Diagnosis of camelina seed yield and quality across an on-farm experimental network

Margot Leclère, Anne-Raphaëlle Lorent, Marie-Hélène Jeuffroy, Arnaud Butier, Christophe Chatain, Chantal Loyce

Diagnosis of camelina seed yield and quality across an on-farm experimental network

Margot Leclère[a] *, Anne-Raphaëlle Lorent[a], Marie-Hélène Jeuffroy[a], Arnaud Butier[a], Christophe Chatain[b], Chantal Loyce[a]

[a] Université Paris-Saclay, AgroParisTech, INRAE, UMR Agronomie, 78850, Thiverval-Grignon, France

[b]Adane, Association de développement agricole du Nord-Est, Rue Adrien-Lhomme, 60400, Noyon, France

* corresponding author: margot.leclere.inra@gmail.com

Bâtiment EGER, UMR Agronomie

Avenue Lucien Brétignières

78 850 Thiverval-Grignon

Abstract

Camelina [*Camelina sativa* (L.) Crantz] is an emerging oilseed crop combining both industrial and agronomic advantages. Camelina seed yield, oil and protein contents, and fatty-acid composition, vary across genotypes, environments, and agricultural practices. However, no studies have been conducted to identify and rank major limiting factors explaining yield and quality variations under on-farm conditions. Camelina performance was measured on 39 experimental strips corresponding to five camelina crop management routes (grown as an intercrop or sole crop), implemented in nine farmers' fields across northern France in 2017 and 2018. The ranking of candidate limiting factors, defined *a priori* from scientific literature, was carried out using a model mixing method based on the Akaike Information Criterion. Main limiting factors of camelina yield (ranging from 62 to 2585 kg ha^{-1}) were nitrogen crop

status at flowering stage and downy mildew. Camelina yield was indeed positively correlated with the Nitrogen Nutrition Index at flowering stage (R^2=0.44, p= 0.007). Oil content varied from 36.6 to 46.5 % and was negatively correlated with protein content. Main indicators explaining oil content variations were grain filling duration and downy mildew. Both poly-unsaturated and linolenic acid contents were positively correlated to grain filling duration, and negatively correlated to temperature during grain filling period. Camelina nitrogen status at flowering stage was mainly explained by N uptake of the intercropped species (pea or barley), and the amount of available inorganic nitrogen in the soil between sowing and flowering. Downy mildew was influenced by both weather conditions and the amount of weed biomass. This study showed a large variability in camelina seed yield and quality under on-farm conditions. The identification of the major limiting factors made it possible to pinpoint ways of improving camelina performance namely choosing genotypes with high resistance to mildew, better managing nitrogen fertilization or delaying camelina sowing date. Finally we also identified major research topics to be addressed to support the adoption of this new crop by farmers as the elaboration of the critical nitrogen dilution curve.

Keywords: *Camelina sativa;* biorefinery; oil content; fatty-acids; nitrogen; downy mildew

1. Introduction

Camelina (*Camelina sativa* (L.) Crantz) is an oilseed crop increasingly studied due to its original seed composition and the diversity of its uses (Chaturvedi et al., 2018; Righini et al., 2016). Camelina is characterized by high contents of seed oil (between 30 and 40 %), poly-unsaturated fatty acids (PUFA, higher than 50%), and mono-unsaturated fatty acids (MUFA, around 30 %) (Belayneh et al., 2015). Main fatty acids (FAs) are linolenic (C18:3, 28-50.3%), linoleic (C 18:2, 16-22.4%), oleic (C18:1, 14.9-18.8%), and ecosenoic (C20:1, 11.6-17.5%) acids (Popa et al., 2017). As camelina seeds are also rich in protein, camelina seed meal contains up to 40 % crude protein, after oil extraction (Zubr, 2003a). Camelina has been widely investigated as feedstock for biofuels (biodiesel or renewable jet fuel) because of its oil properties (Campbell et al., 2013; Mohammad et al., 2018; Mohammed et al., 2017b; Neupane et al., 2018; Tabatabaie et al., 2018). However, there are several other uses reported for camelina oil, meal, or specific compounds, such as human food, feed, or chemical derivatives (Berti et al., 2016; Waraich et al., 2013). Therefore, camelina can be considered as a flex crop, i.e. a crop with multiple uses (food, feed, fuel, fibre, and industrial materials), which allows farmers to adapt themselves to market opportunities (Borras et al., 2016). For instance, camelina oil has been identified as a possible source of polyols and consequently, as an alternative to castor oil, widely used in commercial applications (Omonov et al., 2017). Moreover, camelina meal can either be used in fish diet (Yildiz et al., 2018) or as raw material for bio-adhesive production (Zhu et al., 2017).

Besides its wide range of potential uses, camelina has many agronomic advantages (Berti et al., 2016; Putnam et al., 1993; Vollmann et al., 1996). Camelina is a short lifecycle crop with low water and nutrient requirements, and has shown tolerance to some common pests and diseases of the Brassicaceae family (Hunsaker et al., 2011; Mohammed et al., 2017a; Séguin-Swartz et al., 2009; Soroka et al., 2017). Consequently, camelina has been grown successfully

68 in diverse environments across the world with reported seed yields ranging from 400 to 3300
69 kg ha^{-1} (Berti et al., 2016). Hence, camelina, as a crop suited to low-input managements and
70 marginal lands, and with multiple uses, is clearly a good candidate to address several current
71 environmental and production challenges of agriculture (Murphy, 2016; Sindelar et al., 2017;
72 Zanetti et al., 2013).
73 Camelina seed yield, oil and protein contents, and FAs composition have been shown to vary
74 across genotypes (Gesch, 2014) and environments, i.e. climatic and soil conditions (Vollmann
75 et al., 2007; Zubr, 2003a; Zubr and Matthäus, 2002). Other studies showed that all these
76 agronomic traits are affected by the interaction of genotype with environment (Obour et al.,
77 2017; Zanetti et al., 2017). Camelina performance is also affected by several agricultural
78 practices such as sowing date or rate (Berti et al., 2011; Gesch and Cermak, 2011; Urbaniak et
79 al., 2008), irrigation (Hunsaker et al., 2013), nitrogen and sulphur fertilisation (Jiang et al.,
80 2016, 2013; Wysocki et al., 2013), and harvest time (Walia et al., 2018). However, no studies
81 have been conducted to understand camelina performances variability in on-farm
82 experiments, which could provide useful information to improve management practices
83 (Meynard et al., 2001). Initially developed to understand the variations in crop yield on a
84 regional scale (Doré et al., 1997), the regional agronomic diagnosis has been enlarged to
85 include crop quality factors and to be applied to on-farm experimental network (Casagrande
86 et al., 2009; Dejoux et al., 2003; Doré et al., 2008). In practice, the agronomic diagnosis aims
87 to identify and rank major limiting factors of the crop performance and to understand the
88 impact of the agronomic practices on these limiting factors, thus making it possible to modify
89 them to improve performance (Loyce and Wery, 2006).
90 The objectives of this study were: (i) to describe the variability of camelina seed yield and
91 composition (oil, protein and FAs) across a multi-environment on-farm experimental network

92 in northern France, and (ii) to identify and rank the major causes of this variability, mobilising
93 the methodological framework of the agronomic diagnosis.

2. Materials and methods

2.1. The on-farm experimental network

The experimental network corresponded to five camelina crop management routes, tested in several farmers' fields in 2017 and 2018. Fields were located within an area of 1000 km^2 in northern France (Oise department), ranging from 49.4 to 49.7°N latitude, and 2.86 to 3.13°E longitude, and covered the three main soil types of the region (deep loamy, moderately deep sandy, and shallow calcareous soils, previously described in Leclère et al. (2019)). The area was characterized by an oceanic climate with mean annual temperature and cumulative rainfall respectively equal to 11 °C and 681 mm over the 1981-2010 period. To mimic on-farm conditions, we used an experimental design in strips without replicates, comprised of thirty-nine experimental strips of 2500 m^2 each and spread into 9 environments (Table 1).

The two crop management routes SD and DD corresponded to camelina in pure stand, sown at 4 and 8 kg ha^{-1} respectively. The three others corresponded to camelina (sown at 4 kg ha^{-1}) intercropped with spring pea (*Pisum sativum* L.) sown at a half of the advised rate for sole crop (CP), or with spring barley (*Hordeum vulgare* L.) sown at a half (CB_50), or at a quarter (CB_25) of the advised rate for sole crop (Table 1). The variety used for camelina was Calena. A pre-emergence herbicide (Novall®: 400 $g.l^{-1}$ metazachlor + 100 $g.l^{-1}$ quinmerac) was applied on the SD crop management route only. Based on the balance sheet method, which determines the N rate to be applied, by comparing soil nitrogen supply to the crop's nitrogen requirements during the growing season (Meynard et al., 1997), the experiments did not receive any N fertilisation; nor did they receive irrigation, fungicides, or insecticides, linked to camelina hardiness. The previous crop was winter wheat for all sites, except for Mortemer in 2017 for which previous crop was linseed. Trials were sown by the farmers on the 16th of March in 2017 and on the 23rd of March in 2018, using traditional seed drill (row spacing: 15 cm). For intercrops, a cross seedling was performed, with barley or pea rows

sown perpendicular to the direction in which camelina had been sown (sowing depth: 1cm for camelina, 2-3cm for barley and pea). For both years, trials were harvested on the 17th of July, date at which all the crops (camelina, pea and barley) had reached maturity

2.2. Data collection

Six plots of 0.5 m^2 were randomly sampled all along each strip at camelina flowering and maturity stages (respectively stages 65 and 85 on the BBCH scale; Martinelli and Galasso, 2011). At both dates, the aerial dry biomass (g m^{-2}) of each species (weeds, camelina, pea, and barley) was measured by weighing the samples after a period of 48h of drying at 80°C. At maturity stage, camelina, pea, and barley samples were threshed, and seeds were weighed to measure the yield of each species (pYield, kg ha^{-1}). Sub-samples of all grown species were sent to analysis to determine nitrogen concentration (%) in the whole plants at flowering and in seeds and straws separately at maturity.

Based on these measurements, we calculated the amount of soil-derived nitrogen absorbed by the crops grown in mixture with camelina (NDFS for Nitrogen Derived From Soil, KgN ha^{-1}) using the following equations:

(1) $NDFS_{barley} = aerial\ dry\ biomass\ (kg\ ha^{-1}) * nitrogen\ concentration\ (\%)$

(2) $NDFS_{pea} = [aerial\ dry\ biomass\ (kg\ ha^{-1}) * nitrogen\ concentration\ (\%)] - N_{fix}$

where N_{fix} is the amount of nitrogen resulting from the symbiotic N_2 fixation (KgN ha^{-1}) and estimated using the relation established by Naudin et al. (2011) based on different pea intercropping experiments ($R^2 = 0.86$):

$$N_{fix} = 0.0215 \times pea\ aerial\ dry\ biomass\ (kg\ ha^{-1}) - 0.6986$$

Camelina crude seed protein content (%) was calculated by multiplying nitrogen concentration in camelina seeds by 6.25 (ISO 16634-2:2016, https://www.iso.org). Sub-samples of camelina seeds were also used to measure oil content (%) and to determine the fatty acids (FA) profile, using solvent extraction method and gas chromatography (Puttick et al., 2009). Based on this analysis, the content of each group of FA (PUFA, MUFA and SFA respectively poly, mono-unsaturated FA, and saturated FA) was calculated (%). At maturity, on each strip, three sub-plots of 60 m^2 in which no plants had been previously collected, were mechanically harvested with an experimental combine harvester to measure, after manual separation of the grains of each species, using a sieve, the mechanical yield of camelina (mYield, kg ha^{-1}) corresponding to the yield that could be obtained under on-farm conditions. Eight soil cores (0 to 90 cm depth) were collected on each strip prior to sowing, on February, 22nd in 2017 and March, 5th in 2018. Each core was cut into three layers (0-30, 30-60 and 60-90 cm), and soil inorganic nitrogen (kgN ha^{-1}) was measured for each layer. The total soil inorganic nitrogen prior sowing (0-60cm) was obtained by summing the results of the two first layers. In addition, soil analyses were performed to determine particle size and chemical composition (pH, $CaCO_3$, available P and K, total nitrogen and carbon, and organic matter). Based on these measurements, the amount of inorganic nitrogen available for crops from sowing to camelina flowering (NSOIL, kgN ha^{-1}) was estimated as follows:

$$NSOIL = TotN + Mh + Mr + Mr_{Cc}$$

where $TotN$ is the total soil inorganic nitrogen measured prior sowing (0-60cm), Mh the amount of nitrogen derived from the mineralisation of humus (kgN ha^{-1}), Mr is the amount of nitrogen derived from the mineralisation of the previous crop residues, and Mr_{Cc} is the amount of nitrogen derived from the mineralisation of the cover crop residues, calculated using the COMIFER equations (COMIFER, 2013).

