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Mutualistic functioning of indigenous arbuscular mycorrhizae in spring barley and winter wheat after cessation of long-term phosphate fertilization

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Abstract The influence of 23 years of phosphorus (P) application at three annual rates of 0, 17.5 and 52.5 kg ha^{-1} on arbuscular mycorrhizal (AM) fungal colonization was studied 10 years after the fertilization treatment ended. The annual application of 52.5 kg ha^{-1} was about twice the annual crop P extraction and after 23 years had resulted in a measured increase of 23% in the soil total-P concentration. After 10 and 11 years without fertilization, the total mycorrhizal and arbuscular colonization of the plots previously fertilized at this high rate were still significantly lower than in the plots subjected to the 0 and 17.5 kg ha^{-1} rates. Plots previously fertilized annually at the rate of 52.5 kg ha^{-1} also had a lower benefit:cost ratio for the symbiosis between AM fungi and plants. Furthermore, P-use efficiency was lower in these plots, although no decrease in total dry matter production was found.

Keywords Arbuscular mycorrhiza · Long-term P fertilization · Benefit:cost ratio · P-use efficiency · Mutualism–parasitism continuum

Introduction

The fertilizer used in high-input arable farming systems to boost crop yields leads to nutrient saturation and subsequently to loss of nutrients (Breeuwsma and Silva 1992; Haynes and Williams 1992; Isermann 1990), which causes environmental pollution and degradation of natural conditions (Breeuwsma and Silva 1992; Sharpley and Withers 1994). As a consequence, governments are introducing legislation to minimize nutrient losses by achieving an equilibrium between input and output (Anonymous 1993, 1995; Oenema and van Dijk 1994). It is generally assumed that crop yields will then fall below economically acceptable levels, because decreasing phosphorus (P) application will reduce the availability of this nutrient (Withers et al. 1994).

Organic arable farming systems are assumed to produce profitable crop yields in situations with a low availability of P, because P uptake is stimulated by arbuscular mycorrhizal (AM) fungi (Abbott and Robson 1994; Jensen and Jakobsen 1980; Koide 1991; van der Werff et al. 1995).When P is not growth-limiting, e.g. when P fertilizer is applied, plants may not benefit from extra P taken up by AM fungi (Marschner 1995). Costs of the symbiosis may then exceed benefits, resulting in a parasitic relationship between fungus and plant (Johnson et al. 1997).

Changing farm management from high-input to low-input or organic involves reducing applications of P fertilizer or replacing fertilizer with manure. Reducing or stopping P fertilization will lead to a decrease in P accumulated in soil. The rate at which the AM fungi adapt to these changes in management is not fully understood. Limonard and Ruissen (1989) reported that a change from conventional to low-input agriculture resulted in a large increase in AM root colonization only 4 years after conversion. In studies comparing neighbouring farms with different management regimes, mycorrhizal root colonization was much higher in biological, low-input farming systems than in conventional high-input systems (Mäder et al. 2000; Ryan et al. 1994).

The objective of this study was to assess differences in colonization and functioning of indigenous AM fungi associated with spring barley and winter wheat grown in fields that had not been fertilized for 10 years but had earlier been fertilized at three different P application rates. Two hypotheses were tested: the first was that AM colonization would be lower in previously fer-

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tilized fields and inversely related to the amount of P applied. The second was that high AM colonization in combination with a high P content in soil would coincide with a lower benefit:cost ratio, resulting in lower P-use efficiency and depressed crop yields.

Materials and methods

History of the experimental field

The 'De Schreef' experimental farm was established in Flevoland, The Netherlands in 1962 on land reclaimed from the 'IJsselmeer' (the former 'Zuiderzee') 5 years previously. A long-term study of P fertilizer applications for maintaining the P level in the silty clay loam soil was conducted on the farm and the P demands of various crops were compared (Remmelzwaal and Habekotté 1986). This entailed a randomized block experiment consisting of three blocks. In each block, three P fertilizer rates (0, 17.5 and 52.5 kg ha^{-1} year^{-1}, henceforth referred to as P_0, $P_{17.5}$ and $P_{52.5}$) were randomly assigned. A 4-year crop rotation started with oats and was followed successively by sugarbeet, winter wheat and potatoes (Habekotté 1978). The main conclusion from this experiment, which ran from 1962 to 1985, was that P-water (7.1 mg kg^{-1}) would remain constant under an estimated annual P addition rate of 28.4 kg ha^{-1}. Mean annual P extraction by crops was about 26.2 kg ha^{-1} (Remmelzwaal and Habekotté 1986). Figure 1 shows the mean winter wheat yield at P_0 and $P_{52.5}$ from 1962 to 1985. The yield was calculated with linear regression (from Remmelzwaal and Habekotté 1986) (see Fig. 1). The P fertilization caused the yield in $P_{52.5}$ to increase more than the yield in P_0. Relative yield (y_{rel}) in $P_{52.5}$ (with the yield in P_0 set at 1, and 1962 set as $x = 0$) was calculated from:

