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Winter camelina root characteristics and yield performance under contrasting environmental conditions

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ABSTRACT

A need exists across Europe and the USA for alternative crops to help diversify agricultural systems and promote ecosystem services. Winter camelina is a multipurpose oilseed crop that can be incorporated with staple crops to add biodiversity and other environmental benefits. Little is known about winter camelina productivity across diverse environments, and even less is known about its rooting characteristics under different soils and climates. Therefore, a field study was conducted at Bologna Italy and Morris, Minnesota USA over two growing seasons while applying two seeding rates (500 and 250 seeds m^{-2}) and two sowing dates (early and late) to evaluate the above and belowground productivity of Joelle winter camelina. Winter camelina growth was highly influenced by environmental conditions. Seed yield and oil content were considerably greater at Bologna, averaging 1518 kg ha^{-1} and 419 g kg^{-1}, respectively, as compared with Morris, which averaged 743 kg ha^{-1} and 385 g kg^{-1} during the study. The milder climate of northern Italy was associated with prolonged vegetative growth during winter resulting in root and shoot biomass 1.7-fold greater than in Morris. Plant density at harvest tended to be greater at Bologna but had a negligible effect on productivity at either location. Sowing date only affected seed oil content at Morris, where it was greater in the later sowing. Results confirmed that winter camelina is highly adaptable and can serve as a viable crop in a Mediterranean as well as temperate climate.

1. Introduction

Camelina [*Camelina sativa* (L.) Crantz] is emerging as a multi-purpose oilseed crop both in Europe (Leclère et al., 2018; Zanetti et al., 2017) and northern America (Gesch et al., 2014; Jiang et al., 2014; Schillinger et al., 2012). Camelina's early maturity, low input requirement, high resistance to biotic and abiotic stresses, unique fatty acid profile, and high seed protein content (Berti et al., 2016) are traits that differentiate it from other competing new *Brassica* oilseed crops like Ethiopian mustard (*Brassica carinata* A. Braun), pennycress (*Thlaspi arvense* L.), and crambe (*Crambe abyssinica* R.E. Fries). Camelina oil is rich in polyunsaturated fatty acids (PUFA), mainly linoleic (C18:2) and linolenic (C18:3) acids, which constitute more than 50 % of the total FAs. This high level of unsaturation is counterbalanced by the relevant amount of tocopherol (~800 mg kg^{-1}, Berti et al., 2016), which naturally stabilizes camelina oil against oxidation, allowing multiple uses in food, feed, and bio-based markets (Righini et al., 2016). Camelina press-cake has high potential for the livestock feeding industry, which is looking for alternative protein sources (Nain et al., 2015), because its balance of amino acids and naturally low glucosinolate content (Zubr, 2003).

Camelina exhibits both spring and winter annual biotypes (Mirek, 1980; Anderson et al., 2018). This allows camelina to be integrated as a rotational crop in common cropping systems in Europe or North America. Winter camelina is extremely tolerant to low temperatures (Gesch and Cermak, 2011), and has been identified as a feasible winter annual crop for the northern U.S. where it has been demonstrated to be suitable to precede soybean [*Glycine max* (L.) Merr.] and other short-season summer annuals (Gesch and Archer, 2013; Berti et al., 2015). It has been recently reported by Gesch et al. (2018) that some winter camelina lines, (e.g., Bison and Joelle) can withstand mean monthly temperatures below -15 °C, and thus, can successfully survive under the harsh winter conditions of the northern U.S., being able to achieve seed yields of ≥ 1 Mg DM ha^{-1} (Gesch et al., 2014; Ott et al., 2019).

Winter camelina has not been well studied in Europe, due to limited availability of genetic material (Kurasiak-Popowska et al., 2018), and because greater emphasis has been placed on winter rapeseed (*Brassica napus* L. var. oleifera), the predominant winter oilseed crop in central and northern Europe (Wittkop et al., 2009). Temperatures during the winter in Italy are gener-

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ally warmer than those of the northern U.S., which may allow for greater growth and yield. But in areas with a Mediterranean climate, where winter rapeseed is not extensively grown because of lack of precipitation in late summer/early autumn (George et al., 2017), winter camelina might serve as an alternative. Unlike winter rapeseed, camelina has a much shorter life cycle (about 20 d shorter), which allows it to be double-cropped with short-season summer annual crops like soybean, sunflower (*Helianthus annuus* L.), and millet (*Setaria italica* L.) (Gesch and Archer, 2013). Although spring camelina can be grown as a winter crop in the Mediterranean basin with satisfactory yield (> 2 Mg ha^{-1}) (Cappelli et al., 2019; Masella et al., 2014), experimental studies reporting the suitability of winter camelina for this environment are lacking. As highlighted by Gesch et al. (2018), to properly introduce winter camelina into a new environment a thorough evaluation of agricultural management, like sowing date and seeding rate, should be done to optimize growth and yield for specific growing conditions. In the northern U.S. winter camelina stand establishment is challenged by winter survival (Gesch et al., 2018), while under Mediterranean climate, satisfactory establishment is primarily limited by soil water availability at sowing (George et al., 2017). Thus, the agro-climatic conditions for winter camelina production in the northern U.S. versus that in Southern Europe are different.

Optimal stand establishment and crop productivity are highly dependent on root growth and development, which are often influenced by agronomic practices as well as environment. Although some studies have addressed the root growth of spring camelina under field conditions (Pavlista et al., 2012; Johnson et al., 2018), little information exists for evaluating the rooting characteristics of winter camelina. Furthermore, studies comparing camelina root growth under different climatic and soil environments are lacking. Therefore, a multi-year field study was conducted under a northern temperate continental climate (Morris, Minnesota USA) and a northern Mediterranean climate (Bologna, Italy) to determine the effects of environment, sowing date, and plant population density on *i*) root growth, *ii*) aboveground plant growth and seed yield, and *iii*) seed oil and protein content of winter camelina.

Table 1
Soil texture and characteristics, and main climatic parameters (20-yr historical data, 1995-2015) of the two study sites.

Parameters	Unit	Morris (USA)	Bologna (Italy)
Latitude		45° 35′ N	44° 33′ N
Longitude		95° 54′ W	11°23′ E
Mean annual temperature	°C	5.8	13.4
Mean annual precipitation	mm	663	613
Soil texture		**Fine Loam**	**Clay Loam**
Sand	%	37	18
Loam		39	53
Clay		24	28
pH		6.59	7.46
OM	%	4.27	1.42

2. Materials and methods

2.1. Germplasm and site characterization

The winter camelina cultivar, Joelle (seeds produced in Minnesota and provided by USDA-ARS), was sown in two consecutive growing seasons under field conditions at Bologna, Italy (2015–2017) and Morris, Minnesota, USA (2016–2018). Joelle was chosen for its superior winter survival and higher seed oil content compared to other available winter varieties (Gesch et al., 2018). The soil at the Bologna site was a clay loam (Udic Ustochrepts, mesic), while at the Morris site was a fine loam (mixed, superactive, frigid Calcic Hapludoll). Further characterization of soils is reported in Table 1.

