

# Above- and below-ground competition between barley, wheat, lupin and vetch in a cereal and legume intercropping system

M. Mariotti\*, A. Masoni\*, L. Ercoli† and I. Arduini\*

\*Dipartimento di Agronomia e Gestione dell'Agroecosistema, Pisa University, Italy, and †Scuola Superiore Sant'Anna, Pisa, Italy

## Abstract

The effects of intercropping on dry weight (DW) of herbage and nitrogen (N) nutrition of plants of two winter cereals, barley and wheat, and two legumes, white lupin and common vetch, were investigated, and above- and below-ground competition were separated in a fully factorial additive design. Intercropping increased DW compared with the sole species and the increase was higher for the cereals and lupin than for cereals and vetch intercropping systems. Above-ground competition for light reduced DW of cereals and lupin while it did not influence the DW of vetch. Processes involved in below-ground competition increased shoot growth of cereals and reduced shoot growth of legumes. N nutrition of cereals was enhanced by below-ground competition with legumes and N nutrition of vetch was enhanced by above-ground competition with cereals. Cereals had a higher competitive ability than legumes as a result of their below-ground competitive ability. The interaction between above- and below-competition is not predictable: negative, positive and no interaction (additivity) between different types of competition were found. In low-input intercropping systems, when a N-fixing species is present, the mixture of the roots of components is important for the utilization of the soil resources and, when a climbing species is also present, the mixture of shoots can result in an increased utilization of light.

**Keywords:** above-ground competition, barley, below-ground competition, common vetch, durum wheat, white lupin

Correspondence to: Marco Mariotti, Dipartimento di Agronomia e Gestione dell'Agroecosistema, Via S. Michele degli Scalzi 2, 56124 Pisa, Italy.  
E-mail: marcom@agr.unipi.it

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## Introduction

In temperate climates, mixtures of annual legumes and winter cereals are commonly used for herbage production (Anil *et al.*, 1998). Higher yields associated with intercropping occur when the component crops are complementary to each other, resulting in a more effective use of environmental resources, i.e. light, water and nutrients, compared with when grown alone. Higher yields have been documented for intercropping of beans and maize (Willey and Osiru, 1972), barley and peas (Hauggaard-Nielsen *et al.*, 2001a; Chen *et al.*, 2004), oats and vetches (Ercoli *et al.*, 1997), wheat and peas (Ghaley *et al.*, 2005), and wheat and beans (Ghanbari-Bonjar and Lee, 2003). The higher yield of a mixture may also be due to a facilitation process when one population affects the other population in a positive way (Vandermeer, 1989).

Intercropping of cereals and legumes is widely used in low-input agriculture because the mixture of nitrogen (N)-fixing and non-N-fixing crop species provides complementarities in the utilization of resources (Hauggaard-Nielsen *et al.*, 2003). In Mediterranean countries, intercropping of cereals with legumes has been a common cropping system in short-season rain-fed environments, especially because of their increased productivity and sustainability (Papastyliou, 2004). Recently, Mariotti *et al.* (2006) obtained superior yields and land equivalent ratios (LER) of 1.6 for lupins and 1.4 for vetches in intercropping systems with barley and wheat. Previous research, performed in a conventional farming system, reported lower or no yield advantage and LER of 1.1–1.2 in Canada and of 0.95–1.19 in Spain, respectively, for lupins and wheat, and vetches and oats intercropping systems (Caballero *et al.*, 1995; Jannasch and Martin, 1999).

The complementary use of resources occurs as a result of beneficial interactions between the intercropped species, such as (i) structural support for climbing species, which increases leaf area index and light interception (Robinson, 1969; Keating and Carberry, 1993), (ii) exploitation of a larger soil volume, achieved

by higher length and density of roots or by different spatial distribution of roots (Hauggaard-Nielsen *et al.*, 2001b; Li *et al.*, 2006), (iii) increased efficiency of N fixation by legumes (Izaurrealde *et al.*, 1992; Senaratne *et al.*, 1993; Jensen, 1996b), (iv) transfer of symbiotically fixed N from legume to non-legume intercropping (Jensen, 1996a; Xiao *et al.*, 2004) and (v) reduced weed pressure and pathogen infection because of shading and higher biodiversity (Midmore, 1993; Mitchell *et al.*, 2002).

The physical separation of above-ground competition from below-ground competition enables discrimination between the competition for light and the competition for nutrients and water. The relative strengths of above- and below-ground competition are difficult to predict because they vary with availability of resources (Keddy, 1989; Cahill, 1999), ability of plants to change the allocation patterns of assimilates in order to increase organs that acquire the most limiting resources (Tilman, 1988; Wilson and Tilman, 1993, 1995), and with the plant's relative position within a size hierarchy (Cahill, 1999, 2002). Thus, from previous studies, it has emerged that responses to environmental changes are essentially species-specific (Cahill, 2002). In addition, the effect of full competition (above- and below-ground competition together) can be lower (negative interaction), equal (no interaction), or greater (positive interaction) than a combination of the separate effects of above- and below-ground competition (Cahill, 1999).

To better understand the mechanism of higher yields associated with cereal and legume intercropping, it is necessary to investigate (i) the nature of competition between components, (ii) the attributes that determine their competitive ability and (iii) the limiting resources for which crops compete. In this study, focused on annuals, the productivity, plant nutrition, specifically N uptake, and the competition in forage intercropping between two winter cereals and two legumes were assessed by separating the effects of competition for above-ground and below-ground resources. The species chosen, frequently cultivated in Mediterranean areas,

were barley (*Hordeum vulgare* L.), durum wheat (*Triticum durum* Desf.), white lupin (*Lupinus albus* L.) and common vetch (*Vicia sativa* L.).