$$y_{\mathrm{rel}} = 0.006x + 0.996 \ (R^2_{\mathrm{adj}} = 0.55)$$

When the experiment was ended in 1985, the fertilizer applications were also discontinued. In 1989, the crop rotation was changed to a 6-year rotation: lucerne, lucerne, winter wheat, oats, field bean, and spring barley. No yearly measurements were made between 1985 and 1994 (Remmelzwaal 1989).

Former soil characterization

The soil characteristics and crop yields were measured yearly from 1962 to 1985. Table 1 shows the soil data at 'De Schreef'. Both the $CaCO_3$ and K_2O contents decreased over the 23 years due to natural decalcification and crop uptake. In this period, no calcium carbonate or potassium fertilizers were given because of the relatively high $CaCO_3$ and K_2O content in the soil. The soil bulk density increased as the young silty clay loam soil dried out and 'ripened' (Habekotté 1981; Remmelzwaal and Habekotté 1986).

The soil P contents recorded before our study (between 1962 and 1985) are given in Table 2. Methods used for P analysis are described in the section 'Chemical soil and plant analysis'. The P-water method used nowadays in the Dutch fertilizer advisory scheme was unknown in 1962. P-al and P-citric, especially the latter, are good indicators of the availability of P in soils with a high calcium phosphate content (Remmelzwaal and Habekotté 1986). All extractions showed declining P contents in the P_0 and $P_{17.5}$ treatments in 1985, as was to be expected given that annual P output exceeded input. Significant increase of soil P levels in $P_{52.5}$ was explained by an annual P output which was only half of the P input. After 23 years of the $P_{52.5}$ fertilizer regime, the total-P had increased by 23%, indicating a surplus of P adsorbed to soil particles. The fertilization resulted in P-citric increasing by 56% and P-al by 83% (Remmelzwaal and Habekotté 1986).

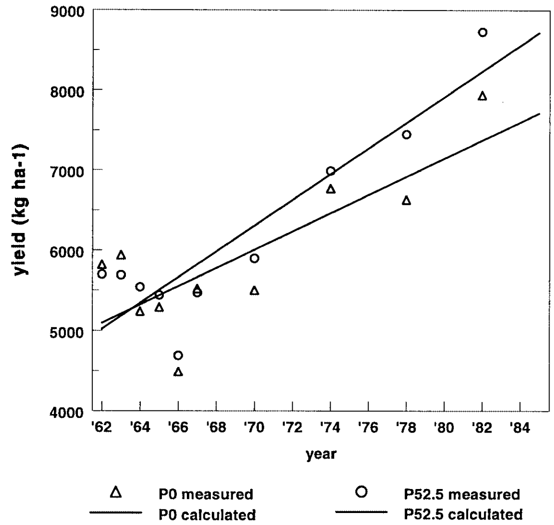

Fig. 1 Measured (*symbols*) and calculated (*lines*) yields of winter wheat following annual P applications of 0 (P_0) and 52.5 ($P_{52.5}$) kg ha^{-1} between 1962 and 1985 (calculated after Remmelzwaal and Habekotté 1986)

Former AM situation

Preliminary investigations of AM fungi in previously fertilized plots at 'De Schreef' were conducted in 1989, 4 years after the experiment with three annual rates of 0, 17.5 and 52.5 kg ha^{-1} P fertilizer ceased. In 1989, soil total-P was 580, 703 and 841 mg kg^{-1}, respectively. AM colonization measured in barley 75 days after sowing was 67, 63 and 56%, respectively (Frissen et al. 1992). No data are available on AM fungi during the experimental period from 1962 to 1985. However, abundance of spores of AM fungi was determined at an experimental farm at Nagele in the neighbouring polder that was reclaimed from the 'IJsselmeer' in the early forties. The soil at Nagele was similar to the soil at 'De Schreef' (a young silty clay loam with loam = 33%; organic matter = 2.4%; $CaCO_3$ = 9%; and pH-KCl = 7.3). Spores of AM fungi were counted after winter wheat in 10 different years between 1951 and 1978. In 1951, an average of 32.2 ± 5.7 mycorrhizal spores g^{-1} dry soil were counted. In the following years, average spore abundance varied between 24.4 and 34.2 mycorrhizal spores g^{-1} dry soil and it was concluded that spore number neither increased nor decreased (Ruissen 1982). Colonization by AM fungi had been assessed in another nearby farm 'De Lovink-

