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REGULAR ARTICLE

White lupin leads to increased maize yield through a soil fertility-independent mechanism: a new candidate for fighting *Striga hermonthica* infestation?

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Abstract Nitrogen (N)-deficiency and lack of phosphorus (P) availability are major constraints to maize yields in Western Kenya. In a two-season field study in the lake Victoria basin, we tested the capacity of white lupin (*Lupinus albus* (L.), *cv.* Ultra), as a nitrogen-fixing crop with a highly efficient P-acquisition capacity, to increase maize yields when used as a companion or cover crop, or as a source of organic matter. Each experiment was performed on three different fields (Vertisols) differing in N/P availability, previous cropping history and in levels of infestation by the parasitic weed *Striga hermonthica* (Del.) Benth. Our results show that white lupin led to significantly higher yields of maize when used as a cover crop. When lupin was grown as a companion crop, it also slightly enhanced the yield of the co-cultivated maize. When lupin shoots were incorporated to the soil, the positive effect of lupin on maize growth was field-dependent and only occurred in the field most heavily infested with *S. hermonthica*. Despite the beneficial impact on maize yield, no clear effect of lupin on soil N and P availability or on maize N/P uptake were observed. In contrast, lupin significantly inhibited infestation of maize by *S. hermonthica:* when lupin was grown together with maize in pots inoculated with *S. hermonthica*, the emergence of the weed was strongly reduced compared to the pots with maize only. This work opens a new range of questions for further research on white lupin and its potential beneficial impact as a *S. hermonthica*-inhibiting crop.

Keywords *Lupinus albus* · *Desmodium uncinatum* · *Striga hermonthica* · *Zea mays* · Soil fertility · Cluster roots

Introduction

Phosphorus (P) deficiency has been estimated to reduce crop yield on more than 30% of the world's arable land (Vance et al. 2003). In order to cope with

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P deficiency, most plants associate with mycorrhizal fungi and take advantage of the symbiosis for their P nutrition (Li et al. 2006; Miller 2000; Rahman et al. 2006). However, there are also some non-mycorrhizal species, which grow well on soils poor in available phosphate. These plants, which belong to different families, have a common root structure, called cluster or proteoid roots (Lamont 2003; Neumann and Martinoia 2002; Purnell 1960; Shane and Lambers 2005). Cluster roots are very densely branched roots that excrete large amounts of organic anions, mostly citrate and malate, which are responsible for phosphate solubilisation. One of these non-mycorrhizal, cluster-root producing plants, is white lupin (*Lupinus albus* (L.)). White lupin's ability to grow on soils where P is present in sparingly soluble forms has been studied intensively for the last 20 years (Gardner et al. 1982, 1983; Neumann et al. 1999; Shane et al. 2003; Shen et al. 2005; Weisskopf et al. 2005, 2006a, b). Furthermore, as a leguminous plant, white lupin has the ability to enrich the soil in nitrogen (N) through symbiotic fixation. Thus, it is a good candidate crop for soils where P and/or N availability is low. However, though white lupin is cultivated in many regions of the world, to our knowledge, no study actually assessed the potential beneficial impact of lupin with respect to its efficient P-acquisition capacity in the field. It is still unclear whether the solubilised P is exclusively recovered by lupin or whether part of it may be exchanged between the rhizospheres of the crops (in the case of intercropping), or become available for the next crops after root organic matter recycling (in the case of crop succession or shoot incorporation to the soil). The only literature data available on this topic come from pot experiments and show contradictory results, possibly due to the difference in the soils used or in the reaction of the following crop (wheat vs. sorghum and maize) to the presence of lupin: El Dessougi et al. (2003) observed a reduced growth and yield of maize when using white lupin both as a companion and as a cover crop. Similarly, Cavigelli and Thien (2003) observed a decreased uptake of P by sorghum after white lupin cropping followed by shoot incorporation into the soil. In contrast, other studies reported that white lupin induced a better growth and P uptake of wheat when used as companion crop (Kamh et al. 1999) and as preceding crop (Kamh et al. 1999; Nuruzzaman et al. 2005). While all these studies were performed in pot experiments, some similar investigations were carried out under field conditions (Horst et al. 2001; Jemo et al. 2006; Kamh et al. 2002), but with other leguminous species. These authors used a collection of leguminous cover crops and observed that the P uptake and yield of maize were increased after pigeon pea (*Cajanus cajan* (L.) Millsp), butterfly pea (*Clitoria ternatea* (L.)), hyacinth bean (*Lablab purpureus* (L.)), cowpea (*Vigna unguiculata* (L.) Walp.) and soybean (*Glycine max* (L.) Merr.). These reports highlight the possibility of certain leguminous crops to combine the advantages of N-enrichment through symbiotic fixation and of P uptake improvement of the co-cultivated or subsequently cultivated crops. Thus, the question of whether white lupin would also show this kind of dual effect in the field, or whether it would be deleterious to co-cultivated or following crops, still remains unsolved.

We chose to address this question in Western Kenya, where soils are extremely poor in nitrogen (N) and available P (P_a) (Okalebo et al. 2006; Sanchez 2002) and where mineral fertilizers are unaffordable to resource-poor farmers. The fact that white lupin can be used as fodder and also for human consumption (Sujak et al. 2006) is an additional advantage of this leguminous crop. However, our first aim in introducing lupin into the farming systems in Western Kenya was to determine whether it could improve growth and yield of the main cash crop maize. To find out the most favourable way to implement lupin into the existing agricultural practices, we tested the effect of lupin on maize by using it in three different cropping systems: as a companion crop, as a cover crop and as a source of organic matter.

In addition to the use of lupin as a companion crop of maize, *Desmodium uncinatum* (Jacq.) DC. (Fabaceae), a comparative leguminous species, was also included in the intercropping experiment. *D. uncinatum* is used as a leguminous fodder crop in Western Kenya and is one of the key species in the "push-pull system" (Khan et al. 2002). In addition to the improvement of soil fertility through symbiotic N fixation, this plant has also been shown to repress maize attacks by lepidopteran stem-borers and by witchweed (*Striga hermonthica* (Del.) Benth.) (Khan et al. 2000; Tsanuo et al. 2003). However, there are indications that some Desmodium species may have high demands in phosphorus (Ascencio 1996; Fist et al. 1987; Johansen et al. 1980). This is why we used it together with lupin as maize companion crops, to test whether the P needs of *D. uncinatum* could be met, at least partly, by lupin.

