305/26

Plant and Soil 91, 221–229 (1986). Ms. 6050

Phosphorus requirements of the wheat plant in various stages of its life cycle

W. RÖMER and G. SCHILLING
Martin-Luther-Universitat Halle-Wittenberg, Sektion Pflanzenproduktion, Wissenschaftsbereich Agrochemie, DDR-4020 Halle/S., Adam-Kuckhoff-Str. 17b, DDR

Received 14 August 1984. Revised July 1985

Key words Daily P uptake per m root length P requirement during life cycle Pot experiment Solution culture Wheat

Summary In pot experiments root growth and P uptake were found to precede shoot growth. The high rate of P uptake in the early stages of the life cycle is not an expression of luxury consumption but reflects a high P requirement in plants. Plants cultivated in nutrient solutions with different P concentrations during various stages of development showed that a high P supply (1 ppm) between Feekes stages 6 and 9 (30 days) caused a higher grain yield than the same P concentration between Feekes stages 11 and 17 (30 days). The early applied P caused a high number of fertile ears per area, a high number of grains per ear, and a high P pool in vegetative parts. The latter could be mobilized during the grain-filling period. Therefore, for high grain yields soil and fertilizers have to meet the high P requirement (about 20 μg P/m root · day) in an early stage of plant growth. During the grain filling period the P supply can be much lower.

Introduction

The complicated behaviour of P in soil[12,13,17] makes it difficult to establish an efficient P fertilizer application policy. Consequently, disagreement exists on the necessary doses of P fertilizers[6,7,20,21,22,27]. Hence, the purpose of the present paper is to quantify the phosphorus requirement of the wheat plant in relation to ontogenesis. Obviously, there is a lack of knowledge on this topic and on time of maximum P demand of wheat[28].

Data contained in the older literature[2,25] show an intensive phosphorus uptake during the early growth stages, but the causes of this phenomenon are not clear. Especially possible changes in the P supply to the root from the rooted soil zones during the growth period have not been taken into account[12].

It appears, therefore, necessary to quantify the required P supply to the root surfaces in times of high P requirement and also during the other stages of plant development. From these data conclusions could be drawn on soil characteristics needed to supply the wheat plants with phosphorus during periods of high and of low requirements. The consequence could be that decisions on fertilizer applications are based not only on soil data but also on physiological ones. But for such investigations it is important to use P concentrations occuring in the soil rather than the higher ones used in nutrient solution cultures[3,28].

Methods

1 Pot experiment

To determine the course of dry matter production and of P uptake by wheat plants during ontogenesis, spring wheat (cv. Hatri) was grown on 40 cm deep Mitscherlich pots. Only 5 plants were grown on each pot. Every 10 to 14 days, the plants of 3 pots were harvested to determine the quantity of dry matter in the shoots and roots, the total length of all roots (measured with a ruler) and the total P uptake. On the basis of these data it was possible to determine the daily average P absorption rate per 1 m root length.

The substrate used was a mixture of 9 kg sandy loam soil (Kühnfield, Halle) and 9 kg quartz sand per pot. Characteristics of the soil were 13% particles $< 0.6\,\mu$m; 1.23% C_t; pH $= 6.1$ (N/10 KCl); 10 mg K/100 g[29] and 7 mg P/100 g[29] substrate. The fertilizer supply consisted of 1 g N (NH_4NO_3), 1 g K (K_2SO_4), 0.3 g Mg ($MgSO_4 \cdot 7H_2O$) for each pot. The moisture level in the substrate was kept at 60% of the maximum water capacity by daily watering. The pots were put on vegetation wagons under open air conditions. Only during the night and when it rains they were taken into the glasshouse.

2 Nutrient solution experiments

To determine the P requirement of the plants at different stages of development, experiments with nutrient solutions were carried out which permitted changes to be made in the P supply in different stages of development of the wheat plants.

The solutions kept in plastic 5 liter containers were renewed every 3 days. The P concentration in the solutions did not exactly correspond to the actual concentration at the root surface (AFS) because the solution was stirred only once per day, but in order to distinguish between times of high and low P requirement, the method can be regarded as adequate.

In January 1980 respective 1981 the winter wheat seeds (cv. Alcedo) were germinated in quartz sand without nutrients (Mitscherlich-pots). When the plants had developed two leaves (middle of March), 16 of them were put in nutrient solution of the following concentration in ppm: 80 N (NH_4NO_3), 70 K (K_2SO_4), 20 Ca ($CaCl_2$), 10 Mg ($MgSO_4 \cdot 7H_2O$), 1 ml A–Z trace element solution according to Hoagland and 0.5 to 5 ppm P (KH_2PO_4) per treatment. The pH was adjusted to 5.8.

