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Interspecific competition for soil N and its interaction with N_2 fixation, leaf expansion and crop growth in pea–barley intercrops

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Abstract

Field experiments were carried out during three successive years to study through a dynamic approach the competition for soil N and its interaction with N_2 fixation, leaf expansion and crop growth in pea–barley intercrops. The intensity of competition for soil N varied between experiments according to soil N supply and plant densities. This study demonstrates the key role of competition for soil N which occurs early in the crop cycle and greatly influences the subsequent growth and final performance of both species. Relative yield values for grain yield and N accumulation increased with the intensity of competition for soil N. Barley competed strongly for soil N in the intercrop. Its competitive ability increased steadily during the vegetative phase and remained constant after the beginning of pea flowering. The period of strong competition for soil N (500–800 degree-days after sowing) also corresponded to the period of rapid growth in leaf area for both species and therefore an increasing N demand. For each species, the leaf area per plant at the beginning of pea flowering was well correlated with crop nitrogen status. Barley may meet its N needs more easily in intercrops (IC) and has greater leaf area per plant than in sole crops (SC). Barley having a greater soil N supply results in an even higher crop N status and greater competitive ability relative to pea in intercrop. Competition by barley for soil N increased the proportion of pea N derived from fixation. The nitrogen nutrition index (NNI) values of pea were close to 1 whatever the soil N availability in contrast to barley. However N_2 fixation started later than soil N uptake of pea and barley and was low when barley was very competitive for soil N. Due to the time necessary for the progressive development and activity of nodules, N_2 fixation could not completely satisfy N demand at the beginning of the crop cycle. The amount of N_2 fixed per plant in intercrops was not only a response to soil N availability but was largely determined by pea growth and was greatly affected when barley was too competitive.

Introduction

Intercropping, the growing of two or more crops simultaneously in the same field during a growing season, is known to improve the use of available resources, and to increase yield and stability compared to sole cropping especially under low-input conditions (Ofori and Stern, 1987; Willey, 1979). This practice is not very widespread in temperate agroecosystems but cereal–legume intercrops are gaining increasing interest in Europe in low-input farming systems especially in organic farming (Anil et al., 1998; Hauggaard-Nielsen and Andersen, 2000). The relative yield total (RYT) is a widely adopted criterion used to quantify and evaluate yield advantage. This relative unit expresses the land area required under sole cropping to give the yields obtained in intercrops (De Wit and Van den Bergh, 1965). RYT values above 1, indicating a benefit of

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intercropping over sole cropping have been reported for many grain legume and cereal intercrops (Jensen, 1996; Ofori and Stern, 1987). Nevertheless performance is usually widely variable and there is a lack of knowledge about the key factors which determine performance and the processes involved in yield advantage.

A yield advantage in species mixtures may occur when component crops differ in their use of growth resources in such a way, that when they are grown together they are able to complement each other and so, make better overall use of resources than when grown separately. A more efficient use of limiting resources in intercrops can occur whether the component crops use resources either at different times, in different parts of the soil profile or aerial canopy or in different forms (Trenbath, 1976; Willey, 1979).

The yield advantage of cereal–legume intercrops is presumed to be mainly associated with the complementary use of N sources by different components. Legumes and non-legumes may complement each other in the use of N sources since although both use soil inorganic N sources, the legume can also fix atmospheric N_2 in symbiosis with rhizobium. This complementary use of soil and atmospheric N sources is of particular interest in cropping systems where inorganic N is a limited resource, e.g. stockless low-input cropping systems.

Previous studies have shown that cereals are more competitive for soil inorganic N. Thus on an individual plant basis, a cereal would gain access to a greater soil N pool in an intercrop as compared to a sole crop (Izaurralde et al., 1992; Jensen, 1996). Moreover observed increases in the contribution of N_2 fixation to total N accumulation (%Ndfa) have often been attributed to the strong competition of cereals for N (Fujita et al., 1992; Jensen, 1996; van Kessel and Harker, 2000; Xiao et al., 2004). This increase in %Ndfa may be seen as an improvement in the complementary use of N and a way to improve N inputs in agroecosystems. However the amount of N_2 fixed in intercrops is generally less than estimations based on intercrop composition and the amount of N_2 fixed in sole crops (Jensen, 1996; Ofori and Stern, 1987; van Kessel and Harker, 2000). The amount of N_2 fixed is probably not solely due to a crop response to soil N availability but also to environmental and management factors that influence crop growth (van Kessel and Harker, 2000).

Soil N availability, N uptake (both fixation and assimilation) and aboveground growth are always interrelated but few authors have simultaneously studied these factors in intercrop systems. Moreover intercrop competition studies usually conclude on the performance from one final harvest of crops and several deal with only one growing season. The species interactions may vary over time and according to environmental conditions, so a dynamic and integrated approach is needed.

The aim of this study was to use a dynamic approach to investigate the competition for soil N in pea–barley intercrops and its interaction with N_2 fixation, leaf expansion and crop growth. This was achieved through a range of field experiments of pea–barley intercrops carried out during three successive years. The intensity of competition for soil N varied between experiments according to soil N supply and plant densities.

Materials and methods

General design

Field experiments were carried out in 2001, 2002 and 2003 at the FNAMS (Fédération Nationale des Agriculteurs Multiplicateurs de Semences) experimental station near Angers, France (47°27′ N, 24°W). In the ploughed layer (0–30 cm), the soil was a sandy loam in 2001 and 2002 and a clay loam in 2003. The soil contained 89, 22 and 71 kg ha^{-1} KCl-extractable inorganic N at 0–70 cm depth at sowing, in 2001, 2002 and 2003 respectively.

Field pea (*Pisum sativum* L., cv. Baccara) and spring barley (*Hordeum vulgare* L., cv. Scarlett) were grown in sole crops (SC) and in alternate row intercrops (IC) with different plant densities (Table 1). Pea sole crop was sown at 80 plants m^{-2} and barley at 250 plants m^{-2} except in 2002 when it was grown at 120 plants m^{-2}.