The two study sites, Bologna (Italy) and Morris (Minnesota, USA), have similar latitudes but are characterized by different climatic conditions during the growing season and soil types (Table 1). Bologna has a typical northern Mediterranean climate (Metzger et al., 2005), with hot, dry summers when daily air temperatures often exceed 30 °C, and mild wet winters, with infrequent snow events and minimum daily temperatures rarely below -13 °C. Morris (Minnesota) is characterized by a temperate continental climate with the majority of precipitation occurring during spring and early summer, while winter is characterized by low temperatures with minimum daily temperatures frequently below -25 °C, and snow cover typically from December through March.

2.2. Experimental design and cultural practices

Joelle camelina was sown at both locations in autumn at two different dates, defined as early and late. Early and late sowing dates were identified considering the typical optimal period for camelina sowing under local climatic conditions, which corresponded to early September to early October at Morris and early to late October at Bologna (Table 2). Two different seeding rates were also tested corresponding to a high density rate (HD) of 500 seeds m^{-2} and an interrow distance of 0.13 m in Bologna, and 0.19 m in Morris, and low density rate (LD) of 250 seeds m^{-2} and an interrow distance of 0.26 m in Bologna, and 0.39 m in Morris. Row spacing varied with seeding equipment available at each location. It is worth noting that the HD treatment (500 seeds m^{-2}) in the present study is within the seeding rate range described as optimal for winter camelina production (Gesch et al., 2018). The designations of HD and LD are used only for the purpose of referring to the seed density rates used in the present study. Seeds were tested for germination prior to sowing and found to have > 90 % germination rate. The previous crop at Morris for both growing seasons was spring wheat (*Triticum aestivum* L.) while at Bologna it was winter wheat. At Morris, seed was sown with a no-till drill with double-disk openers (Great Plains Drill, Salina, KS). Prior to sowing, the drill was

Table 2
Sowing and harvest dates and mean temperatures (Tmin, max, and mean), cumulative precipitation (Prec), cumulative growing degree days (GDD), and growth cycle length (d) from sowing to harvest for Morris (USA) and Bologna (Italy) during two consecutive growing seasons (GS).

Location	GS	SD	Sowing	Harvest	T_{min}	T_{max}	T_{mean}	Prec	GDD_{tot}[a]	GDD_{bf}[b]	GDD_{af}[c]	d
			date		°C			mm				
Morris (USA)	2016/17	Early	9 Sept 2016	30 Jun 2017	−0.5	9.7	4.5	484	1419	841	578	294
		Late	4 Oct 2016	7 Jul 2017	−1.1	9.1	4.0	457	1261	624	637	276
	2017/18	Early	8 Sept 2017	6 Jul 2018	−2.2	8.4	3.2	457	1558	821	737	301
		Late	10 Oct 2017	13 Jul 2018	−3.1	7.5	2.3	317	1345	566	779	276
Bologna (Italy)	2015/16	Early	9 Oct 2015	6 Jun 2016	5.8	14.9	10.1	531	1531	647	884	241
		Late	26 Oct 2015	8 Jun 2016	5.6	14.8	10.0	466	1413	603	809	226
	2016/17	Early	13 Oct 2016	29 May 2017	4.5	14.6	9.4	327	1354	666	688	228
		Late	25 Oct 2016	31 May 2017	4.4	14.6	9.3	272	1287	610	677	230

[a] GDD_{tot} = GDD accumulated from sowing to harvest (base temperature 4 °C).
[b] GDD_{bf} = GDD accumulated from sowing to 50 % flowering stage.
[c] GDD_{af} = GDD accumulated from 50 % flowering.

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run over the seed bed twice for shallow tillage (approximately 0.06 m) and to incorporate 1.13 kg ha^{-1} a.i. of trifluralin into the soil for weed control. At Bologna, seed was sown with a precision mechanical seeder with disks customized for camelina seeds (Vignoli, Italy). The seed bed was prepared by first ploughing to a depth of 0.4 m and then rotary tilling the soil. Prior to sowing, 83 kg ha^{-1} of P_2O_5 as triple superphosphate was incorporated. At both locations the seeding depth was approximately 5–10 mm. In spring, after the soil had thawed (mid-April) and plants were still in the rosette stage, a broadcast application of 78-34–34 kg ha^{-1} of N-P-K (N as urea, P as triple phosphate P_2O_5, and K as potash K_2O) was made at the Morris site, while 50 kg ha^{-1} of N as urea was broadcast applied to plants at the bolting stage in Bologna. Manual weeding was used as necessary at both locations to control weeds. The experimental design at both locations was a split-plot randomized complete block with sowing date as the main plot and seeding rate as sub-plots with blocks replicated four times ($n = 4$). Individual sub-plot size was 1.8m × 6m at Bologna and 3m × 6.1m at Morris.

Weather parameters (daily minimum, T_{min}, maximum, T_{max}, and mean temperatures, T_{mean}, and precipitation) were measured and recorded by automated weather stations located at the both experimental sites. Accumulated growing degree days (GDD, °C d) for 50 % flowering (BBCH 605, Martinelli and Galasso, 2011) and full maturity were calculated as: $GDD = \sum[(T_{max} + T_{min})/2] - T_b$, where T_{max} is daily maximum air temperature, T_{min} is daily minimum air temperature, and T_b is base temperature, for which 4 °C was used (Gesch and Cermak, 2011). Both field experiments were rain fed, no irrigation was used (Table 2).

2.3. Plant sampling and analysis

Plant stand counts were measured in autumn and spring on the same 1-m-row in the center of each plot to determine plant density and winter survival. Autumn counts were made in mid- to late October in Morris and in December in Bologna, before the soil surface froze, and spring counts were done in late April to early May in Morris and in early March in Bologna, after Joelle plants resumed growth. Phenological development was surveyed weekly and main stages were recorded adopting the two-digit BBCH scale of Martinelli and Galasso (2011) for camelina.

When plants reached the 50 % flowering stage (BBCH 65, Martinelli and Galasso, 2011), root sampling was performed at both locations. Soil cores were sampled by using a tipped hydraulic probe to a depth of 0.9 m (internal probe diameter was 72 mm in Bologna and 65 mm in Morris). Two soil cores were taken per plot: one centered over the plant, referred as crown, and one in the inter-row space, referred as center. This sampling method was used to obtain a reasonable weighted average for typical root biomass since plant roots are not uniformly distributed (Drew, 1975). Cores were sectioned into 0–0.1, 0.1–0.2, 0.2–0.3, 0.3–0.6, and 0.6–0.9 m depths and then stored under refrigeration in plastic bags until root material could be hand washed from the soil through sieves (Johnson et al., 2011). Clean root samples were weight fresh and then oven dried at 65 °C to constant weight and used to determine root biomass and density. The sum of the crown and center root biomass is referred to as the total root biomass. Calculating root mass ha^{-1} allowed the estimation of root/shoot ratio on an area basis. On the same day roots were sampled, aboveground biomass (AGB) was collected from the 0.4 m-long row in which the core sampling was carried out, corresponding to 0.05 and 0.10 m^2 at Bologna and 0.08 and 0.15 m^2 at Morris in the HD and LD plots, respectively. The number of plants in the sampled row was counted and after the calculation of dry AGB, by oven drying plant samples at 105 °C until constant weight, the root/shoot ratio was determined.

