K. Ylivainio and T. Peltovuori (2012) 21: 453–461

Phosphorus acquisition by barley (*Hordeum vulgare* L.) at suboptimal soil temperature

Kari Ylivainio[1,2] and Tommi Peltovuori[2]

[1]MTT Agrifood Research Finland, FIN-31600 Jokioinen, Finland

[2]Department of Food and Environmental Sciences, FIN-00014 University of Helsinki, Finland

e-mail: kari.ylivainio@mtt.fi

We studied the effects of soil temperature (8 °C and 15 °C) on barley growth, barley phosphorus (P) uptake and soil P solubility. Barley was grown in a pot experiment in two soils with different P fertilization histories for 22 years. The availability of P was estimated by using ^{33}P-labeled fertilizer and calculating L-values. After cultivation for 22 years at ambient soil temperature without P fertilization (-P), soil L-value had decreased compared to soil that received annual P fertilization (P+). Low soil temperature further reduced the L-values, more in the -P soil than in the +P soil. Our results demonstrated that P fertilization can only partially ameliorate poor growth at low soil temperatures. Thus, applying ample fertilization to compensate for poor growth at low soil temperatures would increase the P content and solubility in the soil, but plant uptake would remain inhibited by cold.

Key words: Phosphorus fractionation, L-value, root growth, ^{33}P fertilization

Introduction

Most cultivated soils in Finland have a cryic temperature regime, with a mean summer soil temperature between 6 °C and 14 °C (Yli-Halla and Mokma 1998). The growing season is short, and low temperatures at the beginning of the growing season often limit plant growth. Spring barley is the most widespread cereal grown in these conditions. Suboptimal temperatures can, to some extent, be alleviated by increasing the plant-available phosphorus (P) concentration in soil (Power et al. 1963). In the recent years, the application levels of P have decreased in Finland due to an awareness of environmental problems related to excessive P fertilization, and adjustments in P fertilization levels have aimed to match plant needs.

Plants acquire P from the soil solution as phosphate ions; however, due to the low P concentration in the soil solution, P must be constantly replenished, either from fertilizers or from soil P reserves. The most significant reserves in soils comprise the P adsorbed on short-range-ordered iron and aluminum oxides and the P precipitated as calcium phosphate (Frossard et al. 1995). These reserves become plant-available through desorption or dissolution, which are both temperature-dependent reactions. The movement of P in soil is primarily controlled by diffusion, also a temperature-dependent process (Lewis and Quirk 1965). In some soils, organic P is a major P reserve, and the release of P from organic material is also hindered by low temperature (Eid et al. 1951).

Soil temperature also affects physiological mechanisms of plant P uptake. Barley root growth is strongly depressed at low soil temperatures (Abbas Al-Ani and Hay 1983, Macduff and Wild 1986), and this reduces the soil volume that the roots explore for nutrients (Gahoonia and Nielsen 1997, Sharratt 1991). This drastically decreases the availability of nutrients transported via diffusion, particularly P (Barber 1961). Sheppard and Racz (1984) concluded that P nutrition had a primary influence on wheat root growth; furthermore, soil P status and temperature had a synergistic effect on plant P uptake. Root hairs play an important role in plant P acquisition. In rye, root hairs were responsible for up to 63% of the P uptake (Gahoonia and Nielsen 1998). Moreover, root hair length affected the P uptake of barley and wheat to a greater extent in soils with a low P availability than in soils with adequate P supply (Gahoonia et al. 1997). Gahoonia and Nielsen (2003) found that, in a soil with low P availability, root-hairless mutants of barley ceased to grow after 30 days; however, the genotype with normal root hairs continued to grow. These factors suggest that a vicious cycle may effectively restrict plant growth at low temperatures in soils with low P status.

In areas of boreal and temperate climates, the effect of low soil temperature on the availability of P is an issue that is currently both agronomically and environmentally relevant, due to escalating fertilizer prices and environmental constraints that limit heavy fertilization. This study aimed to assess the impact of low soil temperature on the availability of both inherent soil P and fertilizer P for barley grown in soils with different P fertilization histories. The study was performed as a pot experiment with labeled ^{33}P fertilizer. Soil temperatures in the pot experiment reflected the typical summer soil temperatures in Southern and Northern Finland (Yli-Halla and Mokma 1998).