Table 1 Physico-chemical characteristics of the upper 20 cm of soil at 'De Schreef', measured in 1962 and 1985 (Remmelzwaal and Habekotté (1986))

Year	Loam (%)	Clay (%)	Organic matter (%)	$CaCO_3$ (%)	K_2O (mg kg^{-1})	pH-KCl	Bulk density (g ml^{-1})
1962	32	53	2.9	10.7	530	–	1.12
1985	32	53	2.9	8.9	340	7.1	1.23

hoeve'. In this experiment, a plot with a low and with a high soil P concentration (P-water = 2 mg kg^{-1} and 11 mg $kg^{-1,}$ respectively) were compared. AM colonization of winter wheat was 57% in the low P plot, and was significantly more than 39% in the high P plot (Ruissen 1982).

Field measurements and sample preparation

The experimental field was cropped with spring barley in 1994 and winter wheat in 1995. Soil, root and plant samples were taken in the field (three fertilizer rates and three replications, i.e. nine observations) while the crops were ripening. Nine soil cores (2 cm diameter and 0–20 cm deep) were taken within the crop row per observation and pooled. Root cores were taken in triplicate per observation. The root core (5.7 cm diameter and 0–20 cm deep) was placed in the crop row, centred on a cut plant. Plant samples were harvested within a frame 79 cm long by 31 cm wide (with the crop row in the middle along the longer axis). The cut material from three samples was pooled to form one plant observation.

Soil samples were dried at 40 C for 24 h before analysis. Stems and ears of the plant material were separated before drying at 70 C for 24 h. Soil and plant samples were ground after drying. Root samples were washed over a 1-mm sieve and fixed in 70% alcohol.

Chemical soil and plant analysis

Soil samples were analysed for P-water (amount of P extracted in water; Sissingh 1971), P-al (P extracted in ammonium lactate-acetic acid; Egnér et al. 1960), P-citric (P extracted in 1% citric acid; Hofstee 1980), total-P (measured as P extracted in a mixture of sulphuric acid and nitric acid in the early years, whereas later P was extracted in a mixture of sulphuric acid – salicylic acid – hydrogen peroxide – selenium; Novozamsky et al. 1984) and total-N (N extracted in a mixture of sulphuric acid – salicylic acid – hydrogen peroxide – selenium; Novozamsky et al. 1984).

Plant samples were examined for dry matter, total-P and total-N (Novozamsky et al. 1983). P-use efficiency (total dry matter divided by P uptake) was calculated (Fageria et al. 1990).

Root length density and AM colonization

Root length density was determined using the grid line intersect method (Tennant 1975). After clearing (10% KOH) and staining (trypan blue in lactoglycerol) (Kormanik and McGraw 1982; Phillips and Hayman 1970), AM colonization was determined by counting 150 root intersections under a light microscope at ×100 and ×200 magnification. Total fractional colonization (AM colonization) was separated into specific colonizations of only hyphae (hyphal colonization, HC), only arbuscules (arbuscular colonization, AC), only vesicles (vesicular colonization, VC) and arbuscules and vesicles together (ACVC) (Giovanetti and Mosse 1980; McGonigle et al. 1990). To estimate mycorrhizal effect on crop production, fractional colonization was multiplied by root length density to give colonized root length density (Brundrett et al. 1996). AC/AM ratio (benefit versus cost of the symbiosis) was calculated to compare the net mycorrhizal effect of the former P fertilizer treatments.

Statistics

Data were tested by a two-way analysis of variance using Genstat 5 (Genstat 5 Committee 1993) with $P<0.05$ or $P<0.10$ for a randomized block experiment with three replications. The percentages of mycorrhizal colonization were arcsine square-root transformed prior to statistical analysis.

Results

Soil P concentrations

After 10 years without fertilization, soil P still reflected the earlier P fertilizer treatments (Table 2). In 1994 and 1995, the soil P levels of the $P_{52.5}$ treatment were significantly higher than those of P_0 and $P_{17.5}$. Between 1985 and 1994 or 1995, the P-water, P-al and total-P showed a clear decline for all P treatments, except for P-water in the P_0 and $P_{17.5}$ treatments.

