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Above- and below-ground competition between intercropped winter wheat *Triticum aestivum* and white clover *Trifolium repens*

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Summary

1. Intercropping of white clover and cereals has recently been promoted for low-input farming systems because it offers several benefits for sustainability, but the practical use of this system has been limited by the relatively low wheat yields. Very little is known about competition between the two species in this intercropping system and its implications for production.

2. To investigate the interaction between white clover and wheat, we separated above- and below-ground competition in the field in a fully factorial additive design. The treatments were with and without clover, with and without below-ground partitions between rows of the two species, and with and without above-ground partitions. Above-ground biomass of both species was harvested three times over the growing season, and the wheat biomass was analysed for nitrogen content.

3. When wheat was grown without clover, its biomass was much reduced by below-ground partitions and slightly reduced by above-ground partitions. Presence of both above- and below-ground partitions did not result in lower wheat biomass than below-ground partitions alone.

4. Total biomass was higher when both species were present, and this biomass was reduced by below-ground partitions and, to a lesser degree, by above-ground partitions. In mixture, below-ground partitions reduced wheat biomass and increased clover biomass at the last harvest, whereas above-ground partitions reduced clover biomass and increased wheat biomass.

5. The interaction between the two species was dominated by competition for soil nutrients, but competition for light influenced the partitioning of biomass production between the two species. Mingling of the roots of both species is important for maximizing soil resource utilization, whereas shoots performed almost as well without mingling.

6. *Synthesis and applications*. The results suggest that competition between wheat and clover for nitrogen is reduced by nitrogen fixation because clover obtains some of its nitrogen from fixation. Increased availability of nitrogen to the intercropped wheat late in the growing season could increase grain protein content. Our results suggest possibilities for improved management of competition between the two species to optimize resource utilization, biomass production and wheat yields. Goals for yield should be based on a specific component, such as total biomass, grain yield and grain quality, because these yield components can behave differently when another species is present.

Key-words: cereal, intercropping, legume, root competition, shoot competition

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Introduction

Intercropping offers the opportunity of utilizing niche differences between crop species when the intercropped species have different resource requirements in time or space (Firbank & Watkinson 1990) or when one species can provide resources to the other (Vandermeer 1988). Other ecological benefits of intercrops include reductions in pests and diseases (Trenbath 1993; Bannon & Cooke 1998), improved soil cover and higher nutrient retention (Altieri 1999). However, few studies on intercropping have addressed the mechanisms of interspecific competition (Connolly, Goma & Rahim 2001).

Intercropping of cereals and legumes is often used in organic or low-input farming systems because the mixture of a nitrogen (N)-fixing and a non-N-fixing crop species provides complementarities in utilization of resources (Hauggaard-Nielsen, Ambus & Jensen 2003). Some experiments have shown clear intercrop advantage in yields, e.g. beans and maize (Willey & Osiru 1972) and pea and barley (Hauggaard-Nielsen, Ambus & Jensen 2001), whereas other studies have not (Jørgensen & Møller 2000; Park, Benjamin & Watkinson 2002). Intercropping of clover and cereals for forage production in temperate climates has received recent attention (Anil *et al.* 1998; Thorsted, Søegaard & Koefoed 2002), although some studies have also looked at grain yield (Thorsted, Koefoed & Olesen 2002). In intercropping systems of cereals and white clover, the cereal is usually established by direct drilling of the cereal seeds into a previously established stand of white clover.

Experiments with white clover–winter wheat intercrops have shown much lower wheat grain yields in the intercrop compared with wheat as a monocrop (Clements & Donaldson 1997; Bergkvist 2003). This yield reduction occurs because of lower wheat density and interspecific competition between clover and wheat.

To understand better the mechanisms of interspecific competition in plants, separation of root and shoot competition can be useful. In the 'row technique' (Schreiber 1967) partitions are used to separate above- and below-ground competition between two species growing in alternating rows. While all methods for the separation of root and shoot competition have their limitations (McPhee & Aarssen 2001), the row technique is often well suited to agricultural investigations, especially when experiments are performed under field conditions with realistic soil volumes and climatic conditions (Wilson 1988). We used the row technique to grow white clover and winter wheat in the four possible combinations of with or without above- and below-ground division. We assumed that the partitions themselves influence plants to the same extent in monocultures as in intercrops. As the most important problem for use of this intercropping system in production is the need to increase wheat yields, we emphasized wheat production in our experimental design.

