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2 **Dynamic analysis of competition and complementarity for light and N use to**
3 **understand the yield and the protein content of a durum wheat-winter pea intercrop**

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10 **Abstract**

11 In a previous paper (Bedoussac and Justes 2009, Plant and Soil DOI: 10.1007/s11104-009-0082-2), we showed that intercropping
12 of durum wheat and winter pea increased the yield and protein concentration of durum wheat when early N availability was less
13 than 120 kg N.ha⁻¹. The aim of the present work was to understand these results by analysing intercrop species dynamics for
14 growth, light and N acquisition. A 2-year field experiment was carried out in SW France with different fertilizer-N levels in order
15 to compare wheat (*Triticum turgidum* L.) and pea (*Pisum sativum* L.) grown as sole crops and as an intercrop in a row substitutive
16 design. The advantages of intercropping in low N conditions were mainly due to: i) better light use (up to 10%) thanks to species
17 dynamic complementarity for leaf area index and height, ii) growth complementarity over time (higher growth rate of wheat until
18 pea flowering and then of pea until wheat flowering), and iii) dynamic complementary N acquisition associated with better wheat
19 N status throughout growth. Disadvantages, underlining poorer complementarity within the intercrop stand, were observed with
20 ample available N in early growth. This induced higher cereal growth during winter which led to increase interspecies
21 competition by reducing pea light absorption and consequently its biomass production.

22 **Keywords**

23 Intercropping, complementary resource use, plant competition, growth dynamics, nitrogen acquisition, land equivalent ratio, light
24 use

25

25 **Introduction**

26 Intercropping (IC) - the simultaneous growing of two or more species in the same field for a significant period of their growth but
27 without necessarily being sown and harvested together (Willey 1979) - is known to increase yield (Y) and grain protein
28 concentration (GPC) in spring-sown crops compared to sole crops (SC), particularly in low N input systems (Willey 1979; Ofori
29 and Stern 1987; Vandermeer 1989; Hauggaard-Nielsen et al. 2003). For these reasons, there has been renewed interest in
30 intercropping since the last decade (Anil et al. 1998; Malézieux et al. 2008).

31 In the previous companion paper (Bedoussac and Justes 2009) we demonstrated that i) intercropping of winter crops such as
32 durum wheat and winter pea can increase dry weight, yield and N acquisition in low N input systems ($< 120 \text{ kg N ha}^{-1}$ available),
33 and ii) the efficiency of intercropping to improve yield and wheat grain protein concentration depends on N availability during
34 early growth. More precisely, we showed that intercrop permits the use of available resources more efficiently than the
35 corresponding sole crops because the two intercropped species do not compete for exactly the same resource niche and thereby
36 tend to use resources - notably N - in a complementary way. This has also been shown for grain legume-cereal spring-sown
37 intercrops (eg. Hauggaard-Nielsen et al. 2001ab). Our previous paper dealing with durum wheat-winter pea intercrops (Bedoussac
38 and Justes 2009) indicated that the durum wheat has a higher interspecific competitive ability at high soil N levels than the winter
39 pea. This result was in good agreement with data observed for various types of intercrops, such as spring barley-pea (Hauggaard-
40 Nielsen and Jensen 2001) or spring wheat-pea (Ghaley et al. 2005). Moreover, as already observed by Ofori and Stern (1987) and
41 Jensen (1996) for spring-sown intercrops, we demonstrated that winter intercrops such as durum wheat-winter pea intercrop also
42 allowed for more N to be taken up by the durum wheat plant, more N to be remobilized into its grain and hence wheat grain
43 protein concentration to increase in the intercrop in comparison to the sole crop. Indeed, the cereal produced less dry weight per
44 square meter when intercropped but it has access to an almost similar amount of soil inorganic N in both the intercrop and the
45 sole crop. This is due to the grain legume's symbiotic N_2 fixation rate increase in intercrop (Bedoussac and Justes, 2009) as
46 already described by Crozat et al. (1994) on spring-sown intercrops. Such results are of particular interest in low N input cropping
47 systems and in organic farming, where soil mineral N is often limiting for cereals with a high N demand, such as durum wheat. It
48 is also interesting for conventional cropping systems, to reduce high levels of N fertilizer amounts generally applied to fulfil
49 durum wheat N requirements and to obtain maximum yield and grain protein content (Garrido-Lestache et al. 2004).

50 Species temporal interactions are complex, varying with, for example, nutrient availability or other environmental factors
51 (Connolly et al. 1990). Thus, intercrop competition studies cannot base their conclusions on data from just one single harvest of
52 crops at maturity and grown at one level of N, for example like Dhima et al. (2007). In particular, intercrops are known to be
53 more efficient in intercepting light (Berntsen et al. 2004; Jahansooz et al. 2007) compared to sole crops because of

54 complementary use of space when crops differ in their aerial architecture (e.g. tall vs. short crops) and of time when crops have
55 life cycles that differ in timing (e.g. early vs. late maturing) (Trenbath 1986; Tsubo et al. 2001). Competitiveness of a given
56 species for solar radiation absorption and consequently its dry weight (DW) and yield depends on its green leaf area index
57 (GLAI), foliar architecture, height and timing, relative to those of its companion crop (Fukai 1993; Midmore 1993).

58 While many references are available on cereal-legume spring-sown intercrops dynamics (e.g. Andersen et al. 2004, Ghaley et al.
59 2005, Corre-Hellou et al. 2006, Jensen 1996) there is no specific reference on wheat-grain legume winter sown intercrops. Now
60 winter sowing are more adapted to conditions of southern Europe particularly to dodge water stress during wheat ripening.
61 Moreover, the growth period of winter crops growth is longer than that of spring crops and hence species dynamics and
62 interactions between crops are certainly different throughout crop growth. The aim of this paper was therefore to analyse the
63 dynamics growth and the resource acquisition along the crop cycle. This will allow explaining the final outcome of a durum
64 wheat-winter pea intercrop such as the proportion of species, the total grain yield and the complementary use of N by
65 components. This analysis should provide the knowledge required to propose further optimal strategies in order to improve the
66 management of durum wheat-winter pea cropping sequences. This paper focuses on species dynamics under different N
67 availabilities modified by N fertilization (quantity and splitting of doses) in a durum wheat-winter pea intercrop compared to their
68 respective sole crops. This was achieved through field experiments conducted in 2005-2006 and 2006-2007 with different soil N
69 availabilities in a substitutive design. We analysed throughout the intercrop growth: i) species aerial biomass dynamics, ii) canopy
70 architecture dynamics (green leaf area index and plant height), iii) N and light use and iv) the potential advantages for biomass, N
71 acquisition and wheat nitrogen nutrition status.

72

72 **Materials and methods**

73 **Site and Soil**

74 The experiment was carried out on the experimental fields of the Institut National de la Recherche Agronomique station in
75 Auzeville (SW France, 43°31'N, 1°30'E) in 2005-2006 (Exp.I) and 2006-2007 (Exp.II). The 25-year mean annual rainfall in
76 Auzeville is 650 mm and the mean annual air temperature is 13.7 °C with a maximum monthly mean daily temperature of 21.9 °C
77 in August and a minimum monthly mean daily temperature of 6.0 °C in January. The rainfall during the growing seasons was 361
78 mm and 468 mm for Exp.I and Exp.II respectively, while the 25-year mean was 489 mm for the same period (November-July).
79 Exp.I was characterized by a cold winter and a dry warm spring, whereas Exp.II was characterized by a warm and dry winter and
80 a rather wet spring. Then, the two years were quite different in terms of climatic conditions indicating a good level of robustness
81 in the dynamic analysis of intercrops.

82 Exp.I was carried out on a loamy soil (24% clay, 29% silt and 47% sand) with an available water capacity of 223 mm (0-150 cm).
83 Exp.II was conducted on a clay loam soil (30% clay, 38% silt and 32% sand) with an available water capacity of 207 mm (0-150
84 cm). For both experiments, phosphorus, potassium and cation exchange capacity values were not limiting (for more details, see
85 Bedoussac and Justes 2009). The four previous crops on the experimental sites were durum wheat (*Triticum turgidum*), sunflower
86 (*Helianthus annuus*), durum wheat and sorghum (*Sorghum bicolor*) for Exp.I and sunflower, durum wheat, sorghum and
87 sunflower for Exp.II.

88 **Experimental design**

89 Durum wheat (W) (*Triticum turgidum* L, cv. Nefer) and winter pea (P) (*Pisum sativum* L., cv. Lucy) were grown as: i) sole crop
90 (SC) sown at the recommended density (336 and 72 seeds m⁻² for durum wheat and winter pea respectively) and ii) intercrop (IC)
91 where each species was sown at half of the sole crop densities in alternate rows.

92 In both experiments, different fertilizer-N sub-treatments were evaluated on wheat sole crop and intercrop while pea sole crop
93 was grown without any N application assuming that N₂ fixation allows fulfilling pea N requirements for optimal growth. In Exp.I
94 three N treatments were compared: i) no fertilizer-N (N0), ii) low N fertilization (N100) split into two applications of 50 kg N ha⁻¹
95 at '1 cm ear' (E1cm, Zadoks 30 (Zadoks et al. 1974)) and 'flag leaf visible' (FLV, Zadoks 37) and iii) moderate N fertilization
96 (N180) split in 3 applications of 30 kg N ha⁻¹ at wheat tillering (Zadoks 23), 100 kg N ha⁻¹ at E1cm and 50 kg N ha⁻¹ at FLV. In
97 Exp.II we carried out four N treatments: i) no fertilizer-N (N0), ii) one application of 60 kg N ha⁻¹ at FLV (N60) to increase grain
98 protein iii) one application of 80 kg N ha⁻¹ at E1cm (N80) to increase yield and iv) a moderate N fertilization (N140) split in two
99 applications of 80 kg N ha⁻¹ at E1cm and 60 kg N ha⁻¹ at FLV. In Exp.II, the previous crop was a rainfed sunflower grown with

100 four levels of fertilizer N: 50, 150, 0 and 100 kg N ha⁻¹ for N0, N60, N80 and N140 respectively, which led to contrasting
101 dynamics of N availability. As a consequence, the N60 treatment was more than the simple effect of a late N supply due to the
102 previous treatment on sunflower, so we chose to name it N60+. Initial mineral N, early mineral N available and mineral N
103 available throughout crop growth for the two experiments are described in Table 1 (for details, see Bedoussac and Justes 2009)[0].
104 The experimental layout for both experiments was a randomized split-plot design with N application as main plots and crops as
105 subplots, with five replicates in Exp.I (four replicates for wheat sole crop in N0 and intercrop in N180) and three replicates in
106 Exp.II (five replicates for pea sole crop in order to control soil variability). Each subplot consisted of 11 rows spaced of 14.5 cm
107 apart. Fungicide-treated seeds were sown on November 8, 2005 (Exp.I) and on November 9, 2006 (Exp.II) using a 6-row
108 pneumatic precision experimental prototype drill with 29 cm row separation. Sowing was done in two passes by moving to the
109 right (14.5 cm) for the second pass and by blocking one row of the drill. The intercrop treatment consisted of 6 rows of wheat and
110 5 rows of pea spaced of 14.5 cm apart, with alternate wheat and pea rows. In Exp.II, 20 mm of irrigation water was applied after
111 sowing because of the low water content in the topsoil. Weeds, diseases and green aphids were controlled as much as possible by
112 application of appropriate pesticides.

