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1 Winter camelina seed quality in different growing environments across Northern America and Europe

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22 Winter camelina [*Camelina sativa* (L.) Crantz], a multifunctional oilseed crop, offers the potential to sustainably
23 diversify cropping systems across the USA and Europe. However, to promote winter camelina as a wide-spread
24 sustainable and profitable crop, it is imperative to know how different environmental conditions impact its seed
25 oil content and fatty acid (FA) composition. The objective of this study was to compare the seed qualitative traits
26 [i.e., 1000-seed weight (TKW), seed oil content, FA profile and saturation] of a winter camelina cv. Joelle, grown
27 across six different environments (Poland, Italy, Greece, Canada, USA, and Spain). Winter camelina seed
28 qualitative traits varied significantly across environments. Average TKW across regions ranged from 0.77-1.07
29 g, with the heaviest and the lightest seeds produced in Poland and Spain, respectively. Joelle seed oil content
30 varied across locations from 35.1 to 41.9%. A significant and negative relationship between seed oil content
31 ($r^2=0.50$, $P\leq 0.05$) and TKW ($r^2=0.44$, $P\leq 0.05$) and growing degree days (GDD)/number of days from sowing to
32 harvest demonstrated that environments with a short growing cycle and high temperatures depressed seed oil
33 content and seed weight. Joelle seed TKW, oil content, linolenic acid (C18:3) content, and omega-3/omega-6
34 FA ratio (n-3/n-6) were promoted when grown in environments with prolonged growing seasons and evenly
35 distributed precipitation. Results indicate that growing conditions should be carefully considered for the future
36 large scale production of camelina as prevailing climate variables will likely influence seed quality, thus affecting
37 the suitability for various end-uses.

38

39 Keywords: seed weight; oil content; fatty acid composition, precipitation; temperature, environment

40

41 Abbreviations: MUFA, monounsaturated fatty acids; PUFA, polyunsaturated fatty acids; SFA, saturated fatty
42 acids; FA, fatty acid; TKW, thousand kernel weight; GDD, growing degree days: n-3/n-6 = omega-3/omega-6.

43

44

45 1. Introduction

46 Camelina [*Camelina sativa* (L.) Crantz] is an ancient oilseed crop once commonly cultivated across parts of
47 Europe and Asia (Zubr, 1997; Berti et al., 2016) before being replaced by canola production (*Brassica napus* L.
48 var. *oleifera*). However, interest in camelina as an oil and protein source for food, feed, and industrial uses has
49 resurged, in part due to its adaptability and fit into modern cropping systems to sustainably intensify crop
50 production while minimizing disruption to food security (Gesch and Archer, 2013; Chen et al., 2015; Leclere et
51 al., 2021; Zanetti et al., 2021). Camelina is a relatively low input crop (Berti et al., 2016) with a short lifecycle
52 that can provide several ecosystem services (Sindelar et al., 2017).

53 Camelina seeds have a distinct oil composition that is high in heart-healthy polyunsaturated FAs, i.e.
54 linoleic, and α -linolenic acids (55-60% of total FA content), which combined with relevant amounts of eicosenoic
55 acid (11-19%), tocopherols (~700 to 800 $\mu\text{g g}^{-1}$ oil), and relatively low erucic acid content (<4%) make it well-
56 suited for multiple uses (Berti et al., 2016; Walia et al., 2018; Zanetti et al., 2021). Biodiesel and renewable
57 aircraft fuel meeting ASTM standards have been made from camelina oil (Moser and Vaughn, 2010; Shonnard
58 et al., 2010; Soriano and Narani, 2012), and it also has great potential for manufacturing biopolymers such as
59 plasticizers, lubricants, polyols, adhesives, coatings, resins, and gums (Kim et al., 2015; Zhu et al., 2017).
60 Moreover, camelina seeds are also known to contain about 25 to 34% protein (Campbell et al., 2013; Sintim et
61 al., 2016; Walia et al., 2018), making its meal, together with the oil, as valuable components in livestock and fish
62 diets (Berti et al., 2016; Zanetti et al., 2021).

63 Genetics and environmental conditions can significantly impact the quantity and quality of seed storage
64 lipids and hence affect the value and use of certain vegetable oils for industrial products and/or food (Singer et
65 al., 2016). Camelina is no exception. Recently, Brock et al. (2020) demonstrated that seed oil content and FA
66 composition significantly differ among *Camelina* species and can substantially differ within the species due to
67 growth conditions, especially temperature. Temperature greatly affects FA synthesis (Singer et al., 2016), and
68 it is common for seed storage lipids to increase in unsaturation under low temperatures and display greater
69 saturation under high temperatures (Linder, 2000). Both temperature and precipitation or water availability,
70 associated with diverse environments, have been implicated in substantial changes in spring camelina seed and

71 oil yields and FA composition (Guy et al., 2014; Obour et al., 2017; Zanetti et al., 2017). For instance, Obour et
72 al. (2017) found that oil content and the proportion of polyunsaturated FAs (PUFA) were greater, and saturated
73 FAs (SFA) and monounsaturated FAs (MUFA) proportions were lower in spring camelina grown at a more
74 northerly latitude in the Great Plains USA compared with a more southerly site. They mainly attributed this to
75 lower temperatures and ample precipitation during flowering and seed development at the northern site.
76 Similarly, in a multi-location trial across Canada and Europe, Zanetti et al. (2017) found that environment rather
77 than genotype affected spring camelina seed yield and quality and also demonstrated that PUFA levels,
78 especially linolenic acid, increased with lower temperatures during seed development and ripening.

79 Most studies addressing the effects of genotype and environment on camelina seed oil quantity and
80 quality have focused on spring biotypes. Winter biotypes, which differ from spring ones in that they require a
81 period of vernalization to transition to flowering (Anderson et al., 2018), have not received much attention yet.
82 Although there is far fewer winter than spring types that have been identified to date, Gesch et al. (2018) have
83 shown that genetic variation for oil yield and FA composition exists for winter camelina. However, to the best of
84 our knowledge, little research has focused on the impact of diverse environments on seed oil content and quality
85 of winter camelina.

86 The cultivar Joelle has been the most extensively studied winter camelina genotype. Joelle has proven
87 to perform well as a cash cover crop to diversify Midwest USA cropping systems (Ott et al., 2019) while providing
88 environmental benefits such as scavenging excess soil N to reduce leaching (Weyers et al., 2019), weed
89 suppression (Hoerning et al., 2020), and forage for pollinators (Eberle et al., 2015). Most field research on winter
90 camelina has been focused on the USA's Corn Belt region, where camelina has been identified as a feasible
91 winter cover crop in typical summer annual-winter fallow cropping systems (Wittenberg et al., 2020). Although
92 winter camelina has not been extensively studied in Europe (Kurasiak-Popowska et al., 2018; Zanetti et al.,
93 2020; 2021), spring camelina can be successfully grown with a autumn/winter cycle in Mediterranean areas of
94 Europe (Masella et al., 2014; Royo-Esnal & Valencia-Gredilla, 2018; Righini et al., 2019; Angelini et al., 2020)
95 surviving winter with negligible damage. Thus, to promote winter camelina as a sustainable and profitable crop
96 throughout Europe and North America, it is imperative to know how different environmental conditions in various

97 regions impact its seed oil content and FA composition. This is one of the first studies to compare seed qualitative
98 traits of a winter biotype camelina grown across such a wide variety of environmental conditions. We hypothesize
99 that winter camelina (cv. Joelle) grown in the various regions (Poland, Italy, Greece, Canada, USA, and Spain)
100 will produce seeds with similar oil content and quality. This study aimed to determine the seed oil quality (oil
101 content and fatty acid profile) of winter camelina (cv. Joelle) as affected by variable environmental conditions
102 throughout Europe and North America regions.

