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► To cite this version:

Margot Leclère, Anne-Raphaëlle Lorent, Marie-Hélène Jeuffroy, Arnaud Butier, Christophe Chatain, et al.. Diagnosis of camelina seed yield and quality across an on-farm experimental network. *European Journal of Agronomy*, 2021, 122, pp.126190. 10.1016/j.eja.2020.126190 . hal-03442252

HAL Id: hal-03442252

<https://hal.inrae.fr/hal-03442252>

Submitted on 7 Nov 2022

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

2

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14

15 **Abstract**

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

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

41

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

43 **1. Introduction**

44 *Camelina* (*Camelina sativa* (L.) Crantz) is an oilseed crop increasingly studied due to its
45 original seed composition and the diversity of its uses (Chaturvedi et al., 2018; Righini et al.,
46 2016). *Camelina* is characterized by high contents of seed oil (between 30 and 40 %), poly-
47 unsaturated fatty acids (PUFA, higher than 50%), and mono-unsaturated fatty acids (MUFA,
48 around 30 %) (Belayneh et al., 2015). Main fatty acids (FAs) are linolenic (C18:3, 28-50.3%),
49 linoleic (C 18:2, 16-22.4%), oleic (C18:1, 14.9-18.8%), and eicosenoic (C20:1, 11.6-17.5%)
50 acids (Popa et al., 2017). As *camelina* seeds are also rich in protein, *camelina* seed meal
51 contains up to 40 % crude protein, after oil extraction (Zubr, 2003a). *Camelina* has been
52 widely investigated as feedstock for biofuels (biodiesel or renewable jet fuel) because of its
53 oil properties (Campbell et al., 2013; Mohammad et al., 2018; Mohammed et al., 2017b;
54 Neupane et al., 2018; Tabatabaie et al., 2018). However, there are several other uses reported
55 for *camelina* oil, meal, or specific compounds, such as human food, feed, or chemical
56 derivatives (Berti et al., 2016; Waraich et al., 2013). Therefore, *camelina* can be considered as
57 a flex crop, i.e. a crop with multiple uses (food, feed, fuel, fibre, and industrial materials),
58 which allows farmers to adapt themselves to market opportunities (Borras et al., 2016). For
59 instance, *camelina* oil has been identified as a possible source of polyols and consequently, as
60 an alternative to castor oil, widely used in commercial applications (Omonov et al., 2017).
61 Moreover, *camelina* meal can either be used in fish diet (Yildiz et al., 2018) or as raw material
62 for bio-adhesive production (Zhu et al., 2017).

63 Besides its wide range of potential uses, *camelina* has many agronomic advantages (Berti et
64 al., 2016; Putnam et al., 1993; Vollmann et al., 1996). *Camelina* is a short lifecycle crop with
65 low water and nutrient requirements, and has shown tolerance to some common pests and
66 diseases of the Brassicaceae family (Hunsaker et al., 2011; Mohammed et al., 2017a; Séguin-
67 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.

94 2. Materials and methods

95 2.1. The on-farm experimental network

96 The experimental network corresponded to five camelina crop management routes, tested in
97 several farmers' fields in 2017 and 2018. Fields were located within an area of 1000 km² in
98 northern France (Oise department), ranging from 49.4 to 49.7°N latitude, and 2.86 to 3.13°E
99 longitude, and covered the three main soil types of the region (deep loamy, moderately deep
100 sandy, and shallow calcareous soils, previously described in Leclère et al. (2019)). The area
101 was characterized by an oceanic climate with mean annual temperature and cumulative
102 rainfall respectively equal to 11 °C and 681 mm over the 1981-2010 period. To mimic on-
103 farm conditions, we used an experimental design in strips without replicates, comprised of
104 thirty-nine experimental strips of 2500 m² each and spread into 9 environments (Table 1).

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

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

122

123 2.2. Data collection

124 Six plots of 0.5 m² were randomly sampled all along each strip at camelina flowering and
125 maturity stages (respectively stages 65 and 85 on the BBCH scale; Martinelli and Galasso,
126 2011). At both dates, the aerial dry biomass (g m⁻²) of each species (weeds, camelina, pea,
127 and barley) was measured by weighing the samples after a period of 48h of drying at 80°C. At
128 maturity stage, camelina, pea, and barley samples were threshed, and seeds were weighed to
129 measure the yield of each species (pYield, kg ha⁻¹). Sub-samples of all grown species were
130 sent to analysis to determine nitrogen concentration (%) in the whole plants at flowering and
131 in seeds and straws separately at maturity.