Methods

Winter wheat *Triticum aestivum* L. cv. Stakado and white clover *Trifolium repens* L. were grown in the field in boxes with and without above-ground and below-ground partitions in four combinations: no partitions, above-ground partitions, below-ground partitions and both above- and below-ground partitions (Fig. 1a). To obtain information on the effects of the partitions themselves on winter wheat, the experiment was performed with and without clover (Fig. 1b). The eight different treatments were placed randomly within three replicate blocks.

The experiment was performed at the Danish Institute of Agricultural Sciences' Foulum experimental station (56 30′ N, 9 35′ E). The soil was a loamy sand classified as a typic hapludult according to the Soil Taxonomy System (Nielsen & Møberg 1985). During the experimental period 1999–2000, the mean temperature was 3·0 C in January and 13·7 C in June, and the annual precipitation was 771 mm (Sørensen, Nielsen & Thysen 2000).

Plants were grown in the field in bottomless boxes made of 12-mm waterproof plywood measuring 111·3 × 121 × 40 cm (width × length × depth). The below-ground partitions were made of the same material and to the same depth. In August 1999 the topsoil (0–20 cm) and subsoil (20–40 cm) were dug up and kept in separate heaps. The soil within each heap was mixed with a shovel. The boxes were placed into the ground and the soil was

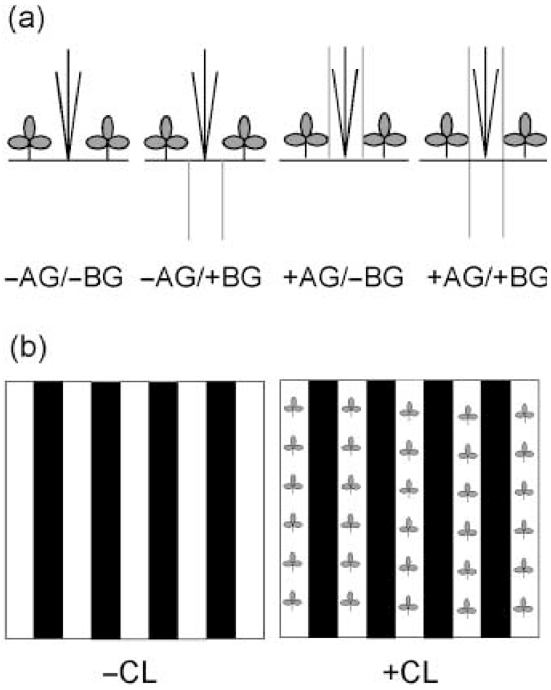

Fig. 1. The four different combinations of white clover and winter wheat with and without above-ground partitions (±AG) and below-ground partitions (±BG) (a), and the layout of boxes with and without clover (±CL) with wheat rows marked in black (b).

filled in with first 20 cm subsoil and then 20 cm topsoil. The soil was gently pressed with a treadle and a wooden stake as it was refilled. The total soil volume was reduced by 8·6% in boxes with below-ground partitions compared with boxes without partitions because of the 12-mm thick plywood.

In each box there were nine 121-cm long rows, four wheat rows and either five rows of clover or bare soil (Fig. 1). The row direction was north–south. The distance between the centres of adjacent wheat rows was 25 cm, and the clover was seeded in 11·3-cm wide bands. White clover cv. Milo (DLF-Trifolium, Roskilde, Denmark) was sown on 17 August 1999 at a rate of 12 kg ha^{-1} by spreading seeds evenly within each band. After making 3-cm deep and 121-cm long rows in the soil, winter wheat was sown on 7–11 October 1999 at a density of 400 seeds m^{-2} (122 seeds in each row). Fertilizer (70 kg N ha^{-1}, 18 kg P ha^{-1}, 53 kg K ha^{-1}) was spread evenly on the surface within the boxes on 31 March 2000. Boxes were placed such that there was one wheat row between them, with the same 25-cm row distance as within the boxes. There was a 40-cm access path between boxes in the other direction, in which a mixture of grasses was sown.