The experiments were arranged in a randomized complete block design with four replications in 2001 and 2002 and three replications in 2003. The size of each plot was 4.20×10 m. The crops were sown on 10 April 2001, 28 March 2002 and 12 March 2003. Weeds, pests and diseases were controlled with appropriate pesticides. Decisions

Table 1. General design, plant density, soil N supplies and soil N competition indexes

Year	Soil type in the ploughed layer	Pea–Barley intercrops			Soil inorganic N at sowing (g N m^{-2}) in 0–70 cm soil layer	N fertilizer (g N m^{-2})	Potential soil N supply (g N m^{-2})	Soil N competition index (g N barley plant^{-1})
		Reference	Plant population (pl m^{-2})					
			Pea	Barley				
2001	Sandy loam	IC1	78	32	8.9	3	13.4	0.42
		IC2	75	69	8.9	3	13.4	0.19
2002	Sandy loam	IC3	55	36	2.2	0	6.6	0.18
2003	Clay loam	IC4	45	100	7.1	0	8.2	0.08
		IC5	91	133	7.1	0	8.2	0.06
		IC6	43	127	7.1	13	13.9	0.11
		IC7	96	118	7.1	13	13.9	0.12

on irrigation and water consumption were based on tensiometer data. Crops were grown without N fertilizer in 2002, with 30 kg N ha^{-1} as starter fertilization in 2001 and either with 130 kg N ha^{-1} or without any fertilizer in 2003. N was supplied in the form of NH_4NO_3 at sowing.

These treatments were assumed to create different levels of competition for soil N by varying soil N supply between years, N fertilizer and using variable densities of legumes and non-legumes in the intercrops.

Plant sampling and analytical methods

Plants were harvested from 0.56 m^2 areas within each plot. In 2001 crops were harvested three times during the crop cycle. In 2002 and 2003, crops were harvested every week corresponding to 11 harvests starting with the development of the fourth leaf and ending at maturity. The IC were sorted according to species and the number of plants of each species was determined at each harvest. Above ground dry matter (DM) was determined after oven drying at 80 °C for 48 h. Samples were ground and N concentration (Nc) was measured by the Dumas procedure (Hansen, 1989) while ^{15}N enrichment was determined by mass spectrometry.

Leaf area was determined on the same harvested area used for the measurement of above-ground DM at the beginning of pea flowering in 2001, five times in 2002 and four times in 2003 (from 6-leaf stage to the end of pea grain formation). The green leaves were separated from the other parts of the plant for each species. The area of a sub-sample of green leaves was determined using a LI3100 area meter (LI-COR Inc., NE, USA). The specific leaf area, which is the ratio of leaf area to leaf dry weight, was determined on this sub-sample. Using this ratio the leaf area of the whole harvested area was calculated.

Soil samples were taken from 0–10, 10–30, 30–50 and 50–70 cm soil layers every 2 weeks below the harvested area in the middle row in 2002 and 2003 and only at sowing and harvest in 2001. Nitrate and ammonium were measured after KCl extraction by standard colorimetric methods (Keeney and Wilson, 1989).

Calculations and statistics

The intensity of competition for soil N was evaluated by a soil N competition index calculated as the ratio of the potential soil N supply and barley plant density (number of plants relying only on soil N for their N nutrition) (Table 1). It ranged from 0.06 to 0.42 g N per barley plant. The lower the competition index, the higher the intensity of competition. The potential soil N supply was determined as the maximum soil N acquisition obtained either in SC or in IC for each year and for each level of fertilization in 2003. It was assumed that pea plants rely mainly on N_2 fixation for their N nutrition in IC and were completely self-sufficient in the case of very low soil N availability. An increase in pea plant density should not therefore increase the intensity of competition for soil N.

The RYT for grain yield and N accumulation for IC of pea and barley was calculated according to De Wit and Van den Bergh (1965). The RYT is the sum of the partial RY values for barley (RY_B) and pea (RY_P): $RY_B = Y_{BP}/Y_{BB}$, $RY_P = Y_{PB}/Y_{PP}$, $RYT = RY_B + RY_P$ where Y_{BP} and Y_{PB} are yields or total N of barley and pea, respectively, in the IC and Y_{BB} and Y_{PP} are the yields of barley and pea in SC, respectively.

The competitive ability of barley for soil N relative to pea was evaluated by using the competitive ratio (CR) of one species with respect to another, as described by Willey and Rao (1980). This ratio ($CR_{B/P}$) indicates the number of times barley is more competitive than pea for soil N and is defined as: $CR_{B/P} = (N_{BP}/N_{BB})/(N_{PB}/N_{PP})$ where N_{BB} and N_{BP} are the amounts of soil N accumulated per barley plant grown in SC and in IC with pea and N_{PP} and N_{PB} are the amounts of soil N accumulated per pea plant grown in SC and in IC with barley.

The amount of N_2 fixed was calculated as the product of pea biomass, %N content and the proportion of plant N derived from N_2 fixation. The percentage of plant N derived from N_2 fixation (%Ndfa) was determined using the ^{15}N natural abundance method for non-fertilized treatments (Amarger et al., 1979). Barley SC was used as reference crop for calculating N_2 fixation in pea SC and pea IC. $\%Ndfa = 100 \times ((\delta^{15}N\ \text{pea} - \delta^{15}N\ \text{barley})/(\beta\text{fix} - \delta^{15}N\ \text{barley}))$ where βfix (−1) (Mariotti et al., 1980) is the isotopic fractionation factor associated with N_2 fixation processes. It corresponds to the ^{15}N enrichment of pea relying only on N_2 fixation. Natural soil enrichment was estimated at 3.5‰, 5.0‰ and 5.5‰ in 2001, 2002 and 2003 respectively by $\delta^{15}N$ in aboveground parts of barley SC which relied totally on soil mineral N. Values of ^{15}N enrichment in crops (pea and barley) were corrected to allow for seed-borne N as an other source of N as described by Jensen et al. (1985):

$$\delta^{15}\text{N corrected}$$
$$= (\delta^{15}\text{N corp} - (\text{QN seed borne}/\text{QN crop})$$
$$\times \delta^{15}\text{N seed borne})/(1 - (\text{QN seed borne}/\text{QN crop}))$$

where it is assumed that 50% of the seed borne N was located aboveground (QN seed borne) and that QN crop is the quantity of N measured in shoots.

A similar approach extended from ^{15}N natural abundance method was used to estimate %Ndfa in fertilized treatments with fertilized barley SC as reference crop. The dilution isotopic method (Rennie and Rennie, 1983) based on the supply of enriched ^{15}N fertilizer ($\delta^{15}N = 365‰$) was also used to estimate %Ndfa in fertilized treatments at two stages (beginning of flowering and maturity of pea).

Soil N acquisition in pea was estimated as the difference between total N accumulated and the amount of N_2 fixed.

Instantaneous soil N uptake and N_2 fixation rates were calculated over the time between two harvests as follows: $(Q_{n+1} - Q_n)/(D_{n+1} - D_n)$ where Q_n is either the quantity of nitrogen originating from the soil or N_2 fixation measured at different dates, D_n expressed in thermal time using cumulative degree-days from sowing (base temperature 0 °C). Instantaneous %Ndfa was defined as the ratio of N_2 fixation rate over total N acquisition rate (Voisin et al., 2002). Changes over time of N_2 fixation and soil N uptake rates in intercrops were also expressed as a proportion of the maximum rates.

