation with winter wheat. Weed control was accomplished with glyphosate applied at 1075 mL ha^{-1} in the fall and spring before camelina planting. Camelina cultivars were planted at 5.6 kg ha^{-1} and 1- to 2-cm deep the first week in April each year using a locally made plot drill. The plot size was 1.5 by 6.0 m with 30 cm row spacing. In mid-May, Assure II (DuPont, Wilmington, DE) (Quizalofop P-Ethyl Ethyl -2-[4-(6-chloroquinoxalin-2-yloxy)-phenoxy] propionate) was applied at 890 mL ha^{-1} to control grass weeds. Urea was broadcasted 2 wk after emergence at 90 kg N ha^{-1}.

Data on flowering date (days to 50% blooming), seasonal temperature and precipitation, and weather conditions at flowering and seed set were recorded at all sites (Table 2). After physiological maturity (when > 90% of the pods had changed color, turned to brown), all plots were harvested to determined seed yield. Harvesting procedure at Hays over the 3 yr was achieved with a small plot combine (Hege 125 plot combine, Wintersteiger Inc., Salt Lake City, UT). At Moccasin harvesting in 2013 and 2014 was accomplished with a plot combine (Wintersteiger Inc., Salt Lake City, UT). However, in 2015, grain yield was calculated from a two 1-m^2 plot area harvested using a hand-held sickle. At all sites, seed yield data was adjusted to 8% moisture content. Two hundred and fifty individual camelina seeds from each plot were counted and data used to determine seed weight adjusted to 8% moisture content.

Oil Content and Fatty Acid Analysis

Seed oil content and fatty acid composition were quantified using a well-established method (Miquel and Browse, 1992) with minor modifications. Briefly, dry seed weight was determined for approximately 20 randomly picked seeds per replicate. These seeds were then briefly homogenized with a polytron (PT2500E, Kinematica AG, Switzerland) in 1.5 mL of toluene, to which 100 µg of triheptadecanoin was added as an internal standard. Total lipids were transmethylated by adding 3 mL of 2.5% (v/v) H_2SO_4/methanol and heating at 80°C for 1h. The fatty acid methyl esters were extracted by adding 2 mL of water and 2 mL hexane and quantified by gas chromatography using a DB-23 column (Agilent J & W GC column, Agilent Technologies, Santa Clara, CA). The oven temperature was initially 200°C for 2 min; then ramped to 240°C at 10°C min^{-1} and held at that temperature for 4 min. Chromatogram peak areas were corrected for flame ionization detector response and oil content determined as described previously (Li et al., 2006). Seed protein content was determined using Fourier transform near-infrared spectroscopy and a specific calibration derived for a scanning monochromator (PertenDA-7200, Perten Instruments, Hägersten, Sweden) similar to Sintim et al. (2016).

Statistical Analysis

Statistical analysis with the Proc Mixed procedure in SAS (SAS Institute, 2012) was used to examine camelina seed yield, oil and protein content, and fatty acid profile as a function of genotype and environment using ANOVA. Year, location, and genotype were the fixed effects while replications and their interactions were considered random effects. The LSMEANS procedure and associated PDIFF were used for mean comparisons. Interaction and treatment effects were considered significant when *F* test *P* values were ≤0.05. Regression analysis were used to show relationships between seed yield, oil content, and fatty acid composition.

RESULTS

Seed Yield

The interaction of year × location × genotype ($P = 0.951$) effect on camelina seed yield was not significant. Similarly, year × genotype ($P = 0.644$; Table 3) interaction had no effect on seed yield. However, year × location ($P = 0.047$) and location × genotype ($P = 0.012$) interaction effects on seed yield were significant. Averaged across years and genotypes, growing camelina at Hays resulted in 54% lower yields than that at Moccasin (Table 4, Fig. 1a). Seed yield ranged from 321 kg ha^{-1} in 2013 at Hays to 1151 kg ha^{-1} in 2013 at Moccasin. Seed yield at

Table 2. Climatic conditions during camelina growth for the different environments in Kansas and Montana.

	Mean growing season air temperature									
	April		May		June		July		August	
Environment	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
	°C									
Hays 2013	2.2	16.5	10.6	25.8	16.6	32.8	18.2	32.9	18.6	31.5
Hays 2014	4.1	19.6	9.5	27.1	16.6	30.1	17.5	31.1	17.8	34.2
Hays 2015	5.4	20.8	10.1	22.6	17.3	31.9	19.4	33.8	16.5	33.0
Moccasin 2013	–4.7	10.5	3.7	18.0	6.8	21.6	11.3	28.9	11.3	29.7
Moccasin 2014	–5.8	12.5	1.7	17.4	5.8	20.0	11.1	29.1	10.2	26.8
Moccasin 2015	–2.1	13.6	2.8	15.6	9.3	24.7	10.2	27.0	9.9	28.7