Manuscript received May 2012

Materials and methods

Soils

Barley (*Hordeum vulgare* cv. 'Loviisa') was grown in a pot experiment in two silty clay soils with different P fertilization histories (Table 1). The soils were obtained from the surface horizon of a P fertilizer trial conducted in Southern Finland. The soils were taken from 1) plots that had received an annual P application of 42 kg ha^{-1} for the first 15 years, then 16 kg ha^{-1} for 7 years (+P) and 2) plots that received no P fertilization for 22 years (-P). The plant-available P concentration was evaluated with water-extraction (1:50 w/v, 1 h, Table 1). Previous results showed a good correlation between water-extractable P (0.7581x + 1.5605, R^2 = 0.85, n = 62, unpublished results, Uusitalo, R.) and the Finnish soil testing method (Acid ammonium acetate, pH 4.65) (Vuorinen and Mäkitie 1955) Therefore, experimental soils could be classified as responsive (+P) or nonresponsive (-P) in terms of P fertilization (Valkama et al. 2009).

Table 1. Properties of experimental soils that received annual P application (+P) or did not receive annual P application (-P) for 22 years.

Soil	-P	+P
pH (0.01 M $CaCl_2$)	5.3	5.0
Organic C, %	2.1	1.9
Particle size distribution, %		
< 0.002 mm	42	42
0.002–0.02 mm	36	36
0.02–0.2 mm	22	20
0.2–2 mm	1	2
Water-extractable P, mg kg^{-1}	2.5	13.1
Exchangeable cations, mg kg^{-1}		
Ca	2116	1663
Mg	678	484
K	127	219
Na	51	25

Barley growth experiment

The experimental soils were sieved (8 mm), homogenized, and placed into pots (5 l soil per pot). To ensure the supply of other essential nutrients, the following elements were mixed into the soil (in mg l^{-1}): 200 N (as NH_4NO_3), 200 K (KCl), 50 Mg ($MgSO_4$), 5 Cu ($CuSO_4$), 4 Mn ($MnSO_4$), 2 Fe ($FeSO_4$), 3 Zn ($ZnSO_4$), 1 B (H_3BO_3), and 1 Mo (Na_2MoO_4). Phosphorus (as $Ca(H_2PO_4)_2 \bullet H_2O$) was added at either 1 mg l^{-1} or 50 mg l^{-1} and labeled with ^{33}P (6.5 * 10^8 Bq ^{33}P pot^{-1}). The lower P concentration served as a carrier for ^{33}P, and it was considered to provide insignificant fertilization (Control). Thirty barley seeds were planted in each pot, and during early development, the shoots were thinned to 20 plants per pot. Each treatment was replicated four times.

The plants were grown outdoors at ambient air temperature under a glass roof. The pots were embedded in metal boxes containing either sand (ambient soil temperature) or circulating, cooled water (aimed to achieve a soil temperature of 8 °C). The metal boxes were covered with a 5 cm styrofoam top, with openings for each experimental pot. Soil and air temperatures were monitored with Pt-100 temperature probes. Soil temperatures were recorded from three randomly selected pots from both soil temperatures at 4 h intervals with a probe placed in the center of the pot at a depth of 10 cm; Table 2 summarizes the temperature readings throughout the experiment. During the experiment, soil moisture was maintained at 70–90% of maximum water holding capacity, which was determined with gypsum blocks (Soil Moisture Equipment) placed in each pot. Plant shoots were harvested at 2 cm above the soil surface at 43 days after planting, when the first awns were visible in the P-fertilized (50 mg P l^{-1}) barley plants in the +P soil at ambient soil temperature.

Table 2. Air and soil temperatures (°C) measured during the pot experiment

	Average*	Range
Air temperature	14.4	6.6 – 23.0
Soil temperature of 15 °C*	14.7	11.0 – 18.0
Soil temperature of 8 °C*	8.0	6.9 – 10.1

*Averages were calculated for three sample pots.

Analysis of barley P

Harvested plant material was dried at 65 °C for 48 h. For P analysis, plant samples were ground with a hammer mill, and duplicate samples were ashed at 500 °C for 2 h. The residue was dissolved in 3 ml of 7 M HNO_3, evaporated to dryness on a sand bath, and heated to 500 °C for 1 h. Next, the residue was dissolved in 10 ml of 6 M HCl and the P concentration was analyzed with an ammonium vanadate method (Jackson 1958). In each batch analyzed, we included a reference sample with a 9.0% coefficient of variation (n = 6). The activity of ^{33}P in the samples was analyzed with a scintillation counter (Wallac 1411), after the addition of the Lumagel (Lumac LSC B.V.) scintillation cocktail. We used the measuring window for ^{45}Ca (maximum energy 257 keV vs. 249 keV of ^{33}P). Background activity was subtracted out, and a correction for the counting efficiency was defined with an external standard (^{152}Eu). The utilization of applied ^{33}P was calculated as the proportion of ^{33}P taken up by the barley biomass compared to the total activity of ^{33}P applied to the soil. Additionally, the apparent utilization of P was calculated by subtracting the total P taken up by plants under the control treatment from the total P taken up by the plants that received P-fertilized treatment; the difference was then compared to the amount of applied P fertilizer. The concentrations of labile P in soils (L-value) were calculated according to the following formula (Russell et al. 1957):

$$L = \frac{^{33}P_{added} * (P_{in\ plant} - P_{in\ seed})}{^{33}P_{in\ plant}} - P_{added}$$

where ^{33}P refers to the total activity (Bq) and P refers to the total amount (mg) of P.