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

135

$$136 \quad (1) \text{NDFS}_{\text{barley}} = \text{aerial dry biomass (kg ha}^{-1}\text{)} * \text{nitrogen concentration (\%)}$$

137

$$138 \quad (2) \text{NDFS}_{\text{pea}} = [\text{aerial dry biomass (kg ha}^{-1}\text{)} * \text{nitrogen concentration (\%)}] - N_{\text{fix}}$$

139 where N_{fix} is the amount of nitrogen resulting from the symbiotic N₂ fixation (KgN
140 ha⁻¹) and estimated using the relation established by Naudin et al. (2011) based on
141 different pea intercropping experiments ($R^2 = 0.86$):

$$142 \quad N_{\text{fix}} = 0.0215 \times \text{pea aerial dry biomass (kg ha}^{-1}\text{)} - 0.6986$$

143 Camelina crude seed protein content (%) was calculated by multiplying nitrogen
144 concentration in camelina seeds by 6.25 (ISO 16634-2:2016, <https://www.iso.org>). Sub-
145 samples of camelina seeds were also used to measure oil content (%) and to determine the
146 fatty acids (FA) profile, using solvent extraction method and gas chromatography (Puttick et
147 al., 2009). Based on this analysis, the content of each group of FA (PUFA, MUFA and SFA
148 respectively poly, mono-unsaturated FA, and saturated FA) was calculated (%). At maturity,
149 on each strip, three sub-plots of 60 m² in which no plants had been previously collected, were
150 mechanically harvested with an experimental combine harvester to measure, after manual
151 separation of the grains of each species, using a sieve, the mechanical yield of camelina
152 (mYield, kg ha⁻¹) corresponding to the yield that could be obtained under on-farm conditions.
153 Eight soil cores (0 to 90 cm depth) were collected on each strip prior to sowing, on February,
154 22nd in 2017 and March, 5th in 2018. Each core was cut into three layers (0-30, 30-60 and 60-
155 90 cm), and soil inorganic nitrogen (kgN ha⁻¹) was measured for each layer. The total soil
156 inorganic nitrogen prior sowing (0-60cm) was obtained by summing the results of the two
157 first layers. In addition, soil analyses were performed to determine particle size and chemical
158 composition (pH, CaCO₃, available P and K, total nitrogen and carbon, and organic matter).
159 Based on these measurements, the amount of inorganic nitrogen available for crops from
160 sowing to camelina flowering (NSOIL, kgN ha⁻¹) was estimated as follows:

$$161 \quad NSOIL = TotN + Mh + Mr + Mr_{cc}$$

162 where *TotN* is the total soil inorganic nitrogen measured prior sowing (0-60cm), *Mh*
163 the amount of nitrogen derived from the mineralisation of humus (kgN ha⁻¹), *Mr* is the
164 amount of nitrogen derived from the mineralisation of the previous crop residues, and
165 *Mr_{cc}* is the amount of nitrogen derived from the mineralisation of the cover crop
166 residues, calculated using the COMIFER equations (COMIFER, 2013).

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

171

172 2.3. Indicators for limiting factors

173 Based on scientific literature and field observations, candidate indicators explaining the
174 variability of camelina performance were defined *a priori*. Yield was assumed to be impacted
175 by nitrogen, water, downy mildew, and hail, whereas oil and protein contents were assumed
176 to be affected by nitrogen, water, downy mildew, and grain filling duration, and PUFA and
177 MUFA contents by nitrogen, water, grain filling duration, and high temperatures (Cappelli et
178 al., 2019; Hergert et al., 2016; Jiang et al., 2013; Vollmann et al., 2001; Zubr and Matthäus,
179 2002).

180

181 2.3.1. *Indicator for nitrogen crop status*

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

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

221
222 At sowing, the soil water content was assumed to be equal to the maximal soil water content,
223 as no water deficit was noticed during the winter.

224
225 *2.3.3. Indicators for yield loss due to mildew and hail*

226 In 2018, symptoms of downy mildew (caused by *Peronospora camelinae*) were observed on
227 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
228 number of pods on ten plants for each replicate, and then by averaging them for each strip.

229
230 On the 12th of July 2017, a hailstorm occurred on the three sites located in the south of the
231 area. This climatic incident caused an opening of pods (Figure 1b). Similarly to downy
232 mildew, an indicator to assess the pod opening due to hailstorm (HAIL, %) was thus used: the
233 ratio between the opened pods and the total number of pods on ten plants for each replicate
234 was calculated, and then averaged for each strip.

235
236 *2.3.4. Indicator for grain filling duration*

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

239
$$CGDD = \sum_{d = \text{flowering stage}}^n GDD_d \text{ (if } GDD_d \geq 0 \text{)}$$

240
$$\text{with } GDD_d = \frac{T_{min_d} + T_{max_d}}{2} - T_{Base}$$

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

244

245 *2.3.5. Indicator for high temperature stress*

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

251

252 2.4. Data analysis

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

256

257 *2.4.1. Step 1*

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

262

263 *2.4.2. Step 2*

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

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

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

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

277
$$w_k = \frac{e^{-0.5(AIC_k - AIC_{\min})}}{\sum_{k=1}^n e^{-0.5(AIC_k - AIC_{\min})}}$$