Above-ground partitions were made of low-density white polyethylene (0·5 mm UV-resistant) fixed between two wooden stakes. The plastic was rolled on the upper stake, and rolled up or down like a curtain to regulate the height of the partitions, and fixed to a wooden stake at the soil surface. Both upper and lower stakes were fixed to stabilize and keep the position of the curtain fixed. The above-ground partitions were placed at a height of 15 cm measured from soil surface on 10 April 2000. The height of the above-ground partition followed the clover height by rolling up more plastic as the clover grew taller. The final height of the above-ground partition was 45 cm above soil surface. All boxes were irrigated with 20 mm water on 24 May 2000 to avoid any drought stress. Weeding was done by hand every week or two in autumn 1999 and throughout the growing season in 2000.

Above-ground wheat and white clover biomasses were harvested on 15 May, 30 May and 22 June 2000. White clover stolons were not harvested. On each sampling date, the above-ground biomass from each separate plant row within each box was harvested at the soil surface and weighed. A subsample of 200 g from each row was dried at 80 °C for 24 h and weighed to determine the percentage dry weight, and this was used to determine the dry weight of the row. Total nitrogen in a sample of plant material from each wheat row was determined for each plant row by the Dumas method (Hansen 1989).

STATISTICAL ANALYSES

The above-ground dry mass of the four wheat rows within each box was used in the statistical analyses. For clover, the mass of the three central plant rows within each box was used, i.e. the outermost rows in each box were excluded.

Data were analysed with analysis of variance. The main factors in the analyses were harvest date, ± above-ground separation and ± below-ground separation, and, in analyses of wheat, also ± clover. To obtain variance homogeneity, wheat biomass and total intercropped (clover + wheat) biomass were log-transformed, and wheat N concentration was arctangent-transformed. Other variables were not transformed.

Results

BIOMASS

The mean total above-ground dry matter production over the three sampling dates was on average 40% higher for the intercrop than for wheat monoculture (Table 1). Both above- and below-ground partitions reduced

Table 1. Means table for wheat mass, wheat N concentration, total wheat N content, clover mass and wheat + clover mass for the three harvest dates, presence (+) vs. absence (–) of above-ground (AG) and below-ground (BG) partitions

			Wheat mass (g m^{-2})		Wheat N concentration (%)		Total wheat N (g m^{-2})		Clover mass (g m^{-2})	Total wheat + clover mass (g m^{-2})
Harvest	BG	AG	Without clover	With clover	Without clover	With clover	Without clover	With clover	With clover	
1	–	–	475	314	1·63	1·59	7·90	5·12	281	595
		+	406	318	1·76	1·52	7·28	4·94	179	496
	+	–	292	233	1·50	1·88	4·40	4·51	248	482
		+	284	256	1·86	1·73	5·33	4·53	210	466
2	–	–	728	483	1·08	1·27	7·83	6·12	319	802
		+	643	478	1·37	1·36	8·84	6·53	291	769
	+	–	427	412	0·99	1·04	4·23	4·27	394	806
		+	419	354	1·05	1·17	4·42	4·16	270	625
3	–	–	1178	854	0·91	0·97	10·75	8·26	426	1280
		+	1104	923	0·93	1·00	10·21	9·21	298	1221
	+	–	717	600	0·84	0·82	6·06	4·95	542	1142
		+	719	682	0·84	0·82	6·05	5·59	403	1084

Table 2. Analysis of variance of log(total intercropped clover + wheat biomass) on block, harvest and presence vs. absence of above-ground partitions and below-ground partitions. Model $r^2 = 0{\cdot}97$. The dominant factors were harvest ($F = 537$), below-ground partitions ($F = 35$) and above-ground partitions ($F = 26$)

Factor	d.f.	SS	*P*
Block	2	0·00057	0·6945
Harvest	2	0·82730	< 0·0001
Above-ground partitions (AG)	1	0·01990	< 0·0001
Harvest × AG	2	0·00173	0·3431
Below-ground partitions (BG)	1	0·02680	< 0·0001
Harvest × BG	2	0·00048	0·7354
AG × BG	1	0·00003	0·8472
Harvest × AG × BG	2	0·00943	0·0077

total above-ground biomass of the intercrop (Table 2). There was no interaction in the effects of above- and below-ground partitions on intercrop biomass production, although there was a significant but weak three-way interaction with harvest date (Table 2).

