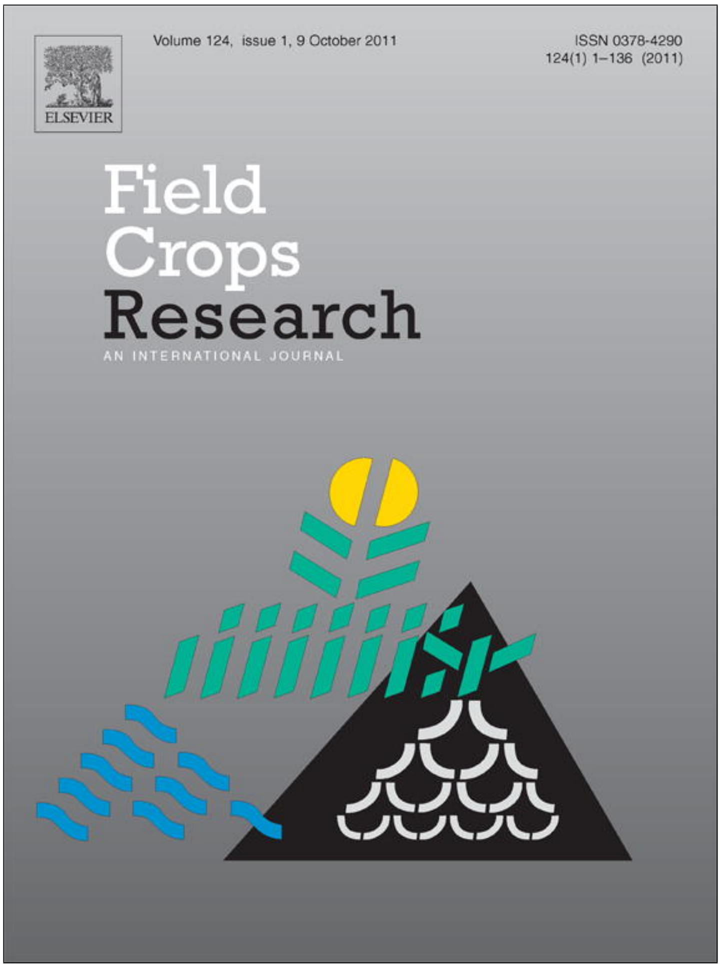
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A comparison of commonly used indices for evaluating species interactions and intercrop efficiency: Application to durum wheat–winter pea intercrops

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ABSTRACT

There are many indices available to evaluate the potential advantages of intercrops and species interactions but correct choice of index is crucial in making accurate interpretations. This study compared and evaluated the relevance in understanding intercrop functioning of some well-known indices (aggressivity, AG; cumulative relative efficiency index, REIc; land equivalent ratio, LER) and other potentially useful indices (change in contribution, CC; interspecific and intraspecific interaction index, IE and IA; comparative absolute growth rate, CGR).

Data collected from a two-year field experiment in SW France with different fertiliser N levels comparing wheat (*Triticum turgidum* L., cv. Nefer) and pea (winter pea, *Pisum sativum* L., cv. Lucy) grown as sole crops or intercrops in a row substitutive design were used to calculate, compare and evaluate the relevance of the selected indices for understanding intercrop functioning.

It was found that AG indices (calculated with or without considering sowing density or actual plant density) did not provide the information generally claimed in the literature (i.e. whether a crop is dominant or dominated). Consequently, their use is clearly unadvisable except when analysed jointly with partial land equivalent ratios. The LER index proved to be clearly relevant, versatile and helpful in illustrating the pattern of competitive outcomes in intercropping experiments, in particular when plotting partial LER values of wheat as a function of those of pea. However, LER cannot identify intraspecific and interspecific interactions. To do so we suggest using the intraspecific and interspecific interaction indices, which can also reveal possible facilitation phenomena and allow description of species change in the contribution index (CC). Interaction dynamics between crops that determine the final balance and the outcome of all competitive interactions occurring between the two crops can be evaluated using the CGR index, which is preferable to REIc, particularly when crops differ greatly in their dry weight.

Careful choice of index and interpretation of the results are thus essential in correctly understanding species interactions (globally and dynamically) and intercrop efficiency compared with sole crops. Such indices can help highlight and reveal cereal and legume traits suited to intercropping and also appropriate cropping sequences and management techniques, allowing efficient intercropping. However, the results must always be related to actual data values (yield, dry weight or N accumulated) because the indices used cannot evaluate intrinsically quantitative performance but only the relative performance of intercrops compared with that of sole crops.

1. Introduction

Modern agriculture has led to many well-known problems such as soil erosion, environmental contamination by fertiliser and pesticides, and disease, pest or weed resistance to pesticides (Griffon, 2006; Jackson and Piper, 1989). There is consequently a need to design new arable cropping systems for greater efficiency and resource conservation. One solution could be to diversify agroecosystems by increasing the number of species grown and using more leguminous crops (e.g. Altieri, 1999; Griffon, 2006; Malézieux et al., 2008).

Intercropping (IC), i.e. the simultaneous growing of two or more species in the same field for a significant period but without necessarily being sown and harvested together (Willey, 1979), is known to: (i) improve soil conservation (Anil et al., 1998), (ii) favour weed control (Banik et al., 2006; Vasilakoglou et al., 2005), (iii) reduce pests and diseases (Altieri, 1999; Trenbath, 1993), (iv) provide better lodging resistance (Anil et al., 1998), (v) improve yield stability (Lithourgidis et al., 2006) and (vi) increase yield and grain protein concentration compared with sole crops (SC), particularly in

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low-input systems (e.g. Bedoussac and Justes, 2010a; Hauggaard-Nielsen et al., 2003; Willey, 1979). Intercrops are common in wild plant communities but due to the intensification of agriculture during the last 50 years, gramineous–legume intercrops are now rarely used in European countries, except in leys for animal feeds.

The advantage of intercrops is that the two intercropped species do not compete for exactly the same resource niche and thereby tend to use resources in a complementary way (Hauggaard-Nielsen et al., 2001a,b; Snaydon and Satorre, 1989). More precisely, the advantages of legume–cereal intercrops are often assumed to arise from the complementary use of N sources by the components of the intercrop (e.g. Bedoussac and Justes, 2010a; Jensen, 1996; Ofori and Stern, 1987). This is of particular interest in low-input cropping systems, where mineral N is a limited resource. In grain legume–cereal intercrops grown at variable N levels, it has been observed that the grain legume has a higher interspecific competitive ability at lower soil N levels, while the cereal component competes better at higher soil N levels (e.g. Bedoussac and Justes, 2010a; Ghaley et al., 2005; Hauggaard-Nielsen and Jensen, 2001). Intercrops are also known to use light more efficiently (Jahansooz et al., 2007) compared with sole crops because of complementary use of: (i) space, when crops differ in their aerial architecture (e.g. tall vs. short crops) and (ii) time, when crops have life cycles that differ in timing (e.g. early vs. late maturing crops) (Poggio, 2005; Trenbath, 1986; Tsubo and Walker, 2004). Species interactions are complex, varying with the nutrient environment and time (Connolly et al., 1990), and depend on the species and cultivars intercropped.