113 **Measurements and analysis**

114 The number of seedlings in four rows of 1 m length was counted one month after emergence.
115 Four (Exp.I) and five (Exp.II) samplings were carried out during the growing season at key development stages (Fig. 1). Outside
116 rows (2 rows on each side of the plot) were not harvested in order to avoid border effects between plots. At each measurement, 7
117 rows of 0.5 m long were harvested from each main plot by cutting plants just above the soil surface. Sampling points were 0.5 m
118 apart. Final harvesting took place at pea physiological maturity for pea sole crop and at wheat physiological maturity (Zadoks 92)
119 for wheat sole crop and intercrop. At maturity, the remaining area (4.5 m x 1.015 m) was mechanically harvested to determine
120 total yield. Except for the final date of sampling, the harvested plant biomass was separated into pea and wheat and into green
121 leaf, stem and senescent material. Senescent parts of green leaves were removed and added to senescent material. Green leaf area
122 was determined using a LI-3100 planimeter (LI-COR Inc., Lincoln, USA). Samples were dried at 80°C for 48 h. Dry weight of
123 aerial biomass and N concentration of plants were determined for every crop sample. At maturity, total dry weight and yield were
124 measured on 150 wheat ears and 20 pea plants, together with N concentration of grain and straw. Total N were analyzed on sub-
125 samples of finely ground plant material using the Dumas combustion method with a Leco-2000 analyzer (LECO Corporation, St.
126 Joseph, USA). Canopy height was measured manually for each treatment considering its maximum height at: i) '1 cm ear' stage
127 of wheat (E1cm), ii) beginning of pea flowering (BPF) and iii) wheat flowering (WF).

128 The photosynthetically active radiation (PAR, 400-700 nm wavebands) was measured using a 30 cm long line sensor PAR-80
 129 (Decagon Devices Inc., Washington, USA) by orientating it perpendicularly to the rows. Incident PAR on the top of the canopy
 130 (PAR_0) and PAR transmitted to the soil (PAR_T) were measured orientating the sensor towards the sky. On the other hand, PAR
 131 reflected by the 'soil-crop' system above the canopy (PAR_R) and PAR reflected from the bare soil (PAR_{RBS}) were measured
 132 orientating the sensor towards the soil at a distance of 30 cm from the surface (canopy or soil). Data were collected regularly
 133 throughout the growing period between 13.00 and 14.00 (GMT+01:00) and only when the sky was totally clear.

134 Calculations

135 The fraction of PAR absorbed by the crop (F_{PARa}) was calculated using the following equations (Hodges and Kanemasu 1977):

$$136 F_{PARa} = \left(\frac{PAR_0 - PAR_T - PAR_R + PAR_{RS}}{PAR_0} \right)$$

$$137 PAR_{RS} = PAR_T \times T_S$$

$$138 T_S = \frac{PAR_{RBS}}{PAR_0}$$

139 where PAR_0 is the incident PAR above the canopy, PAR_T the PAR transmitted to the soil, PAR_R the PAR reflected by the 'soil-
 140 crop' system above the canopy, PAR_{RS} the PAR reflected from the soil, T_S the fraction of PAR_T reflected from the soil and
 141 PAR_{RBS} the PAR reflected from the bare soil. The fraction of PAR absorbed by the crop was regressed against thermal time from
 142 emergence to wheat flowering using a logistic model:

$$143 F_{PARa} = F_{PARmax} \times \frac{\exp(K1 \times (t - K2))}{1 + \exp(K1 \times (t - K2))}$$

144 where F_{PARmax} is the maximum value of F_{PARa} when thermal time approaches positive infinity, $K2$ the thermal time at the point of
 145 inflexion (where F_{PARa} is half of F_{PARmax}), $K1$ the slope of the curve at the point of inflexion and t the thermal time. Parameters
 146 were calculated in order to minimize the root mean square error.

147 PAR absorbed by the canopy (PARa) was then calculated as the sum of daily PAR energy absorbed (dPARa) from emergence
 148 (day 1) to the last measurement (day n) corresponding to 10 and 5 days before wheat flowering in Exp.I and Exp.II respectively:

$$149 PARa = \sum_{i=1}^n dPARa_i = \sum_{i=1}^n 0.48 \times SR_i \times F_{PARai}$$

150 where SR_i is the total incident solar radiation ($MJ m^{-2}$) obtained from the meteorological station on day i , F_{PARai} the fraction of
 151 PAR absorbed by the crop on day i (calculated from the logistic model) and 0.48 the fraction of PAR of the total solar radiation
 152 energy (Varlet-Grancher et al. 1982).

153 In order to compare the species growth dynamics in the intercrop we defined an index called the comparative absolute growth rate
154 (CGR). The CGR compares the dry weight growth rate (GR) within a given time interval (t_1 to t_2), of one species relative to
155 another. Thus, CGR for a wheat-pea intercrop (IC) is the ratio between the growth rate of wheat (GR_w) and pea (GR_p):

$$156 \quad GR_w = \frac{DW_{w-IC}t_2 - DW_{w-IC}t_1}{t_2 - t_1}$$

$$157 \quad GR_p = \frac{DW_{p-IC}t_2 - DW_{p-IC}t_1}{t_2 - t_1}$$

$$158 \quad CGR_{IC} = \frac{GR_{w-IC}}{GR_{p-IC}}$$

159 The same concept was used to compare independent sole crops growth rate as following:

$$160 \quad CGR_{SC} = \frac{GR_{w-SC}}{GR_{p-SC}}$$

161 CGR values were calculated for each time interval between two successive sampling dates during crop growth. At sowing, the
162 total seed weight was taken as total biomass assuming a 1000-grain standard weight of 50 g and 150 g for wheat and pea
163 respectively. CGR_{IC} was calculated separately for each IC replicate. The same was done for CGR_{SC} by using the replicate values
164 of wheat DW for the numerators and the mean pea sole crops values across all replicates for the denominators in order to
165 eliminate the variability inside each block replicate attributed to sole crop pea DW. Moreover, for CGR_{IC} we considered the same
166 N treatment for the wheat and the pea while CGR_{SC} was calculated with the unfertilized pea sole crop as reference hypothesizing
167 that N was not a limiting resource for legumes and did not affect pea DW. $CGR > 1$ indicates a faster growth rate of wheat
168 compared to pea over the time period considered and vice versa when $CGR < 1$.

169 The efficiency of intercrop was evaluated using the land equivalent ratio (LER) which is defined as the relative land area required
170 when growing sole crop to produce the aerial biomass dry weight or yield achieved in intercrop (Willey 1979). Aerial biomass
171 LER for a wheat-pea intercrop (LER_{DW}) is the sum of the partial LER values for wheat (LER_{DW-w}) and pea (LER_{DW-p}) (De Wit
172 and Van Den Bergh, 1965). LER was calculated for each sampling in order to analyse the dynamics of resource use for wheat and
173 pea. Calculations, assumptions and significance are given in a previous paper (Bedoussac and Justes 2009). By analogy, we
174 calculated the LER by considering the shoot N accumulated, and named it LER_N .

175 The nitrogen status of the wheat was characterized using the nitrogen nutrition index (NNI) - an indicator of crop N nutrition
176 status which reveals a possible N deficiency in the crop at the time of observation - which is defined as the ratio between the
177 actual crop N concentration in shoots (%Nact) and the critical crop N concentration in shoots (%Nc) i.e. the minimum N
178 concentration in shoots that allows the maximum shoot biomass production (Lemaire and Gastal 1997):

179
$$NNI = \frac{\% N_{act}}{\% N_c}$$

180 %N_c for a sole crop winter wheat (%N_{c_{w-SC}}) is defined by the critical nitrogen dilution curve proposed by Justes et al. (1994) and
181 validated for durum wheat (Justes et al., 1997).

182
$$\% N_{c_{w-SC}} = 4.4\% \text{ if } DW_{w-SC} < 1.55 \text{ t ha}^{-1} \text{ else } 5.35 \times DW_{w-SC}^{-0.442}$$

183 where DW_{w-SC} is the shoot dry weight per unit area achieved in sole crop for wheat. In intercrops, the biomass of the
184 neighbouring species has to be taken into account because it contributes to: i) the canopy light capture and attenuation and ii) the
185 N dilution according to growth and stages. Hence, Soussana and Arregui (1995) proposed to calculate %N_c for an intercrop using
186 its total biomass. Thus, for the intercropped wheat we used the following equation:

187
$$\% N_{c_{w-IC}} = 4.4\% \text{ if } DW_{IC} < 1.55 \text{ t ha}^{-1} \text{ else } 5.35 \times DW_{IC}^{-0.442}$$

188 where DW_{IC} is the shoot dry weight per unit area of the whole intercrop (pea plus wheat biomasses).

189 A value of NNI of at least one indicates that crop growth was not limited by N supply at this time whereas when NNI is below
190 one N was limiting for crop growth at that specific date.

191 **Statistics**

192 Analysis of variance was carried out using the AOV procedure of the 2.7.1 version of R software (R development Core Team
193 2007) for each year and date of sampling separately, considering N treatments as the main factor, crops as a sub-factor and
194 interaction between N treatments and crops. All data were tested for normal distribution using the Shapiro–Wilk test and pairwise
195 comparisons were performed using a two-tailed t-test (P=0.05 or P=0.10) to compare N treatments within crops and crops within
196 N treatments. According to Sheskin (2004), the significance of differences between treatments can be estimated using simple
197 planned comparisons when these have been planned beforehand, regardless of whether or not the omnibus F value is significant.
198 Finally, confidence intervals for the means of CGR, LER and partial LER values were calculated from replicates assuming
199 normal distribution according to Sheskin (2004) in order to compare the means of CGR and LER with 1 and partial LER values
200 with 0.5.

201

201 **Results**

202 **Growth dynamics**

203 **Emergence and plant density**

204 For both experiments, wheat emerged earlier than pea and the percentage of the cereal emergence was lower than that of the
205 legume (63% and 76% respectively). On average for both species, the emergence was similar for the two experiments (70% and
206 66% for Exp.I and Exp.II respectively) but it was slower in Exp.I. Moreover, for both species, no significant difference ($p>0.10$)
207 was found between sole crops and intercrops. Plant densities are given in Table 1.

208 **Green leaf area index (GLAI)**

209 Without N fertilization (Fig. 2a and 2d), green leaf area index of the pea sole crop was higher than that of the wheat sole crop at
210 the intermediate growth stage (BPF and WF) but lower for earlier stages (WT and E1cm). Moreover, pea sole crop GLAI reached
211 zero (1700 and 2050 °C d⁻¹ after wheat emergence for Exp.I and Exp.II respectively) while wheat sole crop GLAI was still
212 significantly positive.

213 Overall, GLAI of the whole intercrop was greater than that of the wheat sole crop ($p<0.10$) and less than that of the pea sole crop
214 ($p<0.10$) except that in the initial growth stages (WT and E1cm) where it was comparable to that of the wheat sole crop and
215 slightly greater to that of the pea sole crop ($p<0.10$). N fertilization significantly increased wheat GLAI both in sole crop and
216 intercrop (Fig. 2b, 2c, 2e, 2f and 2g), in particular from E1cm to BPF ($p<0.05$). Conversely, in Exp. I no difference between N
217 treatments was observed for the intercropped pea GLAI while in Exp. II the maximum was obtained for N0 ($p<0.05$). Thus the
218 GLAI of the whole intercrop was slightly but not significantly affected by N fertilization ($p>0.10$).

219 **Growth in height**

220 Wheat and pea differed in height, but this difference changed over time (Table 2). Overall, wheat was taller than pea in both the
221 initial (E1cm) and the later (WF) growth stages, but no difference was found at the intermediate growth stage (BPF). No
222 significant difference was neither found between sole crop and intercrop canopy height for both wheat and pea at any of the
223 growth stages ($p>0.10$), except for pea at the BPF stage in Exp.II ($p<0.05$). N fertilization had no effect on pea height except at
224 BPF (Exp.II; $p<0.05$) and WF (Exp.I; $p<0.05$) growth stages and only a slight but significant effect on wheat height at the BPF
225 and WF growth stages ($p<0.05$). Moreover, no pea lodging was observed in intercrop although this occurred in sole crop for both
226 experiments, with a high proportion in Exp.II.