103

104 2. Materials and methods

105 2.1 Germplasm and site characterization

106 The winter camelina cultivar Joelle was used in the present study. It is characterized as winter hardy
107 and relatively high yielding compared with other winter genotypes (Gesch et al., 2018). The seeds of Joelle used
108 at all locations in the study were initially produced in Minnesota and provided by USDA-ARS (Table 1).

109 The six locations were: two in Northern America (Morris, Minnesota - USA, and Morden, Manitoba -
110 Canada), and four in Europe (Bologna - Italy, Aliartos - Greece, Łężany – Poland, Lleida - Spain). The
111 geographical localization of the test environments permitted to grow Joelle in latitudes between 38°22' N
112 (Aliartos) and 53°58' N (Łężany), and in longitudes ranging from 23°06'E (Aliartos) to -98°06'W (Morden). In
113 addition to covering a wide geographical area, the test locations also cover very different climatic conditions
114 (Table 1), ranging from the south Mediterranean climate of Lleida (Spain) and Aliartos (Greece), which both
115 have a mean annual temperature of 15.2 and 16.7°C, respectively, and mean annual precipitation slightly
116 exceeding 400 mm; to the north Mediterranean climate of Bologna (Italy) with a mean temperature of 13.4°C
117 and cumulative precipitation above 600 mm; to the continental climate of Łężany (Poland) with a mean
118 temperature of 8°C and cumulative precipitation of almost 700 mm; to the cold temperate climate of Morden
119 (Canada) and Morris (USA) with a mean temperature of 3.3°C and 5.8°C, respectively, and cumulative
120 precipitation of 500 and 663 mm, respectively. Furthermore, the test locations were characterized by different

121 soil types, being sandy loam in Aliartos (Greece) and Łężany (Poland), clay loam in Bologna (Italy) and Lleida
122 (Spain), loam in Morden (Canada), and fine loam in Morris (USA) (Table 1).

123

124 2.2. Experimental design and cultural practices

125 Joelle was sown at each location at one or multiple sowing dates between early September 2016 (USA)
126 until mid-January 2018 (Spain). In total, 11 field experiments are included in the present study (Table 2). At each
127 test location, the agronomic management was optimized for camelina, based on previous experience of the
128 crop, local agro-ecosystem variances and available equipment. Joelle seeds were tested for germination prior
129 to sowing of each experiment and found to have > 90% germination rate. The same seeding rate was adopted
130 at all locations (500 seeds m⁻²), except for at Lleida (Spain) and Morden (Canada) where a higher rate was used
131 corresponding to 800 and 700 seeds m⁻², respectively. Row spacing varied with seeding equipment available at
132 each location ranging from 0.15 m up to 0.22 m (Table 2). The previous crop at Morris (USA) was spring wheat
133 (*Triticum aestivum* L.), in Lleida (Spain) was winter barley (*Hordeum vulgare* L.), while at the other locations, it
134 was winter wheat (*Triticum aestivum* L.). Seedbed preparation was carried out at each location with typically
135 available equipment, and apart from Morris (USA) where Joelle was no-tillage seeded, elsewhere cultivation
136 and/or disc harrowing was carried out before sowing (Table 2). The seeding depth was approximately 5-20 mm
137 at all locations, and sowing was carried out mechanically except for in Aliartos (Greece) where it was manual.
138 Plot sizes ranged between 7.5 m² in Morden (Canada) to 22.5 m² in Lleida (Spain). The fertilization rate was
139 adjusted locally to soil chemical properties and typical camelina agronomic management. The applied
140 fertilization rates are reported in Table 2. Weeds were managed chemically only at Morden (Canada), where
141 both dicot and grass herbicides were sprayed (i.e. trifluralin and quizalofop-P-ethyl) while at all the other
142 locations, only manual weeding was carried out. All experiments were rainfed. The experimental design was a
143 randomized complete block with four replicates, except in Aliartos (Greece) (n=3).

144 The 50% flowering date was surveyed in some of the trials, as reported in Table 2, following Martinelli
145 and Galasso (2011). At full maturity, Joelle was manually or mechanically harvested, depending on the locally

146 available equipment. Representative seed sub-samples of about 50 g were taken from each plot and cleaned to
147 remove any residual plant parts or external seeds and sent to USDA-ARS, Morris, for qualitative analysis.

148

149 2.3 Meteorological data

150 Meteorological data, including air temperature and precipitation were collected at automated weather
151 stations located on-site or nearby each study site. In particular, daily minimum and maximum temperatures,
152 number of rainy days, and daily precipitation were collected at each site. At all test locations, the accumulated
153 growing degree days from sowing to harvest (GDD; °C d) were calculated [Eq. (1)] using daily maximum air
154 temperature (T_{max}), daily minimum air temperature (T_{min}) and base temperature (T_{base}), for which 4 °C was
155 used for the entire camelina cycle, as suggested by Gesch and Cermak (2011).

$$156 \text{ GDD} = \sum[(T_{max} + T_{min})/2 - T_{base}] \quad \text{Eq. (1)}$$

157 In the experiments where the 50% flowering date was recorded (Table 2) GDD_{AF} was also calculated for the
158 period from 50% flowering to harvest, adopting the same equation as in Eq. (1).

159 Furthermore, to better understand the impact of environmental conditions on Joelle seed quality, additional
160 meteorological variables were calculated, as defined in the following equations:

$$161 \text{ GDD/d} = \sum[(T_{max} + T_{min})/2 - T_{base}] / \text{number of d from sowing to harvest} \quad \text{Eq. (2)}$$

$$162 \text{ Prec/d} = \text{cumulative precipitation from sowing to harvest} / \text{number of d from sowing to harvest} \quad \text{Eq. (3)}$$

$$163 \text{ Prec/rainy d} = \text{cumulative precipitation from sowing to harvest} / \text{number of rainy d} \quad \text{Eq. (4)}$$

164 As for GDD, the meteorological variables defined in equations 2 to 4 were also calculated for the period from
165 50% flowering to harvest (AF), for locations where the 50% flowering date was recorded.

166

167 2.4. Laboratory analyses

168 All qualitative parameters of winter camelina seeds were analyzed in the same laboratory in order to
169 reduce any possible interaction between the analysis techniques and the obtained results. In particular, seed
170 weight and seed oil content were determined at the USDA-ARS laboratory, Morris, (Minnesota, USA) and FA
171 analysis was done at the USDA-ARS laboratory, Peoria, (Illinois, USA).