In view of its efficient P-mobilization strategy and its ability to fix nitrogen, we hypothesised that white lupin would improve the nutrition of maize in the poor fertility soils and low input farming systems of Western Kenya. To test this hypothesis, we developed the following objectives: i) to determine the effect of white lupin on growth and yield of maize under field conditions, ii) to find out the best way of integrating white lupin into the local agricultural practices and, iii) provided positive effects of lupin occurred, to elucidate the mechanisms (e.g. improved N/P uptake) responsible for them.

Furthermore, during the monitoring of the field experiments carried out to investigate the above mentioned questions, we noticed a new positive feature of white lupin: in the fields where maize was cropped together with or following white lupin, less damage was caused by the witchweed *Striga hermonthica. S. hermonthica* is an obligate root parasite (Bouwmeester et al. 2003) that has been estimated to have invaded already 40% of the arable land in sub-Saharan Africa and to cause annual losses of $7 to $13 billions (Khan et al. 2006a). To test the effect of lupin on *S. hermonthica* in conditions where the amounts of *S. hermonthica* seeds could be controlled, a pot experiment was designed to compare the fitness of maize and its resistance to *S. hermonthica* when grown alone or in the presence of lupin.

Material and methods

Study site, soil characteristics and seed material

Study site

The trials were carried out in Western Kenya on the Mbita Point field station of the International Centre of Insect Physiology and Ecology (ICIPE) (00° 25’S, 34° 13’E). The station is situated at 1200 m above see level in the Lake Victoria basin and is characterized by a savannah vegetation. There are two rainy seasons, a short one lasting usually from October to December and a long one from March to July. Average annual rainfall is 1150 mm and mean minimum and maximum temperature are 20°C and 28°C, respectively. The field trials were carried out during the short rainy season, starting in November 2005 and ending in February 2006 and during the long rainy season from March to June 2006. Due to scarce rainfall during the short rainy season of 2005 to 2006, fields were additionally irrigated once a week for 2 h to 3 h. Each experiment was carried out simultaneously on three different fields, differing in soil characteristics (see below) and in cropping history: during the three preceding years, field 1 had maize and soybean, field 2 cassava intercropped with cowpea, and field 3 a mixture of maize and different grasses.

Soil characteristics

In each field, a soil profile was dug and samples were collected from all horizons, air-dried and passed through a 2 mm sieve. All analyses were made according to the procedures adapted to tropical soils as described by Anderson and Ingram (1993). Water pH (pH_{H2O}) was determined using a soil:water ratio of 1:2.5. Loss on ignition (LOI) was performed on 10 g of soil at 450°C to estimate the amount of soil organic matter. Total nitrogen (N_{tot}) and phosphorus (P_{tot}) were measured following a Kjeldahl oxidation. Briefly, 1 g of soil was put into a digestion tube (Büchi, Laboratoriums-Technik AG, Flawil, Switzerland) with two glass balls, a Kjeldahl tablet (Merck, VWR International, Nyon, Switzerland) and 12 ml of H_2SO_4 96%. After digestion at 360°C for 2 h, samples were cooled and 60 ml of de-ionized water were added. After filtration (512 1/2, Schleicher and Schuell AG, Riehen, Switzerland), N was measured by distillation and titration (Anderson and Ingram 1993) while P was determined colorimetrically at 880 nm using the molybdate procedure (Murphy and Riley 1962). Extractable P (P_a, also called available P in the following text) was revealed according to Olsen et al. (1954) by shaking 2.5 g of soil with 60 ml of sodium bicarbonate $NaHCO_3$ (0.5 N, pH 8.5) for 30 min. After filtration (512 1/2, Schleicher and Schuell AG, Riehen, Switzerland), P was determined colorimetrically as above. Total organic carbon (TOC) was quantified by titration (Nelson and Sommers 1982). Briefly, 1 g of soil was oxidized at 150°C for 1 h with 25 ml of a mix of potassium dichromate and sulfuric acid. Then, a reverse titration of $Cr_2O_7^{2-}$ ions was made using an acidified ferrous ammonium sulfate solution. Cation exchange capacity (CEC) was calculated as a result of the combined measurement of exchangeable cations and exchange acidity. For exchangeable cations, 50 ml of HCl 0.1N were added to 2 g of soil and shaken over 45 min before a titration with NaOH 0.1N. Regarding exchange acidity, 50 ml of calcium acetate 1N were mixed with 2 g of soil and shaken over 60 min before a titration with NaOH 0.1N.

The analyses revealed three Vertisols (Table 1) according to the classification of the World Reference Base for soil Resources (IUSS Working Group RB 2006). A typical vertic structure was described with dark-coloured soil layers and large cracks due to the high proportion of clay. In field 2 and 3, vertic horizons (V) were sub-divided because of the increase of massive structure and wide cracks deep in the soil profile and many differences in humidity observed in the field. Global soil characteristics were the following (mean ± standard error) for LAv layers and V layers respectively (the latter in brackets): pH_{H2O} : 7.7±0.1 (7.8±0.1) ; cation exchange capacity (CEC) : 39±4 meq/100 g (62±13); saturation of the complex: 84±2% (90±4); organic carbon (TOC): 1.2±0.04% (1.1±0.1); total nitrogen (N_{tot}): 0.10±0.01% (0.08±0.01); C/N ratio: 11.6±1.3 (15.0±1.7); total phosphorus (P_{tot}): 2.5±0.2 mg/g (2.3±0.3); available phosphorus (P_a): 10.1±2.0 ppm (0.0). The basic water pH increased from the top to the bottom in all the soils studied (7.7 to 8). Regarding both TOC and Ntot values, the amounts of organic matter measured by LOI were very high (4.0±0.5% and 3.8±0.3%, for LAv and V layers, respectively). This may be explained by a loss of carbonates during the ignition from components such as siderite ($FeCO_3$), ankerite ($Ca(Fe, Mg, Mn)(CO_3)_2$) or calcium carbonates ($CaCO_3$). Further analyses should be performed to find the origin of such differences. In addition, the test with HCl 6N confirmed high amounts of carbonates in almost all soil layers from the three fields. As a consequence, the saturation of the complex was qualified as sub-saturated in the first layer (Baize and Girard 1998) and became saturated towards the parent rock material. Regarding cation exchange capacity (CEC), it followed the same pattern for all soils; relatively low in the upper part of the profile (around 30–40 meq/100 g of soil), CEC tended to increase until the deepest horizon reaching 99 meq/100 g of soil in the V_2 horizon of F2. A general N-deficiency was observed in the three soils, but especially for F3 (less than 0.1%) while total organic carbon in the LAv layer varied from 1.13% to 1.25%. P_{tot} concentrations were very high in these three soils, with values between 2 mg/g and 3 mg/g. In contrast, the available part of P (P_a) was extremely low and detected only in the LAv and SV horizons where the root network was best developed and anchored. Furthermore, in F3, no P_a was detected under 18 cm although roots were still present in the deeper layers.