Finally, for each site, local daily weather data, i.e. minimal, maximal, and mean temperatures (Tmin, Tmax, and Tmean, °C), rainfall (RR, mm), and evapotranspiration (ETP, mm), were extracted from a database of Meteo France (https://donneespubliques.meteofrance.fr/). Soil characteristics and weather data for the 9 site-year combinations are summarised in Table 2.

2.3. Indicators for limiting factors

Based on scientific literature and field observations, candidate indicators explaining the variability of camelina performance were defined *a priori*. Yield was assumed to be impacted by nitrogen, water, downy mildew, and hail, whereas oil and protein contents were assumed to be affected by nitrogen, water, downy mildew, and grain filling duration, and PUFA and MUFA contents by nitrogen, water, grain filling duration, and high temperatures (Cappelli et al., 2019; Hergert et al., 2016; Jiang et al., 2013; Vollmann et al., 2001; Zubr and Matthäus, 2002).

2.3.1. Indicator for nitrogen crop status

The Nitrogen Nutrition Index (NNI) has been identified as a reference indicator of the crop nitrogen status (Lemaire and Meynard, 1997). It corresponds to the ratio between the measured nitrogen concentration and the critical nitrogen concentration, estimated with the crop biomass and the critical curve of the species considered (Sadras and Lemaire, 2014). NNI values over 1 indicate a non-limiting crop nitrogen status, while NNI values below 1 indicate that growth is limited by N supply. The lower the NNI value, the higher the nitrogen stress. As no critical nitrogen curve for camelina has been established yet, the NNI for camelina was calculated using the critical dilution curve of oilseed rape (Colnenne, 1998), which is a species close to camelina (Cappelli et al., 2019). NNI was calculated at flowering stage.

192

193 *2.3.2. Indicator for water stress*

194 The indicator for water stress (WS) was calculated from a dynamic water balance between the
195 sowing date and the harvest date. WS equals to 1 indicates that no water stress occurred
196 during the period considered. When WS is lower than 1, the lower the WS value, the higher
197 the water stress.

198 WS was estimated over the entire growing period for yield, and over the grain filling period
199 for seed quality. WS corresponded to the average between sowing date (or flowering stage)
200 and harvest date of a daily stress coefficient (Ks (d), dimensionless) calculated as follows
201 (Itier, 1996):

202 $$Ks(d) = 1 \; if \; SWC(d-1) \geq 2/3 \; SWC_{max}$$

203 $$Ks(d) = SWC(d-1)/SWC_{max} \text{ otherwise}$$

204 where SWC_{max} is the maximal soil water content (mm), i.e. the soil water content at field
205 capacity, estimated for each location with a pedotransfer function (Bruand et al. 2004),
206 and $SWC(d-1)$ is the soil water content on day *d-1* (mm).

207

208 The daily soil water content (SWC, mm) was calculated using the following equation:

209 $$SWC(d) = SWC(d-1) + R(d) - ETR(d)$$

210 where $SWC\ (d)$ is the soil water content (mm) on the day d, $R(d)$ is the amount of
211 rainfall on day *d* (mm), and $ETR(d)$ is the actual evapotranspiration on day *d* (mm) and
212 calculated by:

213 $$ETR(d) = Ks(d) \; x \, Kc(d) \; x \, ETP\ (d)$$

214 where $ETP\ (d)$ is the potential evapotranspiration on day *d* (mm) obtained with
215 weather data, and $Kc(d)$ is a cultural crop coefficient (dimensionless) depending on
216 crop development. For the intercrops, $Kc(d)$ was estimated by weighting the cultural

crop coefficient of each species with its relative importance in the total biomass of the mixture calculated at flowering stage and harvest date (Table 3). Kc values for pea and barley were those proposed by the FAO (Allen et al. 1998), and were extracted from George et al. (2018) for camelina (Table 3).

At sowing, the soil water content was assumed to be equal to the maximal soil water content, as no water deficit was noticed during the winter.

2.3.3. Indicators for yield loss due to mildew and hail

In 2018, symptoms of downy mildew (caused by *Peronospora camelinae*) were observed on camelina (Figure 1a). The incidence and severity of this disease at harvest (MILDEW, %) were assessed by calculating the ratio between the number of diseased pods and the total number of pods on ten plants for each replicate, and then by averaging them for each strip.

On the 12th of July 2017, a hailstorm occurred on the three sites located in the south of the area. This climatic incident caused an opening of pods (Figure 1b). Similarly to downy mildew, an indicator to assess the pod opening due to hailstorm (HAIL, %) was thus used: the ratio between the opened pods and the total number of pods on ten plants for each replicate was calculated, and then averaged for each strip.

2.3.4. Indicator for grain filling duration

Cumulative Growing Degree Days (CGDD) of the grain filling period were calculated for each site-by-year combination as follows:

$$CGDD = \sum_{d\,=\,flowering\ stage}^{n} GDD_d \ \ (if\ GDD_d \geq 0)$$

$$with\ GDD_d = \frac{Tmin_d + Tmax_d}{2} - T_{Base}$$

where n is the harvest date, GDD_d is the growing degree days of the day d, $Tmin_d$ is the minimal temperature of the day d (°C), $Tmax_d$ is the maximal temperature of the day d (°C), and T_{Base} is the base temperature for camelina, i.e. 5 °C (Gesch, 2014).

2.3.5. Indicator for high temperature stress

High temperatures, greater than 25°C, have been reported to affect camelina seed FA composition (Rodríguez-Rodríguez et al., 2013; Zubr and Matthäus, 2002). This possible thermal stress was assessed by the number of days between flowering and harvest with maximal temperatures higher than 25 °C, as proposed for the indicator of winter wheat (Brancourt-Hulmel et al., 1999; Lecomte, 2005).

2.4. Data analysis

Data were analysed through a three-step approach adapted from the on-farm regional agronomic diagnosis (Doré et al., 1997, 2008). All the statistical analyses were run with the R software (version 3.5.1.).

2.4.1. Step 1

The variability of seven variables of interest (camelina yield and seed oil, protein, PUFA, MUFA, linolenic (ALA), and linoleic (LA) contents) across the experimental network was described. The two-by-two relationships between these variables were studied using linear regression models.

2.4.2. Step 2

Candidate indicators of each variable of interest (see 2.3.) were ranked using an AIC-based model mixing method (Burnham and Anderson, 2002) to identify major limiting factors, as it

has been previously proposed to analyse wheat grain protein content and *Miscanthus x giganteus* yield variability (Casagrande et al., 2009; Lesur-Dumoulin et al., 2016). The package MMIX (Morfin and Makowski, 2009) was used. More precisely, the principle of the AIC-based model mixing method is as follows:

(1) First, each variable of interest is related to candidate explanatory variables (limiting factors) using a linear regression model.

(2) Then, all the possible linear combinations of the explanatory variables are fitted and both the Akaike Information Criterion (AIC) value (Akaike, 1974) and the Akaike weight (w_k) are computed for each combination (*mixAIC* function of the MMIX package). The Akaike weight is calculated with the following equation (Burnham and Anderson, 2002):

$$w_k = \frac{e^{-0.5(AIC_k - AIC_{\min})}}{\sum_{k=1}^{n} e^{-0.5(AIC_k - AIC_{\min})}}$$

where w_k is the Akaike weight obtained for the model M_k, corresponding to the k^{th} combination of explanatory variables (among the n possibilities), AIC_k is the Akaike Information Criterion computed for this same model M_k, and $AIC_{\min}$ is the minimal value of AIC obtained across the n model tested.

(3) Finally, the relative importance value of each explanatory variable ($w_+(x)$) is estimated by summing the Akaike weights of all the models tested in which the variable x occurred. The higher the $w_+(x)$ value, the higher the importance of the variable x, meaning that the variable x has a high probability to be in the best model.

In addition, bootstrapping was used to assess the stability of the model mixing method used regarding the dataset (Prost et al., 2008). To do so, the *bootFreq* function of the package MMIX was used. A total of 1000 bootstraps were generated from the initial dataset by

sampling data with replacement (Efron and Tibshirani, 1994), and the AIC-based model mixing method was applied for each bootstrap sample. As a result, for each explanatory variable, four values were computed: the frequency of selection across the bootstrap samples, the mean value of the parameter across the bootstrap samples, the standard deviation of the estimated parameter value across the bootstrap samples, and the mean value of the variable weights.

2.4.3. Step 3

When it was relevant, the effects of environmental conditions and crop management routes on major limiting factors identified in the previous step were analysed using multiple regression models. More precisely, for each major limiting factor, possible effects of environmental conditions or crop management routes were expressed through quantitative variables in order to be tested statistically. For instance, based on literature and field observations, incidence and severity of downy mildew infection at harvest were assumed to be affected by weather conditions and especially cumulative rainfall and mean air temperatures (Desai et al., 2004; Vellios et al., 2017), but also by the amount of (i) camelina biomass (as indicator for the dispersion potential of the disease, Fitt et al., 2006), (ii) intercrop species biomass (as indicator for blocking effect, Boudreau, 2013), and (iii) weeds biomass (as an indicator of the development of the vegetative cover, Wisler and Norris, 2005).

3. Results

3.1. Camelina performance across the experimental network

Camelina yield from experimental plots (pYield) varied from 62 to 2585 kg ha^{-1} with higher yields in 2017 than in 2018, and the lowest yields for the CB_50 and CB_25 crop management routes (Figure 2). For the intercrops, pea yield (also from experimental plots) varied from 449 to 2153 kg ha^{-1}, and barley yield from 753 to 5310 kg ha^{-1}, with higher yields for the CB_50 than for the CB_25 (Figure 2). Camelina mechanical yield (mYield) varied from 77 to 2080 kg ha^{-1} and was highly related to pYield ($p < 0.001$, $R^2 = 0.94$) (data not shown). As a result, all the analyses were run on pYield (named as camelina yield hereafter). No significant correlation was found between camelina yield and oil or protein content (Figure 3a). However, camelina yield was slightly positively correlated to MUFA ($R^2=0.11$, $p < 0.05$) (Table 4).

Oil and protein contents reached average values of 41.7 and 24.1% respectively, and ranged from 36.6 to 46.5%, and from 20.9 to 28.1% respectively. A significant negative correlation was found between these two variables ($R^2=0.44$, $p < 0.001$) (Figure 3b). Protein content was also slightly negatively correlated to MUFA and LA contents, and positively correlated to PUFA and ALA contents (Table 4).

PUFA and MUFA contents respectively varied from 52.1 to 58.5 % (mean = 55.8 %), and from 31.6 to 37.9 % (mean = 34.3 %). A strong negative correlation between PUFA and MUFA contents was found ($p<0.001$, $R^2 = 0.98$) (Table 4). In 2017, camelina oil was characterised by a high content in MUFA and a low content in PUFA, and conversely in 2018 (Figure 3c).

Finally, ALA content varied from 30.9 to 37.8 % and was negatively correlated to LA content (Figure 3d). This negative correlation thus explained the positive correlation between PUFA and ALA, and the negative one between PUFA and LA (Table 4).