Camelina was harvested for seed yield at full maturity, corresponding to BBCH 89 and the residual seed moisture was about 120–140 g kg^{-1}. At both locations, 2 m^2 from the central portion of each plot was manually harvested and weighted to determine total biomass (TB) and then threshed using a plot combine harvester at Bologna (Nursery Master, Wintersteiger, Austria) and using a portable thresher at Morris (LD 350, Wintersteiger, Austria). Residual moisture in the TB and in the seeds was determined by oven drying at 65 °C until constant weight. Seed yield was adjusted to 100 g kg^{-1} moisture content. Average plant height and stand density (plants m^{-2}) were measured in each plot within the harvest area at time of harvest.

2.4. Seed quality analysis

Seed oil content was measure by pulsed nuclear magnetic resonance (NMR) using a mq-10 MiniSpec (Bruker, The Woodlands, TX). The instrument was calibrated with pure camelina oil. Approximately 5 g of seed from each plot was dried for 4 h at 130 °C, cooled in a desiccator for 15 min, transferred to a heating block at 40 °C for approximately 5 min, before immediately measuring in the NMR. The same seed samples were ground to a fine powder using a coffee grinder and approximately 200 mg of the powder was used to determine total C and N content by combustion (LECO TRU SPEC, LECO Corporation, St. Joseph, MO). Crude protein content of seed was estimated by multiplying N content by 6.25.

2.5. Statistical analysis

All data were analyzed using the GLIMMIX Procedure of SAS 9.4 (SAS Institute, Cary, NC) for a split-plot randomized complete block design. Location, sowing date, and seeding rate were treated as fixed effects and year (i.e. growing season) and replication were treated as random effects in the model. When fixed effects or their interactions were significant, means were separated using the LSD test at the $P \leq 0.05$ level of significance.

3. Results

3.1. Meteorological conditions

The mean temperature during camelina growth cycle ranged from 2.3 °C to 4.5 °C in Morris, while in Bologna it ranged from 9.3 °C to 10.1 °C (Table 2). Mean minimum temperature was as low as -3.1 °C in Morris in the late sowing during the 2017/2018 growing season, while in Bologna the lowest mean minimum temperature was 4.4 °C in the late sowing during the 2016/2017 season.

Mean maximum air temperature was stable in Bologna with a difference of only 0.3 °C between the hottest and the coldest year (14.9° versus 14.6 °C in the early sowing of 2015/2016 versus both sowing dates of 2016/2017). Cumulative precipitation during the camelina growing season in Bologna tended to be more variable than Morris, ranging from 272 mm in 2016/2017 late sowing, up to 531 mm in the 2015/2016 early sowing (Table 2). Differences mainly in growing season temperature of the two test sites influenced the length of Joelle's growth cycle, which was generally shorter in Bologna (231 d) than in Morris (287 d) when averaged across growing seasons and sowing dates (Table 2). Differences in growth cycle length based on GDD_{tot} were more pronounced between sowing dates than between environments with a mean value of 1466 °C d for early sowing and 1327 °C d for late sowing, regardless of location and growing season. Averaged across sowing dates and seasons, GDD for winter camelina from sowing to harvest was 1396 °C d at both sites. However, when splitting cumulative GDD between before and after 50 % flowering (GDD_{bf}), greater differences emerged between the two locations. In particular, the GDD_{bf} were consistently greater for the early sowing date in Morris than Bologna. Also worth noting, is that GDD_{bf} values at Bologna were not greatly different between sowing dates averaging about 632 °C d across both seasons, whereas in Morris they tended to be much higher in the early than late sowing (Table 2). The GDD accumulated after 50 % flowering date (GDD_{af}) until harvest varied across locations, sowing dates, and growing seasons, but generally, earlier sowing gave higher values at Bologna while the opposite occurred at Morris with more GDD_{af} accumulated by plants in the later sowings (Table 2).

Mean daily temperatures at Morris during the winter months from November through March were typically much lower than at Bologna (Fig. 1). During this same monthly time period, as can be inferred by the reference line at 4 °C, winter camelina plants at Bologna were still able to grow and accumulate GDDs, while those at Morris remained es-

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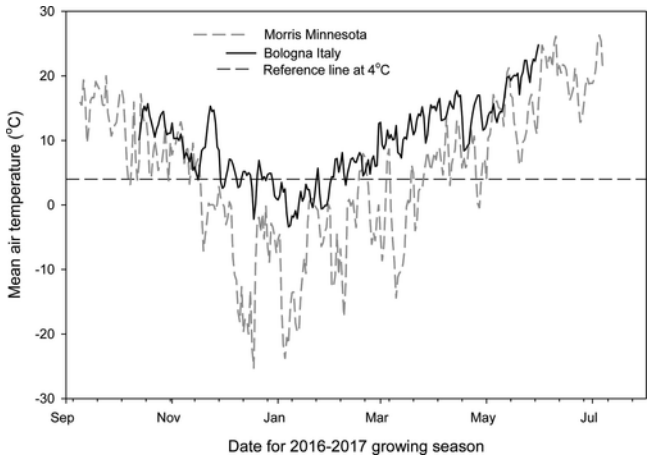

Fig. 1. Growing seasonal mean air temperatures for Morris, Minnesota USA and Bologna Italy. The dashed line is a reference at 4 °C, the base temperature used for growing degree day (GDD) calculations.

3.2. Root biomass

Root and shoot biomass were sampled at 50 % flowering stage at both locations. For root:shoot ratio there was both a location × sowing date and location × seeding rate interaction (Table 3).

The location × sowing date interaction was because the early-sown plants in Morris had a smaller root:shoot ratio (0.9) than early-sown ones in Bologna (1.2), perhaps due to greater growth under milder temperatures in Italy (Table 2). For the location × sowing rate interaction, the low seeding rate at Morris resulted in a greater root:shoot ratio (1.3) than the high rate (0.7). This was likely due to fewer plants at the low rate leading to less competition for soil (i.e., nutrients and moisture) and light resources resulting in greater root growth.