## Materials and methods

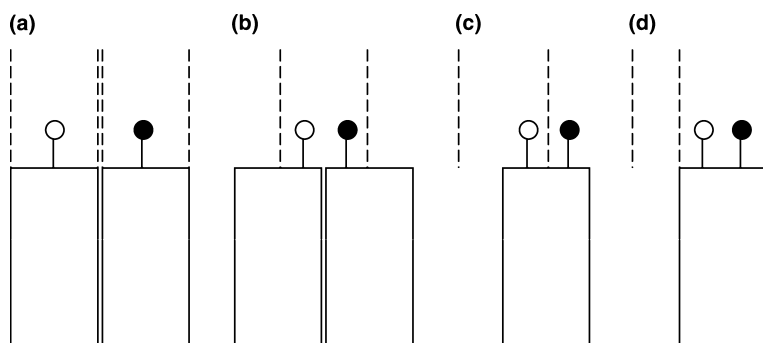
The research was carried out in 2002–2003 and 2003–2004 at the experimental station of the Department of Agronomy and Agroecosystem Management of the University of Pisa, Italy, that is located at a distance of approximately 10 km from the sea (43°41'N, 10°23'E) and 1 m a.s.l.

A 1:1 additive design was used, i.e. the density of each component in any mixture was the same as of the sole crop. The additive design was chosen because it allows interspecific competition to be studied without being confounded by the effects of intraspecific competition, as occurs in replacement designs (Snaydon, 1991).

The separation technique of Donald (1958), modified by Schreiber (1967), was used to separate the effect of above- and below-ground competition between cereals and legumes. The methodology has been utilized successfully to study the nature of root and shoot interactions between crops and weeds (Satorre and Snaydon, 1992), between component crops in intercropping for grain production (Tofinga *et al.*, 1993), and for forage production (Thorsted *et al.*, 2006).

The technique provides four combinations of above and below-ground competition: no competition between species – both shoots and roots separated (Figure 1a); above-ground competition – only roots separated (Figure 1b); below-ground competition – only shoots separated (Figure 1c); and full competition – neither shoots nor roots separated (Figure 1d).

In both years, the experiment was a  $2 \times 2 \times 2 \times 2$  factorial design with three replicates, where the factors were as follows: (i) two cereals; barley, cv. Emilia, and durum wheat, cv. Creso; (ii) two legumes; white lupin, cv. Multitalia, and common vetch, cv. Nitra; (iii) two above-ground competition levels, present or absent;



**Figure 1** The planting arrangements of the intercropping systems between cereals (○) and legumes (●) to give: (a) no competition; (b) above-ground competition; (c) below-ground competition; and (d) full competition.

(iv) two below-ground competition levels, present or absent.

Barley and wheat differ in both shoot and root morphology, and in their competitive ability, when grown in intercropping (Cousens, 1996). White lupin is a legume with a high potential for grain production in Mediterranean areas and can be used in cereal and legume forage mixtures to increase their nutritive value (Jannasch and Martin, 1999; McKenzie and Spaner, 1999). Autumn-sown white lupin is characterized by a rosette stage during which the plant produces leaves without elongation of the corresponding internodes. The rosette stage ends when the main apex becomes floral, which depends on the vernalizing conditions and the vernalization requirements of the genotype under cultivation. Common vetch, an annual legume with a climbing growth habit and high concentrations of crude protein, is widely grown in mixtures with small-grain cereals for hay or herbage production (Lithourgidis *et al.*, 2006). These two legumes differ in growth habit, in both shoot and root morphology, and in their N-fixing capacity (Huyghe, 1991; Caballero *et al.*, 1996; Unkovich and Pate, 2000).

Plants were grown in rows, in aluminium-sided boxes 100 cm long  $\times$  10 cm wide  $\times$  30 cm deep, filled with a soil whose main physical and chemical properties were as follows: 33.9% sand, 20.8% silt and 45.3% clay; pH of 7.2, organic matter content (Walkley and Black method) of 18.5 g kg<sup>-1</sup>, total CaCO<sub>3</sub> content (Scheibler method) of 11.2 g kg<sup>-1</sup>, total N content (Kjeldhal method) of 0.9 g kg<sup>-1</sup>, available P content (Olsen method) of 43 ppm and available K content (ammonium acetate test method) of 167 ppm. The boxes were oriented in a N-S direction and the aerial partitions were made of reflective material. Sowing took place on 31 October 2002 and 25 October 2003, at densities equivalent to 400 viable seeds per m<sup>2</sup> for barley and durum wheat, 100 viable seeds per m<sup>2</sup> for white lupin, and 200 viable seeds per m<sup>2</sup> for common vetch, either for sole crops and intercropping. The symbiosis between white lupin and its specific rhizobium (*Rhizobium lupini*) was promoted by mixing the seeds of white lupin with slightly wet soil where a white lupin crop had been cultivated in the previous year. No use of fertilizers or herbicide was made. To prevent any below-ground competition for water, all boxes were watered daily to field capacity with a drip-irrigation system. The experiment was netted to exclude birds.