When plants had reached Feekes stage 17, the concentration of macronutrients was gradually lowered to zero. At maturity, grain and straw yields and total P absorption were determined.

Results

1 Course of P uptake during ontogenesis (pot experiment)

Figure 1 shows the results obtained in the pot experiment with spring wheat. The curves plotted for the dry matter production of the shoot and the root and for the P uptake reveal some remarkable features:

The growth of the roots clearly precedes the growth of the shoot. When the shoot has developed only 35% of its total dry matter, the root has already reached maximum dry matter production.

P absorption also precedes shoot growth. When the shoots have developed only 20–35% of their total dry matter, already 50–60% of total P has been taken up by the plants.

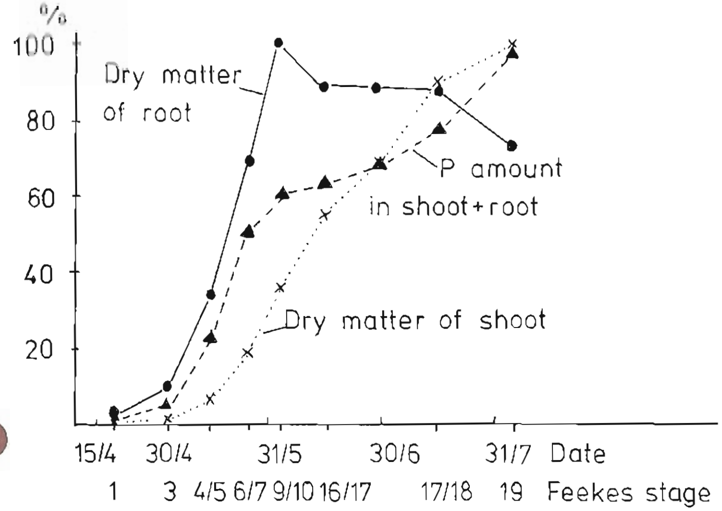

Fig. 1. The course of relative dry matter production of shoot and root and of P uptake for spring wheat (cult. 'Hatri', pot experiment, depth of pots: 40 cm) during a growing season.

Table 1. Dependence of yield and P uptake per pot of spring wheat (cv. Hatri) on P concentration in the nutrient solution

P-concentration in solution (ppm)	Dry matter				Total P uptake	
	Grain		Straw			
	(g)	(rel.)	(g)	(rel.)	(mg)	(rel.)
0.5	14.2	82	15	71	36	46
1	17.4	100	21	100	79	100
5	19.4	111	24	114	217	274
LSD 5% Tukey	2.3	13		14	17	22

The question arose whether the high P absorption rate in the early stages was due to favourable P absorption conditions in the rhizosphere[12] or whether it was a consequence of increased P requirements of the plant (endogenously controlled). This question should be answered by concluding cultivation tests on nutrient solutions.

2 Tests to determine the P requirement of the plants at certain stages of their development (nutrient solution experiments)

The results of preliminary tests (Table 1) showed – with the above-mentioned restriction – that a P concentration in the nutrient solution throughout the vegetation period of 0.5 ppm P could be classified as low, of 1 ppm P as nearly sufficient, and of 5 ppm as high (luxury consumption).

Table 2 shows the results of a nutrient solution experiment with winter wheat (Alcedo). At first all plants were cultivated under equal conditions (1 ppm P). When they reached Feekes stage 6, they were partitioned into 3 treatments. Plants in treatment 1, from that time on up to the stage of maturity were supplied only with the low P concentration of 0.5 ppm. Plants in treatments 2 and 3 received a higher P supply (1 ppm) once during a 30 day period in the course of their development. In treatment 2, they received the higher concentration between Feekes stages 6 and 9, and in treatment 3 as late as between Feekes stages 11 and 17. The following observations were made:

Treatment 2 gave the highest yield (number of grains).

Treatment 3 gave the highest P uptake with a grain yield significantly lower than that of treatment 2. This means that a unit of P absorbed at a late stage contributes less to dry-matter production than one absorbed at an earlier stage.

A yield analysis (Table 2) gives insight into the causes of these results. The higher P supply at an early date (Feekes stages 6 and 9, treatment 2) effected a significant increase in the number of fertile stalks and in the number of grains per ear, but had no influence on the thousand-grain mass (TGM). The higher P supply in Feekes stages 11 to 17 (treatment 3) increased the TGM. This increased TGM, however, could not compensate for the effect of the higher number of ears and grains per unit area (per pot) observed in treatment 2. Furthermore, it should be noted that a significant increase in TGM as a result of increased P supply was observed only in cases (as shown by other tests not referred to in detail here) with a low number of fertile tillers caused by a low P supply after tillering. For this reason, a late increase in P supply cannot generally be considered effective in creating additional crop reserves.