335 Based on these relationships, the AIC-based model mixing method was run for camelina
336 yield, oil content, PUFA content, and ALA content in order to identify their major limiting
337 factors.
338
339 3.2. Major limiting factors of camelina yield and seed quality
340 Overall, the ranks of the limiting factors were preserved after bootstrap (Table 5), and the
341 frequency of selection across the bootstrap samples of all the limiting factors was equal to 1,
342 meaning that the results of the analyses were quite stable regarding the dataset. Major limiting
343 factors, i.e. with a relative importance value equal or close to 1, differed from one variable to
344 another (Table 5).
345 For yield, limiting factors with the higher probability to be in the best model were nitrogen
346 status at flowering (NNI) and pod loss due to mildew (MILDEW), with relative importance
347 values equal to 1 before and after bootstrap (Table 5). Both factors had significant effect on
348 yield (p-values <0.001), and together explained 69% of the yield variability observed. NNI
349 varied from 0.27 to 0.79 and was positively related to yield (Figure 4). The higher NNI values
350 were observed for the crop management route SD, and the lower ones for the camelina-barley
351 intercrops (CB_50 or CB_25) (Figure 4). In 2018, mildew significantly reduced yield with a
352 percentage of diseased pods ranging from 6 to 98% depending on site and crop management
353 route (Figure 4). In the present study, neither water stress during the entire growing period,
354 nor pod loss due to hail were identified as major limiting factors explaining yield variations.
355 Both factors had indeed a low probability to be in the best model (Table 5), and no significant
356 effect on yield.
357 For oil content, both mildew and cumulative growing degree-days during the grain filling
358 period were identified as factors with high probability to be in the best model (w_+= 0.82 and
359 w_+= 0.7 after bootstrap respectively) (Table 5). Both factors had significant effects on oil

content ($p<0.001$ and $p = 3.31\times10^{-2}$ respectively), but they only explained 21% of the variability observed. Overall, oil content slightly increased with longer grain filling period but decreased in 2018 because of downy mildew (Table 5). Neither nitrogen status nor water stress during the grain filling period were identified as major limiting factors for oil content, as their relative importance values were around 0.5 (Table 5).

The same limiting factors were observed for both PUFA and ALA contents (Table 5). Both variables were mainly affected by cumulative growing degree-days during grain filling, high temperatures, and in a less extend by water stress. More precisely, 88% of the PUFA content variability was explained with these three variables ($p<0.001$ for the three factors) and 80% for the ALA content ($p<0.001$ for CGDD and HIGH TEMPERATURES, and $p= 0.03$ for WATER STRESS). PUFA and ALA contents were positively correlated to CGDD during grain filling period, thus explaining the difference between 2017 and 2018 previously described (Table 5, Figure 5). However, a high number of days with maximal temperature above 25 °C appeared to significantly reduce PUFA and ALA contents (Figure 5). Finally, on average, higher PUFA and ALA contents were observed in situations with water stress indicator equal to 1, i.e. without water stress (data not shown).

3.3. Effects of environmental conditions and crop management routes on major limiting factors

Among the candidate limiting factors, four of them, namely nitrogen crop status (NNI), downy mildew, duration of grain filling period (CGDD), and high temperatures, appeared to impact significantly camelina seed yield and/or quality across the on-farm experimental network. As CGDD and high temperatures were indicators directly dealing with climatic conditions, they were not investigated further.

As no nitrogen fertilisation was applied, NNI at flowering stage was assumed to be affected by (i) the amount of available inorganic nitrogen in the soil (NSOIL, kgN ha^{-1}, defined in the section 2.2), (ii) the amount of nitrogen uptake by the other species (barley, pea and/or weeds) at flowering stage, and (iii) water stress between sowing and flowering. For barley and pea, the amount of nitrogen uptake corresponded to NDFS (KgN ha^{-1}, defined in the section 2.2.). For weeds, total weed biomass at flowering (varying from 1 to 272 g m^{-2} depending on the crop management routes, the experimental site and the year) was used as an indicator because we did not measure nitrogen concentration in weeds. The four-factor regression model tested (R^2=0.57, Table 6) showed that NNI was significantly correlated with N uptake of the crops grown with camelina, the quantity of available inorganic nitrogen in the soil, and water stress. No significant effect of weed biomass was found (Table 6). More precisely, NDFS ranged from 5 to 80 kg N ha^{-1}, and was negatively correlated to NNI (Figure 6). Intercrop with pea resulted in higher camelina NNI than intercrop with barley because of lower amount of soil-derived nitrogen absorbed by pea than barley, resulting from the symbiotic N_2 fixation. Conversely, lower NNI were observed for camelina-barley intercrop due to the high amount of nitrogen uptake by barley, except when the quantity of available inorganic nitrogen in the soil was high (Figure 6). NNI was positively correlated to NSOIL and to the indicator of water stress (Table 6) meaning that high amount of nitrogen in soil and no water stress (WATER STRESS = 1) induced higher NNI.

Incidence and severity of downy mildew infection at harvest date appeared to be significantly affected by weather conditions before flowering and by weed biomass at flowering. More precisely, the percentage of diseased pods was positively correlated to cumulative rainfall between sowing and flowering and weed biomass, both explaining together 74 % of the variability observed. Drier weather conditions in 2017 (79 mm (±10) of cumulated rainfall between sowing and flowering on average over the five locations) than in 2018 (140 mm

409 (±19) on average over the four locations) thus explained the absence of disease in 2017. In
410 addition, no significant effect of camelina or intercrop species biomass was found (data not
411 shown). Finally, in 2018, early abundance of weeds induced higher level of diseased pods.

4. Discussion

4.1. Camelina performance variability as an opportunity to develop flexible and adaptive value-chains

The range observed for camelina yields in our network was consistent with previous values reported for the variety Calena except for the low-yielding camelina-barley intercrops. Urbaniak et al. (2008b) found Calena to reach yields between 906 and 2568 kg ha^{-1} in a multi-environment trial in Canada. Without considering CB_50 and CB_25 crop management routes, camelina yield varied from 270 to 2585 kg ha^{-1}, which is close to the range of yields reviewed in Berti et al. (2016) across seven different countries (400 to 3300 kg ha^{-1}). Thus, our on-farm network was successful in exploring some variability, which is useful, in a scientific perspective, to perform an agronomic diagnosis, and then help farmers to reduce this variability by understanding major causes (Doré et al., 1997; Loyce and Wery, 2006). Seed quality was also consistent with previous data. Zanetti et al. (2017) obtained a mean oil content of 41.8 % in a multi-year-location-variety study across Europe and Canada, which is quite similar to the average value we observed in our study (41.7%). In several studies comparing various genotypes, negative genetic correlations between oil and protein contents had been previously observed (Gugel and Falk, 2006; Zanetti et al., 2017) and explained by the competition for carbon and energy during the biosynthesis of fatty acids and amino acids (Gehringer et al., 2006). Here, considering only one genotype, we observed a negative phenotypic correlation, even if the coefficient of correlation was lower than for the genetic correlations in the other studies (respectively r=-0.91 and r=-0.84), suggesting an impact of the environmental conditions on this relation as mentioned by Zubr (2003b). Finally, the negative relationships between PUFA and MUFA, or ALA and LA, observed in our study, have been shown to be the consequence of the relative order of the biosynthesis of the fatty-acids in the developing seeds (Obour et al., 2017; Voelker and Kinney, 2001).

For years, the strategy adopted by the advisors and collectors was to standardize yield and seed quality, in a given supply area, through the use of inputs. But today, the emergence of diversifying flex-crops, with multiple uses, within a context of climate change leading to an increased inter-annual variability, suggests the implementation of a "sustainable commercialisation", defined by Jordan et al. (2016) as a "coordinated innovation process that integrates a new crop into the agriculture of a region, while intentionally addressing economic, environmental and social sustainability challenges via multi-stakeholder governance". In our case study, although contrasting performance was observed between 2017 and 2018, both situations were suitable for a commercial valorisation. Indeed, high level of production combined with oil characterised by a low PUFA/MUFA ratio, i.e. with good properties for industrial uses (Rodríguez-Rodríguez et al., 2013), as in 2017, could be considered to satisfactorily supply an industrial outlet (chemicals or biofuels). On the contrary, low yield but combined with oil rich in omega 3 (ALA), i.e. with high nutritional value (Waraich et al., 2013), as in 2018, would be more adapted to a high-value market (human food or family pet feed). Therefore, in this perspective of "sustainable commercialisation", this inter-annual variability of camelina performances in northern France would argue for the development of a flexible local value-chain in which the uses of camelina would be adapted each year regarding yield and seed quality (Parada et al., 2018). Such kind of coupled innovations (Meynard et al., 2017), will probably require the design of early indicators useful for industrialists to predict, from field measurements, camelina seed quality, and thus future uses, as it has been proposed for the management of the harvest of malting barley at the supplying area scale (Le Bail, 1997).

4.2. Contribution of the agronomic diagnosis to include camelina in cropping systems of northern France

Camelina yield has been shown to respond to nitrogen up to 200 kg ha^{-1} (Jiang and Caldwell, 2016; Solis et al., 2013). In our study, without nitrogen fertilisation, yield varied with nitrogen crop status (NNI), which variations were explained by the amount of inorganic nitrogen available in the soil, as previously reported by Wysocki et al. (2013). Soils in the area of the present study are known to have different capacities in mineral nitrogen supply related to their physico-chemical composition and depth (Begon et al., 1977). In addition, several studies have shown the impact of legume, whether cash or cover crop, on the inorganic nitrogen availability for the following crop (Coombs et al., 2017; Li et al., 2015; Reckling et al., 2016; Stagnari et al., 2017). Therefore, the choice of both soil type and previous crop or cover crop should be considered to introduce camelina in cropping systems, and design low-input management of camelina with satisfying quantitative and qualitative performance.

Our results confirmed the impact of temperatures on camelina seed quality, thus explaining seed quality variations observed across locations, as already mentioned in previous studies (Berti et al., 2011; Vollmann et al., 2007). Here, we specifically showed a significant effect of the number of days with maximal temperature above 25°C on ALA content. With the current climate change, the frequency of periods of heat may widely increase (IPCC, 2018). For instance, in the study area, the number of years, for which there were more than 20 days at a maximal temperature above 25°C during grain filling period, increased from 2 to 5 respectively between the decades of 1996-2005 and 2006-2015 (long term weather data extracted from the on-line platform CLIMATIK for the Estrées-Mons meteorological station, 49.875°N - 3.031°E). In their recent study, Righini et al. (2019) suggested that shifting camelina sowing from spring to autumn in Italy could be a way to enhance oil quality. In a context of climate change, delaying camelina sowing during the autumn or summer could be

an efficient way to avoid these periods of heat occurring in the late spring. More widely, diversifying the way of introducing camelina (as spring, summer, or winter crop) in cropping systems could also contribute to increase the resilience of the developing camelina value-chain (Lin, 2011). Indeed, growing camelina as second crop in France has been shown to reach satisfactory yields (between 600 to 2500 kg ha^{-1}) to sustainably supply a local biorefinery (Leclère et al., 2018). However, further research would be needed to assess the impact of delayed sowing on camelina seed quality, and more widely on the major limiting factors identified in this study for such management conditions. For instance, performance of genotypes known to have higher mildew resistance than Calena (Vollmann et al., 2001) should be investigated, as downy mildew has been shown to be a major limiting factor of camelina yield and oil content, and as it was impacted by weather conditions (Gesch, 2014; Schillinger et al., 2012).

4.3. Contribution of the agronomic diagnosis to design camelina crop management routes suited to northern France

The agronomic diagnosis is a key step to re-design crop management routes because it contributes to identify problems and thus potential levers to overcome them (Loyce and Wery, 2006). In the case of camelina in northern France, the diagnosis of camelina yield and seed quality highlighted three topics that should be addressed to design highly-effective spring camelina crop management routes: (i) nitrogen management, especially for the intercrops with cereals, to limit competition, (ii) weed management to limit nitrogen competition and downy mildew development, and (iii) varietal choice to be better suited to environmental conditions.