Soil analysis

After cutting the barley shoots, soil samples were taken from each pot and dried either at room temperature (ambient soil temperature treatments) or at 5 °C (soil temperature 8 °C), and sieved (2 mm). Soil P was fractioned as duplicates into Chang and Jackson P fractions according to Hartikainen (1979). In brief soil samples were sequentially extracted with 1 M NH_4Cl, 0.5 M NH_4F (pH 8.5), 0.1 M NaOH and 0.25 M H_2SO_4 with a soil-to-solution ratio of 1:50 (w:v). The first extractant removes easily soluble P and exchangeable Ca, followed by P supposedly bound to Al-oxides, Fe-oxides, and finally to Ca (apatitic P). Extraction times were 30 min (1 M NH_4Cl), 1 h (0.5 M NH_4F and 0.25 M H_2SO_4) and 16 h (0.1 M NaOH). After the 2nd and 3rd extractions, soils were washed with 25 ml of saturated NaCl solution. The P concentrations of extractants were analyzed with a molybdenum blue method using stannous chloride reductant. Activities of ^{33}P in the fractions were analyzed with Lumagel Plus (Lumac LSC B.V.) as a scintillation cocktail. Soil pH was determined in a 1:2.5 (v/v) 0.01 M $CaCl_2$ suspension. Soil texture was determined according to Elonen (1971) and the content of organic carbon with a Leco® CNS 1000 analyzer. Exchangeable cations were determined according to Thomas (1982).

Furthermore, we determined water-soluble P concentrations of +P and –P soils by shaking air-dried, sieved (2 mm) soils for one hour in a reciprocal shaker (250 rpm) with a soil-to-water ratio of 1:50 (w:v) at temperatures of 5 °C (± 1 °C), 15 °C (± 1 °C) and 25 °C (± 2 °C). Soils and extractants (water) were tempered at appropriate temperatures for one day before the extractions. A few drops of toluene were added to the centrifuge tubes to depress microbiological growth. The suspensions were filtered through a 0.2 µm filter (Nucleopore® Polycarbonate) at the experimental temperatures and analyzed for P according to Murphy and Riley (1962). Longer extraction times (6 h, 48 h and one week) had no significant effect on water extractable P concentration (data not shown). Also a P adsorption experiment was conducted at the same temperatures, with solution containing 1 mg P l^{-1} (50 mg P kg^{-1} soil). The water extraction and P adsorption experiments were replicated four times.

Results

L-values

The availability of P (L-value) for barley in soil with an ample P fertilization history (+P) was significantly higher than in the soil cultivated for years without P fertilization (-P) (Table 3). In control treatments, at ambient soil temperature, the L-value in the -P soil was 36% of that found in the +P soil. At low soil temperature, the L-value in the -P soil was only 20% of that found in the +P soil. Fresh P fertilization significantly increased the L-value only in the -P soil; the L-values increased by 49 and 24 mg l^{-1} at soil temperatures of 8 and 15 °C, respectively. Nevertheless, the L-values in the -P soil remained less than 50% of those found in the +P soils.

Table 3. Availability of P (L-values, mg l^{-1} soil), shoot dry weight (g), and P content in barley shoots (mg g^{-1} DW) in the pot experiment. Control treatment received 1 mg P l^{-1} soil as a carrier for ^{33}P.

	-P		+P	
	Control	50 mg P l^{-1} soil	Control	50 mg P l^{-1} soil
L-values				
8 °C	35^{a}	84^{bc}	170^{d}	181de
15 °C	69^{b}	93^{c}	191^{e}	192^{e}
Shoot dry weight				
8 °C				
15 °C	2.5^{a}	12.1^{cd}	9.4^{bc}	14.4^{d}
	7.8^{b}	28.6^{e}	26.4^{e}	33.5^{f}
P content				
8 °C	1.9^{a}	3.4^{cd}	3.1^{c}	4.4^{f}
15 °C	2.6^{b}	3.7^{de}	4.0^{ef}	5.6^{g}

Means followed by a common letter were not significantly different ($p < 0.05$, Tukeys HSD test).