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

282

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

287

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

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

297

298 *2.4.3. Step 3*

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

310 3. Results

311 3.1. Camelina performance across the experimental network

312 Camelina yield from experimental plots (pYield) varied from 62 to 2585 kg ha⁻¹ with higher
313 yields in 2017 than in 2018, and the lowest yields for the CB_50 and CB_25 crop
314 management routes (Figure 2). For the intercrops, pea yield (also from experimental plots)
315 varied from 449 to 2153 kg ha⁻¹, and barley yield from 753 to 5310 kg ha⁻¹, with higher yields
316 for the CB_50 than for the CB_25 (Figure 2). Camelina mechanical yield (mYield) varied
317 from 77 to 2080 kg ha⁻¹ and was highly related to pYield ($p < 0.001$, $R^2 = 0.94$) (data not
318 shown). As a result, all the analyses were run on pYield (named as camelina yield hereafter).
319 No significant correlation was found between camelina yield and oil or protein content
320 (Figure 3a). However, camelina yield was slightly positively correlated to MUFA ($R^2 = 0.11$, p
321 < 0.05) (Table 4).

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

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

332 Finally, ALA content varied from 30.9 to 37.8 % and was negatively correlated to LA content
333 (Figure 3d). This negative correlation thus explained the positive correlation between PUFA
334 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

360 content ($p < 0.001$ and $p = 3.31 \times 10^{-2}$ respectively), but they only explained 21% of the
361 variability observed. Overall, oil content slightly increased with longer grain filling period but
362 decreased in 2018 because of downy mildew (Table 5). Neither nitrogen status nor water
363 stress during the grain filling period were identified as major limiting factors for oil content,
364 as their relative importance values were around 0.5 (Table 5).

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

376

377 3.3. Effects of environmental conditions and crop management routes on major limiting 378 factors

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

384 As no nitrogen fertilisation was applied, NNI at flowering stage was assumed to be affected
385 by (i) the amount of available inorganic nitrogen in the soil (NSOIL, kgN ha⁻¹, defined in the
386 section 2.2), (ii) the amount of nitrogen uptake by the other species (barley, pea and/or weeds)
387 at flowering stage, and (iii) water stress between sowing and flowering. For barley and pea,
388 the amount of nitrogen uptake corresponded to NDFS (KgN ha⁻¹, defined in the section 2.2.).
389 For weeds, total weed biomass at flowering (varying from 1 to 272 g m⁻² depending on the
390 crop management routes, the experimental site and the year) was used as an indicator because
391 we did not measure nitrogen concentration in weeds. The four-factor regression model tested
392 (R²=0.57, Table 6) showed that NNI was significantly correlated with N uptake of the crops
393 grown with camelina, the quantity of available inorganic nitrogen in the soil, and water stress.
394 No significant effect of weed biomass was found (Table 6). More precisely, NDFS ranged
395 from 5 to 80 kg N ha⁻¹, and was negatively correlated to NNI (Figure 6). Intercrop with pea
396 resulted in higher camelina NNI than intercrop with barley because of lower amount of soil-
397 derived nitrogen absorbed by pea than barley, resulting from the symbiotic N₂ fixation.
398 Conversely, lower NNI were observed for camelina-barley intercrop due to the high amount
399 of nitrogen uptake by barley, except when the quantity of available inorganic nitrogen in the
400 soil was high (Figure 6). NNI was positively correlated to NSOIL and to the indicator of
401 water stress (Table 6) meaning that high amount of nitrogen in soil and no water stress
402 (WATER STRESS = 1) induced higher NNI.

403 Incidence and severity of downy mildew infection at harvest date appeared to be significantly
404 affected by weather conditions before flowering and by weed biomass at flowering. More
405 precisely, the percentage of diseased pods was positively correlated to cumulative rainfall
406 between sowing and flowering and weed biomass, both explaining together 74 % of the
407 variability observed. Drier weather conditions in 2017 (79 mm (±10) of cumulated rainfall
408 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.

412 4. Discussion

413 4.1. Camelina performance variability as an opportunity to develop flexible and adaptive 414 value-chains

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

437 For years, the strategy adopted by the advisors and collectors was to standardize yield and
438 seed quality, in a given supply area, through the use of inputs. But today, the emergence of
439 diversifying flex-crops, with multiple uses, within a context of climate change leading to an
440 increased inter-annual variability, suggests the implementation of a “sustainable
441 commercialisation”, defined by Jordan et al. (2016) as a “coordinated innovation process that
442 integrates a new crop into the agriculture of a region, while intentionally addressing
443 economic, environmental and social sustainability challenges via multi-stakeholder
444 governance”. In our case study, although contrasting performance was observed between
445 2017 and 2018, both situations were suitable for a commercial valorisation. Indeed, high level
446 of production combined with oil characterised by a low PUFA/MUFA ratio, i.e. with good
447 properties for industrial uses (Rodríguez-Rodríguez et al., 2013), as in 2017, could be
448 considered to satisfactorily supply an industrial outlet (chemicals or biofuels). On the
449 contrary, low yield but combined with oil rich in omega 3 (ALA), i.e. with high nutritional
450 value (Waraich et al., 2013), as in 2018, would be more adapted to a high-value market
451 (human food or family pet feed). Therefore, in this perspective of “sustainable
452 commercialisation”, this inter-annual variability of camelina performances in northern France
453 would argue for the development of a flexible local value-chain in which the uses of camelina
454 would be adapted each year regarding yield and seed quality (Parada et al., 2018). Such kind
455 of coupled innovations (Meynard et al., 2017), will probably require the design of early
456 indicators useful for industrialists to predict, from field measurements, camelina seed quality,
457 and thus future uses, as it has been proposed for the management of the harvest of malting
458 barley at the supplying area scale (Le Bail, 1997).

