

Competitive dynamics in two- and three-component intercrops

METTE KLINDT ANDERSEN,*† HENRIK HAUGGAARD-NIELSEN,†
JACOB WEINER‡ and ERIK STEEN JENSEN†

*Department of Agricultural Sciences, Royal Veterinary and Agricultural University, DK-2630 Taastrup, Denmark; †Biosystems Department, RISØ National Laboratory, DK-4000 Roskilde, Denmark; and ‡Department of Ecology, University of Copenhagen, DK-1958 Frederiksberg, Denmark

Summary

1. Intercropping is receiving increasing attention because it offers potential advantages for resource utilization, decreased inputs and increased sustainability in crop production, but our understanding of the interactions among intercropped species is still very limited.
2. We grew pea *Pisum sativum*, barley *Hordeum vulgare* and rape *Brassica napus* as sole crops and intercrops under field conditions using a replacement design. We collected total dry matter data from sequential harvests and fitted the data to a logistic growth model. At each harvest we estimated the relative Competitive Strength (CS) of the three crops by fitting the data to a simple interspecific competition model.
3. The pea monocrop produced the largest amount of biomass from the middle to the end of the growth period, but pea was not dominant in intercrops.
4. Fitting data to a logistic growth model emphasizes the importance of initial size differences for interactions among intercrops. Barley was the dominant component of the intercrops largely because of its initial size advantage. The competitive effect of barley on its companion crops, measured as CS, increased throughout most of the growing season.
5. The performance of each crop species was very different when it grew with a second species rather than in monoculture, but addition of a third crop species had only minor effects on behaviour of the individual crops.
6. *Synthesis and applications.* Including sequential harvests in experiments on intercropping can provide important information about how competitive hierarchies are established and change over time. Our results suggest that increased understanding of the role of asymmetric competition among species and the resulting advantages of early germination and seedling emergence would be valuable in designing intercrops. More focus on understanding the mechanisms that govern interactions between intercropped species is needed for designing optimized intercropping systems.

Key-words: competition model, complementarity, intercropping, logistic growth, mixtures, plant competition, replacement design.

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Introduction

The importance of interactions among plant species in determining the structure and dynamics of plant communities is widely recognized (Tilman 1988;

Loreau *et al.* 2001). In agriculture, numerous studies on intercropping have been performed to investigate potential agronomic benefits (Hauggaard-Nielsen, Ambus & Jensen 2001a; Zhang & Li 2003; Andersen *et al.* 2004). One of the potential benefits is that differences in the way crop species utilize resources can give intercropping systems improved yields and/or increased sustainability (Vandermeer 1990). In some cases productivity is enhanced in intercrops (Vandermeer 1990;

Fukai & Trenbath 1993), but in the majority of studies intercrop yields are intermediate to the sole crops, or comparable to those of the highest yielding sole crop (Hauggaard-Nielsen *et al.* 2001a; Jensen 1996). Part of the reason for this is that all plants use the same resources (nutrients, water, light), so crops will inevitably compete for these resources. Interspecific competition for resources has therefore been the focus of much research on intercropping (Jensen 1996; Hauggaard-Nielsen, Ambus & Jensen 2001a; Andersen *et al.* 2004). Very few intercrop studies have moved beyond two component mixtures, so little is known about the competitive interactions and performance of more diverse intercrops.

Although one goal has been to investigate ecological interactions in a given intercropping system, most studies have collected data only at the end of a single period of growth. Similarly, most indices used to describe the interaction between species do not address the dynamics of plant growth and competition (Connolly, Wayne & Murray 1990; Turkington & Jolliffe 1996). Studying the growth of intercrops with sequential harvests would provide a dynamic picture of how interspecific interactions develop over the course of the growing season, enabling us to fit growth models (Weigelt & Jolliffe 2003), evaluate the effects of initial conditions on these interactions (Gibson *et al.* 1999; Connolly, Goma & Rahim 2001), and observe changes in competitive interactions over time (Weigelt & Jolliffe 2003). This should help us to develop intercropping systems that better utilize the potential advantages of interactions among crop species.

