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

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Abstract

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

Keywords

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

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Introduction

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

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

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

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

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

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Materials and methods

Site and Soil

The experiment was carried out on the experimental fields of the Institut National de la Recherche Agronomique station in 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 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 in August and a minimum monthly mean daily temperature of 6.0 °C in January. The rainfall during the growing seasons was 361 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). 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 a rather wet spring. Then, the two years were quite different in terms of climatic conditions indicating a good level of robustness in the dynamic analysis of intercrops.

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). 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 cm). For both experiments, phosphorus, potassium and cation exchange capacity values were not limiting (for more details, see Bedoussac and Justes 2009). The four previous crops on the experimental sites were durum wheat (*Triticum turgidum*), sunflower (*Helianthus annuus*), durum wheat and sorghum (*Sorghum bicolor*) for Exp.I and sunflower, durum wheat, sorghum and sunflower for Exp.II.

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Experimental design

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

In both experiments, different fertilizer-N sub-treatments were evaluated on wheat sole crop and intercrop while pea sole crop was grown without any N application assuming that N_2 fixation allows fulfilling pea N requirements for optimal growth. In Exp.I 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} at '1 cm ear' (E1cm, Zadoks 30 (Zadoks et al. 1974)) and 'flag leaf visible' (FLV, Zadoks 37) and iii) moderate N fertilization (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 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 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 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

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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 dynamics of N availability. As a consequence, the N60 treatment was more than the simple effect of a late N supply due to the previous treatment on sunflower, so we chose to name it N60+. Initial mineral N, early mineral N available and mineral N available throughout crop growth for the two experiments are described in Table 1 (for details, see Bedoussac and Justes 2009)[0]. The experimental layout for both experiments was a randomized split-plot design with N application as main plots and crops as subplots, with five replicates in Exp.I (four replicates for wheat sole crop in N0 and intercrop in N180) and three replicates in 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 apart. Fungicide-treated seeds were sown on November 8, 2005 (Exp.I) and on November 9, 2006 (Exp.II) using a 6-row pneumatic precision experimental prototype drill with 29 cm row separation. Sowing was done in two passes by moving to the 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 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 sowing because of the low water content in the topsoil. Weeds, diseases and green aphids were controlled as much as possible by application of appropriate pesticides.

Measurements and analysis

The number of seedlings in four rows of 1 m length was counted one month after emergence.

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

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

Calculations

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

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

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

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

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-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 PAR_{RBS} the PAR reflected from the bare soil. The fraction of PAR absorbed by the crop was regressed against thermal time from emergence to wheat flowering using a logistic model:

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

where F_{PARmax} is the maximum value of F_{PARa} when thermal time approaches positive infinity, K2 the thermal time at the point of 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 were calculated in order to minimize the root mean square error.

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

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

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 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 energy (Varlet-Grancher et al. 1982).

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In order to compare the species growth dynamics in the intercrop we defined an index called the comparative absolute growth rate (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 another. Thus, CGR for a wheat-pea intercrop (IC) is the ratio between the growth rate of wheat (GR_W) and pea (GR_P):

$$GR_W = \frac{DW_{W-IC}t_2 - DW_{W-IC}t_1}{t_2 - t_1}$$

$$GR_P = \frac{DW_{P-IC}t_2 - DW_{P-IC}t_1}{t_2 - t_1}$$

$$CGR_{IC} = \frac{GR_{W-IC}}{GR_{P-IC}}$$

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

$$CGR_{SC} = \frac{GR_{W-SC}}{GR_{P-SC}}$$

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

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

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

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$$NNI = \frac{\%Nact}{\%Nc}$$

%Nc for a sole crop winter wheat ($\%Nc_{W\text{-}SC}$) is defined by the critical nitrogen dilution curve proposed by Justes et al. (1994) and validated for durum wheat (Justes et al., 1997).

$$\%Nc_{W-SC} = 4.4\% \text{ if } \mathrm{DW}_{\text{W-SC}} < 1.55\,\mathrm{t\,ha^{-1}} \text{ else } 5.35 \times \mathrm{DW}_{\text{W-SC}}^{-0.442}$$

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

$$\%Nc_{W-IC} = 4.4\% \text{ if } \mathrm{DW}_{\text{IC}} < 1.55\,\mathrm{t\,ha^{-1}} \text{ else } 5.35 \times \mathrm{DW}_{\text{IC}}^{-0.442}$$

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

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 one N was limiting for crop growth at that specific date.

Statistics

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

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Results

Growth dynamics

Emergence and plant density

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

Green leaf area index (GLAI)

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 the intermediate growth stage (BPF and WF) but lower for earlier stages (WT and E1cm). Moreover, pea sole crop GLAI reached zero (1700 and 2050 °C d^{-1} after wheat emergence for Exp.I and Exp.II respectively) while wheat sole crop GLAI was still significantly positive.

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 ($p<0.10$) except that in the initial growth stages (WT and E1cm) where it was comparable to that of the wheat sole crop and slightly greater to that of the pea sole crop ($p<0.10$). N fertilization significantly increased wheat GLAI both in sole crop and 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 treatments was observed for the intercropped pea GLAI while in Exp. II the maximum was obtained for N0 ($p<0.05$). Thus the GLAI of the whole intercrop was slightly but not significantly affected by N fertilization ($p>0.10$).

Growth in height

Wheat and pea differed in height, but this difference changed over time (Table 2). Overall, wheat was taller than pea in both the initial (E1cm) and the later (WF) growth stages, but no difference was found at the intermediate growth stage (BPF). No significant difference was neither found between sole crop and intercrop canopy height for both wheat and pea at any of the 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 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 and WF growth stages ($p<0.05$). Moreover, no pea lodging was observed in intercrop although this occurred in sole crop for both experiments, with a high proportion in Exp.II.

