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Effect and underlying mechanisms of pea-cereal intercropping on the epidemic development of ascochyta blight

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Abstract Field experiments were conducted in western France for two consecutive years to investigate the effect of pea-cereal intercropping on ascochyta blight, a major constraint of field pea production world-wide. Disease pressure was variable in the experiments. Intercropping had almost no effect on disease development on stipules regardless of disease pressure. In contrast, disease severity on pods and stems was substantially reduced in the pea-cereal intercrop compared to the pea monocrop when the epidemic was moderate to severe. Therefore, a pea-cereal intercrop could potentially limit direct yield loss and reduce the quantity of primary inoculum available for subsequent pea crops. Disease reduction was partially explained by a modification of the microclimate within the intercrop canopy, in particular, a reduction in leaf wetness duration during and after flowering. The effect of intercropping on splash dispersal of conidia was investigated under controlled conditions using a rainfall simulator. Total dispersal was reduced by 39 to 78% in pea-wheat canopies compared to pea canopies. These reductions were explained by a reduction in host plant density and a barrier or relay effect of the non-host plants.

Keywords Canopy architecture · Dispersal gradient · Leaf area index · *Mycosphaerella pinodes* · Rain splash

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Introduction

Ascochyta blight, mainly caused by *Mycosphaerella pinodes* (anamorph: *Ascochyta pinodes*), is a major constraint of field pea production world-wide (Bretag and Ramsey 2001). Provided that weather conditions are conducive to the infection process, disease onset can appear as early as two weeks after emergence, even under extremely low primary inoculum pressure (Schoeny et al. 2007). The disease infects all aerial organs of the plant (leaves, stems, flowers, pods) and can cause significant yield loss (Lawyer 1984; Tivoli et al. 1996). Although ascochyta blight resistance is a research priority in many pea breeding programmes around the world, there are no commercial cultivars with complete or even partial resistance yet available. Therefore, other integrated disease management practices have to be considered to improve disease control. Agronomic practices such as burial of infected stubble, crop isolation from past season's infected stubble, adoption of a suitable crop rotation

or delayed sowing are possible options to reduce primary inoculum, whereas foliar fungicides may be used to limit subsequent disease development (Davidson and Kimber 2007). Using plant and canopy architectural features also appears to be a possible means to slow disease development by modifying pathogen movement within the canopy and/or microclimate (Tivoli and Banniza 2007). Under field conditions, Le May et al. (2009) showed that spring pea cultivars with different architectural features (stem height, branching ability, standing ability) but similar levels of susceptibility to ascochyta blight displayed differences in disease progress on leaves. Under controlled conditions, Schoeny et al. (2008) demonstrated that the leaf area index of a pea canopy could influence the splash dispersal of *M. pinodes* conidia.

Intercropping, also called multiple cropping, is the agricultural practice of cultivating two or more crops in the same space at the same time (Andrews and Kassam 1976). The practice is long-established and still predominates in many tropical and sub-tropical regions. In temperate regions, it is far less widespread and often restricted to low-input farming systems such as organic production. Intercropping is considered a practical application of basic ecological principles such as diversity, competition and facilitation (Hauggaard-Nielsen et al. 2008). Provided that intercrop components display differences in competitive ability for growth factors such as light, water and nutrients, available environmental resources are utilised more efficiently, resulting in yield improvement and increased yield stability compared to monocropping. Grain legume-cereal intercrops perfectly illustrate this complementary use of resources, in particular nitrogen sources. Indeed, leguminous species use atmospheric N_2, whereas non-leguminous species use soil inorganic N. Intercropping may also be efficient in preventing nitrogen leaching (Whitmore and Schröder 2007), reducing weed population density and biomass production (Liebman and Dyck 1993) and controlling pests and diseases (Perrin 1977; Sumner et al. 1981; Trenbath 1993).

Although pea-cereal intercrops have been extensively investigated in terms of fertility, grain quality and yield (Andersen et al. 2004; Carr et al. 1998; Gooding et al. 2007; Hauggaard-Nielsen et al. 2006; Jensen 1996), very few studies have focused on their effects on pests and diseases (Fernandez-Aparicio et al. 2007; Hauggaard-Nielsen et al. 2008). In particular, the relevance of pea-cereal intercropping in the management of ascochyta blight needs to be confirmed and the underlying mechanisms understood. A pea-cereal intercrop and a pea monocrop have drastically different canopy architectures. Does the presence of the cereal plants within the canopy modify the epidemic development of ascochyta blight? Does the magnitude of the effect depend on disease pressure and the nature of the organ assessed? Are microclimate and spore dispersion modified by differences in canopy architecture? To respond to these questions, field trials and experiments under controlled conditions were conducted with the aim of evaluating the effect of pea-cereal intercropping on (i) ascochyta blight development, (ii) canopy microclimate, and (iii) splash dispersal of conidia within the canopy.

Materials and methods

Field experiments

Experimental design and treatments Field experiments were conducted at Le Rheu (48°06′00″ N, 1° 48′00″ W, 30 m above mean sea level), western France. Two experiments involving spring crops were carried out in 2005: PI05 was artificially inoculated and irrigated to favour disease development, and LR05 was conducted under natural ascochyta blight infection. A third experiment involving winter crops (LR06) was conducted under natural ascochyta infection during the 2005–2006 cropping season. Two experimental treatments were compared: pea monocrop and pea-cereal intercrop with pea and cereal seeds sown in alternating rows in a 50:50 ratio (i.e. each species was sown at half the density of the pure stand). Spring pea (cv. Baccara, semi-leafless) and spring barley (cv. Scarlett) were used in PI05 and LR05. Winter pea (cv. Cheyenne, semi-leafless) and winter wheat (cv. Apache) were used in LR06. The target pea plant density was 80–90 plants m^{-2} in the monocrop and 40–45 plants m^{-2} in the intercrop. The target cereal plant density in the intercrop was 125–150 plants m^{-2} for spring barley and 150–175 plants m^{-2} for winter wheat. Experiments were sown on 9 March 2005 (PI05), 10 March 2005 (LR05) and 24 October 2005 (LR06). Experimental treatments were arranged in a randomised complete block design with four replicates. Plots (30 m^2) consisted of five strips (1.2 m wide ×

5 m long) seeded with a six-row drill at 18 cm row spacing.