459

460

461 4.2. Contribution of the agronomic diagnosis to include camelina in cropping systems of
462 northern France

463 Camelina yield has been shown to respond to nitrogen up to 200 kg ha⁻¹ (Jiang and Caldwell,
464 2016; Solis et al., 2013). In our study, without nitrogen fertilisation, yield varied with nitrogen
465 crop status (NNI), which variations were explained by the amount of inorganic nitrogen
466 available in the soil, as previously reported by Wysocki et al. (2013). Soils in the area of the
467 present study are known to have different capacities in mineral nitrogen supply related to their
468 physico-chemical composition and depth (Begon et al., 1977). In addition, several studies
469 have shown the impact of legume, whether cash or cover crop, on the inorganic nitrogen
470 availability for the following crop (Coombs et al., 2017; Li et al., 2015; Reckling et al., 2016;
471 Stagnari et al., 2017). Therefore, the choice of both soil type and previous crop or cover crop
472 should be considered to introduce camelina in cropping systems, and design low-input
473 management of camelina with satisfying quantitative and qualitative performance.

474 Our results confirmed the impact of temperatures on camelina seed quality, thus explaining
475 seed quality variations observed across locations, as already mentioned in previous studies
476 (Berti et al., 2011; Vollmann et al., 2007). Here, we specifically showed a significant effect of
477 the number of days with maximal temperature above 25°C on ALA content. With the current
478 climate change, the frequency of periods of heat may widely increase (IPCC, 2018). For
479 instance, in the study area, the number of years, for which there were more than 20 days at a
480 maximal temperature above 25°C during grain filling period, increased from 2 to 5
481 respectively between the decades of 1996-2005 and 2006-2015 (long term weather data
482 extracted from the on-line platform CLIMATIK for the Estrées-Mons meteorological station,
483 49.875°N - 3.031°E). In their recent study, Righini et al. (2019) suggested that shifting
484 camelina sowing from spring to autumn in Italy could be a way to enhance oil quality. In a
485 context of climate change, delaying camelina sowing during the autumn or summer could be

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

498

499 4.3. Contribution of the agronomic diagnosis to design camelina crop management routes 500 suited to northern France

501 The agronomic diagnosis is a key step to re-design crop management routes because it
502 contributes to identify problems and thus potential levers to overcome them (Loyce and Wery,
503 2006). In the case of camelina in northern France, the diagnosis of camelina yield and seed
504 quality highlighted three topics that should be addressed to design highly-effective spring
505 camelina crop management routes: (i) nitrogen management, especially for the intercrops with
506 cereals, to limit competition, (ii) weed management to limit nitrogen competition and downy
507 mildew development, and (iii) varietal choice to be better suited to environmental conditions.
508 In our network, all camelina NNI values were lower than 1, with a majority of values between
509 0.4 and 0.6, thus suggesting nitrogen deficiency in all situations. However, Wysocki et al.
510 (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,

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

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

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560 **5. Conclusion**

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

570 **Acknowledgments**

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

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

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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.