Wheat produced more above-ground dry matter when there was no clover present (Table 1 and Fig. 2). The reduction of wheat biomass because of the addition of clover was greater without below-ground partitions than with their presence (Figs 2 and 3). Wheat biomass was reduced considerably by the presence of below-ground partitions (and more so in the absence of clover) but was largely unaffected by above-ground partitions (Table 3), although there was slightly lower wheat biomass in the wheat monocrop with above-ground partitions (Table 1 and Fig. 3). Interactions among factors, even when significant, were generally small compared with the main effects.

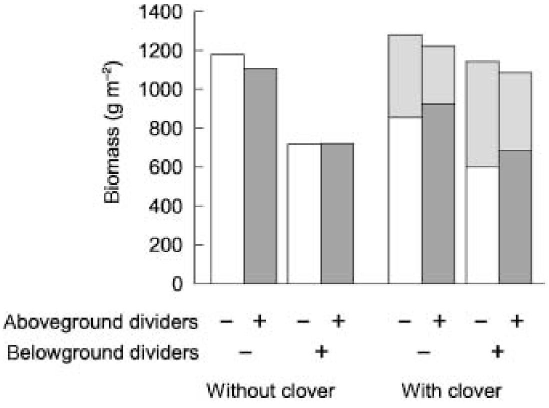

Fig. 2. Dry mass of wheat (white and dark grey bars) and clover (light grey bars) at the third harvest. The strongest effects on wheat biomass were the presence of below-ground dividers ($F = 716{\cdot}2$) and presence of clover ($F = 155{\cdot}2$). Interactions between the presence of clover and above-ground ($F = 20{\cdot}35$) and below-ground ($F = 21{\cdot}00$) dividers were also highly significant but weak compared with the main effects. Both above-ground and below-ground dividers had large and highly significant effects on clover biomass ($F = 27{\cdot}3$ and $18{\cdot}8$, respectively) but there was so interaction between them.

Above-ground dry matter of intercropped clover was reduced by above-ground partitions and was generally higher with below-ground partitions (Tables 1 and 4), especially at the last harvest (Fig. 2).

WHEAT NITROGEN CONTENT

The N concentration of wheat biomass decreased greatly over time (Tables 1 and 5). In the absence of clover, above-ground partitions generally increased N concentration whereas below-ground partitions decreased wheat

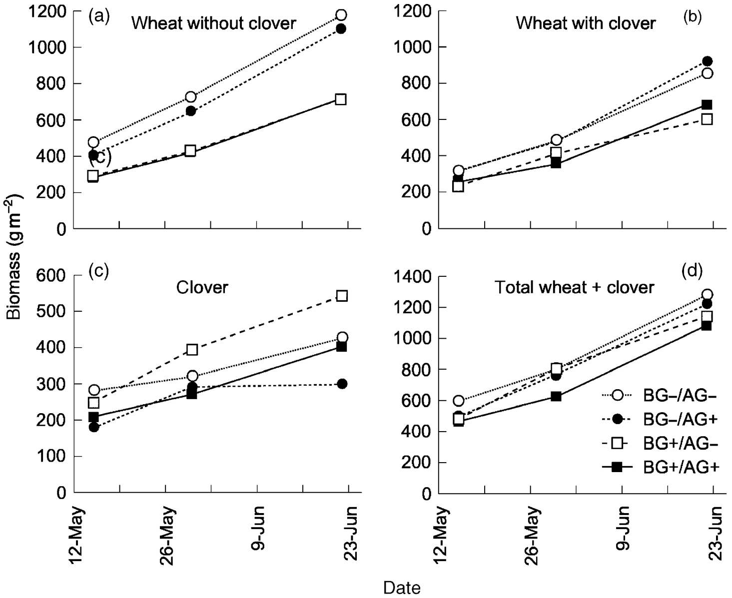

Fig. 3. Biomass accumulation over the three harvest dates for (a) wheat grown without clover, (b) wheat with clover, (c) clover (with wheat) and (d) total intercropped wheat + clover. ○, no partitions; ●, above-ground (AG) partitions; □, below-ground (BG) partitions; ■, both above- and below-ground partitions; –, without; +, with.