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Dry weight of aerial biomass and interspecies dynamics

Without N fertilization (Fig. 3a and 3d), the aerial biomass of sole cropped pea was lower than that of the sole cropped wheat 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 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 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 sole cropped wheat throughout the whole crop growth ($p<0.10$) except at WF stage for N140 ($p>0.10$).

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

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

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 greater than that of pea in intercrop for Exp.I and Exp.II respectively (Table 3). Similar dynamics were observed for the SC with on average CGR values of 1.8 and 4.0 for Exp.I and Exp.II respectively, indicating that competitions between wheat and pea intercropped in rows were weak until E1cm stage.

Afterwards, for both experiments and all treatments, CGR values in intercrop were close to or higher than one during the two following growth periods (E1cm to BPF and BPF to WF) except for N0 between BPF and WF (Table 3), indicating that the growth rate of wheat was similar or slightly higher than that of pea in fertilized intercrops. However, significant lower values than one for N0 treatments indicated higher growth rate of pea in intercrop from BPF to WF. Concerning the sole crops, CGR values 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 for both experiments) from BPF to WF, indicating similar or higher pea growth rate than wheat during this later period.

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 thought in intercrop CGR values were significantly different from one only for N0. On the contrary, in Exp. II, CGR values were

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

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

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

At the four key stages sampled (E1cm, BPF, WF and maturity), LER values calculated from aerial biomass dry weight (LER_{DW}) 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 maturity. These results indicate that throughout the whole crop growth, resources were used for aerial biomass production up to 36% more efficiently in intercrops than in sole crops in low N conditions. On the whole, LER_{DW} values were reduced with N fertilization, particularly for the N180 (Fig. 4c) and the N140 (Fig. 4g) treatments mostly because of the pea partial LER_{DW} (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 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 much higher ($p<0.10$). Moreover, LER_{DW-P} values remained more or less stable throughout the whole crop growth, and similar 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 particular for N0 (Fig. 4d) and N60+ (Fig. 4e).

Resource use dynamics

Light absorption

The fraction of PAR absorbed (F_{PARa}) by sole crops and the whole intercrops increased with crop growth from emergence to WF following a logistic model (Fig. 5). The root mean squared error (RMSE) values (Table 4) were very low (3.6% at maximum) and 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 (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, 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 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.

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 E1cm), itself slightly greater than that of the whole intercrop. Then, from E1cm to WF, the F_{PARa} of intercrop became lower than

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that of pea sole crop and greater than that of wheat sole crop. When N fertilizer was applied, no significant difference was 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 potential of PAR absorption was reached (Table 4). Finally, the cumulative PAR absorbed (Table 4) from sowing to WF was the lowest for the pea sole crop and the highest for the wheat sole crop except for N0 where the maximum was observed for the whole intercrop.

Nitrogen acquisition and wheat nitrogen nutrition index (NNI)

Without N fertilizer and until BPF stage (Fig. 6a and 6d), the pea sole crop accumulated significantly ($p<0.10$) more N in shoots than the wheat sole crop and than the whole intercrop. In N-fertilized treatments, the whole intercrop accumulated more N than 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 accumulated more N than the wheat sole crop except in early stages (WT and E1cm) and at maturity for N180 (Fig. 6c) and N140 (Fig. 6g) ($p>0.10$).

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

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 intercropped wheat was sown at half plant density of the wheat sole crop (fig. 6). The proportion of N uptake in intercrop compared to sole crop was higher for N0 treatment, indicating a higher N availability per wheat plant in intercrop.

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

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Land equivalent ratio for N acquisition (LER_N)

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

Discussion

Various authors have indicated that sequential measurements of crop growth allow a better understanding of the dynamics and mechanisms of competitive interactions in intercrop and sole crop compared to a single measurement of final yield (e.g. Connoly 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 development stages. The following discussion will be largely organized according to the growing periods between these stages because they determined key periods for interspecific competition and complementarity between durum wheat and winter pea.

Our data has shown that for limited early N availability (no fertilizer or a small amount applied after the wheat booting stage) there were significant complementarities between intercropped durum wheat and winter pea for light and nitrogen use. This was clearly due to species differences in their dynamics of growth and to differences in species phenology and physiology which we will demonstrate afterwards.

Early growth dynamics

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

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nutrients) according to e.g. Vocanson et al. (2005) and Voisin et al. (2002) which could have reduced early pea growth. Crop emergence and early growth were slower in Exp.II due to: i) the coarse soil structure, ii) the low soil water content at sowing, only partially compensated by irrigation, and iii) the low winter temperatures. In particular, pea was affected by the coarse soil structure and the low soil water content at sowing in Exp.II possibly explained by a higher water demand due to greater pea seed size. Also, and particularly in Exp.II, pea emerged later and hence at lower temperatures than wheat, increasing the differences between the early growth of the two species as illustrated by higher CGR values in Exp.II than in Exp.I.

In early stages of growth (until wheat stem elongation corresponding to 'ear 1 cm' stage), wheat was much more efficient than pea for light absorption, due to its earlier growth, greater height during winter, tillering and higher green leaf area index, as illustrated by CGR values much higher than one from sowing to E1cm. Similar dynamics were observed for the sole crop and the intercrop indicating that our results are in good agreement with species' phenological and physiological differences. However, pea growth was lower in intercrop than in sole crop during early stages as illustrated by CGR values higher for the intercrop than for the sole crops. This is certainly due to less incoming PAR available for the intercrop pea being partly shaded by the durum wheat.