Inoculation technique Artificial inoculation was achieved using barley grain colonised by a mixture of *M. pinodes* isolates as in Tivoli et al. (1996). Plastic bags containing 250 ml of grain moistened with 200 ml distilled water were autoclaved twice at 120°C for 1 h at a 24 h interval. The fungus was cultured on V8 juice agar for 10–12 days at 20°C with a 12 h photoperiod of white light (wavelength: 350 to 750 nm). Four fungal plugs (1 cm^2) were placed in each bag and incubated at room temperature (20±2°C) under natural light for 4–5 weeks. Bags were gently shaken at least twice a week to achieve a homogenous colonisation of the grain. Plots were inoculated by broadcasting two bags of infected grain per plot, approximately 6 weeks after sowing (18 April 2005, 3-leaf pea stage). A sprinkler irrigation system was operated (total 20 mm water) to promote disease development.

Disease assessments Plants were sampled at several dates during the cropping season (Table 1). At each sampling date, one sample (50 cm×3 rows) was removed per plot, leaving at least 50 cm between two consecutive samples. Ten pea plants were then randomly chosen per sample. Ascochyta blight was assessed on main stems or on branches if the main stems had aborted. For stipules and pods, disease severity was scored at each node using a 0–6 scale adapted from the 0–5 scale previously described by Roger and Tivoli (1996): 0 = no symptoms, 1 = few flecks, 2 = numerous flecks, 3 = coalescing necrotic lesions covering <25% of the organ area, 4 = 25–50% of the organ area necrotic, 5 = 50–75% of the organ area necrotic, 6 = >75% of the organ area necrotic. The mean disease score per plant was calculated by averaging the disease scores of the different nodes. For stems, disease severity was assessed by the percentage of stem length girdled by lesions.

Meso- and microclimate monitoring An automatic weather station was installed shortly after sowing in the field trials conducted under natural ascochyta infection (LR05 and LR06). Mesoclimatic sensors were fixed to a vertical mast at 1.40–2.20 m above ground level. Air temperature and relative humidity (RH) were measured with a temperature and humidity probe (HMP45AC, Vaisala, www.vaisala.com), pre-

Table 1 Sampling dates, climatic variables and pea growth stages of three field experiments (PI05, LR05, LR06) conducted at Le Rheu (France) in 2005 and 2006

Growth stage[a]	PI05			LR05			LR06		
	Date	DD[b]	R[c]	Date	DD	R	Date	DD	R
Sowing	09/03/05	0	0	10/03/05	0	0	24/10/05	0	0
Emergence	28/03/05	187	0	28/03/05	182	0	12/11/05	268	66
3-leaf	–	–	–	–	–	–	06/12/05	400	141
4-leaf	–	–	–	–	–	–	03/01/06	512	166
6-leaf	–	–	–	–	–	–	06/02/06	640	183
7-leaf	02/05/05	549	51	02/05/05	544	51	03/03/06	755	240
10-leaf	16/05/05	715	68	16/05/05	710	68	03/04/06	1,003	317
BF	23/05/05	803	77	23/05/05	797	77	04/05/06	1,332	354
BSF	10/06/05	1,082	102	10/06/05	1,077	102	30/05/06	1,718	384
ESF	–	–	–	–	–	–	06/06/06	1,813	384
BPM	30/06/05	1,476	134	01/07/05	1,488	122	29/06/06	2,251	388

Stipules were assessed at all sampling dates except at BPM when pods and stems were assessed

[a] *BF* beginning of flowering, *BSF* beginning of seed filling, *ESF* end of seed filling, *BPM* beginning of physiological maturity

[b] *DD* degree-days since sowing (basis 0°C)

[c] *R* cumulative rainfall since sowing (in mm)

cipitation was measured with a tipping bucket rain gauge (ARG100, Campbell Scientific Inc., www.campbellsci.com), and wind speed and direction were measured with a wind monitor (model 05103, RM Young, www.youngusa.com). Microclimate was monitored between the 7-leaf pea stage and canopy lodging (5 May–19 June 2005 and 16 March–21 May 2006) in two adjacent plots corresponding to the two experimental treatments. Air temperature was measured with home-made thermocouples and leaf wetness was measured with flat, printed-circuit sensors (model 237, Campbell Scientific Inc.) deployed horizontally. Sensors were placed at three canopy positions: (1) at the base, (2) at mid-height, and (3) at 10 cm above. Two to three sensors of each type were used at each position and in each experimental treatment. Sensors located at mid-height within the canopy and above the canopy were raised periodically as plants grew. Leaf wetness sensors were cleaned weekly with denaturated alcohol. A data logger (CR10X, Campbell Scientific Inc.) scanned the sensors every 10 s and recorded the data as 15-min averages.

Meso- and microclimate data treatment Daily rainfall and daily mean, minimum and maximum air temperatures were calculated for each experiment. They were compared to the long-term data series (1984–2004) collected by the INRA permanent automatic weather station located at a distance of approximately 300 m from the experiments. The treatment of microclimate data differed according to the sensor type. At each 15-min interval, the temperature of the two to three corresponding sensors was averaged and these data used to calculate daily mean, minimum and maximum temperatures per canopy position and experimental treatment. Leaf wetness duration was first calculated per sensor by summing the 15-min data and then daily mean, minimum and maximum leaf wetness durations were calculated per canopy position and experimental treatment by averaging the data of the corresponding sensors.

Experiments in controlled conditions

Plant production Pea (cv. Cheyenne) and wheat (cv. Caphorn) plants were produced in pots (9×9×9.5 cm) containing a non-sterilised sand/peat/soil (1:1:1) mixture. Potted plants were grown for 4, 5 or 6 weeks in a growth chamber with a 12 h photoperiod (photosynthetically active radiation (PAR): 475 µmol m^{-2} s^{-1}), temperature of 15±1°C (night and day), and RH of 80±5% (day), 92±5% (night). Plants were watered weekly to field capacity. From the fifth week of culture, wheat plants were irrigated weekly with 30 ml of Hoagland's complete nutrient solution (Hoagland and Arnon 1938) to avoid nutrient deficiencies. Pea lateral branches were removed to increase homogeneity of plants.

Inoculum preparation A single-spore isolate of *M. pinodes* (*Mp* 91.31.12) was used. A conidial suspension was prepared by culturing the fungus on V8 juice agar for 9–10 days at 20°C with a 12 h photoperiod of white light (wavelength: 350 to 750 nm), flooding the culture with distilled water, gently scraping the agar surface and filtering through four layers of muslin to remove mycelium and agar fragments. The concentration of the conidial suspension was determined with a Malassez cell under an optical microscope (Leitz Dialux 20, magnification ×125) and adjusted with sterile distilled water to 10^6 conidia ml^{-1}. Tween 20 was added to the conidial suspension as a wetting agent (one drop per 250 ml).

