Field Crops Research 347 (2026) 110622

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

The effect of sowing date in establishing *Camelina sativa* as a valuable summer crop in France

Susana Silvestre [a], Anais Da Costa [b], Thomas I. David [c], Frédérique Tellier [b], Javier Prieto [d], Paloma Leon [d], Yuri Herreras Yambanis [d], Richard P. Haslam [a], Jean-Denis Faure [b,*]

[a] Rothamsted Research, Harpenden AL5 2 JQ, United Kingdom
[b] Université Paris-Saclay, INRAE, AgroParisTech, Institut Jean-Pierre Bourgin for Plant Sciences, Versailles 78000, France
[c] University of Cambridge, Centre for Landscape Regeneration, Department of Land Economy, Cambridge CB2 3QZ, United Kingdom
[d] Camelina Company, Camino de la Carrera, 11-11, Fuente el Saz Madrid, 28140, Spain

ARTICLE INFO

Keywords:
Camelina sativa
Seed yield
Fatty acid composition
Sowing time
Sowing type
Harvest techniques

ABSTRACT

Context: European agriculture prioritizes sustainability and land use efficiency to improve economic, social, and environmental benefits by typically improving crop and land management. Intermediate cropping is an approach that can efficiently use available resources with biodiversity, agronomic, and soil health advantages. Lately *Camelina sativa* (L. Crantz, camelina) has been proposed as an intermediate oilseed crop option because of its low agronomic input requirements, short summer cycle, and utility across diverse agribusiness sectors. Recent scientific and industrial interest has increased the value of camelina grain and raised awareness of the considerable plasticity within its varieties, including natural resistance to abiotic stresses such as heat or drought.
Objective: This study explored different agronomic strategies to grow camelina as a summer intermediate crop for optimal seed yield and quality.
Methods: Field trials were conducted with a single camelina genotype in Paris (France), using conventional tillage and minimal inputs, over a period of three consecutive years with three sowing dates (spring, early summer, and summer), two types of sowing (row and broadcast), and two harvest practices (direct combining at harvest maturity and swathing at physiological maturity). Spring sowing (S1) was typically performed in March and the two summer sowings, in mid-June (S2; early summer) and early July (S3; summer).
Results: Sowing time and seasonal weather primarily drove yield (190–1157 kg ha^{-1}), seed composition (oil and protein content of 38–45% and 23–32% dry matter, respectively) and fatty acid composition (higher C18:1 in S1 versus higher C18:3/polyunsaturated fatty acids in S2–S3). Thousand grain weight (TGW) was influenced by sowing date, harvest type, and their interaction, whilst mature harvest and later sowing date produced larger seed.
Conclusions: Our results showed the prospective use of camelina as a summer intermediate crop, and that the selection of the correct sowing time for the intended end-use is crucial for the successful proliferation of the crop. Our study demonstrated the impact of agronomic management on the field performance of a single spring camelina variety, demonstrating the value of incorporating management into typical genetic x environmental camelina germplasm evaluations.

1. Introduction

The optimization of land use or land use efficiency is a priority for European agriculture in the context of agroecological transition and climate change (Chapman et al., 2025). Within this context, optimization of crop management and the introduction of new crops for use on available land throughout the growing season is necessary. Intermediate cropping is a traditional form of efficiently using available land resources by which two or more crops are grown sequentially replacing fallow. It has recognized agronomic and environmental benefits e.g., reducing the use of pesticides by 40–72% while maintaining the gross margin for main crops (Yan et al., 2024), improving plant-soil interactions with a beneficial impact in soil health (Chi et al., 2023), and increasing yields (reviewed in (Toker et al., 2024)). In France, summer

* Corresponding author.
E-mail address: jean-denis.faure@inrae.fr (J.-D. Faure).

https://doi.org/10.1016/j.fcr.2026.110622
Received 23 February 2026; Received in revised form 21 June 2026; Accepted 8 July 2026
Available online 13 July 2026
0378-4290/

Table 1
Sowing (S), flowering (F), and harvest (H) dates for the three growing seasons (2021–2023). S1, spring sowing; S2, early summer sowing; S3, summer sowing; DAS, days after sowing; GDD, growing degree days; Σ, accumulated; Δ, difference. Swathing date refers only to the plots where cutting and swathing (CSH) treatment was applied.

	2021			2022			2023		
	S1	S2	S3	S1	S2	S3	S1	S2	S3
Sowing (*S*) date	29/03/2021	16/06/2021	07/07/2021	23/03/2022	17/06/2022	05/07/2022	28/03/2023	13/06/2023	27/06/2023
Flowering (*F*) date	25/05/2021	20/07/2021	10/08/2021	18/05/2022	20/07/2022	17/08/2022	24/05/2023	21/07/2023	27/07/2023
Swathing date	08/07/2021	25/08/2021	14/10/2021	28/06/2022	23/08/2022	16/09/2022	27/06/2023	23/08/2023	13/09/2023
Harvest (*H*) date	27/08/2021	24/09/2021	09/11/2021	27/07/2022	19/09/2022	10/11/2022	30/08/2023	11/09/2023	04/10/2023
DAS (*S-F*)	57	34	34	56	33	36	57	38	30
DAS (*S-H*)	151	100	125	126	94	128	155	90	99
∑GDD Sowing	8.3	18.9	15.0	6.3	19.8	12.2	3.1	17.1	13.4
∑GDD Flowering	352.3	509.3	514.1	477.2	538.8	624.1	431.5	640.5	484.7
∑GDD Harvest	1699.5	1467.6	1505.7	1505.6	1506.8	1763.3	1960.7	1490.0	1559.7
ΔGDD (*S-F*)	344.0	490.4	499.0	470.9	519.1	611.9	428.4	623.4	471.2
ΔGDD (*F-H*)	1347.2	958.3	991.7	1028.4	967.9	1139.2	1529.2	849.5	1075.0
ΔGDD (*S-H*)	1691.2	1448.6	1490.7	1499.3	1487.0	1751.1	1957.5	1472.9	1546.2
ΣPrecipitation Sowing (mm)	0.0	18.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0
ΣPrecipitation Flowering (mm)	129.0	134.0	98.5	59.5	40.0	26.0	131.0	58.5	67.0
ΣPrecipitation Harvest (mm)	353.0	244.5	254.5	178.5	109.0	162.0	316.5	186.0	237.0
ΔPrecipitation (*S-F*, mm)	129.0	116.0	98.0	59.5	40.0	26.0	131.0	58.5	67.0
ΔPrecipitation (*F-H*, mm)	224.0	110.5	156.0	119.0	69.0	136.0	185.5	127.5	170.0
ΔPrecipitation (*S-H*, mm)	353.0	226.5	254.0	178.5	109.0	162.0	316.5	186.0	237.0

intermediate cropping is usually carried out after winter cereals like barley or legumes (e.g. winter pea), and before the next autumn sowing (Pitchers et al., 2023). Spring and summer double-cropping enables the utilization of available land following winter crops, however, it is often challenged by environmental constraints such as heat or drought that can strongly limit yield and interest from farmers (Pitchers et al., 2023). For a spring double crop, sowing should be implemented between March and April; whilst the summer intermediate crop full cycle should be carried out between mid-June at the earliest and mid-October at the latest. However, as these timings can expose the crop to higher environmental risks such as elevated temperatures (e.g. heat waves) and drought, adapted crop management strategies need to be explored to ensure seed yield and quality.

The potential of *Camelina sativa* (L. Crantz; camelina) to be established as an intermediate crop in France has been previously suggested (Leclère et al., 2018; Pitchers et al., 2023). Camelina has been reported as an effective option for intermediate cropping across Europe and United States, improving biodiversity when sown in the summer (Groeneveld and Klein, 2014), and increasing oil yield as an intermediate crop sown before sunflower (Gesch et al., 2022). Camelina can be cultivated as spring crop for optimal growing conditions (Krzyianiak et al., 2019). Summer cropping can sometimes be considered as suboptimal with the increased likelihood of heat and drought stresses affecting sowing and flowering stages leading to a prematurely reduced growth period. However, in France, intermediate cropping with camelina is classically used either in spring as a mitigation for a failed winter crop or in summer after barley or winter pea (Leclère et al., 2018). Camelina, also known as false flax or gold of pleasure, is a traditional oilseed crop with origins in Southeast Europe and Southwest Asia (Larsson, 2013). An oil content of up to 45% of its seed weight and 20–30% protein (Zubr, 2003), make camelina a suitable crop for many industrial, food and feed applications (Alberghini et al., 2022; Piergiovanni et al., 2025; Tocher et al., 2024). Camelina has long been established as a source of healthy fatty acids (Cahoon, 2009; Zubr, 2003), and in the last few years has gained some traction as a sustainable platform for the production of human health beneficial omega−3 fatty acids (Haslam et al., 2025; Usher et al., 2017). Characterized by high content of polyunsaturated fatty acids (PUFA, 50–60% of total), of which up to 35% is the omega−3 fatty acid α-linolenic acid (ALA, C18:3), and approx. 15% of eicosenoic acid (C20:1) (Krzyianiak et al., 2019; Vollmann et al., 2007). As well as a naturally low content (2–4%) of the highly regulated fatty acid erucic acid (Vollmann et al., 2007; Wang et al., 2022). Camelina shows high plasticity to different environments and growing conditions, with a natural resilience to heat and drought stresses (Alberghini et al., 2025; Masella et al., 2014; Silvestre et al., 2026). This robustness can be associated with the widespread range of varieties adapted for winter and spring/summer growing (Wittenberg et al., 2019; Zubr, 1997). Furthermore, in Mediterranean climates, e.g., southern Europe including Italy and Spain, camelina spring varieties can be sown in Autumn in certain areas, where the climate allows, and achieve higher yields than winter varieties (Codina-Pascual et al., 2025; Zanetti et al., 2021). Typically the camelina lifecycle ranges from 90 to 250 days (reviewed in Zanetti et al. (Zanetti et al., 2021), with the shortest cycles reported for spring/summer sowing (Martinelli and Galasso, 2011), which make camelina an optimal candidate for spring/summer intermediate cropping. The aim of this work was to develop and propose an optimized agronomic strategy (management) for cultivation of camelina as a double crop in France with a focus on yield parameters. To achieve this, field trials were performed over three years using a camelina cultivar adapted to a reduced growth cycle with early flowering (UNT1, provided by Camelina Company, España; CCE). A combination of three sowing times, spring (S1), early summer (S2), and summer (S3); two types of sowing, row (RS) and broadcast (BS); and two harvest techniques, cutting and swathing (CSH) and full maturity (MH), were tested.