Seed material

Lupin seeds (*Lupinus albus* (L.), *cv.* Ultra), were provided by Dr. Muyekho from KARI (Kenyan Agricultural Research Institute). They were supplemented with rhizobial inoculant (*Rhizobia lupini*, Fenaco Winterthur, Switzerland) before sowing. The presence of nodules was verified. Maize seeds (cv. Hybrid 502) and silverleaf desmodium (*Desmodium uncinatum* (Jacq.) DC.) (Fabaceae) seeds were purchased from the Western Seed Company, Kitale, Kenya.

Experimental setup

We designed three separate field trials i) an intercropping experiment carried out during the long rainy season, ii) a crop succession experiment, which was undertaken during both seasons and iii) an organic matter supply experiment carried out during the long rainy season. Each of these three experiments was conducted simultaneously on three different fields separated by at least hundred meters. Plants were planted in nine rows with an intra-row space of at 35 cm and an inter-row space of 37.5 cm (Fig. 1). Three seeds of maize or lupin were planted in each hole and the stand was thinned after 2 weeks to one plant per hole. *D. uncinatum* was planted in 2 cm deep furrows. Weeding was performed twice a month during the first 3 months of the experiment. Plants were harvested 4 months after planting.

Intercropping experiment

In this experiment, *D. uncinatum*, was also included. In each of the three fields, 16 plots were prepared and four different treatments were applied replicated four times: maize planted alone (M), maize intercropped with lupin (ML), maize intercropped with *D. uncinatum* (MD), maize intercropped with lupin and *D. uncinatum* (MLD). The plots (9 m^2) were randomly distributed within each field. They were separated by a 1-meter buffer zone from each other to

Table 1 Field description and physicochemical characteristics of the three Vertisols from the three experimental fields (F1, F2 and F3)

Soil profile description	Horizons	Depth (cm)	pH (H_2O)	LOI (%)	N_{tot} (%)	TOC (%)	C/N	P_{tot} (mg/g)	P_a (ppm)	CEC (meq/ 100 g)	Sat. of the complex (%)
Field 1 (F1)											
Anthropedogenic horizon. Black clayed with sand grains, no cohesive structure (juxtaposition of organic and mineral particles). Many fine roots.	LAvh	0–16	7.7	4.2	0.12	1.17	9.70	2.6	6.3	32	84
Transition towards a vertic horizon. Black coloured layer with a compact and massive structure. Angular blocky structures. Less roots than in LAvh.	SV	16–30	7.6	3.4	0.10	1.27	12.45	2.7	3.6	35	84
Vertic horizon. Compact and massive structure. Wide cracks as a result of shrinking and swelling with wide angular blocky aggregates. Rare fine roots.	Vca	30–55	7.9	4.3	0.07	1.26	17.13	2.1	nd	77	94
Brown sandy clay horizon with a lot of small white stones. Crumbly structure due to the high proportion of sand. Presence of fine roots.	Cca	55–106	7.9	2.1	-	-	-	2.1	nd	-	-
Field 2 (F2)											
Anthropedogenic horizon. Black clayed with sand grains, no cohesive structure (juxtaposition of organic and mineral particles). Many fine roots.	LAvca	0–16	7.7	2.9	0.10	1.13	11.00	2.2	10.9	43	89
Transition towards a vertic horizon B. Enriched in stones (around 30% of the volume) that gives a more pale colour than Ap and B layers. Bigger roots but less numerous than in Ap. Crumbly structure.	SVca	16–42	7.6	2.5	0.07	0.84	11.57	2.2	10.9	41	91
Vertic horizon. Cohesive structure. Wide cracks as a result of shrinking and swelling. Rare roots.	V1	42–59	7.5	3.3	0.09	1.20	14.06	1.6	nd	24	76
Vertic horizon. Compact and massive structure. Wide cracks with wide angular blocky aggregates especially at the bottom of the horizon. No roots.	V2ca	60–96	7.9	3.1	0.09	0.88	9.40	2.1	nd	79	97
Polyedric structure with a high proportion of stones. Transition towards a C horizon.	V2-Cca	97–116	8.0	2.9	0.05	0.78	15.47	2.0	nd	99	100
High proportion of sand and stones. Crumbly structure.	Cca	117–128	8.0	2.4	-	-	-	2.2	nd	-	-
Field 3 (F3)											
Anthropedogenic horizon. Black clay with sand grains, no cohesive structure (juxtaposition of organic and mineral particles). Many fine roots.	LAvhca	0–18	7.6	4.7	0.09	1.25	14.01	2.7	13.3	62	86
Vertic horizon. Compact structure with wide cracks and angular blocky aggregates as a result of shrinking and swelling. Many fine roots.	V1	19–55	7.7	4.5	0.08	1.23	14.81	3.2	nd	39	85
Vertic horizon. Compact and massive structure. Wide cracks. Humidity enhanced compared to the layer B1. Rare roots.	V2ca	56–85	7.9	4.1	0.04	0.84	19.72	2.7	nd	90	96
Polyedric structure with a high proportion of stones and mineral particles. Transition towards a C horizon. Rare roots.	V2-Cca	86–99	7.9	2.0	0.03	0.47	17.52	3.4	nd	134	98
Brown sandy mineral horizon with large proportion of sand and stones. No roots.	Cca	100–119	7.8	0.6	-	-	-	2.2	1.7	-	-