In our network, all camelina NNI values were lower than 1, with a majority of values between 0.4 and 0.6, thus suggesting nitrogen deficiency in all situations. However, Wysocki et al. (2013) suggested that the amount of nitrogen needed to achieve optimum yield would be

511 lower for camelina than for other spring oilseed species. Thus, these absolute values of
512 camelina NNI should be improved by calculating them with a dedicated critical curve for
513 camelina and not with the oilseed rape one. Therefore, it is likely that real camelina NNI
514 values were higher than the calculated ones, questioning the need of nitrogen in camelina pure
515 stand crop management routes (SD or DD). Studies on how camelina responds to nitrogen are
516 numerous, but results appear fluctuating in term of nitrogen rate required to achieve
517 maximum seed yield (from 45 to 200 kg N ha^{-1} depending on growth conditions) (Berti et al.,
518 2016; Righini et al., 2016). Therefore, the design and the assessment of nitrogen fertilisation
519 strategies adapted to local conditions will need further research. It should be especially useful
520 to estimate the nitrogen needs of camelina and to determine the critical dilution curve, which
521 are two indicators useful to quantify crop nitrogen status and reason nitrogen fertilisation
522 (Sadras and Lemaire, 2014). The establishment of a critical dilution curve requires data
523 collection at different crop stages (Flénet et al., 2006; Zhao, 2014). Therefore, additional
524 studies on how camelina responds to nitrogen all along the crop cycle are needed, as the
525 numerous studies previously mentioned are mainly providing data at harvest. In the case of
526 the intercrops, it could be also useful to identify optimal NNI value for camelina to be reached
527 in order to maintain a good balance between the two crops (Bedoussac and Justes, 2010).
528 Weeds did not appear to have a significant effect on camelina NNI, while it is well known
529 that weeds are a major limiting factor of crops because they compete for resources, including
530 nitrogen (Oerke, 2006; Sardana et al., 2017; Yaduraju et al., 2015). We assume that including
531 weed biomass instead of weed nitrogen uptake (kg N ha^{-1}) in our model might have
532 minimized the effect of weeds on camelina NNI and thus on camelina yield. However, in
533 2018, weeds appeared to impact both camelina yield and oil content by increasing downy
534 mildew. Weeds were previously mentioned as a factor favouring fusarium head blight (caused
535 by *Fusarium graminearum*) in wheat (Teich and Nelson, 1983). According to the authors,

weeds might have increased water or nitrogen stress of wheat or modified the crop environment (e.g. by inducing a microclimate). Wisler and Norris (2005) also mentioned that weeds could interact with pathogen management in several ways. A previous study on this experimental network showed that camelina-pea and camelina-barley intercrops significantly reduced weed biomass compared to camelina grown in pure stand (Leclère et al., 2019). Therefore, designing camelina intercrops with legumes or cereals could be promising to limit the effect of downy mildew on camelina performance through the reduction of weeds. In addition, even if it was not statistically shown by our results, blocking effect (diminution of downy mildew dispersion) was observed in the CP and CB crop management routes in two sites over four in 2018, arguing even more in favour of developing such systems.

Varietal choice is a key element mobilized by farmers to adapt their agricultural practices to their local environmental conditions, and even more in a context of climate change (Macholdt and Honermeier, 2017; Parent et al., 2018). In the case of camelina in northern France, the use of a camelina variety with a shorter cycle duration could be an interesting lever to avoid high temperatures during the grain filling period. Lack of availability of improved varieties, as a consequence of strategic choice of breeders focusing on major crops (Parenty, 2018), has been shown to hinder the introduction of diversifying crops into cropping systems (Meynard et al., 2018). Therefore, in the context of a "sustainable commercialisation", defined previously (see 4.1), this diagnosis also could be a useful tool to enhance and design breeding programs on camelina.

5. Conclusion

Camelina yield and seed quality widely varied across our experimental on-farm network. While unstable, oil, protein and fatty-acid contents reached satisfactory levels, suitable for camelina commercialisation. Except for the intercrop with barley, yields were also satisfying and in accordance with previous values reported in experimental stations. Camelina yield was mainly affected by nitrogen crop status and downy mildew, while camelina seed quality was mainly affected by environmental conditions. More widely, this study contributes to better understand agronomic and environmental factors affecting camelina performance under on-farm conditions. These findings should be thus useful to design sustainable and innovative camelina cropping systems and value-chains.

Acknowledgments

This work was performed, in partnership with the SAS P.I.V.E.R.T., within the frame of the French Institute for the Energy Transition (Institut pour la Transition Energétique - ITE) P.I.V.E.R.T. (www.institut-pivert.com) selected as an Investment for the Future ("Investissements d'Avenir"). This work was supported, as part of the Investments for the Future, by the French Government under the reference ANR-001-01.

We thank all the farmers (Mr. Béguin, Mr. Bullot, Mr. Carpentier, Mr. Delacour, Mr. De Smedt, and Mr. Vandeputte) who set up the trials on their farms and contributed significantly to this work. We also thank the technical staff of the lab (Mathieu Bazot, Arnaud Butier, Éléonore Courteau, Richard Gosse, Gilles Grandeau et Véronique Tanneau) who participated in the experimental work.

References

Allen, R. G., Pereira, L. S., Raes, D., Smith, M., 1998. Crop evapotranspiration-Guidelines for computing crop water requirements-FAO Irrigation and drainage paper 56. Fao, Rome, 300(9), D05109.

Akaike, H., 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control, 19, 716–723.

Bedoussac, L., Justes, E., 2010. Dynamic analysis of competition and complementarity for light and N use to understand the yield and the protein content of a durum wheat–winter pea intercrop. Plant and Soil 330, 37–54. https://doi.org/10.1007/s11104-010-0303-8

Begon, J.C., Hardy, R., Mory, A., 1977. Les sols du département de l'Oise. CNRA, Service d'études des sols et de la carte pédologique de France.

Belayneh, H.D., Wehling, R.L., Cahoon, E., Ciftci, O.N., 2015. Extraction of omega-3-rich oil from Camelina sativa seed using supercritical carbon dioxide. J. Supercrit. Fluids 104, 153–159. https://doi.org/10.1016/j.supflu.2015.06.002

Berti, M., Gesch, R., Eynck, C., Anderson, J., Cermak, S., 2016. Camelina uses, genetics, genomics, production, and management. Ind. Crops Prod. 94, 690–710. https://doi.org/10.1016/j.indcrop.2016.09.034

Berti, M., Wilckens, R., Fischer, S., Solis, A., Johnson, B., 2011. Seeding date influence on camelina seed yield, yield components, and oil content in Chile. Ind. Crops Prod. 34, 1358–1365. https://doi.org/10.1016/j.indcrop.2010.12.008

Borras Jr, S.M., Franco, J.C., Isakson, S.R., Levidow, L., Vervest, P., 2016. The rise of flex crops and commodities: implications for research. J. Peasant Stud. 43, 93–115. https://doi.org/10.1080/03066150.2015.1036417

Boudreau, M.A., 2013. Diseases in Intercropping Systems. Annu. Rev. Phytopathol. 51, 499–519. https://doi.org/10.1146/annurev-phyto-082712-102246

Brancourt-Hulmel, M., Lecomte, C., Meynard, J.-M., 1999. A Diagnosis of Yield-Limiting Factors on Probe Genotypes for Characterizing Environments in Winter Wheat Trials 39, 1798–1808. https://doi.org/10.2135/cropsci1999.3961798x

Campbell, M.C., Rossi, A.F., Erskine, W., 2013. Camelina (Camelina sativa (L.) Crantz): agronomic potential in Mediterranean environments and diversity for biofuel and food uses. Crop Pasture Sci. 64, 388–398. http://dx.doi.org/10.1071/CP13054

Cappelli, G., Zanetti, F., Ginaldi, F., Righini, D., Monti, A., Bregaglio, S., 2019. Development of a process-based simulation model of camelina seed and oil production: A case study in Northern Italy. Ind. Crops Prod. 134, 234–243. https://doi.org/10.1016/j.indcrop.2019.03.046

Casagrande, M., David, C., Valantin-Morison, M., Makowski, D., Jeuffroy, M.-H., 2009. Factors limiting the grain protein content of organic winter wheat in south-eastern France: a mixed-model approach. Agron. Sustain. Dev. 29, 565–574. https://doi.org/10.1051/agro/2009015

Chaturvedi, S., Bhattacharya, A., Khare, S.K., Kaushik, G., 2018. Camelina sativa: An Emerging Biofuel Crop, in: Hussain, C.M. (Ed.), Handbook of Environmental Materials Management. Springer International Publishing, Cham, pp. 1–38. https://doi.org/10.1007/978-3-319-58538-3_110-1

Colnenne, C., 1998. Determination of a Critical Nitrogen Dilution Curve for Winter Oilseed Rape. Ann. Bot. 81, 311–317. https://doi.org/10.1006/anbo.1997.0557

COMIFER, 2013. Calcul de la fertilization azote. Guide méthodologique pour l'établissement des prescriptions locales. Cultures annuelles et prairies.

http://www.comifer.asso.fr/images/stories/publications/brochures/BROCHURE_AZOTE_20130705w eb.pdf
Coombs, C., Lauzon, J.D., Deen, B., Van Eerd, L.L., 2017. Legume cover crop management on nitrogen dynamics and yield in grain corn systems. Field Crops Res. 201, 75–85. https://doi.org/10.1016/j.fcr.2016.11.001
Dejoux, J.-F., Meynard, J.-M., Reau, R., Roche, R., Saulas, P., 2003. Evaluation of environmentally-friendly crop management systems based on very early sowing dates for winter oilseed rape in France. Agronomie 23, 725–736. https://doi.org/10.1051/agro:2003050
Desai, A.G., Chattopadhyay, C., Agrawal, R., Kumar, A., Meena, R.L., Meena, P.D., Sharma, K.C., Rao, M.S., Prasad, Y.G., Ramakrishna, Y.S., 2004. Brassica juncea powdery mildew epidemiology and weatherbased forecasting models for India — a case study J. Plant Dis. Prot. 111, 429–438. https://doi.org/10.2307/43216277
Doré, T., Clermont-Dauphin, C., Crozat, Y., David, C., Jeuffroy, M.-H., Loyce, C., Makowski, D., Malézieux, E., Meynard, J.-M., Valantin-Morison, M., 2008. Methodological progress in on-farm regional agronomic diagnosis. A review. Agron. Sustain. Dev. 28, 151–161. https://doi.org/10.1051/agro:2007031
Doré, T., Sebillotte, M., Meynard, J.M., 1997. A diagnostic method for assessing regional variations in crop yield. Agric. Syst. 54, 169–188. https://doi.org/10.1016/S0308-521X(96)00084-4
Efron, B., Tibshirani, R.J., 1994. An Introduction to the Bootstrap. CRC Press.
Fitt, B.D.L., McCartney, H.A., West, J.S., 2006. Dispersal of foliar plant pathogens: mechanisms, gradients and spatial patterns, in: COOKE, B.M., JONES, D.G., KAYE, B. (Eds.), The Epidemiology of Plant Diseases. Springer Netherlands, Dordrecht, pp. 159–192. https://doi.org/10.1007/1-4020-4581-6_6
Flénet, F., Guérif, M., Boiffin, J., Dorvillez, D., Champolivier, L., 2006. The critical N dilution curve for linseed (Linum usitatissimum L.) is different from other C3 species. European Journal of Agronomy 24, 367–373. https://doi.org/10.1016/j.eja.2006.01.002
Gehringer, A., Friedt, W., Lühs, W., Snowdon, R.J., 2006. Genetic mapping of agronomic traits in false flax (Camelina sativa subsp. sativa). Genome 49, 1555–1563. https://doi.org/10.1139/g06-117
George, N., Thompson, S.E., Hollingsworth, J., Orloff, S., Kaffka, S., 2018. Measurement and simulation of water-use by canola and camelina under cool-season conditions in California. Agric. Water Manag. 196, 15–23. https://doi.org/10.1016/j.agwat.2017.09.015
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. https://doi.org/10.1016/j.indcrop.2014.01.034
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. 1 https://doi.org/0.2134/agronj2010.0485
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.
Haefele, S.M., Wopereis, M.C.S., Donovan, C., Maubuisson, J., 2001. Improving the productivity and profitability of irrigated rice production in Mauritania. Eur. J. Agron. 14, 181–196. https://doi.org/10.1016/S1161-0301(00)00094-0
Hergert, G.W., Margheim, J.F., Pavlista, A.D., Martin, D.L., Isbell, T.A., Supalla, R.J., 2016. Irrigation response and water productivity of deficit to fully irrigated spring camelina. Agric. Water Manag. 177, 46–53. http://dx.doi.org/10.1016/j.agwat.2016.06.009