2. Material and methods

2.1. Field trial design

The camelina spring genotype (UNT1) with early flowering and reduced growth cycle used in this study was kindly provided by Camelina Company España (CCE, Spain). Three years of field trials (2021–2023) were performed at the experimental farm of INRAE Versailles-Saclay (48.806 N, 2.086E). The site features silty-clay-loam soil (27% sand, 29% clay, 44% silt, 1.25% organic matter, pH 7). The experimental design of the trial was a split-split plot with three blocks (sowing time) and four replicates, the plot factor was sowing type, and the sub plot factor was harvesting type. The previous crop was cereal (wheat or barley). Three different sowing times were tested, spring (S1), early summer (S2), and summer (S3, dates in Table 1). Two sowing types were used, row sowing (RS) and broadcast sowing (BS). For the RS, seeds were sown at a depth of 1–2 cm with the aid of a mechanical drill (INOTEC) with inter row spacing of 16.5 cm. For BS, seeds were scattered on the surface of the soil. The seeding rate was of 1084 seeds/m^2 for 2021, and 800 seeds/m^2 in 2022 and 2023, and it was kept constant for each sowing date within each year. Two harvesting techniques were applied at the end of the growth cycle, conventional mature harvest (MH) and precocious cutting and swathing (CSH, dates in Table 1) (Pari et al., 2024). In MH, the entire plots were harvested with a combine at full maturity, seed moisture about 8% with fully brown siliques. For CSH, the entire plot was cut at 30 cm (plant height) from the soil when seed moisture was at approximately 35% and the majority (>75%) of siliques were yellow, and then left on the ground for at least two weeks before being manually harvested (Pari et al., 2024). Harvested seed was spread on greenhouse benches and left for further drying for at least a week. For seed moisture, fresh (FW) and dry weight (DW, after overnight drying at 42°C) seeds were collected from ten randomised plants per plot. (Pari et al., 2024) Plants were threshed with a seed thresher (Halldrup LT35–100, Germany), seeds were collected, sieved and cleaned. A total of 48 plots were established for each growing season, and each plot was 16.6 m^2. Agronomic management was performed similarly during the three growing seasons, the seedbed was prepared using conventional cultivation e.g., first soil tilling a couple days before sowing, disk ploughing followed by soil levelling with harrows. Fertilization was incorporated by tillage three weeks to one month before sowing (N50 units/ha YaraBela® Extran® 33.5% N; P50 – K50 – S12 kg ha^{-1} TIMAC AGRO®; N, nitrogen; P, phosphorus; K, potassium; S, sulphur). Excess weeds were removed manually during the trials, and no pesticide nor irrigation was applied during the three years. Plant phenology was assessed using the BBCH scale according to (Martinelli and Galasso, 2011), CSH and MH were carried out respectively at BBCH 805 and BBCH 809.

2.2. Meteorological data collection

The main meteorological data, i.e., air temperature (T_{min}, minimum; T_{max}, maximum) and daily precipitation (mm) were collected throughout the growing seasons by a weather station located in the experimental fields. Growing degree days ($\sum$GDD) were calculated for each trial year from sowing (S1, S2, S3) to harvest date as $\sum GDD = \sum[(T_{max}+T_{min})/2 - T_{base}]$. T_{base} for camelina was defined as 4°C (Gesch and Cermak, 2011).

2.3. Yield parameters

The entire plot was harvested with a combine-harvester, and the seeds were manually cleaned with 1.8 mm sieve, followed by cleaning with an air column. Seed yield was calculated by weighing the cleaned and dried seeds. Thousand grain weight (TGW, g) was determined by averaging the weight of three replicates of 1000 seeds counted with a seed counter (Elmor C3 High Sensitive Seed Counter, Switzerland). Measurements of seed moisture, total oil, and protein content were obtained for each sample with a NIRS device (Near-infrared spectroscopy, FOSS DS2500, Denmark), oil and protein content were corrected for moisture and expressed as percentage of dry matter (% DM). The equations used for these measurements were developed and continuously updated in-house by CCE. Yield parameters' mean ± standard error for every year and trial conditions can be found in Supplementary Table S1.

2.4. Fatty acid analysis

A total of 20 seeds were weighed in a glass tube and mixed with 1.345 mL of fatty acid methyl ester (FAME) buffer [methanol (1 mL), toluene (0.3 mL), sulfuric acid (25 μL) and C17:0 internal standard (20 μL of 10 mg/mL solution)]. The tubes were closed and warmed at 90°C for 90 min. After cooling, water (1.5 mL) and hexane (0.5 mL) were added, and the mix was centrifuged for 5 min at 1600 g. Fifty μL of the organic phase was diluted 1:20 in hexane (1 mL) and 50 μL was transferred into a GC vial for analysis by Gas Chromatography followed by Mass Spectrometry (GC/MS). The samples were injected on an Agilent 7890 A gas chromatograph coupled to an Agilent 5975 C mass spectrometer. The polar column was a BPX70 (SGE) (30 m). Oven temperature ramp was 16 °C/min from 70°C to 160°C, then 4 °C/min up to 240°C and 10 °C/min up to 260°C for 4 min (run length 31,6 min). Helium constant flow was 1.52 mL/min. Temperatures were the following: injector 250 °C, transfer line 290 °C, source 250 °C and quadrupole 150 °C. The peak area of each FAME was normalized to the internal standard and further normalized to the weight of the initial sample. The retention time and identity of each peak was calibrated using the Supelco® 37 Component FAME Mix (certified reference material TraceCERT®, Sigma-Aldrich®). Total FA content was calculated as the sum of all FA present, relative FA composition as percentage of total, leaf relative polyunsaturated FA content (PUFA index) as [*PUFA* (C18:3, C18:2, C20:2)] / [*MUFA* (C18:1, C16:1, C20:1) + *SFA* (C18:0, C16:0, C20:0)]; MUFA, monounsaturated FA; SFA, saturated FA. Detailed FAMES profile (mean ± standard error) for every year and trial conditions can be found in Supplementary Table S2 and S3.

2.5. Statistical analysis

Analysis of variance (ANOVA) was applied to each variable for each year of field trials. Sowing time, sowing type, harvest type, and their interactions were tested. Crop failure in 2022 caused 75% of the data for S3 to be missing, so the analysis and graphs for 2022 were run excluding S3. Significance codes used '***' < 0.001; '**' < 0.01; '*' 0.05; ns, non-significant. RStudio 2024.12.1 + 563 "Kousa Dogwood" release was used for data analysis and graph production (ggplot2). Principal component analysis (PCA) was produced using prcomp package, any missing values were replaced with median of remaining replicates. Linear mixed models were employed to account for year as a random effect. Fixed effects were sowing time, type, and harvest type, and all interactive terms were included. The analysis was performed in RStudio (R version 4.4.1) using the lme4 package (Bates et al., 2015). The full model was refined iteratively through backward elimination of non-significant terms, starting with the highest-level interactive term. At each stage, model residuals and fit were checked with the DHARMa package (Hartig, 2024), and models were compared with Akaike Information Criterion (AIC). This approach was chosen to identify fixed effects that best explained variation in the data, leading to a final model for each response. Post-hoc testing was performed for each response variable, using estimated marginal means (Lenth, 2024), to identify significant differences between fixed effects.

3. Results

3.1. Spring and summer sowings were distinguished by cycle duration and weather patterns

Field trials were carried out over three consecutive years from 2021 to 2023, and within each year three sowing times were tested, two summer sowing dates (S2 and S3) were compared with a spring sowing date (S1). S1 was sown in March while S2 was sown mid-June (early summer), and S3 between end of June to early July (summer, details in Table 1). As expected, S1 was associated with the longest growing period with 151 and 155 DAS (days after sowing) in 2021 and 2023 except for 2022 with a duration comparable to S3 (126 DAS S1, 128 DAS S3; Table 1). In contrast, S2 (early-summer) corresponded to the shortest growing period, whilst S3 was intermediate between S1 and S2. As expected, the length of the growing period was reflected in the growing degree days (GDD, Table 1). The accumulated GDD (ΣGDD) plotted per day of trial for each of the sowing times and years (Supplementary Fig. 1A-C) showed that S2 and S3 paired together throughout the cycle until the later stages. S1 however showed a unique pattern of ΣGDD per DAS characterised by low ΔGDD until flowering (respectively 344, 471, and 428 for 2021–2023 compared to 490, 519, 623 for S2 or 499, 612, 471 for S3) and a longer vegetative period (~57 DAS until