The objective of this study was to ask how competitive interactions between crop species in an intercrop change over time and how crop performance changes as the number of crop species increases from one to three. We chose a three-component mixture of pea, barley and rape. These crops were chosen on the basis of differences in resource utilization: the ability of pea to fix atmospheric nitrogen, the ability of barley and pea, unlike rape, to enter into a mycorrhizal symbiosis, and the longer growing season of rape compared to barley and pea. We fit a logistic growth model to data from a pea–barley–rape intercrop field experiment (Andersen *et al.* 2004). We also fit a competition model to evaluate the relative competitive strength (CS) of the intersown crops. Thus, we extend previous work by modelling competition over time through sequential harvests and by including a third intercropped species, rather than modelling ecophysiological mechanisms (e.g. Kropff & van Laar 1993) or the effects of density (e.g. Park *et al.* 2003).

Materials and methods

The field study was conducted at the experimental farms of the Faculty of Life Sciences, University of Copenhagen in Taastrup, Denmark (55°40'N, 12°18'E) from April to August 2000. The soil type was a sandy loam (Andersen *et al.* 2004).

Using a proportional replacement design (Willey 1979), we grew *Pisum sativum* L. cv. Bohatyr (field pea), *Hordeum vulgare* L. cv. Punto (spring barley) and *Brassica napus* L. cv. Orakel (oilseed rape) as sole crops, in dual-component intercrops, and in a tri-component intercrop, giving a total of seven crop-combination treatments. We used a randomized split-plot design with crop treatment as plot factor and four replicates. Each 18 m² plot consisted of 10 rows of 12 m length spaced 15 cm apart. We tried to achieve sole crop densities of 80 pea, 350 barley and 110 rape plants m⁻². The two and three component intercrops consisted of half and a third of the sole crop densities of each species, respectively.

Crops were sown with a seed drill on 27 April 2000. Pea, barley and rape seeds were sown consecutively in the same rows, spaced 12.5 cm apart. First, the pea seeds were sown at a depth of 6 cm, then barley seeds at 4 cm depth and lastly the rape seeds at a depth of 2 cm. We made a total of five harvests over the course of the growing season, at 33, 42, 61, 77 and 112 days after sowing. At each of the first four harvests, a 0.5 m² subplot was randomly placed within one plot. This same location within the plot was used within all plots at that harvest. At each harvest all plant material from the subplot was harvested at ground level. At the final harvest the harvested area was increased to 1 m². Harvested plant material was sorted into component crops and individual biomass yields determined before and after drying at 80 °C for 24 h.

GROWTH MODEL

Biomass yield data, from all five harvests, were for each crop component of sole- and intercrops fitted to the logistic growth function (Hunt 1982) using least squares.

$$Y_t = (a * e^{b(t-k)}) / (1 + e^{b(t-k)}) \quad \text{eqn 1}$$

where Y is the biomass of a given crop species grown in a given treatment at a given time (t) during the growth season, a is a scale parameter determining the maximum size, b is the initial growth rate, and k determines the location of the curve. These parameters were estimated using the NLIN procedure of the SAS statistical software (SAS 1999).

The assumptions of normal distribution and of variance homogeneity were tested graphically using residual plots. The presence of systematic deviation from the model was also evaluated graphically. The presence of single points with large effects on regression estimates was revealed using Cook's distance (Cook 1977). To attain variance homogeneity and normality, standard model diagnostics were examined and both variables transformed to satisfy model assumptions (Box & Cox 1964).

Using an F -test for lack of fit (Weisberg 1985), no significant differences were found between the within-block and between block variances.

COMPETITION MODEL

To determine the relative competitive ability of the three crops we formulated a simple interspecific competition model, a minimal version of the most widely used class of interspecific competition models:

$$\text{Dual intercrops: } Y_{i(j)} = Y_{i(i)} * (p_i * c_i) / [(p_i * c_i) + (p_j * c_j)] \quad \text{eqn 2}$$

$$\text{Triple intercrops: } Y_{i(jk)} = Y_{i(i)} * (p_i * c_i) / [(p_i * c_i) + (p_j * c_j) + (p_k * c_k)] \quad \text{eqn 3}$$

where Y is the total above-ground dry matter yield of crop components i, j and k , p is the relative proportion of crop component, and c is the competitive coefficient of a given crop. Applying the model to dry matter data from the first harvest, P -values were taken as the target plant density proportions at which the crops were sown. In fitting data from the following harvests, P -values were based on the relative contribution of the component to the total dry matter measured at the previous harvest. The model assumes there is a general competitive effect of a given crop on another, i.e. the competitive ability of a species is defined independently of a specific competing species ($c_{i(j)} = c_{i(jk)}$). This assumption was

tested with a T -test comparing the measured and model predicted yield measures.