679 Hunsaker, D.J., French, A.N., Clarke, T.R., El-Shikha, D.M., 2011. Water use, crop
680 coefficients, and irrigation management criteria for camelina production in arid
681 regions. Irrig. Sci. 29, 27–43. https://doi.org/10.1007/s00271-010-0213-9
682 Hunsaker, D.J., French, A.N., Thorp, K.R., 2013. Camelina water use and seed yield response
683 to irrigation scheduling in an arid environment. Irrig. Sci. 31, 911–929.
684 https://doi.org/10.1007/s00271-012-0368-7
685 Itier, B., 1996. Measurement and Estimation of Evapotranspiration, in: Pereira, L.S., Feddes,
686 R.A., Gilley, J.R., Lesaffre, B. (Eds.), Sustainability of Irrigated Agriculture, NATO
687 ASI Series. Springer Netherlands, Dordrecht, pp. 171–191.
688 https://doi.org/10.1007/978-94-015-8700-6_11
689 Jiang, Y., Caldwell, C.D., 2016. Effect of nitrogen fertilization on camelina seed yield, yield
690 components, and downy mildew infection. Can. J. Plant Sci. 96, 17–26.
691 https://doi.org/10.1139/cjps-2014-0348
692 Jiang, Y., Caldwell, C.D., Falk, K.C., 2014. Camelina seed quality in response to applied
693 nitrogen, genotype and environment. Can. J. Plant Sci. 94, 971–980.
694 https://doi.org/10.4141/cjps2013-396
695 Jiang, Y., Caldwell, C.D., Falk, K.C., Lada, R.R., MacDonald, D., 2013. Camelina yield and
696 quality response to combined nitrogen and sulfur. Agron. J. 105, 1847–1852.
697 https://doi.org/doi:10.2134/agronj2013.0240
698 Jiang, Y., Li, J., Caldwell, C.D., 2016. Glucosinolate Content of Camelina Genotypes as
699 Affected by Applied Nitrogen and Sulphur. Crop Sci. 56, 3250.
700 https://doi.org/10.2135/cropsci2016.01.0018
701 Jordan, N.R., Dorn, K., Runck, B., Ewing, P., Williams, A., Anderson, K.A., Felice, L.,
702 Haralson, K., Goplen, J., Altendorf, K., Fernandez, A., Phippen, W., Sedbrook, J.,
703 Marks, M., Wolf, K., Wyse, D., Johnson, G., 2016. Sustainable commercialization of
704 new crops for the agricultural bioeconomy. Elem. Sci. Anthr. 4, 000081.
705 https://doi.org/10.12952/journal.elementa.000081
706 Le Bail, M., 1997. Maitrise de la qualite des cereales a l'echelle du bassin
707 d'approvisionnement d'une entreprise de collecte-stockage : approche agronomique
708 (thesis). Paris, Institut national d'agronomie de Paris Grignon.
709 Leclère, M., Loyce, C., Jeuffroy, M.-H., 2018. Growing camelina as a second crop in France:
710 A participatory design approach to produce actionable knowledge. Eur. J. Agron. 101,
711 78–89. https://doi.org/10.1016/j.eja.2018.08.006
712 Leclère, M., Jeuffroy, M.-H., Butier, A., Chatain, C., Loyce, C., 2019. Controlling weeds in
713 camelina with innovative herbicide-free crop management routes across various
714 environments. Industrial Crops and Products 140, 111605.
715 https://doi.org/10.1016/j.indcrop.2019.111605
716 Lecomte, C., 2005. L'évaluation expérimentale des innovations variétales. Proposition
717 d'outils d'analyse de l'interaction génotype - milieu adaptés à la diversité des besoins
718 et des contraintes des acteurs de la filière semences. (phdthesis). INAPG
719 (AgroParisTech).
720 Lemaire, G., Meynard, J.M., 1997. Use of the Nitrogen Nutrition Index for the Analysis of
721 Agronomical Data, in: Lemaire, Gilles (Ed.), Diagnosis of the Nitrogen Status in
722 Crops. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 45–55.
723 https://doi.org/10.1007/978-3-642-60684-7_2
724 Lesur-Dumoulin, C., Lorin, M., Bazot, M., Jeuffroy, M.-H., Loyce, C., 2016. Analysis of
725 young Miscanthus × giganteus yield variability: a survey of farmers' fields in east
726 central France. GCB Bioenergy 8, 122–135. https://doi.org/10.1111/gcbb.12247

727 Li, X., Petersen, S.O., Sørensen, P., Olesen, J.E., 2015. Effects of contrasting catch crops on
728 nitrogen availability and nitrous oxide emissions in an organic cropping system.
729 Agric. Ecosyst. Environ. 199, 382–393. https://doi.org/10.1016/j.agee.2014.10.016
730 Lin, B.B., 2011. Resilience in Agriculture through Crop Diversification: Adaptive
731 Management for Environmental Change. BioScience 61, 183–193.
732 https://doi.org/10.1525/bio.2011.61.3.4
733 Macholdt, J., Honermeier, B., 2017. Importance of variety choice: Adapting to climate change
734 in organic and conventional farming systems in Germany. Outlook Agric. 46, 178–
735 184. https://doi.org/10.1177/0030727017722420
736 Martinelli, T., Galasso, I., 2011. Phenological growth stages of Camelina sativa according to
737 the extended BBCH scale. Ann. Appl. Biol. 158, 87–94. https://doi.org/DOI:
738 10.1111/j.1744-7348.2010.00444.x
739 Meynard, J.-M., Charrier, F., Fares, M., Le Bail, M., Magrini, M.-B., Charlier, A., Messéan,
740 A., 2018. Socio-technical lock-in hinders crop diversification in France. Agron.
741 Sustain. Dev. 38, 54. https://doi.org/10.1007/s13593-018-0535-1
742 Meynard, J.-M., Doré, T., Habib, R., 2001. L'évaluation et la conception de systèmes de
743 culture pour une agriculture durable. Comptes Rendus Académie Agric. Fr. 87, 223–
744 236.
745 Meynard, J.-M., Jeuffroy, M.-H., Le Bail, M., Lefèvre, A., Magrini, M.-B., Michon, C., 2017.
746 Designing coupled innovations for the sustainability transition of agrifood systems.
747 Agric. Syst. https://doi.org/10.1016/j.agsy.2016.08.002
748 Meynard, J.-M., Justes, E., Machet, J.-M., Recous, S., 1997. Fertilisation azotée des cultures
749 annuelles de plein champs. In: INRA (ed) Maitrise de l'azote dans les agrosystèmes,
750 Les colloques, Reims, 183-200
751 Mohammad, B.T., Al-Shannag, M., Alnaief, M., Singh, L., Singsaas, E., Alkasrawi, M., 2018.
752 Production of Multiple Biofuels from Whole Camelina Material: A Renewable Energy
753 Crop. BioResources 13, 4870–4883. https://doi.org/10.15376/biores.13.3.4870-4883
754 Mohammed, Y.A., Chen, C., Afshar, R.K., 2017a. Nutrient Requirements of Camelina for
755 Biodiesel Feedstock in Central Montana. Agron. J. 109, 309.
756 https://doi.org/10.2134/agronj2016.03.0163
757 Mohammed, Y.A., Chen, C., Lamb, P., Afshar, R.K., 2017b. Agronomic Evaluation of
758 Camelina (Camelina sativa L. Crantz) Cultivars for Biodiesel Feedstock. BioEnergy
759 Res. 10, 792–799. https://doi.org/10.1007/s12155-017-9840-9
760 Murphy, E.J., 2016. Camelina (Camelina sativa), in: Industrial Oil Crops. Elsevier, pp. 207–
761 230. https://doi.org/10.1016/B978-1-893997-98-1.00008-7
762 Naudin, C., Corre-Hellou, G., Pineau, S., Crozat, Y., Jeuffroy, M. H., 2010. The effect of
763 various dynamics of N availability on winter pea–wheat intercrops: crop growth, N
764 partitioning and symbiotic N2 fixation. Field Crops Research, 119(1), 2-11.
765 https://doi.org/0.1016/j.fcr.2010.06.002
766 Neupane, D., Solomon, J.K.Q., Davison, J., Lawry, T., 2018. Nitrogen source and rate effects
767 on grain and potential biodiesel production of camelina in the semiarid environment of
768 northern Nevada. GCB Bioenergy. https://doi.org/10.1111/gcbb.12540
769 Obour, A.K., Obeng, E., Mohammed, Y.A., Ciampitti, I.A., Durrett, T.P., Aznar-Moreno,
770 J.A., Chen, C., 2017. Camelina Seed Yield and Fatty Acids as Influenced by Genotype
771 and Environment. Agron. J. 109, 947. https://doi.org/10.2134/agronj2016.05.0256
772 Oerke, E.-C., 2006. Crop losses to pests. J. Agric. Sci. 144, 31–43.
773 https://doi.org/10.1017/S0021859605005708
774 Omonov, T.S., Kharraz, E., Curtis, J.M., 2017. Camelina (Camelina Sativa) oil polyols as an
775 alternative to Castor oil. Ind. Crops Prod. 107, 378–385.
776 https://doi.org/10.1016/j.indcrop.2017.05.041

Parent, B., Leclere, M., Lacube, S., Semenov, M.A., Welcker, C., Martre, P., Tardieu, F., 2018. Maize yields over Europe may increase in spite of climate change, with an appropriate use of the genetic variability of flowering time. Proc. Natl. Acad. Sci. 201720716. https://doi.org/10.1073/pnas.1720716115

Parenty, S., 2018. How to organize plant breeding to favor crop's diversification ? Doctoral thesis: Economics and Finance. Université Grenoble Alpes, 148p. https://tel.archives-ouvertes.fr/tel-02071220v2

Prost, L., Makowski, D., Jeuffroy, M.-H., 2008. Comparison of stepwise selection and Bayesian model averaging for yield gap analysis. Ecol. Model. 219, 66–76. https://doi.org/10.1016/j.ecolmodel.2008.07.026

Putnam, D.H., Budin, J.T., Field, L.A., Breene, W.M., 1993. Camelina: a promising low-input oilseed. New Crops Wiley N. Y. 314.

Puttick, D., Dauk, M., Lozinsky, S., Smith, M.A., 2009. Overexpression of a FAD3 desaturase increases synthesis of a polymethylene-interrupted dienoic fatty acid in seeds of Arabidopsis thaliana L. Lipids 44, 753–757.

Reckling, M., Hecker, J.-M., Bergkvist, G., Watson, C.A., Zander, P., Schläfke, N., Stoddard, F.L., Eory, V., Topp, C.F.E., Maire, J., Bachinger, J., 2016. A cropping system assessment framework—Evaluating effects of introducing legumes into crop rotations. Eur. J. Agron. 76, 186–197. https://doi.org/10.1016/j.eja.2015.11.005

Righini, D., Zanetti, F., Martínez-Force, E., Mandrioli, M., Toschi, T.G., Monti, A., 2019. Shifting sowing of camelina from spring to autumn enhances the oil quality for bio-based applications in response to temperature and seed carbon stock. Ind. Crops Prod. 137, 66–73. https://doi.org/10.1016/j.indcrop.2019.05.009

Righini, D., Zanetti, F., Monti, A., 2016. The bio-based economy can serve as the springboard for camelina and crambe to quit the limbo. OCL. https://doi.org/10.1051/ocl/2016021

Rodríguez-Rodríguez, M.F., Sánchez-García, A., Salas, J.J., Garcés, R., Martínez-Force, E., 2013. Characterization of the morphological changes and fatty acid profile of developing Camelina sativa seeds. Ind. Crops Prod. 50, 673–679. https://doi.org/10.1016/j.indcrop.2013.07.042

Sadras, V.O., Lemaire, G., 2014. Quantifying crop nitrogen status for comparisons of agronomic practices and genotypes. Field Crops Res. 164, 54–64. https://doi.org/10.1016/j.fcr.2014.05.006

Sardana, V., Mahajan, G., Jabran, K., Chauhan, B.S., 2017. Role of competition in managing weeds: An introduction to the special issue. Crop Prot., Role of crop competition in weed management 95, 1–7. https://doi.org/10.1016/j.cropro.2016.09.011

Schillinger, W.F., Wysocki, D.J., Chastain, T.G., Guy, S.O., Karow, R.S., 2012. Camelina: planting date and method effects on stand establishment and seed yield. Field Crops Res. 130, 138–144.

Séguin-Swartz, G., Eynck, C., Gugel, R.K., Strelkov, S.E., Olivier, C.Y., Li, J.L., Klein-Gebbinck, H., Borhan, H., Caldwell, C.D., Falk, K.C., 2009. Diseases of Camelina Sativa (false flax). Can. J. Plant Pathol. 31, 375–386. https://doi.org/10.1080/07060660909507612

Sindelar, A.J., Schmer, M.R., Gesch, R.W., Forcella, F., Eberle, C.A., Thom, M.D., Archer, D.W., 2017. Winter oilseed production for biofuel in the US Corn Belt: opportunities and limitations. GCB Bioenergy 9, 508–524. https://doi.org/10.1111/gcbb.12297

Solis, A., Vidal, I., Paulino, L., Johnson, B.L., Berti, M.T., 2013. Camelina seed yield response to nitrogen, sulfur, and phosphorus fertilizer in South Central Chile. Ind. Crops Prod. 44, 132–138. https://doi.org/10.1016/j.indcrop.2012.11.005

Soroka, J.J., Olivier, C., Wist, T.J., Grenkow, L., 2017. Present and Potential Impacts of Insects on Camelina and Crambe. Cabi Publishing-C a B Int, Wallingford.