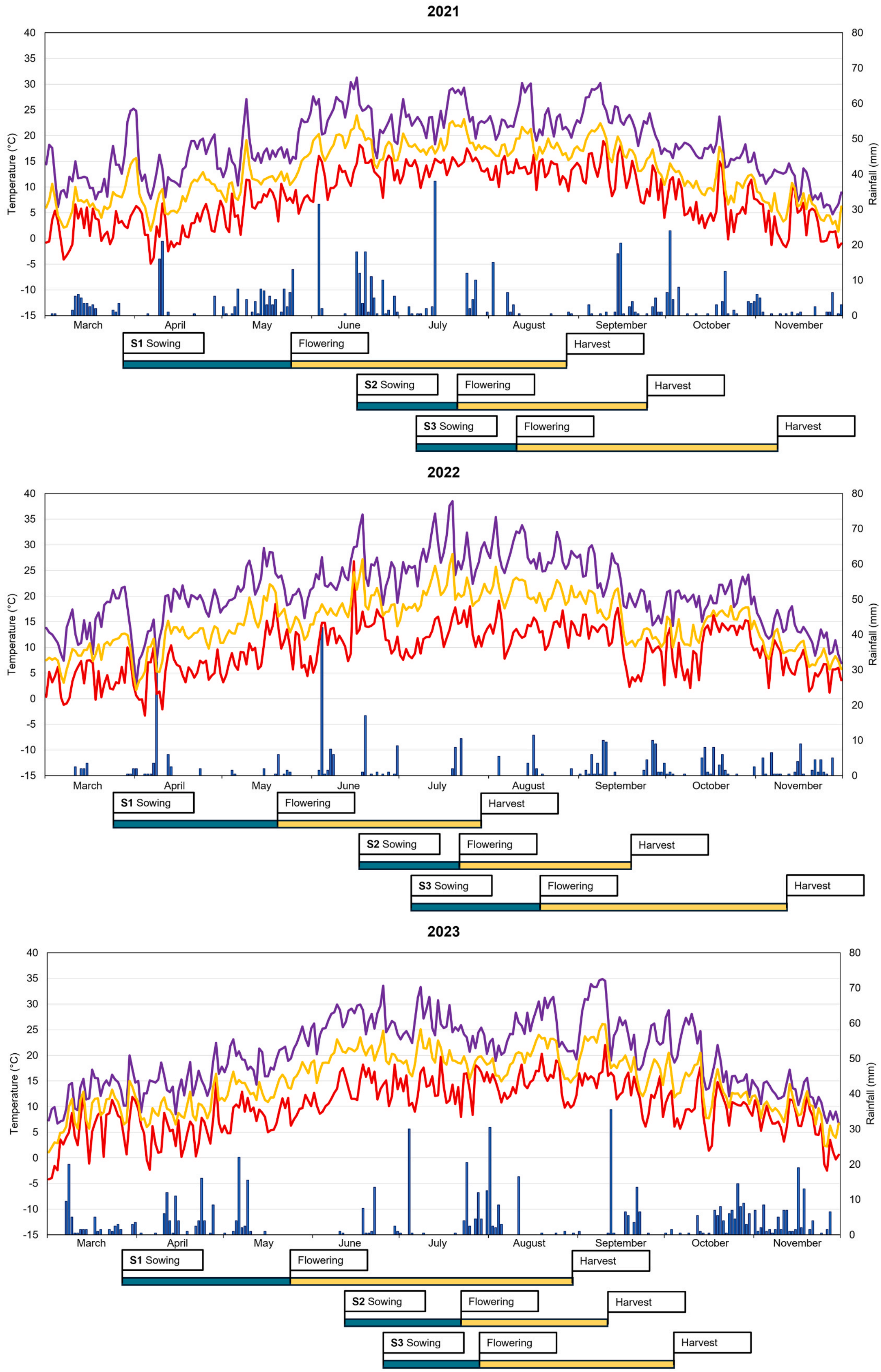

Fig. 1. Temperature and rainfall data for each of the growing season years 2021–2023. Daily minimum (red), maximum (purple), and mean (yellow) temperature (°C), and precipitation (blue, mm) for each growing season between March and November 2021–2023. The three sowing times (S1, S2, S3) are represented below each graph with sowing to flowering (green), and flowering to harvest (yellow) represented.

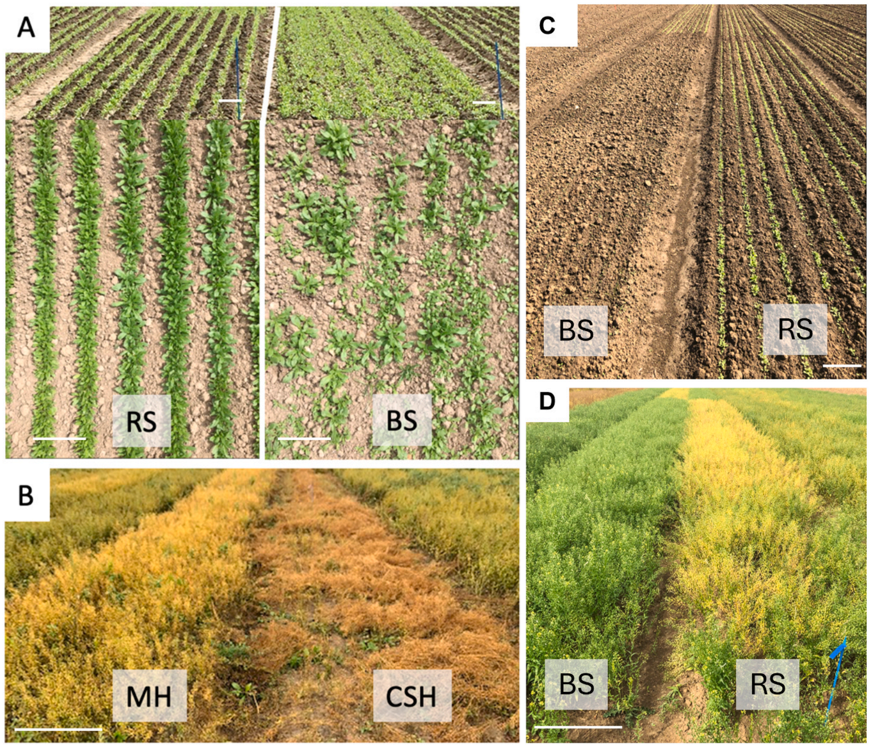

Fig. 2. Comparison of different sowing and harvest management procedures. Row (RS) and broadcast (BS) sowing (A, C, D); conventional harvest at maturity (MH) compared to cutting and swathing (CSH, B). A-B, summer 2021; C-D, 2022 growing season. Growing conditions for 2022 S3 summer sowing date induced a delay in emergence, flowering and seed maturation for broadcast sowing condition compared to row sowing. Scale bar = 20 cm (A, C) and 50 cm (B, D). Photo credits INRAE-AgroParisTech.

flowering stage compared to 30–38 DAS for S2 and S3; Supplementary Fig. 1A-C). This pattern, distinguishing S1 from S2 and S3, was consistently repeated over the three years of field trials. Flowering was influenced by temperature, where the increase in temperature (registered by ΣGDD) observed in S2 and S3 induced flowering earlier at 30–38 DAS, rather than 57 DAS in S1. S1 registered also the highest accumulation of rain between sowing and flowering and the highest overall amount of rain in every year followed by S2 and S3 (Supplementary Fig. 1). Comparing the weather in different years (Fig. 1), 2022 was generally characterised by low rainfall for all sowing times with a maximum of 179 mm in S1, compared to 245 mm and 186 mm, which were the minimum registered for 2021 and 2023, respectively, both in S2 (Table 1). The high temperatures registered in the summer months of 2022 (T_{max} 35.4 – 38.5 °C and T_{mean} 18.4 – 20.8 °C for June – August) had an impact on S3 (summer sowing), which showed the highest ΣGDD for the three years, but did not seem to have had an impact on S1 and S2. In conclusion, across the three years of field trials, S1 was characterised by the longest cycle, the lowest ΣGDD to flowering, the longest DAS to flowering and the highest rainfall. S2 was characterised by the shortest cycle and the lowest overall precipitation. S3 was characterized by the lowest precipitation to flowering. As expected, the summer sowings S2 and S3 showed very similar ΣGDD to flowering and very similar DAS to flowering.

3.2. Analysis of crop management modalities for each sowing time

Row (RS) and broadcast (BS) seeding were tested since the former allowed deeper seeding, which can be more favourable if drought occurs (Fig. 2A, C). Mature harvest (MH) was compared with cutting and swathing (CSH), used to accelerate seed maturation and shorten the growing period (Fig. 2B). Seed yield (kg ha^{-1}), TGW (g), and mature seed oil and protein content (% DM, dry matter) were used as performance variables to evaluate the effect of the different crop management modalities during the three years of trials (Table 2, Fig. 3). Seed quality was investigated by analysing the fatty acid (FA) profile of the seed oil by fatty acid methyl esters (FAMES), which allowed to calculate the polyunsaturated fatty acid index (PUFA; Table 2, Fig. 4). The importance of different crop management was illustrated during the summer of 2022, which was characterized by high temperature and low rain at the end of June and in July (Fig. 1). The severe drought delayed S3 emergence and thus, flowering and seed maturation (Fig. 2C, D). Seed maturation was further reduced by the low temperature registered in September-October 2022, leading to dampened and moulded plants that could not be harvested with the combine. This resulted in crop failure for all S3 conditions except for the combination of RS with CSH, causing 75% of the data for S3 in 2022 to be missing. As this outcome could increase the probability of a type I error in the statistical analysis, these data were excluded from the analysis (mean ± standard error for S3-RS-CSH in 2022 can be found in Supplementary Tables S1-S3).