172

173 2.4.1. Seed weight, oil content, and fatty acid profile determination

174 Seeds were dried to constant weight at 65°C before measuring weight. To determine TKW, three
175 subsamples of 1000 seed per replicated treatment ($n=12$) were counted using an automated seed counter
176 (Series 32669, Seed Processing Holland, Enkhuizen, Netherlands) and then weighed to the nearest tenth of a
177 mg on an analytical balance. The seed oil content was determined on a 5 g of seed sample from each replicated
178 plot using pulsed nuclear magnetic resonance (NMR) (Bruker Minispec mq-10, Bruker, The Woodlands, TX,
179 USA). Prior to measurement, seeds were dried for 3 h at 130 °C and then cooled in a desiccator for 30 min. The
180 NMR was calibrated with pure camelina oil and values of oil contents are reported as a percent.

181 Fatty acid analyses as methyl esters (FAME) was conducted by gas chromatography (GC) on an Agilent
182 Technologies (Palo Alto, CA, USA) 6890N GC using the methods of Isbell et al. (2015). A standard mix of C8 to
183 C30 saturated FAME GLC (Gas-Liquid Chromatography) mixture supplied by Nu-Check Prep (Elysian, MN,
184 USA) which also contained C18:1, C18:2, C18:3, C20:1, and C22:1 was used to identify retention times of methyl
185 esters. Fatty acid methyl esters were synthesized from oil extracted from approximately 50 camelina seeds per
186 sample as previously described by Isbell et al. (2015).

187

188 2.5. Statistical analysis

189 Prior to ANOVA, the homoscedasticity of variance was verified with Bartlett's Test for $P \leq 0.05$. A one-
190 way ANOVA was adopted to test the effect of the different locations on the seed qualitative traits (i.e., TKW,
191 seed oil content, oleic, linoleic, linolenic, eicosenoic, and erucic acids and the n-3/n-6 ratio). Where different

192 sowing dates were tested, at the same location, sowing date was used as a random effect. When ANOVA
193 revealed statistically different means, the LSD's test was used to separate means ($P \leq 0.05$).

194 A linear regression study was conducted to understand the effect of the different meteorological
195 variables, for the whole crop cycle and/or for the 50% flowering to harvest period, on the investigated seed
196 qualitative traits of Joelle. When the regression was found significant for $P \leq 0.05$ the coefficient of determination
197 (r^2) was reported. All the statistical analyses were carried using the Statgraphics Centurion 18 software (ver.
198 18.1.13, Statgraphics Technologies Inc., Virginia, USA).

199

200 3. Results

201 3.1 Weather Conditions

202 Among all the sites tested, Morden (Canada) was the coldest (3.3°C), whereas Aliartos (Greece) was
203 the warmest (16.7°C) over their 20-year mean annual temperatures (Table 1). Considering the whole camelina
204 growing season, the minimum and maximum temperatures were -11.7 and 26°C , respectively (Table 3),
205 surveyed in Canada and Greece. With respect to precipitation, Łężany (Poland) followed by Morris (USA) were
206 the wettest sites, while Lleida (Spain) was the driest with annual precipitation of 683, 663, and 423 mm,
207 respectively, over their 20-year mean cumulative precipitation and also during camelina growing season with
208 cumulative precipitation of 674, 522, and 247 mm, respectively (Tables 1 and 3). The duration of Joelle crop
209 cycle varied significantly across locations (Table 2), lasting 327 d in Łężany (Poland) in the earlier sowing date
210 and only 148 d in Lleida (Spain). The GDD accumulated from sowing to harvest ranged from 1261 in Morris
211 (USA) to 1758 in Aliartos (Greece) in the earliest sowing dates (Table 2). Furthermore, in the trials where
212 flowering date was determined, the GDD accumulated from 50% flowering to harvest varied greatly, ranging
213 from 565 in Morris (USA), in the earliest sowing date, up to 1066 in Łężany (Poland), in the earliest sowing date
214 (Table 2). The delayed harvest could explain the prolonged after-flowering (AF) phase in Poland due to adverse
215 meteorological conditions observed **two** weeks before harvest. In all locations, where more than one sowing

216 date was tested, the earlier one always corresponded to the greatest GDD accumulation from sowing to harvest.
217 However, accumulated GDD from 50% flowering to harvest was not influenced by the sowing date.

218

219 3.2 Seed Qualitative Traits

220 The considered seed qualitative traits of Joelle (i.e., TKW, seed oil content, oleic = C18:1, linoleic =
221 C18:2, linolenic = C18:3, eicosenoic = C20:1, erucic = C22:1 contents, n-3/n-6 ratio, MUFA, PUFA, SFA, and
222 PUFA/MUFA ratio) varied significantly among experimental sites (Table 4), but only TKW, C20:1, C22:1, n-3/n-
223 6, and PUFA/MUFA showed a coefficient of variation higher than 10%. The average TKW across all
224 environments varied from 0.77-1.07 g. Across all environments, the heaviest Joelle seeds were produced at
225 Łęczany, (Poland, 1.07 g), and the lightest in Morris, (USA, 0.81 g), Aliartos, (Greece, 0.79 g), and Lleida, (Spain,
226 0.77 g), without significant difference among those three sites (Fig. 1). Joelle seed oil content varied across the
227 test locations from 35.1% to 41.9%. Across environments, Lleida (Spain) produced a significantly lower amount
228 of seed oil followed by Aliartos, Greece; in contrast to four countries (Italy, Poland, USA, and Canada) where
229 seed oil content was significantly higher but comparable among them, with a mean value of ~ 41%.

230 The FA composition of Joelle varied significantly across test locations (Table 4). The C18:1 content
231 varied from 12.7-14.6%, C18:2 from 14.6-17.8%, C18:3 from 37.1-48.0%, C20:1 from 7.7-14.0%, and C22:1
232 from 0.8-2.7% (Fig. 2). The 18-carbon chain FA's comprised about 68 to 75% of total oil content with the lowest
233 level at Aliartos (Greece) and the highest at Łęczany (Poland). The content of C18:1 was significantly higher at
234 Morden (Canada, 14.6%), Aliartos (Greece, 14.3%), and Bologna (Italy, 14.1%) compared with the other
235 locations; the lowest amount (12.7 %) was found at Łęczany (Poland, Fig. 2). The linoleic acid (C18:2) content
236 was significantly higher in Lleida (Spain, 17.8%) as compared to all other locations, whereas it was again the
237 lowest at Łęczany (Poland, 14.6%). The content of linolenic (C18:3) was greatest for plants grown at Morden
238 (Canada), reporting a value of 48%, followed by Joelle grown at Łęczany (Poland) with a mean value of 40.6%
239 (Fig. 2). In all other environments, the C18:3 content ranged between 37.1% Lleida (Spain) and 38.6% Bologna
240 (Italy) as reported in Figure 2. Also, eicosenoic (C20:1) and erucic acid (C22:1) contents were significantly

241 influenced by growing locations, with Morden (Canada) showing the lowest values for both, corresponding to
242 7.7% and 0.8%, respectively. In all other growing locations, the C20:1 content was almost double compared to
243 that in Morden (Canada) with a mean value of 13.8% across the other five environments. The erucic acid (C22:1)
244 content was **three-fold** higher in all other locations (averaging 2.5%) compared with that in Morden (Canada)
245 with small but significant differences between Łężany (Poland) and Lleida (Spain) versus Bologna (Italy), Aliartos
246 (Greece), and Morris (USA) (Fig. 2).