Stagnari, F., Maggio, A., Galieni, A., Pisante, M., 2017. Multiple benefits of legumes for agriculture sustainability: an overview. Chem. Biol. Technol. Agric. 4, 2. https://doi.org/10.1186/s40538-016-0085-1

Tabatabaie, S.M.H., Bolte, J.P., Murthy, G.S., 2018. A regional scale modeling framework combining biogeochemical model with life cycle and economic analysis for integrated assessment of cropping systems. Sci. Total Environ. 625, 428–439. https://doi.org/10.1016/j.scitotenv.2017.12.208

Urbaniak, S.D., Caldwell, C.D., Zheljazkov, V.D., Lada, R., Luan, L., 2008. The effect of seeding rate, seeding date and seeder type on the performance of Camelina sativa L. in the Maritime Provinces of Canada. Can. J. Plant Sci. 88, 501–508.

Vellios, E., Karkanis, A., Bilalis, D., 2017. POWDERY MILDEW (ERYSIPHE CRUCIFERARUM) INFECTION ON CAMELINA (CAMELINA SATIVA) UNDER MEDITERRANEAN CONDITIONS AND THE ROLE OF WILD MUSTARD (SINAPIS ARVENSIS) AS ALTERNATIVE HOST OF THIS PATHOGEN. Emir. J. Food Agric. 639. https://doi.org/10.9755/ejfa.2017-02-493

Voelker, T., Kinney, A.J., 2001. Variations in the Biosynthesis of Seed-Storage Lipids. Annu. Rev. Plant Physiol. Plant Mol. Biol. 52, 335–361. https://doi.org/10.1146/annurev.arplant.52.1.335

Vollmann, J., Damboeck, A., Eckl, A., Schrems, H., Ruckenbauer, P., 1996. Improvement of Camelina sativa, an underexploited oilseed. Prog. New Crops ASHS Press Alex. VA 1, 357–362.

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. https://doi.org/10.1016/j.indcrop.2007.03.017

Vollmann, Steinkellner, Glauninger, 2001. Variation in Resistance of Camelina (Camelina sativa [L.] Crtz.) to Downy Mildew (Peronospora camelinae Gaum.). J. Phytopathol. 149, 129–133. https://doi.org/10.1046/j.1439-0434.2001.00599.x

Walia, M.K., Wells, M.S., Cubins, J., Wyse, D., Gardner, R.D., Forcella, F., Gesch, R., 2018. Winter camelina seed yield and quality responses to harvest time. Ind. Crops Prod. 124, 765–775. https://doi.org/10.1016/j.indcrop.2018.08.025

Waraich, E.A., Ahmed, Z., Ahmad, R., Ashraf, M.Y., Naeem, M.S., Rengel, Z., 2013. “Camelina sativa”, a climate proof crop, has high nutritive value and multiple-uses: A review. Aust. J. Crop Sci. 7, 1551.

Wisler, G.C., Norris, R.F., 2005. Interactions between weeds and cultivated plants as related to management of plant pathogens. Weed Sci. 53, 914–917. https://doi.org/10.1614/WS-04-051R.1

Wysocki, D.J., Chastain, T.G., Schillinger, W.F., Guy, S.O., Karow, R.S., 2013. Camelina: seed yield response to applied nitrogen and sulfur. Field Crops Res. 145, 60–66.

Yaduraju, N.T., Sharma, A.R., Rao, A.N., 2015. Weeds in Indian Agriculture: Problems and prospects to become self sufficient. Indian Farming 65, 02–06.

Yildiz, M., Eroldogan, T.O., Ofori-Mensah, S., Engin, K., Baltaci, M.A., 2018. The effects of fish oil replacement by vegetable oils on growth performance and fatty acid profile of rainbow trout: Re-feeding with fish oil finishing diet improved the fatty acid composition. Aquaculture 488, 123–133. https://doi.org/10.1016/j.aquaculture.2017.12.030

Zanetti, F., Eynck, C., Christou, M., Krzyżaniak, 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. https://doi.org/10.1016/j.indcrop.2017.06.022

877 Zanetti, F., Monti, A., Berti, M.T., 2013. Challenges and opportunities for new industrial
878 oilseed crops in EU-27: A review. Ind. Crops Prod. 50, 580–595.
879 https://doi.org/10.1016/j.indcrop.2013.08.030
880 Zhao, B., 2014. Determining of a critical dilution curve for plant nitrogen concentration in
881 winter barley. Field Crops Res. 160, 64–72. https://doi.org/10.1016/j.fcr.2014.02.016
882 Zhu, X., Wang, D., Li, N., Sun, X.S., 2017. Bio-Based Wood Adhesive from Camelina
883 Protein (a Biodiesel Residue) and Depolymerized Lignin with Improved Water
884 Resistance. ACS Omega 2, 7996–8004. https://doi.org/10.1021/acsomega.7b01093
885 Zubr, J., 2003a. Dietary Fatty Acids and Amino Acids of Camelina Sativa Seed. J. Food Qual.
886 26, 451–462. https://doi.org/10.1111/j.1745-4557.2003.tb00260.x
887 Zubr, J., 2003b. Qualitative variation of Camelina sativa seed from different locations. Ind.
888 Crops Prod. 17, 161–169. https://doi.org/10.1016/S0926-6690(02)00091-2
889 Zubr, J., Matthäus, B., 2002. Effects of growth conditions on fatty acids and tocopherols in
890 Camelina sativa oil. Ind. Crops Prod. 15, 155–162. https://doi.org/10.1016/S0926-
891 6690(01)00106-6
892

Figure Captions

Figure 1: a) Symptoms of downy mildew observed on camelina at the end of flowering in 2018 (Location: Gury), **and b) opening of pods due to hailstorm in 2017** (Location: Rethondes).

Figure 2: Camelina yield (kg ha^{-1}) as a function of pea or barley yield (kg ha^{-1}) for the thirty-nine experimental strips. Values for yield are those from the experimental plots (pYield). Shape and symbols size respectively represent the crop management route and the year. SD: Camelina single density, DD: Camelina double density, CP: Camelina/Pea intercrop, CB_25 and CB_50: Camelina/Barley intercrop with barley respectively at 25 and 50% of the advised sowing rate for pure crop.

Figure 3: Camelina yield (kg ha^{-1}) and oil, protein, PUFA, MUFA, ALA, and LA contents (%) in camelina seeds across the experimental network: relationships between (a) camelina plot yield and oil content, (b) oil and protein contents, (c) PUFA and MUFA contents, and (d) ALA and LA contents. Shape and symbols size respectively represent the crop management route and the year. SD: Camelina single density, DD: Camelina double density, CP: Camelina/Pea intercrop, CB_25 and CB_50: Camelina/Barley intercrop with barley respectively at 25 and 50% of the advised sowing rate for pure crop. PUFA = polyunsaturated fatty acids, MUFA= monounsaturated fatty acids, ALA = α-linolenic acid, LA = linoleic acid.

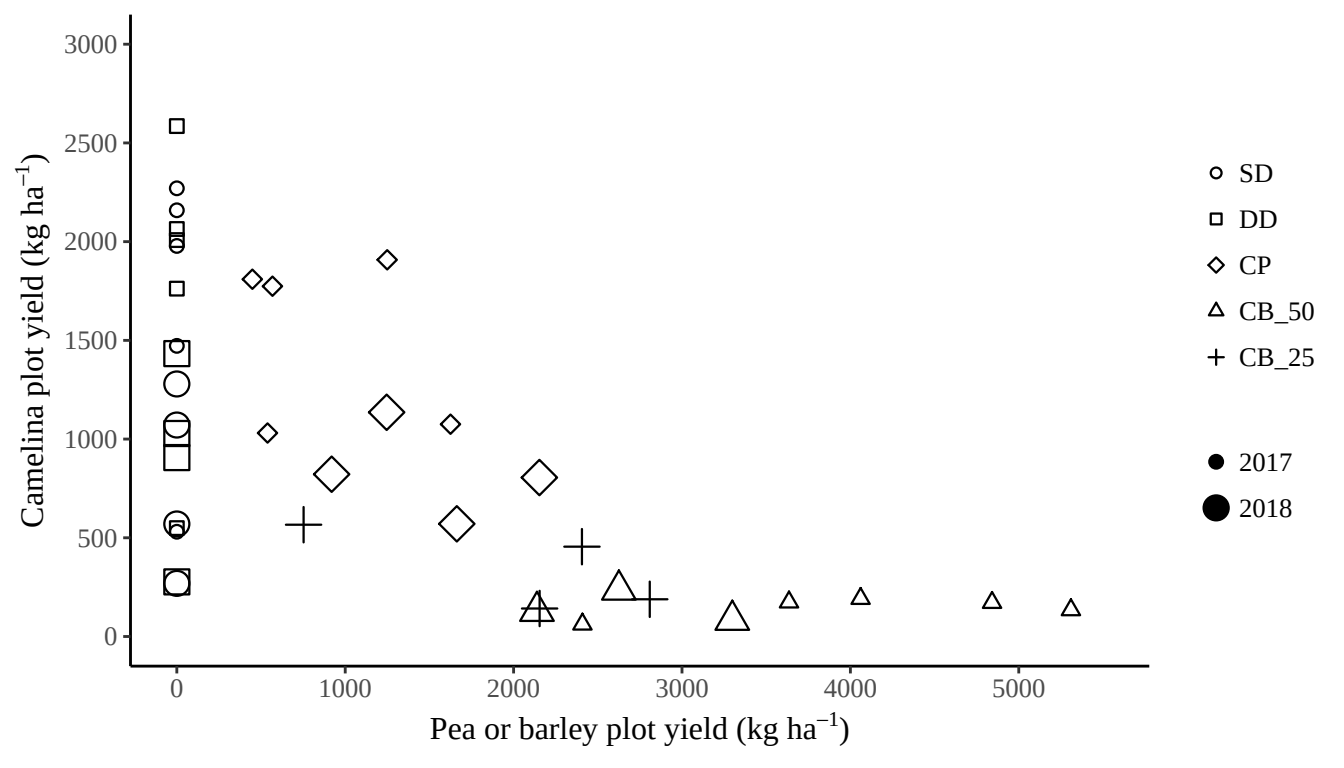
Figure 4: Camelina yield (kg ha^{-1}) as a function of Nitrogen Nutrition Index of camelina at flowering (NNI, unitless) and pod loss due to mildew (%). Symbols shape and size respectively represent the crop management route and the year. Colour gradient represents pod loss due to downy mildew: green corresponds to the lowest values and red to the highest ones. SD: Camelina single density, DD: Camelina double density, CP: Camelina/Pea intercrop, CB_25 and CB_50: Camelina/Barley intercrop with barley respectively at 25 and 50% of the advised sowing rate for pure crop.