227 **Dry weight of aerial biomass and interspecies dynamics**

228 Without N fertilization (Fig. 3a and 3d), the aerial biomass of sole cropped pea was lower than that of the sole cropped wheat
229 until BPF and then higher ($p < 0.05$). Overall, the biomass of the whole intercrop was similar to the sole cropped pea (Fig. 3a and
230 3d) and higher than of the sole cropped wheat for low N availabilities from the WF stage onwards (Fig. 3a, 3b, 3d and 3e). When
231 increasing the amount of fertilizer N (Fig. 3c, 3f and 3g) the biomass of the whole intercrop was similar or lower than that of the
232 sole cropped wheat throughout the whole crop growth ($p < 0.10$) except at WF stage for N140 ($p > 0.10$).

233 During crop growth, sole cropped and intercropped wheat biomass were significantly increased with fertilizer N amount in Exp.I
234 (Fig. 3b and 3c) from BPF stage ($p < 0.05$). In Exp.II, sole cropped wheat biomass at WF stage and maturity were significantly
235 increased ($p < 0.10$) from N0 to N80 ($p < 0.10$) while wheat biomass of intercrop was highest ($p < 0.05$) in N60+ (Fig. 3e) and clearly
236 lowest ($p < 0.05$) in N0 (Fig. 3d). For both experiments, the biomass of intercropped pea was significantly reduced at WF stage and
237 maturity with fertilizer-N compared to N0 ($p < 0.05$) except for N100 (Fig. 3b) at WF stage ($p > 0.10$). As a consequence, total
238 intercrop biomass at WF stage and maturity was increased with N fertilization in Exp.I while in Exp.II the highest total intercrop
239 biomass at maturity was found in N60+ (Fig. 3e) and the lowest in N140 (Fig. 3g). Crop growth was very slow from emergence
240 until E1cm, but increased rapidly from E1cm to WF stage. Moreover, in Exp.II sole crop wheat biomass remained stable between
241 WF and maturity. Finally and more surprisingly the biomass of the sole cropped and intercropped pea decreased in particular for
242 N0 (Fig. 3d) and N140 (Fig. 3g) probably due to the high leave losses.

243 The comparative absolute growth rate (CGR) values were significantly affected by N fertilization ($p < 0.05$) and changed over time
244 ($p < 0.05$) for both sole crops and intercrops.

245 From sowing (S) to 'ear 1cm' stage of wheat (E1cm), the biomass growth rate of wheat was 2.5 to 4.8 times and 4.5 to 11.7
246 greater than that of pea in intercrop for Exp.I and Exp.II respectively (Table 3). Similar dynamics were observed for the SC with
247 on average CGR values of 1.8 and 4.0 for Exp.I and Exp.II respectively, indicating that competitions between wheat and pea
248 intercropped in rows were weak until E1cm stage.

249 Afterwards, for both experiments and all treatments, CGR values in intercrop were close to or higher than one during the two
250 following growth periods (E1cm to BPF and BPF to WF) except for N0 between BPF and WF (Table 3), indicating that the
251 growth rate of wheat was similar or slightly higher than that of pea in fertilized intercrops. However, significant lower values than
252 one for N0 treatments indicated higher growth rate of pea in intercrop from BPF to WF. Concerning the sole crops, CGR values
253 were close to one or more from E1cm to BPF (1.1 and 1.2 on average in Exp. I and II respectively) and close to or below one (0.7
254 for both experiments) from BPF to WF, indicating similar or higher pea growth rate than wheat during this later period.

255 Next, from WF to harvest maturity, wheat growth rate was higher than that of pea in Exp.I for both sole crop and intercrop even
256 thought in intercrop CGR values were significantly different from one only for N0. On the contrary, in Exp. II, CGR values were

257 about 0 for both sole crop and intercrop (except for N60+ in intercrop) due to uncontrolled pests, diseases and lodging in late
258 growth stages.

259 Considering the whole growth period, CGR values were the lowest and close to one in N0 for both experiments in sole crop and
260 intercrop. CGR values were always significantly higher than one in N fertilized plots, without significant difference between N
261 treatments, indicating that wheat growth rate was higher than that of pea with N fertilization. Globally, CGR were higher in
262 Exp.II than in Exp. I (3.4 and 2.4 respectively) indicating pedoclimatic conditions more favourable to wheat during the second
263 experiment.

264 **Dry weight biomass land equivalent ratio (LER_{DW})**

265 At the four key stages sampled (E1cm, BPF, WF and maturity), LER values calculated from aerial biomass dry weight (LER_{DW})
266 were roughly one or more in all treatments ($p < 0.05$) (Fig. 4) except for N180 (Fig. 4c) at E1cm and BPF and for N140 (Fig. 4g) at
267 maturity. These results indicate that throughout the whole crop growth, resources were used for aerial biomass production up to
268 36% more efficiently in intercrops than in sole crops in low N conditions. On the whole, LER_{DW} values were reduced with N
269 fertilization, particularly for the N180 (Fig. 4c) and the N140 (Fig. 4g) treatments mostly because of the pea partial LER_{DW}
270 (LER_{DW-P}) reduction. LER_{DW-P} values were always equal to or significantly below 0.5 ($p < 0.10$), except for N0 in both
271 experiments ($p > 0.10$). For all N treatments and stages, wheat partial LER_{DW} values (LER_{DW-W}) were always at least 0.5 and often
272 much higher ($p < 0.10$). Moreover, LER_{DW-P} values remained more or less stable throughout the whole crop growth, and similar
273 results were found in Exp.I for LER_{DW-W} , while in Exp II, LER_{DW-W} increased until pea flowering and then decreased, in
274 particular for N0 (Fig. 4d) and N60+ (Fig. 4e).

275 **Resource use dynamics**

276 **Light absorption**

277 The fraction of PAR absorbed (F_{PARa}) by sole crops and the whole intercrops increased with crop growth from emergence to WF
278 following a logistic model (Fig. 5). The root mean squared error (RMSE) values (Table 4) were very low (3.6% at maximum) and
279 the bias was nil (0.6% at maximum), indicating a good fit of the data by the model. The parameter values of the logistic model
280 (Table 4) indicate that the thermal time at the point of inflexion (K2) of the pea sole crop was greater than that of the intercrop,
281 itself higher than that of wheat sole crop. The slope of the curve at the point of inflexion (K1) was highest for the pea sole crop
282 and that of the intercrop was higher than that of the wheat sole crop for N60+ and N140 (Exp.II) and lower for N0 in Exp. I.

283 Without N fertilization (Fig. 5a and 5d), F_{PARa} of the pea sole crop was lower than that of wheat sole crop in early stages (until
284 E1cm), itself slightly greater than that of the whole intercrop. Then, from E1cm to WF, the F_{PARa} of intercrop became lower than

285 that of pea sole crop and greater than that of wheat sole crop. When N fertilizer was applied, no significant difference was
286 observed between intercrop and wheat sole crop F_{PARa} (Fig. 5c, 5e, 5f and 5g) and the maximum values of F_{PAR} indicating that the
287 potential of PAR absorption was reached (Table 4). Finally, the cumulative PAR absorbed (Table 4) from sowing to WF was the
288 lowest for the pea sole crop and the highest for the wheat sole crop except for N0 where the maximum was observed for the
289 whole intercrop.

290 **Nitrogen acquisition and wheat nitrogen nutrition index (NNI)**

291 Without N fertilizer and until BPF stage (Fig. 6a and 6d), the pea sole crop accumulated significantly ($p<0.10$) more N in shoots
292 than the wheat sole crop and than the whole intercrop. In N-fertilized treatments, the whole intercrop accumulated more N than
293 the pea sole crop in Exp.I (Fig. 6b and 6c) and a similar or smaller amount in Exp.II (Fig. 6e, 6f and 6g). The whole intercrop
294 accumulated more N than the wheat sole crop except in early stages (WT and E1cm) and at maturity for N180 (Fig. 6c) and N140
295 (Fig. 6g) ($p>0.10$).

296 The wheat N accumulation in sole crop and intercrop were positively correlated with N fertilization in Exp.I (Fig. 6a, 6b and 6c).
297 In Exp.II early N fertilization applied at E1cm (Fig. 6f and 6g) increased the wheat N accumulated in sole crop and intercrop
298 between E1cm and BPF stages. Contrary, N fertilizer applied at flag leaf visible (Fig. 6e and 6g) increased the wheat N
299 accumulated in sole crop and intercrop between BPF and WF stages only for the N60+ treatment (Fig. 6e). The N accumulated by
300 crops increased throughout the growth period in Exp.I while in Exp.II the wheat N uptake of sole crop and intercrop remained
301 more or less stable between WF and maturity whereas that of the pea intercrop decreased.

302 The last point but not the least was that N accumulated by intercropped wheat was 70% to 85% of that of the sole crop despite
303 intercropped wheat was sown at half plant density of the wheat sole crop (fig. 6). The proportion of N uptake in intercrop
304 compared to sole crop was higher for N0 treatment, indicating a higher N availability per wheat plant in intercrop.

305 In Exp.I, for all N treatments, wheat nitrogen status (NNI) was always significantly below one ($p<0.05$) for both sole crops and
306 intercrops (Fig. 7) indicating a significant N deficiency throughout the whole growth period. In Exp.II, NNI values of both wheat
307 sole crops and intercrops were significantly above one ($p<0.05$) at wheat tillering, roughly one or slightly less at E1cm stage of
308 wheat and thereafter significantly lower ($p<0.05$) except at the beginning of pea flowering (BPF) in N80 (Fig. 7f) for the intercrop
309 and in N140 (Fig. 7g) for both sole crop and intercrop. The main result is that the intercropped wheat NNI was always higher or
310 at least statically equal to that of the sole crop for both experiments and all N treatments, indicating that intercropping improved
311 the wheat N status during the growing season. Without N fertilization the wheat NNI of both sole crop and intercrop decreased
312 with development stages and aerial biomass increase, but in Exp.II the wheat NNI remained quite stable from BPF to wheat
313 flowering (WF). Each fertilizer-N application increased the wheat NNI or reduced its decline.

314 **Land equivalent ratio for N acquisition (LER_N)**

315 Whatever the date of sampling or N fertilization regime, LER_N values calculated from N accumulated in shoots (LER_N) were
316 always higher or at least statistically similar than that calculated from aerial biomass (Fig. 4). Throughout the crop growth, LER_N
317 values were roughly one or more in all treatments ($p < 0.05$) except for N140 at maturity (Fig. 4g). This indicates an advantage of
318 intercrop in comparison to sole crop for N acquisition throughout crop growth greater than for biomass production. On the whole,
319 LER_N values were reduced with N fertilization, in particular for N180 (Fig. 4c), N80 (Fig. 4f) and N140 (Fig. 4g). For all N
320 treatments and stages, wheat partial LER_N values ($LER_{N,W}$) were always above 0.5 ($p < 0.10$) except at E1cm in Exp.I, wheat
321 tillering in Exp.II and for N140 at all stages. On the other hand, the values of $LER_{N,P}$ were always equal to or below 0.5 and lower
322 when N fertilizer was applied. The total LER_N values and partial LER_N values changed significantly over time, particularly in
323 Exp.II. LER_N values of wheat were increased until pea flowering and then decreased particularly for the N0 (Fig. 4d), N60+ (Fig.
324 4e) and N80 (Fig. 4f) treatments. In Exp.I, LER_N values of wheat remained more or less stable throughout the crop growth, and
325 similar results were observed for LER_N values of pea. In Exp.II, LER_N values of pea were significantly ($p < 0.10$) reduced between
326 WF and maturity.