Intermediate period of growth dynamics

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

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

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

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

N accumulated by the intercropped wheat was at least 70% and often more of that of the wheat sole crop for half plant density, particularly until the beginning of pea flowering and when little or no N fertilizer was applied. This confirms that the cereal had access to a more than proportionate share of soil mineral N in intercrop per plant as compared to sole crop (Jensen 1996). This result is supported by: i) the increase in pea symbiotic N_2 fixation rate demonstrated in the companion paper (Bedoussac and Justes 2009) and in agreement with several other studies for spring intercrops (e.g. Corre-Hellou 2005; Hauggaard-Nielsen et al. 2003; Corre-Hellou and Crozat 2005), and ii) the lower durum wheat biomass per square meter in intercrop due to light competition exerted by the pea. Consequently and as expected, the intercropped wheat N status (NNI) was always higher than that of the sole crop except when a large amount of N was applied. This confirms that intercrop can improve wheat N status compared to sole crop and consequently the grain protein content in particular with little or no N fertilizer. Moreover, the advantage of intercrop over sole crop seems to increase throughout the growth period due to higher N available per durum wheat plant. The N status of sole cropped and intercropped wheat were mostly below one, in particular in late stages and when little or no N fertilizer was applied, underlining the existence of a nitrogen deficiency in the crop throughout the growing period which confirmed that we were in low N inputs conditions. However, the intercropped wheat had a lower N deficiency which allowed better photosynthesis and hence higher radiation use efficiency (e.g. Justes et al. 2000).

Late growth dynamics

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

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maturity and wheat maturity because wheat biomass was not measured at the pea maturity stage in our experiments. Nevertheless, in late stages, wheat took advantage of the intercrop by remobilizing more N into its grain due to: i) lower grain yield and ii) almost similar N available compared to the sole crop according to the high legume N_2 fixation described in the companion paper (Bedoussac and Justes 2009).

Conclusion

The objective of our paper was to answer to the following question: how the final outcome of the durum wheat-winter pea intercrop can be explained? Thus, we demonstrated that in our experiments the use of environmental resources for plant growth changed over time, indicating that the ability for a crop to exploit resource niches and thereby capture resources varies significantly during the growth cycle. Throughout crop growth, resources were used up to 36% more efficiently in intercrops than in sole crops for aerial biomass in low N conditions and intercrops efficiency for N uptake was greater than for biomass production throughout crop growth at all N fertilization levels. Regardless of N availability, wheat took advantage of intercrop for aerial biomass production more than pea ($LER_{DW\text{-}W} > LER_{DW\text{-}P}$) by using N, light and certainly CO_2 and water more efficiently throughout the growth cycle due to its earlier growth, greater height and higher N demand. CGR and LER dynamic analysis indicated that pea took advantage of intercrop mainly between pea flowering and wheat flowering (near the end of pea grain filling), while wheat took advantage of intercrop between the emergence and the beginning of wheat stem elongation (E1cm stage) and until pea flowering.

Wheat benefited from N fertilization more than pea directly by its faster growth, improving light and water capture and hence suppressing pea growth whatever the amount and the date of N application (Fujita et al. 1992; Jensen 1996; Bulson et al. 1997). Moreover, as shown by many other studies on spring peas, winter pea has a higher interspecific competitive ability at low N levels because of: i) the reduction in N_2 fixation with N supply (Voisin et al. 2002; Ghaley et al. 2005) and ii) the amplification of differences in species growth dynamics with N supply (Hauggaard-Nielsen and Jensen 2001; Ghaley et al. 2005). Durum wheat and winter pea showed interspecific complementarity in good agreement with other studies on cereal-legume spring-sown intercrops (Corre-Hellou and Crozat 2005; Hauggaard-Nielsen et al. 2006; Hauggaard-Nielsen et al. 2009).

However, intercrop efficiency and crops interspecific competitiveness ability depended on the dynamics of N availability throughout the growth cycle of intercrops. N fertilizer applied at the beginning of wheat stem elongation clearly leads to a significant and early decrease in pea N acquisition due to a quantitative reduction in N_2 fixation described in the companion paper (Bedoussac and Justes 2009) and the opposite with no or late N fertilization. As a consequence, the advantage of intercrop for biomass production, yield or accumulated N was maximal under low N fertilization treatments (no or late fertilization) due to good complementarities of durum wheat and winter pea for GLAI and growth dynamics over time.

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

As a practical conclusion, our results indicate that durum wheat-winter pea intercrop productivity can be optimized by adapting cropping sequences, N fertilization in particular, but also by choosing crop species of widely different phenologies and/or morphologies in order to maximize capture and minimize competition for solar radiation. It is essential to prevent an adverse effect on legume growth (involving N_2 fixation) which very much influences the final outcome and total yield potentials of the intercrop.