A principal component analysis (PCA) was applied to all the variables measured over the three years of field trials (Supplementary Fig. S2), where PC1 and PC2 explained 74.8% of the variation found between years and sowing times. 2021 separated from the other two years along PC2, driven by polyunsaturated fatty acids (C20:3, C18:3, and PUFA) and by TGW. Seed yield showed an almost diametrically opposed relationship with TGW, which contributed to the separation of 2022 and 2023 from 2021. The PCA plot (Supplementary Fig. S2) datapoints were labelled with the sowing times S1-S3, where S1 clustered apart from S2 and S3 within each year along PC1 (52.7%). This separation in PC1 was mainly due to the fatty acids in the seed oil (FAMES), except for the PUFA index. Seed oil content aligned with the total amount of measured fatty acids (FA), clustering apart from seed protein content. The observed year separation within the PCA prompted subsequent analysis of measured parameters to be year specific. Following this, linear mixed models were applied to account for the year variance.

Table 2
Analysis of variance (ANOVA) for the measured variables for each year of field trials (2021–2023). Sowing time (S1, S2, S3), sowing (RS, BS) and harvest type (CSH, MH) were tested (":", interactions; d.f., degrees of freedom). Significance: '***' < 0.001; '**' < 0.01; '*' 0.05; ns, non-significant.

		2021				2022				2023			
Variable	Source of variation	d.f.	F-value	P-value		d.f.	F-value	P-value		d.f.	F-value	P-value	
Seed Yield (kg ha^{-1})	Sow Time	2	322.726	< .001	***	1	96.408	< .001	***	2	58.932	< .001	***
	Sow Type	1	10.226	0.003	**	1	6.917	0.015	*	1	3.102	0.087	ns
	Harvest Type	1	0.201	0.657	ns	1	0.458	0.505	ns	1	48.530	< .001	***
	Sow Time: Sow Type	2	17.965	< .001	***	1	7.547	0.011	*	2	2.049	0.144	ns
	Sow Time: Harvest Type	2	0.290	0.750	ns	1	0.068	0.796	ns	2	0.139	0.871	ns
	Sow Type: Harvest Type	1	0.127	0.724	ns	1	0.048	0.828	ns	1	0.456	0.504	ns
	Sow Time: Sow Type: Harvest Type	2	0.707	0.500	ns	1	0.105	0.749	ns	2	0.460	0.635	ns
Thousand Grain Weight (g)	Sow Time	2	404.568	< .001	***	1	351.300	< .001	***	2	94.362	< .001	***
	Sow Type	1	0.417	0.522	ns	1	0.214	0.648	ns	1	0.624	0.435	ns
	Harvest Type	1	13.116	< .001	***	1	12.642	0.002	**	1	22.160	< .001	***
	Sow Time: Sow Type	2	13.657	< .001	***	1	19.722	< .001	***	2	0.008	0.992	ns
	Sow Time: Harvest Type	2	3.762	0.033	*	1	30.770	< .001	***	2	5.493	0.008	**
	Sow Type: Harvest Type	1	2.077	0.158	ns	1	0.763	0.391	ns	1	0.192	0.664	ns
	Sow Time: Sow Type: Harvest Type	2	0.166	0.848	ns	1	0.451	0.508	ns	2	0.273	0.763	ns
Seed Oil Content (%)	Sow Time	2	198.243	< .001	***	1	367.371	< .001	***	2	16.59	< .001	***
	Sow Type	1	3.775	0.060	ns	1	3.940	0.059	ns	1	0.56	0.459	ns
	Harvest Type	1	1.002	0.324	ns	1	1.153	0.294	ns	1	17.94	< .001	***
	Sow Time: Sow Type	2	2.667	0.083	ns	1	6.279	0.019	*	2	2.23	0.122	ns
	Sow Time: Harvest Type	2	0.679	0.513	ns	1	1.450	0.240	ns	2	20.60	< .001	***
	Sow Type: Harvest Type	1	3.189	0.083	ns	1	0.306	0.585	ns	1	2.93	0.096	ns
	Sow Time: Sow Type: Harvest Type	2	7.129	0.002	**	1	0.001	0.974	ns	2	0.45	0.644	ns
Seed Protein Content (%)	Sow Time	2	150.240	< .001	***	1	1145.351	< .001	***	2	314.55	< .001	***
	Sow Type	1	1.170	0.287	ns	1	6.064	0.021	*	1	0.53	0.473	ns
	Harvest Type	1	0.168	0.684	ns	1	9.584	0.005	**	1	4.15	0.049	*
	Sow Time: Sow Type	2	2.060	0.142	ns	1	13.906	0.001	**	2	0.42	0.662	ns
	Sow Time: Harvest Type	2	0.110	0.896	ns	1	6.416	0.018	*	2	4.53	0.018	*
	Sow Type: Harvest Type	1	1.395	0.245	ns	1	0.970	0.334	ns	1	0.28	0.599	ns
	Sow Time: Sow Type: Harvest Type	2	3.864	0.030	*	1	0.000	1.000	ns	2	0.46	0.635	ns
Oleic Acid (mg/g)	Sow Time	2	186.954	< .001	***	1	26.428	< .001	***	2	81.153	< .001	***
	Sow Type	1	31.252	< .001	***	1	23.340	< .001	***	1	1.013	0.321	ns
	Harvest Type	1	0.025	0.876	ns	1	2.781	0.108	ns	1	0.117	0.734	ns
	Sow Time: Sow Type	2	6.653	0.003	**	1	12.090	0.002	**	2	4.190	0.024	*
	Sow Time: Harvest Type	2	13.204	< .001	***	1	0.291	0.594	ns	2	2.760	0.078	ns
	Sow Type: Harvest Type	1	5.587	0.024	*	1	0.153	0.699	ns	1	6.526	0.015	*
	Sow Time: Sow Type: Harvest Type	2	0.951	0.396	ns	1	5.116	0.033	*	2	0.751	0.480	ns
Linolenic Acid (mg/g)	Sow Time	2	24.283	< .001	***	1	3.916	0.059	ns	2	16.574	< .001	***
	Sow Type	1	5.942	0.020	*	1	18.037	< .001	***	1	0.538	0.468	ns
	Harvest Type	1	0.331	0.569	ns	1	0.485	0.493	ns	1	1.407	0.244	ns
	Sow Time: Sow Type	2	7.807	0.002	**	1	8.674	0.007	**	2	4.384	0.020	*
	Sow Time: Harvest Type	2	15.678	< .001	***	1	0.461	0.504	ns	2	0.418	0.662	ns
	Sow Type: Harvest Type	1	18.166	< .001	***	1	0.845	0.367	ns	1	11.060	0.002	**
	Sow Time: Sow Type: Harvest Type	2	4.735	0.015	*	1	1.734	0.200	ns	2	2.792	0.075	ns
Relative PUFA Content	Sow Time	2	195.040	< .001	***	1	12.385	0.002	**	2	228.137	< .001	***
	Sow Type	1	15.150	< .001	***	1	14.092	0.001	**	1	5.679	0.023	*
	Harvest Type	1	0.125	0.726	ns	1	5.505	0.028	*	1	0.680	0.415	ns
	Sow Time: Sow Type	2	5.474	0.008	**	1	7.927	0.010	*	2	2.569	0.091	ns
	Sow Time: Harvest Type	2	7.638	0.002	**	1	0.220	0.643	ns	2	2.246	0.121	ns
	Sow Type: Harvest Type	1	0.125	0.726	ns	1	0.055	0.816	ns	1	2.615	0.115	ns
	Sow Time: Sow Type: Harvest Type	2	2.319	0.113	ns	1	6.661	0.016	*	2	0.124	0.884	ns
Total FA Content (mg/g)	Sow Time	2	108.009	< .001	***	1	8.348	0.008	**	2	11.662	< .001	***
	Sow Type	1	13.163	< .001	***	1	21.680	< .001	***	1	0.737	0.397	ns
	Harvest Type	1	0.226	0.637	ns	1	0.969	0.335	ns	1	1.193	0.282	ns
	Sow Time: Sow Type	2	4.983	0.012	*	1	9.579	0.005	**	2	4.415	0.020	*
	Sow Time: Harvest Type	2	20.374	< .001	***	1	0.671	0.421	ns	2	0.480	0.623	ns
	Sow Type: Harvest Type	1	14.573	< .001	***	1	0.648	0.429	ns	1	10.504	0.003	**
	Sow Time: Sow Type: Harvest Type	2	2.943	0.066	ns	1	2.744	0.111	ns	2	1.931	0.161	ns

3.3. *Sowing time was the main factor affecting seed yield and quality within each year*

Seed yield showed high variability according to trial year and agronomic practices, ranging from 191 kg ha^{-1} for S2-RS-MH in 2021–1158 kg ha^{-1} for S2-RS-MH in 2023 (Supplementary Table S1). Sowing time and type, and their interaction, had a significant impact on seed yield in 2021 and 2022 (Table 2). Contrasting responses were observed in the data (Table 2) e. g., S1 showed the highest yield in 2021, but the lowest in 2022. However, in both years RS consistently produced