There are many indices used in the literature to evaluate the potential advantages of intercrops and species interactions. Such indices have been reviewed by a number of authors (e.g. Dhima et al., 2007; Willey, 1979; Weigelt and Joliffe, 2003) for both replacement and additive designs, sometimes taking into account crop density, which is known to affect plant performances (e.g. yield, dry weight, N accumulated). The choice of index and its use and significance are crucial in making accurate interpretations. The land equivalent ratio (LER; Willey and Osiru, 1972), an index well known to agronomists, is widely used (in about 11% of articles on intercrop or intercropping published since 2000; ISI Web of Science, 2010) to compare the efficiency of sole crops and intercrops for yield or dry weight production. However, the full potential of the LER index is rarely explored and it is usually used simply to investigate whether the intercrop is producing more than the sole crops. However, as pointed out by Williams and McCarthy (2001), this index could be much more useful because it can allow the competitive advantage of one species over the other, mutual interference and facilitation interactions to be distinguished. Moreover, there are examples in the literature where the use of indices lacks a sound scientific basis or where the results are given a partially erroneous meaning if some hypothesis is not verified. For example, aggressivity (AG), defined as the difference between partial LER values (first define by McGilchrist and Trenbath, 1971 and adapted by Snaydon, 1991), has often been used (in 2% of articles on intercrop or intercropping published since 2000; ISI Web of Science, 2010) to conclude that a crop is dominant or dominated, but without giving a clear definition of these terms. Moreover they often do not consider that crop dominance can change over time while a better understanding of dynamic competitive interactions and mechanisms within intercropped species is allowed only by sequential measurements of crop growth (Andersen et al., 2004; Bedoussac and Justes, 2010b; Connolly et al., 1990). For that reason, the relative efficiency index (REIc, Connolly, 1987) is sometimes used to compare the relative biomass production performance of crops over the growth period but without referring to the actual absolute dry weight of the crops.

The value of these indices is thus questionable due to some difficulties in their interpretation. The aim of the present study was to compare and evaluate the relevance in understanding intercrop functioning of some of the most commonly used indices (LER, AG and REIc) with other indices that are rarely used despite being easily understood and potentially relevant. The latter were: (i) the change in contribution (CC) used to compare the proportion of a species in a mixture with that in sole crops (Williams and McCarthy, 2001) and which could be relevant to help for designing cropping sequences, (ii) the interspecific and intraspecific interaction index (IA and IE, respectively; Jacquard, 1968) allowing evaluation of these interactions separately and then a better understanding of species interactions and (iii) the comparative absolute growth rate (CGR; Bedoussac and Justes, 2010b) as an alternative to the REIc index to compare the dynamics of species growth considering their growth rate (an indicator commonly used by agronomist).

The study focused on dry weight dynamics, final grain yield and final N accumulated in shoots to compare the selected indices. The results were then used to: (i) identify the most suitable index (ought to be clear relevant, specific and consistent in meaning) and (ii) evaluate the potential advantages of a durum wheat–winter pea intercrop compared with the sole crops by analysing crop interactions (competitive ability, severity of competition and complementarity for the use of resources) both globally and dynamically. Furthermore, we considered various N availabilities modified by N fertilisation (quantity and split doses) in order to increase the range of competitive pattern. Indeed, growing a grain legume–cereal intercrop at various N levels shows that the grain legume has a higher interspecific competitive ability at lower soil N levels, whereas that of the cereal is lower (Bedoussac and Justes, 2010a; Ghaley et al., 2005; Hauggaard-Nielsen and Jensen, 2001).

2. Materials and methods

2.1. Site and soil

The experiment was carried out on the two experimental fields of the Institut National de la Recherche Agronomique station in Auzeville (SW France, 43°31′N, 1°30′E) in 2005–2006 (Experiment I) and 2006–2007 (Experiment II). Experiment I was characterised by a cold winter and a dry, warm spring, whereas in Experiment II the winter was warm and dry and the spring was particularly wet. In Experiment I, soil water content was lower during the growing season and water stress higher in spring. Experiment I was carried out on a loamy soil plot (24% clay, 29% silt and 47% sand) with an available water capacity of 223 mm (0–150 cm) and Experiment II was conducted on a clay loam soil plot (30% clay, 38% silt and 32% sand) with an available water capacity of 207 mm (0–150 cm).

2.2. Experimental design

Durum wheat (W) (*Triticum turgidum* L., cv. Nefer) and winter pea (P) (*Pisum sativum* L., cv. Lucy) were grown as: (i) sole crops (SC) sown at the recommended density (336 and 72 seeds m^{-2}, respectively), (ii) half-density sole crops (SC1/2) sown at half the sole crop density and (iii) mixed crops (IC) in a row substitutive design (each species sown at half the sole crop density in alternating rows).

In both experiments, different fertiliser N sub-treatments (N*x* where '*x*' represents N applied in kg N ha^{-1}) in terms of quantity and split doses were evaluated on durum wheat sole crops, durum wheat half-density sole crops and intercrops, while pea sole crops and pea half-density sole crops were grown without any N application (for details see Bedoussac and Justes, 2010a).

The number of replicates for each treatment varied from three to six except for durum wheat SC1/2 in Experiment I (only two replicates) due to a problem at sowing identified after emergence.

Fungicide-treated seeds were sown on 8 November 2005 (Experiment I) and on 9 November 2006 (Experiment II). In Experiment II, 20 mm of irrigation water were applied after sowing because of the low water content in the topsoil. Weeds, diseases and green aphids were controlled as much as possible with appropriate pesticides.

2.3. Measurements and analyses

Four samplings were carried out during the growing season (for details see Bedoussac and Justes, 2010a) at key development stages: (i) 1 cm ear (E1 cm) of wheat (Zadoks 30; Zadoks et al., 1974), (ii) beginning of pea flowering (Zadoks 37), (iii) wheat flowering (Zadoks 69) and (iv) crop physiological maturity (pea maturity for sole cropped pea crops and wheat maturity for the intercrops and wheat sole crops).

2.4. Definition and calculation of indices

2.4.1. Cumulative relative efficiency index and comparative absolute growth rate

The relative performance of durum wheat and winter pea for biomass production was evaluated (Table 1) by calculating for each time interval between two successive sampling dates: (i) the cumulative relative efficiency index (Connolly, 1987) and (ii) the comparative absolute growth rate (Bedoussac and Justes, 2010b).

Within a given time interval ($t_1 - t_2$), the REIc compares the proportional change in total dry weight (K) of one species relative to another, while the CGR compares their dry weight growth rate (GR). At sowing, for both REIc and CGR, 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.

2.4.2. Land equivalent ratio for yield (LER_Y) or nitrogen accumulated in shoots (LER_N)

The land equivalent ratio is defined as the relative land area required when growing sole crops to produce the yield (LER_Y) or the N accumulated (LER_N) achieved in an intercrop (Willey and Osiru, 1972). LER for a durum wheat–winter pea intercrop is the sum of the partial LER values for wheat (LER_W) and pea (LER_P) (see Table 1).

To illustrate the pattern of competitive outcomes in intercrop experiments, Williams and McCarthy (2001) suggested plotting partial LER values for the first species (i.e. winter pea here) as a function of the partial LER of the second intercropped species (i.e. durum wheat here), which allows the distinction of areas of interest for the two species (see Fig. 1 for details).

2.4.3. Interspecific and intraspecific interaction index for yield (IE_Y and IA_Y) or nitrogen accumulated in shoots (IE_N and IA_N)

The effect of one winter pea row on one contiguous durum wheat row (interspecific interactions) was evaluated by calculating the wheat interspecific interaction index for yield (IE_{Y-W}) or N accumulated in shoots (IE_{N-W}) according to Jacquard (1968) (Table 1).

Similarly, we evaluated the effect of the presence of one wheat row on another contiguous wheat row (intraspecific interactions) by calculating the wheat intraspecific interaction index for yield (IA_{Y-W}) or N accumulated in shoots (IA_{N-W}) (Table 1).

For the IA index the half-density sole crop values were multiplied by two in order to compare sole crops and half-density sole crops on a similar plant or row basis, as with the IE index.

2.4.4. Change in contribution for yield (CC_Y) or nitrogen accumulated in shoots (CC_N)

Williams and McCarthy (2001) proposed the index 'change in contribution', which we calculated for each species separately (Table 1) using a simplified equation according to the experimental design. CC is the proportion of grain yield (CC_Y) or N accumulated in shoots (CC_N) of a species reached in intercrop divided by the expected grain yield or N accumulated proportion estimated from sole crop data. Subtracting 1.0 from this value gives the proportional change in contribution in an intercrop compared with the sole crops.

