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A simple model of P uptake by crops as a possible basis for P fertilizer recommendations

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Abstract

In the Netherlands the Pw value, based on an extraction of soil P with water, is used as a basis for P-fertilizer recommendations for arable crops. Using a simple, mechanistic model of P transport in the soil the Pw value required for adequate P uptake by crops can be calculated on the basis of daily uptake requirements, root area index, P-adsorption isotherms and total amount of P taken up during a growing season. Calculated Pw values for adequate uptake are in the same range as the present recommendation scheme based on field experiments. Possible refinements of the model are discussed. For each soil the Pw value can be calculated that corresponds to the P concentrations in the soil solution according to standards set to reduce environmental pollution. Our model predicts that, unless the root area index of non-cereal crops is considerably improved, these standards cannot be met in the plough layer without affecting crop production levels. Calculations show that the present method of determining the Pw value yields a reasonable compromise between a measurement of intensity and capacity of P supply in the soil.

Keywords: root length density, root area index, phosphorus availability, phosphate adsorption, barley, bean, maize, onion, potato, sugar beet, wheat

Introduction

The major aim in soil fertility research in the Netherlands in the past century has been to raise existing soil fertility levels to the point where nutrient supply is non-limiting. Increasing the phosphorus supply was one of the first priorities in N.W. Europe, and still is in many tropical countries. The first question, still relevant, was at what soil fertility level supply is non-limiting. In our present definition this is the level where, per unit root, the supply is equal to demand throughout the growing season. The critical level thus depends on plant factors that affect total demand, on the size of the root system, and on soil factors determining supply.

For a fertilizer recommendation scheme we also need to know how serious growth reductions are at soil fertility levels slightly below the critical level and what the relative effectiveness of various soil amendments (e.g. manure, cattle slurry) is. Furthermore, current fertilizer recommendation schemes are based on fertilizer/product price ratios, on maintenance of desirable soil fertility levels and on the crop rotation used. Nowadays, avoidance of environmental pollution should be included in the recommendations. In the present Dutch national environmental policy, a P concentration not exceeding 0.15 mg l^{-1} in surface water and 0.40 mg l^{-1} in the upper m of the groundwater on sandy soils (van Duijvenbooden et al., 1989) is aimed at. The first question we will deal with is whether or not these environmental standards are reconcilable with adequate P supply to crops.

In view of the large number of factors influencing both supply and demand, it seems unlikely that any single soil test can be used for establishing a criterion for adequacy of P supply to crops. Still, establishment of simple soil test procedures from which the amount of 'available' nutrients can be determined for each crop, preferably without further information on soil factors, has been the focus of much research and debate. In the history of Dutch P fertility research a number of extraction techniques have been used, leading to a water extraction method known as the Pw value technique (van der Paauw, 1971). It gives the amount of phosphate extractable from 1 cm^3 of soil with 60 ml of water after 22 h of incubation with 2 ml water (Sissingh, 1971). It is expressed in mg P_2O_5 per liter soil and is currently used for arable soils. In the current scheme (van der Paauw, 1973) a target Pw value of 30 is used for diluvial sandy soils, cut-over peat soils, basin clay and loess, and of 25 for marine clays and alluvial sands, for crop rotations with potato as the crop requiring the highest P status of the soil. When the Pw value is equal to or slightly above this target value the recommended rates of P fertilization for a crop rotation slightly exceed the amount of P expected to be removed with the products harvested. If the Pw value is higher than the target value, the recommended rate of P fertilization is lower and the Pw value will consequently decrease; if the Pw value is below the target, the recommended rate of P fertilization considerably exceeds expected removal. In the recommendation scheme, four groups of crops are identified based both on differences in P-response curves and differences in fertilizer/crop price ratios. From the scheme a Pw value can be derived for each crop where expected crop removal and recommended fertilization are equal. This Pw value we will indicate as the apparent equilibrium point of the recommendation scheme. The second question we will discuss is to what extent the P status of the soil obtained at the apparent equilibrium point of the recommendation scheme for each crop, is in agreement with results of a simple, mechanistic model (de Willigen & van Noordwijk, 1987) of P transport in soil and uptake by roots. The third question we will deal with is whether it is possible to obtain acceptable results with a single soil test, in spite of the large differences between soils in buffer capacity for P. Finally, we will discuss which process description is minimally required to predict the long-term P balance of arable soils.