Barley biomass yield, P concentration, and ^{33}P utilization

The low soil temperature dramatically depressed barley growth and delayed barley development. The dry weights of shoots harvested at 8 °C soil temperature were only 32 to 43% of those for shoots harvested at ambient soil temperature (Table 3). The effects of P fertilization history and fresh P fertilization were also evident in the shoot dry weight. Without P fertilization (control treatment), at both soil temperatures, the harvested biomass of plants grown in the -P soil was less than 30% of that found in plants grown in the +P soil. Fresh P fertilization quadrupled the shoot dry weight of plants grown in the -P soil and raised it to about 85% of the yield achieved with the +P soil (Table 3). Although L-values were not affected, P-fertilization also significantly increased the biomass of barley grown in the +P soil.

The concentrations of P in barley shoots reflected the accumulation of shoot dry weight. The soil temperature, P fertilization history, and fresh P fertilization all had marked effects on plant P concentration (Table 3). The barley shoots grown in the -P soil without P fertilization had P concentrations below 3 mg g^{-1} of dry matter; this concentration indicated P deficiency (Bergmann 1992).

The utilization of added ^{33}P at ambient soil temperature was 15.2% in the -P soil and 16.1% in the +P soil. Less ^{33}P was utilized at 8 °C; 5.8% in the -P soil and 5.6% in the +P soil. The apparent P utilization rates were much higher, but were not affected by prior P fertilization history. On average, the apparent utilization was 33% at ambient soil temperature and 14% at the low soil temperature. Regardless of soil temperature, approximately 36% and 22% of the P taken up by barley shoots originated from fresh ^{33}P fertilization in the -P and +P soils, respectively.

Soil P fractions after the experiment

Omitting P fertilization for 22 years had decreased the NH_4F-extractable P concentration in the -P soil to one third of that found in the +P soil (Table 4). In the NaOH fraction, the lack of P fertilizer had quantitatively decreased the P concentration by about the same amount, but the relative decrease was only 26%. The inferior P status of the -P soil compared to the +P soil, also suggested in the concentrations of NH_4Cl-soluble P, was clearly demonstrated in the L-values and biomass accumulation of barley (Table 3).

Addition of ^{33}P fertilizer clearly increased the amount of P found in the NH_4Cl-, NH_4F- and NaOH-extractable fractions (Table 4). The P concentration in the two most soluble P fractions tended to be higher in soils incubated at 8 °C than in soils incubated at 15 °C; however, this was only statistically significant in the NH_4F-extractable fraction from the +P-soil. Most (68–86%, Table 4) of the ^{33}P applied to the soils was retained in the NH_4F- and NaOH-extractable P fractions. The NaOH fraction of the -P soil retained ^{33}P more efficiently than the NaOH fraction of the +P soil; in contrast, the opposite was true for the NH_4F-extractable fractions.

The most soluble (NH_4Cl-extractable) P fraction contained a very small proportion of the added ^{33}P. However, NH_4Cl extracted significantly more ^{33}P from the +P soil compared to the -P soil (Table 4). At the low soil temperature, among the P fractions, the addition of ^{33}P fertilizer (50 mg l^{-1}) caused a significant increase only in the NH_4Cl-extractable ^{33}P content for both -P and +P soils. Only H_2SO_4 extracted more P from the -P than from the +P soil, but this fraction contained at most 5.5% of the added ^{33}P. The difference was probably due to the fact that the -P soil had a slightly higher level of exchangeable Ca and a higher soil pH (Table 1) than the +P soil; this favored the formation of calcium phosphates. After the pot experiment, considering both the harvested biomass and the soil P fractionation, the total recoveries of ^{33}P from the -P and +P soils were 94% and 97%, respectively, at the ambient soil temperature and 88% and 95%, respectively, at the lower soil temperature.

Table 4. P recoveries from sequential extractions were analyzed in Chang and Jackson P fractions (mg kg^{-1}) from experimental soils (-P and +P) at the beginning (start) and after the pot experiment.