Total decrease of P in the upper 20 cm of the soil between 1985 and 1994 (or 1995) was 231 (or 235) kg ha^{-1} for fertilizer treatment P_0, 251 (or 214) kg ha^{-1} for $P_{17.5}$ and 381 (or 363) kg ha^{-1} for $P_{52.5}$. Thus, the decrease in P was greatest in the $P_{52.5}$ treatment. In $P_{17.5}$ and $P_{52.5}$.the total-N concentration in soil was significantly higher during the growth of winter wheat.

Root length density and AM colonization

Root length density of spring barley was significantly higher at the highest fertilizer level (Table 3). This trend was also visible (but not significant) in winter wheat. AM and AC were significantly higher in P_0 than $P_{52.5}$ in both spring barley and winter wheat (Table 3). VC and ACVC were near detection level.

HC was only significantly different in barley when colonization was expressed as root length density (Table 4). AM, AC and VC expressed as colonized root length density were not significantly different for any fertilizer treatment in spring barley or winter wheat. The lower AM and AC at $P_{52.5}$ were compensated by a greater root length density. In both spring barley and winter wheat, the AC/AM ratio was significantly higher in P_0.

Plant analysis

The ear dry matter content of spring barley and of winter wheat was significantly higher in $P_{52.5}$. The stem dry matter content of spring barley and of winter wheat was not significantly different. P concentrations in stems and ears were significantly higher in $P_{52.5}$. N concentrations in stems and ears of both spring barley and winter wheat were not significantly different, except for stems of winter wheat in $P_{17.5}$, which had a significantly higher N concentration (Table 5).

Calculated total dry matter production, total P uptake and total N uptake are given in Table 6. No significant effect was found among the former fertilizer treatments on the stems and the ears of either spring barley or winter wheat. The P-use efficiency was significantly lower in these plant fractions in $P_{52.5}$.

Table 2 Phosphorus (P) contents in the upper 20 cm of soil as affected by P application of 0, 17.5 and 52.5 kg ha^{-1} year^{-1} in 1962 (first year of application), 1985 (last year of application) [calculated from Remmelzwaal and Habekotté (1986)], 1994 and 1995 (10 and 11 years after last application, respectively). Different letters within one year and measurement denote significant differences at $P<0.05$

Year (crop)	P application 1962–1985 (kg ha^{-1} year^{-1})	P-water (mg kg^{-1})		P-al (mg kg^{-1})		P-citric (mg kg^{-1})		Total-P (mg kg^{-1})		Total-N (mg kg^{-1})	
1962	0	–		94	a	183	a	651	a	–	
	17.5	–		–	–	–	–	–	–	–	
	52.5	–		104	a	197	a	664	a	–	
1985 (sugar. beet)	0	1.8	a	55	a	101	a	581	a	–	
	17.5	2.9	a	74	a	133	a	620	a	–	
	52.5	12.6	b	189	b	306	b	817	b	–	
1994 (barley)	0	2.7	a	45	a	–		487	a	1365	a
	17.5	3.6	a	61	a	–		518	a	1346	a
	52.5	7.7	b	153	b	–		662	b	1349	a
1995 (wheat)	0	2.3	a	39	a	–		494	a	1507	a
	17.5	2.6	a	51	a	–		541	a	1543	b
	52.5	8.7	b	124	b	–		683	b	1564	b

Table 3 Root length density, percentage of total (*AM*), hyphal (*HC*), arbuscular (*AC*), vesicular (*VC*), and arbuscular and vesicular colonization (*ACVC*) in spring barley and winter wheat as affected by P fertilizer treatments applied until 1985. Different letters within one year and measurement denote significant differences at $P<0.05$

Year (crop)	Former P-treatment (kg ha^{-1} year^{-1})	Root length density (cm ml^{-1})		AM (%)		HC (%)		AC (%)		VC (%)		ACVC (%)	
1994 (barley)	0	3.51	a	78	a	38	a	35	a	3	a	2	a
	17.5	4.01	ab	72	ab	43	a	26	ab	2	a	1	a
	52.5	4.98	b	60	b	39	a	18	b	1	a	1	a
1995 (wheat)	0	4.18	a	92	a	52	a	38	a	2	a	1	a
	17.5	5.04	a	87	ab	61	a	24	b	1	a	1	a
	52.5	5.76	a	75	b	53	a	20	b	1	a	0	a