	Growing season total precipitation, mm				
Site	April	May	June	July	August
Hays 2013	27	55	69	180	15
Hays 2014	23	21	240	60	41
Hays 2015	24	164	19	104	12
Moccasin 2013	17	81	96	43	25
Moccasin 2014	16	30	62	35	171
Moccasin 2015	38	94	45	44	14

	Mean air temperature during flowering and seed filling, °C				
Site	1 wk pre-flowering	1 wk post-flowering	2 wk post-flowering	3 wk post-flowering	4 wk post-flowering
Hays 2013	27.1	26.4	25.0	29.3	25.4
Hays 2014	23.3	25.9	23.3	24.8	25.0
Hays 2015	24.2	32.6	30.3	35.2	32.0
Moccasin 2013	20.7	19.5	20.2	20.7	18.9
Moccasin 2014	14.8	21.3	20.3	20.9	20.3
Moccasin 2015	22.8	17.5	19.1	19.0	17.8

	Total precipitation during flowering and seed filling, mm				
Site	1 wk pre- flowering	1 wk post-flowering	2 wk post-flowering	3 wk post-flowering	4 wk post-flowering
Hays 2013	7	0	15	15	1
Hays 2014	55	7	0	15	1
Hays 2015	9	2	70	27	0
Moccasin 2013	51	16	36	36	1
Moccasin 2014	13	24	47	50	0
Moccasin 2015	39	1	11	5	1

Table 3. Analysis of variance summary of the effects of year, location and genotype on camelina seed yield, protein, oil content, and fatty acid content over three growing seasons at Hays and Moccasin.

Treatment effect	Yield	Seed weight	Protein	Oil	SFA†	MUFA	PUFA	Linoleic	Linolenic
Year (Y)	0.3891	**<0.0001‡**	0.0985	**0.0212**	**0.0003**	**0.0397**	**0.0021**	**0.0008**	**0.0001**
Location (Loc)	**<0.0001**	0.0632	**0.0006**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
Y × Loc	**0.0474**	**<0.0001**	0.6346	**0.0062**	**<0.0001**	**0.0016**	**0.0002**	**<0.0001**	**<0.0001**
Genotype (G)	**0.0251**	**<0.0001**	**0.0272**	0.2801	**0.0113**	**<0.0001**	**<0.0001**	**<0.0001**	**0.0002**
Y × G	0.6435	**0.0003**	0.1722	0.3848	**0.0273**	**0.0333**	**0.0178**	**<0.0001**	**0.0009**
Loc × G	**0.0119**	**0.0047**	**0.0269**	0.7286	**0.0007**	**0.0059**	**0.0002**	**<0.0001**	**<0.0001**
Y × Loc × G	0.9506	0.1263	0.2442	0.2951	0.2476	**0.004**	**0.0001**	**<0.0001**	0.001

† SFA = saturated fatty acid; MUFA = monounsaturated fatty acid; PUFA = polyunsaturated fatty acid.

‡ Treatment effects in bold are significant at $P \leq 0.05$.

Table 4. Location and genotype effects on camelina seed yield, protein, oil content and fatty acid composition.

Location	Seed yield	Seed weight	Protein content	Oil content	SFA†	MUFA	PUFA	Linolenic acid	Linoleic acid
	kg ha^{-1}	g	g kg^{-1}						
Hays	447.9b‡	0.93a	297.8a	274.6b	11.6a	35.6a	51.4b	27.9b	22.1a
Moccasin	972.9a	0.95a	285.1b	335.1a	10.2b	34.1b	54.3a	32.2a	20.7b
SE§	53.8	0.01	2.4	6.1	0.1	0.1	0.2	0.2	0.2
Genotype									
Blaine Creek	775.0a	1.06a	293.4a	300.3a	10.7b	34.4b	53.4	29.6b	22.3a
Pronghorn	697.0ab	0.85c	292.3a	303.7a	11.0a	35.6a	52.0	30.7a	20.1c
Shoshone	659.3b	0.92b	288.6b	310.6a	11.0a	34.6a	53.1	29.9b	21.8b
SE	41.3		1.8	6.5	0.1	0.2	0.1	0.2	0.2

† SFA = Saturated fatty acid; MUFA = monounsaturated fatty acid; PUFA = polyunsaturated fatty acid.

‡ Means followed by the same letter (S) within a column (location or genotype) are not significantly different using the least squares means (LSMEANS) multiple comparison procedure ($P < 0.05$).

§ SE = standard error of the mean.

Moccasin was not different over the 3 yr of the study, whereas yields in 2013 at Hays were significantly lower than 2014 and 2015 seasons (Fig. 1a). Seed yield differed among the camelina genotypes when grown at Hays. Average yield of Blaine Creek was 625 kg ha^{-1}, 17 and 42% greater than Pronghorn (519 kg ha^{-1}) and Shoshone (361 kg ha^{-1}), respectively (Fig. 1b). However, seed yield of the camelina genotypes were not different when grown at Moccasin (Fig. 1b).