Rain simulator The Deltalab Microprocessor Controlled Spray System, EID 330, manufactured under Orstom licence (Asseline and Valentin 1978) was used in all experiments to simulate rain events in still air. As previously described by Schoeny et al. (2008), rainfall was generated by an oscillating nozzle (Deltalab, Tec Jet SS 6560) positioned at a height of 3.8 m in a closed shed. Displacement was at constant speed with a sweep angle of 180°, providing a rainfall intensity of 40 mm h^{-1}. For each experiment, the system was operated for 3 min to simulate a 2 mm rain event. Splash dispersal was investigated on plants within the centre m^2 area, where intensity and drop diameter distribution of the simulated rain were most homogenous.

Experimental design Experiments were designed to investigate the effect of intercropping on the splash dispersal of *M. pinodes* conidia. Pea and pea-wheat canopies (1 m^2) were constituted by potted plants at two growth stages (5–7 or 8–10 nodes per plant for the pea) and placed in two grid configurations (9×9 or 11×11 quadrats m^{-2}) (Fig. 1). The central plant was replaced by an empty pot supporting a Petri dish containing 40 ml of conidial suspension (10^6 conidia ml^{-1}). For each

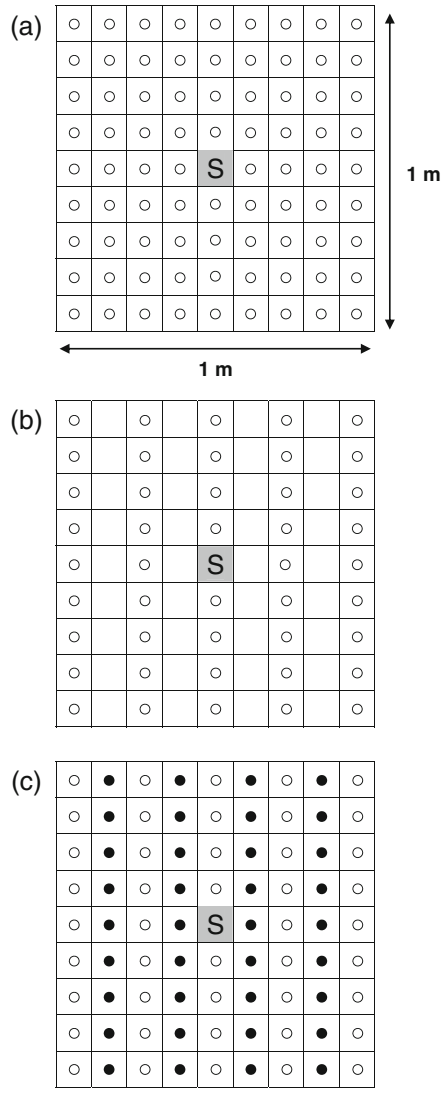

Fig. 1 Schematic layout of treatments used to investigate the effect of pea-wheat intercropping on the splash dispersal of *Mycosphaerella pinodes* conidia in controlled conditions (grid configuration 9×9 quadrats m^{-2}). Potted pea (○) and wheat (●) plants were placed around a central conidial suspension (S) and subjected to 2 mm simulated rainfall. Three canopies were compared: **a** full density pea monocrop; **b** reduced density pea monocrop; **c** pea-wheat row intercrop

growth stage x grid treatment, the splash dispersal of *M. pinodes* conidia was investigated in a series of three canopies: a full density pea monocrop, a reduced density pea monocrop and a pea-wheat row intercrop. The reduced density pea monocrop corresponded to the intercrop design without the wheat rows. The combination of the three canopies allowed discrimination between the two potential effects of the intercrop: (i) the 'density reduction' or 'dilution' effect resulting in an increased distance between the inoculum source and the target pea plants and, (ii) the 'barrier/relay' effect of the wheat plants. Each series was repeated three times. Pea canopies were characterised by their leaf area index (LAI). LAI (dimensionless) is the ratio of the total leaf area of the canopy (m^2) divided by the area of ground covered by the canopy (m^2). The total leaf area of each canopy was calculated by multiplying the number of plants constituting the canopy by the number of leaves per plant and the mean leaf area (7.48 cm^2) (Schoeny et al. 2008).

Post-splash incubation conditions and disease assessment After rainfall simulation, pea plants were incubated in a dew chamber (12 h photoperiod, 21± 1°C night/day, 100% RH) for five days. The number of lesions was counted on those stipules that had been present on the day of the splash experiment. Under similar experimental conditions, Schoeny et al. (2008) showed that the age of the stipules (i.e. their position along the stem) did not bias lesion counts. Therefore, lesions counted five days after incubation derived solely from splash dispersal and not from an interaction between splash dispersal and tissue susceptibility.

Statistical analyses

All statistical analyses were done with the Statistical Analysis System software (SAS Institute Inc., Cary, NC). Analyses of variance (ANOVAs) were performed using the GLM procedure to test the effect of intercropping on the development of ascochyta blight on different pea organs (stipules, pods and stems) under field conditions. Data distributions were examined with the UNIVARIATE procedure. In particular, the Shapiro-Wilk W statistic was used to test the assumption of normality. Levene's test was used to confirm homoscedasticity (homogeneity of variances). Means were compared by Fisher's least significant difference test.

Splash dispersal gradients achieved in controlled conditions were described by the negative exponential model:

$$y = a \exp^{-bx}$$

where y is the mean number of lesions per plant, x is the distance from inoculum source (in cm), and a and b are the parameters of the model. Parameter a is the value of y at x=0 (i.e. the source). Parameter b characterises the slope of the gradient (in cm^{-1}). Parameters a and b were estimated by nonlinear regression using the NLIN procedure. As results obtained with this empirical model should not be extrapolated outside the observed range (Fitt et al. 1987), no emphasis was put on parameter a. The coefficient of determination R^2 was used to estimate the goodness of fit of each model. R^2 was computed with the following equation:

$$R^2 = 1 - \frac{\text{Residual sum of squares}}{\text{Corrected total sum of squares}}$$

The fitting was performed for each experiment (primary dispersal gradients) and for each experimental treatment whenever possible (mean dispersal gradients). The relationship between the slope estimate of the primary dispersal gradient and the LAI of the pea canopy was investigated by linear regression analysis using the REG procedure.