Water pH, organic matter through loss on ignition (LOI, in %), total nitrogen (Ntot, in %), total organic carbon (TOC, in %), C/N ratio, total phosphorus (Ptot, in mg/g), available phosphorus (Pa, in ppm), cation exchange capacity (CEC, in meq /100 g of soil), and saturation of the complex (in %)

avoid interactions between treatments. The planting arrangement is shown in Fig. 1. In the plots intercropped with *D. uncinatum* (MD, and MLD) four *D. uncinatum* rows were intercropped with five rows of maize (MD), or with five rows of maize and lupin planted alternatively in the same rows (MLD). In ML plots, four rows of lupins were intercropped with five rows of maize. The advantage of this design was that all plots contained a similar number of plants. The disadvantage was that the numbers of maize plants per plot were different between the treatments. This is why we calculated the yield per maize plant and not per plot.

Crop succession experiment

Each of the three fields harboured 12 randomly placed plots, with four replicates of three different treatments: during the first cropping season, either maize (M) or lupin (L) was planted or the plots were left unplanted and kept free of weeds (B). At harvest, the plants were cut and removed, and the soil was hand hoed and prepared for the next crop. During the second cropping season, maize was planted everywhere, allowing for the following treatments: maize after maize (M/M), maize after lupin (M/L) and maize after bare land (M/B). We used bare land instead of natural fallow as a control to be able to evaluate the changes in N/P soil concentrations due to the cropping of maize or lupin and to compare them with plots without any plant P/N uptake and/or N fixation. The treatments were replicated four times.

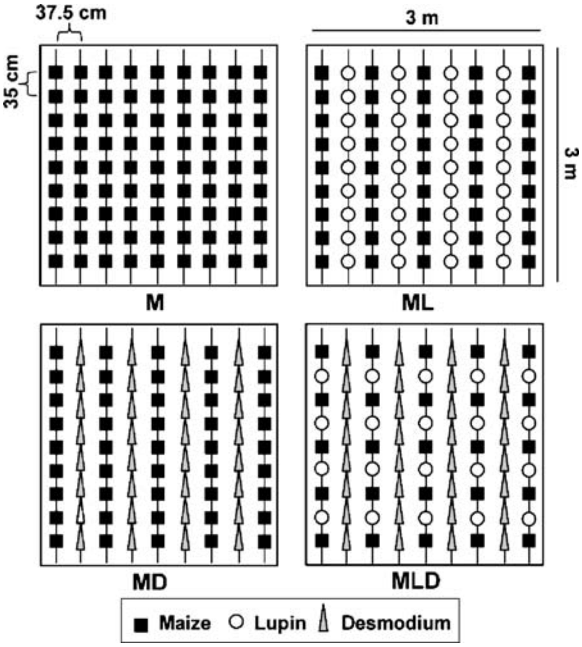

Fig. 1 Planting arrangement for the intercropping experiment. M maize monocrop, ML maize intercropped with lupin, MD maize intercropped with *D. uncinatum*, MLD maize intercropped with lupin and *D. uncinatum*. Maize planting density was maximal for M, intermediary for ML and MD and minimal for MLD

Lupin shoot incorporation experiment

The treatments were lupin added to the soil a few days before planting maize, whereby lupin shoots were air-dried and cut into 2 cm pieces, and untreated plots, which constituted the control plots. The treatments were replicated four times on each of the three fields.

Plant analyses

In all experiments, maize height was recorded at harvest and mid-harvest in a non-destructive manner on four randomly picked plants per plot. In the intercropping experiment, four maize plants were randomly collected at harvest for determination of the biomass and nutritional status. Ears were removed and dried together with the ears of the remaining plants in the plots for yield assessment; the stem and the leaves were air-dried, weighed and separately ground for further analyses (total N and P concentrations). In the crop succession and the lupin shoot addition experiment, the same procedure was carried out, but eight plants were randomly picked both at harvest and at 56 days after planting for evaluation of biomass and nutritional status. For yield assessment, ears were oven-dried for 3 days at 65°C. They were then weighed, shelled and the damaged grains were separated from the undamaged grains and weighed separately. The yield was calculated based on the weight of undamaged grains.

Striga hermonthica pot experiment

To test the effect of lupin on *S. hermonthica*, a pot experiment was designed with two different substrates, namely sand and the soil from field 2, taken from an area where *S. hermonthica* was not present. About 3000 *S. hermonthica* seeds were then incorporated into the pots. For each substrate, we had two treatments i) pots with maize only (i.e., six seeds later thinned to two plants per pot), and ii) pots with lupin and maize whereby 2 weeks before maize planting, eight seeds of lupin later thinned to four plants were planted. Pots planted with maize or maize and lupin without prior addition of *S. hermonthica* seeds were used as controls to check for natural infestations of *S. hermonthica* in the two substrates. This experiment was performed using five replicates per treatment. Maize height and number of emerged *S. hermonthica* were scored twice a month for 3 months after planting.

Statistical analyses

ANOVA was carried out separately for each experiment, with field and cropping treatment as explanatory variables. In the pot experiment, means were compared using a Student's T test. Statistical analyses were performed using the S-PLUS statistical software v. 7.0 (Insightful Corporation, Seattle, USA), using a significance level of $P<0.05$.

Results

Soil P and N fertility and maize shoot P and N uptake

Very few significant effects were observed both in soil P/N concentrations and in the uptake of P/N by maize. The maize leaves contained sufficient amounts of both elements and no sign of nutrient deficiency was observed on the plants. The results for the changes in soil available P/N concentrations as well as in maize leaves P/N concentrations for each experiment are supplied as electronic supplementary material.