Models and parameters

Calculation of the Pw value from adsorption isotherms

Inorganic phosphorus in the soil can be considered to consist of three fractions:

phosphorus in the soil solution, phosphorus in the labile pool and non-labile phosphorus. The labile phosphorus mainly consists — we shall assume exclusively — of reversibly adsorbed phosphate (Olsen & Khasawneh, 1980). The non-labile phosphorus is contained in poorly soluble minerals and/or is irreversibly adsorbed. Transfer from the non-labile to the labile pool and vice versa occurs so slowly that it may be neglected during a growing season, as a first approximation (Barber, 1984). The relation between labile phosphate and phosphates in solution can be given by an adsorption isotherm. For our present purpose, adsorption can be considered as instantaneous (de Willigen, 1981).

Figure 1 gives phosphate adsorption isotherms for eight Dutch soils, determined in 0.005 M $CaCl_2$ for 24 h, at a solution-to-soil volume ratio of 20. These isotherms can be described by a two-site Langmuir equation, for which no mechanistic interpretation is given here (Holford & Mattingley, 1975):

$$C_a = \frac{A_1 B_1 C}{1 + B_1 C} + \frac{A_2 B_2 C}{1 + B_2 C} \qquad (1)$$

where:

C_a = adsorbed phosphate in g P dm^{-3} soil
C = the concentration of phosphate in the soil solution in g P l^{-1}
A_1, A_2 = adsorption maxima in g dm^{-3}
B_1, B_2 = parameters in l g^{-1}

The parameters fitted to the adsorption isotherms in Figure 1 are listed in Table 1. The slope of the adsorption isotherm (dC_a/dC) can be defined as buffer capacity. It has a maximum for $C = 0$, equal to $K_a = A_1 B_1 + A_2 B_2$. K_a varies 28-fold in

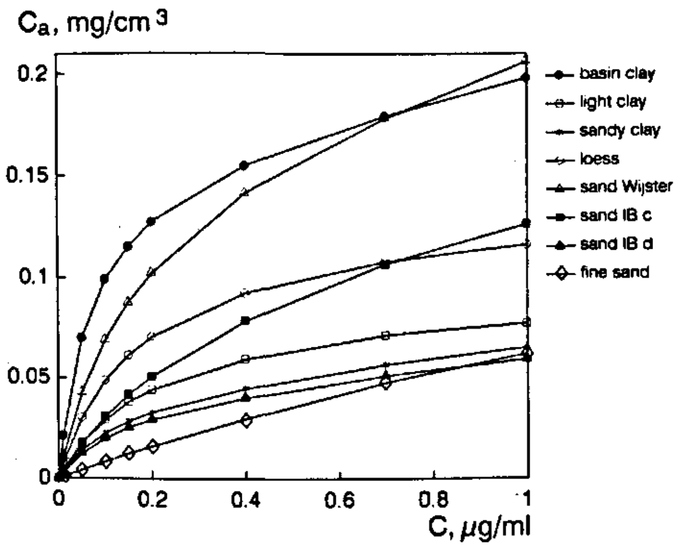

Fig. 1. Adsorption isotherms for eight Dutch soils; for parameters see Table 1.

Table 1. Parameters of 24-hour P-adsorption isotherms for eleven Dutch soils, arranged according to maximum buffer capacity K_a; Pw(n1) and Pw(n2) are the calculated Pw values (in P_2O_5, mg l^{-1}) corresponding to the standard of a solution P concentration of 0.15 and 0.4 mg l^{-1}, respectively; the ratio r_ϱ, of the bulk density during the determination of the Pw value and the bulk density in the field, the assumed water content θ at field capacity is shown as well as the resulting effective diffusion constant, D_e, used in the calculations for Table 3.