Table 3. Analysis of variance of log wheat biomass on block, harvest and presence vs. absence of clover, above-ground partitions and below-ground partitions. Model r^2 = 0·97. The dominant factors were harvest (F = 3240), below-ground partitions (F = 1368), clover (F = 500). Interaction effects were much weaker, even when significant

Factor	d.f.	SS	P
Block	2	0·0206	0·0004
Harvest	2	8·4237	< 0·0001
Clover	1	0·6500	< 0·0001
Harvest × clover	2	0·0096	0·0259
Above-ground partitions (AG)	1	0·0053	0·0443
Harvest × AG	2	0·0277	< 0·0001
Clover × AG	1	0·0260	< 0·0001
Harvest × clover × AG	2	0·0161	0·0023
Below-ground partitions (BG)	1	1·7783	< 0·0001
Harvest × BG	2	0·0071	0·0666
Clover × BG	1	0·1139	< 0·0001
Harvest × clover × BG	2	0·0081	0·0448
AG × BG	1	0·0087	0·0101
Harvest × AG × BG	2	0·0092	0·0305
Clover × AG × BG	1	0·0087	0·0103
Harvest × clover × AG × BG	2	0·0080	0·0466

Table 4. Analysis of variance of clover biomass on block, harvest and presence vs. absence of above-ground partitions and below-ground partitions. Non-significant high-order interactions were removed from the analysis. Model r^2 = 0·62. The dominant factors were harvest (F = 59·0) and above-ground partitions (F = 45·3). Below-ground partitions had less of effect (F = 10·8; interaction with harvest F = 5·4)

Factor	d.f.	SS	P
Block	2	27 283	0·0721
Harvest	2	595 499	< 0·0001
Above-ground partitions (AG)	1	228 353	< 0·0001
Below-ground partitions (BG)	1	54 631	0·0014
Harvest × BG	2	54 099	0·0062

N concentration. In the presence of clover, above-ground partitions had only minor effects on N concentration, whereas below-ground partitions reduced wheat N concentration at the second and third harvest. At the third harvest, wheat N concentration was higher in the presence than in the absence of clover when there were no below-ground partitions, and lower when there were below-ground partitions

Table 5. Analysis of variance of arctangent wheat N concentration on block, harvest and presence vs. absence of clover, above-ground partitions and below-ground partitions. Model r^2 = 0·89. The dominant factors were harvest (F = 959), below-ground partitions (F = 46·1, interaction with harvest F = 46·9) and above-ground partitions (F = 26·7)

Factor	d.f.	SS	P
Block	2	0·0088	0·1436
Harvest	2	4·2903	< 0·0001
Clover	1	0·0202	0·0030
Harvest × clover	2	0·0169	0·0248
Above-ground partitions (AG)	1	0·0643	< 0·0001
Harvest × AG	2	0·0365	0·0004
Clover × AG	1	0·0264	0·0007
Harvest × clover × AG	2	0·0301	0·0015
Below-ground partitions (BG)	1	0·1063	< 0·0001
Harvest × BG	2	0·2058	< 0·0001
Clover × BG	1	0·0010	0·4993
Harvest × clover × BG	2	0·0426	0·0001
AG × BG	1	0·0017	0·3851
Harvest × AG × BG	2	0·0069	0·2160
Clover × AG × BG	1	0·0003	0·7043
Harvest × clover × AG × BG	2	0·0269	0·0028