	-P		+P	
P fractions	8 °C	15 °C	8 °C	15°C
NH_4Cl				
Start	n.d.*		2.8	
Control	n.d.* (0.5^{a})	n.d.* (0.6^{a})	2.6^{bc} (3.4^{c})	3.2^{c} (2.0^{bc})
50 mg ^{33}P l^{-1}	1.0^{ab} (2.2^{bc})	0.7^{a} (0.9^{ab})	5.9^{d} (5.2^{d})	5.8^{d} (3.2^{c})
NH_4F				
Start	27.5		88.8	
Control	29.4^{a} (35.0^{ab})	29.1^{a} (29.3^{a})	93.4^{c} (44.9^{cd})	89.1^{c} (34.6^{ab})
50 mg ^{33}P l^{-1}	42.5^{b} (36.1^{abc})	41.6^{b} (29.3^{a})	116.3^{e} (51.3^{d})	106.6^{d} (40.3^{bc})
NaOH				
Start	144.5		196.9	
Control	145.7^{a} (51.1^{cd})	144.1^{a} (54.6^{d})	202.0^{cd} (32.3^{ab})	192.2^{c} (33.6^{ab})
50 mg ^{33}P l^{-1}	160.4^{b} (40.4^{abc})	160.9^{b} (44.4^{bcd})	203.5^{cd} (30.4^{a})	206.3^{d} (34.1^{ab})
H_2SO_4				
Start	304.4		271.9	
Control	303.1^{b} (4.8^{cd})	306.3^{b} (5.5^{d})	269.1^{a} (2.5^{ab})	272.5^{a} (3.0^{abc})
50 mg ^{33}P l^{-1}	302.5^{b} (3.1^{abc})	312.5^{b} (4.2^{bcd})	277.8^{a} (2.2^{a})	271.3^{a} (3.2^{abc})
Sum				
Start	476.6		560.4	
Control	478.2 (91.3)	479.5 (90.0)	567.0 (83.1)	557.0 (72.6)
50 mg ^{33}P l^{-1}	506.5 (81.8)	515.7 (78.7)	603.4 (89.1)	589.8 (80.8)

Barley had been grown in control soil (nominally treated with 1 mg P l^{-1} soil as a carrier for ^{33}P) and fertilized soil (50 mg ^{33}P l^{-1}) at different soil temperatures; the percentage of ^{33}P recovered from the applied amount in fertilizer is shown in parenthesis.

* below the detection limit

Means within the P fractions followed by a common letter were not significantly different ($p < 0.05$, Tukeys HSD test).

Temperature effects on water-soluble P and P adsorption

The water-soluble P concentration increased with increases in extraction temperature from 5 °C to 25 °C, both in the -P and in the +P soils (Table 5). However, at the lower range (from 5 °C to 15 °C), the concentration of water-soluble P concentration increased significantly only in the +P soil (Table 5). This increase corresponded to that observed in the L-values (about 10%) as the extraction temperature increased from 8 °C to 15 °C. In the -P soil, the L-value doubled, but the water-extractable P concentration increased by only about 18%. Phosphorus adsorption was about three-fold higher in the -P soil than in the +P soil. As the extraction temperature increased from 15 °C to 25 °C, P adsorption increased only in the -P soil (Table 5).

Table 5. Water-soluble P and P adsorption (mg kg^{-1}) in experimental soils (-P and +P soils) at three temperatures. Adsorption of P (mg kg^{-1}) was determined by adding 50 mg P kg^{-1} soil to an extraction solution (water). Adsorption of P (Pads) was calculated as: Pads = initial P (50 mg P kg^{-1}) – P concentration in the extraction solution on a soil weight basis (mg P kg^{-1}) after 1 h.

	Extraction temperature		
	5 °C	15 °C	25 °C
Water-soluble P			
-P	1.4[a]	1.7[a]	2.5[b]
+P	9.2[c]	10.4[d]	13.1[e]
Adsorbed P (Pads)			
-P	22.8[b]	24.6[b]	28.9[c]
+P	8.6[a]	6.9[a]	8.5[a]

Means followed by a common letter were not significantly different ($p < 0.05$, Tukeys HSD test).

Discussion

This study showed that a decrease in soil temperature from 15 °C to 8 °C halved the L-value in soil with low plant-available P content. In contrast, soil with larger P reserves was relatively unaffected by temperature. The main mechanism behind this outcome was probably that low soil temperatures depressed the root growth (Mackay and Barber 1984, Macduff and Wild 1986, Kaspar and Bland 1992); poor root growth reduced the soil volume available for P uptake, which is a critical factor in soils with low plant-available P (Sheppard and Racz 1984).