Total root biomass of winter camelina (sum of center + crown biomass, Mg DM ha^{-1}) was significantly influenced by location, soil depth, and the interactions between sowing date x seeding rate, location x depth, and sowing date x seeding rate x depth (Table 3). Joelle grown at Bologna produced significantly greater total root biomass (7.75 Mg ha^{-1}) than that grown at Morris (4.66 Mg ha^{-1}) within the 0–0.9 m profile, presumably in relation to milder temperatures and possibly soil conditions. Moreover, the interaction (Table 3) between location and soil depth (Fig. 2), revealed that plants grown at Bologna had greater root biomass deeper within the soil profile than at Morris. For instance, at Bologna, the 0.3–0.6 m depth contained about 22 % of camelina's total root biomass. Conversely, at Morris, more than the 50 % of the total root biomass was concentrate in the 0–0.1 m depth, while only 14 % of root mass was found at the 0.3–0.6 m depth. Furthermore, the three-way interaction of sowing date x seeding rate x soil depth (Table 4) showed that plants sown earlier and with a lower density presented a very unevenly distributed root system within the soil profile, compared to the other combination of factors. This trait is often related to a poorer soil colonization by the roots, which might reduce resource interception even at deeper layers.

Table 3
ANOVA table with *F* values and statistical significance of the root parameters measured at the 50 % flowering stage of camelina over two growing seasons at Bologna (Italy) and Morris (Minnesota, USA). Loc = locations (Bologna vs. Morris), SD = sowing dates (early vs. late sowing dates), SR = seeding rates (HD 500 vs. LD 250 seeds m^{-2}), Depth = soil depths (0-0.1, 0.1-0.2, 0.2-0.3, 0.3-0.6, 0.6-0.9 m).

Factors	Root:shoot ratio	Total crown + center root biomass
Loc	0.71 ns	46.04***
SD	0.05 ns	0.09 ns
SR	3.9 ns	0.02 ns
Depth	–	141.89***
Loc*SD	4.82*	1.65 ns
Loc*SR	7.52**	0.40 ns
SD*SR	0.46 ns	4.55*
Loc*SR*SD	0.07 ns	2.15 ns
SD*Depth	–	0.75 ns
SR*Depth	–	0.66 ns
Loc*Depth	–	6.48***
SD*SR*Depth	–	2.71*
Loc*SD*SR*Depth	–	1.32 ns

*, **, *** Significant at the 0.05, 0.01, and 0.001 probability levels, respectively (LSD test); ns = not significant.

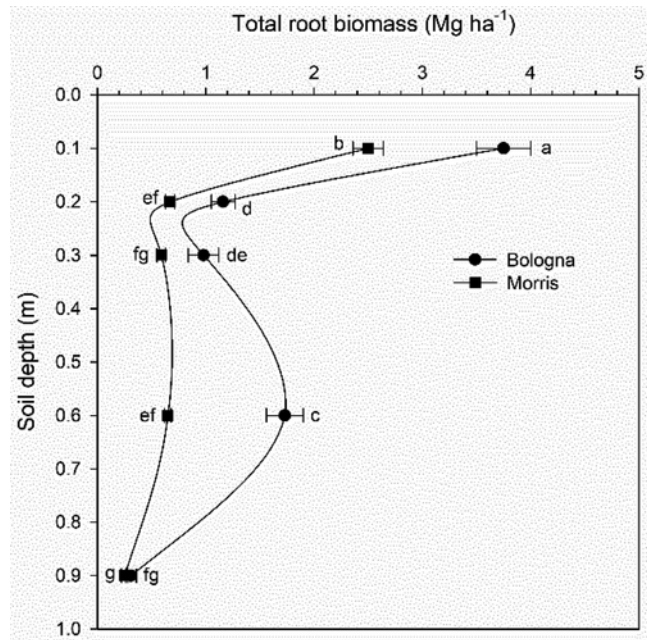

Fig. 2. Joelle camelina root biomass (crown + center) as affected by the interaction location x soil depth over two growing seasons at Bologna (Italy) and Morris (Minnesota, USA). Values at each depth for a given location are averaged across both sowing dates and seeding rates ± standard errors. Values followed by the same letters are not statistically different (LSD Test, $P \leq 0.05$).

Table 4
Joelle camelina root biomass (crown + center) as affected by the interaction of sowing date x seeding rate x soil depth. SR = seeding rates (HD 500 vs. LD 250 seeds m^{-2}). Values are means ± standard errors. Values within the column of a specific sowing date followed by the same letters are not statistically different (LSD Test, $P \leq 0.05$).

Sowing date	Seeding rate	Depth (m)	Total root biomass (crown + center, Mg DM ha^{-1})
Early	LD	0–0.1	2.92 ± 0.24 ab
		0.1–0.2	0.59 ± 0.07 D-g
		0.2–0.3	0.93 ± 0.31 c-e
		0.3–0.6	1.31 ± 0.29 c
		0.6–0.9	0.24 ± 0.07 fg
	HD	0–0.1	3.34 ± 0.31 a
		0.1–0.2	1.06 ± 0.11 cd
		0.2–0.3	0.78 ± 0.10 c-e
		0.3–0.6	1.33 ± 0.31 c
		0.6–0.9	0.18 ± 0.03 g
Late	LD	0–0.1	3.52 ± 0.43 a
		0.1–0.2	1.12 ± 0.17 cd
		0.2–0.3	0.75 ± 0.08 c-f
		0.3–0.6	1.22 ± 0.015 c
		0.6–0.9	0.30 ± 0.06 e-g
	HD	0–0.1	2.59 ± 0.29 b
		0.1–0.2	1.01 ± 0.16 cd
		0.2–0.3	0.77 ± 0.10 c-e
		0.3–0.6	1.14 ± 0.16 cd
		0.6–0.9	0.41 ± 0.05 e-g

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3.3. Plant growth, yield, and seed qualitative traits

Winter survival was significantly (Table 5) greater in Bologna than in Morris, i.e., 73 versus 68 %, respectively. A significant interaction between location and sowing date emerged (Table 5), with early-sown plants at Morris having lower winter survival than those in Bologna but no difference in survival between late-sown camelina at Morris compared with either sowing date at Bologna (data not shown). The 50 % flowering date was significantly influenced by location, sowing date, and the interaction between sowing date and location (Table 5). By late March, 50 % flowering had occurred in Bologna, while in Morris, it occurred about 45 d later. With respect to the location by sowing date interaction, 50 % flowering differed by just 3 d between sowing dates in Bologna (91 versus 94 DOY, early versus late sowing), while they differed by 7 d at Morris (142 versus 149 DOY, early versus late sowing).

At harvest, plant height and population density were significantly affected by location and by the interaction between location and seeding rate (Table 5). Joelle plants grown at Bologna were significantly taller (0.97 m; $P \leq 0.05$) than those at Morris (0.68 m). Furthermore, plants at Bologna were taller in the LD plots (1.00 m; $P \leq 0.05$) than the HD seeding rate (0.95 m). In addition to greater winter survival, the population density at harvest, when averaged across all treatments, was more than three-fold greater at Bologna (187 plants m^{-2}; $P \leq 0.05$) than at Morris (51 plants m^{-2}). In Bologna, population density of Joelle was 239 plants m^{-2} in the HD plots and 135 plants m^{-2} in the LD ones, while in Morris, the HD treatment was 64 plants m^{-2} and LD was 37 plants m^{-2}, confirming the significant interaction between seeding rate and location ($P \leq 0.05$). This also demonstrates that the HD seeding rate did lead to approximately double the plant density as the LD rate at both locations.