327 **Discussion**

328 Various authors have indicated that sequential measurements of crop growth allow a better understanding of the dynamics and
329 mechanisms of competitive interactions in intercrop and sole crop compared to a single measurement of final yield (e.g. Connolly
330 et al. 1990; Andersen et al. 2004). In our study, we sampled four (Exp.I) and five (Exp.II) times during the growing season at key
331 development stages. The following discussion will be largely organized according to the growing periods between these stages
332 because they determined key periods for interspecific competition and complementarity between durum wheat and winter pea.
333 Our data has shown that for limited early N availability (no fertilizer or a small amount applied after the wheat booting stage)
334 there were significant complementarities between intercropped durum wheat and winter pea for light and nitrogen use. This was
335 clearly due to species differences in their dynamics of growth and to differences in species phenology and physiology which we
336 will demonstrate afterwards.

337 **Early growth dynamics**

338 We observed that wheat growth was earlier than that of pea for both sole crops and intercrops and the better start of wheat was
339 mostly the result of faster seedling emergence. Furthermore, wheat early advantage over pea was probably due to i) its faster and
340 deeper root growth and ii) higher N demand than those of pea (Fujita et al. 1992; Corre-Hellou 2005; Hauggaard-Nielsen et al.
341 2003; Corre-Hellou and Crozat 2005).[0] It was also certainly due to the establishment of costly pea nodulation (in energy and

342 nutrients) according to e.g. Vocanson et al. (2005) and Voisin et al. (2002) which could have reduced early pea growth. Crop
343 emergence and early growth were slower in Exp.II due to: i) the coarse soil structure, ii) the low soil water content at sowing,
344 only partially compensated by irrigation, and iii) the low winter temperatures. In particular, pea was affected by the coarse soil
345 structure and the low soil water content at sowing in Exp.II possibly explained by a higher water demand due to greater pea seed
346 size. Also, and particularly in Exp.II, pea emerged later and hence at lower temperatures than wheat, increasing the differences
347 between the early growth of the two species as illustrated by higher CGR values in Exp.II than in Exp.I.
348 In early stages of growth (until wheat stem elongation corresponding to 'ear 1 cm' stage), wheat was much more efficient than
349 pea for light absorption, due to its earlier growth, greater height during winter, tillering and higher green leaf area index, as
350 illustrated by CGR values much higher than one from sowing to E1cm. Similar dynamics were observed for the sole crop and the
351 intercrop indicating that our results are in good agreement with species' phenological and physiological differences. However,
352 pea growth was lower in intercrop than in sole crop during early stages as illustrated by CGR values higher for the intercrop than
353 for the sole crops. This is certainly due to less incoming PAR available for the intercrop pea being partly shaded by the durum
354 wheat.

355 **Intermediate period of growth dynamics**

356 From wheat '1 cm ear' stage to wheat flowering, the intercrop as a whole was more efficient for light absorption than wheat sole
357 crop thanks to light absorption by the intercropped pea in late stages in particular without N fertilization. Indeed, legume
358 efficiency for light absorption in late stage was due to: i) the later growth of the legume and also ii) the small effect of senescence
359 on pea light interception; this compartment of pea was ever shown for sole crop by Guilioni and Lecoer (2005) who
360 demonstrated that pea leaves did not fall, maintained their orientation and their area was only reduced by 5-10% allowing higher
361 light absorption compared to wheat close to cereal flowering stage. The later growth of the legume was observed for both sole
362 crop and intercrop, as illustrated by lower CGR values compared to the period from sowing to 'ear 1cm' stage of wheat indicating
363 that phenological difference can play a central role in shaping the observed dynamics (Berntsen et al. 2004).

364 When N fertilizer was applied early (wheat tillering or stage 'ear 1cm' of wheat), we observed a slightly increase in the cereal
365 growth in winter but a strong increase in early spring. Hence, when the growth of the intercropped legume was expected to
366 increase markedly - like in sole crop - there was less light available to it, which reduced its aerial biomass production and
367 consequently that of the whole intercrop. However, N fertilization had only a small effect on the F_{PARa} of intercrop because it was
368 already close to the potential without N fertilization, indicating a good complementary absorption of incoming PAR of the two
369 species under these N conditions. This suggests that the efficiency of intercrop in N fertilized treatments was mostly due to wheat
370 light absorption - certainly related to the effect of N fertilization for wheat green leaf area index and biomass increase - which

371 markedly reduced pea growth due to light competition. This result was coherent with the positive correlation observed in both
372 experiments between wheat sole crop and intercrop green leaf area index and N fertilization as already described by many authors
373 for other graminaceous crops (e.g. Gastal et al. 1992; Wilman and Pearse 1984).

374 On the contrary, in low N availability conditions, no harmful competition of wheat for light was observed on the legume as
375 indicated by low CGR values, because wheat early growth was limited by a lack of available mineral N in the soil. Then, unlike
376 spring barley-pea intercrop (Corre-Hellou 2005), durum wheat-winter pea allowed a similar or better use of light compared to
377 sole crops throughout the growth period, especially with low N supply. These conclusions are strengthened by the fact that similar
378 results were obtained for both experiments while weather conditions were very different. This also confirms that, in N fertilized
379 treatments, wheat has a higher and pea a lower interspecific competitive ability when intercropped and this difference was
380 increased as soil N availability was enhanced.

381 N accumulated by the intercropped wheat was at least 70% and often more of that of the wheat sole crop for half plant density,
382 particularly until the beginning of pea flowering and when little or no N fertilizer was applied. This confirms that the cereal had
383 access to a more than proportionate share of soil mineral N in intercrop per plant as compared to sole crop (Jensen 1996). This
384 result is supported by: i) the increase in pea symbiotic N₂ fixation rate demonstrated in the companion paper (Bedoussac and
385 Justes 2009) and in agreement with several other studies for spring intercrops (e.g. Corre-Hellou 2005; Hauggaard-Nielsen et al.
386 2003; Corre-Hellou and Crozat 2005), and ii) the lower durum wheat biomass per square meter in intercrop due to light
387 competition exerted by the pea. Consequently and as expected, the intercropped wheat N status (NNI) was always higher than that
388 of the sole crop except when a large amount of N was applied. This confirms that intercrop can improve wheat N status compared
389 to sole crop and consequently the grain protein content in particular with little or no N fertilizer. Moreover, the advantage of
390 intercrop over sole crop seems to increase throughout the growth period due to higher N available per durum wheat plant. The N
391 status of sole cropped and intercropped wheat were mostly below one, in particular in late stages and when little or no N fertilizer
392 was applied, underlining the existence of a nitrogen deficiency in the crop throughout the growing period which confirmed that
393 we were in low N inputs conditions. However, the intercropped wheat had a lower N deficiency which allowed better
394 photosynthesis and hence higher radiation use efficiency (e.g. Justes et al. 2000).

395 **Late growth dynamics**

396 From wheat flowering (WF) to maturity, durum wheat seems to be the most efficient, certainly due to: i) the earlier initiation of
397 seed filling and maturity of pea (physiological maturity of the legume was observed 3 weeks before that of the durum wheat) and
398 ii) the effect of the diseases and pests of pea which were not perfectly controlled by pesticide applications. However, it was not
399 possible to know precisely if the greater efficiency of wheat in late stages occurred between WF and pea maturity or between pea

400 maturity and wheat maturity because wheat biomass was not measured at the pea maturity stage in our experiments. Nevertheless,
401 in late stages, wheat took advantage of the intercrop by remobilizing more N into its grain due to: i) lower grain yield and ii)
402 almost similar N available compared to the sole crop according to the high legume N₂ fixation described in the companion paper
403 (Bedoussac and Justes 2009).

404 **Conclusion**

405 The objective of our paper was to answer to the following question: how the final outcome of the durum wheat-winter pea
406 intercrop can be explained? Thus, we demonstrated that in our experiments the use of environmental resources for plant growth
407 changed over time, indicating that the ability for a crop to exploit resource niches and thereby capture resources varies
408 significantly during the growth cycle. Throughout crop growth, resources were used up to 36% more efficiently in intercrops than
409 in sole crops for aerial biomass in low N conditions and intercrops efficiency for N uptake was greater than for biomass
410 production throughout crop growth at all N fertilization levels. Regardless of N availability, wheat took advantage of intercrop for
411 aerial biomass production more than pea ($LER_{DW-W} > LER_{DW-P}$) by using N, light and certainly CO₂ and water more efficiently
412 throughout the growth cycle due to its earlier growth, greater height and higher N demand. CGR and LER dynamic analysis
413 indicated that pea took advantage of intercrop mainly between pea flowering and wheat flowering (near the end of pea grain
414 filling), while wheat took advantage of intercrop between the emergence and the beginning of wheat stem elongation (E1cm
415 stage) and until pea flowering.

416 Wheat benefited from N fertilization more than pea directly by its faster growth, improving light and water capture and hence
417 suppressing pea growth whatever the amount and the date of N application (Fujita et al. 1992; Jensen 1996; Bulson et al. 1997).
418 Moreover, as shown by many other studies on spring peas, winter pea has a higher interspecific competitive ability at low N
419 levels because of: i) the reduction in N₂ fixation with N supply (Voisin et al. 2002; Ghaley et al. 2005) and ii) the amplification of
420 differences in species growth dynamics with N supply (Hauggaard-Nielsen and Jensen 2001; Ghaley et al. 2005). Durum wheat
421 and winter pea showed interspecific complementarity in good agreement with other studies on cereal-legume spring-sown
422 intercrops (Corre-Hellou and Crozat 2005; Hauggaard-Nielsen et al. 2006; Hauggaard-Nielsen et al. 2009).

423 However, intercrop efficiency and crops interspecific competitiveness ability depended on the dynamics of N availability
424 throughout the growth cycle of intercrops. N fertilizer applied at the beginning of wheat stem elongation clearly leads to a
425 significant and early decrease in pea N acquisition due to a quantitative reduction in N₂ fixation described in the companion paper
426 (Bedoussac and Justes 2009) and the opposite with no or late N fertilization. As a consequence, the advantage of intercrop for
427 biomass production, yield or accumulated N was maximal under low N fertilization treatments (no or late fertilization) due to
428 good complementarities of durum wheat and winter pea for GLAI and growth dynamics over time.

429 Another point concerns the reduction of pea lodging which is of great importance in order to obtain good yield. Indeed, pea is
430 very sensitive to lodging, mainly because of diseases like pea ascochyta (*Mycosphaerella pinodes*) which usually attacks the
431 stems. Hence pea sole crop must be harvested soon after maturity, which may be difficult in bad weather or with severe lodging.
432 In intercrop, pea maturity occurred around 3 weeks before durum wheat and due to lodging, pests and diseases this can be very
433 prejudicial to the pea harvest efficiency. However, in our conditions, no lodging was observed for pea in intercrop because the
434 legume clings to the durum wheat with its tendrils, creating a dense and stable network.

435 As a practical conclusion, our results indicate that durum wheat-winter pea intercrop productivity can be optimized by adapting
436 cropping sequences, N fertilization in particular, but also by choosing crop species of widely different phenologies and/or
437 morphologies in order to maximize capture and minimize competition for solar radiation. It is essential to prevent an adverse
438 effect on legume growth (involving N₂ fixation) which very much influences the final outcome and total yield potentials of the
439 intercrop.