Some studies have suggested that low P solubility in soil is the dominant mechanism for hindering plant growth at low soil temperature. According to Singh and Jones (1977), the reduced desorption of P in cold soil played a major role in the variations in P uptake by lettuce at temperatures that ranged from 12.7 to 29.4 °C; thus, they suggested that physiological factors played only a minor role. In our study, however, even ample ^{33}P fertilization in +P soil was unable to compensate for the growth retardation caused by low soil temperature. It is probable that the P status of the +P soil was at the level where no significant increases in yield could be obtained with additional P, because the L-value at low soil temperature after P application was the same as the availability observed in the fertilized and unfertilized treatments at ambient soil temperature. Low soil temperature also reduced the L-values more than would be expected based on the water-extractable P concentration measured in the -P soil. This indicated that physiological factors must have been the main cause for the reduced P uptake, rather than P availability *per se*. Indeed, there is evidence that the activation energy of ion uptake can drastically increase when the temperature falls below 10 °C (Carey and Berry 1978). According to Macduff and Jackson (1991) there are temperature-sensitive mechanisms that may hinder plant growth at low soil temperatures and contribute to reduced nutrient uptake.

Cultivation of the -P soil for years without P fertilization had decreased the water soluble P concentration to less than 20% of that found in the +P soil; consequently, barley growth was dramatically depressed. Growth was, however, restored to the level of +P soil with fresh P fertilization; nevertheless, the L-value remained less than half of that found in the +P soil. This indicated that the growth of barley in soil with a low plant available P content could be restored with a single P application.

Calculation of the L-value is based on the assumption that ^{33}P has reached equilibrium with the soil P (Larsen 1952). According to Frossard et al. (1994), when the carrier application is large compared to an isotopically exchangeable P pool, it will modify the P exchange kinetics, and this may lead to an overestimation of the actual L-value. In the present study, the P adsorption test showed that the low soil temperature may have depressed the adsorption of P in the -P soil. This was supported by the higher proportion of ^{33}P found in the NH_4Cl –extractable fraction at the low soil temperature. Thus, the L-value may have been overestimated, because the increase in the L-value equaled the amount of added fertilizer P (49 mg l^{-1} vs. 50 mg l^{-1}, Table 3), which suggested that ^{33}P may not have reached equilibrium with soil P at the low soil temperature. This notion was supported by the fact that the most soluble P fraction (NH_4Cl-P) of the P fertilized soil contained significantly more ^{33}P than the NH_4Cl-P fraction of the control soil.

Regardless of previous P fertilization history, increases in soil temperature significantly increased the L-values in both soils. This was probably the result of increased P desorption and enhanced root growth (Sheppard and Racz 1984), which increased the utilization of indigenous P sources, particularly in the -P soil. Contrary to the -P soil, the L-values of the +P soil were not affected by P fertilization at either soil temperature.

In this experiment, barley shoots were harvested at different growth stages. The L-values were probably only slightly affected by this procedure. For maize, a slight decrease in the L-value was observed as growth advanced from the 7th to the 10th leaf stage (Munyinda et al. 1982). Equal L-values suggested that additional P fertilization was not required in the +P soil, despite the significant increases in barley biomass yields. Higher yields could partly be explained by different growth stages at harvest. Some studies have shown that deviations in early growth rates do not necessarily result in grain yield differences. For instance, Power et al. (1970) observed that barley growth rate was accelerated in the early growth stage at higher soil temperatures, and the heading stage was achieved sooner at a soil temperature of 15.5 °C than at a soil temperature of 9 °C. Nevertheless, the grain grown at those soil temperatures produced equivalent final yields. In field experiments, it was shown that P fertilization provided equal yield increases in Southern and Northern Finland (Valkama et al. 2009).

Exhaustion of indigenous P reserves had depressed the L-value and increased the P adsorption capacity of the -P soil. Nevertheless, the calculated utilization of ^{33}P in both soils, irrespective of soil temperature, was very similar. It was somewhat surprising that the large difference in P fertilization over the last 22 years (742 kg ha^{-1} vs. 0 kg ha^{-1}) had such a small effect on the utilization efficiency of ^{33}P in terms of the P adsorption capacity of the soils. This result indicated that fresh P fertilizer was not immediately fixed into an unavailable form, even in soil with a low P status. Utilization of ^{33}P in +P soil may have been depressed by the slightly lower soil pH compared to that found in -P soil. High utilization of P fertilizer in the -P soil increased barley yields by more than triple; consequently, the yield approached that obtained in the +P soil.

In the Chang and Jackson P fractionation procedure, the NH_4F-P and NaOH-P fractions presumably represented P bound to short-range-ordered Al- and Fe-oxides, respectively (Hartikainen 1979). These fractions, particularly the NH_4F-extractable P, regulate the concentration of soluble P in non-alkaline soils (MacKenzie 1962, Hartikainen 1979, Frossard et al. 1995). We also found that most of the added ^{33}P was present in these fractions, and cultivation for 22 years without P fertilizer had depleted proportionately more NH_4F- than NaOH-extractable P. Continuous P fertilization in the +P soil had maintained the P saturation of the Fe- oxides, and P bound to the Al –oxides probably provided most of the plant P requirements. In contrast to the +P soil, the -P soil had provided a higher proportion of P from Fe-oxides to fulfill plant P requirements. Deviations in P saturation caused more of the fresh ^{33}P fertilizer to be adsorbed onto the Fe-oxides and less onto the Al-oxides in the -P soil; and the opposite occurred in +P soil.