Seed weight was affected by year × location interaction (Table 3). Except for the 2014 growing season, seed weight of camelina genotypes was greater at Moccasin than at Hays (Fig. 2a). Seed weight in 2013 was lower than 2014 and 2015 growing seasons at both study locations. The interaction of location × genotype had a significant effect on seed weight. The 1000-seed weight of Blaine Creek was greater than Pronghorn and Shoshone at both Hays and Moccasin in the 3 yr of the study (Fig. 2b). At Moccasin, 1000-seed weight of Pronghorn was lower than the other camelina genotypes. Similarly, year × genotype effect on seed was significant. This interaction occurred because of the seed weight differences between Pronghorn and Shoshone in 2015. Blaine Creek had the heaviest seed weight among the camelina genotypes over the 3-yr study. Averaged across locations, 1000-seed weight ranged from 0.76 for Pronghorn in 2013 to 1.18 for Blaine Creek in 2014 (Fig. 2c).

Protein and Oil Content

Genotype × year × location ($P = 0.244$) interaction had no effect on camelina protein content. However, location × genotype interaction ($P = 0.027$; Table 3) had a significant effect on protein content. Averaged across years, protein content was greater at Hays compared to when camelina was grown at Moccasin (Table 4, Fig. 3a). Protein content of Blaine Creek (303 g kg^{-1}) was greater than Pronghorn (297 g kg^{-1}) and Shoshone (294 g kg^{-1}) at Hays. However, protein content was not different among camelina genotypes when grown at Moccasin (Fig. 3a). Oil content was not different among camelina genotypes. However, location ($P < 0.0001$) and year × location interaction ($P = 0.006$, Table 3) had an effect on oil content. This interaction occurred because oil content differed among years within each study location. In general, growing camelina at Hays resulted in less oil content relative to the Moccasin site (Table 4). Oil content ranged from 262 g kg^{-1} at Hays to 359 g kg^{-1} at Moccasin during the 2015 growing season (Fig. 3b).

Fatty Acid Composition

Genotype ($P < 0.05$) and location ($P < 0.05$) had an effect on SFAs, MUFAs, and PUFAs composition (Table 3). The proportion of PUFAs (linoleic acid, linolenic acid, and eicosadienoic acid) ranged from 49 to 55%, and was greater at Moccasin compared to the Hays site (Tables 4 and 5). Similarly, MUFAs (oleic acid, gondoic acid, and erucic acid) ranged from 33.2 to 37.6%, with greater concentrations at the Hays site (Tables 4 and 5). The proportions of SFAs (palmitic acid, stearic acid, and arachidic acid) constituents were merely 10 to 12% (Fig. 4), and were generally greater at Hays (Table 4). Blaine Creek produced the greatest proportion of PUFAs among the camelina genotypes (Table 4). However, MUFAs was greatest in

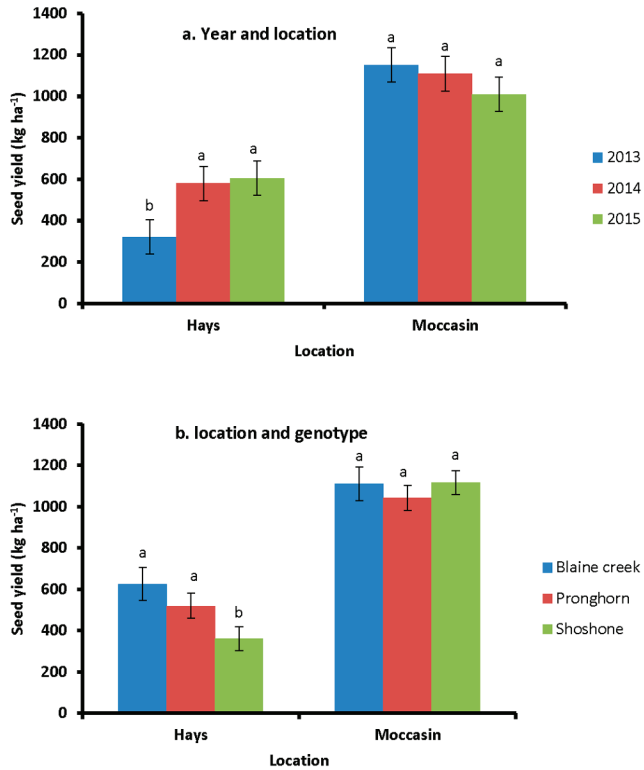

Fig. 1. Camelina seed yield as affected by (a) year and (b) genotype at Hays, KS, and Moccasin, MT. Means followed by the same letter within a location are not significantly different using the least squares means (LSMEANS) multiple comparison procedure ($P < 0.05$). Error bars represent 1 SE.