There were strong (Table 1 and Fig. 4) and highly significant (Table 6) effects of the presence of both clover and below-ground partitions on total above-ground wheat N, whereas above-ground partitions had much less of an effect. Total wheat N over the three sampling dates was higher without than with clover, and it was lower with than without below-ground partitions. There was almost no effect of the presence of clover on total wheat N when there were below-ground partitions (Fig. 4). Total wheat N was highest without clover and without below-ground partitions. Total wheat N remained almost constant over time in the treatments with below-ground partitions, whereas the N content increased by 60% from the first to the last sampling date in the treatments without below-ground partitions (Fig. 4). Wheat in monoculture without below-ground barriers contained much more N at the first harvest than the other treatments, whereas the negative effect of clover on total wheat N was lower at the third harvest. Thus, the rate of N accumulation without below-ground partitions over the three harvests was significantly higher with clover than without clover (Fig. 4).

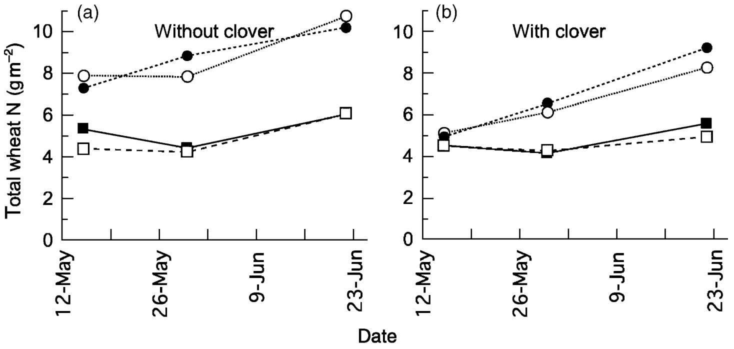

Fig. 4. Total N in above-ground wheat mass over the three harvest dates for (a) wheat grown without clover and (b) wheat with clover. ○, no partitions; ●, above-ground partitions; □, below-ground partitions; ■, both above- and below-ground partitions.

Table 6. Analysis of variance of total wheat N on block, harvest and presence vs. absence of clover, above-ground partitions and below-ground partitions. Non-significant high-order interactions are removed from the analysis. Model $r^2 = 0{\cdot}82$. The dominant factors were below-ground partitions ($F = 678$), harvest ($F = 154$) and clover ($F = 131$). Interactions effects were much weaker, even when significant

Factor	d.f.	SS	*P*
Block	2	6·14	0·0062
Harvest	2	181·24	< 0·0001
Clover	1	77·28	< 0·0001
Harvest × clover	2	1·24	0·3515
Above-ground partitions (AG)	1	2·36	0·0470
Harvest × AG	2	1·01	0·4263
Clover × AG	1	0·22	0·5473
Harvest × clover × AG	2	5·26	0·0127
Below-ground partitions (BG)	1	400·11	< 0·0001
Harvest × BG	2	45·14	< 0·0001
Clover × BG	1	34·30	< 0·0001
AG × BG	1	0·18	0·5838
Harvest × AG × BG	2	5·08	0·0147

Discussion

EFFECTS OF CLOVER AND PARTITIONS ON BIOMASS PRODUCTION

Without any partitions, total above-ground biomass of the wheat + white clover intercrop was 16% higher than the wheat monocrop, which is comparable to yield increases observed in other experiments with cereal–legume intercrops (Anil *et al.* 1998; Hauggaard-Nielsen & Jensen 2001). There was no significant interaction between the effects of above- and below-ground partitions on total intercrop biomass (Table 2), which means the effects of above- and below-ground competition on total biomass production were generally additive.

The largest total biomass was obtained in the absence of both above- and below-ground partitions, when the two species were allowed to fully interact and thus gain access to all available above- and below-ground resources. This suggests that further increases in total biomass production may be possible if the species were even more intermingled than in the standard practice of alternate rows.

The increase in total above-ground biomass from the addition of clover was only 16·3% without any partitions and 17·4% with above-ground partitions only (Fig. 2). Addition of clover had a much larger effect on total biomass in the presence of below-ground partitions (71·3%), because below-ground partitions restricted wheat root growth and biomass. This indicates that it is essential for productivity that plants have access to the entire soil volume. Because of the additive design, it is not possible to know if the same total biomass would have been achieved by increasing the density of wheat. Future studies should investigate the optimal density for both components in this system, as this is one of the basic management tools in intercropping.