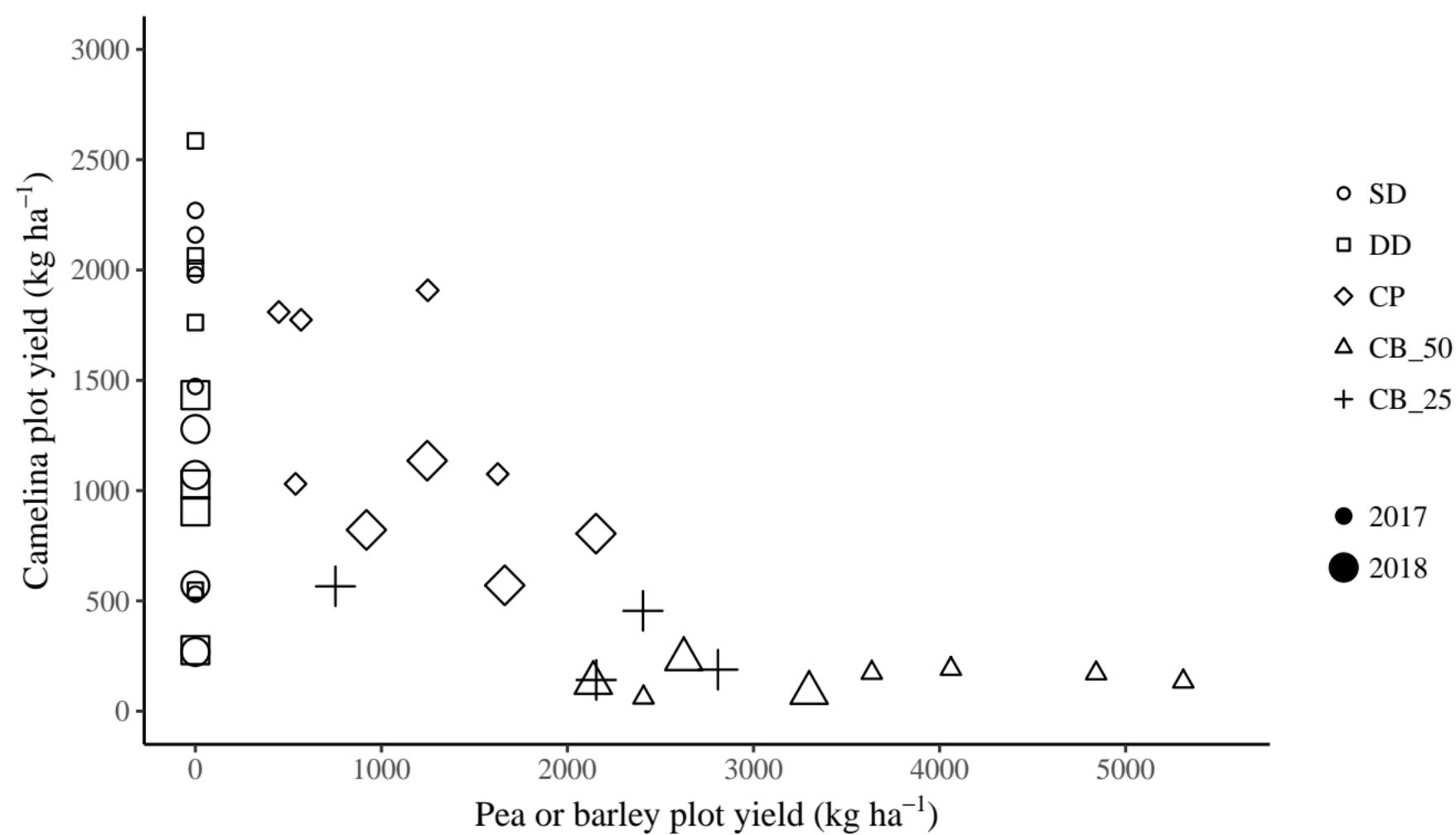
Figure 3: Camelina yield (kg ha^{-1}) and oil, protein, PUFA, MUFA, ALA, and LA contents (%) in camelina seeds across the experimental network: relationships between (a) camelina plot yield and oil content, (b) oil and protein contents, (c) PUFA and MUFA contents, and (d) ALA and LA contents. Shape and 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.

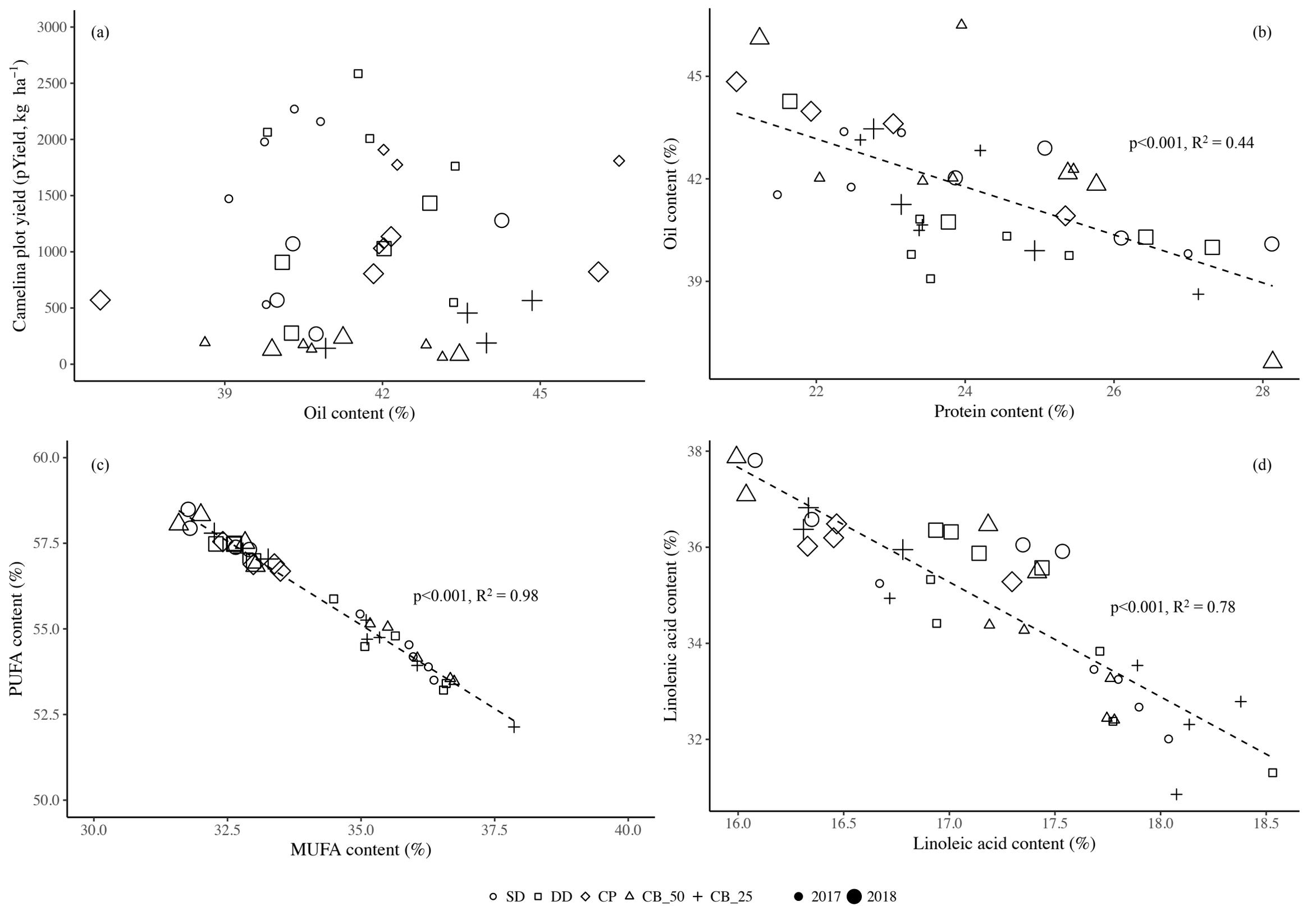
Figure 4: Camelina yield (kg ha^{-1}) as a function of Nitrogen Nutrition Index of camelina at flowering (NNI, unitless) and pod loss due to mildew (%). Symbols shape and size respectively represent the crop management route and the year. Colour gradient represents pod loss due to downy mildew: green 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.