247 The average contents of MUFAs in Joelle camelina oil varied from 23.5 to 31.1%, PUFAs from 55.5 to
248 65.3%, SFAs from 8.6 to 10.1%, PUFA/MUFA ratio from 1.79 to 2.8, and n3/n6 ratio from 2.1 to 3.0 (Fig. 3) over
249 the different environments. In Morden (Canada) the contents of PUFA (65.3%), PUFA/MUFA (2.8), and n3/n6
250 ratios (3.0) were substantially greater than at all other sites. Conversely, contents of MUFA (23.5%) and SFA
251 (8.6%) were considerably lower in Morden (Canada) as compared with other locations (Fig. 3). This
252 demonstrates that camelina produced under the coldest climate (Morden, Canada) increased PUFA content,
253 which constitutes >65% of the total FAs in Joelle oil at the expense of MUFA and SFA (Fig. 3). However, contents
254 of PUFA, MUFA, SFA, PUFA/MUFA, and n3/n6 ratios were found to vary only marginally across the other five
255 locations averaging 56.3%, 30.4%, 9.7%, 1.9%, and 2.4%, respectively (Fig. 3).

256 To better understand the relationships between Joelle seed qualitative traits and specific meteorological
257 conditions characterizing each experiment (Table 3), a regression study was conducted (Table 5). Earlier studies
258 have reported that Significant regressions ($P \leq 0.05$) were observed among the qualitative seed traits (i.e. TKW,
259 seed oil content, C18:1, C18:2, C18:3, n-3/n-6 ratio, and SFA) and specific meteorological variables. But, for the
260 other seed qualitative traits (C20:1, C22:1, MUFA, PUFA, and PUFA/MUFA ratio), no significant regressions
261 were identified with the studied meteorological variables. Joelle 1000-seed weight (TKW) was significantly
262 ($P \leq 0.05$) and negatively correlated with GDD/d, Prec/rainy d, and Prec_{AF}/rainy d_{AF} (Table 5). Likewise, seed
263 oil content was significantly and negatively correlated with GDD/d. Interestingly, none of the variables calculated
264 for the 50% flowering to harvest (AF) period were found significantly correlated to Joelle seed oil content.

265 Concerning the FA composition, oleic acid (C18:1) content was significantly ($P \leq 0.05$) and negatively
266 related with Prec/rainy d, highlighting that wet seasons (high amount of precipitation over the entire growing
267 season) led to a decrease of this FA (Table 5). The linoleic (C18:2) and linolenic acid (C18:3) contents were
268 positively and negatively related ($P \leq 0.05$) with Prec/rainy d, respectively (Table 5), confirming how these two
269 FAs are inversely related, with C18:3 being directly derived from C18:2 through desaturation. The results also
270 revealed that linoleic acid content was not only positively related ($P \leq 0.05$) with Prec/rainy d from sowing to
271 harvest but also with Prec_{AF}/rainy d_{AF}. Linoleic acid accumulation in Joelle seeds was enhanced in locations
272 where precipitation was high and concentrated in fewer days. As expected, the n-3/n-6 ratio showed the opposite
273 behavior of that for linoleic acid, increasing in environments where precipitation was lower and more diffused
274 over the entire growing season as well as in AF period. Finally, the saturated fatty acid content (SFA) was found
275 to be positively related ($P \leq 0.05$), similar to linoleic acid, with the meteorological variables linked to precipitation,
276 in particular Prec_{AF}/d_{AF}, Prec/rainy d, and Prec_{AF}/rainy d_{AF} (Table 5).

277

278 4. Discussion

279 Joelle winter camelina was able to grow at all six test environments surviving to very low winter
280 temperatures, as in Morden (Canada), but also to the mild conditions in Lleida (Spain), and Aliartos (Greece),
281 confirming its extensive environmental adaptability. Joelle seed yield varied greatly among test environments
282 ranging from 704 kg DM ha⁻¹ in Leida up to 2095 kg DM ha⁻¹ in Morden, while seed yield data for Bologna and
283 Morris have already been published by Zanetti et al. (2020). The present study demonstrated how the seed
284 quality of Joelle was highly influenced by growing environment, modifying seed weight, total oil content, and the
285 relative percentages of the main FAs substantially. Nevertheless, it is possible that differences in agronomic
286 management among test locations might have also influenced Joelle seed quality. However, previous studies
287 have shown that winter camelina seed quality traits (e.g., oil content and profile) are more greatly affected by
288 environment than management practices such as seeding rate and tillage (Gesch and Cermak, 2011; Gesch et

289 al., 2018). In the present study, the management used for growing camelina was considered optimal or near
290 optimal for the given region and its soil condition.

291 Results for seed weight and oil content are in line with the available literature for camelina. In particular,
292 results confirmed that Joelle seed is characterized by relatively small size, as in the study by Wittenberg et al.
293 (2020), who found that the TKW ranged from 0.96-1.28 g across different years and sowing dates in the US
294 Great Plains. However, winter camelina varieties with larger seed size are available, like Bison, but when
295 compared with Joelle, it showed lower winter survival (Gesch et al., 2018), and a study by Canak et al. (2020)
296 indicates that Bison may be more susceptible to drought during germination and emergence. The seed weight
297 of Joelle in the present study increased when precipitation was more evenly distributed throughout the crop's
298 growth cycle, including the 50% flowering to harvest period (Table 4), confirming that camelina is susceptible to
299 heavy moisture conditions causing a general decrease in its qualitative performance (Gesch and Cermak, 2011).

300 Similar to Gesch et al. (2014), who reported an average seed oil content of Joelle sown in Minnesota,
301 USA, ranging from 38.8 to 42.1%, in the present study, the content was in a comparable range (~ 35-42%). In
302 comparison, studies on spring camelina have shown seed oil content to range from 40 to 44% (Zubr 2003;
303 Waraich et al. 2013). Oil contents in the range of 30 to 40% have also been reported for spring camelina grown
304 under dryland conditions in the US Great Plains (Pavlista et al., 2012; Jiang et al., 2014; Sintim et al., 2016).
305 With respect to Joelle winter camelina, Wittenberg et al. (2020) reported a lower seed oil content (~30%) grown
306 in North Dakota, which was attributed to heat stress that occurred at the seed filling stage. This strongly agrees
307 with our regression analysis that reported a significant negative relation between seed oil content and the GDD/d,
308 explaining how environments characterized by a short growing cycle and high temperatures depressed Joelle
309 seed oil content (i.e. Lleida, Spain, and Aliartos, Greece, in the later sowing date). A similar response to
310 environmental conditions is reported in other winter annual *Brassicaceae* such as oilseed rape (Bouchet et al.,
311 2016) and pennycress (Gesch et al., 2016), confirming that an extended vegetative growth phase allowed plants
312 to accumulate more carbohydrates and nitrogen translating to increased yield.