2.4.5. Aggressivity for yield (AG_Y) or nitrogen accumulated in shoots (AG_N)

Aggressivity, first defined by McGilchrist and Trenbath (1971) was calculated for each species (Table 1) according to the equation proposed by Snaydon (1991), which we simplified according to the experimental design. AG, defined as the difference between component crop partial LER values is often used to evaluate how aggressively a species behaves in an intercrop. More precisely, AG quantifies how much the relative yield (AG_Y) or N accumulated in shoots (AG_N) of a species is greater than that of the other species.

This calculation allows comparison of species aggressivity on an area basis, which equates to comparing the aggressivity of the whole wheat population with that of pea. Indeed, in our situation we considered that both species occupied the same area in the intercrop due to the systematic alternation of wheat and pea rows in the mixture.

2.4.6. Sowing plant aggressivity and actual plant aggressivity for yield ($SPlantAG_Y$ and $APlantAG_Y$) or nitrogen accumulated in shoots ($SPlantAG_N$ and $APlantAG_N$)

Adapting the equation proposed by Snaydon (1991) for AG (Table 1) we also calculated the aggressivity corrected by: (i) species sowing density in the mixture for yield ($SPlantAG_Y$) or N accumulated in shoots ($SPlantAG_N$) because of the great difference between durum wheat and winter pea sowing density in the mixture and (ii) actual plant densities in the mixture for yield ($APlantAG_Y$) or N accumulated in shoots ($APlantAG_N$) because plant density can be very different from sowing density (until stand establishment after winter frost).

2.5. Statistics

LER, AG and CC values were calculated separately for each intercrop replicate using the replicate values for the numerators and the mean sole crop values across all replicates for the denominators to eliminate the variation in the ratio attributable to sole crop variability. For the same reason, IE and IA indices were calculated considering the respective values of intercrops and sole crops and the mean half-density sole crop values across all replicates. Indeed, half-density sole crop variability is often high due to the difficulty in achieving homogeneous plant cover with half the number of seeds.

Moreover, we used the same N treatment for sole cropped durum wheat, half density durum wheat and the intercrops, while we always considered the unfertilised treatment for the sole cropped pea and half density pea assuming that N is not a limiting resource for legumes and did not affect pea grain yield and N accumulated (Sagan et al., 1993; Voisin et al., 2002a).

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, considering N treatment as the main factor, crop 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 to

Table 1
Name, symbol, source, formula and meaning of the various indices. Abbreviations as follows: W (durum wheat), P (winter pea), SC (sole crop), SC1/2 (half density sole crop), IC (intercrop), t_1 and t_2 (time), X (yield, dry weight (DW) or N accumulated in shoots per unit area), $R_{W\text{-}IC}$ and $R_{P\text{-}IC}$ (sowing proportions in intercrops of durum wheat and winter pea, respectively), $R'_{W\text{-}IC}$ and $R'_{P\text{-}IC}$ (actual plant density proportions in intercrops of durum wheat and winter pea, respectively).

Full name	Symbol	Source	Formula	Meaning
Cumulative relative efficiency index	REIc	Connolly (1987)	$K_W = DW_{W-IC}t_2/DW_{W-IC}t_1$ $K_P = DW_{P-IC}t_2/DW_{P-IC}t_1$ $REIc = K_W/K_P$	REIc > 1 indicates a greater proportional growth of wheat than pea over the time period considered and vice versa when REIc < 1
Comparative absolute growth rate	CGR	Bedoussac and Justes (2010b)	$GR_W = (DW_{W-IC}t_2 - DW_{W-IC}t_1)/(t_2 - t_1)$ $GR_P = (DW_{P-IC}t_2 - DW_{P-IC}t_1)/(t_2 - t_1)$ $CGR = GR_W/GR_P$	CGR > 1 indicates a faster growth rate of wheat then pea over the time period considered and vice versa when CGR < 1
Land equivalent ratio	LER	Willey and Osiru (1972)	$LER_W = X_{W-IC}/X_{W-SC}$ $LER_P = X_{P-IC}/X_{P-SC}$ $LER = LER_W + LER_P$	See Fig. 2 for details
Aggressivity	AG	Snaydon (1991)[a]	$AG_W = 2 \times (LER_W - LER_P) = -AG_P$	If $AG_W > 0$ ($\Leftrightarrow LER_W > LER_P$) than the relative grain yield, dry weight or N accumulated of wheat is greater than that of pea and vice versa if $AG_W < 0$
Sowing plant aggressivity	SPlantAG	Adapted from Snaydon (1991)[a]	$SPlantAG_W = 2 \times (LER_W/R_{W-IC} - LER_P/R_{P-IC}) = -SPlantAG_P$	Similar to that of AG_W except that $SPlantAG_W$ compares species efficiency in mixtures on seeds sown basis instead of on area basis
Actual plant aggressivity	APlantAG	Adapted from Snaydon (1991)[a]	$APlantAG_W = 2 \times (LER_W/R'_{W-IC} - LER_P/R'_{P-IC}) = -APlantAG_P$	Similar to that of AG_W except that $APlantAG_W$ compares species efficiency in mixtures on actual pant densities basis instead of on area basis
Interspecific interaction index	IE	Jacquard (1968)	$IE_W = X_{W-IC}/X_{W-SC1/2}$ or $IE_P = X_{P-IC}/X_{P-SC1/2}$	If $IE_W < 1$ intercropped wheat row yield, dry weight or N accumulated is lower than that of the half density sole cropped wheat row due to interspecific competition and vice versa if $IE_W > 1$
Intraspecific interaction index	IA	Adapted from Jacquard (1968)	$IA_W = X_{W-SC}/(2 \times X_{W-SC1/2})$ or $IA_P = X_{P-SC}/(2 \times X_{P-SC1/2})$	If $IA_W < 1$ simple spaced wheat row yield, dry weight or N accumulated is lower than that of the half density sole cropped wheat row due to intraspecific competition and vice versa if $IA_W > 1$
Change in contribution for yield	CC	Williams and McCarthy (2001)	$CC_W = \frac{X_{W-IC}/(X_{W-IC}+X_{P-IC})}{X_{W-SC}/(X_{W-SC}+X_{P-SC})} - 1 = (CC_P + 1) \times \frac{LER_W}{LER_P} - 1$	If $CC_W > 0$ ($\Leftrightarrow LER_W > LER_P$) then the grain yield, dry weight or N accumulated proportion of wheat in the mixture is greater than wheat proportion in the sole crops and vice versa if $CC_W < 0$

[a] Aggressivity was first defined by McGilchrist & Trenbath (1971) as: $A_W = 1/2 \times [(Z_{W-IC}/Z_{W-SC}) - (Z_{P-IC}/Z_{W-SC})]$ where Z is the yield per plant for a replacement series, but can be modified for partial additive series (designs sensu Gibson et al., 1999) by two (Snaydon, 1991). Moreover, in our experiment each species was sown in intercrop at half its sole crop density and we considered that the ability of the species to emerge is not a characteristic determined by interaction in seed germination in an intercrop (here species were sown in alternate rows and no allelopathic effects are known for pea and durum wheat.).