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

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Tables

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 0-120 cm, ii) calculated apparent available N on 0-120 cm from sowing to the beginning of pea flowering (S to BPF) and from 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 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

Table 2. Canopy height (cm) of sole crops (SC) and intercrops (IC) measured at '1 cm ear' stage of wheat (E1cm), beginning of pea flowering (BPF) and wheat flowering (WF) for the unfertilized plots (N0) or considering the mean of all N treatments. Values 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

Table 3. Comparative absolute growth rate (CGR) calculated for the time interval corresponding to the dates of sampling: sowing to '1cm ear' stage of wheat (E1cm), E1cm to the beginning of pea flowering (BPF), BPF to wheat flowering (WF), WF to maturity harvest (Harvest) and for the whole growth period (Sowing to Harvest) for the different N treatments (Nx where 'x' represents N applied in kg N ha^{-1}) of experiments I and II. Values are the mean ± standard error. Single plus (+) and single 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 +

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Table 4. Values of fitted parameters, cumulative PAR absorbed, root mean square error, bias and PAR land equivalent ratio calculated from the logistic model: $F_{PARa} = F_{PAR\max} \times \frac{\exp(K1 \times (t - K2))}{1 + \exp(K1 \times (t - K2))}$ for the whole intercrop (IC), pea sole crop (P 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	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	

Figures

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

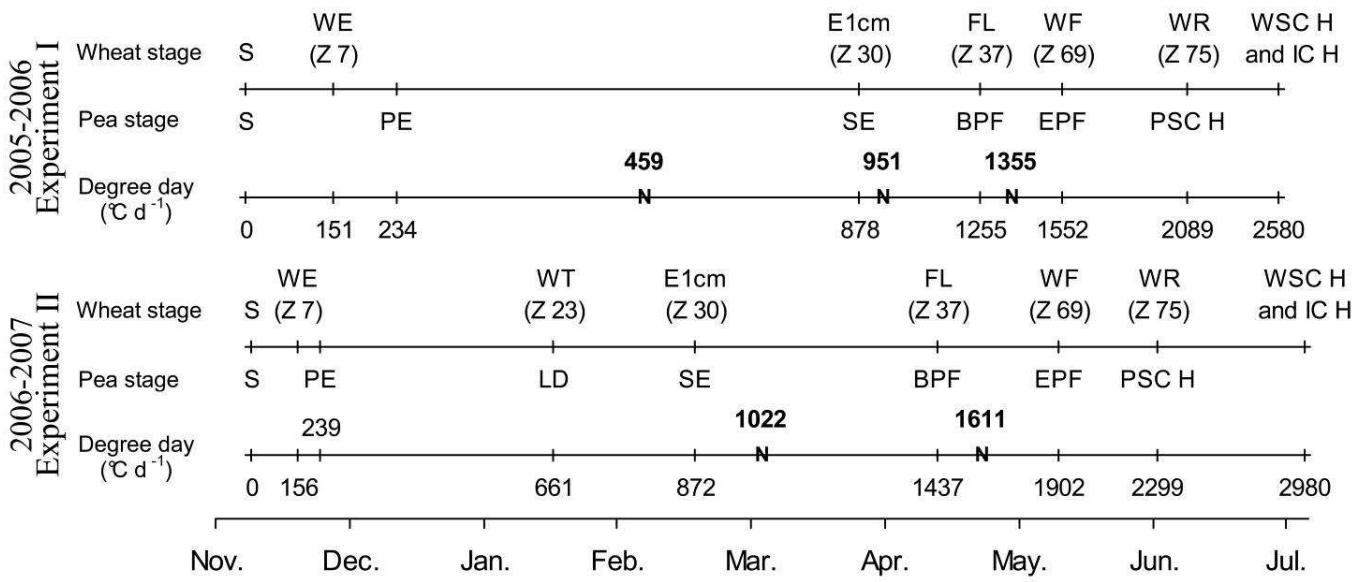

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Figure 2. Dynamics of green leaf area index (GLAI) of sole crops (SC) and intercrops (IC) of pea and wheat for the different N treatments (Nx where 'x' represents N applied in kg N ha^{-1}) and dates of sampling. Values are means (n=3 to 5). For each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