Pronghorn. The proportion of MUFAs was similar in Blaine Creek and Shoshone (Table 4). Nominal differences in SFAs were observed among the camelina genotypes (Table 4). All two-way interactions (year × location, year × genotype, and location × genotype) had a significant effect on the proportion of SFA, MUFA, and PUFA (Table 3). This occurred because the fatty acid composition of the genotypes varied over the growing seasons at each location.

The genotype × location × year interaction had an effect on MUFAs, PUFA, linoleic and linolenic acid constituents (Table 3). Average PUFA content ranged from 51% at Hays in 2013 to 55% in 2015 at Moccasin (Table 5). At Hays, the linoleic acid content of Blaine Creek and Shoshone were not different in most of the 3 yr but tend to be greater than Pronghorn. Blaine Creek had the highest proportion of linoleic acid at Moccasin over the 3 yr (Table 5). Except in 2013, linolenic acid content of Blaine Creek was greater than Pronghorn and Shoshone at Hays (Table 4). At Moccasin, Pronghorn had greater proportion of linolenic acid than Blaine Creek and Shoshone over the 3 yr (Table 4). Average linolenic acid content ranged from 27 to 34%, and was generally greater when camelina was grown at the Moccasin site (Tables 4 and 5). Unlike PUFA, proportion of total MUFA tended to be greater at Hays than Moccasin (Tables 4 and 5).

Total SFA content of camelina genotypes was greater when grown at Hays relative to Moccasin (Table 4, Fig. 4). Location × genotype and year × location interaction had an effect on SFA content (Table 3). The proportion of SFA was not different among camelina genotypes at Moccasin. At Hays however, the SFA content of Blaine Creek was significantly lower than that of Pronghorn and Shoshone (Fig. 4a). Total SFA content in 2013 and 2015 at Hays were not different but significantly greater than 2014. Proportion of SFA differed over the 3 yr at Moccasin with the highest SFA content observed in 2013 (Fig. 4b). Similarly, year × genotype interaction had an effect on SFA. This occurred because of the reduced SFA content of Blaine Creek in 2014 (Fig. 4c).

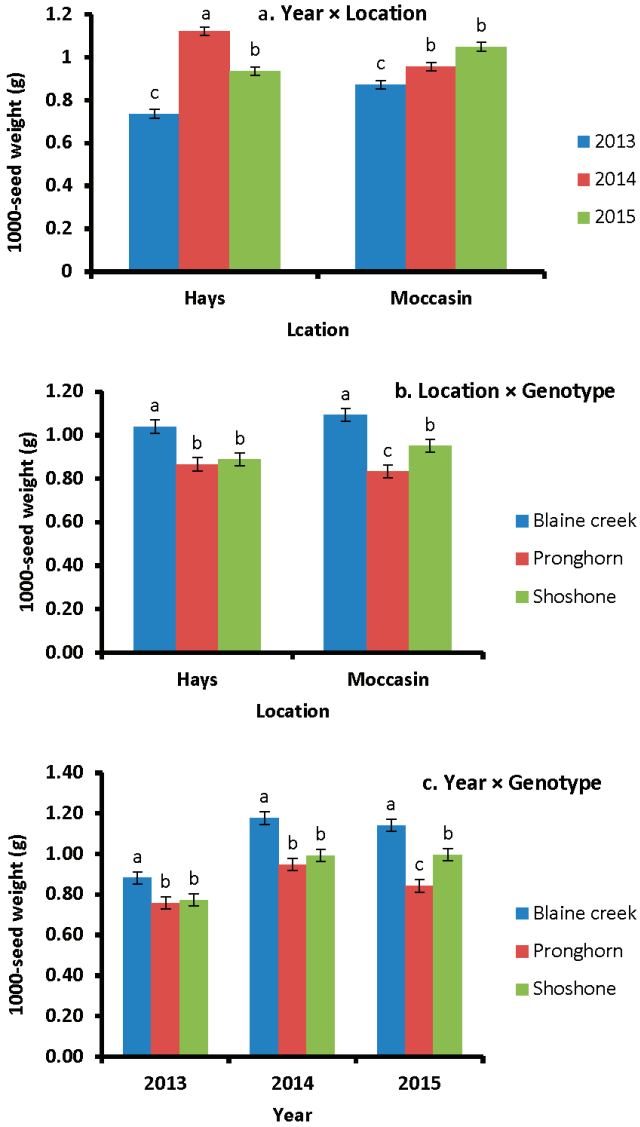

Fig. 2. Thousand seed weight of camelina as influenced by (a) year and location, (b) location and genotype, and (c) year and genotype. Means followed by the same letter within a location or year are not significantly different using the least squares means (LSMEANS) multiple comparison procedure ($P < 0.05$). Error bars represent 1 SE.