Soil type[1]	B_1 ($l\ g^{-1}$)	B_2 ($l\ g^{-1}$)	A_1 ($g\ dm^{-3}$)	A_2 ($g\ dm^{-3}$)	K_a ($l\ dm^{-3}$)	Pw standards n1	n2	r_ϱ	θ ($dm^3\ dm^{-3}$)	D_e ($cm^2\ d^{-1}$)
Fine sand	500	8.5	0.16	0.91	88	12	29	1	0.25	0.084
Sand IB d	8056	142	0.039	0.19	342	14	29	0.77	0.25	0.084
Sand IB c	4430	340	0.073	0.26	413	17	40	0.74	0.25	0.084
Loess	6600	44	0.12	0.26	439	16	34	1	0.40	0.14
Sand Wijster	7860	220	0.133	0.49	1150	17	40	1	0.25	0.084
Sandy clay	8590	177	0.043	0.17	1250	15	30	0.77	0.40	0.14
Light clay	5000	20	0.087	0.18	1570	15	30	1	0.40	0.14
Basin clay	16000	130	0.15	0.49	2460	17	37	1	0.40	0.14

[1] Origin of the soils used: *fine sand*: Zeijen; *sand IB c and d*: IB-farm Haren, adjacent fields; *loess:* Wijnandsrade; *sand Wijster*: IB 1920; *sandy clay:* Noordoostpolder, Lovinkhoeve IB 0013; *light clay:* Warffum; *basin clay:* Hedel.

the soils examined. The maximum adsorption $A_1 + A_2$ occurs as $c \rightarrow \infty$ and varies 5-fold, from 0.21 for the sandy clay to 1.07 g dm^{-3} for the fine sand.

As described by de Willigen & van Noordwijk (1978), the amount of P extracted during measurement of the Pw value can be calculated from the adsorption isotherm of a soil and the total amount of labile P measured with exchange resin or with non-limiting amounts of iron-hydroxide-impregnated filter paper (van der Zee et al., 1987; Menon et al., 1989) from a well-mixed slurry (water-to-soil volume ratio 20, in 0.005 M $CaCl_2$) in 24 h. The calculation is based on the assumption that the amount of labile P does not change during extraction, that desorption isotherms are equal to adsorption isotherms and that effects of background electrolyte concentration on the adsorption/desorption process may be neglected. These assumptions lead to:

$$S = C_a + \Theta\ C = C_a^* + V_w\ C^* \tag{2}$$

where:

S = total amount of labile phosphorus per dm^3 of soil (g dm^{-3})
Θ = water content of the soil ($dm^3\ dm^{-3}$)
V_w = volume ratio of water to soil used during extraction; $V_w = 60$ for the Pw value as defined by Sissingh (1971)
C_a^*, C^* = equivalent of C_a and C, during determination of the Pw value

Combination of Equations 1 and 2 gives a cubic equation in C^*, which can be solved iteratively, given the parameters of the adsorption isotherm and S. The Pw value, expressed in mg P_2O_5 per liter of soil, is calculated as $1000 \times (142/62) \times C^* \times V_w$.

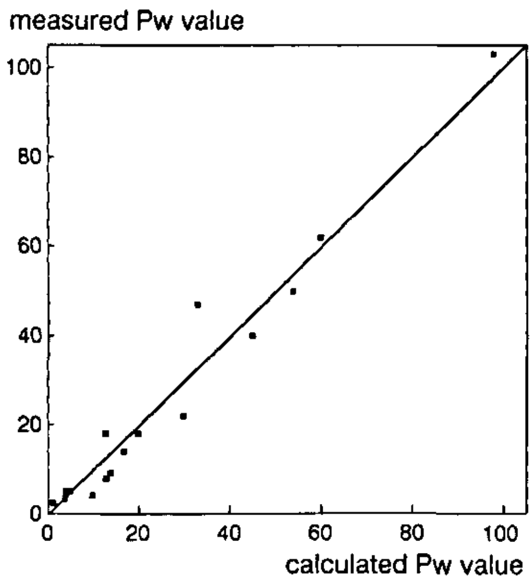

Fig. 2. Calculated versus measured Pw values; for several soils more than one P level is included; data on three soils not mentioned in Table 1 are included.