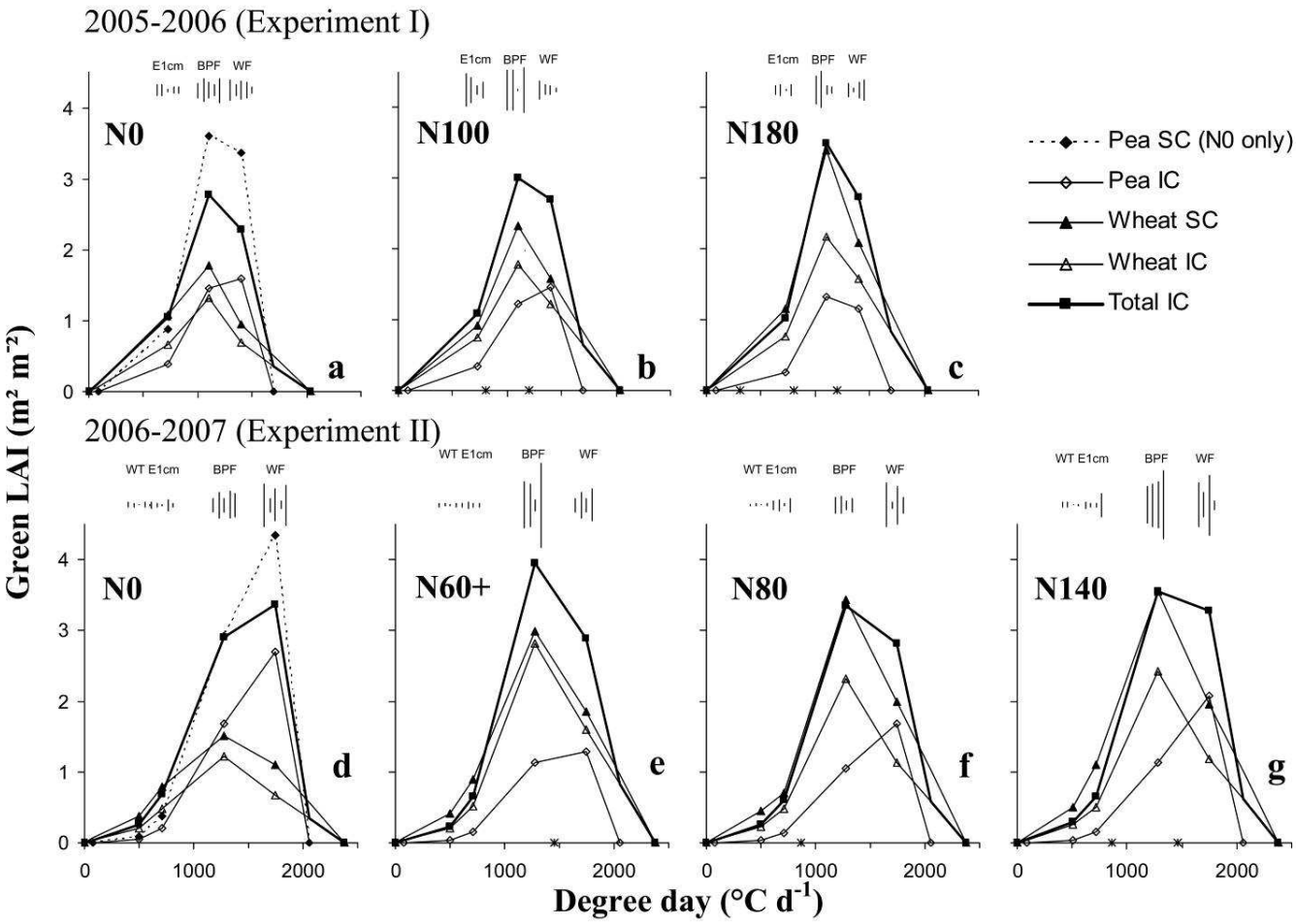

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Figure 3. Evolution of total shoot dry weight (DW) production in t ha^{-1} of sole crops (SC) and intercrops (IC) of pea and wheat for the different N treatments (Nx where 'x' represents N applied in kg N ha^{-1}) and dates of sampling. Values are means (n=3 to 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 IC, Wheat SC and Pea SC (N0 only) respectively. Asterisks on the x-axis indicate fertilizer-N applications.

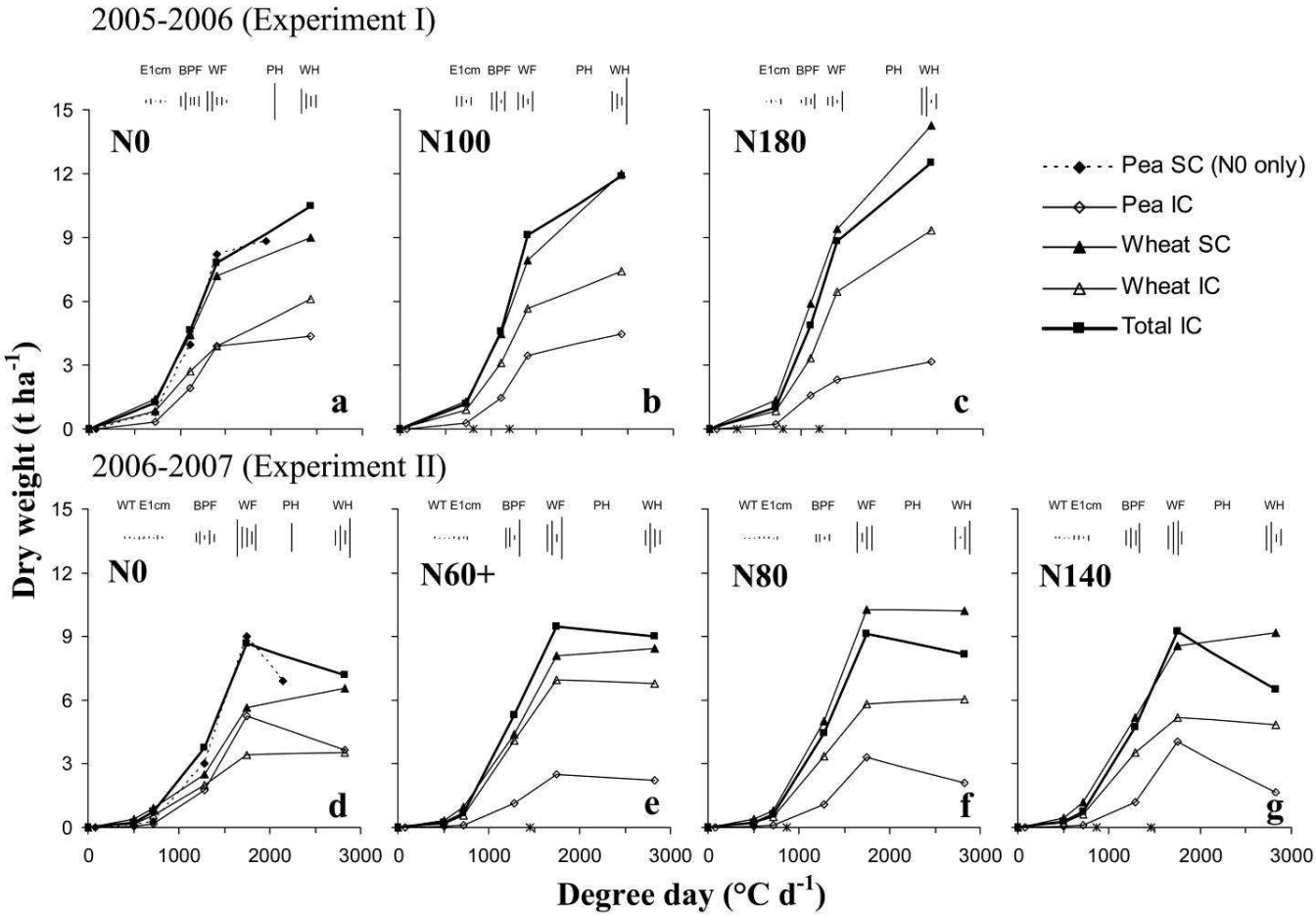

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Figure 4. Partial land equivalent ratio (LER) of wheat and pea calculated from dry weight (LER_{DW}) and N accumulated (LER_N) for the two experiments and N treatments (Nx where 'x' represents N applied in kg N ha^{-1}) for the different dates of sampling: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