The P fertilization history and soil temperature had a significant effect on how ^{33}P was distributed among the extracted P fractions. Cool soil temperature caused more ^{33}P to be adsorbed onto the Al-oxides, particularly in the +P soil. This was probably related to the observation that P was less strongly retained at low soil temperatures (Barrow 1979, Hartikainen 1979). This hypothesis was supported by our results, which showed that the NH_4Cl-P concentration increased after P fertilization only at the low soil temperature (8 °C). The role of NH_4F-P was probably accentuated by depressed barley growth and decreased P uptake at the low soil temperature. Despite the low P saturation in the –P soil, P fertilization increased the biomass of barley to that obtained with the +P soil at ambient soil temperature. This result suggested that the level of readily soluble P content in the +P soil after ^{33}P fertilization was above the optimum level; consequently, the high P saturation increased the P leaching potential of the soil. Thus, over-fertilization may adversely impact the environment more at low than at high temperatures, due to the reduced P uptake. This study implied that suboptimal growing temperatures cannot be overcome with P fertilization. Keeping this in mind, P fertilization should be targeted to fields that are responsive to P fertilization; this strategy would ensure the best results, both environmentally and economically.

Conclusions

Our results demonstrated that a low soil temperature significantly depressed the early development of barley, particularly in soils with a low P status. The adverse effects of suboptimal soil temperatures on plant growth can only be partly ameliorated with P fertilization. However, at a given soil temperature, the productivity of soil with a low content of plant-available P can be restored with P fertilization; in fact, it can be restored to the level of a soil with an optimal level of plant-available P content. From environmental and economical points of view, P fertilization should be adjusted according to the responsiveness of a given crop. At suboptimal soil temperature, P fertilization increases P solubility, and this may increase the P leaching potential, particularly in soils with a high content of readily soluble P.

Acknowledgements

We thank Kaj-Roger Hurme, laboratory technician, and Antti Uusi-Rauva, chief engineer, for their guidance in using ^{33}P. We also thank Kemira Agro Oyj, currently Yara Suomi Oy, for providing the soils for the experiment and a grant for the laboratory analyses. Financial support for publishing this work was partly provided by the research project, Baltic Forum for Innovative Technologies for Sustainable Manure Management (Baltic Manure), a project that was partly financed by the European Union (European Regional Development Fund), the Baltic Sea Region Programme 2007-13.

References

Abbas Al-Ani, M.K. & Hay R.K.M. 1983. The influence of growing temperature on the growth and morphology of cereal seedling root systems. *Journal of Experimental Botany* 34: 1720-1730.

Barber, S.A. 1961. A diffusion and mass-flow concept of soil nutrient availability. *Soil Science* 93: 39-49.

Barrow, N.J. 1979. Three effects of temperature on the reactions between inorganic phosphate and soil. *Journal of Soil Science* 30: 271-279.

Bergmann, W. 1992. *Nutritional disorders of plants - development, visual and analytical diagnosis*. Jena: Gustav Fischer. 741 p.

Carey, R.W. & Berry, J.A. 1978. Effects of low temperature on respiration and uptake of rubidium ions by excised barley and corn roots. *Plant Physiology* 61: 858-860.

Eid, M.T., Black, C.A. & Kempthorne, O. 1951. Importance of soil organic and inorganic phosphorus to plant growth at low and high soil temperatures. *Soil Science* 71: 361-370.

Elonen, P. 1971. Particle-size analysis of soil. *Acta Agralia Fennica* 122: 1-122.

Frossard, E., Brossard, M., Hedley, M.J. & Metherell, A. 1995. Phosphorus in the global environment. In: Tiessen, H. (ed.). *Reactions controlling the cycle of P in soils*. New York: John Wiley & Sons. p. 107-137.

Frossard, E., Fardeau, J.C., Brossard, M. & Morel, J.L. 1994. Soil isotopically exchangeable phosphorus: A comparison between E and L values. *Soil Science Society of America Journal* 58: 846-851.

Gahoonia, T.S., Care, D. & Nielsen, N.E. 1997. Root hairs and phosphorus acquisition of wheat and barley cultivars. *Plant and Soil* 191: 181-188.