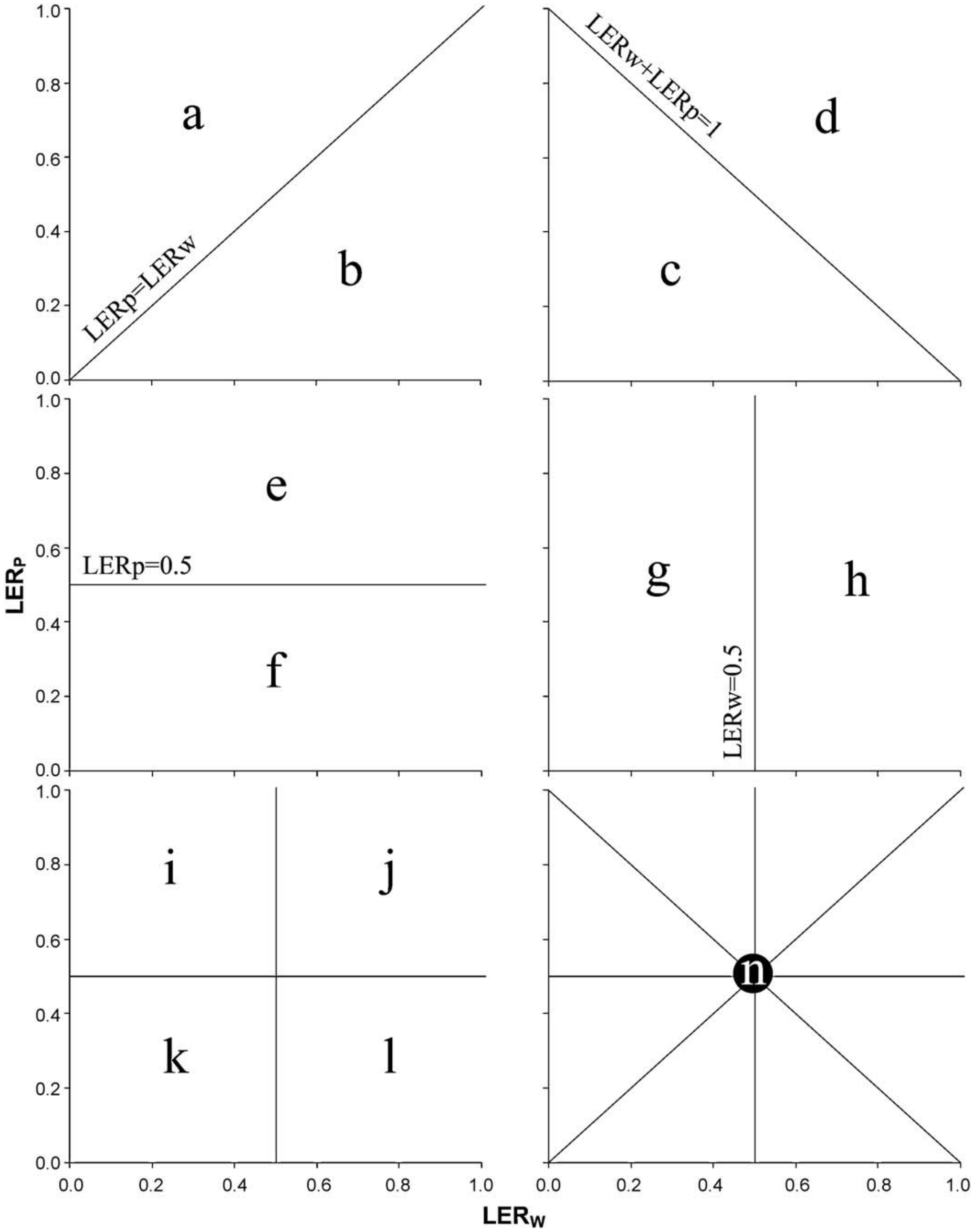

Fig. 1. Graphical representation of all possible outcomes of an interaction experiment with two species in a substitutive design (each species sown at half the sole crop density). The diagonal line corresponding to $LER_{Y-W} = LER_{Y-P}$ separates the areas of the graph in which winter pea has a competitive advantage over durum wheat for grain yield production (a) and vice versa (b). The other diagonal corresponding to $LER_Y = LER_{Y-W} + LER_{Y-P} = 1$ separates the areas of the graph where sole crops are more efficient than the intercrop for grain yield production (c) and vice versa (d). Areas corresponding to partial LER values below 0.5 for winter pea (f) and for durum wheat (g) indicate that species grain yield (per plant or row) is less in the mixture than in the sole crop because each species was sown in the intercrop at half its sole crop density. Conversely, areas corresponding to values above 0.5 for winter pea (e) and for durum wheat (h) represent situations where species grain yield (per plant or row) is higher when intercropped. Area (i) corresponds to situations in which winter pea suppresses durum wheat; the reverse is true in area (l). Finally, in area (k) both species are suppressed in the mixture due to competition while in area (j) both species grow better in the mixture (per plant or row) than they did as sole crops, indicating so-called 'facilitation'. The neutral point (n) at $LER_{Y-W} = LER_{Y-P} = 0.5$ indicates situations in which the grain yield (per plant or row) of the two species is similar in the mixture and in sole crops.

compare N treatments within crops and crops within N treatments at a significance threshold of $p = 0.10$. This threshold was chosen to take into account the variability within some measurements in our experiments, in particular for data sampled at various stages and analysed in terms of dynamics. According to Sheskin (2004), the significance of differences between treatments can be estimated using simple pre-planned comparisons, regardless of whether the omnibus F value is significant. Finally, confidence intervals for the means of AG, SPlantAG, APlantAG, CC, LER, IE, IA, REIc and CGR values were calculated from replicates assuming a normal distribution according to Sheskin (2004) but we could have considered others statistical solutions relevant to intercropping research (Mead and Riley, 1981).

3. 3 Results and discussion

3.1. *Interspecies growth dynamics (REIc and CGR)*

Sequential measurements of crop growth allow better understanding of competitive interactions in intercrop and sole crop

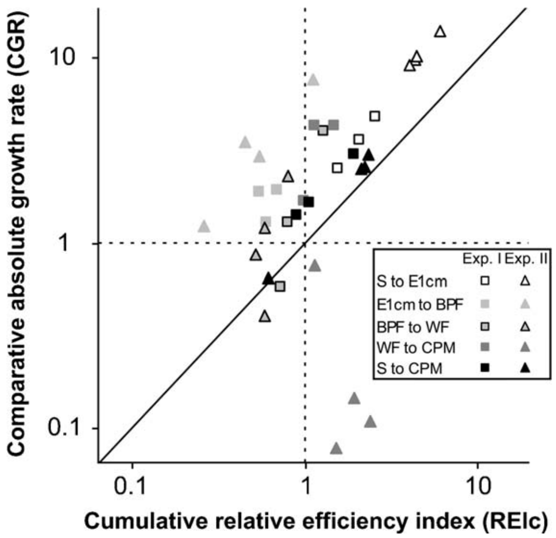

Fig. 2. Comparative absolute growth rate as a function of cumulative relative efficiency index calculated for the time interval corresponding to the date of sampling: sowing (S) to '1 cm ear' stage of durum wheat (E1 cm), E1 cm to the beginning of winter pea flowering (BPF), BPF to durum wheat flowering (WF), WF to crop physiological maturity (CPM) and for the whole growth period (S to CPM) for the different N treatments (N*x* where '*x*' represents N applied in kg N ha^{-1}) of Experiments I and II. Values are the mean (n = 3–5).

dynamics compared with a single measurement of final yield (Andersen et al., 2004; Connolly et al., 1990) and indices such as REIc and CGR can therefore be useful.

In the present work, both REIc and CGR indicated that species dynamics changed over time. From sowing (S) to the beginning of durum wheat stem elongation (E1 cm), REIc and CGR values were above 1 in all experiments and N treatments (Fig. 2). Moreover, CGR values were greater than REIc values. This indicates that the proportional changes in total dry weight (K) and dry weight growth rate of durum wheat were greater than those of winter pea. In particular they showed that durum wheat had a better start than pea, at least until durum wheat stem elongation, which was undoubtedly the result of faster seedling emergence and root growth of the cereal (Corre-Hellou and Crozat, 2005; Hauggaard-Nielsen et al., 2003; Jensen, 1996).