The nitrogen status of the crops was assessed at the beginning of pea flowering by calculating a nitrogen nutrition index (NNI) (Lemaire and Meynard, 1997). The NNI at this stage is considered as an indicator of the level of satisfaction of crop N demand and a good indicator of the nitrogen nutrition of the crop with regard to leaf growth. The NNI was calculated as the ratio between the measured concentration of N in the aerial DM and the critical Nc determined from the DM by the equation proposed by Ney et al. (1997) for pea: if $DM < 1\ t\ ha^{-1}$, $Nc = 5.08\%$; if $DM > 1\ t\ ha^{-1}$, $Nc = 5.08 \times (DM)^{-0.32}$. The equation established for wheat was used for barley: if $DM < 1.55\ t\ ha^{-1}$, $Nc = 5.35\%$; if $DM > 1.55\ t\ ha^{-1}$, $Nc = 5.35 \times (DM)^{-0.442}$ (Justes et al., 1997).

Analyses of variance were performed and means were compared using the least significant difference test (LSD) at the 0.05 probability level.

Results

Grain yield and N accumulation

Pea SC produced higher yields than barley SC ($P < 0.05$) except with the highest nitrogen supply

(Table 2). Nitrogen fertilization increased barley grain yield ($P < 0.05$) but had no significant effect on pea grain yield. The grain yields of pea–barley IC were 30% greater than those of barley SC and were significantly higher than that of pea SC only in 2003 ($P < 0.05$). Yield of the IC was more stable than that of pea and barley SC. Fertilizer N addition (IC4–IC6 and IC5–IC7) increased barley and reduced pea yield in the IC ($P < 0.05$) but did not influence total IC grain yield. The increase in pea plants (IC4–IC5 and IC6–IC7) increased pea yield but reduced barley yield as well as the total IC yield. The increase in barley plants (IC1–IC2) increased barley yield but reduced pea yield in the IC and slightly increased the total IC yield.

The average relative grain yield total was 1.24 indicating an average grain yield advantage of 24% in IC compared with SC. Nitrogen fertilization increased the contribution of barley in the IC and decreased the RYT values ($P < 0.05$) as a result of the large decrease in the partial relative yield of pea (IC4–IC6 and IC5–IC7). The increase in pea plant density increased RY_P, decreased RY_B and decreased RYT (IC4–IC5 and IC6–IC7). The increase in barley plant density increased RY_B, decreased RY_P and increased RYT (IC1–IC2).

Table 2. Grain yield, N accumulation, N2 fixation and %Ndfa of pea (P) and barley (B) grown as sole crops (SC) and as intercrops (IC), total and partial relative yields of pea and barley for grain yield and N accumulation (RYT, RYp, RYb), and coefficient of variation (cv %)

	2001			2002		2003					Mean	cv (%)
						0N		N				
Grain yield (g m^{-2})												
PSC	570		*74*	620	*62*	415		360		*113*	491	25
BSC	440			390		380		530			435	16
	IC1	IC2		IC3		IC4	IC5	IC6	IC7			
IC	540	570		470		630	560	660	510		563	12
PIC	350	300	*NS*	340	–	430	490	210	320	*114*	349	34
BIC	190	270	*85*	130	–	200	70	450	190	*48*	214	58
Relative yields												
RY p	0.61	0.53	*NS*	0.55	–	1.04	1.18	0.58	0.89	*0.30*	0.77	39
RY b	0.43	0.61	*0.15*	0.33	–	0.53	0.18	0.85	0.36	*0.12*	0.47	51
RYT	1.05	1.14	*NS*	0.88	–	1.56	1.36	1.43	1.25	*0.13*	1.24	36
N accumulation (g m^{-2})												
PSC	23.4		*3.5*	25.1	*2.7*	26.4		29.0		*3.8*	26.0	9
BSC	10.8			6.6		5.3		13.9			9.2	43
	IC1	IC2		IC3		IC4	IC5	IC6	IC7			
IC	20.0	20.5		21.7		26.6	29.1	22.0	26.3		23.7	15
PIC	13.9	12.5	*NS*	18.2	–	21.7	26.3	10.9	17.1	*4.1*	17.2	40
BIC	6.1	8.0	*NS*	3.5	–	3.4	2.8	11.1	9.2	*3.1*	6.3	51
Relative yields												
RY p	0.59	0.53	*NS*	0.73	–	0.82	1.00	0.38	0.59	*0.10*	0.66	41
RY b	0.56	0.74	*0.1*	0.53	–	0.64	0.53	0.80	0.66	*0.17*	0.64	37
RYT	1.16	1.27	*NS*	1.26	–	1.46	1.52	1.17	1.25	*0.20*	1.30	32
N_2 fixed (g m^{-2})												
PSC	11.0			18.6		20.4		17.4			16.9	24
PIC	8.1	7.1	*NS*	15.1	–	19.8	20.9	9.5	12.9	*3.1*	12.1	52
%Ndfa												
PSC	47.0		*5.2*	74.2	*6.3*	77.2		59.9		*7.2*	64.6	22
PIC	58.0	57.0		83.0		91.2	79.5	87.2	75.4		75.9	18

Means of four replicates in 2001 and 2002 and three replicates in 2003. (0N) no nitrogen supply, (N) with N supply, numbers in italic indicate LSD ($P < 0.05$), (NS) non-significant.

Pea SC accumulated much more N than barley SC in all situations ($P < 0.05$) (Table 2). The variability in the amount of N accumulated by pea between years was very low (cv 9%). The amount of N accumulated by barley SC was much more variable: from 5.3 to 13.9 g m^{-2} (cv 43%). All intercrops accumulated more nitrogen than barley SC ($P < 0.05$) and with less variability (cv 15%). Intercrops accumulated on average only 8% less N than pea SC. N addition reduced the total N accumulated as well as the contribution of pea N in the intercrop (IC4–IC6 and IC5–IC7) ($P < 0.05$). Increasing the plant density of either crop in IC increased its contribution to total N accumulation (IC1–IC2, IC4–IC5 and IC6–IC7). The RYT N values indicated that N was used 16–52% (mean: 30%) more efficiently than in SC. N fertilization decreased N accumulation and RYT N values (IC4–IC5 and IC6–IC7) ($P < 0.05$). RYT for grain yield and N accumulation were plotted against soil N competition index estimated by the ratio of potential N supply and plant density of barley (Figure 1). RYT values tended to increase from 1.0 to 1.6 when the intensity of competition for soil N increased from a soil N supply per barley plant of 0.2–0.05 g N. RYT values tended to remain stable and close to 1.0 for values of soil N competition index higher than 0.2.