DISCUSSION

Seed Yield

The present study showed camelina seed yield is differentially affected by genotype and environment. This observation corresponds well with the different climatic conditions at each growing environment (Table 2). Total growing season precipitation at Hays was greater than that at Moccasin, but this did not correspond to any yield increase. Greater daily air temperatures and relatively uneven distribution of rainfall during

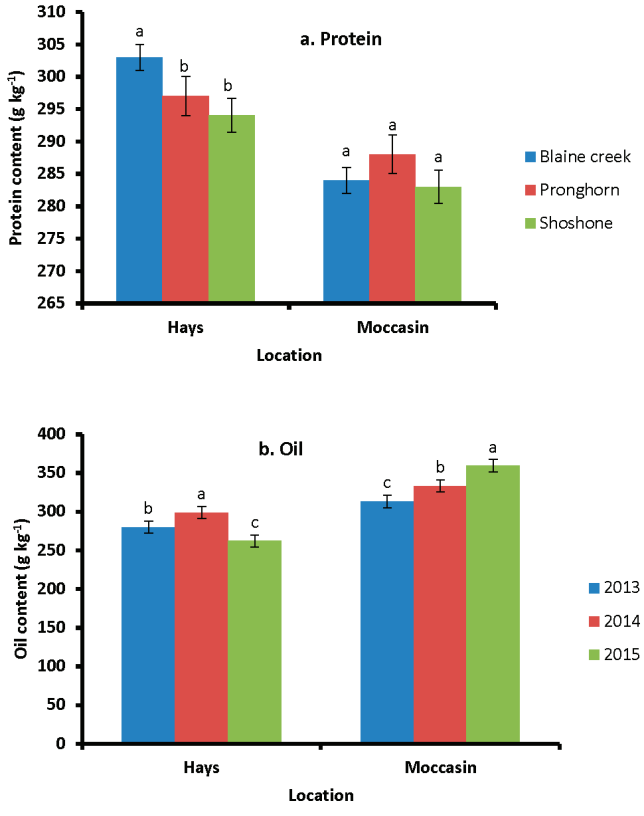

Fig. 3. (a) Camelina protein and (b) oil content as influenced by growing environment. Means within location followed by the same letter are not significantly different using the least squares means (LSMEANS) multiple comparison procedure ($P < 0.05$). Error bars represent 1 SE.

Table 5. Fatty acid composition as affected by camelina genotypes and year at each growing environment.

	Linoleic acid (C18:2; %)						Linolenic acid (C18:3; %)					
	Hays			Moccasin			Hays			Moccasin		
Variety	2013	2014	2015	2013	2014	2015	2013	2014	2015	2013	2014	2015
Blaine creek	23.2a†	20.4b	22.8ab	24.4a	23.8a	19.4ab	26.1a	32.0a	27.5a	28.4c	29.5c	34.0b
Pronghorn	22.1b	20.4b	22.0b	19.4c	18.5c	18.3b	26.3a	30.2b	25.9b	32.8a	33.6a	35.3a
Shoshone	23.0ab	22.0a	23.3a	21.3b	20.7b	20.3a	27.2a	29.0c	26.9ab	30.7b	32.1b	33.6b
Mean	22.8	20.9	22.7	21.7	21.0	19.3	26.5	30.4	26.8	30.6	31.7	34.3
SE	0.6	0.3	0.5	0.6	0.3	0.5	0.76	0.43	0.5	0.76	0.43	0.5
	MUFA‡, %						PUFA, %					
	Hays			Moccasin			Hays			Moccasin		
	2013	2014	2015	2013	2014	2015	2013	2014	2015	2013	2014	2015
Blaine creek	36.0b	34.1b	35.3b	33.2b	33.7b	34.3a	50.7b	54.0a	51.8a	54.5a	54.9a	54.9a
Pronghorn	37.1a	35.3a	37.6a	34.4a	34.9a	34.4a	49.5c	51.9b	49.1b	53.5b	53.4c	54.9a
Shoshone	35.3c	34.8a	35.1b	34.2a	34.3ab	33.6a	51.5a	52.5b	51.5a	53.4b	54.2b	55.4a
Mean	36.2	34.7	36.0	33.9	34.3	34.1	50.6	52.8	50.8	53.8	54.1	55.0
SE	0.39	0.37	0.45	0.39	0.37	0.45	0.32	0.32	0.41	0.32	0.32	0.41

† Means followed by the same letter are not significantly different using the least squares means (LSMEANS) multiple comparison procedure ($P < 0.05$).
‡ MUFA = monounsaturated fatty acid; PUFA = polyunsaturated fatty acid.

flowering and seed set (Table 2) could account for smaller yields observed at Hays. Aiken et al. (2015) showed yields of oilseed crops including camelina grown under dryland conditions in the central Great Plains to be limited by available soil moisture and heat stress at flowering and during seed formation. In western Nebraska, increased soil moisture availability increased camelina seed yield significantly from 890 kg ha^{-1} for rain-fed to 2540 kg ha^{-1} by adding 27 cm of water through irrigation over the season (Pavlista et al., 2016).