After E1 cm, for all N treatments and experiments, REIc values were close to 1 and often lower during the two following spring growth periods (E1 cm to BPF and BPF to WF), while CGR values were always close to 1 and mainly higher (except for N0 between BPF and WF for Experiments I and II). In summary, until durum wheat flowering, the proportional change in total dry weight of pea was faster than that of durum wheat but its growth rate was slower, leading to apparent contradictory information from the REIc and CGR indices. This is because unlike REIc, which is based on the proportional dry weight increase of the species, CGR is based on the absolute growth rate of one species relative to the other.

Later, from WF to crop physiological maturity (CPM), durum wheat proportional growth was faster than that of pea in all treatments, even though REIc values were significantly greater than 1 only for N0 (Experiment I) and N140 (Experiment II). Similar results were found for CGR in Experiment I, while CGR values were about 0.1 in Experiment II (except for N60, where CGR was equal to 1). Finally, considering the whole growth period, REIc and CGR values were the lowest (less than 1) in N0 for both experiments (except CGR in Experiment I) and about 1 or more in N-fertilised plots and no significant difference was found between N-fertilised treatments.

To conclude, both REIc and CGR are useful to analyse species dynamics but we recommend analysing REIc in terms of the absolute value of dry weight to avoid misinterpretation, which is not necessary for CGR. More precisely, when the dry weight of intercrop species differs considerably, we suggest using the CGR index instead of REIc to compare species relative performance, crop dynamics and crop competitiveness.

3.2. Intercropping advantages for yield and nitrogen accumulated

3.2.1. Yield and nitrogen accumulated in shoots

As expected, yield and N accumulated in shoots of sole cropped, half-density sole cropped and intercropped durum wheat were significantly increased by fertiliser N compared with the unfertilised treatments in both experiments (Table 2). For both experiments, intercropped winter pea yield and N acquisition were significantly reduced with N fertilisation compared with N0 (except for N100 in Experiment I).

The yield and N accumulated in shoots of the total intercrop were higher than those of the durum wheat sole crops for treatments with little or no N fertiliser application (N0 and N100 in Experiment I; N0 and N60 in Experiment II) but were lower or similar when large amounts of N fertiliser were applied (N180 in Experiment I and N140 in Experiment II). Finally, the whole intercrop yield was always higher or similar to that of the unfertilised sole cropped pea, while the whole intercrop accumulated more N than the sole cropped pea in Experiment I (except for N0) and less or a similar amount in Experiment II.

3.2.2. Land equivalent ratio for yield (LER_Y) or nitrogen accumulated in shoots (LER_N)

The land equivalent ratio for yield (LER_Y) or N accumulated in shoots (LER_N) is a relevant indicator, not to interpret interference but to quantify mixture productivity compared with the sole crops (Jolliffe, 2000), either for grain yield or N acquired.

In our experiment, except for LER_Y in N80 and N140 and for LER_N in N140, LER values were above the diagonal line corresponding to LER = 1 (Fig. 3a and b). This indicates that resources were ultimately used up to 21% more efficiently on average for yield production compared with sole crops and confirmed that intercrops can increase the use of N sources by up to 32%, especially when little or no N fertiliser is applied or when N was applied late in the crop cycle. The adverse effect of N availability at the end of winter on intercrop behaviour confirms that intercropping is more suitable in low N input situations (Bulson et al., 1997; Fujita et al., 1992; Jensen, 1996). However, the LER depends on the sole crop reference is calculated on (Mead and Willey, 1980; Jolliffe, 2000). Thus indices must always be related to their original data values and in particular those of the sole crop (e.g. yield, dry weight or N accumulated) since relative and absolute productions are not necessarily linked. For example, species mixtures with highest LER values do not necessarily have highest absolute productivity (Garnier et al., 1997; Jolliffe and Wanjau, 1999).

Plotting partial LER values for the first species as a function of the partial LER of the second intercropped species is a way to illustrate the pattern of competitive outcomes in intercrop experiments. In our experiment, partial LER values were always below the diagonal line corresponding to $LER_P = LER_W$, i.e. in the area corresponding to a competitive advantage of durum wheat over peas (except for LER_Y in N0 in Experiment II) and more precisely, to situations where durum wheat suppressed pea (i.e. $LER_W > 0.5$ and $LER_P < 0.5$).

Our results also indicate that pea crop had higher interspecific competitive ability at low N levels, while the reverse was true for durum wheat at high N levels. Indeed, LER_{Y-P} were negatively correlated with N availability and were always above or sometimes

Table 2
Grain yield ($t\,ha^{-1}$) and N accumulated in shoots ($kg\,N\,ha^{-1}$) for the sole crops (SC), the half-density sole crops (SC1/2) and the intercrops (IC) in Experiments I and II for the different N treatments (N*x* where '*x*' represents N applied in $kg\,N\,ha^{-1}$). Values are the mean (n = 3–5) ± standard error.

Year	Specie	N	Grain yield I ($t\,ha^{-1}$)			N accumulated in shoots ($kg\,N\,ha^{-1}$)		
			Wheat	Pea	Total IC	Wheat	Pea	Total IC
2005–2006 (Experiment I)	IC	N0	2.6 ± 0.3	2.2 ± 0.3	4.8 ± 0.6	67 ± 12	81 ± 13	148 ± 18
		N100	3.3 ± 0.5	2.4 ± 0.2	5.7 ± 0.4	106 ± 19	99 ± 14	206 ± 16
		N180	4.4 ± 0.9	1.6 ± 0.0	6.0 ± 0.8	137 ± 17	75 ± 5	211 ± 14
	SC	N0	3.8 ± 0.3	4.4 ± 0.8		77 ± 7	177 ± 30	
		N100	5.2 ± 0.5			155 ± 23		
		N180	6.9 ± 0.3			209 ± 18		
	SC1/2	N0	3.4 ± 0.3	3.2 ± 0.7		72 ± 9	132 ± 26	
		N100	4.7 ± 0.4			139 ± 22		
		N180	6 1 ± 0.6			202 ± 21		
2006–2007 (Experiment II)	IC	N0	1.4 ± 0.4	2 1 ± 0.3	35 ± 0.2	44 ± 12	81 ± 10	124 ± 7
		N60	2.7 ± 0.6	1.2 ± 0.5	4.0 ± 0.1	116 ± 39	48 ± 21	164 ± 17
		N80	1 ± 1.2	1.2 ± 0.5	3.6 ± 95	95 ± 6	48 ± 20	143 ± 22
		N140	2.2 ± 0.4	0.8 ± 0.1	2.9 ± 0.2	93 ± 26	40 ± 9	
	SC	N0	2.8 ± 0.5	3.3 ± 1.0		70 ± 12	173 ± 37	133 ± 14
		N60	3.7 ± 0.2			116 ± 23		
		N80	4.3 ± 0.3			122 ± 16		
		N140	3.6 ± 0.9			143 ± 37		
	SC1/2	N0	2.4 ± 0.3	3.4 ± 0.8		61 ± 9	161 ± 28	
		N60	3.7 ± 0.8			116 ± 32		
		N80	3.3 ± 0.2			106 ± 18		
		N140	3.7 ± 0.9			178 ± 25		

similar to their respective LER_{N-P} values. Conversely, LER_{Y-W} values were only slightly negatively correlated with N availability and were always below or at least similar to their respective LER_{N-W} values. The adverse effect of N fertilisation was undoubtedly the result of two main factors: (i) the reduction in N_2 fixation with early N application (Ghaley et al., 2005; Voisin et al., 2002b) and (ii) the amplification of differences in species growth dynamics with N supply (Ghaley et al., 2005; Hauggaard-Nielsen and Jensen, 2001; Bedoussac and Justes, 2010b).