440 Further research are needed to investigate the effect of wheat and pea cultivars on interspecies dynamics, hypothesizing that short
441 or late wheat cultivars would be more suited for intercrop than tall or early ones and vice versa for pea cultivars. Furthermore,
442 intercrop competition analysis - considering various legumes species, crop densities, sowing dates (eventually shifting wheat and
443 pea sowing date) and N fertilization - seems critical in order to optimize these innovative agro-ecosystems. Moreover, defining
444 specific objectives (grain or biomass production, grain protein concentration increase, reduction of N leaching and chemical use
445 etc.) would lead to different choices for the optimal combination of cultivars of the two species, their density and fertilization-N
446 strategies.

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452

452 **References**

- 453 Andersen M K, Hauggaard-Nielsen H, Ambus P, Jensen E S (2004) Biomass production, symbiotic nitrogen fixation and
454 inorganic N use in dual and tri-component annual intercrops. *Plant Soil* 266:273-287
- 455 Anil L, Park J, Phipps R H, Miller F A (1998) Temperate intercropping of cereals for forage: a review of the potential for growth
456 and utilization with particular reference to the UK. *Grass Forage Sci* 53:301-317
- 457 Bedoussac L, Justes E (2009) The efficiency of a durum wheat-winter pea intercrop to improve yield productivity and wheat
458 grain protein concentration depends on N availability during early growth. *Plant Soil*. DOI 10.1007/s11104-009-0082-2
- 459 Berntsen J, Hauggaard-Nielsen H, Olesen J E, Petersen B M, Jensen E S, Thomsen A (2004) Modelling dry matter production
460 and resource use in intercrops of pea and barley. *Field Crops Res* 88:69-83
- 461 Bulson H, Snaydon R, Stopes C (1997) Effects of plant density on intercropped wheat and field beans in an organic farming
462 system. *J Agric Sci* 128:59-71
- 463 Connolly J, Wayne P, Murray R (1990) Time course of plant-plant interactions in experimental mixtures of annuals - Density,
464 frequency, and nutrient effects. *Oecologia* 82:513-526
- 465 Corre-Hellou G (2005) Acquisition de l'azote dans des associations pois-orge (*Pisum sativum* L. – *Hordeum vulgare* L.) en
466 relation avec le fonctionnement du peuplement. Thèse de doctorat en sciences agronomiques de l'école doctorale d'Angers
- 467 Corre-Hellou G, Crozat Y (2005) Assessment of root system dynamics of species grown in mixtures under field conditions using
468 herbicide injection and N-15 natural abundance methods: A case study with pea, barley and mustard. *Plant Soil* 276:177-192
- 469 Corre-Hellou G, Fustec J, Crozat Y (2006) Interspecific competition for Soil N and its interaction with N₂ fixation, leaf
470 expansion and crop growth in pea-barley intercrops. *Plant Soil* 282:195-208
- 471 Crozat Y, Aveline A, Coste F, Gillet J, Domenach A (1994) Yield performance and seed production pattern of field-grown pea
472 and soybean in relation to N nutrition. *Eur J Agron* 3:135-144
- 473 De Wit C T, Van Den Bergh J P (1965) Competition between herbage plants. *Neth J Agric Sci* 13:212-221
- 474 Dhima K V, Lithourgidis A S, Vasilakoglou I B, Dordas C A (2007) Competition indices of common vetch and cereal intercrops
475 in two seeding ratio. *Field Crops Res* 100:249-256

476 Fujita K, Ofosubudu K G, Ogata S (1992) Biological nitrogen fixation in mixed legume-cereal cropping systems. *Plant Soil*
477 141:155-175

478 Fukai S (1993) Intercropping - Bases of productivity - Introduction. *Field Crops Res* 34:239-245

479 Garrido-Lestache E, López-bellido R J, López-bellido L (2004) Effect of N rate, timing and splitting and N type on bread-making
480 quality in hard red spring wheat under rainfed Mediterranean conditions *Field Crops Res* 85:213-236

481 Gastal F, Belanger G, Lemaire G (1992) A model of leaf extension rate of tall fescue in response to nitrogen and temperature.
482 *Ann Bot.* 70:437-442

483 Ghaley B B, Hauggaard-Nielsen H, Høgh-Jensen H, Jensen E S (2005) Intercropping of wheat and pea as influenced by nitrogen
484 fertilization. *Nutr Cycl Agroecosyst* 73:201-212

485 Guillioni L, Lecoq J (2005) Acquisition du carbone à l'échelle du peuplement. In: *Agrophysiologie du pois protéagineux*.
486 INRA-ARVALIS-UNIP-ENSAM, Paris, pp 65-80

487 Hauggaard-Nielsen H, Andersen M K, Jørgensen B, Jensen E S (2006) Density and relative frequency effects on competitive
488 interactions and resource use in pea-barley intercrops. *Field Crops Res* 95:256-267

489 Hauggaard-Nielsen H, Ambus P, Jensen E S (2001a) Temporal and spatial distribution of roots and competition for nitrogen in
490 pea-barley intercrops - a field study employing P-32 technique. *Plant Soil* 236:63-74

491 Hauggaard-Nielsen H, Ambus P, Jensen E S (2001b) Interspecific competition, N use and interference with weeds in pea-barley
492 intercropping. *Field Crops Res* 70:101-109

493 Hauggaard-Nielsen H, Ambus P, Jensen E S (2003) The comparison of nitrogen use and leaching in sole cropped versus
494 intercropped pea and barley. *Nutr Cycl Agroecosyst* 65:289-300

495 Hauggaard-Nielsen H, Gooding M, Ambus P, Corre-Hellou G, Crozat Y, Dahmann C, Dibet A, Von Fragstein P, Pristeri A,
496 Monti M, Jensen E S (2009) Pea-barley intercropping for efficient symbiotic N₂-fixation, soil N acquisition and use of other
497 nutrients in European organic cropping systems. *Field Crops Res* 113:64-71

498 Hauggaard-Nielsen H, Jensen E S (2001) Evaluating pea and barley cultivars for complementarity in intercropping at different
499 levels of soil N availability. *Field Crops Res* 72:185-196

500 Hodges T, Kanemasu E T (1977) Modeling daily dry-matter production of winter-wheat. *Agron J* 69:974-978

501 Jahansooz M R, Yunusa I A M, Coventry D R, Palmer A R, Eamus D (2007) Radiation- and water-use associated with growth
502 and yields of wheat and chickpea in sole and mixed crops. *Eur J Agron* 26:275-282

503 Jensen E (1996) Grain yield, symbiotic N₂ fixation and interspecific competition for inorganic N in pea-barley intercrops. *Plant*
504 *Soil* 182:25-38

505 Justes E, Denoroy P, Gabrielle B, Gosse G (2000) Effect of crop nitrogen status and temperature on the radiation use efficiency of
506 winter oilseed rape. *Eur J Agron* 13:165-177

507 Justes E, Jeuffroy MH, Mary B (1997) Wheat, Barley and Durum wheat. In: *Diagnosis of the nitrogen status in crops*. Lemaire G,
508 Springer, pp 73-91

509 Justes E, Mary B, Meynard J, Machet J, Thelier-Huche L (1994) Determination of a critical nitrogen dilution curve for winter
510 wheat crops. *Annals of Botany* 74:397-407

511 Lemaire G, Gastal F (1997) N uptake and distribution in plant canopies. In: *Diagnosis of the nitrogen status in crops*. Lemaire G,
512 Springer, pp 3-43

513 Malézieux E, Crozat Y, Dupraz C, Laurans M, Makowski D, Ozier-Lafontaine H., Rapidel B, de Tourdonnet S, Valantin-Morison
514 M (2008) Mixing plant species in cropping systems: concepts, tools and models. A review. *Agron Sustain Dev* 29:43-62.

515 Midmore D J (1993) Agronomic modification of resource use and intercrop productivity. *Field Crops Res* 34:357-380

516 Ofori F, Stern W R (1987) Cereal-legume intercropping systems. *Adv Agron* 41:41-90

517 R Development Core Team (2007) *A language and Environment for Statistical Computing*. R Foundation for Statistical
518 Computing, Vienna

519 Sheskin D J (2004) *Handbook of parametric and nonparametric statistical procedures*. Third edition. Chapman and Hall/CRC,
520 Boca Raton

521 Soussana J F, Arregui M C (1995) Effect of mixed cropping on the nitrogen nutrition and growth of perennial ryegrass and white
522 clover. *Agronomie* 15:81-96

- 523 Trenbath B R (1986) Resource use by intercrops. In: Francis C A (ed) Multiple cropping systems. MacMillan, New York, pp 57-
524 81
- 525 Tsubo M, Walker S, Mukhala E (2001) Comparisons of radiation use efficiency of mono-/inter-cropping systems with different
526 row orientations. Field Crops Res 71:17-29
- 527 Vandermeer J (1989) The ecology of intercropping. Cambridge university press, Cambridge
- 528 Varlet-Grancher C, Bonhomme R, Chartier M, Artis P (1982) Efficiency of solar energy conversion by a plant canopy. Acta
529 Oecologica, Oecologia Plant 3:3-26
- 530 Vocanson A, Munier-Jolain N, Voisin A S, Ney B (2005) Nutrition azotée. In: Agrophysiologie du pois protéagineux. INRA-
531 ARVALIS-UNIP-ENSAM, Paris, pp 81-106
- 532 Voisin A S, Salon C, Munier-Jolain N G, Ney B (2002) Quantitative effects of soil nitrate, growth potential and phenology on
533 symbiotic nitrogen fixation of pea (*Pisum sativum* L.). Plant Soil 243:31-42
- 534 Willey R (1979) Intercropping - its importance and research needs. 1. Competition and yield advantages. Field Crop Abstr 32:1-
535 10
- 536 Wilman D, Pearse P J (1984) Effects of applied nitrogen on grass yield, nitrogen-content, tillers and leaves in field swards. J
537 Agric Sci 103:201-211
- 538 Zadoks J C, Chang T T, Knocak C F (1974) A decimal code for the growth stages of cereals. Weed Res 14:415-421
- 539

539 **Tables**

540 **Table 1.** For the different N treatments (Nx where 'x' represents N applied in kg N ha⁻¹): i) soil N mineral content at sowing on 0-
 541 120 cm, ii) calculated apparent available N on 0-120 cm from sowing to the beginning of pea flowering (S to BPF) and from
 542 sowing to maturity harvest (S to H) and iii) plant densities of wheat and pea in sole crop (SC) and intercrop (IC) (for details, see
 543 Bedoussac and Justes 2009)[0].

		2005-2006 (Experiment I)			2006-2007 (Experiment II)				
		N0	N100	N180	N0	N60+	N80	N140	
Initial mineral N on 0-120 cm (kg N ha ⁻¹)		37	40	35	30	52	28	46	
Mineral N available on 0-120 cm (kg N ha ⁻¹)	S to BPF	60	77	129	60	91	129	161	
	S to H	90	168	223	94	144	150	171	
Plant densities (plants m ⁻²)	Pea	SC	51		56				
		IC	26	27	28	29	28	25	28
	Wheat	SC	224	229	224	211	198	190	207
		IC	111	114	112	105	99	95	104

544
 545 **Table 2.** Canopy height (cm) of sole crops (SC) and intercrops (IC) measured at '1 cm ear' stage of wheat (E1cm), beginning of
 546 pea flowering (BPF) and wheat flowering (WF) for the unfertilized plots (N0) or considering the mean of all N treatments. Values
 547 are the mean of (n=3 to 5) ± standard error.