Competition for soil nitrogen during the vegetative phase

Pea and barley displayed quite similar patterns of soil N acquisition over time indicating that they compete simultaneously for this resource (Figure 2). In all situations, the acquisition of soil N per plant in pea IC was lower than in pea SC (Figure 2a). Differences in soil N uptake per plant between pea SC and pea IC occurred during the vegetative phase, from 600 degree-days after sowing. At the beginning of pea flowering (800 degree-days after sowing), soil N uptake per plant in pea IC was from 35 to 63% lower than in pea SC. The decrease was greatest when soil N supply was high (IC1, IC2, IC6, IC7).

In contrast to pea, barley accumulated a significantly higher amount of soil N per plant in IC than in SC from 600 degree-days onwards (Figure 2b). At the beginning of pea flowering, soil N acquisition per plant in barley IC was increased by 32% up to 179% with highest soil N supplies compared with barley SC. With or without N fertilizer soil N acquisition in pea IC was similar (IC4–IC6 and IC5–IC7) whereas soil N acquisition in barley IC was more than four times higher with than without N fertilizer.

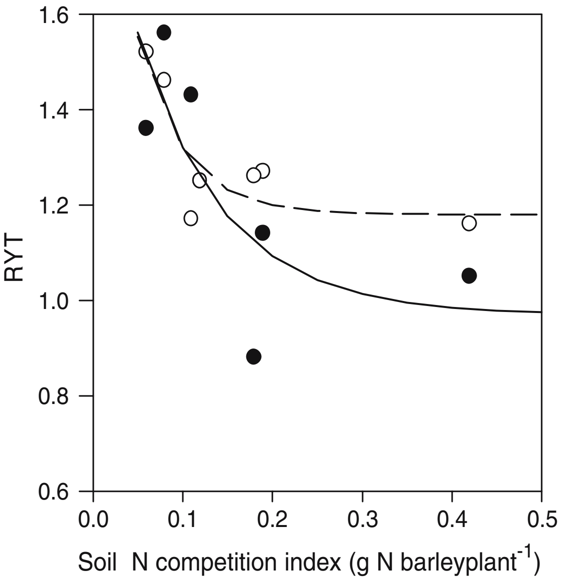

Figure 1. Total relative yield (RYT) for grain yield (closed symbols) and for N accumulation (open symbols) in relation to soil N competition index defined as the ratio of potential N supply to barley plant density. Values are means of four replicates in 2001 and 2002 and three replicates in 2003. —— RYT grain yield = exp(−10.5 soil N competition index) + 0.97, $R^2 = 0.60$; – – – – RYT N = exp(−19.7 soil N competition index) + 1.18, $R^2 = 0.74$.

The CR for soil N indicated that barley was more competitive than pea for this resource in all intercrops (Figure 2c). The competitive ability of barley relative to pea for soil N increased regularly with time during the vegetative phase and except in 2001 remained constant after the beginning of the flowering. At this stage, barley was 2–6 times more competitive than pea for soil N in intercrops. The competitive ability of barley relative to pea was higher with high soil N supplies (IC1, IC2, IC6, IC7). An increase in barley plant density decreased the CR for soil N of barley relative to pea (IC1–IC2) whereas a variation in pea plant density did not affect significantly the CR (IC4–IC5 and IC6–IC7). The competitive ability of barley relative to pea for soil N decreased with the decrease in soil N competition index (IC1–IC2, IC4–IC6, IC5–IC7).