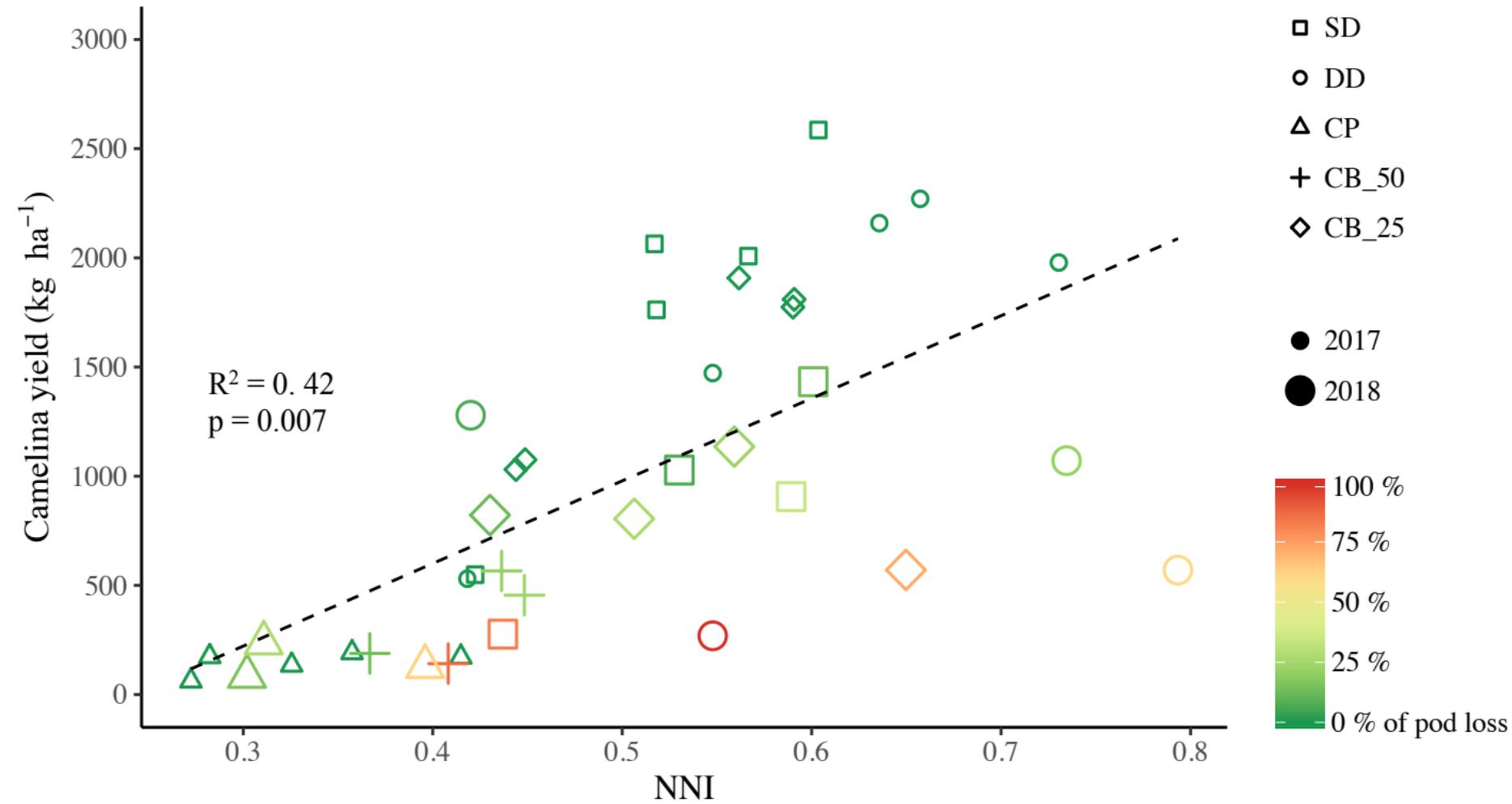
Figure 5: Linolenic content (%) as a function of grain filling duration ($^{\circ}\text{Cd}$) and high temperatures. Symbols shape and size respectively represent the crop management route and the year. Colour gradient represents the number of days with maximal temperature above 25°C : blue tones correspond 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.