Results

Ascochyta blight epidemics in pea monocrops

In the two experiments involving spring crops sown in early March (LR05 and PI05), the first symptoms were observed in late April, approximately one month after emergence. In LR05, mean disease score on stipules remained extremely low until the beginning of flowering (Table 2; SC treatment). It increased slightly after this growth stage to reach a mean level of 1.4 at the beginning of seed filling. In PI05, artificial inoculation induced rapid disease development in May and the mean disease score was 3.0 at the beginning of flowering and 3.5 at the beginning of seed filling. In the experiment involving winter crops sown in late October (LR06), disease onset occurred in early December, approximately three weeks after emergence. Disease progress was gradual during winter but was particularly intense in March due to unusually high rainfall (81 mm, whereas the third quartile of the 1984–2004 period was 62 mm). Mean disease score reached 4.0 at the beginning of flowering and 4.7 during seed filling.

The three epidemics were classified as slight (LR05), moderate (PI05) and severe (LR06) on the

Table 2 Mean disease score (0–6) on stipules in pea monocrop (MC) and pea-cereal intercrop (IC) in field experiments conducted at Le Rheu (France) in 2005 and 2006

Trial (epidemic pressure)	Treatment	Pea growth stage[a]							
		3-leaf	4-leaf	6-leaf	7-leaf	10-leaf	BF	BSF	ESF
PI05 (moderate)	MC	–	–	–	1.56 a	2.86 a	2.99 a	3.54 a	–
					(0.19)	(0.15)	(0.11)	(0.14)	
	IC	–	–	–	1.58 a	2.88 a	3.04 a	3.86 a	–
					(0.18)	(0.19)	(0.13)	(0.17)	
LR05 (slight)	MC	–	–	–	0.36 a	0.35 b	0.36 a	1.41 a	–
					(0.10)	(0.10)	(0.10)	(0.12)	
	IC	–	–	–	0.45 a	0.65 a	0.56 a	1.24 b	–
					(0.12)	(0.10)	(0.13)	(0.10)	
LR06 (severe)	MC	0.17 a	0.49 a	0.86 a	1.23 a	2.75 a	3.99 a	4.74 a	4.73 a
		(0.04)	(0.04)	(0.11)	(0.07)	(0.26)	(0.03)	(0.06)	(0.06)
	IC	0.25 a	0.52 a	0.61 b	0.89 b	2.26 a	4.00 a	4.51 a	4.59 a
		(0.06)	(0.01)	(0.06)	(0.08)	(0.28)	(0.07)	(0.15)	(0.05)

Standard errors of the mean are in brackets. Means within trial and stage followed by the same letters are not significantly different at P=0.05

[a] *BF* beginning of flowering, *BSF* beginning of seed filling, *ESF* end of seed filling

basis of the disease score at the beginning of flowering, a key stage in the yield component formation (Garry et al. 1998b). This range of disease variability provided good experimental conditions to investigate the effect of intercropping on ascochyta blight development.

Effect of intercropping on ascochyta blight development

The intercropping effect differed according to the plant organ assessed and the severity of the epidemic. When the epidemic was slight to moderate (LR05 and PI05), intercropping had nearly no effect on disease progress on stipules (Table 2). When the epidemic was severe (LR06), a slight reduction of disease was observed on stipules at the 6–7 leaf stage but disappeared thereafter.

Mean disease scores on pods at the beginning of physiological maturity ranged from 0.9 to 4.1 (Table 3). Intercropping had no significant effect on disease score on pods when the epidemic was slight. In contrast, when the epidemic was moderate to severe, disease score on pods was reduced on average by 19–50% in the intercrop compared to the pea monocrop, although these reductions were not always statistically significant. Disease score on pods at the first fructiferous node was 32% less in the intercrop than in the pea monocrop in PI05 and 43% less in LR06. When disease pressure was slight, the disease profile on pods showed a rapid decrease along the stem between the first fructiferous node and the next (Fig. 2). Under more intense disease pressure, the reduction in symptoms was not as rapid, as demonstrated by the steeper regression slopes.

The percentage of stem height girdled at the beginning of physiological maturity ranged from 5.9 to 21.2% (Table 4). Intercropping had no significant effect on ascochyta blight development when the epidemic was slight (LR05), whereas significant and substantial reductions of 32% and 49% were observed in the moderate (PI05) and severe (LR06) epidemics, respectively.

Effect of intercropping on microclimate

Differences between the air temperature within the canopy (base or mid-height) and the air temperature

Table 3 Mean disease score (0–6) on pods at the beginning of physiological maturity in pea monocrop (MC) and pea-cereal intercrop (IC) in field experiments conducted at Le Rheu (France) in 2005 and 2006

Trial	Treatment	Rank of first fructiferous node	Mean number of fructiferous nodes	Fructiferous node						
				1	2	3	4	5	6	7
PI05	MC	12.0 a	6.8 a	4.1 a	3.4 a	3.0 a	2.8 a	2.2	2.0	1.7
		(0.5)	(0.4)	(0.4)	(0.5)	(0.4)	(0.4)	(0.5)	(0.5)	(0.5)
	IC	12.3 a	3.6 b	2.8 b	2.6 a	2.2 b	1.7 b	–	–	–
		(0.5)	(0.5)	(0.4)	(0.4)	(0.5)	(0.5)			
	P=	*>0.10*	*0.0001*	*0.029*	*>0.10*	*0.027*	*0.004*	–	–	–
LR05	MC	11.4 a	6.1 a	3.9 a	3.4 a	2.7 a	2.2 a	1.4 a	1.4	–
		(0.4)	(0.6)	(0.6)	(0.6)	(0.6)	(0.6)	(0.5)	(0.5)	
	IC	11.2 a	4.9 b	3.7 a	3.3 a	2.9 a	2.0 a	1.3 a	–	–
		(0.4)	(0.6)	(0.3)	(0.6)	(0.5)	(0.6)	(0.5)		
	P=	*>0.10*	*0.058*	*>0.10*	*>0.10*	*>0.10*	*>0.10*	*>0.10*	–	–
LR06	MC	17.9 a	7.1 a	3.0 a	2.5 a	2.3 a	1.6 a	1.8 a	1.4	1.3
		(0.2)	(0.5)	(0.2)	(0.3)	(0.2)	(0.3)	(0.2)	(0.1)	(0.2)
	IC	16.4 b	5.0 b	1.7 b	1.5 a	1.4 a	1.3 a	0.9 b	–	–
		(0.1)	(0.3)	(0.2)	(0.3)	(0.3)	(0.1)	(0.1)		
	P=	*0.010*	*0.074*	*0.035*	*>0.10*	*>0.10*	*>0.10*	*0.078*	–	–