A last key point is that all the indices based on N accumulated were calculated from the total N in shoots (N from soil and N_2 from air). It would be interesting to consider only the N accumulated from soil by the legume as a way to reveal competitions within intercropped species since competition for N between durum wheat and pea occurs only for soil mineral N and not for N_2. Conversely, considering the whole N accumulated by the legume (N from the soil and N_2 from air) allow to evaluate species complementarity for the use of N pools. In a previous paper (Bedoussac and Justes, 2010a), we found that the percentage of N acquired by the legume derived from air (biological N_2 fixation) was ~80% in the intercrop and only ~60% in sole crops. As a consequence, the partial LER_N of pea considering only mineral N will be about 0.5 of that calculated from both N sources $[(1-0.8)/(1-0.6)]$. This indicates that if we considered only the N derived from soil, durum wheat would appear much more competitive than winter pea compared to the conclusion of our paper (indices calculated from the total N accumulated in shoots). This result is most probably due to faster and deeper root growth and higher N demand of the cereal, as already observed by many authors for others cereal–grain legume intercrops (e.g. Corre-Hellou and Crozat, 2005; Hauggaard-Nielsen et al., 2003; Jensen, 1996).

In summary, bivariate diagrams are useful to illustrate competitive outcomes (Snaydon and Satorre, 1989; Williams and McCarthy, 2001). Nevertheless, partial LER values only compare single-spaced rows of pure crops with a mixed crop and therefore consider the balance between intraspecific and interspecific interactions (Cruz and Soussana, 1997).

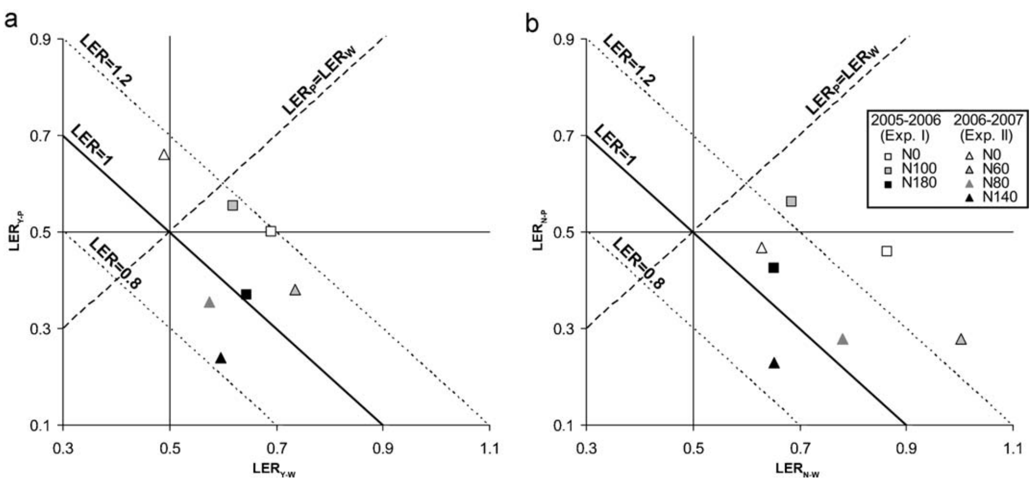

Fig. 3. Partial land equivalent ratio of winter pea (LER_P) as a function of the partial land equivalent ratio of durum wheat (LER_W) calculated from: (a) grain yield or (b) shoot N accumulated for the different N treatments (N*x* where '*x*' represents N applied in $kg\,N\,ha^{-1}$) of Experiments I and II. Values are the mean (n=3–5).

3.3. Severity of competition for yield and nitrogen accumulated (IE, IA and CC)

3.3.1. Intraspecific and interspecific interaction effects on yield (IA_Y and IE_Y) or on nitrogen accumulated in shoots (IA_N and IE_N)

In order to evaluate such interactions separately, Cruz and Soussana (1997) proposed comparing single-spaced pure crops (SC) and intercrops (IC) with double-spaced pure crops (SC1/2) which can be considered as the reference crop. Indeed, variations between single- and double-spaced pure crops of species A allow the study of intraspecific interactions, i.e. the effect of the presence of species A on A. Conversely, the study of interspecific interactions, i.e. the effect of the presence of species B on A and vice versa, can be performed comparing variations between double-spaced pure crops and mixture.

In our work, IE_Y and IA_Y values were always below 1 (Fig. 4a) and similar results were found for IE_N and IA_N (Fig. 4b) except that IE_N was ~1.0 in N60 (Experiment II). This indicates that both interspecific and intraspecific competition reduced durum wheat yield (on a row basis) compared with the half-density sole crop. Moreover, all values were above the diagonal line corresponding to IE = IA, revealing that a durum wheat row reduced the yield and N accumulated of the adjacent row of durum wheat more than a pea row. This shows that in our substitutive row experiment, a durum wheat row competed better than a pea row relative to the yield and N accumulated in shoots by the half-density sole cropped wheat, i.e. intraspecific competition was stronger than interspecific competition for both grain yield and N accumulated in shoots.

Considering all N treatments and experiments, the variability in IE indices was greater than their respective IA indices, as indicated by the coefficient of variation (16% and 11%, respectively, on average for yield and N in shoots for both experiments). We also observed higher coefficients of variation for indices calculated from N in shoots compared with those calculated from yield (16% and 10%, respectively, on average for IE and IA for both experiments). These results indicate that intraspecific competition, is almost at a similar intensity whatever the N availability and experiment because a durum wheat sole crop is always an homogeneous stand while interspecific competition depends strongly on N availability. Indeed, N application (especially in the early stages) has a large positive effect on intercropped durum wheat growth and consequently a negative effect on pea growth due to less incoming photosynthetically active radiation available (Bedoussac and Justes, 2010b).

To conclude, IE and IA indices are more versatile than the partial LER values because they allow to distinguish intraspecific and interspecific interactions and it can be demonstrated that $IE_W/IA_W = [X_{W-IC}/X_{W-SC1/2}]/[X_{W-SC}/(2 \times X_{W-SC1/2})] = 2 \times X_{W-IC}/X_{W-SC} = 2 \times LER_W$ (where X is the yield, N accumulated in shoots or dry weight per unit area).

3.3.2. Consequences of intraspecific and interspecific interactions on the change in contribution for yield (CC_Y) or nitrogen accumulated in shoots (CC_N)

The change in contribution index, representing the proportional change in contribution of grain yield or N accumulated in an intercrop compared with sole crops, has a clear meaning and it is not size biased (Williams and McCarthy, 2001).

In our experiments, CC_Y and CC_N were always close to or higher than 1 (Fig. 5a and b) except for N0 in Experiment II, indicating that grain yield proportion of durum wheat in the intercrop was greater than that in the sole crops. As already observed for aggressivity and plant aggressivity, CC_N values were always higher than their respective CC_Y values (except for N180 in Experiment I) and CC values depended on N fertilisation. More precisely, the contribution of durum wheat in the intercrop was increased by 19% for grain yield and 43% for N accumulated compared with the sole crops which confirms that durum wheat benefited more from intercropping than pea. CC index seems efficient to demonstrate whether one crop is more efficient than another under given conditions. However, unlike LER, the CC index cannot define the overall intercrop performance.

We also demonstrated that CC_Y and CC_N could not be estimated in a satisfactory way from only durum wheat intraspecific and interspecific interaction indices (Fig. 5a and b), as illustrated by the high RMSE values (0.124 and 0.126, respectively). Conversely, estimating CC values from durum wheat and pea intraspecific and interspecific interaction indices (Fig. 6a and b) allowed a significant reduction in the RMSE (0.041 and 0.039, respectively). This shows that CC index depends not only on durum wheat interspecific and intraspecific interactions (IE_W and IA_W), i.e. the effects of durum wheat on durum wheat and of pea on durum wheat, but also on pea interspecific and intraspecific interactions (IE_P and IA_P), i.e. the effect of pea on pea and of pea on durum wheat. However, the weight of pea interspecific and intraspecific indices in CC estimation was lower than that of durum wheat indices, as illustrated by the lowest IE_P and IA_P coefficient absolute values (−0.94 and 0.58, respectively on average for yield and N accumulated) compared with the IE_W and IA_W coefficient absolute values (0.82 and −1.17, respectively on average for yield and N accumulated).