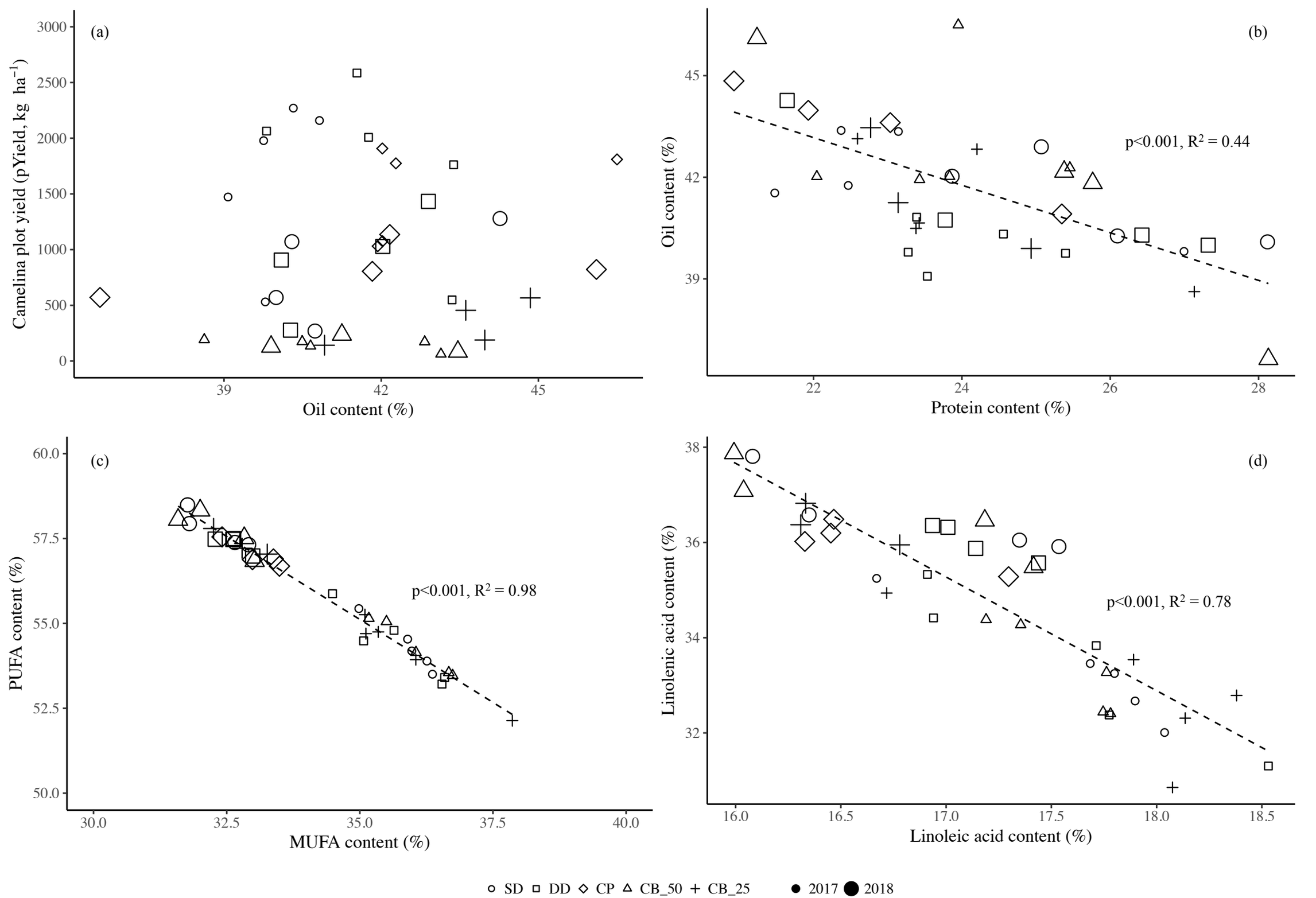
Figure 5: Linolenic content (%) as a function of grain filling duration (°Cd) and high temperatures. Symbols shape and size respectively represent the crop management route and the year. Colour gradient represents the number of days with maximal temperature above 25°C: blue tones correspond to lower values (<17 days), green tones to intermediate values (between 17 and 20 days), and red-pink tones to higher values (>20 days). SD: Camelina single density, DD: Camelina double density, CP: Camelina/Pea intercrop, CB_25 and CB_50: Camelina/Barley intercrop with barley respectively at 25 and 50% of the advised sowing rate for pure crop.

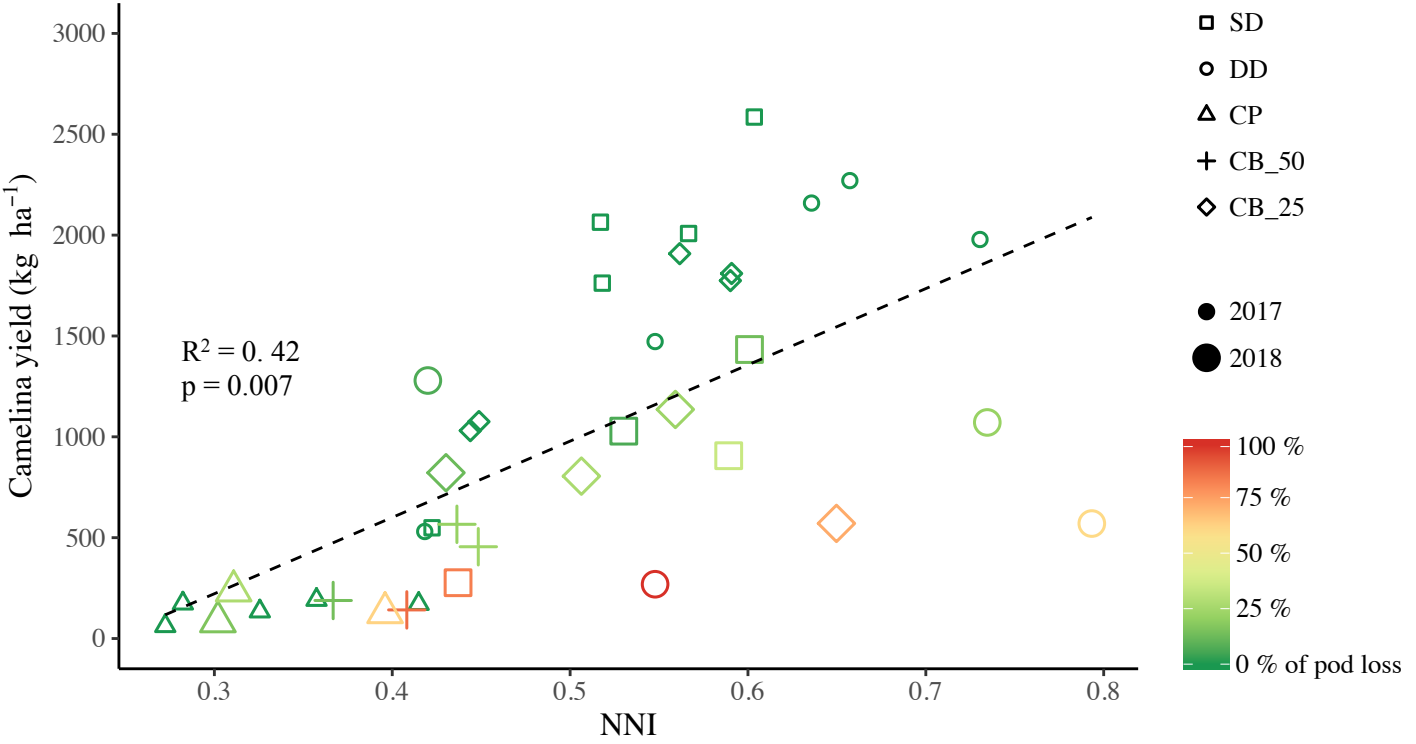
Figure 6: Nitrogen Nutrition Index (NNI) as a function of the amount of uptake nitrogen by the intercrop species at flowering stage (NDFS, kgN ha^{-1}) and the total nitrogen available in soil (Nsoil, kg N ha^{-1}). Symbols shape and size respectively represent the crop management route and the year. Colour gradient represents Nsoil: blue and green tones correspond to lower values (<75 kg N ha^{-1}), yellow-orange tones correspond to intermediate values (between 75 and 115 kg N ha^{-1}), and red tones to higher values (>115 kg N ha^{-1}). SD: Camelina single density, DD: Camelina double density, CP: Camelina/Pea intercrop, CB_25 and CB_50: Camelina/Barley intercrop with barley respectively at 25 and 50% of the advised sowing rate for pure crop.

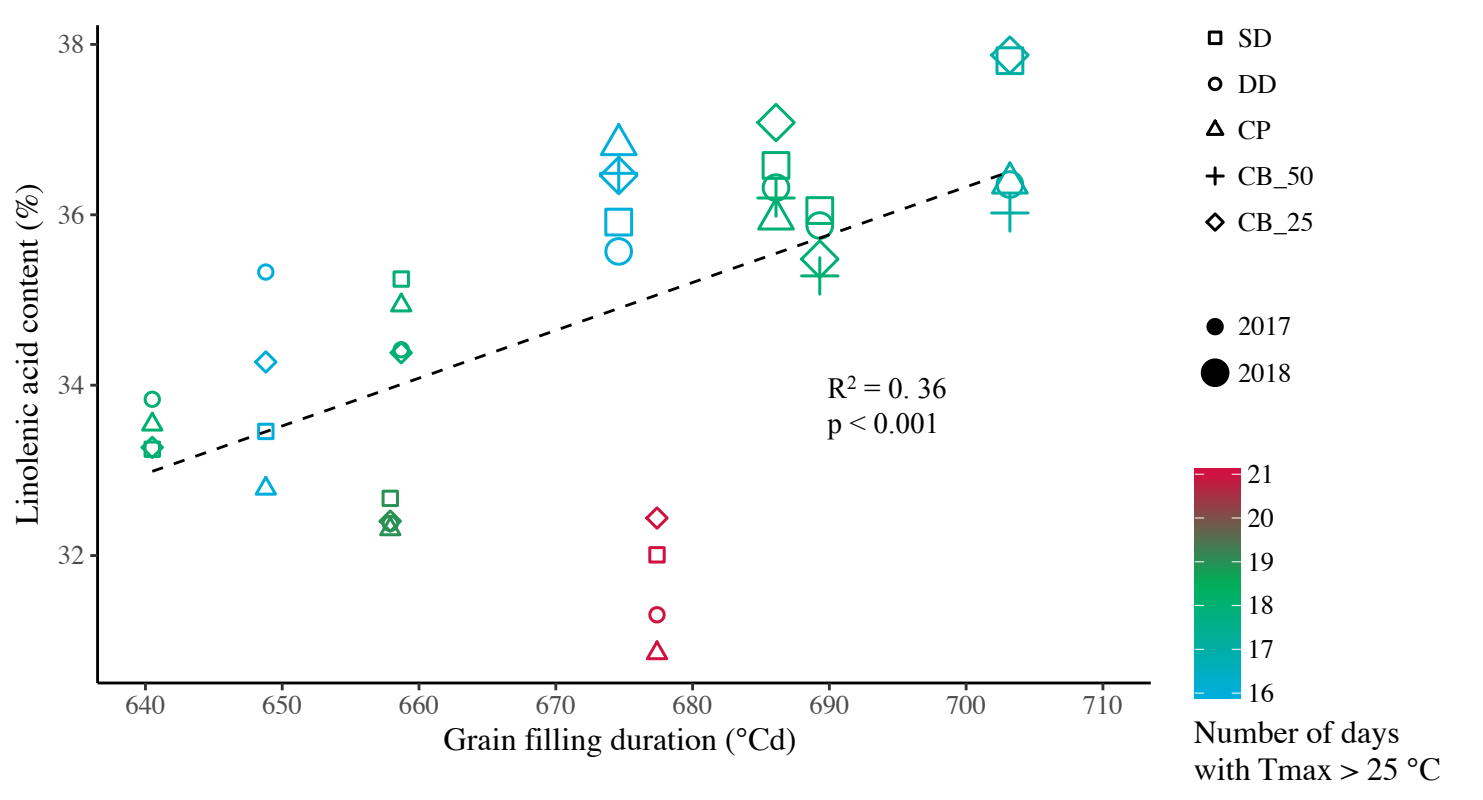

a)


b)


Camelina plot yield (kg ha^{-1})
3000
2500
2000
1500
1000
500
0
0
1000
2000
3000
4000
5000
Pea or barley plot yield (kg ha^{-1})
SD
DD
CP
CB_50
CB_25
2017
2018


(a)
Camelina plot yield (pYield, kg ha^{-1})
Oil content (%)
(b)
Oil content (%)
Protein content (%)
p<0.001, R^2 = 0.44
(c)
PUFA content (%)
MUFA content (%)
p<0.001, R^2 = 0.98
(d)
Linolenic acid content (%)
Linoleic acid content (%)
p<0.001, R^2 = 0.78
SD DD CP CB_50 CB_25
2017 2018


Camelina yield (kg ha^{-1})
3000
2500
2000
1500
1000
500
0
0.3
0.4
0.5
0.6
0.7
0.8
NNI
R^2 = 0. 42
p = 0.007
SD
DD
CP
CB_50
CB_25
2017
2018
100 %
75 %
50 %
25 %
0 % of pod loss


Linolenic acid content (%)
38
36
34
32
640
650
660
670
680
690
700
710
Grain filling duration (°Cd)
R² = 0. 36
p < 0.001
SD
DD
CP
CB_50
CB_25
2017
2018
21
20
19
18
17
16
Number of days
with Tmax > 25 °C