Sole crops and intercropping systems were harvested at the dough-ripening stage of cereals (decimal code 83–85 of the scale of Zadoks *et al.*, 1974), while white lupin and common vetch were harvested at the pod-filling stage. Within each species, no difference in phenological stage was recorded between sole crops and intercropping systems. The herbage grown in each box

was cut at ground level and was separated into cereals and legumes. Winter cereal and legume plants were divided into stems plus leaves (referred to as the vegetative part in the rest of the text), spikes or pods (reproductive part), and roots. Throughout the rest of the text, 'shoot' refers to the sum of the vegetative and reproductive plant parts. The roots were separated from the soil by gently washing with water. Plant parts were oven-dried for determination of dry weight (DW) at 75°C to constant weight and analysed for N concentration (NC) by the microKjeldahl method. N yield (NY) was obtained by multiplying NC by DW.

The resource complementarity was measured by the relative total yield (RYT) and, according to De Wit and Van Den Bergh (1965), was expressed as  $RYT = (Y_{ab}/Y_{aa}) + (Y_{ba}/Y_{bb})$ , where  $Y_{ab}$  is the yield (mass of plant material per unit land area) of crop 'a' growing in association with crop 'b' in intercropping,  $Y_{ba}$  is the yield of crop b growing in association with crop a in intercropping, and  $Y_{aa}$  and  $Y_{bb}$  are the yields of crop a and crop b respectively in sole cropping (i.e. no competition).

The competitive ability of a crop in intercropping, relative to the other, was measured by the Competitive Balance Index (Cb) and, according to Wilson (1988), was expressed as  $Cb = \ln[(Y_{ab}/Y_{aa})/(Y_{ba}/Y_{bb})]$ .

## Statistical analyses

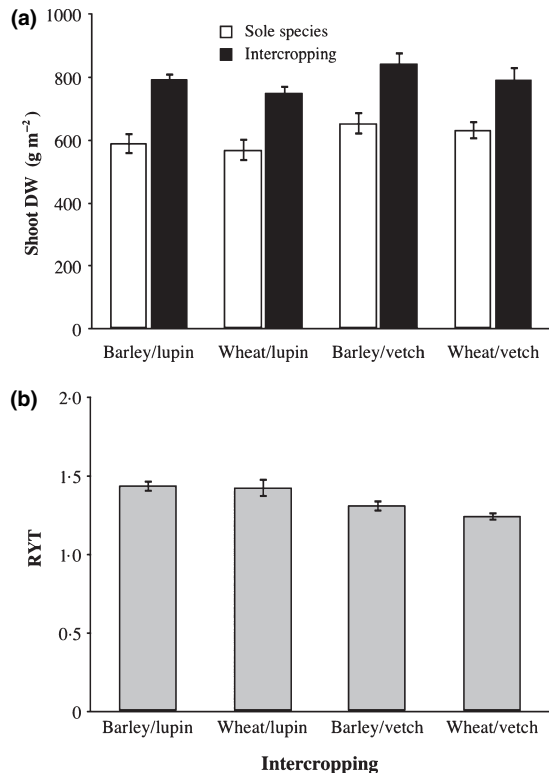
Data were analysed statistically by analysis of variance (ANOVA), using COSTAT statistical package (version 6.4, CoHort Software, Monterey, CA, USA). For each cereal and legume intercropping system, ANOVAs on plant DW, NC and NY were performed as a 2  $\times$  2  $\times$  2 factorial design (i.e. 2 years  $\times$  two levels of above-ground competition  $\times$  two levels of below-ground competition) with three replicates. ANOVAs on RYT and Cb were performed as a 2  $\times$  3 factorial (i.e. 2 years  $\times$  three types of competition – above-, below- and full competition) with three replicates.

No statistically significant year effect or year  $\times$  competition treatment interactions were recorded, so data reported are the means of the 2 years. The treatments received an optimal water supply in both years, which probably caused the effect of year to be non-significant. Significantly different means were separated at  $P < 0.05$  by the least significant difference test (Snedecor and Cochran, 1980).

## Results

### Resource complementarity

The DW of the four sole species, obtained in conditions of no competition between components, were similar,



**Figure 2** (a) Shoot dry weight (DW) and (b) relative total yield (RYT) of barley and white lupin (lupin), wheat and white lupin, barley and common vetch (vetch), and wheat and common vetch, intercropping systems. Values for intercropping systems were obtained in conditions of full competition. Shoot DW data were calculated on the basis of the same surface area: the values for sole species were averaged and the values for intercropping systems were pooled. Vertical bars indicate standard error of mean.

ranging from 5.7 t ha<sup>-1</sup> recorded for wheat and white lupin to 6.5 t ha<sup>-1</sup> for barley and common vetch (Figure 2a). In conditions of full competition between components, shoot DW of intercropping systems was higher than for sole species with the highest difference proportionately being recorded in the barley and white lupin intercropping system (+0.35) and the lowest in wheat and common vetch intercropping system (+0.25). To make a correct comparison, data in Figure 2a were calculated on the same surface area, and not on a species basis, so the sole species values were averaged and the intercropping values were pooled. Resource complementarity of intercropping was evidenced by RYT values that were always higher than 1.0, with slightly higher values for the cereals and white lupin intercropping systems than for the cereals and common vetch intercropping systems (Figure 2b).