The general picture observed is. The capability of the wheat plants to utilize the absorbed P for a higher crop yield is obviously pronounced in the first half of ontogenesis, most probably till Feekes stage 9. This does not imply that the plants have no demand for P at the time of grain filling. But the P supply required at the root surface to enable them to form many fertile flowers per unit area is obviously higher than the P supply required for the physiological process at the time of grain filling. This has been clearly demonstrated recently for winter wheat by other authors as well[28]. For the last stages of development, the plant

Table 2. Dependence of yield and its components of winter wheat on variations in P supply during several stages of plant growth (Experiment with solution culture)

Treatment No.	P-supply during various stages of growth according to Feekes (F) (ppm P) F2–F6	F6–F9	F9–F11	F11–F17	Grain yield per pot (g)	(rel.)	P-amount in grain + straw (mg/ pot)	(rel.)
1	1	0.5	0.5	05	34.2	100	80	100
2	1	1	0.5	0.5	39.5	115	98	122
3	1	0.5	0.5	1	36.6	107	108	135
LSD 5% Tukey					2.7	7.9	8	10

Treatment No.	Number of fertile tillers/ pot	Number of grains Main shoot	Fertile tiller	1000 grain mass (g) Main shoot	Tiller
1	16.3	37	18	39.5	37.5
2	20.0	40	19	39.8	37.7
3	15.3	37	17	43.7	41.9
LSD 5% Tukey	1.4	1.3	1.5	2.1	1.1

Table 3. Changes in dry matter and P content of spring wheat over a 7-day-period during grain filling (P concentration in the nutrient solution: 5 ppm)

Date of harvest	Dry matter of 2 plants (g) Ears	Straw	P-concentration (mg P/g dry matter) Ears	Straw	Total P in 2 plants (mg) Ears	Straw	Straw rel.
5.9.81	1.68	7.12	4.32	2.16	7.8	15.4	(100)
12.9.81	3.05	8.16	4.16	1.55	12.7	12.6	(82)
LSD 5%	0.64	1.45	0.64	0.31	3.0	2.0	(12)

can also make use of phosphate absorbed at earlier stages of development which can now be translocated into the growing seeds. Related experiments revealed that during the grainfilling period within one week 18% of the absorbed P are translocated from the vegetative parts to the ears (Table 3). Taking into account the fact that in this period root growth is severely restricted (degradation is greater than new growth!) (*cf.* Fig. 1) and that for plants grown in the field nutrient diffusion to the roots is often restricted by shortage of water, the significance of P redistribution within the plant becomes quite clear.

3 Estimation of the necessary P supply to the roots at times of high requirement

Knowledge of quantity of P taken up per root unit in case of highly productive plants permits an estimation to be made of the demands of plant's need for soil P. Since the plants in the pot experiment (Fig. 1) were grown under conditions (36 cm deep root space, 5 plants per pot, 7 mg DL-P/100 g of substrate) which permitted them to form maximum grain yields (5 g per plant) it should be possible to use their P absorption rate as a measure of the P requirement in the individual stages of development. Table 4 shows daily P uptake per root unit and the root density at different Feekes stages (F). Some results are interesting:

The intensity of P uptake per unit of root is not constant. It increases to a maximum at approximately Feekes stage 3 and decreases afterwards.

The maximum P uptake rate amounts to nearly 20 μg P/m root · day.

The root density 1 cm/cm^3 for a good crop growth[31] at a 'normal P level' is reached for the total pot volume at F3 and the maximum value is reached at F9. In field experiments Böhm[5] observed these values for winter wheat at F5/6 and F11 respectively.

Discussion

The experiments carried out have confirmed the well known fact that the phosphate uptake by wheat is greatest during the early growth stages (until the end of shooting)[2,11,20,22,25].

In addition to this, the results obtained show that the high uptake rate in this period is not an expression of luxury consumption but of a high P requirement.

Therefore earlier suggestions[22] are confirmed by the present experiments, and the effect of starter P-dressings[6,15] becomes understandable. This effect is valid for both winter and spring wheat because their yields decreased when P-supply was scarce in the early stages of plant development[3,28].