		2005-2006 (Experiment I)				2006-2007 (Experiment II)			
		N0		N		N0		N	
		SC	IC	SC	IC	SC	IC	SC	IC
E1cm	Wheat	25 ± 0	26 ± 2	25 ± 0	27 ± 3	23 ± 0	23 ± 2	25 ± 0	23 ± 4
	Pea	10 ± 0	10 ± 0		10 ± 0	6 ± 1	8 ± 1		5 ± 0
BPF	Wheat	58 ± 2	55 ± 1	62 ± 4	61 ± 3	45 ± 4	47 ± 2	54 ± 4	57 ± 2
	Pea	56 ± 4	55 ± 5		58 ± 3	41 ± 3	47 ± 2		52 ± 3
WF	Wheat	70 ± 0	70 ± 0	77 ± 3	75 ± 4	92 ± 7	91 ± 6	100 ± 2	98 ± 2
	Pea	63 ± 3	60 ± 0		66 ± 6	76 ± 4	73 ± 5		74 ± 2

548
 549 **Table 3.** Comparative absolute growth rate (CGR) calculated for the time interval corresponding to the dates of sampling: sowing
 550 to '1cm ear' stage of wheat (E1cm), E1cm to the beginning of pea flowering (BPF), BPF to wheat flowering (WF), WF to
 551 maturity harvest (Harvest) and for the whole growth period (Sowing to Harvest) for the different N treatments (Nx where 'x'
 552 represents N applied in kg N ha⁻¹) of experiments I and II. Values are the mean ± standard error. Single plus (+) and single
 553 asterisks (*) indicate that CGR are significantly different from one at P=0.10 and P=0.05 respectively.

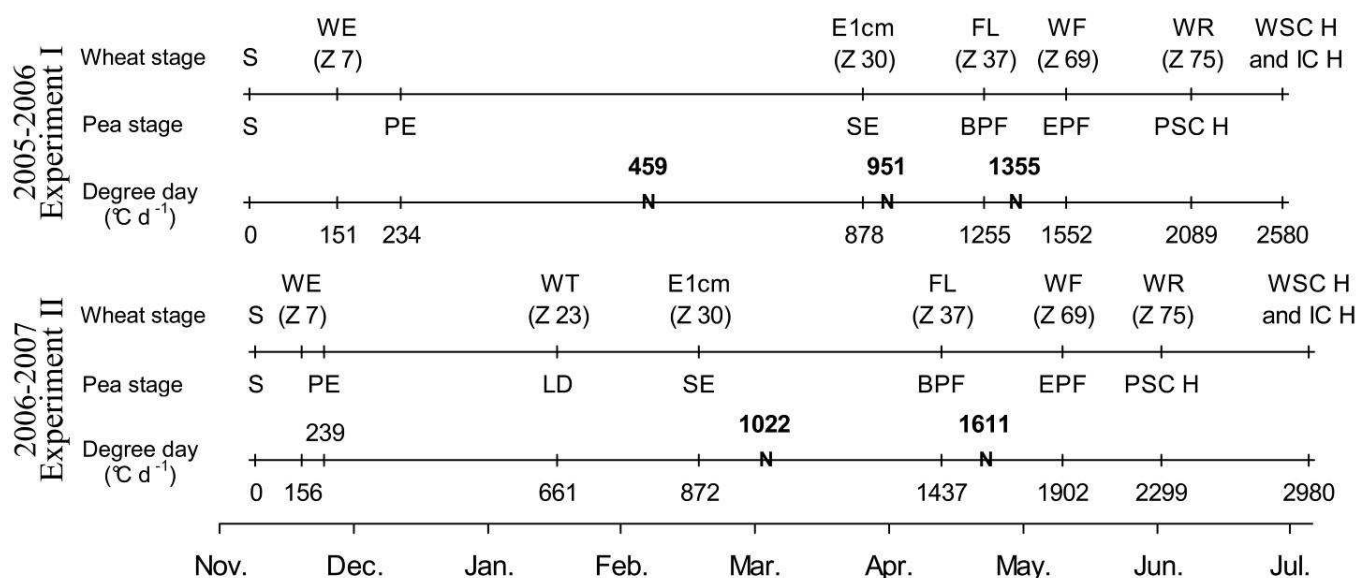
	2005-2006 (Experiment I)						2006-2007 (Experiment II)							
	N0		N100		N180		N0		N60+		N80		N140	
	SC	IC	SC	IC	SC	IC	SC	IC	SC	IC	SC	IC	SC	IC
Sowing to E1cm	1.9 ± 0.1 *	2.5 ± 0.7 *	1.7 ± 0.4 *	3.6 ± 1.4 *	1.8 ± 0.2 *	4.8 ± 0.8 *	3.8 ± 0.8 *	4.5 ± 1.1 *	4.0 ± 0.4 *	11.7 ± 5.5 *	3.1 ± 0.4 *	9.8 ± 5.5 *	5.1 ± 1.0 *	8.3 ± 2.8 *
E1cm to BPF	0.9 ± 0.1	1.3 ± 0.5	1.0 ± 0.2	1.9 ± 0.5 *	1.4 ± 0.1 *	1.9 ± 0.4	0.6 ± 0.2 *	0.9 ± 0.4	1.3 ± 0.6	3.3 ± 0.5 *	1.6 ± 0.1 *	3.0 ± 0.4 *	1.5 ± 0.4 *	4.3 ± 3.3
BPF to WF	0.7 ± 0.1	0.6 ± 0.1 *	0.8 ± 0.1 *	1.3 ± 0.3	0.8 ± 0.2	4.0 ± 0.3 *	0.5 ± 0.1 *	0.4 ± 0.0 *	0.6 ± 0.2 *	2.3 ± 1.0	0.9 ± 0.2	1.2 ± 0.4	0.6 ± 0.3 *	0.7 ± 0.7
WF to Harvest	2.3 ± 0.7	4.3 ± 1.6 *	7.0 ± 2.3 *	1.5 ± 0.6	8.4 ± 1.6 *	4.3 ± 1.1	-0.4 ± 0.5 *	0.0 ± 0.1 *	-0.2 ± 0.5 *	0.8 ± 0.3	0.0 ± 0.2 *	0.1 ± 0.3 *	-0.3 ± 0.1 *	0.1 ± 0.1 *
Sowing to Harvest	1.0 ± 0.1	1.4 ± 0.0 *	1.4 ± 0.2 *	1.6 ± 0.2 *	1.6 ± 0.1 *	3.2 ± 0.5 *	0.9 ± 0.2	1.0 ± 0.4	1.2 ± 0.1 *	3.5 ± 1.4 *	1.5 ± 0.2 *	3.3 ± 1.1 *	1.3 ± 0.1 *	3.3 ± 1.4 *

555 **Table 4.** Values of fitted parameters, cumulative PAR absorbed, root mean square error, bias and PAR land equivalent ratio
 556 calculated from the logistic model: $F_{PARa} = F_{PARmax} \times \frac{\exp(K1 \times (t - K2))}{1 + \exp(K1 \times (t - K2))}$ for the whole intercrop (IC), pea sole crop (P
 557 SC) and wheat sole crop (W SC) for the different N treatments (Nx where 'x' represents N applied in kg N ha⁻¹).

	2005-2006 (Experiment I)						2006-2007 (Experiment II)									
	N0		N100		N180		N0		N60+		N80		N140			
	IC	W SC	P SC	IC	W SC	IC	W SC	IC	W SC	P SC	IC	W SC	IC	W SC		
K1*10 ⁵	743	923	1030	693	665	767	757	809	813	967	834	711	960	1018	927	769
K2 (°C)	671	569	782	653	581	652	589	842	755	967	865	813	832	790	826	764
F _{PARmax} (%)	89	74	93	91	83	93	87	86	73	91	94	90	93	92	94	97
PAR absorbed (MJ m ⁻²)	342	333	289	359	366	369	380	400	373	367	427	432	441	457	450	486
RMSE (%)	3.1	2.1	1.8	1.9	2.3	2.7	3.3	1.6	2.4	1.3	2.6	1.6	2.9	3.6	1.7	1.6
Bias (%)	-0.2	-0.1	0.4	-0.2	-0.2	-0.2	-0.2	0.2	0.2	0.4	0.3	0.1	0.2	0.6	0.3	0.2
LER _{PAR}		1.10		1.10		1.10		1.08			1.07		1.07			1.06

559 Figures

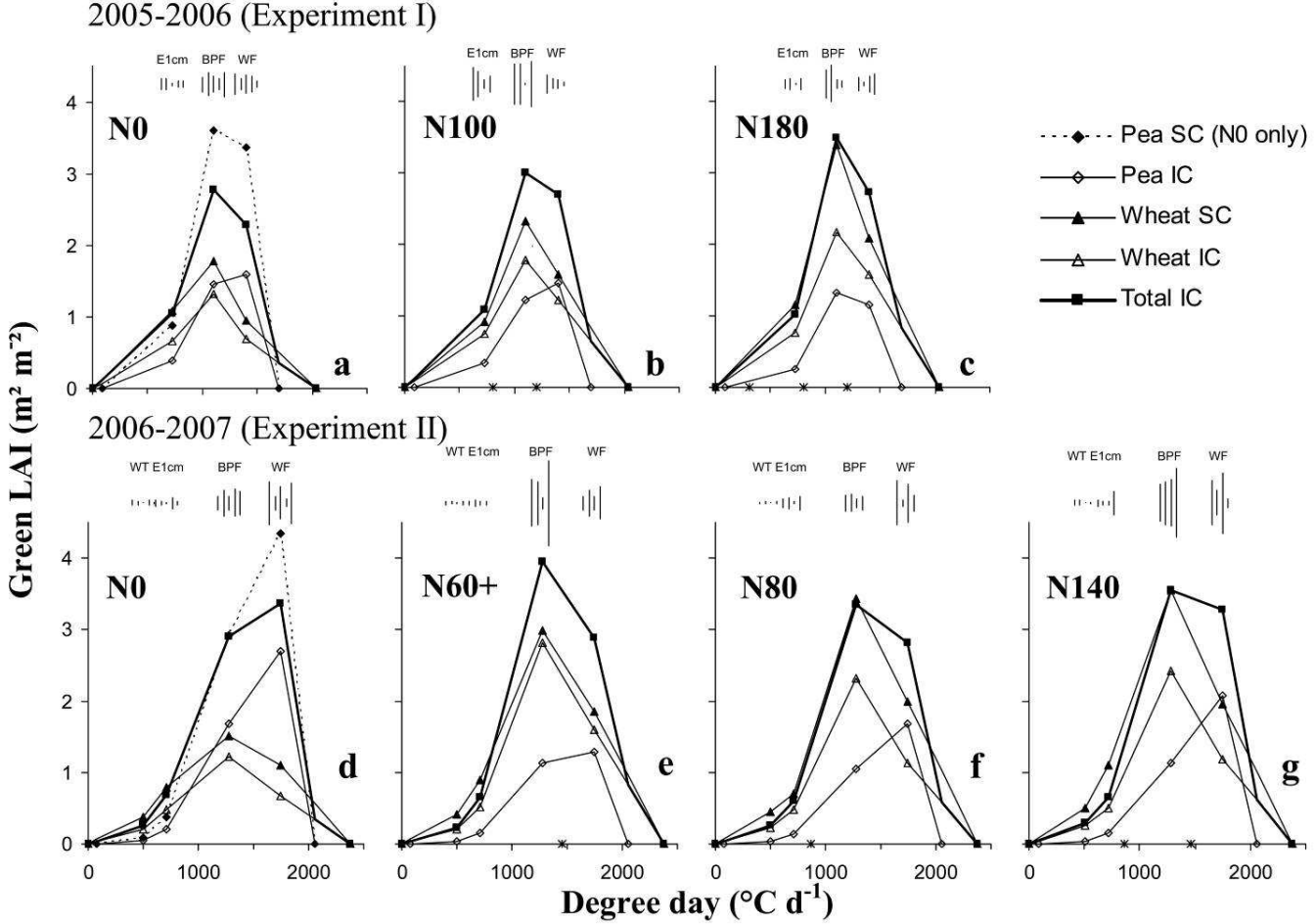
560 **Figure 1.** Major stages and sampling dates which occurred during the experimental periods represented on a calendar scale
 561 coupled with a degree day scale (base 0°C) scale: sowing (S), wheat emergence (WE), pea emergence (PE), wheat tillering stage
 562 (WT), pea leaf development (LD), '1 cm ear' stage of wheat (E1cm), beginning of pea stem elongation (SE), 'visible flag leaf'
 563 stage of wheat (FL), beginning of pea flowering (BPF), wheat flowering (WF), end of pea flowering (EPF), wheat ripening (WR),
 564 final harvest (maturity) for pea sole crop (PSC H) and final harvest (maturity) for wheat sole crop and intercrop (WSC and IC H).
 565 Wheat stages are indicated with a 'Z' (for Zadoks scale) followed by the number of the stage e.g. 'Z 30'. Dates of fertilizer-N
 566 application are indicated with a bold 'N' for both experiments.