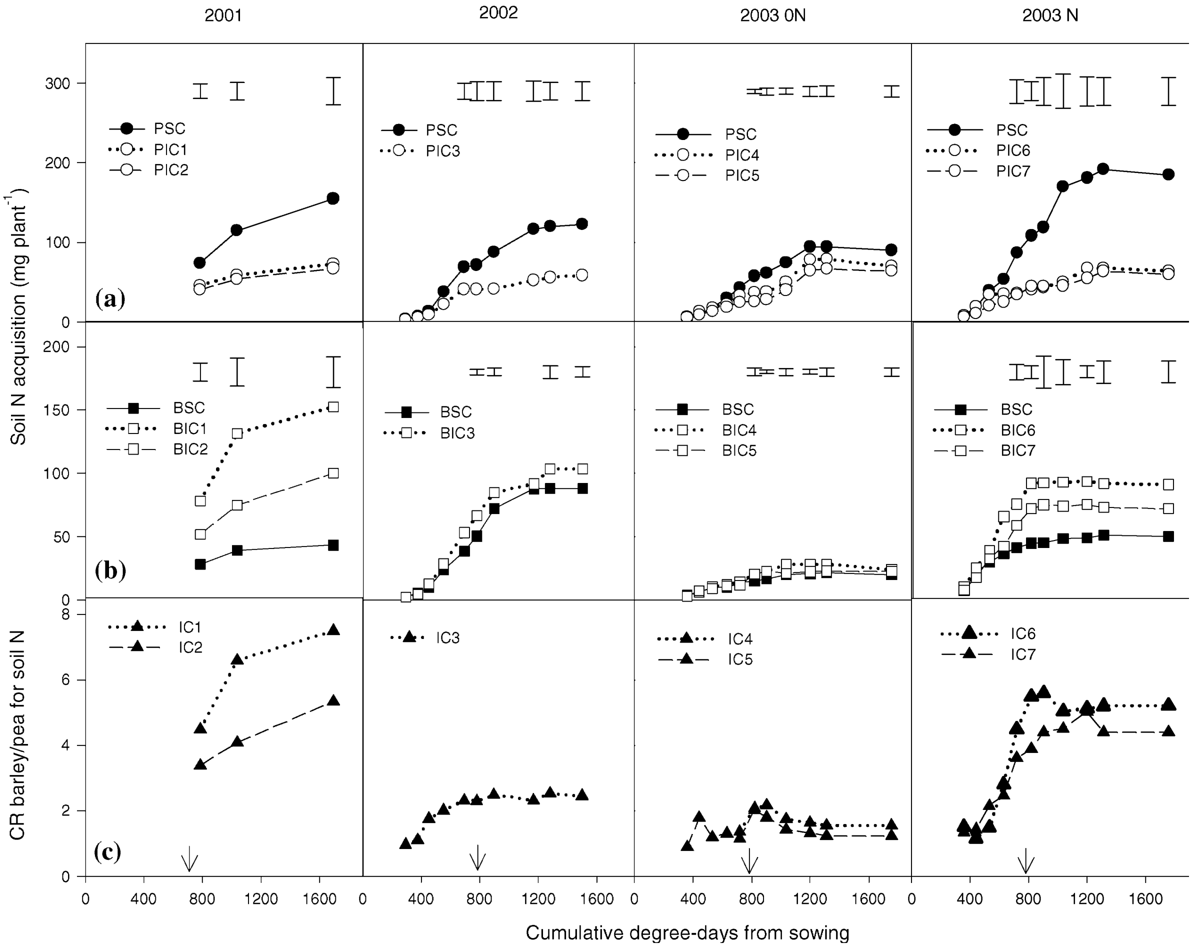

Figure 2. Cumulative soil N acquisition per plant of pea (a) and barley (b) as sole crops (SC) and intercrops ($IC_{1 \to 7}$) and competitive ratio (CR) of barley relative to pea for soil N (c), in 2001, 2002, without N in 2003 (0N) or with N supply in 2003 (N). Values are means of four replicates in 2001 and 2002 and three replicates in 2003. Vertical bars represent LSD ($P < 0.05$). ↓: Beginning of pea flowering. (P) pea, (B) barley.

N_2 fixation

The amount of N_2 fixed at maturity varied from 11 to 20.4 g m^{-2} and from 7.1 to 20.9 g m^{-2} in pea SC and in pea IC respectively (Table 2). %Ndfa varied from 47 to 77% and from 58 to 91% in pea SC and in pea IC respectively. %Ndfa increased by on average 21% in pea IC compared to pea SC. The increase was the greatest with N supply. %Ndfa and the amount of N_2 fixed decreased with soil N supply in SC and in IC. The decrease in the amount of N_2 fixed with N supply was lower in SC than in IC. On the contrary, the decrease in %Ndfa with N supply was greater in pea SC than in pea IC. %Ndfa decreased with the increase in pea plants but the amount of N_2 fixed slightly increased.

Similar %Ndfa were obtained for fertilized treatments at two stages (beginning of pea flowering and maturity) with the dilution isotopic method and the extension of the natural abundance method. Therefore the study of the dynamic of N_2 fixation throughout the cycle using the principle of the natural abundance method was feasible for all the treatments.

For all treatments, instantaneous %Ndfa and N_2 fixation rate increased gradually with thermal time to a maximum during the flowering (800–900 degree-days) (Figure 3a and b). The maximum contribution of N_2 fixation to total N accumula-

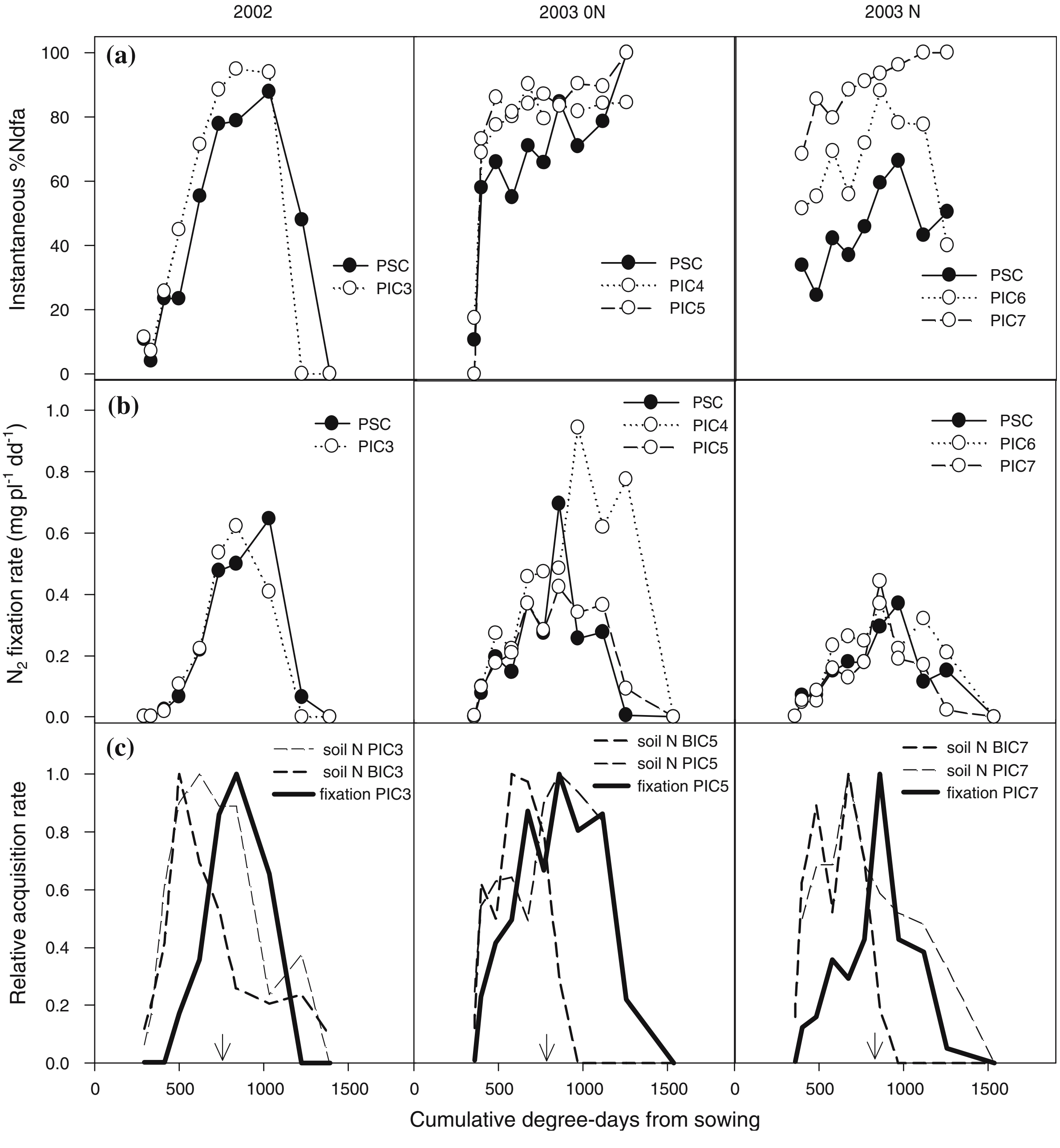

Figure 3. Instantaneous %Ndfa (a), N_2 fixation rate (b) and relative N acquisition rate (c) in pea (P) and barley (B) grown as sole crops (SC) or as intercrops (IC) in 2002, without N in 2003 (0N) or with N supply in 2003 (N). Values are means of four replicates in 2002 and three replicates in 2003.