INTERACTIONS BETWEEN WHEAT AND CLOVER

The biomass of wheat was reduced by the presence of clover (Table 3 and Fig. 2), which is prima facie evidence of interspecific competition: the negative effects of clover on wheat biomass were stronger than any positive effects (small but significant interactions notwithstanding). The reduction of wheat biomass because of the presence of the clover was considerably greater when there were no below-ground partitions, indicating strong below-ground competition from clover (Figs 2 and 3). Below-ground competition for resources was generally thought to be more intense than above-ground competition in agricultural fields (Wilson 1988).

The clover biomass at the last sample date was significantly increased and wheat biomass decreased by the presence of below-ground partitions (Fig. 2). This could be because wheat is a stronger competitor for one or more below-ground resources, such that wheat obtains more of these resources at the expense of clover when roots of both species are allowed to interact. With partitions, clover gets all of the resources in its 'own' soil volume, in which it does not have to compete with wheat. Alternatively, higher clover biomass with below-ground partitions on the last sampling date could be the result of an interaction between above- and below-ground competition. If the presence of below-ground partitions restricted the growth of wheat, it would then reduce the wheat's above-ground biomass and leaf area, and therefore wheat's ability to compete for light. We know very little about the interactions among competition for different resources.

The clover grew vigorously in the spring and quickly developed a dense canopy. If the clover was sown in the previous spring instead of early autumn, it may have been even more competitive because of a larger root system and greater above-ground biomass when competition began. On the other hand, if the clover crop had been older it may have supplied more N because of decay of senesced clover leaves and roots (Akhonzada *et al.* 2001), as white clover plant material is considered to have a fast release of N during decay (Breland 1994).

The results of any intercropping experiment can be contingent on the densities of the component species (Vandermeer 1988). There is no reason to expect that the results presented here would be very different for other densities that might be appropriate for production, but neither can this possibility be ruled out.

ABOVE- VS. BELOW-GROUND INTERACTIONS

The presence of below-ground partitions, which reduced soil volume available to wheat in the top 40 cm of the soil by 59%, reduced wheat biomass by 32% (Fig. 3) and total wheat N by 37% (Fig. 4). While the mingling of roots of both species is important for biomass production, canopies seem to produce almost the same amount of biomass when they do not interact. This may be because there are numerous below-ground resources and therefore numerous possibilities for niche differentiation in nutrient uptake between the species, whereas plants compete above-ground for only one resource: light. Also, light is directional whereas soil resources are usually distributed in three dimensions. While it is possible that differences in canopy structure or photosynthetic pigments can provide more effective utilization of light and therefore increased biomass production in species mixtures, it may be that each species by itself can effectively utilize the light resource, and that the benefits of intercropping for resource utilization occur primarily below-ground.

NITROGEN ECONOMY

The results are consistent with the hypothesis that interspecific competition for soil and fertilizer N is important. A modest N fertilizer rate was used in the experiment, and it is possible that results would have been different at higher or lower fertilizer rates. At low N levels, N fixation by legumes gives them an advantage, and an increase in N fertilization in grass–clover mixtures usually decreases clover's contribution to total biomass production (Martin & Field 1984). Higher N fertilization can decrease competition for N, and total dry matter yields and grain yields in wheat–clover intercropping are usually increased by higher N fertilizer rates (Jones & Clements 1993; Bergkvist 2003). At higher N supply above-ground competition is likely to become more important (Wilson & Tilman 1991).

The observed effects of clover on wheat N (Fig. 4) are net effects of competition for N between the two species and possible transfer of N through the soil from the clover to the wheat, and it is not possible to distinguish between these effects. Biological N fixation by clover in a mixture reduces competition for soil N. This may be much more important for the N economy of grass–legume mixtures than the actual transfer of N from legume to grass. From the perspective of plant strategies, one would expect a species capable of N-fixation to be a weak competitor for soil N. Higher competitiveness of cereals over legumes for soil N has been observed in a barley–pea intercrop, where pea only acquired 6% of the total soil N taken up by the intercrop (Jensen 1996). An alternative explanation for these results would be differential responses to the presence of partitions (Peach, Benjamin & Mead 2000), such that wheat plants spread under the boxes and obtained more resources from the area between the boxes. While this possibility cannot be ruled out, it seems unlikely because (i) it would require that wheat roots not only grew laterally beyond the boxes but also upwards to the N-richer shallow soil layers, and (ii) N fertilizer was only applied within the boxes.