313 The significant variation in all the main FAs of Joelle oil reported in the present study differ from the
314 results of Kurasiak-Popowska et al. (2020a), which highlighted the high compositional stability of different winter
315 and spring camelina lines grown in the same environment in Poland over three consecutive growing seasons.
316 However, differences among growing environments in the present study were greater than that in the Poland
317 study.

318 Even though there was variation among the contents of oleic and linoleic acids across locations, their
319 contents were similar to those reported previously by Gesch and Cermak (2011) for Joelle grown in Minnesota,
320 USA, which averaged 15 and 20%, respectively. These findings suggest that oleic and linoleic acid contents of
321 Joelle seeds remained relatively stable over different environments across Northern America and Europe.
322 Conversely, there was a high variation in the linolenic acid content, in particular between Morden (Canada) and
323 all the other locations, where C18:3 accumulation was about 20% greater (Fig. 2). Being that the expression of
324 the FAD3 desaturase enzyme is promoted by low temperatures at seed filling stages (Rodriguez-Rodriguez,
325 2013), this likely increased the biosynthesis of linolenic acid at locations like Morden (Canada) and Łężany
326 (Poland), where growing-season temperatures were typically lower, and linolenic acid content was greater
327 (Schulte et al., 2013). Furthermore, in Canada, the contents of eicosenoic and erucic acids were significantly
328 less (7.7 and 0.8%, respectively), presumably in relation to environmental conditions that promoted FAD3
329 desaturase expression to such an extent that it may have strongly competed with the function of FAE1, which is
330 involved in the elongation of C18:1 to C20:1 and C22:1. Similar results were obtained in mutagenized camelina
331 when the FAE1 activity was genetically blocked (Ozseyhan et al., 2018). Otherwise, among the other locations,
332 the amounts of linolenic, eicosenoic, and erucic acids averaged 38.2, 13.6%, and 2.5%, respectively, similar to
333 values reported previously for Joelle winter camelina (Walia et al., 2018), as well as for a study where spring
334 camelina was grown under a winter cycle (Righini et al. 2019). The concentration of erucic acid across several
335 spring camelina genotypes have been shown to be approximately 3% (Zubr 1997, Zubr 2003; Kirkhus et al.,
336 2013). However, Zubr (1997) provided some of the first evidence that winter-types may tend to have lower erucic
337 content than spring-types. In that study, the mean erucic content was 2.5% across five winter varieties, while
338 that across six spring-types averaged 3%. Moreover, Walia et al. (2018) reported erucic levels as low as 1.1 and

339 2.0% at physiological maturity of winter camelina grown at two different locations in Minnesota US, which is
340 below or equal to the 2% threshold desired for food-grade oil in the US (Abbott et al., 2003) and 5% in Europe
341 (Council Directive 76/621/EEC, 1976). Also, Kurasiak-Popowska et al. (2020b) confirmed the valuable trait of
342 winter camelina types to accumulate low erucic acid content making their oil a suitable feedstock for
343 multipurpose biobased applications without incurring possible restrictions in their use due to the erucic acid level.

344 The regression study highlighted significant relationships between the seed qualitative traits studied and
345 the growing environments' meteorological conditions. Interestingly, the valuable and positive qualitative traits of
346 Joelle were negatively related with the same meteorological variables enabling authors to identify environments
347 possibly more suitable for growing winter camelina. A significant and negative relation between seed weight with
348 GDD/d, Prec/rainy d, and Prec_{AF}/rainy d_{AF}, indicates that Joelle seed weight was impaired by conditions in
349 which the growing season was short and hot, expressed as GDD/d, and also where precipitation is high and
350 erratic, both along the whole crop cycle and from 50% flowering to harvest (Table 5). The present study also
351 corroborates that TKW, seed oil content, linolenic content, and the n-3/n-6 ratio all increased when Joelle was
352 grown in environments characterized by prolonged growing season and even precipitation distribution. These
353 traits are particularly appreciated by the biobased industry, which is looking for seeds with high weight, high oil
354 content, and increased amounts of linolenic acid and n-3 FAs, fulfilling the needs for producing plasticizers,
355 biopolymers, and biolubricants (Jeon et al. 2019). Likewise, these same traits are being sought by the
356 aquaculture industry (Hixson et al., 2014). Similar to linoleic acid, a positive and significant relation exists
357 between SFA and precipitation, showing that higher rainfall favors the higher SFA content in their oils, which are
358 known to store more energy than unsaturated fatty acids (Linder, 2000).

359

360 5. Conclusions

361 The present results confirm that Joelle winter camelina is highly adaptable, being able to grow across
362 very different environmental conditions in the US Great Plains, Canadian Prairies, Mediterranean Europe, and
363 continental Europe. Winter camelina's seed oil qualitative traits were highly influenced by growing conditions,

364 and this should be carefully considered in the possible future scale-up of winter camelina since some areas
365 might be more suitable than others for specific end-uses related to different FA composition. This response to
366 growing conditions might be further exploited in developing different end products for specific biobased markets,
367 but of course, it should be more carefully considered to geographically scale up winter camelina worldwide.

368

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382

383 CRediT authorship contribution statement

384 **Maninder K. Walia**: Conceptualization, Data curation; Formal analysis; Writing - original draft; **Federica Zanetti**:
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386 **Gesch**: Conceptualization; Data curation; Software; Supervision; Writing - review & editing; **Michal Krzyżaniak**:
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390 editing, **Terry Isbell**: Data curation; Methodology; Writing - review & editing; **Andrea Monti**: Funding acquisition;
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392

393 7. References

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543 Figure captions

544 Figure 1. The thousand-seed weight (g) and total seed oil content (%) of Joelle camelina grown at the six test
545 locations. Individual values are means \pm standard errors. Values followed by the same letters are not statistically
546 different for the same parameter (LSD test, $P \leq 0.05$).

547 Figure 2. Main FAs (C18:1 = oleic acid, C18:2 = linoleic acid, C18:3 = linolenic acid, C20:1= eicosenoic acid,
548 C22:1= erucic acid) characterizing the oil of Joelle camelina grown at the six test locations. Individual values are
549 means \pm standard errors. Values followed by the same letters are not statistically different for the same
550 parameter (LSD test, $P \leq 0.05$).

551 Figure 3. Unsaturated FA contents (MUFA and PUFA), PUFA/MUFA ratio, n-3/n-6 ratio (ratio between omega-
552 3 and omega-6 FAs), and Saturated (SFA) of Joelle camelina grown at each test location. Individual values are
553 means \pm standard errors. Values followed by the same letters are not statistically different for the same
554 parameter (LSD test, $P \leq 0.05$).