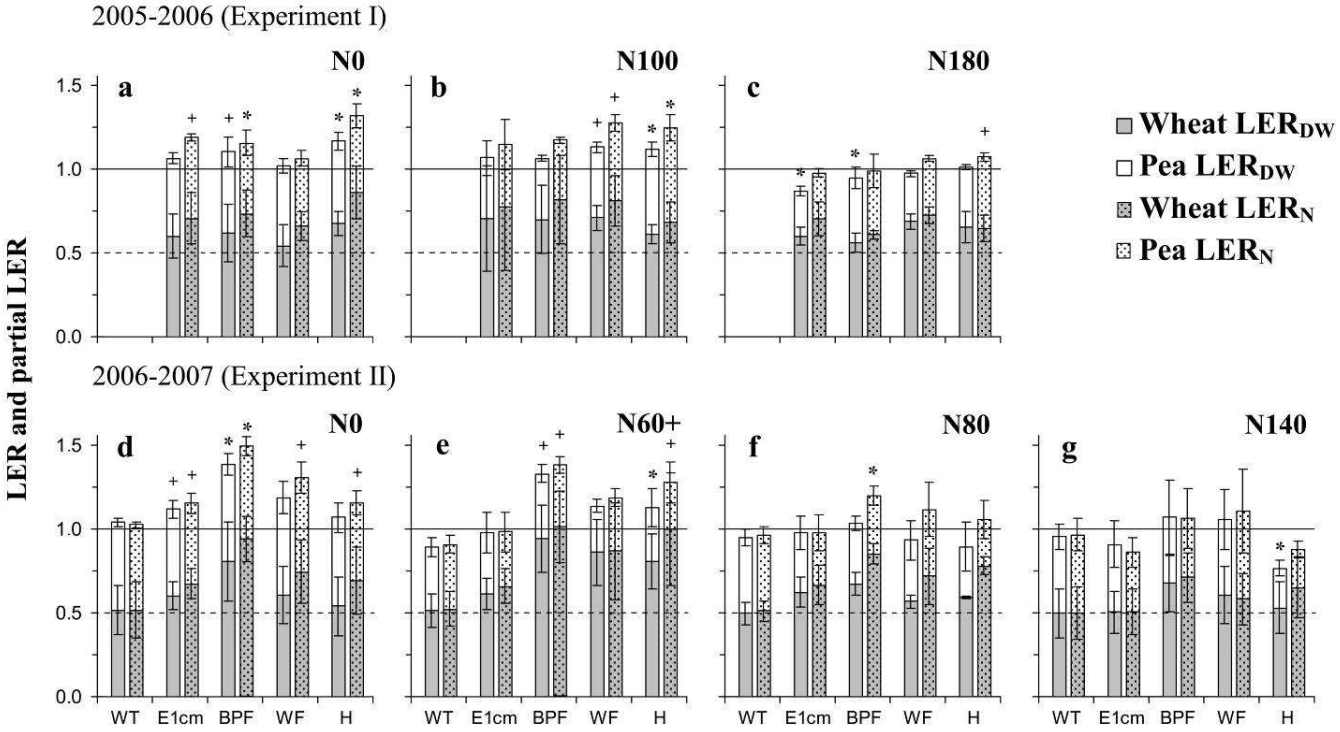

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Figure 5. Evolution of the PAR fraction absorbed of sole crops (SC) of pea or wheat and of the whole intercrop (IC) measured throughout crop growth for the different N treatments (Nx where 'x' represents N applied in kg N ha^{-1}). Values are means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

$F_{PARa} = F_{PAR\max} \times \frac{\exp(K1 \times (t - K2))}{1 + \exp(K1 \times (t - K2))}$. For each date of sampling, vertical bars on the top of the figure correspond to standard deviation of the total IC, Wheat SC and Pea SC (N0 only) respectively. Asterisks on the x-axis indicate fertilizer-N application.