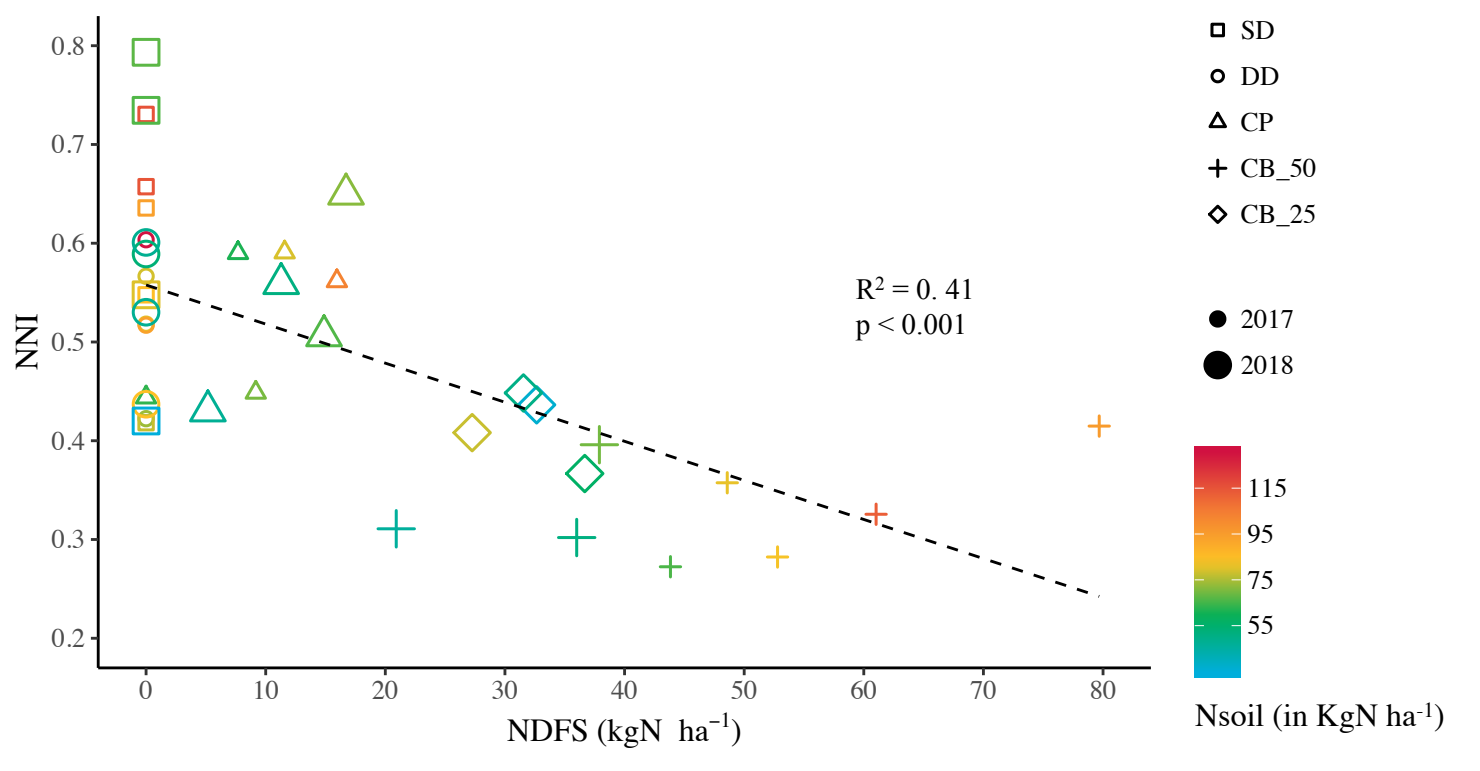

NNI
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0
10
20
30
40
50
60
70
80
NDFS (kgN ha^{-1})
R^2 = 0. 41
p < 0.001
SD
DD
CP
CB_50
CB_25
2017
2018
115
95
75
55
Nsoil (in KgN ha^{-1})

Table 1: Description and location of the thirty-nine experimental strips. Each location is identified by a three-letter code corresponding to the municipality where the field is located: AMY for Amy (49.655°N, 2.825°E), AUT for Autrêches (49.444°N, 3.126°E), GUR for Gury (49.570°N, 2.799°E), MOU for Moulin-sous-Touvent (49.456°N, 3.072°E), MOR for Mortemer (49.570°N, 2.680°E), RET for Rethondes (49.417°N, 2.939°E). The field used to set the trial within a same municipality differs across years (for instance AMY in 2017 corresponds to a different field than AMY in 2018).

Crop management routes tested	**Number and location of the trials in 2017**	**Number and location of the trials in 2018**
SD – Pure camelina sown at Single Density (*4 kg ha^{-1}*)	5 AMY, AUT, MOU, MOR, RET	4 AMY, AUT, GUR, MOU
DD – Pure camelina sown at Double Density (*8 kg ha^{-1}*)	5 AMY, AUT, MOU, MOR, RET	4 AMY, AUT, GUR, MOU
CP – Camelina (*4 kg ha^{-1}*) intercropped with spring Pea (*100 kg ha^{-1}*)	5 AMY, AUT, MOU, MOR, RET	4 AMY, AUT, GUR, MOU
CB_50 – Camelina (4 kg ha^{-1}) intercropped with spring Barley (*70 kg ha^{-1}*)	5 AMY, AUT, MOU, MOR, RET	3 AMY, AUT, MOU
CB_25 – Camelina (*4 kg ha^{-1}*) intercropped with spring Barley (*35 kg ha^{-1}*)	0	4 AMY, AUT, GUR, MOU

Table 2: Main soil characteristics and weather conditions during the growing period for the nine site/year combinations of the experimental network. Experimental site are named by a three-letter code corresponding to the corresponding to the municipality where the field was located: AMY for Amy (49.655°N, 2.825°E), AUT for Autrêches (49.444°N, 3.126°E), GUR for Gury (49.570°N, 2.799°E), MOU for Moulin-sous-Touvent (49.456°N, 3.072°E), MOR for Mortemer (49.570°N, 2.680°E), RET for Rethondes (49.417°N, 2.939°E). Soil texture, amount of $CaCO_3$, and total soil inorganic nitrogen prior sowing are results from soil analyses. Maximal soil water content was estimated with a pedotransfer function (Bruand et al. 2004). Growing period corresponds to the period between sowing and harvest, thus varying between years. RR = Cumulative rainfall during the growing period (mm); ETP = Cumulative evapotranspiration during the growing period (mm).

Year	**Experimental site**	**Soil characteristics**				**Weather data during the growing period**		
		Soil texture	**CaCO3 (%)**	**Total soil inorganic nitrogen (0-90cm) prior sowing (kgN ha^{-1})**	**Maximal soil water content, SWC_{max} (mm)**	**Average of mean temperatures (°C)**	**RR (mm)**	**Climatic weather balance (RR – ETP) (mm)**
2017	AMY	Silt loam	3	76	149	14.3	141	-216,4
2017	AUT	Silt loam	32	54	117	14.4	185	-227,2
2017	MOU	Silt loam	5	60	155	14.4	151	-239,5
2017	MOR	Loam	2	102	154	14.0	180	-164,7
2017	RET	Loamy sandy	18	35	120	14.8	147	-249,7
2018	AMY	Sandy loam	<1	31	120	15.3	186	-177
2018	AUT	Silt loam	15	35	100	15.5	149	-266,4
2018	GUR	Sandy clay loam	60	43	95	15.3	195	-167,2
2018	MOU	Silt loam	1	26	157	15.3	197	-164

Table 3: Kc values for camelina, pea and barley and equations used for Kc calculation for the intercrops. *Kc_ini* is for the period during sowing and fifteen days before flowering, *Kc_max* is for the period between -15 and +15 days around flowering and *Kc_end* is for the period between 15 days after flowering until harvest. *KcC* = Kc value for camelina, *KcI*= Kc value for the intercrop (Pea or Barley), *MSc_flo* = Measured aerial dry matter of camelina at flowering, *MSc_harv*= Measured aerial dry matter of camelina at harvest, *MSi_flo* = Measured aerial dry matter of the intercrop species (pea or barley) at flowering, *MSi_harv* = Measured aerial dry matter of intercrop species (pea or barley) at harvest.

	Camelina	Barley	Pea	Camelina intercropped with barley or pea
Kc_ini	0.28	0.3	0.5	$\frac{MSc_{flo}}{MSc_{flo}+MSi_{flo}} \times KcC_{ini} + \frac{MSb_{flo}}{MSc_{flo}+MSi_{flo}} \times KcI_{ini}$
Kc_max	0.43	1.15	1.15	$\frac{MSc_{flo}}{MSc_{flo}+MSi_{flo}} \times KcC_{max} + \frac{MSb_{flo}}{MSc_{flo}+MSi_{flo}} \times KcI_{max}$
Kc_end	0.2	0.25	0.3	$\frac{MSc_{harv}}{MSc_{harv}+MSi_{harv}} \times KcC_{end} + \frac{MSb_{harv}}{MSc_{harv}+MSi_{harv}} \times KcI_{end}$

Table 4: Results of the linear regression models between the quantitative and qualitative variables studied. Values above the diagonal line represent the p-value and the R-square of the model, and values below the diagonal line are the values of the slope estimated by the model. pYield= yield estimated from experimental plots, PUFA = polyunsaturated fatty acids, MUFA= monounsaturated fatty acids, ALA = α-linolenic acid, LA = linoleic acid, ns indicates that no significant relationship was found between the two variables.

Variables of interest	pYield	Oil content	Protein content	PUFA content	MUFA content	ALA content	LA content
pYield	-	ns	ns	$p<0.1$ $R^2=0.08$	$p < 0.05$ $R^2= 0.11$	ns	ns
Oil content	ns	-	$p < 0.001$ $R^2= 0.44$	ns	ns	ns	ns
Protein content	ns	-0.7	-	$p < 0.05$ $R^2= 0,16$	$p < 0.05$ $R^2= 0.15$	$p<0.01$ $R^2=0.20$	$p<0.01$ $R^2=0.17$
PUFA content	-118.6	ns	+0.44	-	$p < 0.001$ $R^2= 0.98$	$p<0.001$ $R^2=0.94$	$p<0.001$ $R^2=0.58$
MUFA content	+137.07	ns	-0.41	-0.98	-	$p<0.001$ $R^2=0.87$	$p<0.001$ $R^2=0.48$
ALA content	ns	ns	+0.45	+0.92	-0.90	-	$p<0.001$ $R^2=0.78$
LA content	ns	ns	-1.14	-1.95	+1.80	-2.39	-

Table 5: Relationship between yield, oil content, PUFA content, or ALA content and their candidate limiting factors estimated with model mixing method combined with bootstrap. Relative importance value is given before and after bootstrap to see the stability of the ranking, but parameter estimation and standard deviation (StdD) are the values after bootstrap.

Variable of interest	Potential limiting factors [1]	Parameter estimation	StdD	Relative importance value	
		After bootstrap	After bootstrap	Before bootstrap	After bootstrap
Yield					
	NNI	3624.14	793.29	1	1
	MILDEW	-16.67	3.93	1	1
	WATER STRESS[2]	2204.32	1650.10	0.69	0.67
	HAIL	-0.45	2.77	0.3	0.41
Oil content					
	MILDEW	-0.03	0.01	0.87	0.82
	CGDD (grain filling)	0.03	0.02	0.73	0.7
	NNI	-2.21	2.20	0.48	0.53
	WATER STRESS[2]	0.24	2.53	0.3	0.41
PUFA content					
	CGDD (grain filling)	0.06	0.01	1	1
	HIGH TEMPERATURES	-0.81	0.07	1	1
	WATER STRESS[2]	3	1.47	0.97	0.86
	NNI	-0.35	0.81	0.34	0.45
ALA content					
	CGDD (grain filling)	0.06	0.01	1	1
	HIGH TEMPERATURES	-0.80	0.11	1	1
	WATER STRESS[2]	1.85	1.77	0.67	0.64
	NNI	0.88	1.15	0.44	0.49

[1] NNI = Nitrogen Nutrition Index; CGDD = Cumulative Growing Degrees Days.

[2] Depending on the variable, WATER STRESS is calculated either over the entire growing period (for yield), or over the grain filling period (for oil, PUFA, and ALA contents).

Table 6: Parameter estimation, standard deviation and p-value of the four-factor linear model defined to explain the effect of environmental conditions and crop management routes on NNI (R^2 = 0.57). NDFS is the quantity of nitrogen uptake from the soil by the intercropped species at flowering stage, NSOIL is the quantity of available nitrogen in soil between sowing and flowering, WATER STRESS is the value of WS calculated between sowing date and flowering stage, and BM WEEDS is the total aerial biomass of weeds at flowering stage.

Variable tested	Parameter estimation	Standard deviation	p-value
NDFS	-0.0041	0.0007	< 0.001
NSOIL	0.0021	0.0007	0.004
WATER STRESS	0.63	0.26	0.020
BM WEEDS	-0.00045	0.00028	0.11