tion in pea SC reached 93% for the lowest soil N availability (2002) and only 66% for the highest soil N availability (2003 N). From 400 degree-days to the end of the crop cycle, the contribution of N_2 fixation to total N uptake was higher in pea IC than in pea SC (Figure 3a). Even with N fertilizer maximum instantaneous %Ndfa in pea IC was higher than 80% (Figure 3a). When instantaneous %Ndfa was plotted against instantaneous nitrate availability in the ploughed layer for all 2002 and 2003 treatments, the differences in instantaneous %Ndfa between pea SC and pea IC and changes

Table 3. Nitrogen nutrition values (NNI) of pea (P) and barley (B) grown as sole crops (SC) and as intercrops (IC) at the beginning of flowering of pea in 2001, 2002, 2003 without N supply (0N) and 2003 with N supply (N)

	2001		2002	2003				Mean	cv
				0N		N			
PSC	0.92		0.96	1.07		1.08		1.01	8
BSC	0.62		0.52	0.35		0.76		0.56	31
	IC1	IC2	IC3	IC4	IC5	IC6	IC7		
PIC	0.81	0.73	0.91	0.89	0.99	0.73	0.89	0.85	11
BIC	0.67	0.59	0.65	0.44	0.49	0.84	0.81	0.64	29
LSD (0.05)	0.07		0.10		0.09				

Values are means of four replicates in 2001 and 2002 and three replicates in 2003.

over time were mainly explained by differences in soil nitrate availability in the 0–30 cm soil layer. Instantaneous %Ndfa decreased linearly ($R^2 = 0.65$, $n = 26$) from 100 to 0% as soil nitrate availability varied from 0 kg N ha^{-1} to about 70 kg N ha^{-1}. Although a higher contribution of N_2 fixation to total N accumulation was observed in pea IC, pea SC and pea IC displayed quite similar patterns of N_2 fixation rate per plant with thermal time (Figure 3b). Changes over time in N_2 fixation and soil N uptake of pea and barley IC were compared using rates expressed as a proportion of the maximum (Figure 3c). The peak of N_2 fixation rate in IC was achieved during flowering, corresponding to on average 100 degree-days and 250 degree-days after the peak of soil N uptake rate in pea and barley respectively. Only 35% of the total N_2 fixation took place before flowering. When barley began to compete strongly for soil N in IC (from 500 degree-days), N_2 fixation rate of pea was still low (only 20–40% of the maximum N_2 fixation rate).

Crop N status, leaf growth and their relation to N acquisition

The nitrogen nutrition status (NNI) assessed at flowering was always higher in pea ($P < 0.05$) than in barley SC (Table 3). In all situations, nitrogen nutrition of barley was sub-optimal. The NNI values of barley SC ranged from 0.35 to 0.76 in SC whereas the NNI values of pea SC were close to 1 in all situations. N fertilizer increased the NNI values of barley SC ($P < 0.05$) but did not modify those of pea SC. In intercrops, at least one species and more often the two species displayed a NNI lower than 1 indicating that N supply (from soil, fertilizer and air) was always insufficient to meet the N demand of the two species grown together.

The NNI values increased on average by 14% for barley IC and decreased by 16% for pea IC compared with SC. In intercrops, N fertilization increased markedly the NNI values of barley and decreased slightly those of pea ($P < 0.05$).

The period of strong competition for soil N (500–800 degree-days) also corresponded to the period of fast growth in leaf area for the both species (Figure 4). Barley IC produced a greater leaf area per plant than barley SC and pea IC produced a lower leaf area than pea SC. For each species the leaf area per plant at the beginning of pea flowering was well correlated with crop nitrogen status (Figure 5). The differences in the amount of N_2 fixed per plant in the different intercrops were not only due to the response to available soil nitrate but also depended to a great extent on differences in crop biomass (Figure 6). Thus, for example, N addition decreased %Ndfa by 22% in SC but by only 15% in IC due to the greater depletion of soil N by barley. However N addition entailed a decrease in the amount of N_2 fixed of 14% in SC and 45% in IC because it strongly affected pea growth in IC but not in SC. A significantly greater N_2 fixation rate in IC compared with SC occurred only in 2003, in an intercrop (IC4) without added N and having 45 pea plants and 100 barley plants per square metre (Figure 3). The advantage of this IC in terms of N_2 fixation occurred at the end of the crop cycle and corresponded also to a situation where the leaf growth went on later than in the SC (Figure 4).