With increasing V_w, more P would be extracted from the soil, but the degree to which this happens would depend on soil type and P status of the soil.

Figure 2 shows that calculated Pw values agree well with measured Pw values for the same soils. We will therefore assume that Pw values can be calculated on the basis of adsorption isotherms and total amount of labile P. In the calculations for Figure 2 we used the bulk density of each soil as measured during a Pw value determination; for further calculations we used the bulk density under field conditions, insofar as estimates were available.

Calculations of P uptake by crops

The total amount of labile P is available for instantaneous uptake by a root system of infinite density and negligible volume. Root systems of finite density can only extract a certain fraction from the soil at the rate required for crop growth (the unrestrictedly available amount). The remainder is restrictedly available, i.e. at a rate determined by transport processes in the soil (de Willigen & van Noordwijk, 1987). To predict what available amount in the soil is necessary to have just sufficient unrestrictedly available P in the soil, we have to specify crop demand, root density and activity.

Figure 3 shows the time course of P uptake by potatoes with adequate or suboptimal P supply, as measured by van der Paauw (1948). By far the largest part of the dry matter produced by a crop is synthesized during the linear growth period. The major part of P is also taken up at a constant daily rate. The same is true for other

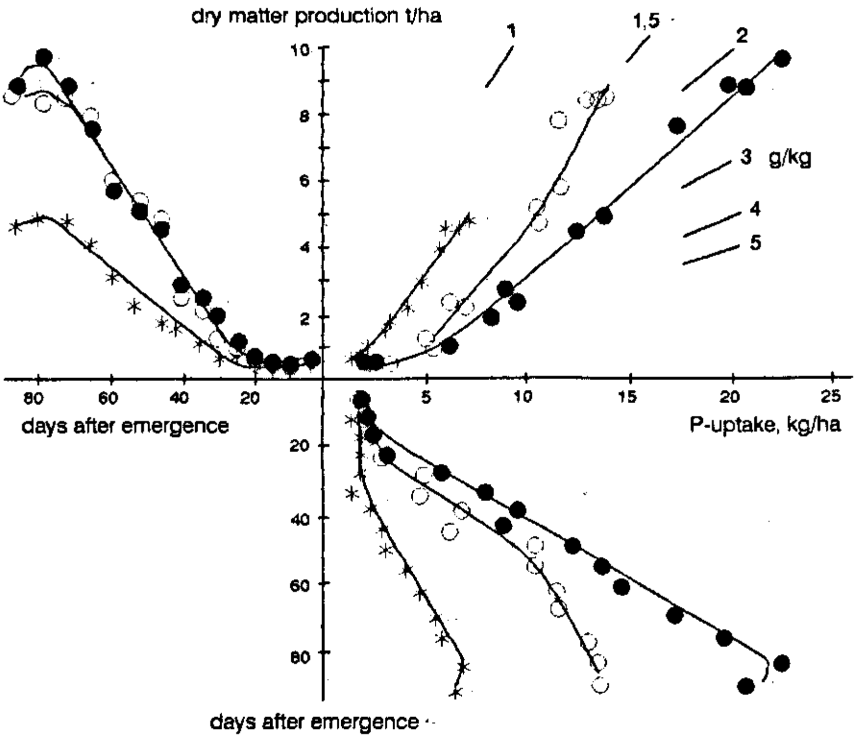

Fig. 3. Time course of P uptake and dry matter production of potato at three levels of P supply in the soil (data from van der Paauw, 1948). In quadrant I, P concentrations of 1 to 5 ‰ are indicated as slopes.

crops and other nutrients as follows from Figure 4, based on measurements by van Itallie (1937) of crops under non-limiting nutrition. Uptake is generally two weeks ahead of dry matter production, so P contents are gradually decreasing despite constant daily dry matter production and P uptake. As the root system is at first approximation constant in size during the linear growth period of the crop, the daily uptake requirement per unit root length is constant for a considerable length of time (de Willigen & van Noordwijk, 1987).