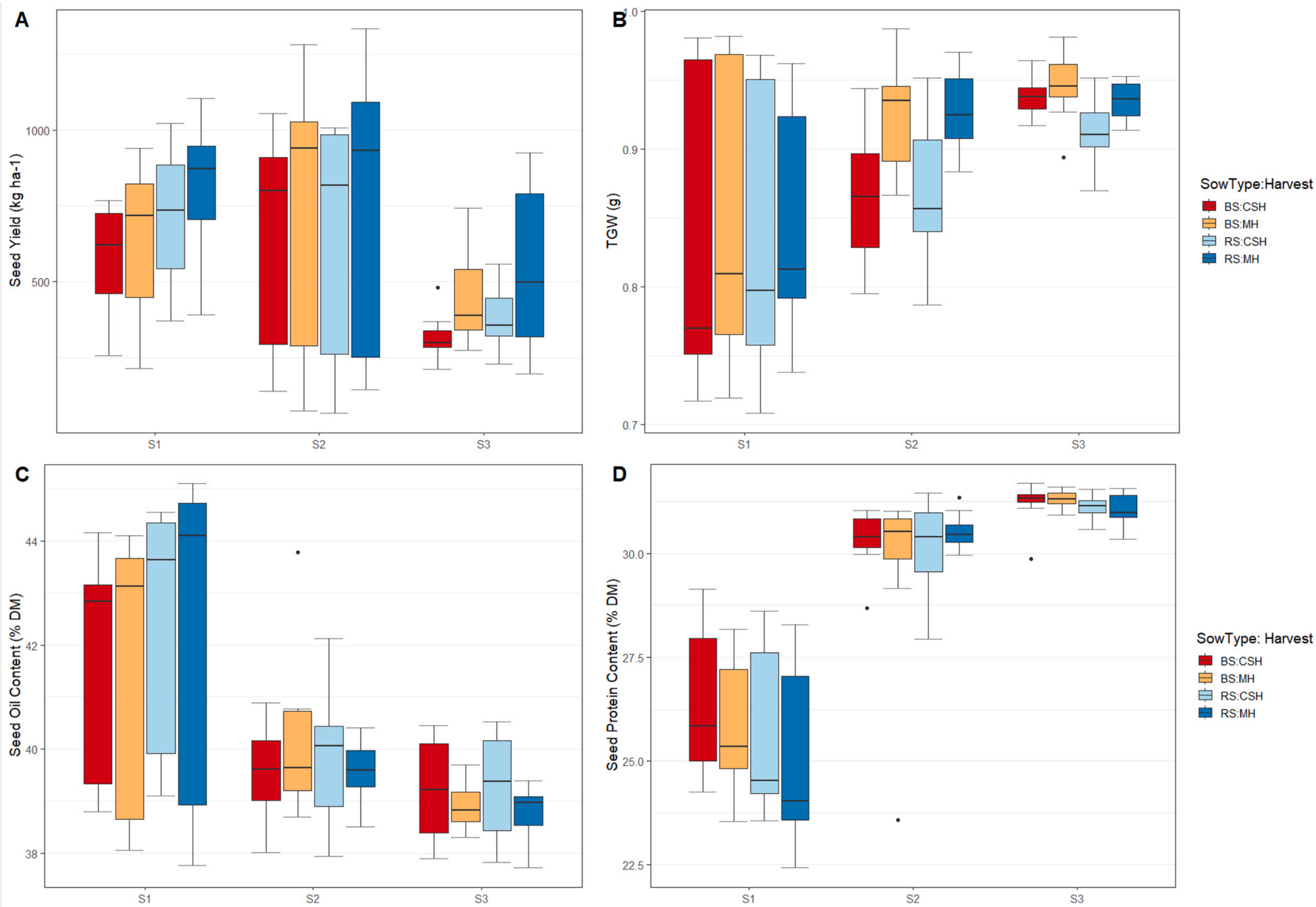

Fig. 3. Yield parameters measured over the three years of field trials shown by sowing time (S1, S2, S3). (A) seed yield (kg ha^{-1}); (B) thousand grain weight (TGW, g); seed oil (C) and protein (D) content (% dry matter, DM). Different treatment combinations of sowing type (row, RS; broadcast, BS) and harvest type (cut and swathing, CSH; mature, MH) are shown in color gradient coded on the right. The box represents the interquartile range (IQR), horizontal lines mark the median, whiskers extend to 1.5 × the IQR, dots indicate individual outliers, N = 12. Mean ± standard error for each year and treatment combinations can be found in Supplementary Table S1.

30–50% higher yields than BS (Fig. 3A). Noteworthy in 2023, harvest type had a significant impact on seed yield, alongside sowing time (Fig. 3A). In this growing season harvesting the mature plants generated higher yields in all sowings, with the highest overall seed yield achieved in the early summer sowing of 2023 (S2-RS-MH 1158 kg ha^{-1}). Contrary to seed yield, TGW was more stable in all three years with significant effect of sowing time, harvest type, and their interaction (Fig. 3B, Table 2). The combination of summer sowings (S2 or S3) in combination with MH produced the highest TGW for 2021 (S3-BS-MH 0.961 g) and 2023 (S2-BS-MH 0.934 g; Supplementary Table S1). However, in 2022 the hot and dry weather experienced in the summer seemed to invert this tendency (considering the only data for S3-RS-CSH 0.926 g compared to 0.975 g for S1-BS-CSH).

The seed oil content under the tested conditions varied from an average of 38% DM up to 45% DM (Fig. 3C), while protein content varied from an average of 23% DM up to 32% DM (Fig. 3D; Supplementary Table S1). As with seed yield and TGW, sowing time had a significant impact in seed oil and protein content within each of the three years of trials (Table 2). S1 favoured the accumulation of oil in the first two years of trials, while in 2023 the latter summer sowing (S3) seemed to produce higher oil accumulation. In contrast, S1 produced the lowest seed protein content in all three years, with the summer sowing (S3) producing 30% or more of protein in the seed (Fig. 3D, Supplementary Table S1). In the last two years of trials (2022 and 2023), the type of harvest, alongside sowing time and their interaction, was significant for seed protein accumulation with CSH in S1 yielding higher content (Fig. 3D, Table 2).

Seed total FA content ranged from 25% to 43% seed weight (from 264 mg/g to 427 mg/g of seed) with a significant effect of sowing time, type and their interaction in all three years of trials (except in 2023, sowing type was non-significant, Table 2). In most tested conditions, summer sowing times S2 and S3 led to lower FA content compared to spring S1 (Fig. 4A). The relative polyunsaturated fatty acid (PUFA) content was used as a measure of FA remodelling, reflecting the response to the different growing conditions through FA desaturation (Fig. 4B). Comparing years, 2021 resulted in distinctive PUFA content with a decrease of 17–23% from 1.32 to 1.02–1.09 in 2022 and 2023 (Supplementary Table S2). The two summer sowings (S2 and S3) showed the highest PUFA content in 2021 and 2023 (insufficient data in 2022) which was 10–13% higher than S1 (Supplementary Table S2). Fig. 4 (C-D) shows oleic (OA, C18:1) and linolenic acid (ALA, C18:3) content (mg/g) in the mature seed. OA however showed an opposite result to ALA and relative PUFA contents, with a higher content in S1 in all three years (Fig. 4C).

3.4. Sowing time determined yield and seed composition across growing seasons

Linear mixed models were applied to the measured variables to account for the year-to-year variation (Tables 3 and 4). The analysis confirmed that, independently of year, sowing time was the most significant treatment in all the measured variables. Seed yield and TGW