555

556

557 Table 1. Country, location, soil type, and main climatic characteristics (20-year historical data) of the six study
 558 sites.

| Country | Location | Coordinates | Soil type | Mean annual precipitation (mm) | Mean annual temperature (°C) |
|---------|----------|-----------------------|------------|-----------------------------------|---------------------------------|
| USA | Morris | 45° 35' N, -95° 54' W | Fine Loam | 663 | 5.8 |
| Canada | Morden | 49° 11' N, -98° 06' W | Loam | 500 | 3.3 |
| Italy | Bologna | 44° 33' N, 11° 23' E | Clay Loam | 613 | 13.4 |
| Greece | Aliartos | 38° 22' N, 23° 06' E | Sandy Loam | 485 | 16.7 |
| Poland | Łężany | 53° 58' N, 21° 09' E | Sandy Loam | 683 | 8.0 |
| Spain | Lleida | 41° 37' N, 0° 37' E | Clay Loam | 423 | 15.2 |

559

560 Table 2. Sowing, 50% flowering (50% F) and harvesting dates, cycle duration, GDD (Growing Degree Days) from sowing to harvest, GDD_{AF} (from 50% flowering to
 561 harvest), and the main agronomic practices adopted in the 11 experiments with Joelle across six locations in Europe, Canada, and USA. Sowing and harvest years
 562 were 2016 and 2017, respectively for all locations, except Spain where 2018 the year for both sowing and harvest.

| Country | Location | Sowing | Harvest | 50% F# | Cycle | GDD* | GDD _{AF} * | Seeding rate | Row spacing | Tillage | NPK |
|---------|----------|---------|---------|--------|-------|------|---------------------|--------------------------|-------------|------------------------|------------------------|
| | | | Date | | (d) | | | (seeds m ⁻²) | (m) | | (kg ha ⁻¹) |
| USA | Morris | 6 Sept | 30 Jun | 19 May | 297 | 1473 | 565 | 500 | 0.19 | None | 78-34-34 |
| | | 4 Oct | 07 Jul | 28 May | 276 | 1261 | 625 | | | | |
| Canada | Morden | 21 Sept | 24 Jul | 25 May | 306 | 1359 | 837 | 700 | 0.22 | Disk + harrow | 67-44-0 |
| Italy | Bologna | 13 Oct | 29 May | 02 Apr | 228 | 1360 | 679 | 500 | 0.13 | Plough + rotary till | 50-83-0 |
| | | 25 Oct | 31 May | 07 Apr | 218 | 1290 | 662 | | | | |
| Greece | Aliartos | 27 Oct | 31 May | 22 Mar | 216 | 1758 | 949 | 500 | 0.15 | Plough + rotary till | 83-45-45 |
| | | 17 Nov | 06 Jun | 04 Apr | 201 | 1651 | 967 | | | | |
| | | 13 Dec | 10 Jun | 17 Apr | 179 | 1583 | 907 | | | | |
| Poland | Łężany | 09 Sept | 02 Aug | 12 May | 327 | 1603 | 1066 | 500 | 0.15 | Plough + rotary till + | 30-14-30 |
| | | 29 Sept | 09 Aug | N/A | 314 | 1501 | N/A | | | harrow + roll | |
| Spain | Lleida | 16 Jan | 13 Jun | N/A | 148 | 1322 | N/A | 800 | 0.18 | Plough+ rotary till | 0-0-0 |

563 N/A= data not available

564 #Flowering year was 2017 for all locations, except Spain where it was in 2018.

565 *Tbase for GDD calculation 4°C (Gesch and Cermak, 2011)

566

567 Table 3. Mean monthly air temperature and accumulated precipitation during the study period at each location.

| Months | Morris (USA)* | | Morden (Canada)* | | Bologna (Italy)* | | Aliartos (Greece)* | | Łężany (Poland)* | | Lleida (Spain)** | |
|----------------|----------------|----------------|------------------|----------------|------------------|----------------|--------------------|----------------|------------------|----------------|------------------|----------------|
| | Mean temp (°C) | Total ppt (mm) | Mean temp (°C) | Total ppt (mm) | Mean temp (°C) | Total ppt (mm) | Mean temp (°C) | Total ppt (mm) | Mean temp (°C) | Total ppt (mm) | Mean temp (°C) | Total ppt (mm) |
| September | 16.7 | 42.9 | 14.4 | 89.8 | - | - | - | - | 14.7 | 46.2 | - | - |
| October | 9.6 | 87.1 | 6.9 | 28.4 | 13.5 | 103.6 | 18.1 | 21.0 | 6.6 | 151.4 | - | - |
| November | 4.8 | 42.2 | 4.2 | 32.9 | 9.2 | 83.6 | 13.2 | 25.5 | 2.4 | 86.2 | - | - |
| December | -9.2 | 32.5 | -11.7 | 41.0 | 4.5 | 32.2 | 6.8 | 31.0 | 1.2 | 48.1 | - | - |
| January | -9.1 | 13.2 | -10.7 | 17.8 | 1.3 | 5.0 | 4.7 | 55.7 | -3.2 | 17.4 | 7.9 | 24.6 |
| February | -2.8 | 11.4 | -7.9 | 13.0 | 6.5 | 51.2 | 9.9 | 20.7 | -1.2 | 34.0 | 5.9 | 30.2 |
| March | -0.8 | 11.7 | -5.1 | 14.0 | 11.6 | 9.6 | 11.9 | 71.6 | 4.9 | 60.0 | 10.5 | 32.4 |
| April | 7.6 | 65.0 | 5.4 | 7.9 | 14.2 | 33.4 | 15.5 | 21.3 | 7.0 | 53.8 | 14.7 | 69.8 |
| May | 13.5 | 92.5 | 12.4 | 21.9 | 18.3 | 55.8 | 21.4 | 111.6 | 13.3 | 19.8 | 18.5 | 63.0 |
| June | 19.8 | 101.1 | 17.9 | 64.7 | - | - | 26.2 | 38.2 | 16.7 | 67.0 | 22.9 | 14.9 |
| July | 22 | 22.6 | 19.7 | 38.3 | - | - | - | - | 17.7 | 90.4 | 26.0 | 12.1 |
| Avg/Cumulative | 6.6 | 522.2 | 4.1 | 369.7 | 9.9 | 374.4 | 14.2 | 396.6 | 7.3 | 674.3 | 15.2 | 247.0 |

568 * refer to 2016/17 Joelle growing cycle

569 **refer to 2018 Joelle growing cycle

570

571 Table 4. ANOVA results (F-value) for all the considered camelina seed qualitative traits (i.e. TKW = 1000-
 572 seed weight, C18:1 = oleic acid, C18:2 = linoleic acid, C18:3 = linolenic acid, C20:1= eicosenoic acid, C22:1=
 573 erucic acid, n-3/n-6 = ratio between omega 3 and omega 6 FAs, MUFA = monounsaturated fatty acids,
 574 PUFA= polyunsaturated fatty acids, SFA = saturated fatty acids) and the coefficient of variation (CV) in the
 575 Joelle camelina study across six study locations.

| Factors | Location ¹ | Significance | CV(%) |
|-------------|-----------------------|--------------|-------|
| TKW | 71.12 | *** | 13.6 |
| Oil content | 16.91 | *** | 5.86 |
| C18:1 | 18.93 | *** | 5.38 |
| C18:2 | 36.47 | *** | 6.92 |
| C18:3 | 126.28 | *** | 8.40 |
| C20:1 | 111.26 | *** | 14.4 |
| C22:1 | 116.60 | *** | 22.5 |
| n-3/n-6 | 106.32 | *** | 12.7 |
| MUFA | 83.71 | *** | 7.6 |
| PUFA | 78.23 | *** | 5.0 |
| SFA | 71.90 | *** | 5.9 |
| PUFA/MUFA | 66.12 | *** | 15.7 |

576 ¹At Morris (USA), Bologna (Italy), Aliartos (Greece) and Lezeny (Poland) multiple sowing dates have been
 577 considered.