Effect of lupin as a companion crop

A highly significant field effect was observed on maize height, biomass and yield (Fig. 2 and Table 2), field 2 being the best and field 3 the worst field in terms of maize growth and yield. While it was not affecting other parameters, cropping treatment had a highly significant effect on maize yield: yields were maximal when maize was intercropped with both lupin and *D. uncinatum* (MLD), followed by the intercrop with a single leguminous species (ML or MD) and lowest yields were observed for maize alone (M).

Effect of lupin as a cover crop

As in the first experiment, the field had a significant effect on height, biomass and yield of maize, with the maize growing best in field 2 and worst in field 3 (Fig. 3, Table 3). The height of maize (Fig. 3a,b) was not significantly affected by the cropping treatment, but the biomass was, both at mid-harvest and at

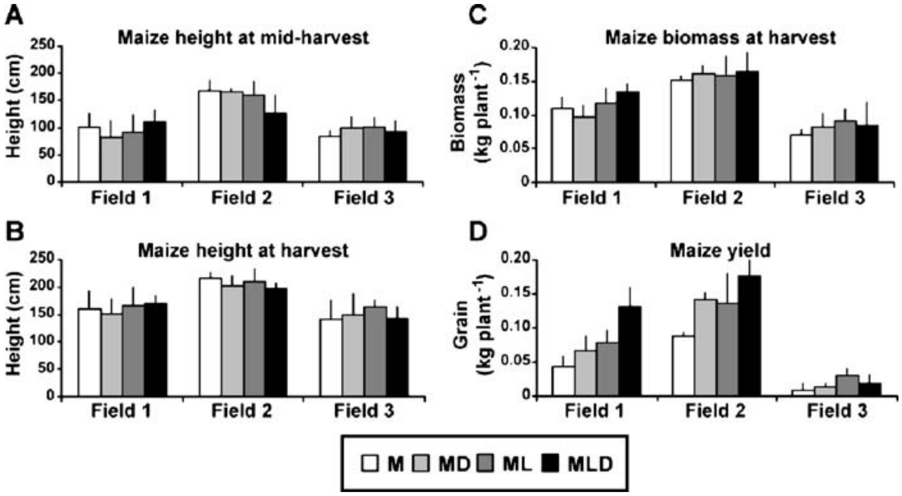

Fig. 2 Maize height (**a**–**b**), biomass (**c**) and yield (**d**) in various intercropping systems. M maize monoculture, ML maize intercropped with lupin, MD maize intercropped with *D. uncinatum*, MLD maize intercropped with lupin and *D. uncinatum*. **a**–**b** Bars are means ± SE of four replicates, each representing one plot where four randomly picked plants were measured at mid-harvest (56 days) and at harvest (112 days). **c**–**d** Bars are means ± SE of four replicates, each representing one plot where the biomass and the yield of four randomly picked plants were assessed at harvest. See Table 2 for significance of the treatments

Table 2 Significant effects of treatments on maize height, biomass and yield

Intercropping experiment

		Height (mid-harvest)		Height (harvest)		Biomass (harvest)		Yield	
	df	F	*P*	F	*P*	F	*P*	F	*P*
Field	2	30.8	***	24.73	***	55.55	***	95.64	***
Cropping treatment	3	0.24	ns	0.64	ns	1.68	ns	13.26	***
Residuals (MS)	42	614		579.3		$4.36\cdot10^{-4}$		$5.89\cdot10^{-4}$	

The analysis performed was a two-way ANOVA with field and cropping treatment as explanatory variables

df degrees of freedom, *MS* mean square

**P*<0.05, ***P*<0.01, ****P*<0.001

harvest: at mid-harvest, in field 3, there was a higher biomass for maize grown after lupin or after bare land than for maize grown after maize, while at harvest, in field 2, maize grown after lupin had a higher biomass than the two other cropping treatments. Maize yield was also significantly affected by the cropping treatment, with the highest yield after lupin cropping in all the fields (Fig. 3e).

Effect of addition of lupin shoots to the soil

Maize height, biomass and yield varied significantly in function of the fields (Fig. 4, Table 4), with the same tendencies as observed for the two first experiments: best growth in field 2 and worst growth in field 3, field 1 being intermediary (Fig. 4). Adding to the soil lupin shoot pieces prior to maize cropping had a significant positive effect on maize height at mid-harvest and at harvest, as well as on biomass at mid-harvest (Table 4). There was no general significant effect of incorporating lupin shoots on maize yield (probably due to the high variation between the fields), but in field 3, adding lupin shoots to the soil led to a 3-fold increase in maize yield (Fig. 4e). In general, the effects of addition of lupin shoots were more marked in field 3 than in the two other fields (Fig. 4).