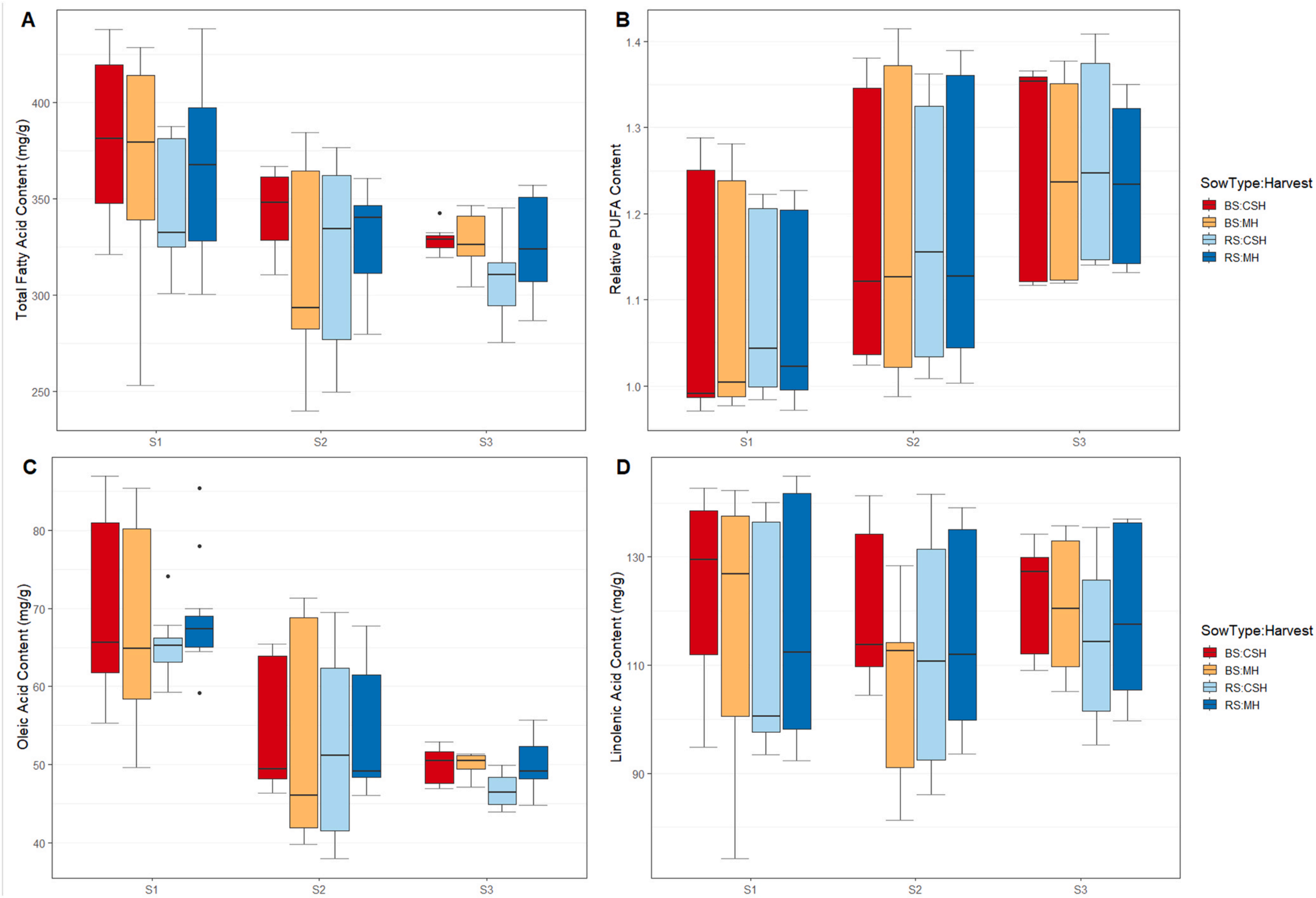

Fig. 4. Seed fatty acid (FA) composition measured over three years of field trials shown by sowing time (S1, S2, S3). (A) total fatty FA content (mg/g); (B) Relative polyunsaturated FA (PUFA) content; (C) oleic acid (mg/g); (D) linolenic acid (mg/g). Treatment combinations of sowing type (row, RS; broadcast, BS) and harvest type (cut and swathing, CSH; mature, MH) are shown in color gradient coded on the right. The box represents the interquartile range (IQR), horizontal lines mark the median, and whiskers extend to 1.5 × the IQR, dots indicate individual outliers. Mean ± standard error for each year and treatment combinations can be found in Supplementary Tables S2, S3.

were also influenced by harvest type (Table 3). Seed yield was significantly lower in S3 when compared to S1 and S2, and MH independently increased yield (Table 4, Fig. 3A, Supplementary Fig. S3A). S3 significantly increased TGW independently of the type of harvest, while S2 only when combined with MH resulted in higher TGW comparable to S3 (Table 4, Fig. 3B, Supplementary Fig. S3B). Seed oil and protein content showed contrasting responses with S1 favouring oil content, while S2 and S3 favoured protein content, and the combination of S3 and BS showing a further increase (Tables 3–4, Fig. 3C-D, Supplementary Fig. S3C-D). OA, ALA, and total FA were significantly increased by S1 (ALA also in S3), independently of any other treatments (Table 4, Fig. 4A, C, D, Supplementary Fig. S4A, C, E). However, an interaction between sowing and harvest types were found for these three components (Table 3). OA showed to be increased by RS and MH, whilst ALA and total FA by CSH and BS (Table 4, Supplementary Fig. S4B, D, F). PUFA was only significantly affected by sowing time, with S2 and S3 increasing PUFA content reflecting FA remodelling associated with summer growing conditions (Table 4, Fig. 4B, Supplementary Fig. S4G).

4. Discussion

Summer double cropping systems could be more prone to face environmental challenges that impact agronomic performance with low and variable yields as demonstrated in our study. The high variability of yield due to environmental constraints has previously been reported in other studies in Europe (Krzyianiak et al., 2019; Kurasiak-Popowska et al., 2018; Zanetti et al., 2017) and Northern America (Gesch, 2014; Gugel and Falk, 2006). Camelina is nonetheless well positioned to be used across multiple agribusiness sectors, including the more recent expansion into biofuels with potential yields of 1.5 t ha^{-1} demonstrating its economic value as a summer double crop in France (Allard, 2024). In an earlier study (Leclère et al., 2018), the potential and limitations of growing camelina as a second crop in France were evaluated by using original on-farm participatory design research. Farmers noted that emergence was highly determined by sowing method and depth, with deep or broadcast sowing leading to heterogeneous emergence times or rates, respectively. The study also identified late maturity as an important issue for camelina summer intermediate cropping that could be managed with an earlier sowing date, and by using cutting and swathing before harvest to accelerate seed maturity. The three-year study of camelina grown in open field presented here showed that sowing time had the greatest impact on yield and TGW. The last sowing date (S3) was clearly associated with the lowest yield and the largest seeds (Fig. 5) meaning that a difference of 2–3 weeks for sowing time has a large effect. Indeed, S3 was often associated with the most unfavorable conditions with dry and hot conditions at sowing and flowering stages and cool and humid conditions for seed maturation. Changes in temperature, relative humidity and precipitation, both in terms of trends and distribution patterns, were more pronounced at the trial site in spring and summer, with a globally higher temperature (in particular for summer) and lower relative humidity (Ringard et al., 2019). Therefore, the observed ranges for agronomic data in the study (e.g., seed yield

Table 3
Analysis of variance (ANOVA) for the Mixed Effect Model applied to the measured variables using year as a random effect, and sowing time, sowing and harvest types as fixed effects. *NumDF* is the numerator degrees of freedom, derived from the number of parameters of each tested effect. *DenDF* is the denominator degrees of freedom used to approximate the error term in the F-test, derived from the number of observations. *F value* is the ratio of variance explained by the fixed effect to the residual variance, and *Pr(>F)* is the likelihood of significance. Significance: '***' < 0.001; '**' < 0.01; '*' 0.05; '.' 0.05–0.1.

Variable	Fixed Effects	NumDF	DenDF	F value	Pr(>F)	
Seed Yield (kg ha^{-1})	Sow Time	2	120.85	13.31	< 0.0001	***
	Sow Type	1	120.05	2.99	0.086	.
	Harvest Type	1	120.05	6.69	0.011	*
TGW (g)	Sow Time	2	120.75	13.95	< 0.0001	***
	Harvest Type	1	119.97	7.87	0.006	**
	Sow Time: Harvest Type	2	119.97	2.45	0.091	.
Seed Oil Content (%)	Sow Time	2	123.41	47.98	< 0.0001	***
Seed Protein Content (%)	Sow Time	2	120.73	268.19	< 0.0001	***
	Sow Type	1	120.04	1.62	0.205	
	Sow Time: Sow Type	2	120.04	2.70	0.072	.
Oleic Acid (mg/g)	Sow Time	2	118.18	89.18	< 0.0001	***
	Sow Type	1	117.99	1.56	0.214	
	Harvest Type	1	118.00	0.85	0.358	
	Sow Type: Harvest Type	1	118.00	3.86	0.052	.
Linolenic Acid (mg/g)	Sow Time	2	118.10	4.79	0.010	**
	Sow Type	1	118.00	3.14	0.079	.
	Harvest Type	1	118.01	0.20	0.654	
	Sow Type: Harvest Type	1	118.01	9.90	0.002	**
Relative PUFA Content	Sow Time	2	121.02	123.96	< 2.20E−16	***
Total FA Content (mg/g)	Sow Time	2	118.25	25.4923	6.24E−10	***
	Sow Type	1	118	3.8816	0.051	.
	Harvest Type	1	118.01	0.0509	0.822	
	Sow Type: Harvest Type	1	118.01	8.5012	0.004	**

190–1157 kg ha^{-1}; oil 38–45% DM; protein 23–32% DM; and FA composition changes) represent site- and season-specific outputs, rather than generalised camelina performance benchmarks. Temperature is clearly an important parameter, with higher yield observed in cooler years (Gesch, 2014; Gugel and Falk, 2006). The conditions encountered during the summer of 2022 (temperature exceeding 35°C, rainfall less than 10 mm per month), impacted both spring as well as summer sowing conditions but for different reasons. High temperature observed in June and July 2022 could impact flowering and seed set for spring sowing and emergence for summer sowing. Delayed emergence compromised the harvest as previously noted by other studies (Kurasiak-Popowska et al., 2018; Zanetti et al., 2017). Contrary to seed yield and TGW, protein and oil content (including total fatty acid content) showed consistent sowing time effect for the three years investigated with higher oil content for spring sowing and higher protein content for summer sowing. This could be due to cooler conditions for spring sowing as observed previously (Gesch, 2014) while warmer and wetter growing season resulted in lower oil content. Seed oil content was described to be affected by environmental conditions (Krzyianiak et al., 2019; Vollmann et al., 2007). Higher temperature during seed filling combined with longer seed maturing period could explain the higher oil content for spring sowing. As expected, the protein content showed the opposite trend with higher accumulation for summer sowing. Sowing time also impacted seed oil quality by modifying its fatty acid profile with higher content of OA for spring sowing and conversely higher amount of ALA for summer sowing. The opposite trend between both fatty acids is consistent with the fact that OA is a precursor of ALA synthesis. It was previously noted that camelina genotypes were able to accumulate more C18:3 when grown in regions characterized by low temperatures during seed filling compared to warmer regions (Zanetti et al., 2017). Conversely, high temperature decreased C18:3 content in oil of large collection of genotypes capturing camelina diversity which could be associated with the effect of polyunsaturated fatty acids on membrane fluidity (Silvestre et al., 2026; Murakami et al., 2000). Relative PUFA content reported here is in accordance with other field trials reported for France (Silvestre et al., 2026). In conclusion, sowing time condition could not completely mitigate the high temperature effect on yield but had a significant impact on seed quality.

Contrary to sowing time, sowing type did not have a significant effect on yield, seed weight or seed composition except for the combination of row seeding with mature harvest that increased oleic acid content (Fig. 5). The higher relative density of plants in RS compared to BS could impact seed set and fatty acid metabolism that would also be enhanced by longer seed maturation in the case of MH. Sowing type did also show an effect on PUFA level but it varied according to the trial years most probably correlated with temperature (Zanetti et al., 2017). French summer-intermediate cropping practices for camelina recomends direct sowing or at shallow depth to preserve residual soil moisture. Our study suggest that shallow depth sowing mitigates better summer cropping risks since it would allow better access to moisture availability at emergence, improve emergence and reduce risk of delayed harvest.