Although precipitation amounts differed over the 3 yr at Moccasin (Table 2), seed yield did not differ significantly among years. This is attributed to relatively cooler growing season temperatures that favor camelina production. Soil moisture availability resulting from more even rainfall distribution at flowering and seed set explained the greater seed yield at Hays in 2014 and 2015 seasons compared with 2013. Yields in the present study at Hays were smaller than previously reported camelina yield in the Great Plains, which range from 900 to 2200 kg ha^{-1} (Moser, 2010). However, in northwestern Kansas (Colby, KS) and western Nebraska (Sidney, NE) spring camelina seed yield ranged from 340 to 1000 kg ha^{-1} (Aiken et al., 2015), which is within the range of yields reported for this study at Hays. Seed yield at Moccasin was similar to average yields of camelina (1000–1200 kg ha^{-1}) planted in northwestern Wyoming (Sintim et al., 2016).

Seed yield varied among camelina genotypes, consistent with previous studies (Gugel and Falk, 2006; Urbaniak et al., 2008; French et al., 2009; Vollmann et al., 2007). Average yields ranged from 843 to 1018 kg ha^{-1} for Blaine Creek, 858 to 1068 kg ha^{-1} for Pronghorn, and 720 to 932 kg ha^{-1} for Shoshone when planted in northwestern Wyoming (Sintim et al., 2016). The latter seed yield ranges were consistent with yields reported in this study for the same cultivars at Moccasin but not at Hays. Seed yields at

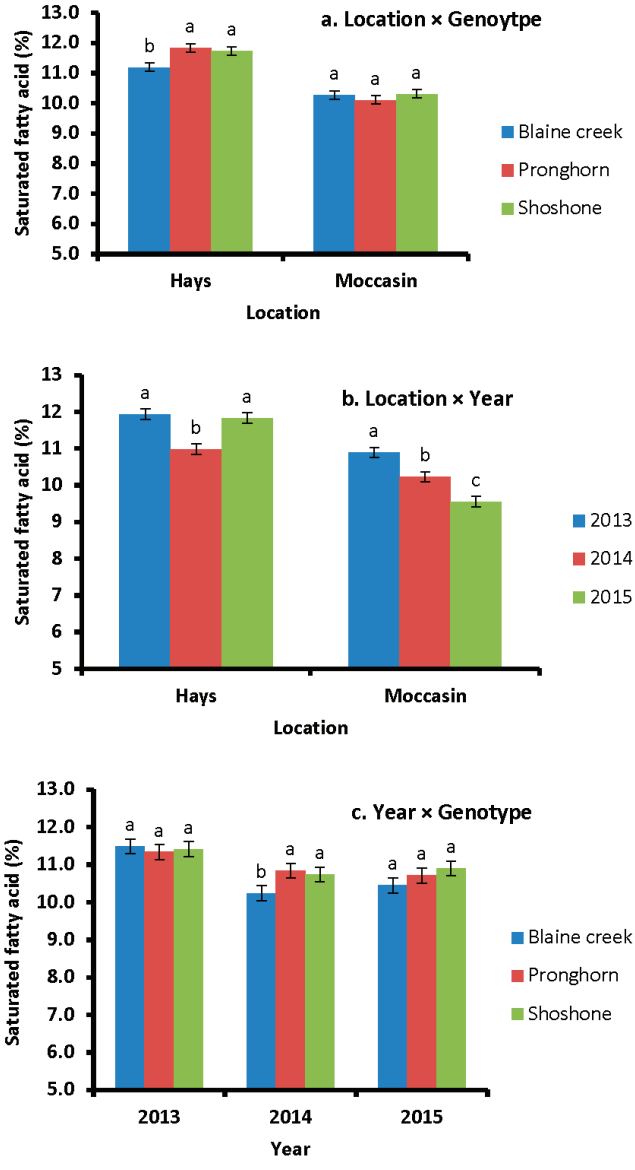

Fig. 4. Camelina saturated fatty acid content as affected by (a) genotype and location, (b) location and year, and (c) year and genotype. Means followed by the same letter within a location or year are not significantly different using the least squares means (LSMEANS) multiple comparison procedure ($P < 0.05$). Error bars represent 1 SE.