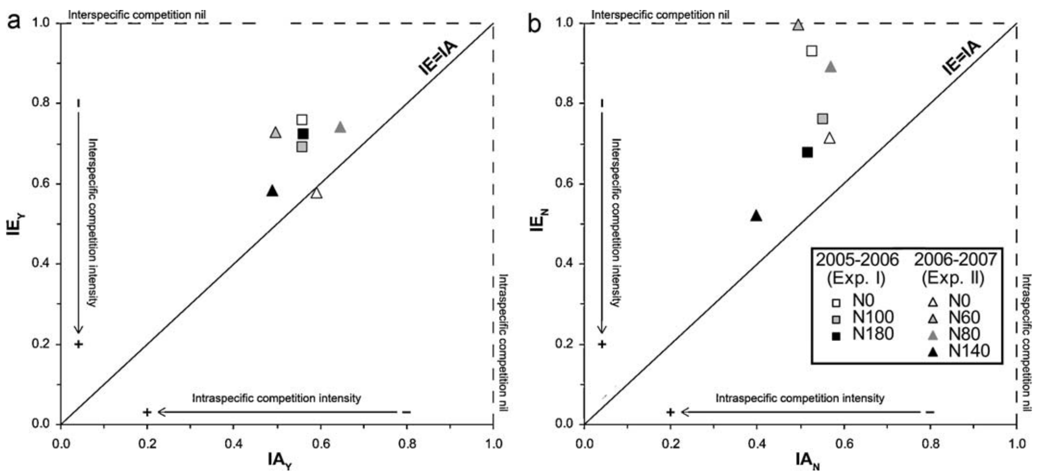

Fig. 4. Durum wheat interspecific interaction index (IE) as a function of durum wheat intraspecific interaction index (IA) calculated from: (a) grain yield or (b) shoot N accumulated for the different N treatments (N*x* where '*x*' represents N applied in kg N ha^{-1}) of Experiments I and II. Values are the mean (n=3–5).

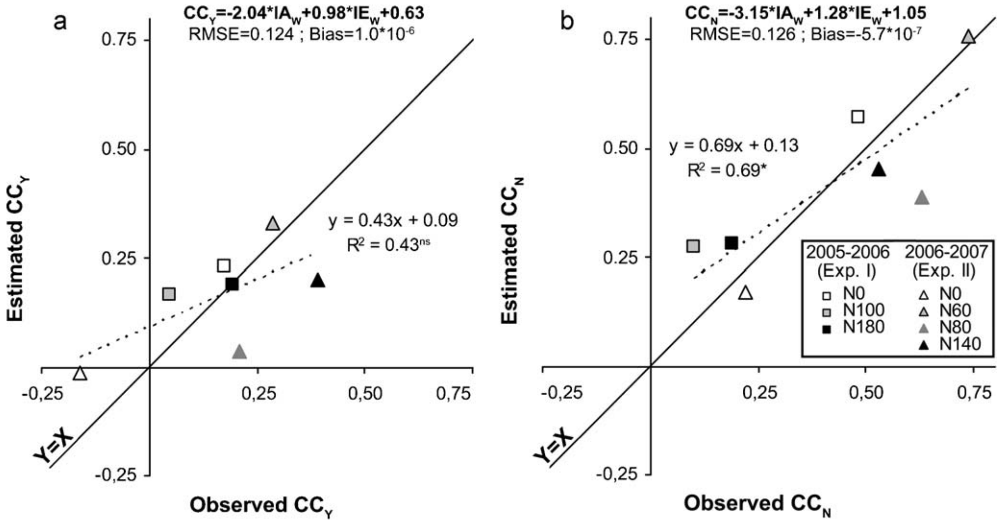

Fig. 5. Change in contribution as a function of interspecific and intraspecific interaction indices of durum wheat calculated from: (a) grain yield or (b) shoot N accumulated for the different N treatments (N*x* where '*x*' represents N applied in kg N ha^{-1}) of Experiments I and II. Values are the mean (n=3–5).

In summary, our results confirms that crop interactions in intercrops can only be revealed and well interpreted, i.e. without misinterpretation, by comparing within the same experimental design sole crops, half-density sole crops and intercrops, as postulated by Cruz and Soussana (1997).

3.4. Competitive ability for yield and nitrogen accumulated (AG, SPlantAG and APlantAG)

Aggressivity, defined here as the difference between durum wheat and pea partial LER values, quantifies how much the relative yield or the relative N accumulated by one crop is greater than that of another. This index is often used to evaluate how aggressively a species behaves in a mixture, but its meaning is not always clearly defined and adequately used in the literature. Many authors (e.g. Dhima et al., 2007) consider that: (i) both crops are equally competitive when AG is zero, (ii) durum wheat is the dominant crop when AG is positive and (iii) durum wheat is the dominated crop when AG is negative. A major limitation of this index is that it needs a clear definition of 'dominant' and 'dominated', but too few papers contain satisfactory definitions and do not consider AG values in dynamic situations where a species could be dominant during early growth stages but could be dominated later as we observed in our experiments.

Moreover, Williams and McCarthy (2001) demonstrated that AG is not a relevant index because functional curves of AG values are parallel to the diagonal where $LER_W = LER_P$ and may cross over with different competition scenarios which was clearly confirmed by our results. For example, $AG > 0 \Leftrightarrow LER_W > LER_P$ could be obtained with various types of intercrop interactions, such as: (i) beneficial to both species but more for durum wheat than for pea ($LER_W > LER_P > 0.5$), (ii) beneficial to durum wheat and harmful to pea ($LER_W > 0.5 > LER_P$) or (iii) harmful to both crops but less so for durum wheat than for pea ($0.5 > LER_W > LER_P$). Considering our experimental data and on an area basis, using AG index we could only draw conclusions on the following points: (i) wheat did better in the intercrop than pea compared with their respective sole crops, (ii) durum wheat's advantage was higher for N accumulated

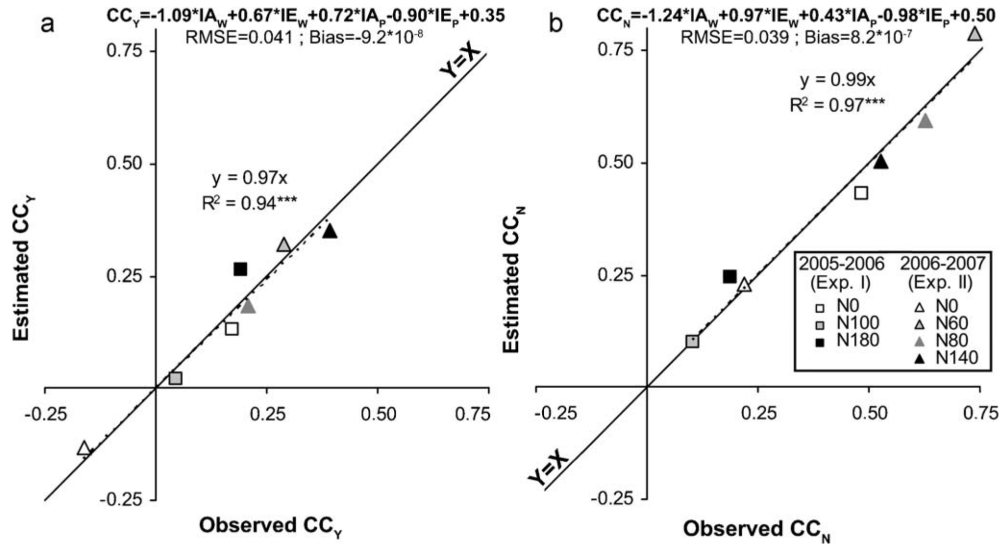

Fig. 6. Change in contribution as a function of interspecific and intraspecific interaction indices of durum wheat and winter pea calculated from: (a) grain yield or (b) shoot N accumulated for the different N treatments (N*x* where '*x*' represents N applied in kg N ha^{-1}) of Experiments I and II. Values are the mean (n=3–5).