Standard errors of the mean are in brackets. Means within trial and node followed by different letters are significantly different at the given *P* value

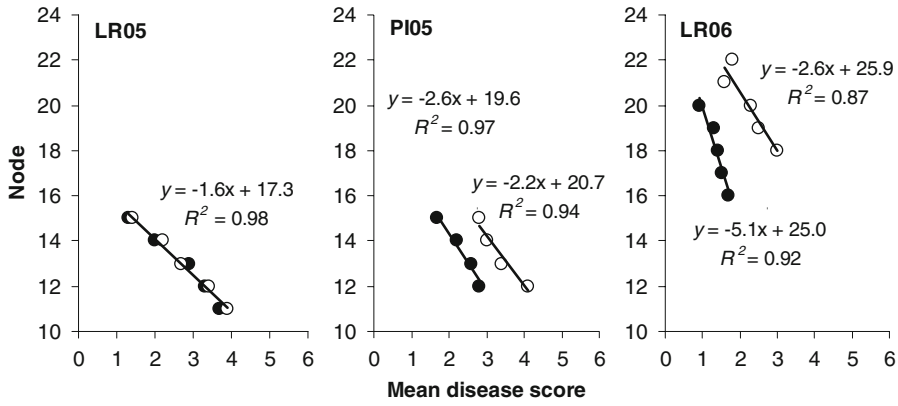

Fig. 2 Mean disease score on pods at the beginning of physiological maturity in pea monocrop (○) and pea-cereal intercrop (●) in field experiments conducted at Le Rheu (France) in 2005 and 2006

above the canopy were sorted according to the air temperature above the canopy. For temperatures <14°C, the absolute temperature difference generally was <0.5°C suggesting a limited modification of the air temperature by the pea canopy (data not shown). In contrast, for above-canopy temperatures >14°C, temperature differences up to 2.2°C were observed, suggesting a slight cooling effect by the pea canopy. In addition, temperatures within the canopy were cooler at the base than at mid-height. This cooling effect was less marked in the intercrop canopy (data not shown). As a consequence, the temperature at the base of the intercrop canopy was frequently higher than the temperature at the base of the pea monocrop canopy, particularly from the beginning of the flowering (data not shown). Nevertheless, differences remained low and did not exceed 1.7°C in LR05 and 0.7°C in LR06.

With regard to leaf wetness duration, a drastic change occurred at the beginning of pea flowering. Before this stage leaf wetness duration was usually longer within the intercrop than within the pea monocrop (Fig. 3). However, after this stage, the trend was reversed and leaf wetness duration was usually shorter within the intercrop than within the pea monocrop.

Table 4 Mean percentage of stem height girdled by lesions at the beginning of physiological maturity in pea monocrop (MC) and pea-cereal intercrop (IC) in field experiments conducted at Le Rheu (France) in 2005 and 2006

Trial	Treatment	% stem height girdled
PI05	MC	13.1 (2.9) a
	IC	8.9 (1.2) b
	P=	*0.062*
LR05	MC	5.9 (0.8) a
	IC	6.2 (1.1) a
	P=	*>0.10*
LR06	MC	21.2 (0.8) a
	IC	10.8 (0.5) b
	P=	*0.012*

Standard errors of the mean are in brackets. Means followed by different letters are significantly different at the given *P* value

Effect of intercropping on splash dispersal of conidia

Splash dispersal was assessed indirectly through the number of conidia that had successfully germinated and induced lesions. Splash dispersal occurred in all experiments but its magnitude was highly variable. The number of lesions counted per plant generally decreased with increasing distance from the source. In 28 out of 36 experiments (78%), primary dispersal gradients were satisfactorily described by a negative exponential model explaining >91% of the variance (Table 5). For the other experiments (all of them involving a pea monocrop canopy at reduced density or a pea-wheat canopy), the model failed to fit the data, probably because of a poor overall splash dispersal. Indeed, splash dispersal was drastically reduced in both the pea monocrop at reduced density and the intercrop compared to the pea monocrop at full density. Mean dispersal gradients were fitted for the pea monocrop canopies at 81 and 121 plants m^{-2} (Fig. 4). The fitted models accounted for 71 to 88% of the variance. For a given growth stage, the slope was steeper at 121 than at 81 plants m^{-2}. For a given density, the slope was steeper for plants at the 5–7-