The relative competitive strength (CS) of the crops is defined as the ratio of the competition coefficient of one species to the competition coefficient of the other: $CS_{ij} = c_i/c_j$. We estimated CS by fitting the equation

$$Y_{i(j)} = Y_{i(i)} * (p_i) / [p_i + (p_j * CS_{ij})] \quad \text{eqn 4}$$

using pea as a standard.

As with the growth model, we tested the assumptions of the competition model through analysis of variance and normality. To attain variance, homogeneity and normality variables were log-transformed.

PARTIAL LER

On the basis of actual measured dry matter yields at the final harvest, partial Land Equivalent Ratio (L) values were calculated for the component crops of the triple intercrop. These indices were calculated to ask whether average yield per sown plant of crops grown in a tri-component intercrop was predictable on the basis of their performance in sole crop or dual intercrop, so partial LER values were for each component crop calculated in two ways: first, taking sole crop yield as reference (eqn 5) and second, taking the yield of the crop grown in dual intercrop as reference (eqn 6).

L for species i intercropped with j and k :

$$\text{Yield of } i(i) \text{ as reference: } L_{i(jk)} = Y_{i(jk)} / Y_{i(i)} \quad \text{eqn 5}$$

$$\text{Yield of } i(ij) \text{ as reference: } L_{i(jk)} = [Y_{i(jk)} * (3/2)] / (Y_{i(ij)} * 2) \quad \text{eqn 6}$$

The multiplicative factors in the numerator and denominator in equation 6 ensure comparability to values calculated with equation 5. Each component crop gave rise to three L -values, one in which the sole crop yield served as reference and two L -values using yields in dual intercrop as a reference. All L -values were calculated for each block, giving a total of four replicates for each estimate. L -values less than 0.33 indicate that the crop performed better in the reference crop than in the triple intercrop, values greater than 0.33 indicate the opposite.

Results

CROP GROWTH AND PRODUCTIVITY

Dry matter accumulation for all components of sole- and intercrops over the five harvests fit the logistic growth model well ($P < 0.0001$). The final dry matter yields of all crop components estimated from the logistic model were consistent with the yields measured (Fig. 1). With the exception of rape growing with barley, the fitting of growth data to the model gave rise to very