The parallelism of phosphorus uptake and phosphorus requirement might lead to the conclusion that the amount of P absorbed by the plant is controlled by the plant's requirement[8,26]. However, it appears improbable that the two quantities are strictly coupled as suggested in the statement[31] 'that plant requirement completely regulates nutrient uptake rate'. Our experiments[26] with wheat plants have shown that an enhancement of shoot growth by an increased supply of CO_2 or by a rise of temperature (from 10 to 22°C, unpublished) in the first days only resulted in an enhanced translocation of P from roots and older leaves to the growing centres. One or two weeks later an increased ^{32}P uptake by these plants was observed. Therefore, the P pool in roots

Table 4. Daily P absorption rate per m root length of spring wheat (cv. Hatri) during various stages of growth as well as the root density in the soil layer of the pot from 0 to 36 cm (pot experiment, cf. Fig. 1)

Vegetation period	Stage of ontogenesis by Feekes (F)	P uptake (μg P/m · day[a])	Root density (cm/cm^3)
21 April–4 may	Beginning of tillering (F2)	14	0.27
5 May–14 May	Tillering (F3)	18	1.04
15 May–25 May	2nd node is detectable (F7)	12	3.02
26 May–3 June	Flag leaf ligule is visible (F9)	3.4	3.88
3 June–16 June	Flowering (F16/17)	n.d. [2]	2.41
	LSD 5% Tukey	3.1	n.c. [3]

[a] The daily P uptake per plant was calculated from the P content of shoot and root of a single plant and the number of days between two harvest dates. The average root length was calculated from the root length per plant (average of 3 replicates) at the corresponding harvest dates. Thus, the value for daily P uptake rate could be divided by that for average root length.

[2] n.d. = not determined.

[3] n.c. = not calculated, the variation of the 5 figures was 6 to 15%.

(probably the inorganic phosphate or specific organic P compounds[8,18,19]) seems to regulate the P influx/P efflux ratio. P uptake and P consumption are then looked upon as relatively independent processes that are loosely coupled via enzyme-regulated equilibria.

The results of ^{32}P uptake tests performed on divided or shortened root systems[9,10,16] could also be integrated into such a theoretical concept. These tests revealed a time-delayed increase in ^{32}P uptake per unit of root when the P demand of the shoot was met with the use of a smaller root surface area.

In our experiments the maximum daily P uptake rate of 18 μg P (= 0.6 μM) per m of root occurred at the end of tillering. This value is very close to data obtained by Bole[4] using another method. Therefore, this value could be a reference value for the required P supply to roots in an early stage of plant growth. The P requirement at a later stage is markedly lower. When evaluating the absolute level of this value the size of the root system (*e.g.* the root density in cm/cm^3 of soil)[23,24] and its activity[30] may be important. Whether the used cultivar Hatri has an optimal root density or not cannot be decided. Presumably a plant with a larger root surface area will require smaller uptake rates per unit of surface area and lower P concentrations in the soil[23] than a plant with a smaller root surface. But we know, that the ability of adaptation to different P levels in soils varies between cultivars[1]. Therefore, the size of the root systems under field conditions will decide whether the maximum P demand of plants may considerably deviate from the value mentioned above (18 μg P/m · d). Soil inhomogeneities regarding the P content might change the required P amount of distinct root parts, but we might be able to save fertilizers when we bring the soil P-intensity and P-buffercapacity at a level sufficient for plants during their later growth stages, and when we cover the peak of P requirement by additions of readily soluble P fertilizers[14,16].