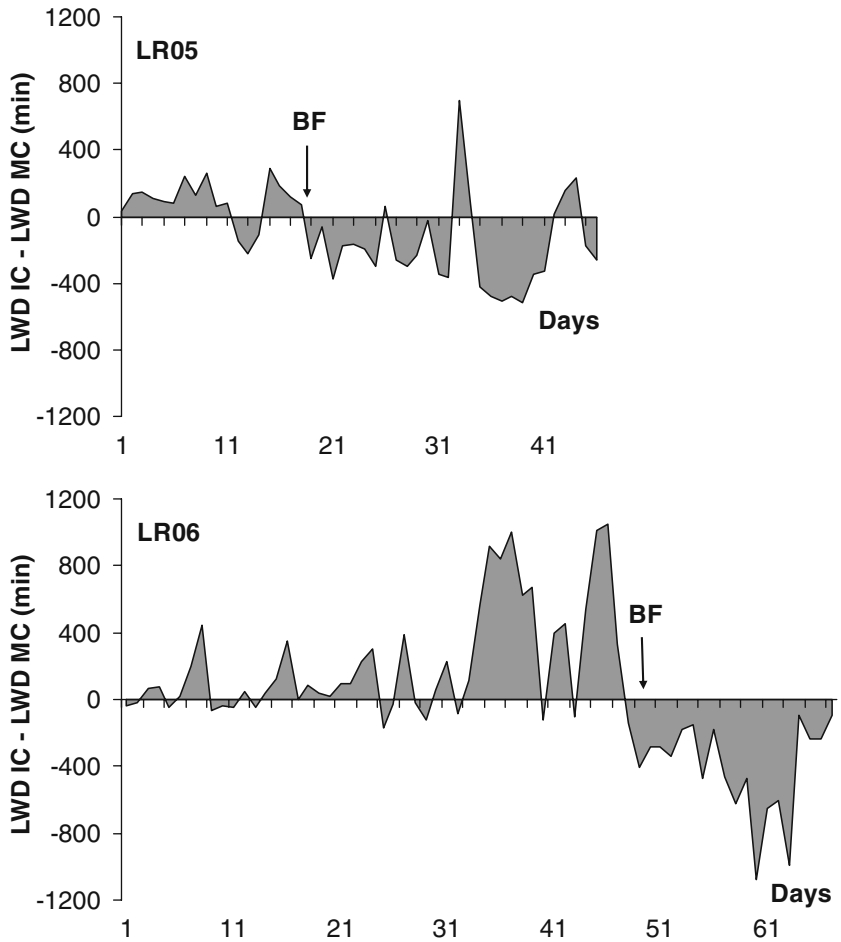

Fig. 3 Difference in mean leaf wetness duration (LWD) between a pea-cereal intercrop (IC) and a pea monocrop (MC) over time. Leaf wetness was monitored at the base of the canopies between the 7-leaf pea stage and canopy lodging (5 May–19 June in LR05 and 16 March–21 May in LR06). BF indicates the beginning of flowering. A value of 1,440 min signifies a full day of leaf wetness

leaf stage than at the 8–10-leaf stage. This trend was confirmed when plotting the slope estimates of primary dispersal gradients as a function of the LAI of the corresponding pea monocrop canopies (Fig. 5). For pea monocrop canopies at 81 and 121 plants m^{-2}, the slope estimate decreased linearly with increasing LAI. At these densities, LAI explained 68 to 70% of the variability of the slope estimate. At lower densities, there was no relationship between the slope estimate and LAI.

Due to the difficulty in comparing the three canopy types on the sole basis of their dispersal gradients, the total dispersal, i.e. the total number of lesions counted m^{-2}, was considered (Table 6). Compared to the pea monocrop at full density, total dispersal was reduced by 39 to 78% in the intercrop. These reduction percentages represent the global effect of intercropping on dispersal (hereafter referred to as 'intercropping effect'). In the same manner, the reduction percentages of total dispersal in the pea monocrop canopy at reduced density compared to that achieved in the monocrop canopy at full density represent the effect of density reduction on dispersal (hereafter referred to as 'dilution effect'). Comparisons between these two effects allowed us to characterise the nature of the underlying mechanisms involved. An intercropping effect higher than a dilution effect means that non-host plants reinforced the dilution effect by playing a role of physical barrier to splash dispersal of conidia (data in bold). In contrast, an intercropping effect lower than a dilution effect means that non-host plants partially compensated for the dilution effect by playing a role of relay for successive splashes. In our experimental conditions, the intercrop displayed a

Table 5 Slope estimates of primary dispersal gradients of *M. pinodes* conidia in three types of canopies (pea monocrop at full density, pea monocrop at reduced density and pea-wheat intercrop)

Treatment/Repetition	Full density pea monocrop		Reduced density pea monocrop		Pea-wheat intercrop	
	Slope (cm^{-1})[a]	R^2	Slope (cm^{-1})	R^2	Slope (cm^{-1})	R^2
S5–7 G81						
1	0.21 (0.01)[b]	0.99	0.13 (0.02)	0.91	0.17 (0.03)	0.96
2	0.39 (0.02)	0.99	…[c]		…	
3	0.27 (0.02)	0.99	0.21 (0.02)	0.99	0.24 (0.01)	0.99
S5–7 G121						
1	0.46 (0.03)	0.99	0.19 (0.04)	0.92	0.19 (0.02)	0.98
2	0.26 (0.04)	0.95	0.19 (0.01)	0.99	0.18 (0.03)	0.93
3	0.26 (0.02)	0.98	0.27 (0.01)	0.99	0.13 (0.02)	0.94
S8–10 G81						
1	0.20 (0.02)	0.96	…		0.16 (0.02)	0.98
2	0.12 (0.02)	0.92	0.21 (0.03)	0.98	0.17 (0.01)	0.99
3	0.16 (0.02)	0.97	…		0.15 (0.03)	0.94
S8–10 G121						
1	0.26 (0.02)	0.99	0.24 (0.02)	0.99	…	
2	0.16 (0.01)	0.99	…		0.14 (0.02)	0.93
3	0.30 (0.03)	0.98	…		…	

Canopies were constituted by potted plants at two growth stages (5–7 or 8–10 nodes per plant for the pea) and placed in two grid configurations (9×9 or 11×11 quadrats m^{-2}).

[a] Slope (parameter b) was estimated by fitting the equation $y = ae^{-bx}$ in which y is the mean number of lesions per plant and x is the distance from inoculum source (in cm) to experimental data

[b] Standard errors of the means are given in brackets

[c] No satisfactory fitting was obtained

barrier role in 7 out of 12 cases (mainly for plants at the 5–7-leaf stage) and a relay role in 5 cases (mainly for plants at the 8–10-leaf stage).

Discussion

The experimental methodology of this study permitted us to investigate the effect of pea-cereal intercropping on the epidemic development of ascochyta blight under various disease pressures. The choice of the disease assessment method appeared to be central to the evaluation. Indeed, the efficiency of intercropping to control the disease depended on the pea organ assessed. Intercropping had almost no effect on disease development on stipules regardless of disease pressure. In contrast, disease severity on pods and stems was substantially lower in the pea-cereal intercrop compared to the pea monocrop under moderate and severe epidemics. Part of this differential response might be explained by the time-lag between the two methods of disease assessment: stipules being assessed before or during flowering (after this stage, physiological senescence biases disease assessment of the lowest nodes), whereas pods and stems were assessed later, at the beginning of physiological maturity. Ascochyta blight affects yield either indirectly through reduction of photosynthetic leaf area and the photosynthetic efficiency of the remaining green leaf area (Garry et al. 1998a), leading to a reduced biomass production (Béasse et al. 2000; Le May et al. 2005), or directly through pod infection (Béasse et al. 1999). Consequently, although intercropping had almost no effect on disease development on stipules, which represent the main photosynthetic organs of the compound leaf in semi-leafless pea cultivars, it may limit direct yield loss by limiting disease development on pods. On the other hand, the reduced level of disease observed on stems in the pea-cereal intercrop compared to the pea monocrop