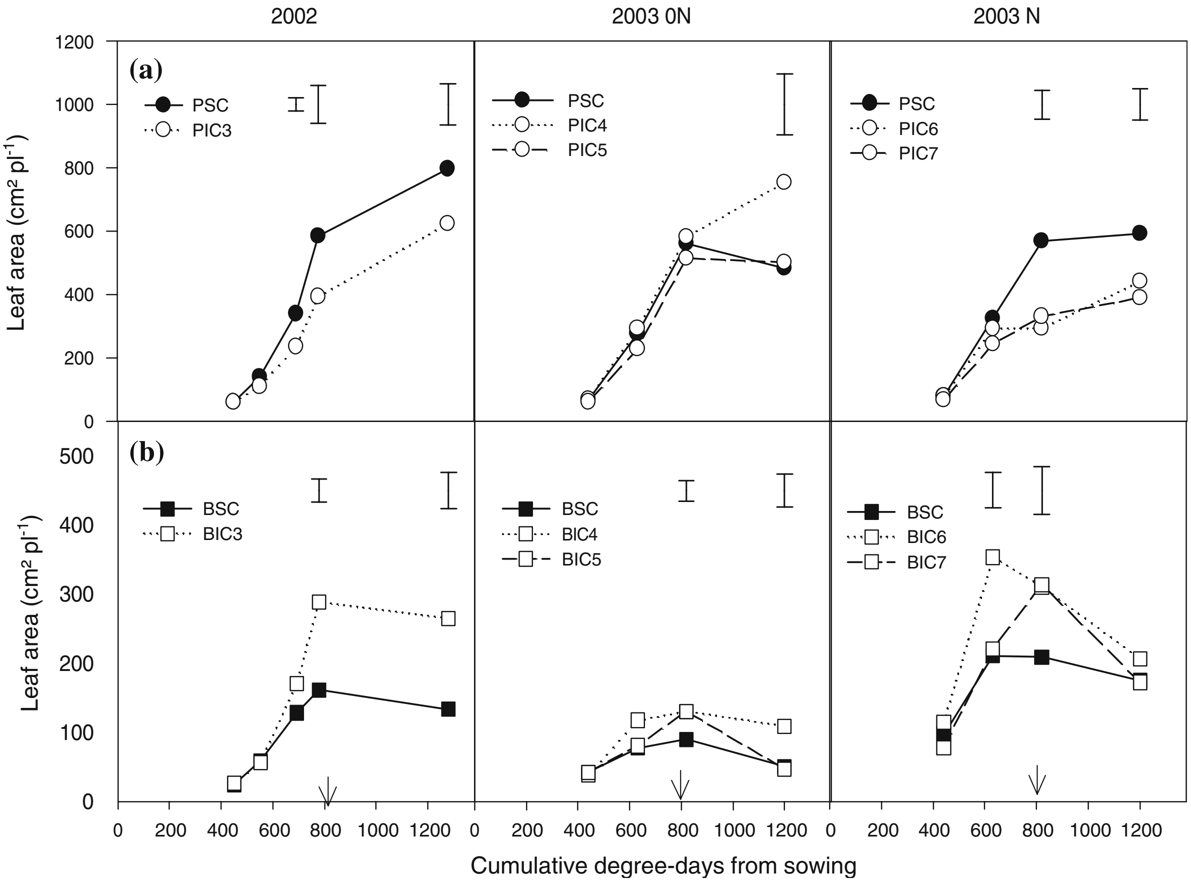

Figure 4. Leaf area dynamics per plant of pea (a) and barley (b) as sole crops (SC) and as intercrops (IC) in 2002, 2003 without N supply (0N) and 2003 with N supply (N). Values are means of four replicates in 2002 and three replicates in 2003. Vertical bars represent LSD ($P < 0.05$). ↓: Beginning of pea flowering. (P) pea, (B) barley.

Discussion

Relative yields greater than 1 (on average 1.2) were obtained in pea–barley intercrops in this study. The yield advantage of pea–barley IC over SC may be actually associated with the complementary use of N sources by components as shown by the RYT values for N accumulation from 1.16 to 1.52. N addition (i) did not increase the total pea–barley intercrop yield, (ii) decreased the contribution of pea, and (iii) decreased RYT values which remain nevertheless higher than 1. These results are in agreement with other studies on the effect of N fertilizer in intercrops based on legumes and another species (Jensen, 1996; Katayama et al., 1995; Leitch and Musa, 1998; Waterer et al., 1994). Through the use of a soil N competition index, it was shown that RYT values for grain yield and N accumulation remain constant (close to 1) at very low levels of competition and tend to increase while the intensity of competition for soil N increases. The highest RYT values were obtained when competition between plants relying on soil N alone was high. The competition index is considered as a suitable criterion to compare the intensity of competition for soil N in intercrops grown with varying soil N supplies and plant densities. Nevertheless the relationship between this index and RYT needs to be confirmed with a larger range of soil N supplies and/or plant densities, particularly in order to identify a possible threshold after which RYT values remain constant.

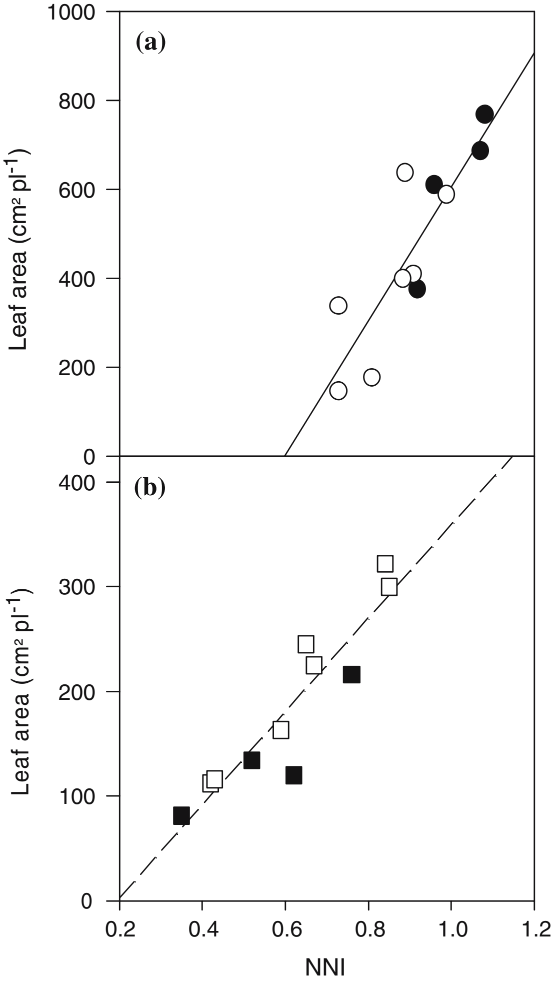

Figure 5. Effect of crop N status assessed by nitrogen nutrition index (NNI) on leaf area per plant for pea (a) and barley (b) as sole crops (closed symbols) and as intercrops (open symbols) at the beginning of pea flowering. Values are means of four replicates in 2001 and 2002 and three replicates in 2003. —— Pea leaf area per plant = 1057.5 NNI – 901.9, $R^2 = 0.75$; $n = 11$; – – – – Barley leaf area per plant = 446.3 NNI – 86.9, $R^2 = 0.85$; $n = 11$.

An analysis of the satisfaction of N demand has rarely been achieved in competitive studies assessing the intensity of competition between intercropped species. In the present study NNI values were used to estimate the level of satisfaction of N demand of each species. Similar nitrogen dilution curves were used to assess crop nitrogen status both in SC and IC assuming that the structure of the canopy, particularly the proportion of leaves and stems at a given stage, did not change significantly between SC and IC. As shown by its NNI values close to 1, pea N acquisition appeared to be more driven by crop growth than by N supply. Conversely with NNI values varying from 0.44 to 0.84 differences between N accumulation situations for barley IC were due mainly to differences in soil N supply. Barley IC has a lower N demand than barley SC due to a lower plant density than in SC and obtains a more than proportional share of soil inorganic N due to its high competitive ability for soil N whereas pea may obtain N through symbiotic fixation. Therefore barley may meet its N needs more easily in IC than in SC as shown by the increase in its NNI value. This increase in NNI in barley IC entails a greater leaf area per plant than in barley SC increasing its competitive ability for light. It strengthens barley growth, N demand and its competitive ability for soil N. A greater soil N supply entails an even higher crop N status of barley and an even greater competitive ability. By using a dynamic approach, our study demonstrates the key role of the early competition on the subsequent growth and final performance of the both species. Competition, once initiated, tends to be magnified by a system of positive feedbacks when simultaneous shoot and root competition are occurring (Donald,