### Dry weight of cereals

Above-ground competition with white lupin reduced shoot and root DWs of barley by proportionately 0.36 and 0.29 and shoot and root DWs of wheat by 0.41 and 0.43, with respect to treatments excluding competition (Figure 3). Below-ground competition with white lupin increased shoot DWs of barley and wheat by 0.26 and 0.14 and reduced root DWs of barley and wheat by 0.10 and 0.18 respectively. Above-ground competition with common vetch reduced shoot and root DWs of both cereals by about 0.45 while below-ground competition increased slightly shoot DW and reduced root DW of both cereals.

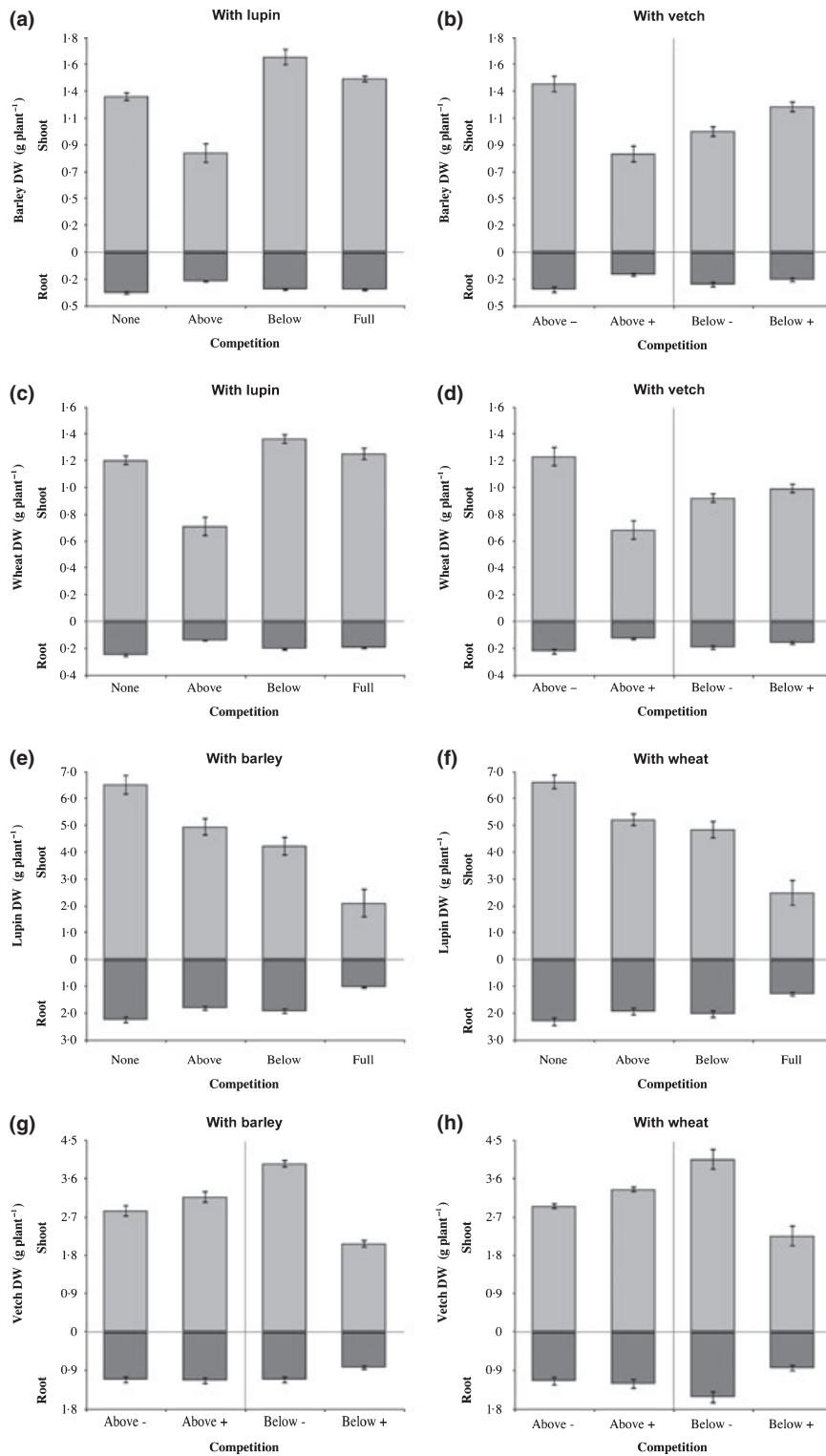
The effect of full competition with white lupin was lower than expected on the basis of the separate effects of above- and below-ground competition (the above- $\times$  below-ground interaction was negative), leading to a slight increase in shoot DWs of barley and wheat (+0.11 and +0.04 respectively) and to a modest decrease in root DWs (-0.08 and -0.22). Full competition with common vetch gave no evidence of interaction between above- and below-ground competition.

Above-ground competition did not modify allocation patterns of biomass between roots and shoots of cereals. On the contrary, below-ground competition with both legumes modified the root:shoot ratios of cereals from about 0.26 to 0.20 in barley and from 0.21 to 0.15 in wheat (data not shown).

### Dry weight of legumes

Legumes responded to competition from cereals in a different way. In white lupin plants, shoot and root DWs were reduced by competition with cereals (Figure 3). Above-ground competition with both cereals reduced shoot and root DWs of white lupin proportionately by about 0.23 and 0.18 respectively. Below-ground competition with barley reduced shoot DW of white lupin by 0.36 and root DW of white lupin by 0.15, while below-ground competition with wheat reduced shoot and root DWs of white lupin by 0.26 and 0.11 respectively. The effect of above- and below-ground competition together (full competition) was greater than a mathematical combination of the separate effects (positive interaction): full competition with cereals reduced shoot and root DWs of white lupin by 0.65 and 0.55 respectively. Below-ground and full competition with cereals reduced shoot DW more than root DW, so that the root:shoot ratio was increased (from 0.35 to about 0.48 with both cereals).