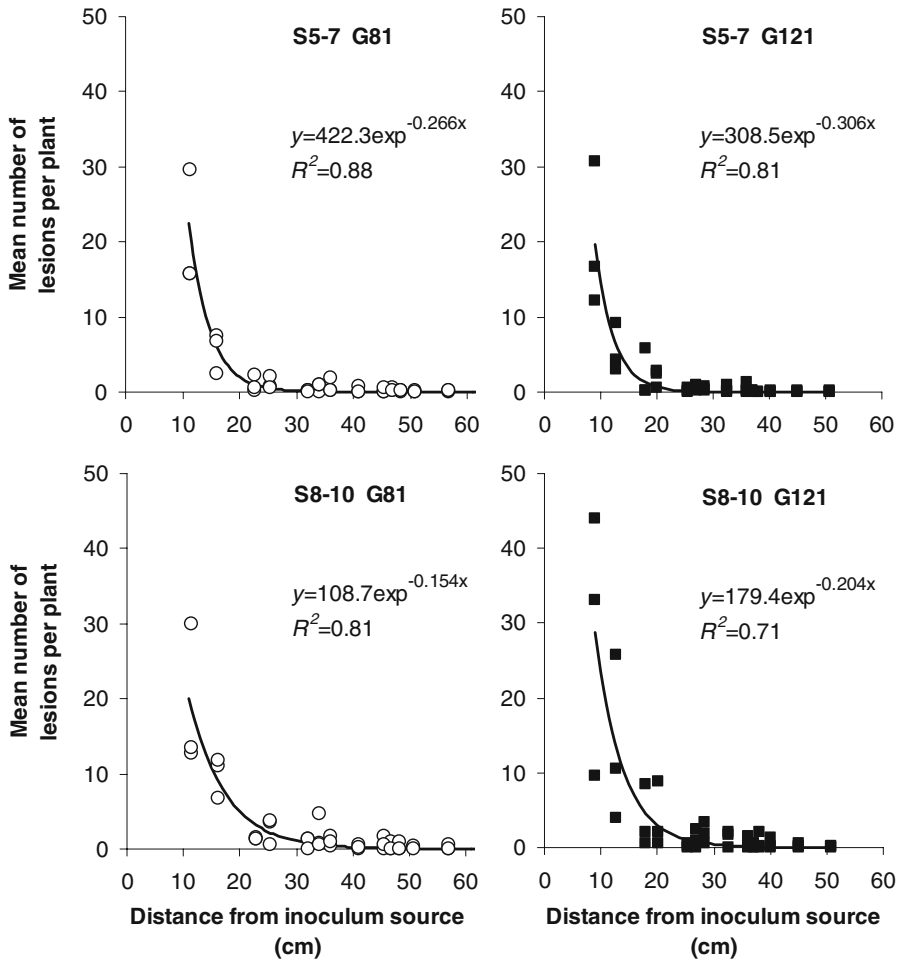

Fig. 4 Mean dispersal gradients of *M. pinodes* conidia in canopies composed of potted pea plants at two growth stages S (5–7 and 8–10 nodes) and placed according two grid organisations G (9×9 or 11×11 quadrats m^{-2}). Symbols are observed means for each replicate. Lines are fitted curves

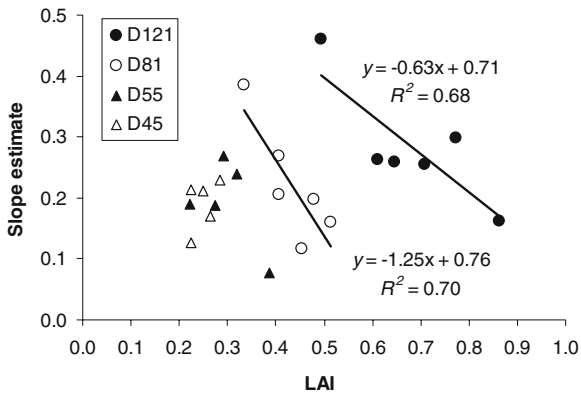

Fig. 5 Relationships between the slope estimate of the dispersal gradients of *M. pinodes* conidia and the leaf area index (LAI) of pea canopies at four plant densities (45, 55, 81 and 121 plants m^{-2}). LAI (dimensionless) is the ratio of the total leaf area of the canopy (m^2) divided by the area of ground covered by the canopy (m^2)

probably had no impact on yield but is likely to play an important role in subsequent epidemics. Indeed, infected pea stubble constitutes a major source of primary inoculum for subsequent pea crops. When left at the soil surface after harvest, stubble releases ascospores that can be wind-dispersed to neighbouring fields up to a distance of 1.6 km (Lawyer 1984). When buried, stubble induces the formation of survival structures such as chlamydospores (Dickinson and Sheridan 1968) that can survive in the soil for many years (Wallen et al. 1967) and infect the next pea crop in the rotation. Thus, by reducing stem damage, intercropping also reduces the risk of inoculum build-up and disease recurrence.

Microclimate monitoring revealed consistent trends among years. Under the experimental conditions of this study, the pea canopy provided a slight cooling effect when above-canopy air temperatures >14°C. This cooling effect was more marked at the base of

Table 6 Total number of ascochyta blight lesions counted on pea plants after splash dispersal in three types of canopies (pea monocrop at full density, pea monocrop at reduced density and pea-wheat intercrop)

Treatment	Canopy type	Rep1		Rep2		Rep3	
S5–7 G81	Full density pea monocrop [81]	107		84		206	
	Reduced density pea monocrop [45]	35	**(−67%)**	50	**(−40%)**	133	**(−35%)**
	Pea-wheat intercrop [45]	27	**(−75%)**	24	**(−71%)**	84	**(−59%)**
S5–7 G121	Full density pea monocrop [121]	91		101		228	
	Reduced density pea monocrop [55]	20	(−78%)	64	**(−37%)**	153	**(−33%)**
	Pea-wheat intercrop [55]	23	(−75%)	39	**(−61%)**	128	**(−44%)**
S8–10 G81	Full density pea monocrop [81]	262		150		107	
	Reduced density pea monocrop [45]	74	(−72%)	66	**(−56%)**	15	(−86%)
	Pea-wheat intercrop [45]	144	(−45%)	38	**(−75%)**	31	(−71%)
S8–10 G121	Full density pea monocrop [121]	70		453		261	
	Reduced density pea monocrop [55]	40	(−43%)	157	(−65%)	90	**(−66%)**
	Pea-wheat intercrop [55]	43	(−39%)	195	(−57%)	58	**(−78%)**