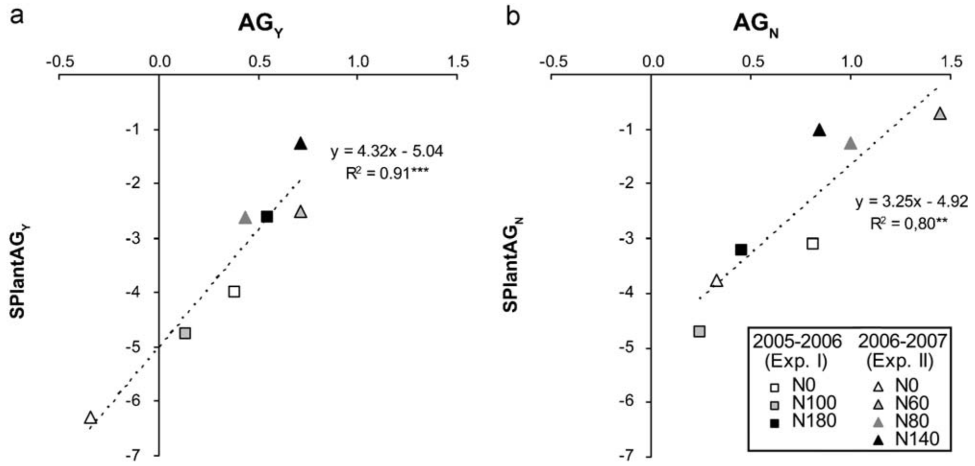

Fig. 7. Sowing plant aggressivity as a function of the aggressivity for: (a) yield or (b) shoot N accumulated for the different N treatments (N*x* where '*x*' represents N applied in kg N ha^{-1}) of Experiments I and II. Values are the mean (n = 3–5).

than for grain yield and (iii) durum wheat's advantage was higher for the N-fertilised treatments.

Another critical point concerning AG (and others indices calculated from species performance on an area basis) is that the density of each species in the intercrop is not taken into account. This is a key point in experiments where the sowing densities of the component species are very different. In our study, pea plants represented only 21% of the intercropped plant population. As a consequence, AG_Y and AG_N values were always close to or higher than 0 (Fig. 7a and b), except for AG_Y in N0 (Experiment II), while $SPlantAG_Y$ and $SPlantAG_N$ values (which consider the sowing proportion of the species based on sowing seeds) were always lower than 0 leading to apparent contradictory information between these two indices. In fact, this suggests that a pea seed grows more efficiently than a durum wheat seed compared with their respective sole crops. Moreover, AG and SPlantAG values were significantly affected by N fertilisation and values for N accumulated in shoots were higher than those for yield except for N180 in Experiment I. The choice between AG and SPlantAG depends on whether we take into account the whole population or a single seed which is also a key point when considering the LER (Willey and Osiru, 1972) or the relative yield total (De Wit, 1960; De Wit and Van den Berg, 1965). Nevertheless, as with AG, SPlantAG cannot determine whether a single seed of durum wheat or pea is dominant or dominated, or explain the dynamics of species.

Now, the choice between SPlantAG and APlantAG depends on whether the process of emergence is taken into account in the analysis which is also true for indices based on species proportion. The ability of the species to emerge is probably not a characteristic determined by interaction in seed germination in an intercrop, at least in our experiment. Indeed, here species were sown in alternate rows, i.e. not mixed within the same row, and no allelopathic effects are known for pea and durum wheat, particularly for a 14.5 cm row spacing. Whatever the experiment, APlantAG and SPlantAG were positively correlated and APlantAG values were always higher than the respective SPlantAG values for both yield and N accumulated (Fig. 8) because the percentage emergence of pea was higher than that of wheat (75% and 63%, respectively). The *X*-axis values at the origin were close for both experiments and the slope of the curve was close to 1 for Experiment I (0.98) and slightly lower than 1 for Experiment II (0.87). This result indicates that the two indices varied in the same manner and were here equally useful because the percentage emergence of species was not affected by N treatment because N fertiliser was not applied at sowing time but during crop growth.

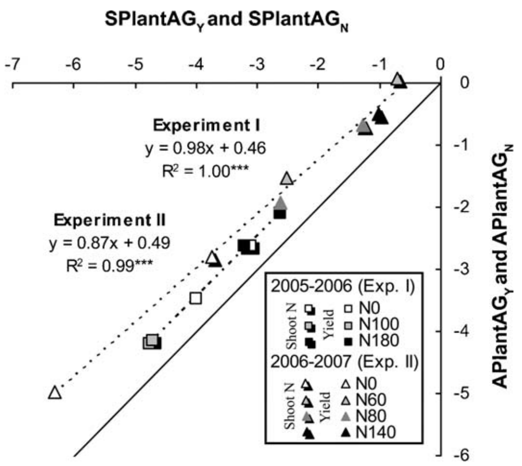

Fig. 8. Actual plant aggressivity for yield and shoot N accumulated as a function of the sowing plant aggressivity for yield and shoot N accumulated for the different N treatments (N*x* where '*x*' represents N applied in kg N ha^{-1}) of Experiments I and II for the durum wheat. Values are the mean (n = 3–5).

4. Conclusions

Intercrops are more suited to low N input systems due to a high level of complementary N use between the two species compared with conventional highly N-fertilised systems. This work showed that the choice of index is important in correctly understanding species interactions, competitiveness and intercrop efficiency compared with sole crops.

We demonstrated that the significance of AG, SPlantAG and APlantAG is unclear and cannot be analysed separately without simultaneous analysis of partial land equivalent ratios. Also, the choice within these indices depends on whether we want to consider the whole population, a single seed or a single plant. The commonly used LER index is a relevant and versatile indicator to quantify mixture productivity compared with the sole crops and is helpful in illustrating the pattern of competitive outcomes in intercropping experiments when plotting values in the LER space. However, intra and interspecific interactions (estimated by IA and IE indices) can only be relevantly analysed by comparing intercrops with sole crops sown at half-density and not directly with sole crops sown at normal density and allow description of species change in contribution index (CC). Finally, these indices based on the final performance (e.g. grain yield or N accumulated) can be considered as indicators of the final outcome of all competitive interactions between the two crops throughout the growth period and such indices are useful for comparing crop interactions and crop efficiency.

However, since the ability to exploit resource niches and thereby to capture available resources varies with developmental stages of the two species indices such as REIc and CGR may be helpful. To avoid misinterpretation in data analysis we suggest using CGR rather than REIc due to its clearer meaning and to its capacity to allow comparison of crop efficiency as regards the total biomass produced. We can also suggest that plotting IE as a function of IA (calculated from dry weight) at key development stages could be worthwhile in order to: (i) analyse interspecific and intraspecific interactions separately; (ii) evaluate dynamic interactions, (iii) identify possible facilitation behaviour, (iv) reveal when competition occurred during growth, (v) explain the consequences of interactions for a given species on yield components and (vi) determine key development stages involved in complementary or competitive interactions.

To conclude, some of the indices studied here can be useful and relevant to evaluate the efficiency of durum wheat intercropped with pea at different levels of N availability, provided that their equations are always defined and their meaning clearly explained. Finally, using appropriate indices could identify cereal and legume traits suited to intercropping and also appropriate cropping sequences and management techniques, e.g. sowing density of each specie and N fertilisation practices, allowing efficient intercropping.

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