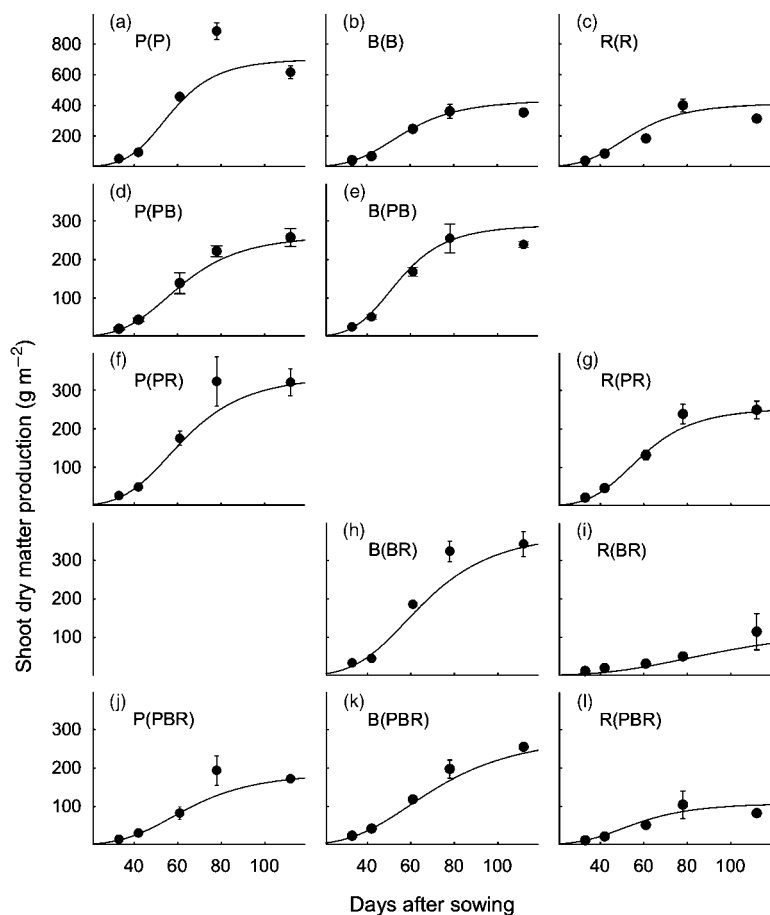


Fig. 1. Measured (symbols) and modelled (lines) total shoot dry matter production (g m^{-2}) of intercropped and sole cropped pea (a, d, f, j), barley (b, e, h, k) and rape (c, g, i, l). Measured values are means ($n = 4$) \pm SE.

Table 1. Relative proportions (as percentage) of component crops in the total dry matter biomass harvested from each of the four studied intercrops: pea–barley (PB); pea–rape (PR); barley–rape (BR); pea–barley–rape (PBR) 33 and 112 days after sowing (DAS). Values are the mean ($n = 4$) \pm SE

	Crop component	Intercrop treatment			
		PB	PR	BR	PBR
33 DAS	Pea	45 (± 3)	56 (± 6)		29 (± 3)
	Barley	55 (± 3)		75 (± 4)	48 (± 3)
	Rape		44 (± 6)	25 (± 4)	23 (± 3)
112 DAS	Pea	49 (± 3)	56 (± 3)		34 (± 1)
	Barley	51 (± 3)		75 (± 3)	50 (± 1)
	Rape		44 (± 7)	25 (± 7)	16 (± 1)

similar b and k parameter values for all components (Table 2). Differences in the model expressions of the crop components were largely a result of differences in the estimated a values (Table 2).

Plant counts performed 2 weeks after germination confirm that the intended relative proportions of component crops in the four studied intercrops were generally achieved (data not shown). By the first harvest, the barley component contributed over-proportionally to biomass in the three-component intercrop and the dual intercrop with rape, and the relative proportions of the component crops in the harvested biomass remained more or less unchanged throughout the growing season (Table 1). From the third harvest and onwards, the pea sole crop produced significantly more biomass than the two non-legume sole crops, but pea was not dominant when grown with them (Fig. 1).

Rape grew much better when grown in combination with pea alone (Fig. 1g) than in dual or triple intercrop with barley (Fig 1i and l, respectively), where a clear dominance of barley was evident from the third harvest and subsequently.

The greatest total above-ground dry matter yield was reached in the sole crop pea treatment, the lowest in the

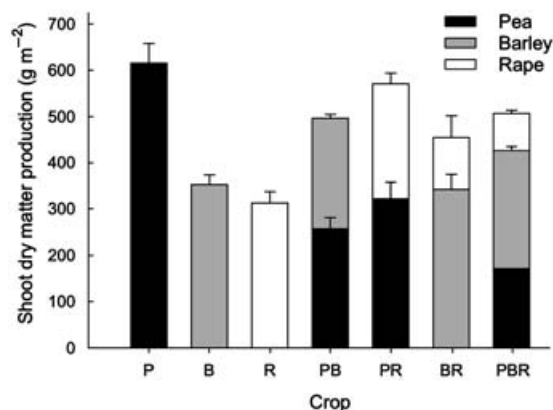


Fig. 2. Total above-ground dry matter yields of pea (P, black), barley (B, grey) and rape (R, white) grown as sole crops (SC) and in dual- and tri-component intercrops (IC). Values are means ($n = 4$) \pm SE.

other two sole crops. All intercrops produced yields that were intermediate (Fig. 2). Since the total yields of the intercrops were not significantly different from one another, there was no direct effect of species number on biomass productivity.