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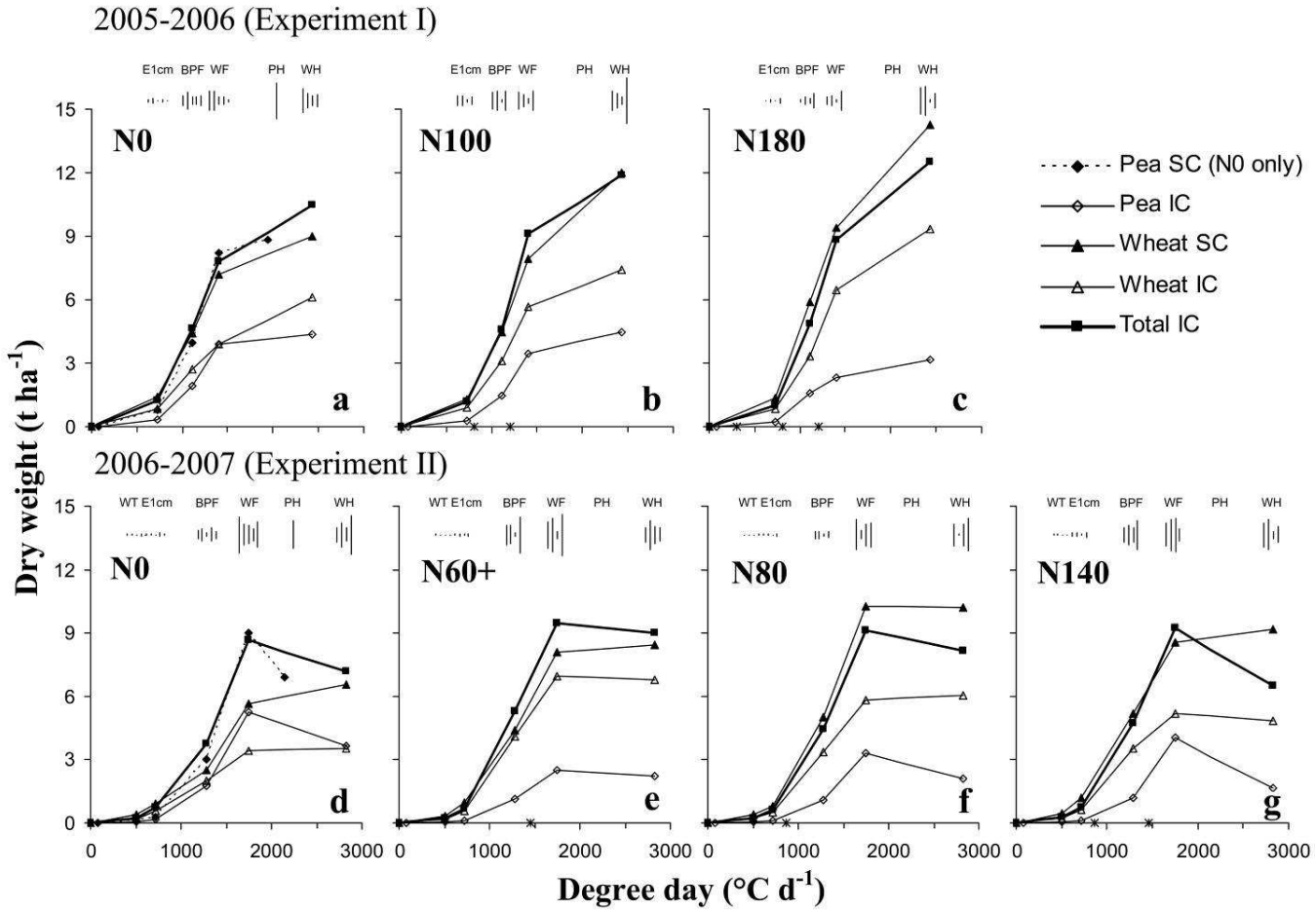
568

568 **Figure 2.** Dynamics of green leaf area index (GLAI) of sole crops (SC) and intercrops (IC) of pea and wheat for the different N
 569 treatments (Nx where 'x' represents N applied in kg N ha⁻¹) and dates of sampling. Values are means (n=3 to 5). For each date of
 570 sampling, vertical bars on the top of the figure correspond to standard deviation of the total IC, Wheat IC, Pea IC, Wheat SC and
 571 Pea SC (N0 only) respectively. Asterisks on the x-axis correspond to fertilizer-N application.



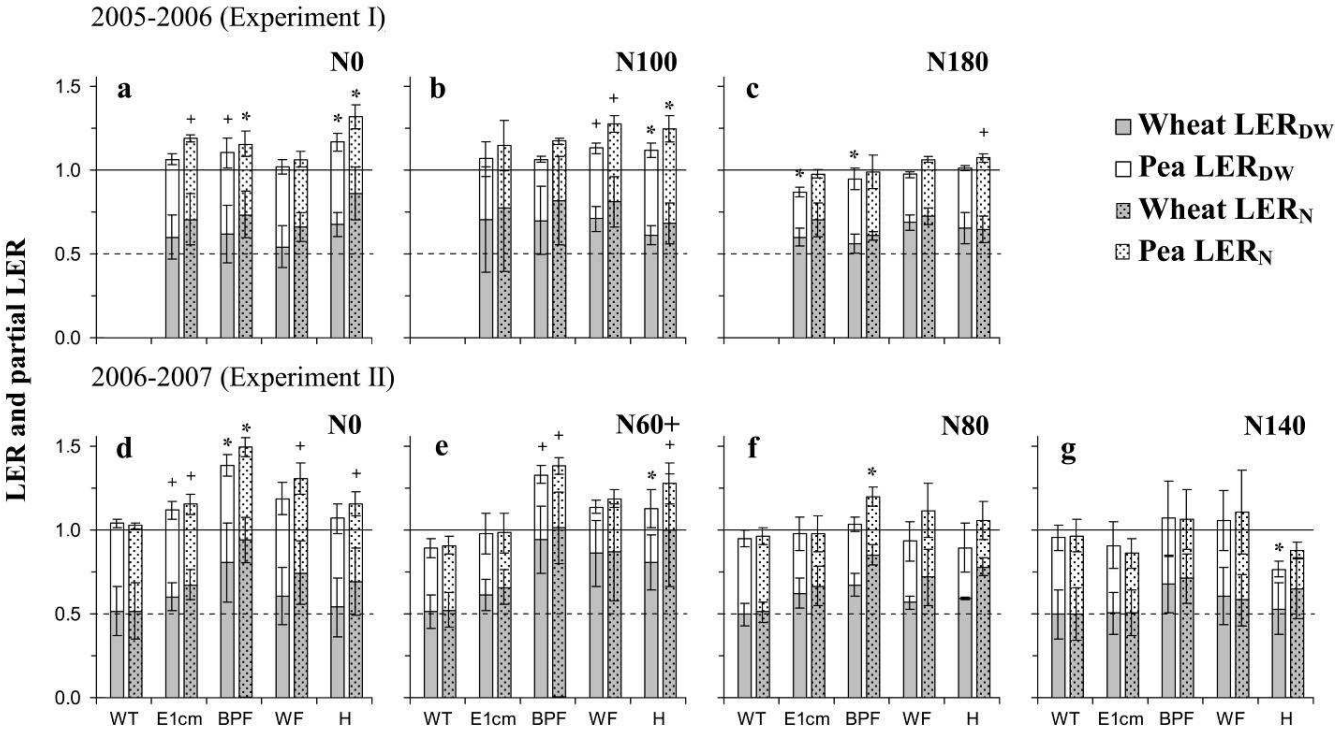
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573

573 **Figure 3.** Evolution of total shoot dry weight (DW) production in $t\ ha^{-1}$ of sole crops (SC) and intercrops (IC) of pea and wheat
 574 for the different N treatments (Nx where 'x' represents N applied in $kg\ N\ ha^{-1}$) and dates of sampling. Values are means (n=3 to
 575 5). For each date of sampling, vertical bars on the top of the figure correspond to standard deviation of the total IC, Wheat IC, Pea
 576 IC, Wheat SC and Pea SC (N0 only) respectively. Asterisks on the x-axis indicate fertilizer-N applications.



577
 578

578 **Figure 4.** Partial land equivalent ratio (LER) of wheat and pea calculated from dry weight (LER_{DW}) and N accumulated (LER_N)
 579 for the two experiments and N treatments (Nx where 'x' represents N applied in kg N ha⁻¹) for the different dates of sampling: i)
 580 wheat tillering (WT), ii) 'ear 1cm' stage of wheat (E1cm), iii) beginning of pea flowering (BPF), iv) wheat flowering (WF) and v)
 581 harvest maturity (H). Values are the mean (n=3 to 5) ± standard error. Single plus (+) and single asterisks (*) indicate that LER is
 582 significantly different from one at P=0.10 and P=0.05 respectively.