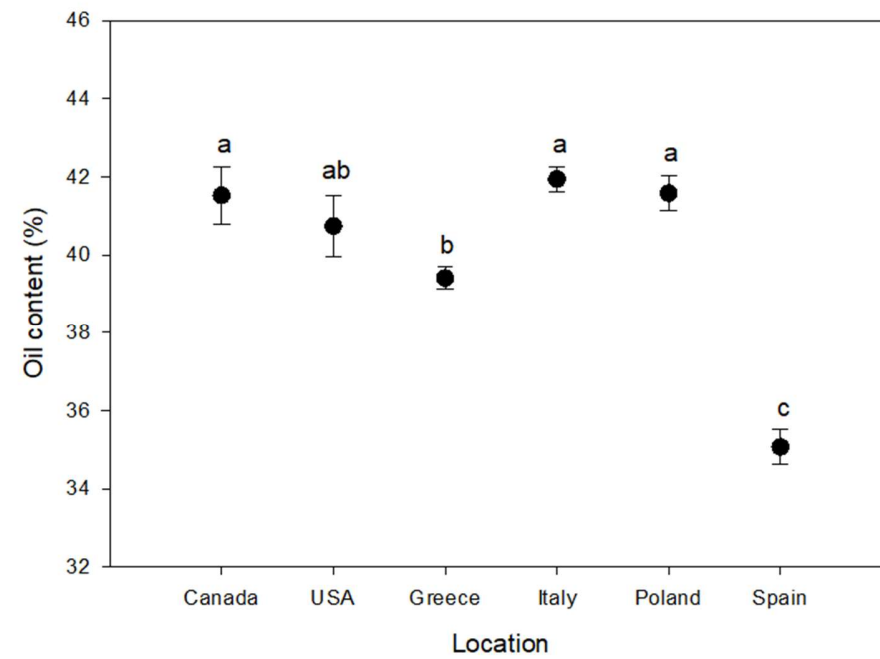
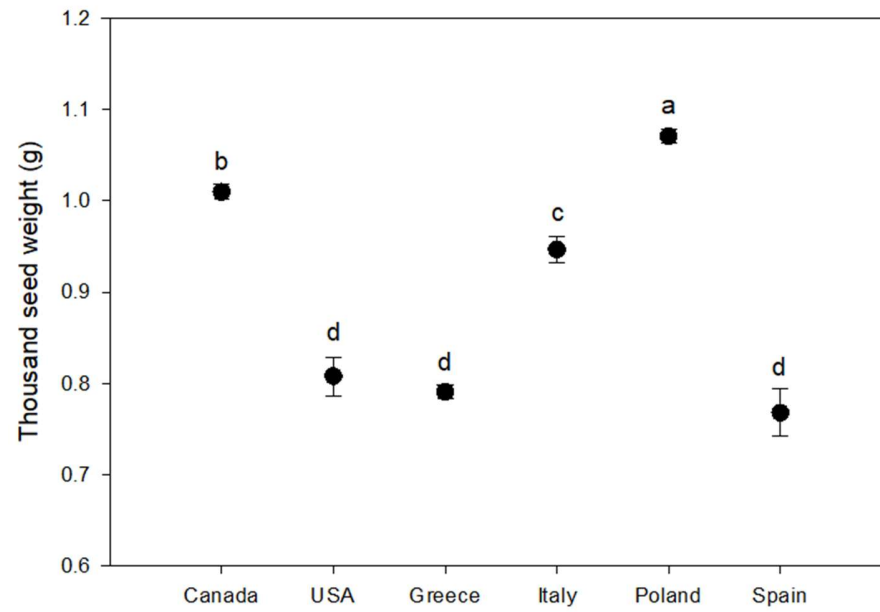
578 *** Significant at 0.001 probability level.

579 Table 5. Coefficients of determination (r^2) and P -values (*in parenthesis*) for the significant linear regressions between the meteorological variables,
 580 calculated for the entire crop cycle and for the 50% flowering to harvest (AF) period, and Joelle seed qualitative traits.

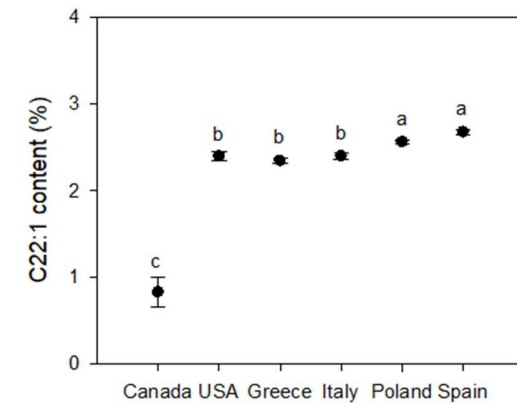
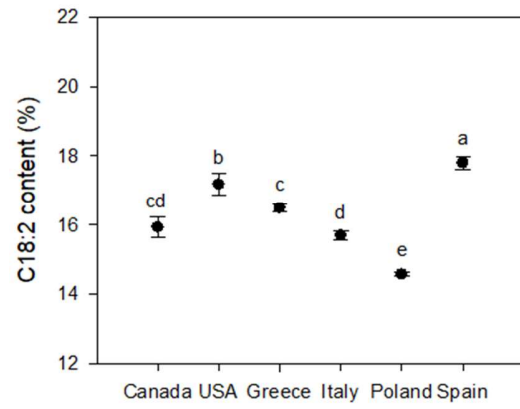
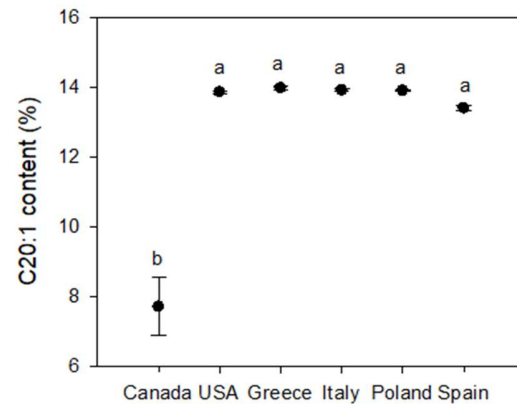
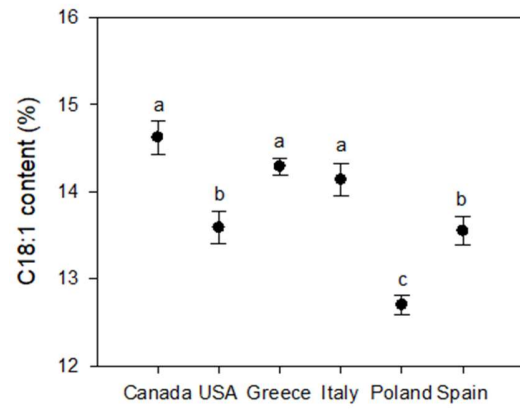
| Variables | GDD/d | Prec/d | Prec _{AF} /d _{AF} | Prec/rainy d | Prec _{AF} /rainy d _{AF} |
|-------------|--------------|--------------|-------------------------------------|---------------|---|
| TKW | 0.44 (0.025) | - | - | 0.86 (<0.001) | 0.88 (<0.001) |
| Oil content | 0.50 (0.016) | - | - | - | - |
| C18:1 | - | 0.52 (0.013) | - | - | - |
| C18:2 | - | - | 0.53 (0.026) | 0.56 (0.008) | 0.70 (0.005) |
| C18:3 | - | - | - | 0.37 (0.048) | - |
| n-3/n-6 | - | - | - | 0.65 (0.003) | 0.71 (0.004) |
| SFA | - | - | 0.55 (0.023) | 0.74 (<0.001) | 0.87 (<0.001) |