RELATIVE COMPETITIVE STRENGTH

The competition model assumes that competition is general in the sense that a crop species has the same effect on each of the other species, so one competition coefficient was calculated for each crop at each harvest, using pea as a standard (Table 3). The relative competitive strengths (CS) of each crop relative to the others were calculated from these coefficients. Since CS of species i relative to species j is the reciprocal of the CS of species j to species i , only one of two CS values corresponding to a pair of species is shown (Fig. 3). Barley exerted a significant and similar competitive pressure on both pea and rape throughout the growth season. Values of CS for pea relative to rape were around 1,

Table 2. Parameters (a , b and k) estimated from fitting shoot dry matter from each crop component (P, pea; B, barley, R, rape) of each inter- and sole-crop treatment (PB, PR, BR, PBR, P, B and R) to the logistic growth curve described in the text (eqn 1). All values are given with \pm SE

Crop treatment	Crop component	Estimated model parameters		
		a	b	k
P	P	742 (± 96)	0.115 (± 0.015)	57.1 (± 3.5)
B	B	384 (± 51)	0.096 (± 0.015)	56.3 (± 4.2)
R	R	348 (± 46)	0.098 (± 0.017)	54.7 (± 4.2)
PB	P	264 (± 36)	0.096 (± 0.013)	59.5 (± 4.1)
	B	257 (± 33)	0.106 (± 0.017)	54.8 (± 3.9)
PR	P	346 (± 48)	0.095 (± 0.012)	60.2 (± 4.1)
	R	257 (± 34)	0.103 (± 0.014)	58.1 (± 3.8)
BR	B	376 (± 54)	0.089 (± 0.011)	61.6 (± 4.3)
	R	107 (± 27)	0.048 (± 0.009)	78.1 (± 2.2)
PBR	P	190 (± 27)	0.091 (± 0.012)	61.2 (± 4.3)
	B	266 (± 40)	0.080 (± 0.011)	63.0 (± 4.9)
R	R	89 (± 12)	0.090 (± 0.016)	55.5 (± 4.6)

Table 3. Competitive coefficients (c) of barley and rape estimated from fitting shoot dry matter data from each crop component: pea (P), barley (B), rape (R) of each intercrop treatment (PB, PR, BR and PBR) to the competition model described in the text. The competitive coefficient for pea (c_{pea}) was set to 1. Values are given with SE

Time of harvest	Estimated competition coefficient (relative to pea)	
	Barley	Rape
33 DAS	1.83 (± 0.33)	0.88 (± 0.19)
42 DAS	2.09 (± 0.38)	0.95 (± 0.21)
61 DAS	3.87 (± 0.78)	1.46 (± 0.36)
77 DAS	3.44 (± 0.82)	1.01 (± 0.32)
112 DAS	2.44 (± 0.49)	1.01 (± 0.25)

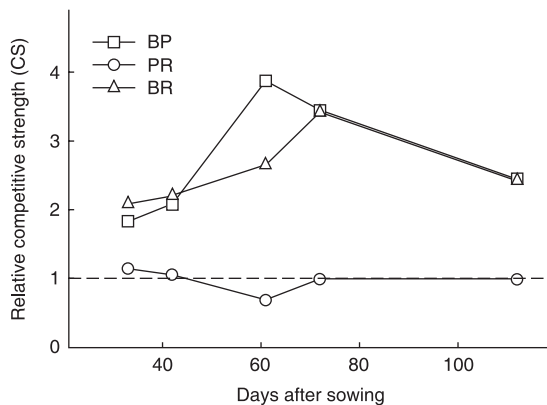


Fig. 3. Relative competitive strength (CS) of barley towards pea (BP), pea towards rape (PR) and barley towards rape (BR). Calculations based on parameters estimated in the competition model described in the text.

implying that the two crops had a similar competitive impact on one another throughout the growth period.

INTERCROP DIVERSITY AND CROP PERFORMANCE

When partial LER values for the components of the triple intercrop were calculated with sole crop yields as reference, they were all very different from the 0.5-value, indicating that crop performance differed in sole and intercrop (Table 4). With an L -value of 0.72, barley clearly benefited from being intercropped whereas both rape and pea suffered from the presence of companion crops. Using yields of crop grown in dual intercrop as reference in the calculation of L it was evident that the values differed greatly depending on the composition of the reference intercrop. The performance of both pea and rape in triple intercrop was more predictable on the basis of their growth in dual intercrop with barley than with one another. Barley in triple intercrop performed much better than in dual intercrop with pea whereas when the barley-rape intercrop served as a reference barley performance was only slightly improved.