Actual uptake patterns such as in Figure 3 cannot be explained by mechanistic models of nutrient uptake where the uptake rate is described as a function of external concentration (Nye & Tinker, 1977; Barber, 1984), unless the physiological parameters governing uptake are described as a function of internal P content in the plant or are derived as a function of plant age for plants growing under identical field conditions. Internal regulation of P uptake by the plant (Alberda, 1948) has recently been rediscovered by plant physiologists (Clarkson, 1985). In our model (van Noordwijk & de Willigen, 1979; de Willigen & van Noordwijk, 1987) we assume internal regulation of uptake rates to be complete and we describe the uptake rate as either demand-governed (equal to total demand divided by total root length) or supply-governed (equal to supply by mass flow and diffusion to a cylindrical 0-

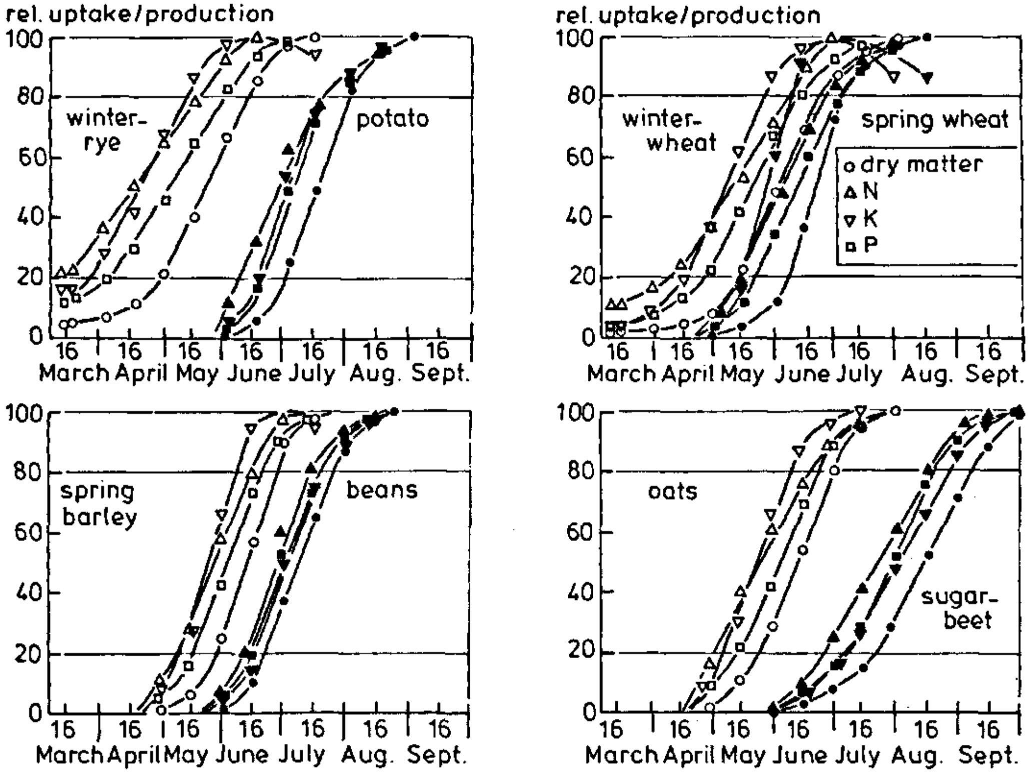

Fig. 4. Time course of N, P and K uptake and dry matter production of eight crops under non-restricted supply (van Itallie, 1937).

sink). We further assume roots to be regularly distributed and in complete contact with the soil.

Phosphorus uptake from a soil is highly dependent on root development of the crop. In two stages of crop development, P uptake may lag behind P demand for maximum growth rates: during initial growth, when the demand per unit root length usually is high, and during the second half of the growing season, when root growth stops and the root environment has been partially depleted, while P demand continues. We will concentrate here on the P level of the soil required to avoid deficiency in the second half of the growing season, but for crops with high shoot:root ratios in the initial stages (especially high shoot weight per unit root length) the P level initially required may be higher than that calculated here.