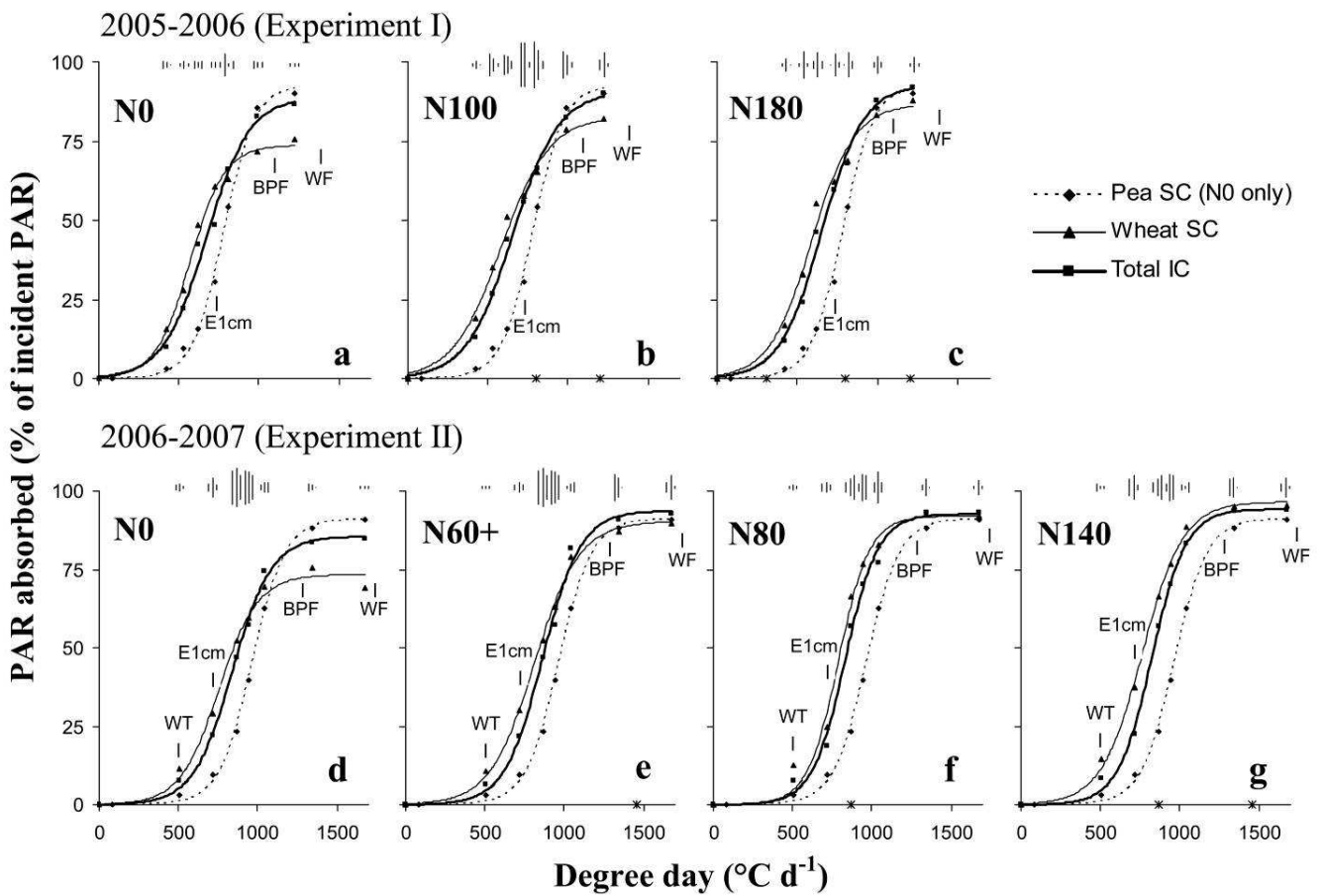


583
584

584 **Figure 5.** Evolution of the PAR fraction absorbed of sole crops (SC) of pea or wheat and of the whole intercrop (IC) measured
 585 throughout crop growth for the different N treatments (Nx where 'x' represents N applied in kg N ha⁻¹). Values are means (n=3 to
 586 5) and curves are regressed non-linearly against thermal time using the following logistic model:

587
$$F_{PARa} = F_{PARmax} \times \frac{\exp(K1 \times (t - K2))}{1 + \exp(K1 \times (t - K2))}$$
 For each date of sampling, vertical bars on the top of the figure correspond to

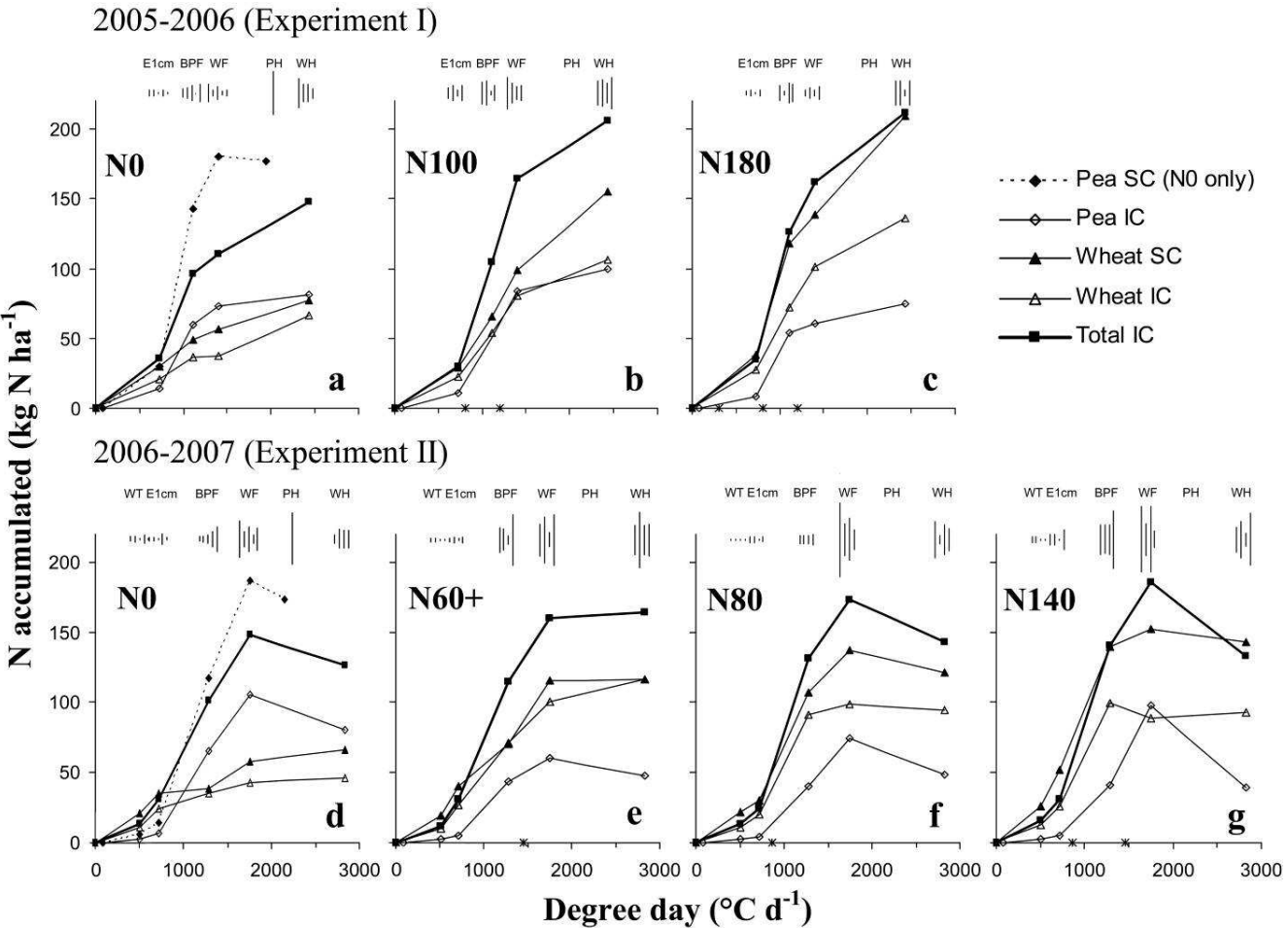
588 standard deviation of the total IC, Wheat SC and Pea SC (N0 only) respectively. Asterisks on the x-axis indicate fertilizer-N
 589 application.



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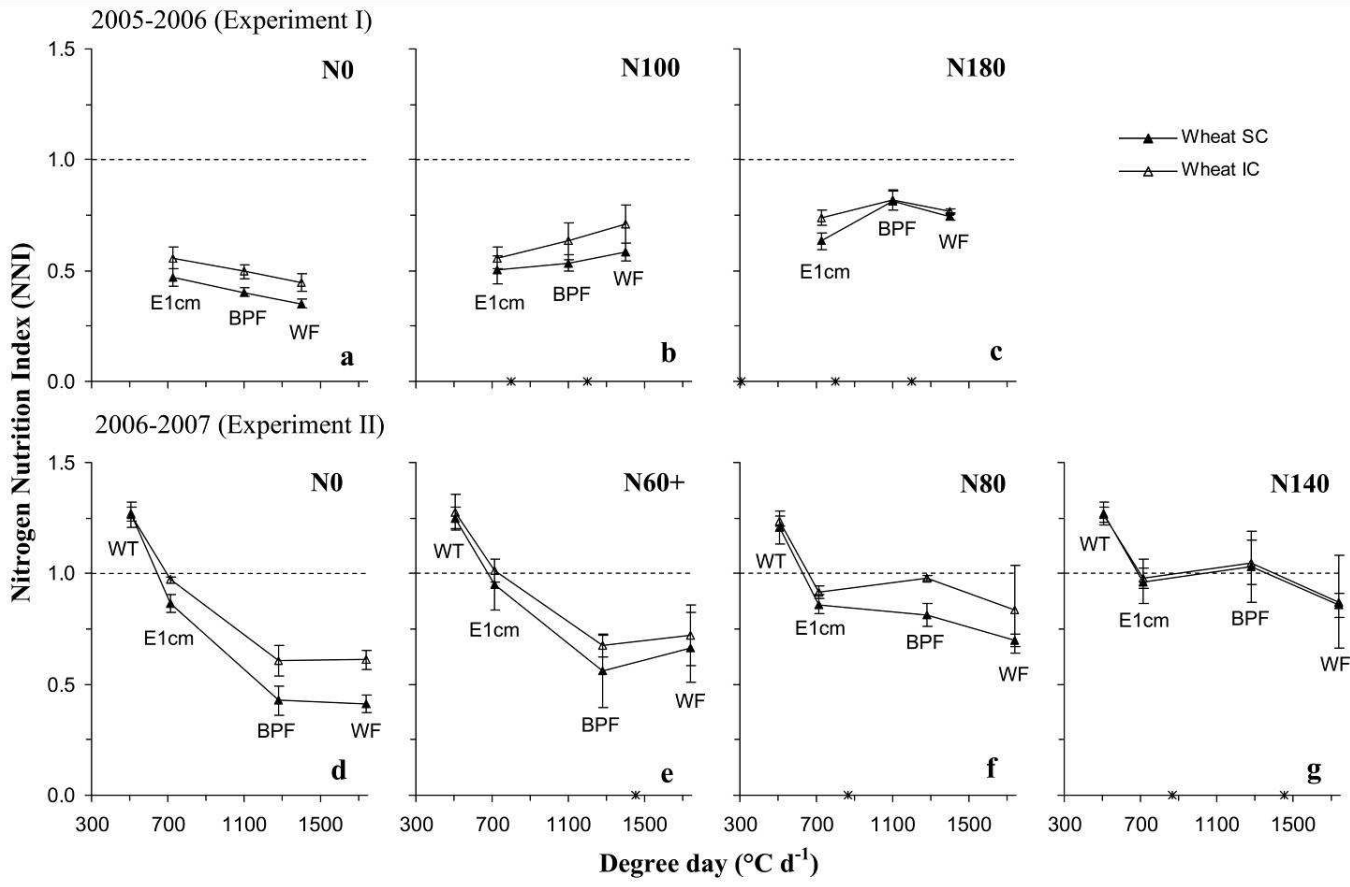
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591 **Figure 6.** Total shoot N accumulation in kg N ha⁻¹ of sole crops (SC) and intercrops (IC) of pea and wheat for the different N
 592 treatments (Nx where 'x' represents N applied in kg N ha⁻¹) and dates of sampling. Values are means (n=3 to 5). For each date of
 593 sampling, vertical bars on the top of the figure correspond to standard deviation of the total IC, Wheat IC, Pea IC, Wheat SC and
 594 Pea SC (N0 only) respectively. Asterisks on the x-axis indicate fertilizer-N application.



595
596

596 **Figure 7.** Nitrogen nutrition index (NNI) of wheat in a sole crop (SC) and intercrop (IC) for the different N treatments (Nx where
 597 'x' represents N applied in kg N ha⁻¹) and dates of sampling. Values are means (n=3 to 5) ± standard error. Asterisks on the x-axis
 598 indicate fertilizer-N application.



599