Table 4. Partial LER values of the component crop (P, pea; B, barley; R, rape) dry matter yields at final harvest for the triple intercrop (PBR). Calculations were based on eqns 5 and 6, using sole crop (SC) and dual intercrop (IC) yields as reference, respectively. Values are means ($n = 4$) \pm SE

	Partial LER values of the triple IC		
	P	B	R
Calculations based on SC yields			
P SC	0.28 (± 0.01)		
B SC		0.72 (± 0.07)	
R SC			0.26 (± 0.02)
Calculations based on dual IC yields			
PB IC	0.42 (± 0.05)	0.57 (± 0.05)	
PR IC	0.51 (± 0.06)		0.26 (± 0.04)
BR IC		0.80 (± 0.04)	0.60 (± 0.30)

Discussion

CROP GROWTH AND PRODUCTIVITY

Questions about the outcome of competition have not been clearly differentiated from questions regarding how much neighbouring species affect each other and the mechanisms through which this occurs (Connolly, Wayne & Bazzaz 2001). Including the dynamics of growth helps to illuminate the underlying mechanisms to a degree that single harvest data cannot. In the present study, the fitting of sequential harvest data to a logistic growth model showed that all but one component crop, rape grown in dual intercrop with barley, displayed similar growth rates (b) and reached the point of inflexion (k) at approximately the same time, differing primarily in the maximum size (a) they achieved. The model is formulated such that the relative growth rate at a given time is similar for all crops throughout the growing season, so differences in initial size play an important role in estimating a . Growth dynamics prior to the first harvest would have been useful for explaining the observed balance between the intercropped crops. The observation that biomass ratios determined at the first harvest remained more or less stable throughout the growing season (Table 1) supports this. Several researchers have emphasized the important role of initial growth in shaping the competitive dynamics between species (Tofinga, Paolini & Snaydon 1993). Initial growth is affected by differences in seed (Marañón & Grubb 1993; Rees 1995; Rees & Westoby 1997) and therefore seedling size (Schwinning & Fox 1995), relative time of emergence (Cousens *et al.* 1987; Radosevich & Roush 1990; Kropff & Spitters 1991) and early root establishment (Bellostas *et al.* 2003; Hauggaard-Nielsen, Ambus & Jensen 2001b). In the present study, the barley crop grew well in all intercrops, accounting for an equal or greater proportion of the final yield compared to its companion crops (Fig. 2), suggesting that barley had an early competitive advantage. In a pot experiment

with these same three species, a competitive advantage of barley relative to pea and rape as early as 2 weeks after seedling emergence was observed (Bellostas *et al.* 2003).

A clear dominance of barley in the barley–rape intercrop in comparison with the more equal distribution of components in the pea–barley intercrop suggests that competition for soil nitrogen may have been an important structuring factor. It is likely that a quicker establishment of the barley crop gave it a head start in the competition for soil nitrogen, giving rise to a strong suppression of the less competitive rape, whereas pea, due to its ability to fix atmospheric nitrogen, was less suppressed.

RELATIVE COMPETITIVE STRENGTH

Competition in mixtures of plant species has been a focus in attempts to link competitive ability to relative abundance and dynamics in natural plant communities (Goldberg 1996). In an agronomic setting, the focus is more short-term, and increased knowledge of interspecies dynamics is of interest with respect to designing intercrops that maximize some aspect of yield at the end of the growing season. Few studies have fit explicit mathematical models of competition to data from intercrop studies (Park *et al.* 2003), and when it has been done, the primary purpose has been to study the effects of cropping density and relative component crop frequency on the competitive dynamics between the crop species (Helenius & Jokinen 1994; Hauggaard-Nielsen *et al.* 2006). The competitive impact of barley on both pea and rape, tracked as *CS*, increased during the first half of the growing season, and continued to increase until the fourth harvest when the companion crop was rape (Fig. 3). As discussed above, it is likely that size-related traits resulting in an early growth advantage were the basis for this competitive dominance. Size-asymmetric competition between species (Connolly & Wayne 1996; Freckleton & Watkinson 2001) tends to compound such an initial size advantage, so initial differences in size may explain the increasing competitive impact of barley towards its companion crops throughout most of the cropping season. This suggests the possibility of influencing the relative dominance of components of an intercrop by manipulating the initial advantage in competition, for example through differences in sowing times, depths or densities. A few days difference in sowing date, for example, could allow farmers to alter the competitive balance among intercropped species.