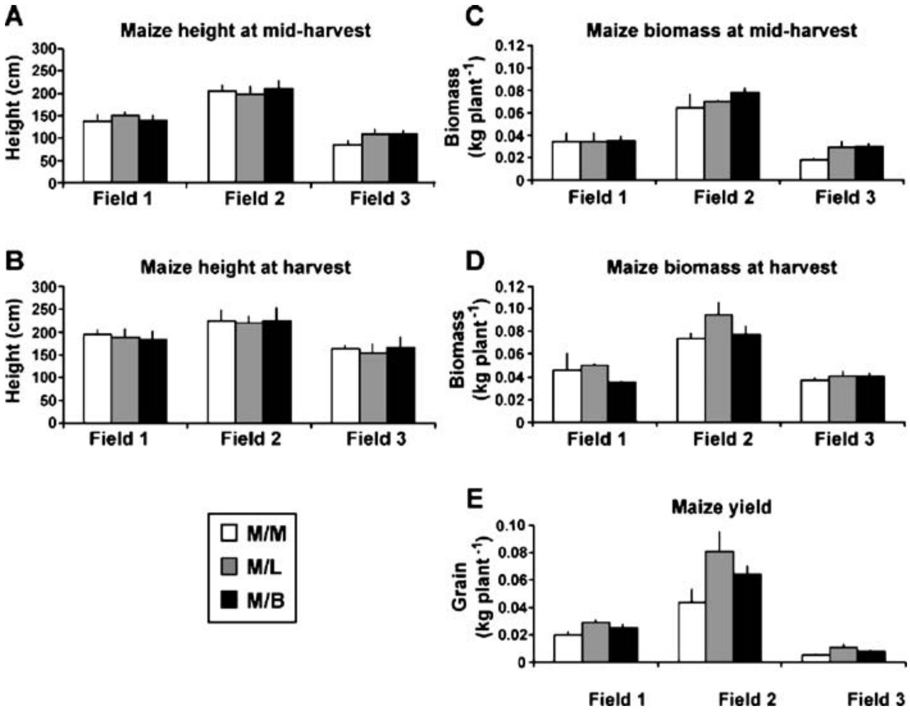

Fig. 3 Maize height (**a**–**b**), biomass (**c**–**d**) and yield (**e**) as affected by previous cropping. M/M maize after maize, M/L maize after lupin, M/B maize after bare land. **a**–**d** Bars are means ± SE of four replicates, each representing one plot where four randomly picked plants were measured at mid-harvest (56 days) and at harvest (112 days). **e** Bars are means ± SE of four replicates, each representing one plot where the yield of four randomly picked plants was assessed at harvest. See Table 3 for significance of the treatments

Table 3 Significant effects of treatments on maize height, biomass, and yield

Crop succession experiment

		Height (mid-harvest)		Height (harvest)		Biomass (mid-harvest)		Biomass (harvest)		Yield	
	df	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Field	2	185.28	***	38.89	***	172.44	***	107.4	***	127.74	***
Cropping treatment	2	1.91	ns	0.43	ns	5.99	**	7.13	**	11.4	***
Residuals (MS)	31	173		303.4		$0.39\cdot10^{-4}$		$0.61\cdot10^{-4}$		$0.75\cdot10^{-4}$	

The analysis performed was a two-way ANOVA with field and cropping treatment as explanatory variables

df degrees of freedom, *MS* mean square

*$P<0.05$, **$P<0.01$, ***$P<0.001$

Effect of lupin on *Striga hermonthica*

S. hermonthica infestation was present in our fields, but differed much in intensity between the fields, as revealed by total counts of *S. hermonthica* performed five times across the growth period, yielding cumulative numbers of approximately 25000 plants in field 3, 20000 in field 1, and only 2500 in field 2. These differences in *S. hermonthica* infestation fit very well with the differences in height, biomass and yield obtained in the different fields in all three experiments (e.g. the yield of maize was highest in field 2 and lowest in field 3, field 1 being intermediate, see also Figs. 2d, 3d and 4d). During monitoring of the field experiments, we observed that in some plots intercropped with lupin, *S. hermonthica* emergence was reduced. However, a direct comparison of the *S. hermonthica* infestation in the different treatments was not possible because of the high variability in *S. hermonthica* occurrence between the plots situated at the border of the fields and the plots situated at the centre (with drastically more *S. hermonthica* at the border than at the centre of the field). We thus designed a pot experiment with controlled amounts of *S. hermonthica* seeds to evaluate the effect of lupin on *S. hermonthica*. Planting lupin together with maize in pots inoculated with *S. hermonthica* led to a drastic reduction of the damage caused to maize by *S. hermonthica* (Fig. 5a). In the right pot (M), where no lupin was planted, the two maize plants showed

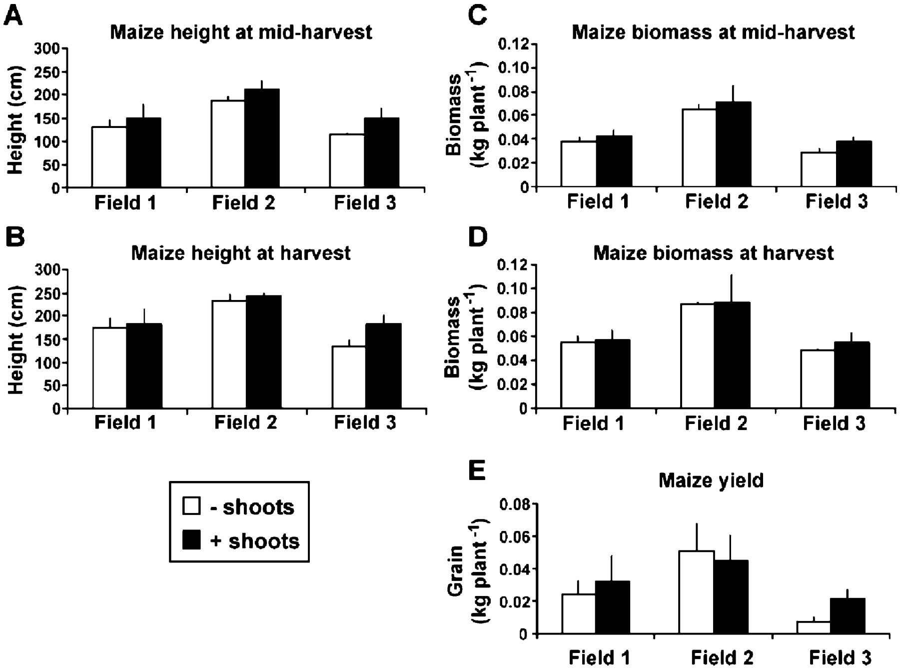

Fig. 4 Maize height (**a**–**b**), biomass (**c**–**d**) and yield (**e**) as affected by lupin shoot addition to the soil. **a**–**d** Bars are means ± SE of four replicates, each representing one plot where four randomly picked plants were measured at mid-harvest (56 days) and at harvest (112 days). **e** Bars are means ± SE of four replicates, each representing one plot where the yield of four randomly picked plants was assessed at harvest. See Table 4 for significance of the treatments

Table 4 Significant effects of treatments on maize height, biomass and yield

Shoot incorporation experiment

		Height (mid-harvest)		Height (harvest)		Biomass (mid-harvest)		Biomass (harvest)		Yield	
	df	F	*P*	F	*P*	F	*P*	F	*P*	F	*P*
Field	2	28.27	***	29.48	***	56.26	***	26.81	***	12.7	***
Lupin shoot addition	1	9.76	**	5.3	*	5.82	*	0.45	ns	0.77	ns
Residuals (MS)	18	343.2		432.3		$0.42\cdot10^{-4}$		$0.11\cdot10^{-4}$		$1.60\cdot10^{-4}$	

The analysis performed was a two-way ANOVA with field and cropping treatment (lupin shoot addition) as explanatory variables

df degrees of freedom, *MS* mean square

**P*<0.05, ***P*<0.01, ****P*<0.001

signs of heavy *S. hermonthica* parasitism (reduced growth and early drying) and the *S. hermonthica* plants developed well until the flowering stage. In the left pot (ML) in contrast, no *S. hermonthica* was observed and the maize developed normally, showing no signs of parasitism. This positive lupin effect is also demonstrated in the amounts of *S. hermonthica* found in lupin-planted and lupin-unplanted pots (B) in both substrates tested. No *S. hermonthica* emergence was observed in the pots not supplemented with *S. hermonthica* seeds (data not shown).