Both total aboveground biomass and seed yield at harvest were significantly affected ($P \leq 0.05$) by growing location and seeding rate (Table 5 and Fig. 3A and B). Bologna had higher accumulation of aboveground biomass (5383 kg ha^{-1}; $P \leq 0.05$) than Morris (3221 kg ha^{-1}), which also translated to greater seed yield in Italy as well (1518 kg ha^{-1} at Bologna versus 743 kg ha^{-1} at Morris, $P \leq 0.05$). Also, the HD seeding rate promoted a greater accumulation of aboveground biomass and seed yield (Fig. 3B). Averaged across locations and sowing dates, Joelle camelina under the HD seeding rate yielded 24 % more seed than the LD rate (1212 versus 977 kg ha^{-1}, for HD and LD, respectively, $P \leq 0.05$).

Perhaps due to lesser aboveground biomass accumulation, the harvest index (HI) was significantly greater at Morris than Bologna (0.22 versus 0.16, for Morris and Bologna, respectively, $P \leq 0.05$) (Fig. 4). Additionally, a significant interaction between location and sowing date emerged for HI (Fig. 4). Harvest index at Bologna was relatively stable between early and late sowing (0.16 versus 0.17, for early and late sowing, respectively), but at Morris, late sowing was associated with significantly greater HI (0.20 versus 0.24, for early and late sowing, respectively, $P \leq 0.05$).

Seed oil content was significantly affected by location and the interaction between location and sowing date (Table 5). Joelle grown at Bologna contained significantly greater oil content than that grown at Morris (419 versus 385 g kg^{-1}, for Bologna and Morris, respectively, $P \leq 0.05$). Late-sown Joelle at Morris had significantly greater seed oil content than the earlier sowing (392 versus 375 g kg^{-1}, for late and early sowing, respectively, $P \leq 0.05$), while at Bologna oil contents were consistently above 410 g kg^{-1} (Fig. 5).

Seed protein content showed an inverse relationship with oil content and was significantly influenced by location, sowing date, and the interactions of location x seeding rate and sowing date x seeding rate (Table 5). Seed protein was greater at Morris than Bologna (274 versus 253 g kg^{-1}, for Morris and Bologna, respectively, $P \leq 0.05$), and earlier sowing led to increased protein content (269 versus 259 g kg^{-1}, for early and late sowing date, respectively, $P \leq 0.05$). Protein was slightly greater at Bologna when Joelle was grown under HD, while the opposite occurred at Morris (Fig. 6A, $P \leq 0.05$). Concerning the interactive effect between sowing date and rate (Fig. 6B), seeds from the early sowing had the highest protein (271 g kg^{-1}) under HD, while the lowest was found in the late-sown HD plots (257 g kg^{-1}).

4. Discussion

Little information exists for comparing either the above or belowground growth characteristics and seed yield of winter camelina across such diverse environments as used in this study. Results of the present study demonstrated that winter camelina produced greater seed and biomass yields under the Mediterranean climate and soil conditions of Bologna (Italy) than Morris (Minnesota, USA). Aboveground biomass produced by plants in Bologna was 1.7 times greater than that in Morris, and during the 2015/2016 growing season in Italy, Joelle camelina produced an average seed yield of 2059 kg ha^{-1}. Seed yields at Bologna are generally greater than those previously reported for winter camelina (Gesch and Cermak, 2011; Johnson et al., 2017; Gesch et al., 2018), although Berti et al. (2015) reported average yields as high as 1745 kg ha^{-1} for Joelle grown in the northern Great Plains, USA. Seed yields for Joelle winter camelina at Morris for this study are similar to that reported by Gesch et al. (2018), which averaged 865 kg ha^{-1} across a range of seeding rates from 334 to 1000 seeds m^{-2}.

Similar to aboveground plant growth, total belowground root mass for winter camelina grown at Bologna was approximately 1.7 times greater than that at Morris. Also striking, was that root biomass at Bologna was considerably greater at lower depths in the soil profile than for plants at Morris, especially at the 0.3–0.6 m depth. Gesch and Johnson (2015) reported that 82 % of Joelle winter camelina's root density was found in the 0–0.3 m soil depth in a previous study conducted at Morris (Minnesota) and concluded that it possessed a meager root system that partly explained its relatively low water use. In the present study, 81 % of camelina root mass was found in the 0–0.3 m depth at Morris, while only 74 % was found at the same depth in Bologna in a clay loam soil. In Arizona on a sandy clay loam soil, Hunsaker et al. (2011) found that roots of spring camelina extend as deep as 1.4 m allowing them to extract soil water from relatively deep in the soil profile. The much greater root mass deeper in the soil for winter camelina grown at Bologna likely allowed plants access to more soil resources (i.e., nutrients and water) than those at Morris. Thus, this greater root growth in part led to the greater aboveground biomass and seed yield of plants at Bologna. Greater growth and yield are often associated with plants that have deeper, more extensive root systems (Den Herder et al., 2010; Vamerali et al., 1999). Conversely, because the soil at Morris has a higher OM%, plants may have been able to extract ample nutrients for

Table 5
ANOVA table with *F* values and statistical significance of the parameters surveyed during camelina growth and at harvest over two growing seasons at Bologna (Italy) and Morris (Minnesota, USA). Loc = locations (Bologna vs. Morris), SD = sowing dates (early vs. late sowing dates), SR = seeding rates (HD 500 vs. LD 250 seeds m^{-2}).

Factors	Winter survival	50 % flowering DOY	Plant height	Population density	Total biomass	Seed yield	Harvest index	Oil content	Protein content
LOC	6.92*	3120***	133.31***	113.43***	30.64***	10.14**	8.81**	24.67***	69.16***
SD	0.28 ns	63.67***	2.44 ns	10.82*	2.07 ns	5.74 ns	21.58***	4.46 ns	21.28**
SR	0.26 ns	0.74 ns	0.31 ns	65.51***	13.22***	11.18**	1.12 ns	1.06 ns	0.38 ns
Loc*SD	5.17*	5.92*	0.25 ns	0.87 ns	2.97 ns	0.35 ns	7.99**	4.83*	0.07 ns
Loc*SR	0.12 ns	0.74 ns	6.71*	22.52***	0.05 ns	0.12 ns	3.09 ns	3.5 ns	5.01*
SD*SR	1.54 ns	0 ns	0.2 ns	5.91*	0.03 ns	0 ns	0.02 ns	0.01 ns	5.42*
Loc*SR*SD	0.01 ns	0 ns	0.48 ns	1.89 ns	0 ns	0.07 ns	0.07 ns	0.64 ns	2.15 ns

*, **, *** Significant at the 0.05, 0.01, and 0.001 probability levels, respectively (LSD test); ns = not significant.