Hays are lower than the ranges reported above, confirming environmental conditions have significant effect on yield performance of camelina genotypes. Greater seed weight at Hays in 2014 did not translate into greater seed yield, with yields lower than that at Moccasin in all 3 yr (Fig. 1a). The latter outcome suggests that seed weight might have limited value in predicting seed yields in camelina. This agrees with Vollmann et al. (2007) who found a negative correlation between camelina seed yield and 1000-seed weight in a study conducted over three growing seasons in Austria. The 1000-seed weights of up to 1.17 g found in the present study are within the range of 1000-seed weight (0.8–1.81 g) reported for camelina (Vollmann et al., 2007; Solis et al., 2013).

Protein and Oil content

The protein contents observed in the present study are similar to the range (29–32%) reported for camelina grown in northwestern Wyoming (Sintim et al., 2016) but lower than the 42 to 45% reported in Europe (Zubr, 2003). The protein content of camelina seeds grown in Canada ranged from 24 to 29% (Jiang et al., 2014) similar to that reported in the present study. Oil content did not differ among camelina genotypes but differed across locations suggesting that growing environment rather than genotype is the major determinant of seed oil content in camelina. Growing camelina at Hays resulted in lower seed oil content compared to growing at Moccasin (Table 4, Fig. 2b), possibly due to relatively greater daily air temperatures during flowering and seed set at Hays (Table 2). The present results support previous findings that showed increased air temperature conditions at seed development reduced oil content in camelina and other oilseed crops (Canvin, 1965; Pavlista et al., 2011; Kirkhus et al., 2013; Schulte et al., 2013).

The oil contents observed in the present study were within the range from 27 to 34% reported in studies conducted in western Nebraska (Pavlista et al., 2011; Pavlista et al., 2016). Nonetheless, camelina oil content >40% has been reported in other environments (Zubr, 2003; Vollmann et al., 2007; Gesch, 2014). In the present study, environments where camelina synthesized high protein in the seed tended to have significantly lower seed yield and oil content. There was a significant negative correlation between camelina protein and oil content at both Hays and Moccasin (Table 5). In addition, regression analysis showed a significant linear relationship between mean air temperature at flowering and seed set, and camelina protein content with a correlation coefficient of 0.82 (Fig. 5). Relatively greater air temperatures contributed in part to greater camelina protein content observed at Hays. It is unclear why increased air temperature is positively correlated with protein accumulation and negatively correlated with oil content. One proposed mechanism suggests that at higher temperatures, more N is available for protein synthesis, which then competes for the C skeletons also used for lipid production (Canvin, 1965; Singer et al., 2016).

Fatty Acid Composition

The range of fatty acid profile results presented here are consistent to that reported in previous studies (Zubr and Matthaus, 2002; Vollmann et al., 2007; Kirkhus et al., 2013; Jiang et al., 2014). All fatty acid constituents in the present study were influenced by genotype and location interactions. Growing camelina at Hays increased SFAs and MUFAs content at the expense of

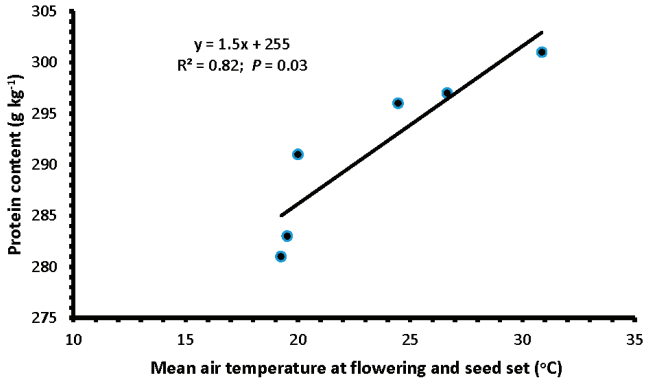

Fig. 5. Relationship of mean air temperature at flowering and seed set with camelina seed protein content measured at Hays and Moccasin over three growing seasons.

PUFAs, which constitute >50% of the total fatty acids in camelina oil (Tables 4 and 5, Fig. 4). Air temperatures >25°C during seed development caused a significant reduction in PUFAs in camelina (Zubr and Matthaus, 2002). Several days during flowering and seed filling at Hays (June through to mid-July at Hays and late June through July at Moccasin) had a mean temperature above 25°C (Table 2). The elevated temperature during seed development is a plausible explanation for the observed decreased oil content and the proportion of linolenic acid in camelina seed produced at Hays. Pearson correlation analysis showed a significant positive association between the seed oil content and proportion of linolenic acid (Table 6). Conversely, high seed oil content decreased SFAs at both locations and and MUFAs contents at Hays. Higher oil content in oilseed flax resulted in a significant increase in linolenic acid content (Zhang et al., 2016), which is consistent with findings in the present study. Fatty acid profile can influence the quality of biodiesel produced. Greater content of MUFAs and SFAs (such as oleic and palmitic acids) are considered to be more desirable than PUFAs (linolenic and linolenic acids) in terms of biodiesel oxidation stability, cetane number, and fuel cold weather performance (Pinzi et al., 2009). Therefore, reduced levels of linolenic acid content of camelina seed produced at Hays could be desirable in terms of biodiesel application. Notwithstanding, camelina genotypes tolerant to heat stress will be needed to boost seed oil content when grown in relatively warmer environments similar to Hays.