Table 4 Total (*AM*), hyphal (*HC*), arbuscular (*AC*), vesicular (*VC*), arbuscular and vesicular colonized root length density (*ACVC*) and ratio of arbuscular root length to total colonized root length in spring barley and winter wheat as affected by P fertilizer treatments applied until 1985. Different letters within one year and measurement denote significant differences at $P<0.05$

Year (crop)	Former P-treatment (kg ha^{-1} year^{-1})	AM (cm ml^{-1})		HC (cm ml^{-1})		AC (cm ml^{-1})		VC (cm ml^{-1})		ACVC (cm ml^{-1})		AC:AM ratio	
1994 (barley)	0	2.73	a	1.32	a	1.23	a	0.10	a	0.08	a	0.45	a
	17.5	2.85	a	1.70	b	1.03	a	0.08	a	0.04	a	0.36	b
	52.5	3.00	a	1.96	b	0.91	a	0.06	a	0.07	a	0.30	b
1995 (wheat)	0	3.87	a	2.16	a	1.60	a	0.07	a	0.03	a	0.41	a
	17.5	4.39	a	3.09	a	1.23	a	0.05	a	0.03	a	0.28	b
	52.5	4.39	a	3.07	a	1.24	a	0.06	a	0.02	a	0.27	b

Discussion

The soil P in all the fertilizer treatments decreased after 1985, the year that P application ceased. Given the mean crop extraction reported by Remmelzwaal and Habekotté (1986), a decrease of 223 kg ha^{-1} (in P_0 and $P_{17.5}$) and of 266 kg ha^{-1} (in $P_{52.5}$) would have been expected over a period of 10 years. The decreases in soil P we found in plots that previously received P_0 (231 or 235 kg ha^{-1}) or $P_{17.5}$ (251 or 214 kg ha^{-1}) were close to the expected values. However, in plots that previously received $P_{52.5}$, we found a much greater decline in soil P (381 or 363 kg ha^{-1}). Although plant P concentration was significantly higher in the $P_{52.5}$ treatment, total P uptake did not differ between the various fertilizer treatments. Bergmann (1988) and Fageria et al. (1990) reported that the plant P concentration in the former $P_{52.5}$ treatment was adequate, so luxury uptake was unlikely. We attribute the greater decrease of total soil P in the former $P_{52.5}$ over a period of 10 years to a greater

Table 5 Dry matter content and the concentrations of P and N in stems and ears of spring barley and winter wheat as affected by P fertilizer treatments applied until 1985. Different letters within one year and measurement denote significant differences at $P<0.10$ (letters in parenthesis), and $P<0.05$, respectively

Year (crop)	Former P-treatment (kg ha^{-1} year^{-1})	Dry matter content				P concentration				N concentration			
		Stem (g kg^{-1})		Ear (g kg^{-1})		Stem (g kg^{-1})		Ear (g kg^{-1})		Stem (g kg^{-1})		Ear (g kg^{-1})	
1994 (barley)	0	295	a	484	(a)	550	a	2540	(a)	4.68	a	11.63	a
	17.5	300	a	497	(b)	581	ab	2821	(ab)	4.35	a	12.36	a
	52.5	296	a	496	(b)	865	b	3021	(b)	4.88	a	12.55	a
1995 (wheat)	0	298	a	464	ab	626	a	2537	(a)	3.86	a	10.79	a
	17.5	301	a	457	a	818	ab	2577	(a)	5.64	b	11.84	a
	52.5	309	a	480	b	932	b	2891	(b)	4.19	a	10.87	a

Table 6 Total dry matter production, total P uptake and P-use efficiency of stems and ears of spring barley and winter wheat as affected by P fertilizer treatments applied until 1985. Different letters within one year and measurement denote significant differences at $P<0.10$

Year (crop)	Former P-treatment (kg ha^{-1} year^{-1})	Total dry matter production				Total P uptake				P-use efficiency			
		Stem (kg ha^{-1})		Ear (kg ha^{-1})		Stem (kg ha^{-1})		Ear (kg ha^{-1})		Stem (kg ha^{-1}		Ear (kg ha^{-1})	
1994 (barley)	0	5533	a	8189	a	3.09	a	20.8	a	1880	a	396	a
	17.5	5257	a	8146	a	3.04	a	23.0	a	1748	ab	355	ab
	52.5	4981	a	7767	a	4.32	a	23.6	a	1195	b	333	b
1995 (wheat)	0	5886	a	10101	a	3.70	a	25.6	a	1607	a	395	a
	17.5	5356	a	9370	a	4.37	a	24.2	a	1263	b	389	a
	52.5	4936	a	9302	a	4.67	a	27.0	a	1070	b	347	b

loss of P induced by a higher soil P content (Haynes and Williams 1992).