In common vetch plants, there was no interaction between above- and below-ground competition. Above-ground competition with barley and wheat did not modify significantly the DWs of shoot and root,



**Figure 3** Shoot and root dry weight (DW) of barley, wheat, white lupin (lupin) and common vetch (vetch) as affected by the interaction [(a), (c), (e) and (f)], or by the mean effect [(b), (d), (g) and (h)] of above- and below-ground competition. Vertical bars indicate standard error of mean.

**Table 1** Proportion of shoot mass represented by the pods, number of pods per plant and dry weight (DW) per pod of legumes, as affected by types of competition with cereals (barley and wheat).

Legume	Type of competition	With barley			With wheat		
		Proportion as pods	No. pods plant <sup>-1</sup>	DW per pod (mg)	Proportion as pods	No. pods plant <sup>-1</sup>	DW per pod (mg)
White lupin	Above–	0.158 <sup>a*</sup>	4.3 <sup>a</sup>	222.2 <sup>a</sup>	16.0 <sup>a</sup>	4.3 <sup>a</sup>	225.0 <sup>a</sup>
	Above+	0.105 <sup>b</sup>	1.5 <sup>b</sup>	251.9 <sup>a</sup>	8.9 <sup>b</sup>	1.5 <sup>b</sup>	234.6 <sup>a</sup>
	Below–	0.226 <sup>a</sup>	3.2 <sup>a</sup>	413.9 <sup>a</sup>	21.2 <sup>a</sup>	3.3 <sup>a</sup>	395.7 <sup>a</sup>
	Below+	0.037 <sup>b</sup>	2.6 <sup>a</sup>	60.2 <sup>b</sup>	3.7 <sup>b</sup>	2.5 <sup>b</sup>	64.0 <sup>b</sup>
Common vetch	Above–	0.144 <sup>b</sup>	4.7 <sup>b</sup>	88.8 <sup>b</sup>	15.2 <sup>b</sup>	4.8 <sup>b</sup>	95.4 <sup>b</sup>
	Above+	0.262 <sup>a</sup>	6.1 <sup>a</sup>	137.1 <sup>a</sup>	27.5 <sup>a</sup>	6.4 <sup>a</sup>	145.7 <sup>a</sup>
	Below–	0.226 <sup>a</sup>	6.5 <sup>a</sup>	136.7 <sup>a</sup>	23.0 <sup>a</sup>	6.8 <sup>a</sup>	137.5 <sup>a</sup>
	Below+	0.179 <sup>b</sup>	4.3 <sup>b</sup>	89.2 <sup>b</sup>	19.7 <sup>b</sup>	4.3 <sup>b</sup>	103.7 <sup>b</sup>

\*In each legume and type of competition, values followed by the same letter are not significantly different at  $P \leq 0.05$ .

while below-ground competition reduced shoot DW proportionately by about 0.45 and root DW by about 0.35 (Figure 3). Below-ground competition with both cereals increased the root:shoot ratio of common vetch from 0.37 to 0.44.

Competition from cereals negatively affected the reproductive plant parts of white lupin more than the vegetative ones, owing to a reduced partitioning of dry matter to pods (Table 1). The effect was higher with below-ground than with above-ground competition and was caused by DW per pod for the former and by number of pods per plant for the latter. In the common vetch, above-ground competition with cereals increased the reproductive parts as a proportion of the total plant, owing to an increase in the proportion of shoot DW represented by the pods from 0.15 to 0.27 (Table 1): the effect was caused by an increase in the DW per pod and by the number of pods per plant. In the common vetch, below-ground competition with both cereals reduced the contribution of pods to total shoot DW, an effect that was caused by the decrease in both DW per pod and number of pods per plant.

### Competitive ability

Cereals had a higher below-ground competitive ability than legumes, and legumes had a higher above-ground competitive ability than cereals (Table 2). In conditions of full competition, the competitive ability of cereals was higher than that of white lupin but the same as that of common vetch. Values for barley were a little higher than values for wheat with all types of competition.

### Nitrogen yield

Nitrogen concentration showed little variation between the different types of competition. Consequently, the

**Table 2** Competitive balance index (on dry weight basis) of four intercropping systems as affected by type of competition.

Type of competition	Intercropping system			
	Barley and white lupin	Wheat and white lupin	Barley and common vetch	Wheat and common vetch
Above	-0.17 <sup>c*</sup>	-0.30 <sup>c</sup>	-0.61 <sup>c</sup>	-0.70 <sup>c</sup>
Below	0.67 <sup>b</sup>	0.43 <sup>b</sup>	0.93 <sup>a</sup>	0.72 <sup>a</sup>
Full	1.24 <sup>a</sup>	1.01 <sup>a</sup>	0.16 <sup>b</sup>	-0.06 <sup>b</sup>

\*In each column, values followed by the same letter are not significantly different at  $P \leq 0.05$ .

pattern of NY was similar to that of DW. Significant variations, however, were recorded in cereals and white lupin intercropping systems: The NC of cereals was increased by below-ground competition with white lupin, whereas NC of white lupins was decreased by all type of competition with cereals (Table 3).