581 Qualitative traits: TKW = 1000-seed weight, C18:1 = oleic acid, C18:2 = linoleic acid, C18:3 = linolenic acid, n-3/n-6 = ratio between omega 3 and
 582 omega 6 FAs, SFA = saturated fatty acids.

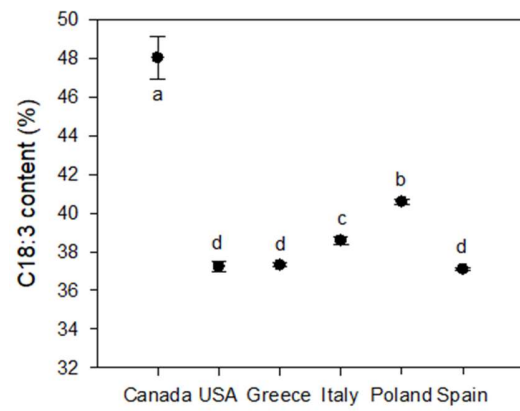
583 Meteorological variables: GDD/d = Growing degree days/number of d from sowing to harvest, Prec/d= cumulative precipitation from sowing to harvest
 584 / number of d from sowing to harvest, Prec_{AF}/d_{AF}= cumulative precipitation from 50% flowering to harvest / number of d from 50% flowering to harvest,
 585 Prec/rainy d = cumulative precipitation from sowing to harvest / number of rainy d, Prec_{AF}/rainy d_{AF}= cumulative precipitation from 50% flowering to
 586 harvest / number of rainy d from 50% flowering to harvest.



588 Figure 1. The thousand-seed weight (g) and total seed oil content (%) of Joelle camelina grown at the six test locations. Individual values are means
589 \pm standard errors. Values followed by the same letters are not statistically different for the same parameter (LSD test, $P \leq 0.05$).
590

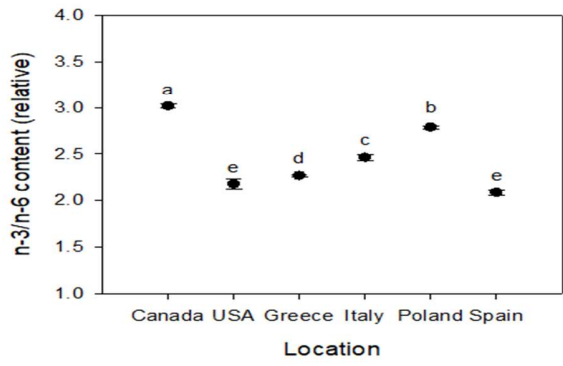
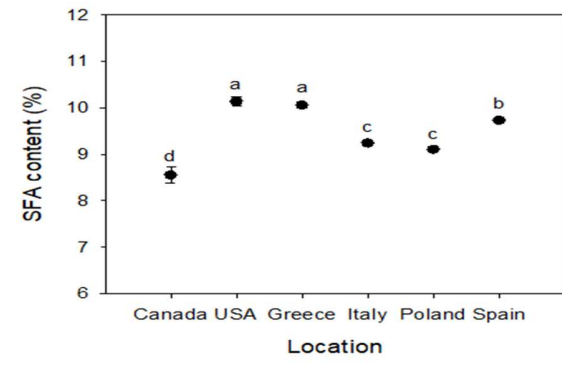
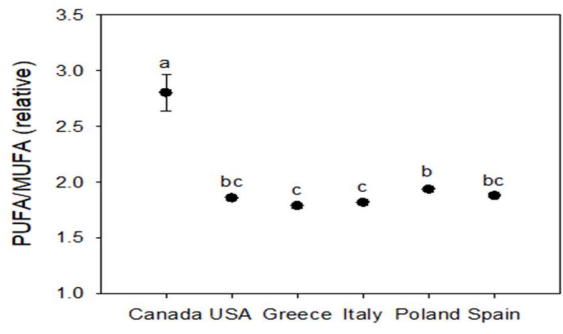
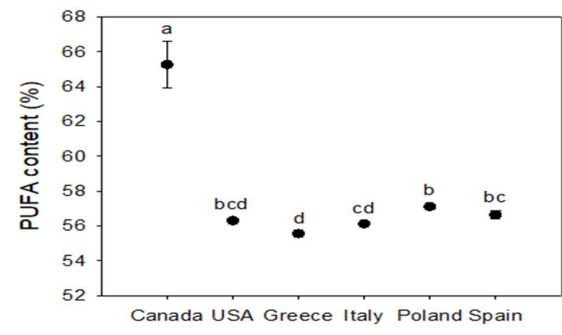
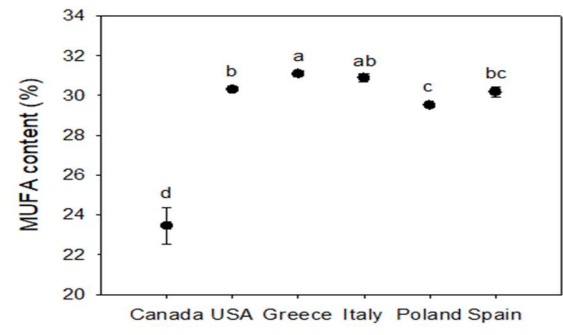


Location



Location

592 Figure 2. Main FAs (C18:1 = oleic acid, C18:2 = linoleic acid, C18:3 = linolenic acid, C20:1= eicosenoic acid, C22:1= erucic acid) characterizing the oil
593 of Joelle camelina grown at the six test locations. Individual values are means \pm standard errors. Values followed by the same letters are not statistically
594 different for the same parameter (LSD test, $P \leq 0.05$).



595

596 Figure 3. Unsaturated FA contents (MUFA and PUFA), PUFA/MUFA ratio, n-3/n-6 ratio (ratio between omega 3 and omega 6 FAs), and Saturated
597 (SFA) of Joelle camelina grown at each test location. Individual values are means \pm standard errors. Values followed by the same letters are not
598 statistically different for the same parameter (LSD test, $P \leq 0.05$).
599