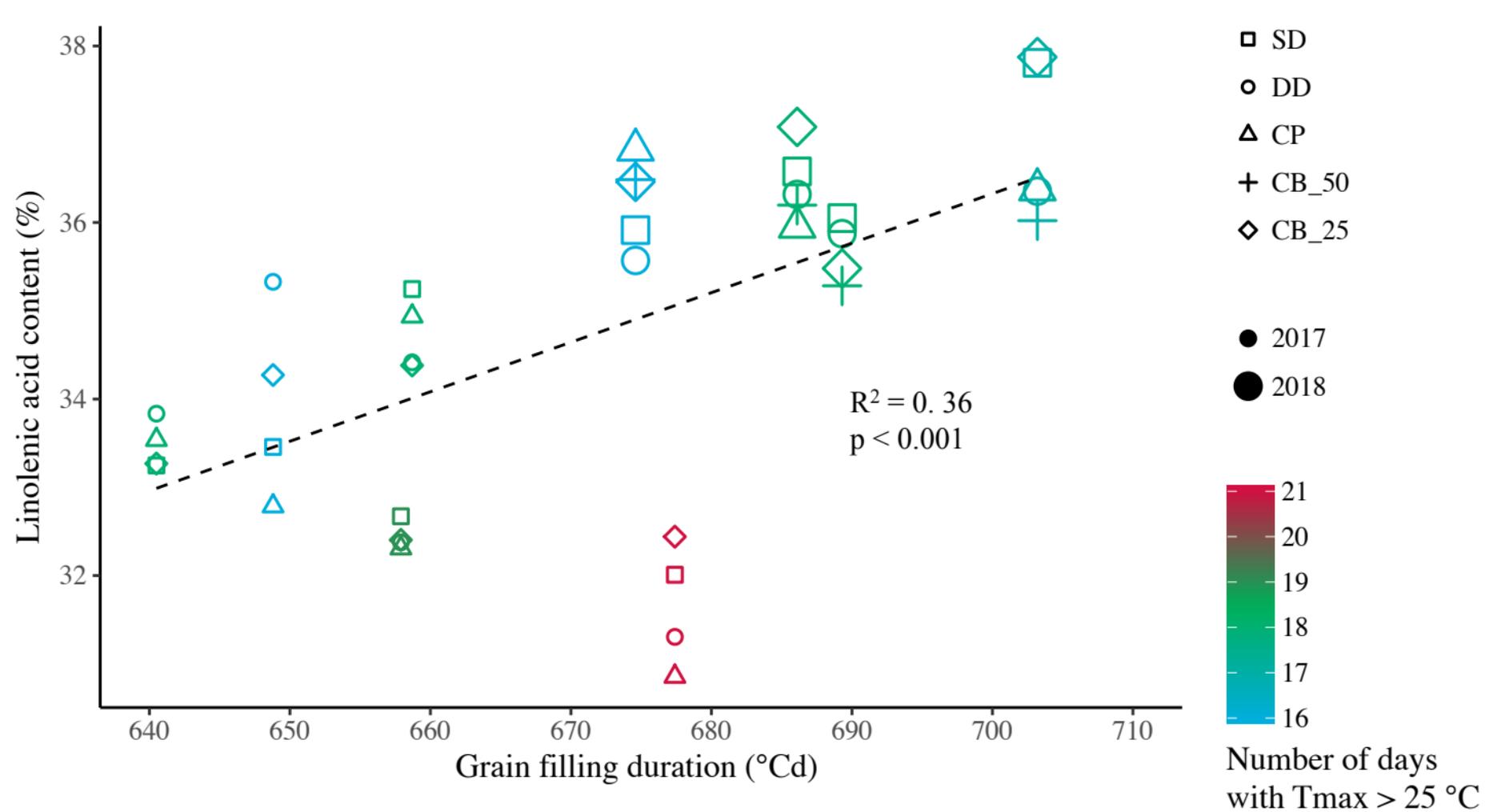
Figure 6: Nitrogen Nutrition Index (NNI) as a function of the amount of uptake nitrogen by the intercrop species at flowering stage (NDFS, kg N ha^{-1}) and the total nitrogen available in soil (Nsoil, kg N ha^{-1}). Symbols shape and size respectively represent the crop management route and the year. Colour gradient represents Nsoil: blue and green tones correspond to lower values ($<75 \text{ kg N ha}^{-1}$), yellow-orange tones correspond to intermediate values (between 75 and 115 kg N ha^{-1}), and red tones to higher values ($>115 \text{ kg N ha}^{-1}$). 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.