Discussion

Where soils are becoming more and more deficient in mineral elements essential for plant growth and where farmers cannot afford fertilizers, as it is the case in many African countries, it is of utmost importance to find alternative ways to help restoration and maintenance of soil fertility. Nitrogen deficiency and lack of availability of phosphorus are major causes for poor yields, in addition to biotic factors such as herbivore damage or weeds. Intercropping with legumes has been shown to drastically reduce pest infestation on maize (Chabi-Olaye et al. 2005; Khan et al. 2006b). In addition, it appears relevant to make use of leguminous crops, either as cover crops or as companion crops, to increase the N nutrition of the crop of interest, with the additional advantage of legumes as food, fodder or as a source of organic matter. Furthermore, if a leguminous crop can also enhance P uptake by the crop of interest, as for instance has previously been observed for cowpea and soybean (Jemo et al. 2006), then the leguminous crops become even better candidates for use as and low-input soil fertility improvement measures. A promising candidate is white lupin, with its highly efficient P-

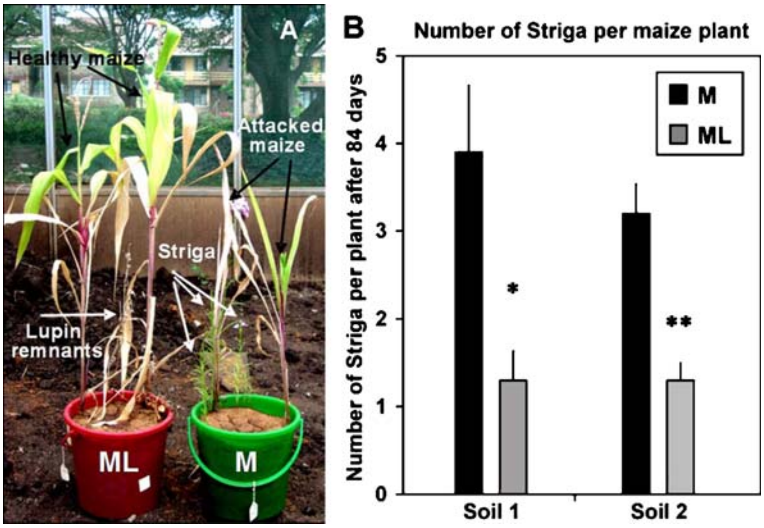

Fig. 5 Effect of lupin on the damage caused to maize by *Striga hermonthica*. **a** 3 month old maize planted either alone (right pot) or 2 weeks after lupin (left pot) grown in sand. **b** Number of emerged *S. hermonthica* per maize plant in pots inoculated with *S. hermonthica* seeds after 84 days of growth. M maize alone, ML maize planted 2 weeks after lupin. Bars are means ± SE of five replicates. **P*<0.05, ***P*<0.01 (Student's T test)

acquisition strategy relying on the formation of cluster roots that excrete high amounts of P-solubilising carboxylates (Neumann and Martinoia 2002).

Effect of lupin on soil fertility and P/N uptake of maize

Only very few significant differences were observed in soil available P and N concentrations in all experiments (see supplementary material). Moreover, despite the low available P concentrations in the three fields, maize plants showed amply shoot P concentrations, suggesting that maize fitness was not limited by soil fertility constraints, but by other parameters (see below, effect of lupin on *S. hermonthica*). In the intercropping experiment, the absence of a negative impact of lupin on P uptake of maize suggests that in our field conditions, lupin's efficiency in P-acquisition did not cause a depletion of P in the rhizosphere of maize, which would lead to a decreased uptake, as observed by Cavigelli and Thien (2003) in pot experiments. Moreover, lupin led to more biomass being produced by maize in several cases, in the crop succession as well as in the shoot incorporation experiment. Since the P and N concentrations were not significantly different in maize plants grown with lupin and in maize grown without, it is suggested that maize was able to take up more P and N when lupin was present or had been planted previously. Nevertheless, even in these cases, no net changes in soil P and N availability were observed at our time scale. We can thus conclude from our data that lupin did not lead to improved soil P/N fertility, but cannot exclude that in a longer term or in soils more deprived of P and N, the expected positive effect of lupin on pools of available P and N would take place.

Effect of lupin on maize growth and yield

Out of the three cropping strategies (companion crop, cover crop and shoot supply) that we tested to assess the effect of lupin on maize growth and yield, the beneficial effect of lupin on maize yield was most evident when used as a cover crop (Fig. 3e). This increase of maize yield after lupin cropping is in line with the findings of Kamh et al. (1999) and Nuruzzaman et al. (2005) who reported better growth of wheat after lupin cropping in a pot experiment. It contrasts however with the observations of El Dessougi et al. (2003), where the previous growth of lupin in pots caused a lower yield of the following maize. This might be due to differing soil properties and fertility or to the fact that the positive effect of lupin in the field was due to other factors beyond soil fertility (see below, effect of lupin on *S. hermonthica*).