Because of the combined effect of DW and N concentration, below-ground and full competition enhanced NY of barley by +5 and +2 mg N plant<sup>-1</sup> respectively, for below-ground and full competition and NY of wheat by +3 and +2 mg N plant<sup>-1</sup>, and reduced that of white lupin, compared with treatments excluding competition (Figure 4).

In the cereals and common vetch intercropping system, the above-ground competition reduced NY of both cereals by about 4 mg N plant<sup>-1</sup> while it enhanced NY of common vetch by 8 mg N plant<sup>-1</sup> with barley and 12 mg N plant<sup>-1</sup> with wheat as a companion species (Figure 4). With below-ground competition, NY of barley and wheat was unchanged, with respect to treatments excluding competition, and NY of common vetch was lower.

**Table 3** Cereals and white lupin intercropping systems: nitrogen concentration ( $\text{g kg}^{-1}$  DM) of shoots of barley, wheat and white lupin as affected by type of competition.

Type of competition	Nitrogen concentration			
	Barley	Wheat	White lupin	
			With barley	With wheat
None	7.9 <sup>b*</sup>	7.3 <sup>b</sup>	15.7 <sup>a</sup>	16.1 <sup>a</sup>
Above	8.1 <sup>b</sup>	7.6 <sup>b</sup>	13.2 <sup>b</sup>	14.4 <sup>b</sup>
Below	9.2 <sup>a</sup>	8.7 <sup>a</sup>	11.5 <sup>b</sup>	12.5 <sup>c</sup>
Full	8.3 <sup>ab</sup>	8.4 <sup>a</sup>	9.0 <sup>c</sup>	9.9 <sup>d</sup>

\*In each column, values followed by the same letter are not significantly different at  $P \leq 0.05$ .

## Discussion

Intercropping is an old and widespread practice in agriculture which is based on the management of plant interactions to maximize production of DW (Trenbath, 1974; Ofori and Stern, 1987). Higher yields result from resource complementarity producing more efficient resource use via niche separation (Wilson, 1988) or facilitative interactions between components (Hauggaard-Nielsen and Jensen, 2005).

In this study, all intercropping systems had higher shoot DWs than sole species and consequently RYT values greater than 1.0, regardless of the type of competition and the species, indicating that the complementary facilitation dominated over the competitive interference. This is important because the research was carried out without the application of fertilizer and, in this situation, enhanced productivity of herbage with a high nutritive value is desirable. The results in this study are comparable to increases in yield observed in other experiments with the same cereal and legume intercropping species (Jannasch and Martin, 1999; Mariotti *et al.*, 2006; Dhima *et al.*, 2007).

Although intercropping always gave higher yields than sole species, the single components of the mixture responded to the types of competition in different ways, and often with a reduction in their DW. Indeed, RYT values higher than 1.0 and lower than 2.0 indicate that resource complementarity and competition interference between companion crops occurred at the same time.

Barley and wheat showed similar behaviour in intercropping systems, although response in yield and competitive ability of barley were slightly higher than those of wheat, i.e. barley gained slightly more advantage and suffered slightly less competition from legumes than wheat. Growth characteristics that allow more rapid establishment of barley plants than wheat plants,

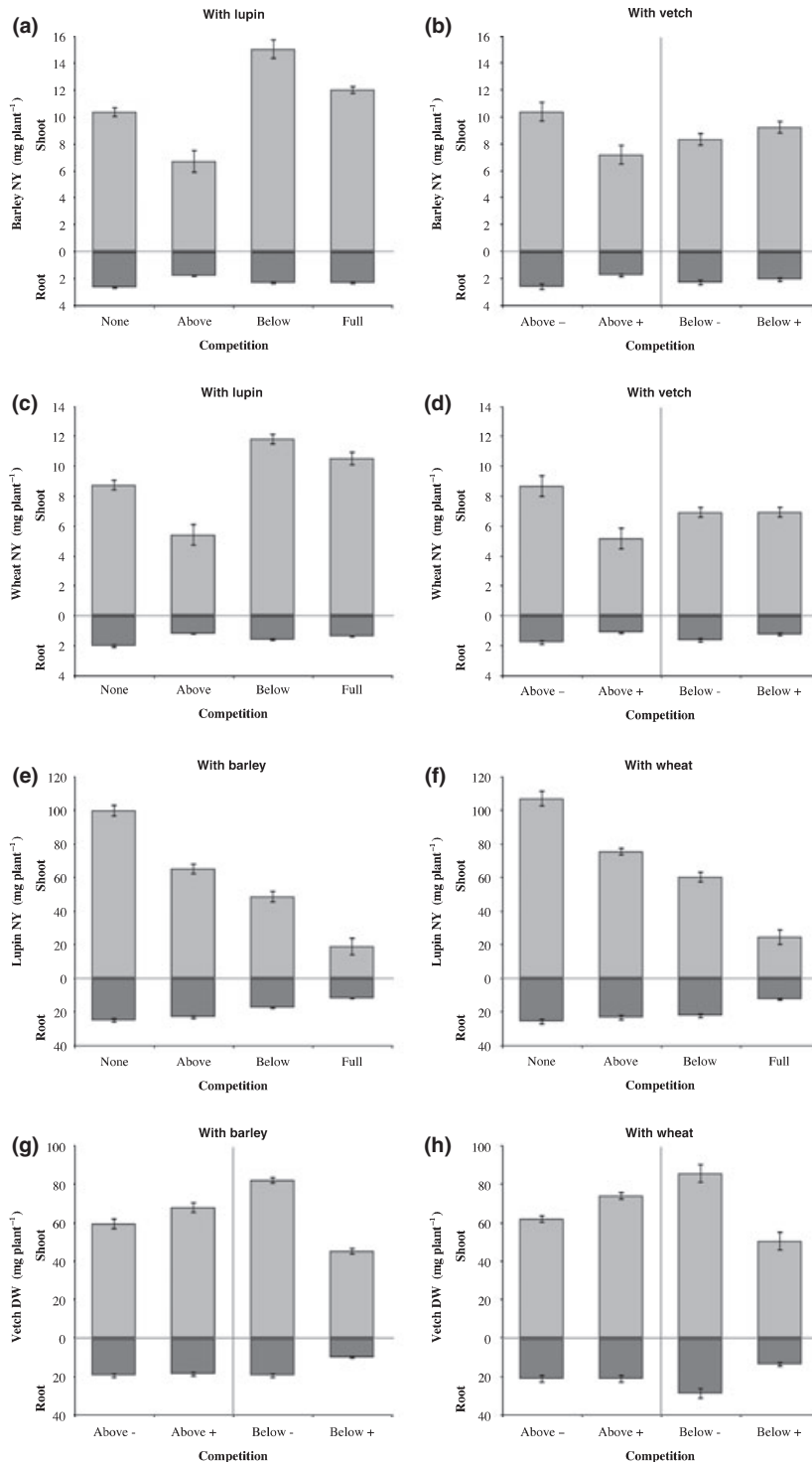
such as an earlier rate of leaf production, are likely to be the determining factors leading to the observed dominance exerted by this species when intercropped (Cousens, 1996; Jensen, 1996b).