Gahoonia, T.S. & Nielsen, N.E. 1997. Variation in root hairs of barley cultivars doubled soil phosphorus uptake. *Euphytica* 98: 177-182.

Gahoonia, T.S. & Nielsen, N.E. 1998. Direct evidence on participation of root hairs in phosphorus (^{32}P) uptake from soil. *Plant and Soil* 198: 147-152.

Gahoonia, T.S. & Nielsen, N.E. 2003. Phosphorus (P) uptake and growth of a root hairless barley mutant (*bald root barley, brb*) and wild type in low- and high-P soils. *Plant, Cell and Environment* 26: 1759-1766.

Hartikainen, H. 1979. Phosphorus and its reaction in terrestrials soils and lake sediments. *Journal of the Scientific Agricultural Society of Finland* 51: 537-624.

Jackson, M.L. 1958. Phosphorus determinations for soils. In: *Soil chemical analyses*. Englewood Cliffs, N.J: Prentice-Hall, Inc. p. 134-182.

Kaspar, T.C. & Bland, W.L. 1992. Soil temperature and root growth. *Soil Science* 154: 290-299.

Larsen, S. 1952. The use of P^{32} in studies in the uptake of phosphorus by plants. *Plant and Soil* 4: 1-10.

Lewis, D.G. & Quirk, J.P. 1965. Diffusion of phosphate to plant roots. *Nature* 205: 765-766.

Macduff, J.H. & Jackson, S.B. 1991. Growth and preferences for ammonium or nitrate uptake by barley in relation to root temperature. *Journal of Experimental Botany* 42: 521-530.

Macduff, J.H. & Wild, A. 1986. Effects of temperature on parameters of root growth relevant to nutrient uptake: measurements on oilseed rape and barley grown in flowing nutrient solution. *Plant and Soil* 94: 321-332.

Mackay, A.D. & Barber, S.A. 1984. Soil temperature effects on root growth and phosphorus uptake by corn. *Soil Science Society of America Journal* 48: 818-823.

MacKenzie, A.F. 1962. Inorganic soil phosphorus fractions of some Ontario soils as studied using isotopic exchange and solubility criteria. *Canadian Journal of Soil Science* 42: 150-156.

Munyinda, K., Karamanos, R.E. & Bettany, J.R. 1982. The determination of "L" values by discrete and integrated sampling procedures. *Communications in Soil Science and Plant Analysis* 13: 1061-1069.

Murphy, J. & Riley, J.P. 1962. A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta* 27: 31-36.

Power, J.F., Grunes, D.L., Reichman, G.A. & Willis, W.O. 1970. Effect of soil temperature on rate of barley development and nutrition. *Agronomy Journal* 62: 567-571.

Power, J.F., Grunes, D.L., Willis, W.O. & Reichman, G.A. 1963. Soil temperature and phosphorus effects upon barley growth. *Agronomy Journal* 55: 389-392.

Russell, R.C., Russell, E.W. & Marais, P.G. 1957. Factors affecting the ability of plants to absorb phosphate from soils I. The relationship between labile phosphate and absorption. *Journal of Soil Science* 8: 248-267.

Sharratt, B.S. 1991. Shoot growth, root lenght density, and water use of barley grown at different soil temperatures. *Agronomy Journal* 83: 237-239.

Sheppard, S.C. & Racz, G.J. 1984. Effect of soil temperature on phosphorus extractability II. Soil phosphorus in six carbonated and six non-carbonated soils. *Canadian Journal of Soil Science* 64: 255-263.

Singh, B.B. & Jones, J.P. 1977. Phosphorus sorption isotherm for evaluating phosphorus requirements of lettuce at five temperature regimes. *Plant and Soil* 46: 31-44.

Thomas, G.W. 1982. Exchangeable cations. In: Page, A.L., Miller, R.H. & Keeney, D.R. (eds.). *Methods of Soil Analysis. Part 2 - Chemical and Microbiological Properties*. Madison, Wisconsin, USA: American Society of Agronomy, Inc. p. 159-165.

Valkama, E., Uusitalo, R., Ylivainio, K., Virkajärvi, P. & Turtola, E. 2009. Phosphorus fertilization: A meta-analysis of 80 years of research in Finland. *Agriculture, Ecosystems & Environment* 130: 75-85.

Vuorinen, J. & Mäkitie, O. 1955. The method of soil testing in use in Finland. *Agrogeological Publications* 63: 1-44.

Yli-Halla, M. & Mokma, D. 1998. Soil temperature regimes in Finland. *Agricultural and Food Science in Finland* 7: 507-512.