References

1 Augustin J 1984 Untersuchungen zur Beeinflussung des Wurzelwachstums von Weizenkeimpflanzen durch exogene und endogene Faktoren. Diss. A der Landw. Fakultät Halle/S.
2 Bierei E 1931 Die Düngung der Getreidearten. *Aus* Handbuch der Pflanzenernährung und Düngerlehre. Hrgb. F. Honcamp, Berlin, S. 711–720.
3 Boatwright G O and Viets F G 1966 Phosphorus absorption during various growth stages of spring wheat and intermediate wheat grass. Agron. J. 58, 185–188.
4 Bole J S 1977 Uptake of ^{3}HHO and ^{32}P by roots of wheat and rape. Plant and Soil 46, 297–307.
5 Böhm W 1978 Untersuchungen zur Wurzelentwicklung bei Winterweizen Z. Acker. Pflanzenbau 147, 264–269.
6 Buchner A 1976 Die Ertragswirkung der Phosphate – früher und heute. Die Bodenkultur 27, 244–255.
7 Buchner A und Sturm H 1980 Gezielter Düngen. Frankfurt/Main.
8 Clarkson D T 1981 Nutrient demand as the pacemaker for nutrient absorption and root development. *In* Aspects of Crop Growth, Agronomy Conference. Org. Agric. Dev. and Adv. Serv. at Bournemouth pp 1–14.
9 Drew M C and Saker L R 1974 Further studies on the modification to root growth and ion uptake caused by localized enrichment of phosphate in the rooting zone of barley plants. Letcombe Laboratory Ann. Rep., 8–10.
10 Drew M C and Saker L R 1975 Further studies on the modification of root growth and ion uptake brought about by enrichment of phosphate over narrow zones of the root system. Letcombe Laboratory Ann. Rep., 15–16.
11 Erdei L, Olah Z and Berczi A 1983 Nutrition of winter wheat during the life cycle. II. Influx and translocation of potassium and phosphorus. Physiol. Plant. 58, 131–135.
12 Floßmann R and Richter D 1982 Extraktionsmethode zur Charakterisierung der Kinetik der Freisetzung von P aus der festen Phase des Bodens in die Bodenlösung. Arch. Acker. Pflanzenbau Bodenkunde 26, 703–709.
13 Hendriks L 1980 Veränderung der Phosphatkonzentration des Bodens in der Umgebung lebender Pflanzenwurzeln. Ph. Thesis. Hannover.
14 Judel G K, Gebauer W G und Mengel K 1982 Einfluß der Löslichkeit verschiedener Phosphatdüngemittel auf die Phosphataufnahme und den Ertrag von Sommerweizen. Z. Pflanzenernaehr. Bodenkd. 145, 296–303.
15 Jung J und Dressel J 1981 Zur Wirkung von langjährig angereichertem Bodenphosphat im Vergleich zu frisch zugeführtem Düngerphosphat im Modellversuch. Z. Acker. Pflanzenbau 150, 382–389.
16 Jungk A and Barber S A 1974 Phosphate uptake rate of corn roots as related to the proportion of the roots exposed to phosphate. Agron. J. 66, 554–557.
17 Keerthisinghe D G 1980 Die Bedeutung der Phosphatpufferung und der Phosphatkonzentration der Bodenlösung für die Phosphataufnahme der Pflanzen. Ph. Thesis. Gießen.

18 Lefebvre D D and Glass A D M 1982 Regulation of phosphate influx in barley roots: effects of phosphate deprivation and reduction of influx with provision of orthophosphate. Physiol. Plant. 54, 199–206.

19 Loughman B 1981 Metabolic aspects of the transport of ions by cells and tissues of roots. Plant and Soil 63, 47–55.

20 Matzel W and Sunthcim L 1982 Die P-Aufnahme des Getreides, Arch. Acker. Pflanzenbau Bodenkd. 26, 425–436.

21 Mengel K 1982 Factors of plant nutrient availability relevant to soil testing. Plant and Soil 64, 129–138.

22 Munk H 1976 Die Stellung der Phosphorsäure in der Pflanze. Die Bodenkultur, 27, 229–243.

23 Noordwijk M van and Willigen P de 1979 Calculation of the root density required for growth in soil of different P-status. *In* The Soil-Root-Interface. Eds. J Harley and R S Russell. Acad. Press. pp 381–390.

24 Noordwijk M van 1983 Functional interpretation of root density in the field for nutrient and water uptake. *In* Root Ecology and its Application. Int. Symp. Gumpenstein Austr. pp 207–226.

25 Primost E 1965 Die Düngung im Getreidebau, A. Weizen. *In* Handbuch der Pflanzenernährung und Düngung, Springer-Verlag Wien, New York, III/1, pp 174–238.

26 Römer W 1983 Einfluß von Sproß-und Wurselwachstum auf die Phosphataufnahme. Tagung der Kommission Bodenchemie und Pflanzenernährung der Bodenkd. Gesell. der DDR in Berlin, 8. 12. 1983.

27 Schachtschabel P und Beyme B 1980 Löslichkeit des anorganischen Bodenphosphors und Phosphatdüngung. Z. Pflanzenernaehr. Bodenkd. 143, 306–316.

28 Sutton P J, Peterson G A and Sander D H 1983 Dry matter production in tops and roots of winter wheat as affected by phosphorus availability during various growth stages. Agron. J. 75, 657–663.

29 Thun R 1955 Die Untersuchung von Böden. Methodenbuch Band 1, Radebeul und Berlin, p 177.

30 Wiersum L K 1981 Problems in soil fertility characterization by means of plant nutrient requirements. Plant and Soil 61, 259–267.

31 Willigen P de, Noordwijk M van 1978 Calculations on P-uptake by crops in relation to rooting density and P-status of the soil. Institut voor Bodemvruchtbaarheid Haren-Gr. Rapport 1978, 1–63.