Above-ground competition reduced the DW of the cereals and white lupin, with the relative magnitude of this effect being greatest in wheat and lowest in white lupin while it did not influence the DW of common vetch. However, in all species, above-ground competition did not alter root:shoot ratios, because modifications in biomass allocation to roots were similar to those in shoots. This indicates that the lowered carbohydrate synthesis arising from limited light availability reduced root and shoot growth equally.

Higher yields by mixtures have often been attributed to a more efficient use of light by their canopy (Keating and Carberry, 1993). Among above-ground factors, the components that affect the light regime of plant canopies are the amount and quality of incident radiation, the canopy architecture (LAI and leaf orientation) and the optical properties of leaves (pigment content and absorbance of incident radiation) (Ercoli *et al.*, 1993; Sinoquet and Caldwell, 1995).

The reductions in DW reported for cereals and white lupin with above-ground competition are probably related to the limited light intercepted by the reduced canopies, and similar results for cereals have been obtained by Tofinga *et al.* (1993). Also in white lupin Strydhorst *et al.* (2008) reported that the amount of light available at the top of the canopy was reduced proportionately by about 0.50 in the presence of barley. In addition, considering that NC is closely related to chlorophyll concentration, absorbance of incident radiation and photosynthetic capacity in a wide range of crops (Sinclair and Horrie, 1989; Ercoli *et al.*, 1993), it is argued from the data reported in Table 3 that photosynthetic capacity of white lupins was also reduced by above-ground competition. The DWs of common vetch were not modified by above-ground competition, probably because companion cereals provide structural support and contribute to increase light interception (Ercoli *et al.*, 1997).

Conversely, below-ground competition increased shoot growth of cereals and decreased that of legumes, while it reduced root growth in all species. Thus, below-ground competition modified the pattern of biomass allocation in the plant, and the root:shoot ratio decreased in cereals and increased in legumes. A decrease in root:shoot ratio is generally considered an indicator of an increase of availability of soil nutrients, as plants adjust their root weight in response to environmental conditions to maximize relative growth rate (Martin and Field, 1984; Aerts *et al.*, 1991). In cereals, the effect was probably because of the facilitative effects of mixing their roots with those of



**Figure 4** Shoot and root nitrogen yield (NY) of barley, wheat, white lupin (lupin) and common vetch (vetch) as affected by the interaction [(a), (c), (e) and (f)], or by the mean effect [(b), (d), (g) and (h)] of above- and below-ground competition. Vertical bars indicate standard error of mean.



leguminous plants, mainly arising from the transfer of N from the legumes (Xiao *et al.*, 2004). In this study, although it was not possible to quantitatively determine the N transfer from legumes to cereals, either directly or indirectly, NY of cereals was increased by 10–20 kg N ha<sup>-1</sup> when cereal roots were intermingled with those of legumes. Other possible facilitation effects recorded for roots of white lupin have been reported by Suong *et al.* (2005). In the legumes, the increase in the root:shoot ratio because of below-ground competition indicates the responses of the plants to the lower fertility conditions caused by the roots of the cereals.

The balanced-growth hypothesis of Shipley and Meziane (2002), which states that plants preferentially allocate resources to the organs acquiring the most limiting resources, is confirmed by the results obtained with below-ground competition. On the contrary, the data on above-ground competition do not support this hypothesis, as the root:shoot ratio was unchanged in all cereal and legume intercropping systems. Crucial to this hypothesis is the assumption that light interception and nutrient uptake are proportional to leaf and root, and shoot biomasses, although light interception depends on leaf area and nutrient uptake depends on root surface area. Consequently, it is not possible to exclude morphological adaptive strategies in the plants.