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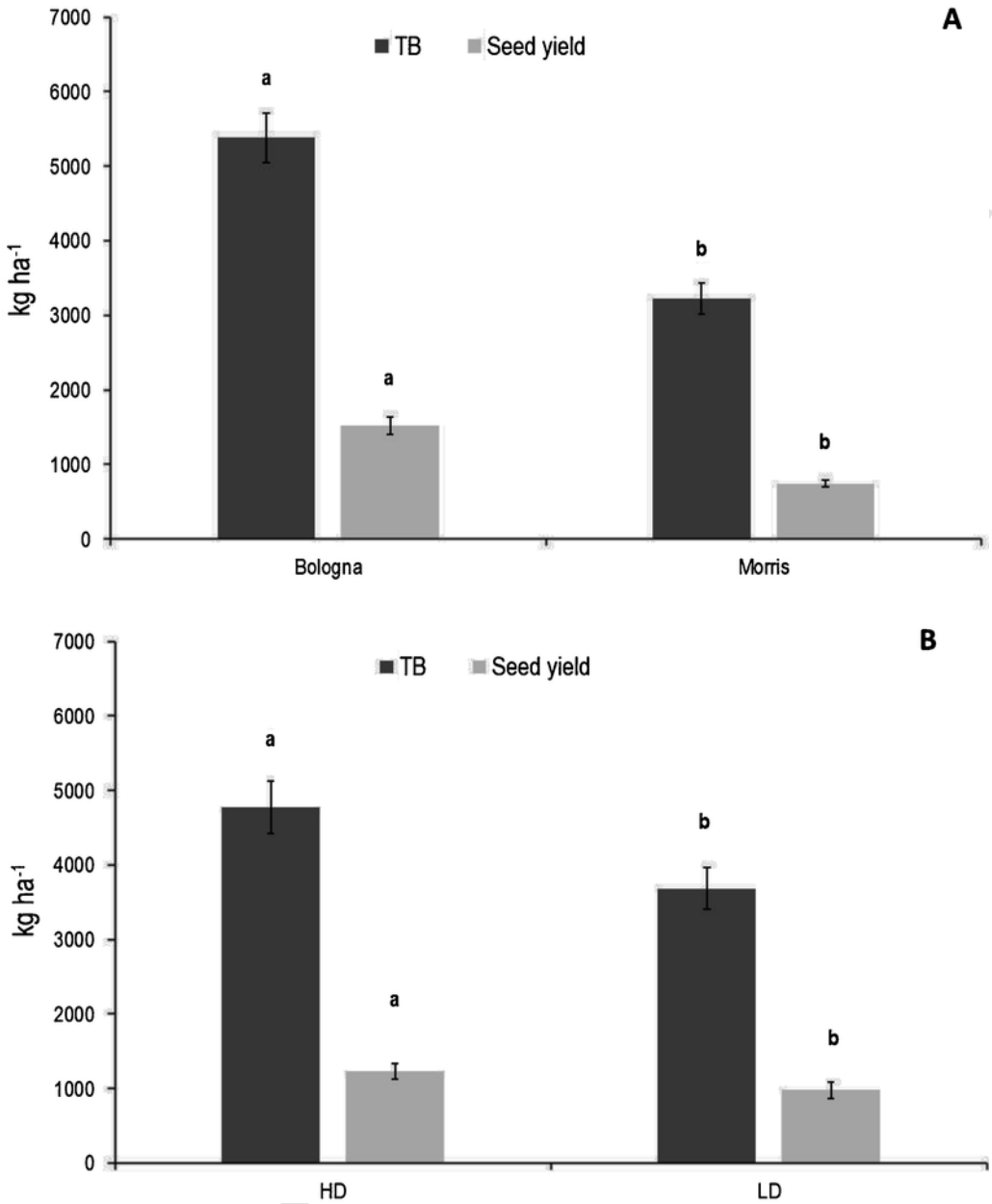

Fig. 3. Total aboveground biomass (TB) and seed yield at 10 % moisture content (kg ha^{-1}) of Joelle camelina grown over two growing seasons as affected by: A) location (Bologna, Italy vs. Morris, USA), and B) by seeding rate (HD: 500 seeds m^{-2} vs. LD: 250 seeds m^{-2}). Vertical bars are means ± standard errors. Values followed by the same letters are not statistically different for the same parameter (LSD test, $P \leq 0.05$).

growth without having to extend their roots deeper into the profile. Classic root architecture studies such as that of Drew (1975) demonstrated that root systems respond to spatial availability of nutrients. This might also partially explain the much greater root mass in the 0.3–0.6 m layer at Bologna, where presumably organic residues would be more available due to the deeper ploughing application. To understand the mechanism(s) causing the shift in root growth and architecture would require finer resolution of soil properties.

The mild winter temperatures characteristic of the Mediterranean climate undoubtedly had a substantial influence on the greater growth and yield of camelina grown at Bologna as compared with Morris. Even though camelina was sown later and harvested earlier in Bologna, the number of total accumulated GDD did not greatly differ between locations. In fact, when averaged over seeding dates and growing seasons, the number of GDD for both locations was 1396 °C d, but GDD distribution over the growing season differed (Table 2). The two locations differed with respect to total crop cycle length (i.e. sowing to harvest) and total number of days with active growth (Tmean > 4 °C). Bologna had the shortest crop cycle (231 d) but the longest period of active growth (197 d), while Morris showed the opposite trend (287 and 139 d, respectively). Plants grown at Bologna, particularly between December and March typically were able to accumulate GDDs, while those at Morris remained essentially dormant (i.e., no growth) during this time, and resumed growth in early April (Fig. 1). This extended period of vegetative growth during the winter months is likely the reason for taller and generally larger plants at the Bologna site. A longer vegetative phase typically allows crops to accumulate more carbohydrates and nitrogen, which are later translocated from vegetative tissues to reproductive organs to increase seed yield (Bouchet et al., 2016). Moreover, the longer flowering period in Bologna, indicated by a greater accumulation of GDD after 50 % flowering (an average of 765 °C d compared with 683 °C d at Morris) coupled with an extended vegetative growth over winter, translated into greater seed yield than in Morris. Our re-