The fertilizer N input in the present experiment, 70 kg N ha^{-1}, is lower than the recommended N rate of *c.* 150 kg N ha^{-1} for wheat in conventional farming in Denmark, but is similar to the N supply from manure allowed in organic farming (Danish Plant Directorate 2004). N limitation may have restricted the growth of the wheat crop, thus leaving more resources available for the clover, which can compensate for the low N availability by symbiotic N_2 fixation. A low N supply will increase the transfer of N from clover to wheat when roots can interact. One of the problems facing the development of grass–legume intercropping systems is that N transfer from the legume to the grass, one of the objectives of the system, is highest under low productivity, N-limiting conditions. Increasing productivity through N fertilization reduces this desirable interaction.

High N availability early in cereal crop development results in faster growth and usually higher yield, but it can lead to lower plant N concentration and grain protein content later, as these are more influenced by N availability later in development when vegetative growth has slowed down or ceased. This makes the relationships between wheat biomass, N concentration and total wheat N difficult to interpret. The higher N concentration of wheat in the presence of clover at the last harvest (without below-ground partitions) suggests that there was some transfer of N from clover to wheat late in the growth period. The last leaf of the wheat was fully extended on 25 May, and N uptake between the two last sample dates would therefore not affect the crop leaf area and thus have little effect on biomass yield, but could be important for grain protein content (Thorsted, Koefoed & Olesen 2002), which would be advantageous for wheat quality in organic farming systems.

The probable importance of competition for N in this system suggests that cereal–clover intercrops may be advantageous in low-input farming in temperate climates, if the clover can be manipulated to maximize total N use by reducing competition for N by clover and maximizing transfer of N from clover to wheat. Competition between clover and intercropped wheat may be manipulated through the spatial structure of the intercrop (e.g. row width and seeding density; Thorsted, Olesen & Weiner 2006a), temporally through sowing date of the cereal, or directly through cutting of the clover prior to or during the growing season (Thorsted, Olesen & Weiner 2006b).

OTHER EFFECTS OF PARTITIONS

Both the above- and below-ground partitions have numerous effects on crop growth, and caution should therefore be taken in directly comparing results with and without partitions (McPhee & Aarssen 2001). Above-ground partitions may affect the microclimate by reducing heat and water fluxes in the canopy, increasing both air temperature and humidity. Acrylic above-ground partitions increased crop canopy temperature by 7 °C (Brede & Duich 1986). In our experiment, the higher temperature and shading by the partitions may have led to increased senescence of clover and wheat leaves, and the mineralization of these senesced leaves may have contributed N to the wheat crop causing the slightly higher N concentration in wheat when there was above-ground division.

The below-ground partitions primarily restricted the available soil volume with resulting effects on water and nutrient uptake. Effects on water uptake were probably not important in this experiment, as the roots of both the clover and the wheat had reached below the partition depth (40 cm) by onset of spring, and the boxes were kept irrigated during dry periods. Partitions affected access to mineral nutrients including N, and prevented any potential transfer of N from the clover to the wheat intercrop. The 40-cm depth of the partitions was reasonable, as most of the competition for N and the transfer between the two species will occur in the topsoil, where both the root density and the turnover of soil organic matter is largest. It is not possible to separate effects of competition for N from transfer of N between the species.

CONCLUSIONS

Our results confirm that competition for soil resources is very important in low-input intercropping systems, even if a N-fixing species is intercropped. The intermingling of roots of the component species is important for optimal resource utilization, while there is little evidence for improved utilization of light because of intermingling of shoots. Shoot competition between the species can, however, influence the partitioning of biomass between the species. Goals for yield should be based on a specific component, such as total biomass, grain yield or grain quality, because these yield components can behave differently when another species is present.

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