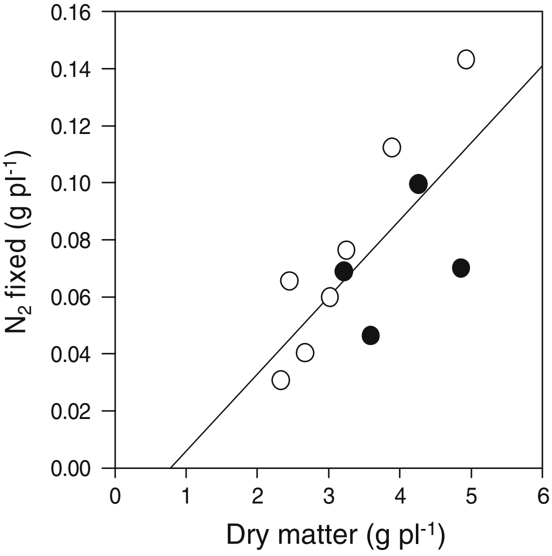

Figure 6. Effect of crop growth on N_2 fixation by pea as sole crops (closed symbols) and as intercrops (open symbols) at the beginning of pea flowering. Values are means of four replicates in 2001 and 2002 and three replicates in 2003. —— N_2 fixed = 0.027 pea dry msatter – 0.021, $R^2 = 0.54$; $n = 11$.

1958). Barley component accounted for a greater relative proportion of soil N accumulated and aerial DM at the high N level as previously observed in pea–barley intercrops (Andersen et al., 2005; Jensen, 1996). When two species compete for a given source, e.g. water or nutrients, an addition of that resource may reduce its deficiency and so reduce the intensity of competition (Vandermeer, 1989). However as discussed by Wilson (1988), the addition of a resource does not necessarily decrease competition since the growth of the dominant crop component may be favoured thereby negatively affecting the growth of the other component. In any case, the effect of N addition on competition level should not be considered without taking into account the N demand of each species.

By using partitions to separate the effects of root and shoot interactions, several studies dealing with interferences between species have led to the conclusion that root competition for nutrients is determinant and has usually a much greater effect on the relative performance of two interacting species than shoot competition for light in cereal–legume intercrops (Li et al., 1999; Martin and Snaydon, 1982; Wilson, 1988; Xiao et al., 2004). Nevertheless, as shown in the present study, root competition for soil resources and shoot competition for light are occurring simultaneously and are always interrelated. It is clear that N acquisition by the two components in IC depends both on N supply and crop growth and that competition occurs when there is a combined need in excess of the supply. In our results, three phases may be distinguished during the crop cycle. The first one occurred up to 500 degree-days after sowing during which no significant competition for soil N was observed, soil N supply being probably largely sufficient to cover the still low N demand. The second phase from 500 to 900 degree-days corresponded to a period of strong competition for soil N which increased steadily with time; it was also a period of rapid growth in leaf area and therefore of an increasing N demand. Third, after 900 degree-days the competition for soil N remained constant.

The poor competitive ability of grain legumes for soil N compared with cereals has already been reported by several authors (Hauggaard-Nielsen et al., 2001; Jensen, 1996; Trenbath, 1976). Several factors may influence the competitive balance for soil N between species grown in mixture such as root depth penetration rate, root density, time and rate of N demand (Casper and Jackson, 1997; Haynes, 1980; Trenbath, 1974). In a previous article on root methods, based on the same experiments, we showed that barley has a faster root depth penetration and a higher root biomass compared to pea in intercrops (Corre-Hellou and Crozat, 2005). Other authors have also demonstrated the advantage of cereals relatively to legumes in terms of root development in intercrops (Hauggaard-Nielsen et al., 2001; Izaurralde et al., 1992; Katayama et al., 1995). Moreover the crop growth of barley takes place earlier than that of pea (Andersen et al., 2005; Bellostas et al., 2003). During the initial growth phase, a species which grows faster than the others, may progressively dominate resource acquisition. Thus, a better root access to soil resources and a higher N demand at the beginning of the crop cycle are probably the main explanations for the much higher competitive ability of barley for soil N.

Competition by barley for soil N clearly increased the proportion of pea N derived from fixation as previously observed in cereal–pea intercrops (Andersen et al., 2005; Jensen, 1996; Rauber et al., 2001; Xiao et al., 2004). The dynamic study of instantaneous %Ndfa and soil N availability indicated that the increase in %Ndfa in IC was correlated with the quick depletion of soil N by barley leading to lower soil N availabilities than in pea sole crops. Instantaneous %Ndfa declined linearly with soil N availability as previously reported for pea with a quite similar relationship (Voisin et al., 2002). However the increase in %Ndfa observed in IC was not always associated with an increase in the amount of N_2 fixed per plant. N_2 fixation started later than soil N uptake of pea and barley and was low when barley was very competitive for soil N. Due to the time necessary for the progressive development and activity of nodules (Tricot et al., 1997; Voisin et al., 2002), N_2 fixation could not completely satisfy N demand at the beginning of the crop cycle in intercrops. N_2 fixation is affected by soil N availability but is also directly related to photosynthesis and N demand (Bethlenfalvay and Phillips, 1977; Voisin et al., 2002). In our study, whereas the amount of N_2 fixed per plant in pea SC was largely determined by soil N availability, the amount of N_2 fixed per plant in intercrops was largely determined by pea growth and was dependant on the competitive strength of barley for light. Thus, as previously observed (Andersen et al., 2005; Jensen, 1996; Ofori and Stern, 1987), the potential intercropping practice as a means of increasing the contribution of N derived from fixation was lost as fertilization level was increased. Other studies have shown the role of competition for light affecting pea growth and thereby N_2 fixation in intercrops. When soybean was intercropped with a tall sorghum rather than a shorter cultivar, light interception and consequently pea growth and N_2 fixation were decreased (Wahua and Miller, 1978). In a sorghum–groundnut intercrop system, partial defoliation of sorghum increased the amount of light for the associated legume and enhanced fixation (Nambiar et al., 1983).

Conclusion

To increase the performance of pea–barley intercrops, it would be necessary to try to better satisfy the needs of each species. We have shown that this is not possible through N addition because it increases soil N uptake by barley, but decreases N_2 fixation by pea. Other strategies might encourage the complementary use of N. Sowing the pea crop earlier might favour its growth and N nutrition without the strong competition of barley and N_2 fixation activity might be sufficiently high when barley would begin to take up soil nitrogen.

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