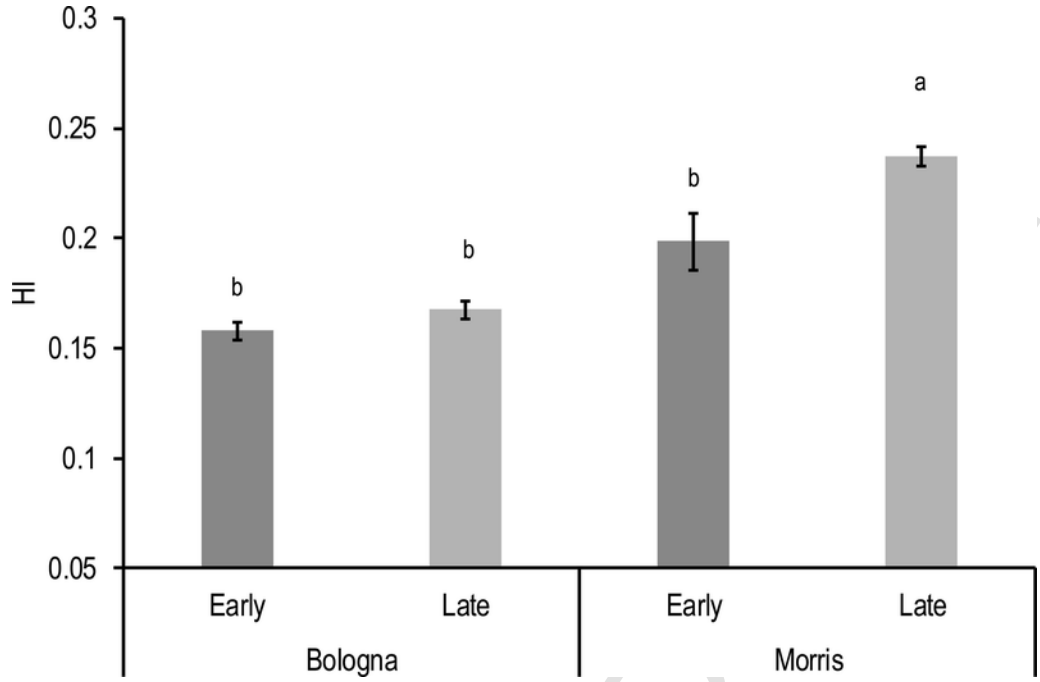

Fig. 4. Harvest index (HI) of Joelle camelina grown as affected by the interaction of location (Bologna, Italy vs. Morris, USA) and planting date (early vs. late sowing). Vertical bars are means ± standard errors. Values followed by the same letters are not statistically different (LSD test, $P \leq 0.05$).

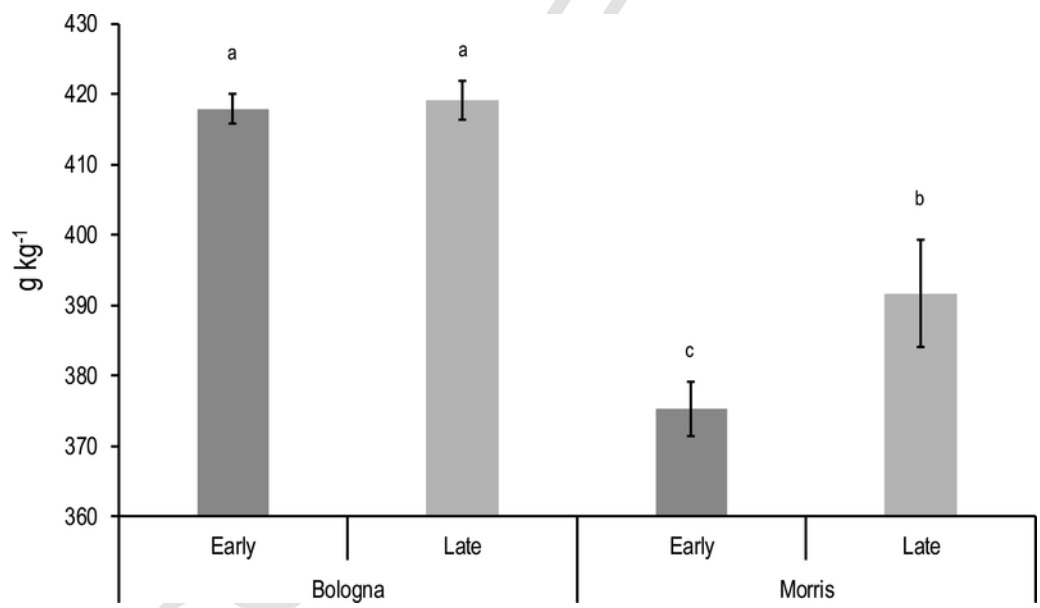

Fig. 5. Joelle camelina seed oil content (g kg^{-1}) as affected by the interaction between location (Bologna, Italy vs. Morris, USA) and sowing date (early vs. late sowing). Vertical bars are means ± standard errors. Values followed by the same letters are not statistically different (LSD test, $P \leq 0.05$).

sults corroborate those of Royo-Esnal et al. (2017) who compared growth fitness parameters of pennycress (*Thlaspi arvense* L.) and camelina grown as winter annual crops in Teruel and Almenar (Spain) with the same species grown in Minnesota USA. They also reported that plants were consistently taller and larger when grown in Spain as compared with the USA, and further demonstrated that this translated to greater reproductive growth.

Plant densities at harvest differed between the locations, and thus, cannot be ruled out as potentially influencing yield. Bologna consistently had greater plant densities at harvest than Morris, which may have been due to better fall emergence of seedlings at Bologna. For instance, during the study, fall emergence (data not shown) at Bologna averaged 141 and 337 plants m^{-2} for the LD and HD treatment, respectively, while in Morris, emergence averaged 70 and 146 plants m^{-2} for the LD and HD, respectively. Variable emergence of camelina under differing soils and climatic conditions, especially relative to available soil moisture for germination, has been cited as an issue (McVay and Khan, 2011; Schillinger et al., 2012). However, winter camelina plant density over a wide range has been shown to have little effect on seed and oil yield. Gesch et al. (2018) demonstrated over a two-year field study with winter camelina that seeding rates of 334, 668, and 1000 seeds m^{-2}, resulting in final stands of 113, 161, and 201 plants m^{-2}, did not significantly impact seed and oil yield due to growth and yield compensation of plants. This was due to greater production of seed weight $plant^{-1}$ at lower densities (Gesch et al., 2018), presumably in relation to increased branching, and hence, more silicles and seed $plant^{-1}$, although seed size might have also been a factor. Similarly, McVay and Khan (2011) have reported little yield variation for spring