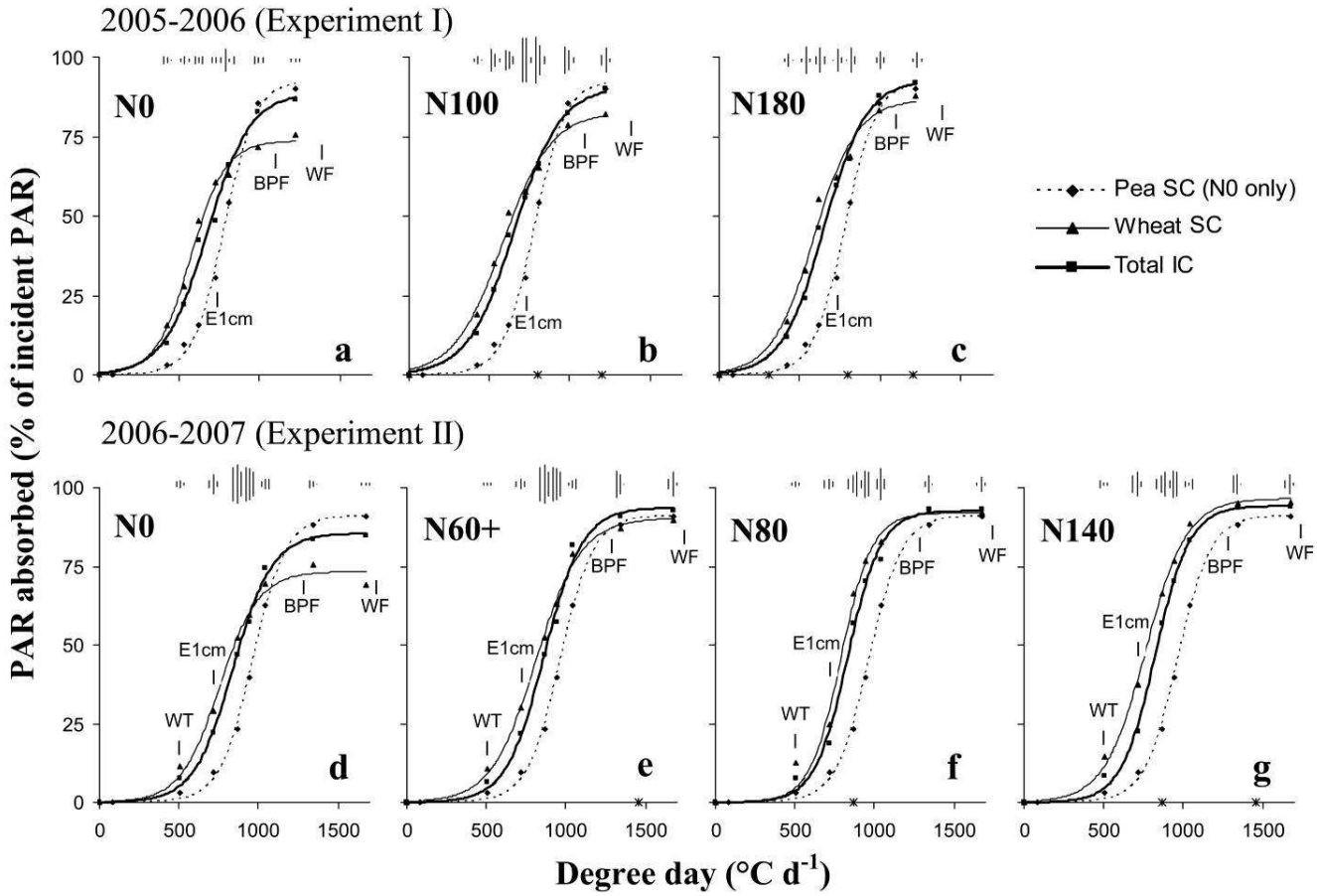

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Figure 6. Total shoot N accumulation in kg N ha^{-1} of sole crops (SC) and intercrops (IC) of pea and wheat for the different N treatments (Nx where 'x' represents N applied in kg N ha^{-1}) and dates of sampling. Values are means (n=3 to 5). For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