Finally, harvest type has an effect on seed yield with higher yield observed in MH compared with CSH. It must be noted that harvest was manual after cutting and swathing which could have reduced the expected seed loss of this practice. Mature harvest enhanced TGW in several conditions (2021 S2 and S3; 2022 S2; 2023 S1), most probably by allowing more time for seed filling. However, MH would only have an impact when the seed maturation conditions are more favourable usually in August and September. When the culture cycle is extended or delayed (late sowing, delayed emergence), MH could have no positive effect or even not been possible and CSH could be a valuable alternative in these conditions given physiological maturity has been reached before cutting.

5. Conclusion

Altogether, this work demonstrated that summer cropping is a viable alternative in northern France. In the conditions tested with minimal input (no irrigation or pesticides and limited fertilization), intermediate cropping with summer sowing is still competitive compared with classical spring sowing. Out of the different modalities tested, sowing time had the greatest impact on yield and oil profile. The most advantageous time of sowing would be from mid to end of June. Row sowing would be preferentially selected since it could minimize the impact of low soil moisture. Cutting and Swathing is a technically challenging process at the farm scale but could be of use as mitigation, in the case of

Table 4
Post-hoc analysis of the Estimated Marginal means pairwise contrasts. Only the significant contrasts are shown (i.e., not between S1-S2). Est is the estimate difference between the pairwise contrast, SE is the standard error of this estimate. 95% CI is the confidence interval of the Estimate. If the 95% CI is either positive or negative, there is statistical evidence to say they are different, if they overlap 0 (i.e., Sow Type contrast has 95% CI of −164–11) then the p value will be > 0.05. Significance: '***' < 0.001; '**' < 0.01; '*' 0.05; '.' 0.05–0.1.

Variable	Fixed Effects	Contrast	Est	SE	95% CI	P-value	
Seed Yield (kg ha^{-1})	Sow Time	S1 – S3	+262.8	60.1	[120.0, 405.4]	0.0001	***
		S2 – S3	+289.2	59.8	[147, 431.0]	< 0.0001	***
	Sow Type	BS - RS	−76.4	44.2	[−164, 11]	0.086	.
	Harvest Type	CSH - MH	−114	44.2	[−202, −26.8]	0.0109	*
TGW (g)	Harvest Type CSH	S1 – S3	−0.117	0.019	[−0.162, −0.074]	< 0.0001	***
		S2 – S3	−0.081	0.019	[−0.127, −0.035]	0.0002	***
	Harvest Type MH	S1 – S2	−0.084	0.017	[−0.124, −0.045]	< 0.0001	***
		S1 – S3	−0.120	0.019	[−0.166, −0.075]	< 0.0001	***
	Sow Time S2	CSH – MH	−0.060	0.017	[−0.093, −0.027]	0.0005	***
Seed Oil Content (%)	Sow Time	S1 – S2	+2.35	0.28	[1.70, 2.99]	< 0.0001	***
		S1 – S3	+2.57	0.32	[1.18, 3.33]	< 0.0001	***
Seed Protein Content (%)	Sow Time S1	BS – RS	0.854	0.334	[0.193, 1.515]	0.0117	*
	Sow Type BS	S1 – S2	−3.98	0.334	[−3.19, −11.92]	< 0.0001	***
		S1 – S3	−5.17	0.383	[−6.08, −4.26]	< 0.0001	***
		S2 – S3	−1.19	0.383	[−2.10, −0.28]	0.0067	**
	Sow Type RS	S1 – S2	−5.07	0.334	[−5.86, −4.28]	< 0.0001	***
		S1 – S3	−5.85	0.383	[−6.75, −4.94]	< 0.0001	***
Oleic Acid (mg/g)	Sow Time	S1 – S2	14.33	1.16	[11.58, 17.07]	< 0.0001	***
		S1 – S3	13.43	1.37	[10.18, 16.68]	< 0.0001	***
	Harvest Type CSH	BS - RS	3.23	1.45	[0.37, 6.10]	0.0272	*
Linolenic Acid (mg/g)	Sow Time	S1 – S2	4.66	1.75	[0.51, 8.81]	0.0236	*
		S2 – S3	−5.23	2.06	[−10.12, −0.35]	0.0326	*
	Harvest Type CSH	BS - RS	7.48	2.19	[3.15, 11.80]	0.0009	***
	Sow Type BS	CSH - MH	5.47	2.17	[1.17, 9.77]	0.0132	*
Relative PUFA index	Sow Time	S1 – S2	−0.092	0.0068	[−0.108, −0.076]	< 0.0001	***
		S1 – S3	−0.107	0.0081	[−0.126, −0.088]	< 0.0001	***
Total FA Content (mg/g)	Sow Time	S1 – S2	38.1	5.47	[25.2, 51.11]	< 0.0001	***
		S1 – S3	28.2	6.48	[12.9, 43.61]	0.0001	***
	Sow Type BS	CSH - MH	14.9	6.79	[1.49, 28.39]	0.0298	*
	Sow Type RS	CSH - MH	−12.8	6.66	[0.04, −1.92]	0.0571	.
	Harvest Type CSH	BS - RS	23.2	6.84	[9.69, 36.77]	0.0009	***

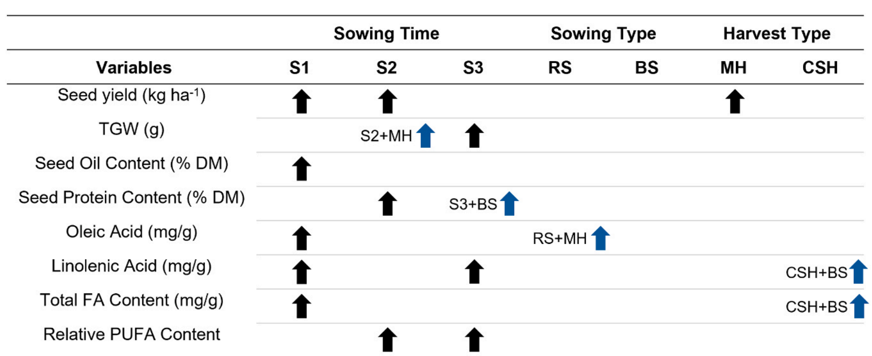

Fig. 5. Summary of the applied treatments with a significant impact on the measured traits. Positive impact marked with an arrow; black arrows show significance with no interaction, and blue arrows show significance with interaction between treatments. Values and statistical analysis in Tables 1–4, and Supplementary Tables S1-S3.

unfavorable conditions for seed maturation in September/October. The combination of row seeding and cutting and swathing was indeed the only modality able to rescue 2022 S3 harvest illustrating its potential use for any sowing date in case of adverse climatic conditions that summer intermediate cropping systems are more likely to observe in the future. An important issue in summer intermediate cropping is the ability to complete the growth cycle till full harvest. Since sowing and harvest could take place in sub-optimal conditions, appropriate management is necessary to mitigate the risk of reduced yield or even crop losses. Considering the short growing season, the crop cycle would have to be optimized by promoting efficient emergence (with irrigation if necessary) and precocious harvest if sub-optimal conditions occur. Future trials using new genotypes and locations, together with establishment metrics, will be needed to contextualise yield variability and management interactions over a wider range of environments. The development of early flowering varieties and testing of agronomic practices such as seed coating systems or relay cropping to promote early emergence under drought conditions, or the immediate sowing after the main food crop harvest would be important to better fit camelina into summer intermediate cropping conditions.

Author contributions

All measurements, sampling, and data acquisition were performed by ADC, FT, JDF. TID ran the linear mixed model analysis. SS, JDF wrote the manuscript with edits from all authors.

CRediT authorship contribution statement

Yuri Herreras Yambanis: Writing – review & editing. **Richard P. Haslam:** Writing – review & editing, Funding acquisition, Conceptualization. **Jean-Denis Faure:** Writing – original draft, Project administration, Methodology, Funding acquisition, Conceptualization. **David Thomas:** Formal analysis. **Frédérique Tellier:** Investigation. **Javier Prieto:** Writing – review & editing. **Paloma Leon:** Writing – review & editing. **Susana Silvestre:** Writing – original draft, Visualization, Formal analysis. **Anais Da Costa:** Methodology, Investigation.

Funding

This study (all authors) received funding support from the European Union's Horizon 2020 Research and Innovation Action programme under UNTWIST project grant agreement number 862524 (doi 10.3030/862524). RPH and SS were further supported by the Biotechnology and Biology Sciences Research Council (BBSRC, UK) funded Institute Programme Grant (Green Engineering, BB/X010988/1; BBS/E/RH/230002B).

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Jean-Denis Faure reports financial support was provided by the European Union Horizon 2020 Research and Innovation Action programme. Javier Prieto, Paloma Leon, Yuri Herreras Yambanis reports a relationship with Camelina Company España that includes: employment. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors thank Camelina company Espana for providing the seeds and NIRS analysis and **Jennifer Dillion from** the statistics Team at Rothamsted Research for the statistical support.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2026.110622.

Data availability

Please find the data available at: https://www.camelina-hub.org/home.

References

Alberghini, B., Vicino, M., Zanetti, F., Silvestre, S., Haslam, R., Zegada-Lizarazu, W., Monti, A., 2025. Assessing different physiological, seed yield and quality responses of camelina lines to drought. Ind. Crops Prod. 234.