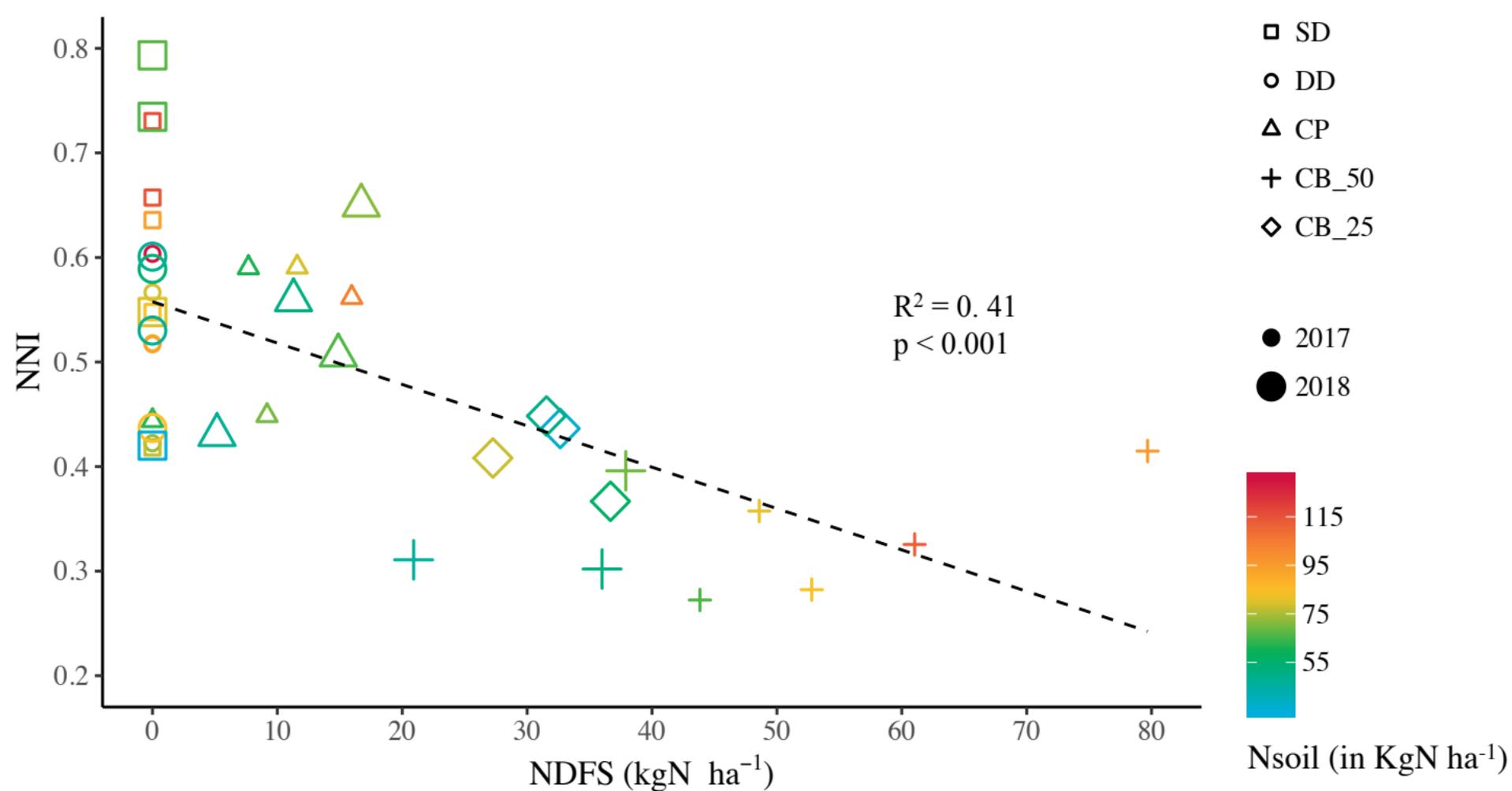


Table 1: Description and location of the thirty-nine experimental strips. Each location is identified by a three-letter code corresponding to the municipality where the field is located: AMY for Amy (49.655°N, 2.825°E), AUT for Autrêches (49.444°N, 3.126°E), GUR for Gury (49.570°N, 2.799°E), MOU for 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 CaCO₃, 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	CaCO ₃ (%)	Total soil inorganic nitrogen (0-90cm) prior sowing (kgN ha ⁻¹)	Maximal soil water content, <i>SWC</i> _{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