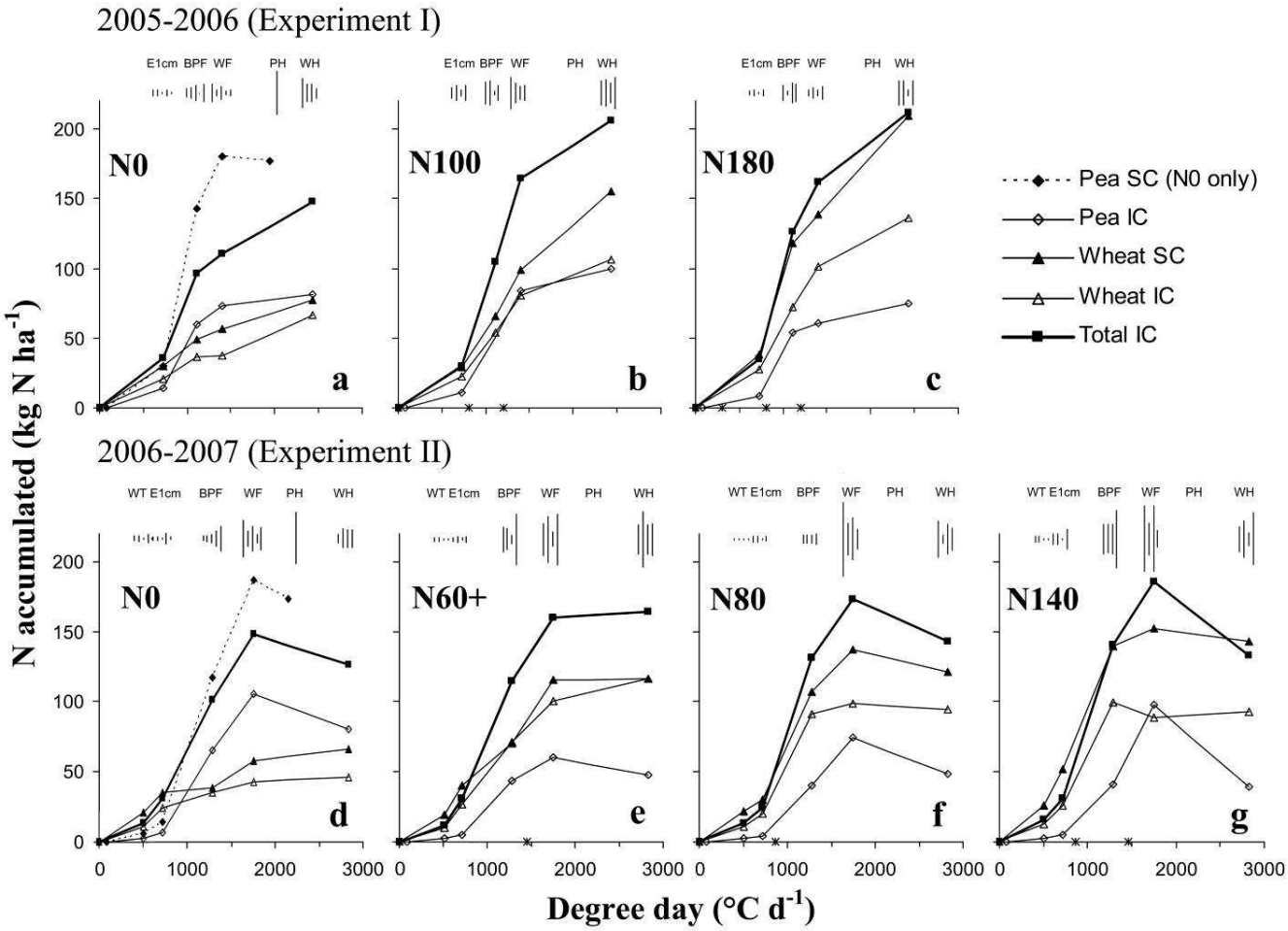

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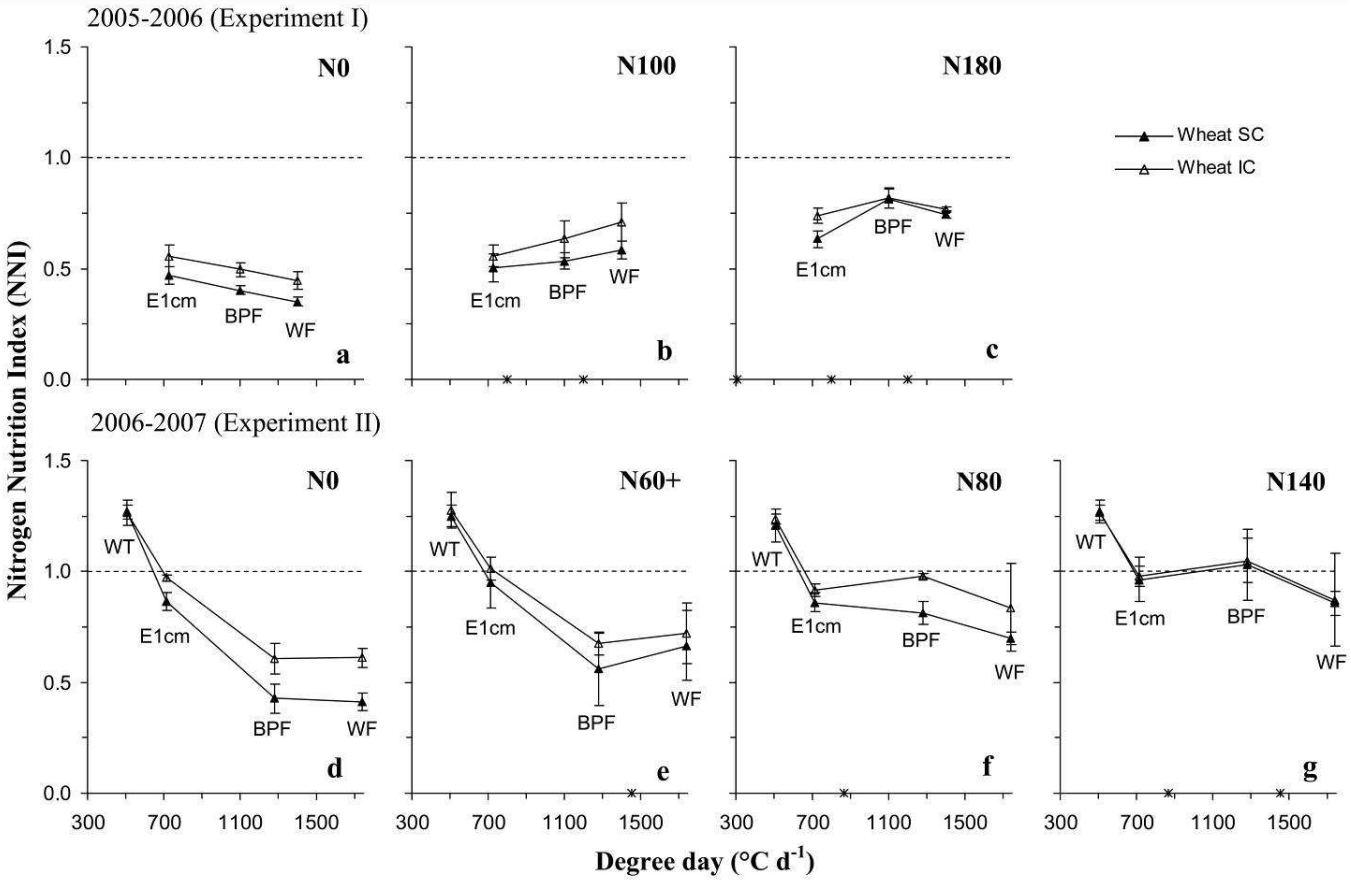
Figure 7. Nitrogen nutrition index (NNI) of wheat in a sole crop (SC) and intercrop (IC) for the different N treatments (Nx where 'x' represents N applied in kg N ha^{-1}) and dates of sampling. Values are means (n=3 to 5) ± standard error. Asterisks on the x-axis indicate fertilizer-N application.



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