Alberghini, B., Zanetti, F., Corso, M., Boutet, S., Lepiniec, L., Vecchi, A., Monti, A., 2022. Camelina [*Camelina sativa* (L.) Crantz] seeds as a multi-purpose feedstock for bio-based applications. Ind. Crops Prod. 182.

Allard, L.M., 2024. Guide de culture Cameline - conventionnel et biologique. Terres Inovia.

Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting Linear Mixed-Effects Models Using lme4. J. Stat. Softw. 67, 1–48.

Cahoon, E.B., 2009. Camelina sativa, A Potential Oilseed Platform for the Production of High-value Industrial Oils. Vitr. Cell. & Dev. Biol. -Anim. 45, S22. –S22.

Chapman, M., Jung, M., Leclere, D., Boettiger, C., Augustynczik, A.L.D., Gusti, M., Ringwald, L., Visconti, P., 2025. Meeting European Union biodiversity targets under future land-use demands. Nat. Ecol. & Evol. 9.

Chi, B.J., Liu, J., Dai, J.L., Li, Z.H., Zhang, D.M., Xu, S.Z., Nie, J.J., Wan, S.M., Li, C.D., Dong, H.Z., 2023. Alternate intercropping of cotton and peanut increases productivity by increasing canopy photosynthesis and nutrient uptake under the influence of rhizobacteria. Field Crops Res. 302.

Codina-Pascual, N., Cantero-Martínez, C., Romero-Fabregat, M.P., De La Fuente, G., Royo-Esnal, A., 2025. Growth conditions but not the variety, affect the yield, seed oil and meal protein of camelina under Mediterranean conditions. Eur. J. Agron. 162.

Gesch, R.W., 2014. Influence of genotype and sowing date on camelina growth and yield in the north central US. Ind. Crops Prod. 54, 209–215.

Gesch, R.W., Cermak, S.C., 2011. Sowing date and tillage effects on fall-seeded camelina in the northern corn belt. Agron. J. 103, 980–987.

Gesch, R.W., Mohammed, Y.A., Walia, M.K., Hulke, B.S., Anderson, J., 2022. Double-cropping oilseed sunflower after winter camelina. Ind. Crops Prod. 181.

Groeneveld, J.H., Klein, A.M., 2014. Pollination of two oil-producing plant species: Camelina (*Camelina sativa* L. Crantz) and pennycress (*Thlaspi arvense* L. double-cropping in Germany. Glob. Change Biol. Bioenergy 6, 242–251.

Gugel, R.K., Falk, K.C., 2006. Agronomic and seed quality evaluation of Camelina sativa in western Canada. Can. J. Plant. Sci. 86, 1047–1058.

Hartig, F. 2024. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models(Version 0.4.7) [Computer software]. doi:10.32614/CRAN.package.DHARMa.

Haslam, R.P., Michaelson, L., Eastmond, P.J., Napier, J.A., 2025. Born of frustration: the emergence of *Camelina sativa* as a platform for lipid biotechnology. Plant. Physiol. 197.

Krzyianiak, M., Stolarski, M.J., Tworkowski, J., Puttick, D., Eynck, C., Zaluski, D., Kwiatkowski, J., 2019. Yield and seed composition of 10 spring camelina genotypes cultivated in the temperate climate of Central Europe. Ind. Crops Prod. 138.

Kurasiak-Popowska, D., Tomkowiak, A., Czlopinska, M., Bocianowski, J., Weigt, D., Nawracala, J., 2018. Analysis of yield and genetic similarity of Polish and Ukrainian *Camelina sativa* genotypes. Ind. Crops Prod. 123, 667–675.

Larsson, M., 2013. Cultivation and processing of *Linum usitatissimum* and *Camelina sativa* in southern Scandinavia during the Roman Iron Age. Veget Hist. Archaeobot.

Leclère, M., Loyce, C., Jeuffroy, M.H., 2018. Growing camelina as a second crop in France: A participatory design approach to produce actionable knowledge. Eur. J. Agron. 101, 78–89.

Lenth, R. 2024. _emmeans: Estimated Marginal Means, aka Least-Squares Means_. R package version 1.10.4, https://CRAN.R-project.org/package=emmeans.

Martinelli, T., Galasso, I., 2011. Phenological growth stages of Camelina sativa according to the extended BBCH scale. Ann. Appl. Biol. 158, 87–94.

Masella, P., Martinelli, T., Galasso, I., 2014. Agronomic evaluation and phenotypic plasticity of Camelina sativa growing in Lombardia, Italy. Crop. & Pasture Sci. 65, 453–460.

Murakami, Y., Tsuyama, M., Kobayashi, Y., Kodama, H., Iba, K., 2000. Trienoic fatty acids and plant tolerance of high temperature. Science 287 (5452), 476–479.

Pari, L., Cozzolino, L., Marsac, S., Hermet, L., Bergonzoli, S., 2024. Effect of Swathing or Direct Combining on Yield, Seed Losses and Costs of Camelina. Agron. -Basel 14.

Piergiovanni, A.R., Alberghini, B., Zanetti, F., Ponzoni, E., Brambilla, I.M., Galasso, I., 2025. The effect of year and variety on the nutritional value of *Camelina sativa* meal. Eur. Food Res. Technol. 251, 841–849.

Pitchers, J., Ferrand, N., Pull, M., Minette, S., Abella, M., Debaeke, P., 2023. Opportunities and risks of double cropping in southwestern France with a focus on soybean and sunflower crops☆. Ocl-Oilseeds Fats Crops Lipids 30.

Ringard, J., Chiriaco, M., Bastin, S., Habets, F., 2019. Recent trends in climate variability at the local scale using 40 years of observations: the case of the Paris region of France. Atmos. Chem. Phys. 19, 13129–13155.

Silvestre, S., Prigent, S., Pétriacq, P., Hassall, K.L., Le Boulch, M., Da Costa, A., Tellier, F., Alberghini, B., Aldorino, E., Hallab, A., Großkinsky, D., Cassan, C., Monti, A., Prieto, J., Leon, P., Yambanis, Y.H., Gibon, Y., Usadel, B., Faure, J.D., Zanetti, F., Jonak, C., Haslam, R.P., 2026. Assessment of phenotypic trait plasticity in the oilseed Camelina sativa using integrated early-stage abiotic stress and field studies. Plant. Physiol.

Tocher, D.R., Sprague, M., Han, L.H., Sayanova, O., Norambuena, F., Napier, J.A., Betancor, M.B., 2024. Inclusion of oil from transgenic *Camelina sativa* in feed effectively supplies EPA and DHA to Atlantic salmon (*Salmo salar*) grown to market size in seawater pens. Food Chem. 456.

Toker, P., Canci, H., Turhan, I., Isci, A., Scherzinger, M., Kordrostami, M., Yol, E., 2024. The advantages of intercropping to improve productivity in food and forage production - a review. Plant. Prod. Sci. 27, 155–169.

Usher, S., Han, L.H., Haslam, R.P., Michaelson, L.V., Sturtevant, D., Aziz, M., Chapman, K.D., Sayanova, O., Napier, J.A., 2017. Tailoring seed oil composition in the real world: optimising omega-3 long chain polyunsaturated fatty acid accumulation in transgenic Camelina sativa. Sci. Rep. 7.

Vollmann, J., Moritz, T., Kargl, C., Baumgartner, S., Wagentristl, H., 2007. Agronomic evaluation of camelina genotypes selected for seed quality characteristics. Ind. Crops Prod. 26, 270–277.

Wang, P.D., Xiong, X.J., Zhang, X.B., Wu, G., Liu, F., 2022. A Review of Erucic Acid Production in Brassicaceae Oilseeds: Progress and Prospects for the Genetic Engineering of High and Low-Erucic Acid Rapeseeds (*Brassica napus*). Front. Plant. Sci. 13.

Wittenberg, A., Anderson, J.V., Berti, M.T., 2019. Winter and summer annual biotypes of camelina have different morphology and seed characteristics. Ind. Crops Prod. 135, 230–237.

Yan, E., Munier-Jolain, N., Martin, P., Carozzi, M., 2024. Intercropping on French farms: Reducing pesticide and N fertiliser use while maintaining gross margins. Eur. J. Agron. 152.

Zanetti, F., Alberghini, B., Jeromela, A.M., Grahovac, N., Rajkovic, D., Kiprovski, B., Monti, A., 2021. Camelina, an ancient oilseed crop actively contributing to the rural renaissance in Europe. A review. Agron. Sustain. Dev. 41.

Zanetti, F., Eynck, C., Christou, M., Krzyzaniak, M., Righini, D., Alexopoulou, E., Stolarski, M.J., Van Loo, E.N., Puttick, D., Monti, A., 2017. Agronomic performance

and seed quality attributes of Camelina (Camelina sativa L. crantz) in multi-environment trials across Europe and Canada. Ind. Crops Prod. 107, 602–608.
Zubr, J., 1997. Oil-seed crop: *Camelina sativa*. Ind. Crops Prod. 6, 113–119.
Zubr, J., 2003. Dietary fatty acids and amino acids of *Camelina sativa* seed. J. Food Qual. 26, 451–462.

Glossary

ALA: α-Linolenic Acid
BS: Broadcast Sowing
CSH: Cutting and Swathing Harvest
CCE: Camelina Company España
EU: European Union
FA: Fatty Acid
FAMES: Fatty Acid Methyl Esters
GDD: Growing Degree Days
INRAE: National Research Institute for Agriculture, Food and Environment, France
MH: Mature Harvest
OA: Oleic Acid
PCA: Principal Component Analysis
PUFA: Polyunsaturated Fatty Acids
RS: Row Sowing
S1: spring sowing
S2: Early summer sowing
S3: summer sowing
TGW: Thousand Grain Weight