Canopies were constituted by potted plants at two growth stages (5–7 or 8–10 nodes per plant for the pea) and placed in two grid configurations (9×9 or 11×11 quadrats m^{-2}). The actual number of pea plants present in each canopy type is given in square brackets. For each growth stage × grid treatment, the three canopies were splashed the same day and could therefore be compared. Reduction percentages are given in brackets. Percentages in bold indicate the cases where the barrier effect induced by the wheat plants reinforced the dilution effect induced by the reduction in pea density

the canopy than at mid-height. The air temperature gradient within the canopy was larger in the pea monocrop than in the intercrop. As a consequence, the temperature at the base of the canopy was slightly higher in the intercrop than in the pea monocrop particularly from the beginning of pea flowering onwards. At the same time, the leaf wetness duration was usually shorter within the intercrop than within the pea monocrop. These results are consistent with the current understanding of the development of humidity within a canopy (Castro et al. 1991). Air humidity is generally higher within a closed than within an open canopy because there are more transpiring leaves, and because humidity is trapped in a dense canopy. Leaves remain wet longer during the daytime after a rainfall or morning dew within a closed than within an open canopy for two reasons: (1) evaporation is lower due to a lower wind speed and radiation penetration, and (2) the frequency of dew formation is higher due to a larger air temperature gradient within the canopy. In our experimental conditions, pea canopy closure coincided approximately with the beginning of flowering. After this stage, the homogeneous pea canopy appeared denser than the heterogeneous intercrop canopy. In hindsight, assessing the progression of the LAI of both canopies would have been useful to reinforce these visual observations. Monitoring of PAR was performed in both years but results were inconsistent, probably due to sensor failure, which made interpretation unreliable. Even though not supported by LAI or PAR measurements, the higher air temperature and shorter leaf wetness duration observed within the intercrop was likely to have resulted from a slightly more open canopy, which allowed higher radiation penetration. The differences in microclimate between both canopies might explain the differences in ascochyta blight development. In particular, the shorter leaf wetness duration (a highly important microclimatic factor in the infection process) observed in the intercrop after the beginning of pea flowering might explain the lower level of disease on pods and stems.

Experiments conducted under controlled conditions provided complementary results on the effect of intercropping on the splash dispersal of *M. pinodes* conidia. For a given overall plant density, total dispersal was reduced by 39 to 78% in the pea-wheat intercrop compared to the pea monocrop. So, the drastic change in canopy architecture induced by the replacement of host plants by non-host plants led to substantial reductions in total dispersal. By comparing the total dispersal achieved in the three canopy

types, it was possible to assess the contribution made by reduced host density (dilution effect) to the lowered levels of dispersal in the intercrop. The combination of addition series (i.e. differences in treatments are achieved by adding host plants) and replacement series (i.e. differences in treatments are achieved by replacing host plants by non-host plants) had already been considered by Burdon and Chilvers (1982) as a convenient way to investigate the underlying mechanisms of species mixtures through an assessment of the relative contribution of the reduction in host density and the presence of non-host plants. More recently, this approach was applied to cultivar mixtures by Finckh et al. (1999). In our experimental conditions, reductions in host density were responsible to a large extent for the reductions in total dispersal. A strong effect of host density reduction was also observed by Burdon and Chilvers (1977) when studying the effect of barley-wheat mixtures on barley mildew. In our study, depending on the experimental treatment, the host dilution effect was reinforced or mitigated by a direct effect of non-host plants. Thus, the host dilution effect was predominantly reinforced (additional reduction of 8 to 31%) for canopies at growth stage S5–7 suggesting that non-host plants could provide a physical barrier to conidial movement within the intercrop canopy early in the cropping season. In contrast, the host density effect was predominantly mitigated (compensation of 3 to 27%) for canopies at growth stage S8–10 suggesting that non-host plants could also allow for successive splashes through a relay effect. Older canopies (i.e. higher LAI values) may enhance the formation of rain droplets which in turn may promote re-splashing events and increase the dispersion tail. This would also explain the linear decrease in primary dispersal gradient slope with increasing LAI observed in pea monocrop canopies. Our results demonstrated that even if the reduction in host density is a major underlying mechanism to explain lowered disease levels in the intercrop, the presence of non-host plants may considerably complicate the analysis.

In this study, intercropping of pea with a cereal affected ascochyta blight development on pea by modifying both splash dispersal and microclimate. An early effect on splash dispersal of conidia could explain the early transitory effect of intercropping on disease severity on stipules, whereas the late modification of microclimate observed after canopy closure could explain the late effect on disease severity on pods and stems. These results confirm that, under some conditions, pea-cereal intercropping could usefully contribute to the management of ascochyta blight. Other elements of the cropping system could potentially contribute to increase the intercropping effect. For instance, Bouws and Finckh (2008) showed that the choice of the non-host species and the planting direction to the main wind direction are of particular importance in limiting late blight severity on potatoes.

In this study, intercropping was only evaluated from the epidemiological point of view. The effect of intercropping on yield and the disease-yield loss relationship was not investigated. First, the experimental design was not adapted to carry out such agronomic investigation. Indeed, field experiments involved both spring and winter pea crops in order to achieve a wide range of epidemics. As with other crops, winter sowings can result in higher, more stable yields than spring sowings (Lejeune-Hénaut et al. 1999). The differences in potential yield make the comparisons between experiments very difficult. Second, the branching ability permits pea plants to compensate for density variations quite easily. These competitive interactions between hosts and non-host plants could lead to unexpected results (Finckh et al. 1999). At last, overall yield assessment usually requires putting the emphasis on the yield formation of both host and non-host crops to calculate the land equivalent ratio (LER), i.e. the relative land area growing monocrops required to produce the yields achieved when growing intercrops (Hauggaard-Nielsen et al. 2008). Indeed, assessing the effect of intercropping on the pea yield only would generally lead to the conclusion that the benefit of intercropping on yield is nil, whereas LER values would indicate an advantage from intercropping in terms of the use of environmental resources for plant growth compared to monocrops. As a consequence, intercropping is more suitable for organic farming where there is an interest in a gross crop product (for example, the feed industry) than for more conventional farming where separation of crop products is required.

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