The importance of an initial size advantage in competition among species underlines the limits of simple competition indices. Many researchers have pointed out that an index of competition between two species can be altered by the density of each component and by resource levels, but our results suggest that any factor that alters initial size differences may have major effects on the outcome. Small differences in initial conditions

may explain why interspecific competition experiments, when repeated, sometimes produce surprisingly different results.

The *CS* of barley dropped towards the end of the growing season, which may partly be due to differences in the phenology of the associated crops (Fig. 3). The growing season of component species in an intercrop is frequently longer than that of sole crops (Ofori & Stern 1987), as observed in maize–soybean (Chui & Shibles 1984) and pigeon pea–sorghum (Natarajan & Willey 1980) intercrops.

INTERCROP DIVERSITY AND CROP PERFORMANCE

As in most intercrop studies, the crops included in this study were chosen on the basis of assumed differences in their structural and biogeochemical traits, differences that are expected to result in complementary use of available growth resources and possibly greater biomass productivity than the comparable sole crops. We found that all intercrops yielded intermediately to the sole crops and that the total yields of dual and tri-component intercrops were not significantly different. Partial LER values calculated using sole crop yields and dual intercrop component crop yields as reference indicated that the performance of the individual crops was most affected by a change from sole crop to intercrop, and less by a further increase in diversification. The performance of the three components of the triple intercrop was generally predictable on the basis of dual intercrop performance. While our results are consistent with some of the proposed advantages of intercropping, much more research is needed before we can determine if the potential advantages of three over two component crops can justify the additional management effort required.

The results might have been different under different cropping conditions, such as different densities of the components (Snaydon 1991). In a recent study (Hauggaard-Nielsen *et al.* 2006), the relative competitive strength of intercropped pea and barley was clearly affected by changes in both the relative frequency and density of the component crops. Ideally, one would like to vary the density of each component separately (Park *et al.* 2003), but this requires very large experiments.

Understanding how crop species grow and interact in the context of their abiotic and biotic environment is important for developing intercropping systems that can utilize the advantages of species interactions (Connolly, Goma & Rahim 2001). Here, we have shown that a dynamic picture of the growth and competition dynamics in an intercrop is an important step in achieving this understanding. Our results suggest an important role for the initial advantage in competition among intercropped species. These initial conditions can be influenced by sowing practices, which present opportunities for manipulating intercrop competition to achieve specific objectives.

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Corrigendum

Andersen, M.K., Hauggaard-Nielsen, H., Weiner, J. & Jensen, E.S. (2007) Competitive dynamics in two- and three-component intercrops. *Journal of Applied Ecology*, **44**, 545–551.

There was an error in equation 6 and the following sentence, and in Table 4.

Eqn 6 should be

$$L_{i(jk)} = Y_{i(jk)} / (Y_{i(j)} * 2)$$

The factor of 2 in the denominator in equation 6 ensures comparability to the values calculated in equation 5.

Table 4. Partial LER values of the component crop (P: pea; B: barley; R: rape) dry matter yields at final harvest for the triple intercrop (PBR). Calculations were based on equations 5 and 6, using sole crop (SC) and dual intercrop (IC) yields as reference, respectively. Values are means ($n = 4$) \pm SE

	Partial LER values of the triple IC		
	P	B	R
Calculations based on SC yields			
P SC	0.28 (\pm 0.01)		
B SC		0.73 (\pm 0.07)	
R SC			0.26 (\pm 0.02)
Calculations based on dual IC yields			
PB IC	0.34 (\pm 0.04)	0.53 (\pm 0.03)	
PR IC	0.28 (\pm 0.04)		0.17 (\pm 0.03)
BR IC		0.38 (\pm 0.03)	0.57 (\pm 0.19)

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Jacob Weiner, Department of Agriculture and Ecology, University of Copenhagen.

Henrik Hauggaard-Nielsen and Erik Steen Jensen, Technical University of Denmark.

*Correspondence author. E-mail: jw@life.ku.dk