As shown elsewhere (de Willigen & van Noordwijk, 1987), the assumption of a constant daily uptake requirement per unit root surface area leads to the development of steady rate profiles of the concentration around each root, for nutrients where the fraction adsorbed is independent of the concentration. For phosphate with a non-linear adsorption isotherm we found that the concentration in the soil solution around each root can be satisfactorily approximated by a steady-rate profile as well. At the time when the concentration at the root surface decreased to C_{min}, the steady-rate profile is given by:

$$C(r) = C_{min}\, r^{2\nu} + \frac{F_a R_o}{D} \left[\frac{\varrho^{2\nu+2}\,(r^{2\nu} - 1)}{2\,\nu\,(\varrho^{2\nu+2} - 1)} + \frac{r^{2\nu} - r^{2\nu+2}}{2\,(\varrho^{2\nu+2} - 1)} \right] \quad (3)$$

where:
$C(r)$ = concentration at distance r (mg l^{-1})
C_{min} = concentration required at the root surface to maintain sufficiently high uptake rates (mg l^{-1})
r = R/R_o = dimensionless distance in the soil cylinder
R_o = root radius (cm)
ϱ = $(R_o \sqrt{\pi L_{rv}})^{-1}$
L_{rv} = root length density (cm cm^{-3})
F_a = required uptake rate per unit root surface area (μg cm^{-2} day^{-1})
D = effective diffusion constant (cm^2 day^{-1})
ν = $-E_a R_o/2D$
E_a = transpiration rate per unit root surface area (cm day^{-1})

The amount S of available P which should be present in the soil at the start of the growing season to allow uptake at the required rate during the whole growing season can now be formulated as:

$$S = U + T + M \quad (4)$$

where U is total crop uptake during the growing season, T is the amount required to allow a sufficiently high rate of P transport to the root surface and M is the

Table 2. Estimates of parameters determining the uptake required per unit root surface area for seven crops. Total P uptake by each crop is based on Anon. (1989). The period in which 60 % of total uptake occurs, $t_{20\text{-}80}$, was derived from Fig. 3. Root length data, L_{rv}, based on de Willigen & van Noordwijk (1987), and estimates of root radius, R_o partly based on Jungk & Claassen (1989), were used to calculate the root area index, RAI. Daily demand during the linear growth phase, A, has been combined with root data to obtain the required inflow per unit root length, I_l, and the required flux per unit root surface area, F_a.

	P removal (kg ha^{-1})	P uptake (kg ha^{-1})	$t_{20\text{-}80}$ (d)	A (kg ha^{-1})	L_{rv} (cm cm^{-3})	R_o (mm)	RAI	I_l (μg cm^{-1} d^{-1})	F_a (μg cm^{-2} d^{-1})
Bean	18	20	34	0.35	0.8	0.15	1.9	0.175	1.86
Potato	24	34	31	0.65	1.5	0.15	3.5	0.173	1.84
Onion	20	23	45	0.31	0.8	0.25	2.5	0.155	0.99
Sugar beet	41	42	43	0.58	2	0.10	3.1	0.116	1.23
Maize	35	37	45	0.50	2.5	0.10	3.9	0.080	0.85
Barley	19	23	33	0.41	4	0.10	6.3	0.041	0.65
Wheat	24	28	52	0.32	6	0.10	9.4	0.022	0.35

amount corresponding to the term with C_{min}. For phosphate, C_{min} is approximately 1 μmol l^{-1} or 0.031 mg l^{-1} (de Willigen & van Noordwijk, 1987). The amount T + M can be calculated by substitution of Equation 3 into Equations 1 and 2, and integration of the resulting equation over the soil cylinder. The amount T + M (in g dm^{-3}) is given by the integral:

$$T + M = \frac{1}{1000\,(\varrho^2 - 1)} \int_1^{\varrho} 2r(C_a + \Theta C)\,\mathrm{d}r \tag{5}$$

where C is given by Equation 3 and C_a by Equation 1. The integral can be evaluated by numerical integration.