In the legumes, the competition modified the biomass allocation between reproductive and vegetative organs, with generally negative effects being more pronounced in white lupin than in common vetch, and with below-ground competition greater than above-ground competition. Other authors have reported that white lupin responds to environmental stress primarily by decreasing reproductive organs (Herbert, 1977; Withers, 1979), and similar results have been reported for intercropping with white lupin (Carruthers *et al.*, 2000). A greater effect of below-ground than above-ground competition on inflorescence was also reported by Tofinga *et al.* (1993). In common vetch, a species with a climbing growth habit, an increase in the incidence of pods was observed with above-ground competition, probably because of the greater amount of radiation intercepted by lower parts of the stem when a cereal plant provided physical support (Ercoli *et al.*, 1997). The greater sink strength (through increased number and mass of pods) that resulted, promoted a higher N demand and was probably the cause of the enhanced NY of common vetch (Figure 4).

Nitrogen nutrition of legumes requires some consideration. In previous studies carried out with full competition between legume and non-legume intercropping, it emerged that the non-legume was found to be more competitive than the legume for soil N, forcing the legume to rely mainly on N<sub>2</sub> fixation for its N

nutrition. In these conditions, the legume's proportion of N derived from the atmosphere increases as a result of intercropping with a non-legume crop, although the amount of N accumulated in the plant will be lowered (Danso *et al.*, 1987; Schmidtke *et al.*, 2004). Clearly these results were caused by below-ground and not by above-ground competition (Tofinga *et al.*, 1993). In this study, although no data about N<sub>2</sub> fixation were collected, these findings can help to explain the N nutrition of common vetch, because in this species it seems that competition did not reduce the ability to obtain N from soil and/or from N<sub>2</sub> fixation, and the competition effect on the N nutrition appeared indirect, because of variations in DW. Instead in white lupin, all types of competition from cereals reduced both NC and NY: thus it seems that white lupin and cereals competed highly for soil N, but also that competition reduced the N<sub>2</sub>-fixing capacity of the legume.

Cereals had higher below-ground competitive ability than legumes and this was apparently not caused by differences in allocation of biomass to the roots, and legumes presented higher above-ground competitive ability than cereals, again not apparently because of differences in shoot allocation: no clear pattern emerges on the relative cause and effect between competitive ability and biomass allocation pattern. Higher below-ground competitive ability of cereals than legumes can be the result of the much finer roots of cereals (Martin and Snaydon, 1982), resulting in more efficient exploration of the soil volume, a faster development of roots (Hauggaard-Nielsen *et al.*, 2001b) and a higher N-uptake capacity (Jensen, 1996a; Karpenstein-Machan and Stuelpnagel, 2000). The higher above-ground competitive ability of legumes, compared with cereals, can be ascribed to the climbing growth habit of common vetch and to the greater size of the shoots of white lupin (about six times larger than the shoot of cereals – see Figure 3). As mentioned before, the competitive ability of a plant may not be directly correlated to the pattern of allocation of biomass because plants grown in conditions of limiting resources may adopt adaptive strategies, without modifying their allocation of DW (Aerts *et al.*, 1991; Grime *et al.*, 1991).

Above- and below-ground competition can have additive and non-additive effects on plant growth and the non-additive effect may be positive or negative (Cahill, 1999). A negative interaction results when one type of competition mitigates the negative effect of the other type of competition. In this study, negative interaction was found in cereals that compete below-ground with white lupin, probably because cereals compete better for the aerial space with legumes when they have intermingled roots because, in these conditions, the increased N nutrition of cereals (Table 2 and

Figure 4), arising from a real below-ground facilitation, allows an increase in shoot growth, thus reducing the severity of above-ground competition.

A positive interaction was also found between above- and below-ground competition. This occurred in white lupin intercropped with cereals. Positive interaction can result because below-ground competition reduced NC and NY in white lupin (Table 2). In these conditions, there was possibly a lower photosynthetic capacity of the leaves and thus the negative effect of the shading (above-ground competition) was enhanced (Cahill, 2002).

There was no interaction between above- and below-ground competition when the cereals were intercropped with common vetch. The N transfer from common vetch to graminaceous plants is low and sometimes uncertain (Papastylianou and Danso, 1991; Kurdali *et al.*, 1996) and the climbing growth habit of legumes can confer a high above-ground competitive ability (Tofinga *et al.*, 1993). In these conditions, where a low below-ground facilitation and a high above-ground competition from the companion species do occur, the mitigation effect of one type of competition (below-ground) on the other type (above-ground) is not possible.

In conclusion, this study showed that competition had different effects on the different species and that the interaction between above- and below-ground competition varied among species from negative to positive synergy and additivity. Thus, the distinct differences in the canopy structure and root activity of different components of intercropping systems can affect the relative importance of above- and below-ground competition, and their interaction. Interspecific competition and facilitation can exist simultaneously. The results suggest that, in low-input intercropping systems, when a N-fixing species is present, the intermingling of root of the component species is important for utilization of soil nutrients, while there is little evidence for increased utilization of light because of intermingling of shoots, although the species with climbing growth habit, like common vetch, can benefit. Modifying sowing time of the components (delaying the seeding time of the species with the higher competitive ability) and/or the design of the intercropping system, such as modifying the seeding ratio or row configuration, could possibly reduce the competition and enhance facilitation effects, with increased yield and nutritive value of the herbage.

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