The present study showed highly significant negative association between linolenic acid content and the proportion of linoleic acid, SFAs, and MUFAs contents in camelina oil (Table 6). These results are consistent with the relative order of synthesis of these fatty acids in developing seeds. For example, linolenic acid is formed by the desaturation of linoleic acid, explaining the inverse relationship between the levels of these two fatty acids. Lower temperatures during seed development seem to favor greater levels of PUFAs in the seed and explain in part the generally greater linoleic acid, SFAs, and MUFAs found in camelina seeds produced at Hays. Consistent with our results, previous work also showed that temperature during seed filling was positively correlated with linoleic in camelina (Vollmann et al., 2007). As regulation of desaturase activity by temperature at both the transcriptional and post-transcriptional levels has been noted in other plant species (Singer et al., 2016), a similar effect on fatty acid desaturase (FAD3) activity in camelina may explain the relatively high levels of linoleic acid grown in Hays. In addition, soil

Table 6. Correlation of protein content, oil content and fatty acid contents of camelina seed from different locations.

Parameter	Oil content	Protein	SFA†	MUFA	PUFA	Linoleic acid
			Hays			
Protein	–0.36‡					
SFA	–0.53	ns				
MUFA	–0.30	ns	0.44			
PUFA	0.45	ns	–0.73	–0.93		
Linoleic	–0.49	ns	0.67	ns§	–0.35	
Linolenic	0.56	ns	-0.84	-0.69	0.85	–0.79
			Moccasin			
Protein	–0.58					
SFA	–0.68	0.68				
MUFA	ns	ns	ns			
PUFA	0.48	–0.49	–0.61	–0.62		
Linoleic	–0.31	ns	0.56	0.51	ns	
Linolenic	0.48	ns	–0.77	–0.72	ns	–0.94

† SFA = saturated fatty acid; MUFA = monounsaturated fatty acid; PUFA = polyunsaturated fatty acid.

‡ Correlation coefficient values reported for those R values that are significant at $P < 0.05$.

§ ns = nonsignificant ($P > 0.05$).

water availability through irrigation was found to increase proportion of linolenic acid in camelina from 32 to 35% but the amount of linoleic acid decreased slightly from 20 to 19%, respectively (Pavlista et al., 2016). The greatest amounts of linolenic acid were observed when precipitation was above normal during flowering and seed filling (Kirkhus et al., 2013). The authors observed that 53% of the variation in oil quality parameters could be explained by the differences in seasonal temperature and precipitation. Precipitation at Moccasin was uniformly distributed with relatively cooler temperatures, thus drought and heat stress periods were limited during seed development. Heat and drought stresses were more extensive at Hays, which could ultimately alter fatty acid composition in camelina.

The contents of linoleic acid, reported for camelina grown in the central Great Plains are 19 to 20% (Pavlista et al., 2016). The linoleic acid values reported here in the present study are slightly greater than the range reported by the above authors. Although camelina has been promoted for biodiesel feedstock production, results from the present study and others underscore the great potential of camelina oil in human nutrition due to the high contents of linolenic acid (up to 35% in the present study). However, the presence of high erucic acid may limit its use as vegetable oil in human food (Zubr and Matthaus, 2002).

CONCLUSIONS

Our results confirm that camelina seed yield, oil content, and fatty acid composition are significantly affected by genotype × environment. Seed yield and oil content were greater when camelina was grown at Moccasin MT, which had relatively cooler growing season temperatures (and more specifically during seed development). However, protein content was reduced at Moccasin compared to when camelina was grown at the Hays site. Linolenic acid, the major fatty acid constituent in camelina was highest at Moccasin but the proportion of linoleic acid, SFAs, and MUFAs were decreased at this location. Oil content was not different among the camelina genotypes studied, suggesting that the growing condition had a major effect on camelina oil content. Nevertheless, high yielding camelina genotypes are desirable, as seed yield affects the overall biodiesel produced. We reject our hypothesis based on the findings of the study and conclude that oil content and fatty acid profile of camelina grown in the central Great Plains are inferior to that grown in the northern Great Plains. Nonetheless, the relatively greater MUFAs and lower PUFAs content in camelina produced at Hays, KS, may be more desirable for biodiesel production. Findings of this study suggest that plant-breeding efforts should aim at selecting camelina genotypes tolerant to heat stress to improve seed yield, oil content, and fatty acid profile of camelina grown across the Great Plains.

ACKNOWLEDGMENTS

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