Using white lupin as a companion crop of maize led to higher maize yields, both intercropped as a companion species or in a mix with *D. uncinatum*, another leguminous species. Except in field 3, where intercropping maize with lupin alone led to the best maize yields, yields were generally highest when maize was intercropped with the two leguminous species together. In addition to beneficial effects of *D. uncinatum* and lupin, this increased yield might also be due to the maize planting density, which was lowest in the MLD treatment (see also Fig. 1). Intercropping maize with lupin did not lead to a decrease in maize yield in any of the fields in our experiment. This is in line with the findings of Kamh et al. (1999) and Nuruzzaman et al. (2005), but contrasts with the observations of Härdter and Horst (1991) and Horst and Härdter (1994) with cowpea and of Jannasch and Martin (1999) with lupin, who reported a reduction of maize yield in intercropped plots due to interspecific competition. This difference might be explained by differing soil P/N fertility: Jannasch and Martin (1999) used external NK fertilizers while Härdter and Horst (1991) as well as Horst and Härdter (1994) observed interspecific competition in both absence and presence of N or P fertilizers, but they used cowpea, which might be a more aggressive competitor for maize than lupin. Since no sign of nutrient deficiency was observed in our field conditions, it can be assumed that there was no competition for nutrients between maize and lupin. The situation might have been different on soils with a more severe P/N depletion. Moreover, longer-term trials would give a more reliable idea of how lupin influences maize growth and soil fertility. However, the short term trials (two seasons) presented here give very encouraging first results and indicate that white lupin is having a beneficial impact on maize yield already at the beginning of the intercropping strategy, with a potential for more significant effects over a longer period of time through additional improvement of soil fertility.

Finally, adding homogenised lupin shoots to the soil prior to maize cropping led to significantly better growth of maize (height, biomass). These beneficial effects were most marked in field 3, in the field where plants generally produced less grain. In this field, the yield of maize was three times higher in plots supplemented with lupin shoots than in control plots.

Field effects

In all three experiments, large variations in maize growth and yield occurred depending on the field where plants were grown. While the average soil characteristics were similar in all three fields, the cultivation history was quite different: during the three preceding years, maize and soybean had been grown in field 1. In field 2, cassava, which has been shown to improve soil fertility (Adjei-Nsiah et al. 2007) was intercropped with cowpea, which has been reported to increase yield of the following maize (Jemo et al. 2006), whereas in field 3, maize and grasses had been cropped. In addition (and probably partly due to these different cropping histories), the infestation with the parasitic weed *Striga hermonthica*, which plays a key role in maize growth and health, also varied a lot between the three different fields and this factor might well explain the differences observed in maize growth and yield in the three fields. In fields 1 and 3, *S. hermonthica* infestation was most severe, which is not surprising considering that fields had been planted with the host plant maize. In contrast, in field 2, *S. hermonthica* infestation was minimal, probably due to the absence of the host plant and to the presence of cowpea, which has been shown to reduce *S. hermonthica* population (Khan et al. 2007). Thus, it appears that the *S. hermonthica* infestation, rather than the soil N and P fertility, explained the varying plant fitness we observed, with highest fitness in field 2 (almost no *S. hermonthica* pressure), intermediate fitness in field 1 (higher *S. hermonthica* pressure) and lowest fitness in field 3 (highest *S. hermonthica* pressure).

Effect of lupin on *S. hermonthica* infestation

Despite the fact that the use of lupin led to a better maize growth and yield in our three different experiments, no significant effect of lupin could be observed on the P and N nutritional status of maize or on the pools of available P and N in the soil, suggesting that lupin was acting via a soil fertility-independent mechanism. Our observations that there was less emergence of *S. hermonthica* in some plots planted with lupin compared with other plots where lupin was absent led us to perform a pot experiment with controlled amounts of *S. hermonthica* seeds to test the impact of lupin on the damage caused to maize by the parasitic weed. The results of this pot experiment showed a significant reduction of *S. hermonthica* damage when lupin was planted with maize. This newly discovered effect of white lupin against *S. hermonthica* opens a whole new set of questions, as to the underlying mechanisms and the potential signalling metabolites involved in the plant-parasite interactions (Bouwmeester et al. 2003). A first key question is to whether lupin acts directly on germination and/or development of the *S. hermonthica* seeds or whether the action takes place in an indirect way, through an improved nutrition of maize, which is then better able to defend itself against the weed. The latter seems unlikely in our case, since maize was not suffering from N or P deficiency as indicated by the levels of N and P in the shoots (see supplementary material). From what has been reported for other leguminous species, and especially for *D. uncinatum* (Khan et al. 2000, 2007), possible mechanisms of action are the stimulation of *S. hermonthica* seed germination, which leads to premature death of the parasite if the host is not present, as well as the inhibition of haustoria formation. We are currently trying to elucidate the mechanisms underlying this promising new feature of white lupin.

Conclusion

At the start of the study, we hypothesised that white lupin would improve the growth and yield of maize through a better P and N nutrition. To test this hypothesis, three objectives were formulated: i) to assess the effect of lupin on maize growth and yield in field conditions, ii) to find the best way of introducing white lupin into the local agricultural practices and, provided positive effects were observed, iii) to elucidate the mechanisms underlying these effects. Our results clearly demonstrate that the use of white lupin led to higher yields of maize in all three cropping strategies. From the results obtained during our two-season experimental period, it appears that the beneficial effect on the maize yield per plot was highest when lupin was used as a cover crop. However, the simultaneous intercropping of white lupin and maize also led to good results in terms of maize yield per plant and might even prove more successful when used on a longer period of time, through slow but continuous improvement of soil fertility and/or decrease of damages due to *S. hermonthica*. This intercropping strategy also has the advantage, for the great majority of local farmers who have no irrigation system, to rely only on the long rain season, whereas the crop succession also involves the short rain season, where water supply is much less reliable. As to the mechanisms underlying the positive effect of lupin on maize, we observed that they were surprisingly not linked to an improvement of soil fertility or maize P/N uptake in our field conditions and time scale, but to a reduction of the damage caused by *S. hermonthica*. Longer term studies, involving bigger plots and different fertilizer treatments, are needed to provide more information on putative long-term effects of white lupin on N/P soil availability and on the N/P uptake of the co-cultivated or subsequently cultivated crops. The newly discovered inhibiting impact of white lupin on *S. hermonthica* opens a new and promising research area and will hopefully lead to a better understanding of the mechanisms underlying this effect and to the best possible use of white lupin as a *S. hermonthica*-inhibiting leguminous crop.

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