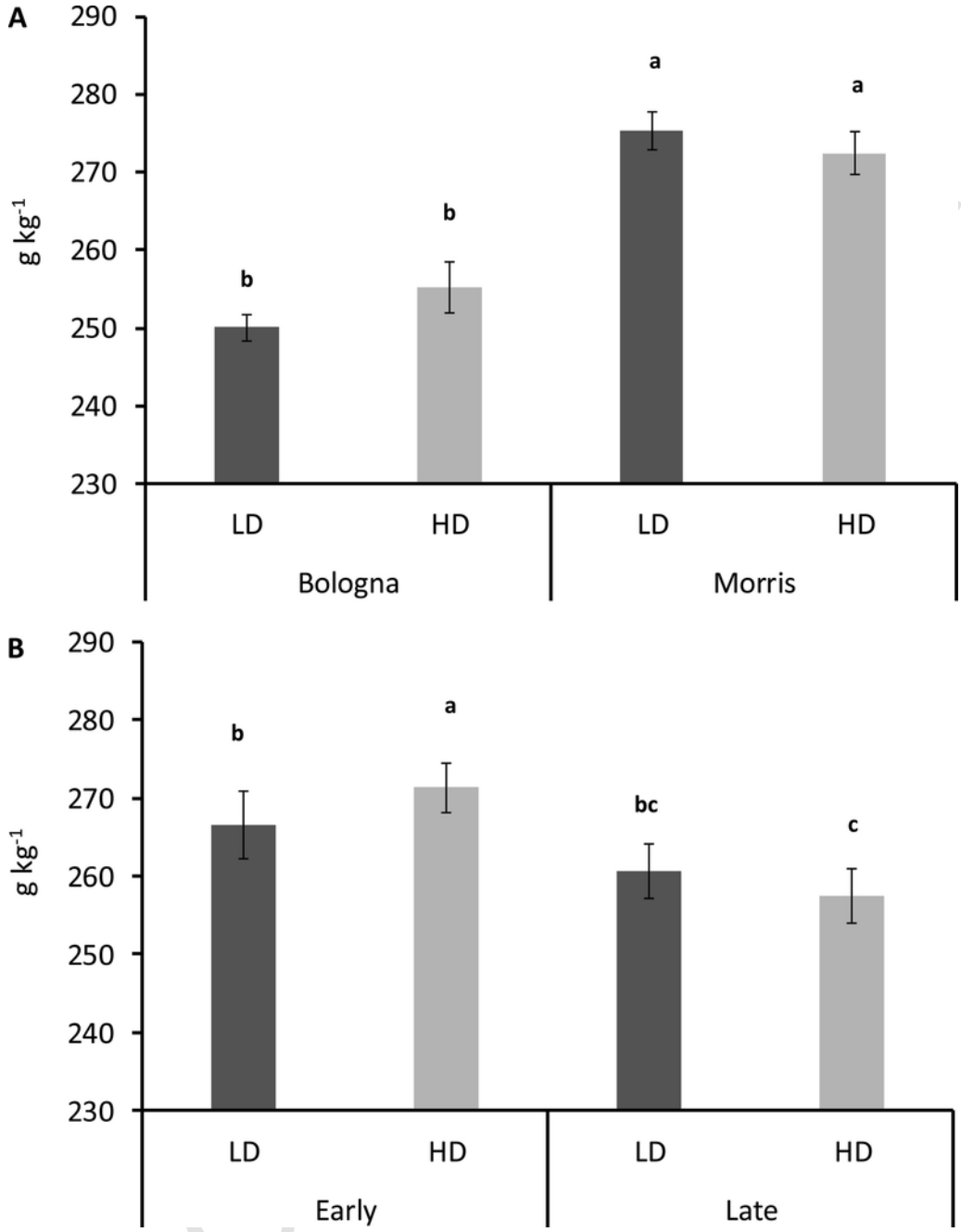

Fig. 6. Joelle camelina seed protein content (g kg^{-1}) as affected by: A) the interaction between location (Bologna, Italy vs. Morris, USA) and seeding rate (HD: 500 seeds m^{-2} vs. LD: 250 seeds m^{-2}); B) the interaction between planting date (early vs. late sowing) and seeding rate (HD vs. LD). Vertical bars are means ± standard errors. Values within a graph followed by the same letters are not statistically different (LSD test, $P \leq 0.05$).

camelina over a wide range of plant densities. Stand densities in the present study are within the range of those reported in these previous studies. However, in the present study, there was a slight but significant increase in yield associated with the HD treatment (Fig. 3B). This response tended to be more pronounced at Bologna. Nevertheless, the differences in plant growth, yield, and seed quality are believed to have been influenced more by location variances in climate and soil than by plant density, as reported by Zanetti et al. (2017) for spring camelina grown at different locations in Europe and Canada.

Differences in climate, especially growing season temperatures, also likely had the greatest influence on seed oil and protein content. Mild temperatures during reproductive growth of camelina are often associated with greater seed oil content as well as increased yield (Gugel and Falk, 2006; Sintim et al., 2016; Obour et al., 2017). Plants at Bologna were flowering by late March when temperatures were relatively low as compared with when plants were flowering in Morris, which was not until mid- to late May when temperatures were rapidly increasing (Fig. 1). The higher oil content of seeds produced at Bologna (Fig. 5) was likely due to seeds developing under lower temperatures than at Morris (Righini et al., 2019). Seeds of other Brassicaceae species have also been shown to increase in oil content when development occurs under low temperatures (Pavlista et al., 2011). Conversely, the greater seed protein content measured for seeds produced at Morris was presumably due to development of seeds at higher temperatures caused by later flowering than at Bologna (Fig. 6A). Greater seed protein is often associated with development under high temperatures, and as noted by Sintim et al. (2016), there tends to be an inverse relationship between protein and oil content in camelina seed. The seed oil and protein contents measured in this study are within the range of

those previously reported for Joelle winter camelina (Gesch and Cermak, 2011; Gesch et al., 2014, 2018).

In the present study, although sowing date did not affect seed or biomass yield, it did tend to influence seed oil content at Morris. The later sown plants at Morris produced seed that had about a 5% greater oil content than those sown earlier. This result agrees with Gesch and Cermak (2011) who also found that winter camelina sown in late September to mid-October generally produced greater oil content than plants seeded in early September. Also, the HI of winter camelina measured in the present study are within the range previously reported (Gesch and Cermak, 2011). However, HI was consistently higher at Morris (0.22) than at Bologna (0.16). This may have been due to the much greater vegetative growth of camelina grown in Bologna as compared with Morris. Winter camelina HI is still quite low compared with other Brassicaceae, such as oilseed rape (Fan et al., 2017) and may be an important trait to target in future breeding efforts.

5. Conclusions

Much like the Corn Belt region of the United States, many European countries are searching for low input, alternative winter oilseed crops that can diversify current cropping systems and promote ecosystem services to bolster greater agricultural sustainability. Results of this study demonstrated that winter camelina is a viable oilseed crop for Mediterranean climates and soil conditions like that of northern Italy. Generally, Joelle camelina exhibited greater above and belowground (i.e., roots) growth, and produced more seed and oil in Bologna Italy than Morris, Minnesota USA. This largely was attributed to mild Mediterranean winters experienced in Bologna which resulted in a longer vegetative period that translated to greater reproductive growth. Closely coupled to this growth was a much larger root system that extended deeper in the soil for plants grown at Bologna consistent with greater exploration and capture of soil resources supporting greater overall plant productivity. Camelina's versatility as either an industrial or feed/food-use crop should aid to expand Its market potential. However, more research will be required to select genotypes with higher HI that more efficiently translate vegetative growth to seed and oil yield. Moreover, additional investigation is needed to better understand camelina's rotational fit in European and USA cropping systems and its potential use in double- and relay-cropping scenarios.

Uncited reference

Berti et al. (2017).

CRediT authorship contribution statement

Federica Zanetti: Conceptualization, Methodology, Investigation, Writing - original draft, Writing - review & editing. **Russ W. Gesch:** Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft, Writing - review & editing. **Maninder K. Walia:** Methodology, Investigation, Writing - review & editing. **Jane M.F. Johnson:** Methodology, Supervision, Writing - review & editing. **Andrea Monti:** Resources, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.fcr.2020.107794.

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