In 1994 and 1995, the soil P in plots that previously received $P_{52.5}$ was still significantly higher than in P_0 and $P_{17.5}$. These higher soil P levels gave a significantly higher root length density in spring barley, an effect previously described by Goedewaagen (1955). The standard deviations in the results for root length density of winter wheat were large and differences in root length are not significant. In all treatments, AM colonization was (very) high, although AM (due to differences in AC) was significantly lower in the former $P_{52.5}$ treatment than in P_0 and $P_{17.5}$. Jensen and Jakobsen (1980) described the influence of long-term fertilization on mycorrhizal colonization and also found lower AM colonization with higher total P in soil. Thomson et al. (1992) investigated the effect of different fertilization rates after 6 years without fertilizer and found that colonization of *Scutellospora calospora* was inversely related to increasing residual P from fertilizer applications.

Mycorrhizal root length density was calculated because it might be more directly correlated with the benefits and costs of the symbiosis (Brundrett et al. 1996). As a result of the contrasting behaviour of roots and mycorrhizal fungi to P addition, total mycorrhizal and arbuscular root length density were not different between fertilizer treatments. Amijee et al. (1989) observed that the net effect of P fertilization on mycorrhizal root length density was initially positive (the positive effect of P on root length being larger than the negative effect on fractional colonization) but was negative at higher P applications. In a comparison between conventional and alternative farming systems in Australia, Ryan (1998) noted that both root length density and fractional colonization of wheat plants were greater on the alternative farms, which magnified the differences found between farming systems.

Arbuscular root length density apparently declined in the $P_{52.5}$ plots but the results are not significant, mainly because significant differences in AM and AC vanished when multiplied by the results for root length density, which had high standard deviations. Johnson et al. (1997) proposed that a mutualistic relationship can change into a parasitic relationship when benefits decrease and costs remain unchanged. Decreased benefits of mycorrhizal colonization would be expected if fertilization eliminates nutrient limitation. If mycorrhizal colonization does not decrease at the same time, net costs will remain unchanged. Consideration of the AC/AM ratio may help to answer the question of whether this difference in mycorrhizal functioning occurs in such fields. If AC is considered an indicator of the benefit of mycorrhizae to the plant (arbuscules being the sites of nutrient exchange) and AM is an indicator of the cost to the plant (fungal biomass depending on the carbohydrates supplied by the plant), the AC/AM ratio would reflect the benefit:cost ratio. This ratio was significantly lower in the $P_{52.5}$ plots, from which we infer that even 10 years after fertilizer application ceased, mutualistic functioning was still lower in these nutrient-rich plots. The transformation of high-input agricultural systems to low-input systems can apparently take a long time.

If the AM fungi were showing truly parasitic behaviour, crop production in $P_{52.5}$ would have been significantly lower than recorded. As we found no significant difference in total dry weight of stem and ear in barley or wheat, parasitism is unlikely. On the other hand, P-use efficiency in both barley and wheat was significantly lower in the $P_{52.5}$ plots. In the these plots, the high soil P content brought about a higher root length density, which led to an improved capacity for P uptake by the root system (de Willigen and van Noordwijk 1987). It may, therefore, be possible that the AM fungi in the P_0 and $P_{17.5}$ plots were able to supply the plants with the P needed for growth, whereas the P availability in the $P_{52.5}$ plots was sufficient for growth even of non-mycorrhizal plants. It could take a long time before such soils become low in P and, thus, mycorrhizae will be an important component of nutrient uptake processes.

In summary, we conclude that fractional mycorrhizal colonization remains low in fields previously fertilized. Mycorrhizal colonization, and especially arbuscular colonization, were inversely related to the amount of P applied. This effect was cancelled out by higher root length density as a consequence of higher P availability. No direct effect on dry weight production of either crop was observed. However, looking at the mycorrhizal benefit:cost ratio, the mycorrhizal association shifted along the mutualism-parasitism continuum towards lower plant benefit in plots that previously received 52.5 kg P ha^{-1} $year^{-1}$. This shift was accompanied by a lower P-use efficiency by the crops.

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