By assuming average values for the respective parameters for seven crops (Table 2), we can now calculate the required amounts of available P and the corresponding Pw values on the various soil types. Daily uptake requirement in the period of constant daily uptake was estimated from the number of days $t_{20\text{-}80}$ between 20 and 80 % of the cumulative uptake in Figure 4 and realistic values of total uptake. We assumed for each crop a P-containing plough layer of 25 cm with homogeneously distributed roots, with complete root-soil contact but no root hairs penetrating the soil. An average root diameter was estimated for each crop. The water content of the soil has a major effect on transport by diffusion; we took the estimated value at field capacity (pF 2.0) for each soil. Calculated Pw values corresponding to S as defined above are listed in Table 3 for each crop/soil combination. For comparison

Table 3. Calculated values of the Pw value required in eight soils at field capacity for non-P-limited growth of seven crops. For comparison the range of Pw values is included which are obtained after P fertilization when the soil is at the 'apparent equilibrium' point where recommended P application equals the expected uptake by the crop in the current P-recommendation scheme (Anon., 1986). The scheme distinguishes two classes of soils: diluvial sands, cut-over peat soils, loess and basin clay (I) and marine clay soils and alluvial sands (II).

	Bean	Potato	Onion	Sugarbeet	Maize	Barley	Wheat
I. Wijster sand	88	87	72	73	53	29	19
IB sand c	68	54	45	46	34	19	13
Fine sand	71	73	59	64	48	27	21
IB sand d	41	44	35	39	31	18	14
Basin clay	58	59	48	51	38	21	14
Loess	51	54	44	49	38	21	15
II. Light clay	46	50	42	48	37	21	16
Sandy clay	32	34	27	31	24	14	11
Current scheme							
Apparent eq. I	63	47	59	33	44	45	24
+ P-fert.	65-72	53-58	64-69	42-51	55-60	50-54	28-34
Apparent eq. II	62	46	59	29	44	31	18
+ P-fert.	70-72	57	69-70	45	60	38	25

the apparent equilibrium points of the present recommendation scheme are given as well as the range of Pw values resulting for different soils from an addition of P equal to the amount removed in harvested products. Of the three terms in Equation 4, the term T has the largest value in all situations considered.

Results

Pw values corresponding to pollution standards

As shown in Table 1, a P concentration of 0.15 mg l^{-1} occurs at different Pw values in different soils, varying from 18 on the Wijster sand to 12 on the fine sand; the Pw values corresponding to a concentration of 0.4 mg l^{-1} vary between 26 for the IB sand d and 41 for the Wijster sand. Although predictions of P leaching behaviour in soils are more complicated as relatively slow fixation processes have to be taken into account (Raats et al., 1982), the leachate from a sandy soil with a Pw value higher than the calculated value will have a P concentration exceeding the maximum permissible value. The target values of the present P recommendation scheme for arable crops imply that the inorganic P concentration of the leachate from the plough layer will be higher than allowed in surface water, and for sandy soils slightly higher than allowed in the upper meter of groundwater. As a certain amount of organic P will be present in solution as well, the maximum permissible total P concentration is likely to be exceeded in leachates from a plough layer on sandy soils with a Pw value above 20. At the (much) higher Pw values recommended for vegetable crops, environmental standards cannot be met.

Pw values required for different crops

Table 3 shows that the calculated Pw values required are of the same order of magnitude as the Pw values obtained at the apparent equilibrium points of the present P-recommendation schemes. In Figure 5 the average calculated Pw value for each crop is compared with the average Pw value according to the recommendation scheme, for the two classes of soils distinguished in the scheme. The calculated values for the different crops allow a distinction between crops with a high and with a low demand similar to that in the present scheme. Table 2 shows that differences among crops in uptake required per unit root surface area are largely determined by differences in root length density. To obtain non-P-limited growth on sandy soils which meet the environmental standards, a potato crop should have a root length density comparable to that of a wheat crop, a nice target for plant breeders.

Empirical evidence shows that barley requires a higher soil P status than wheat. Our calculations confirm the difference as the required influx is higher for barley than for wheat (Jungk & Claassen, 1989) due to a lower root length density of barley (Weaver, 1926; Schjørring & Nielsen, 1987), but the difference we calculated is smaller than the difference in the present recommendation scheme.

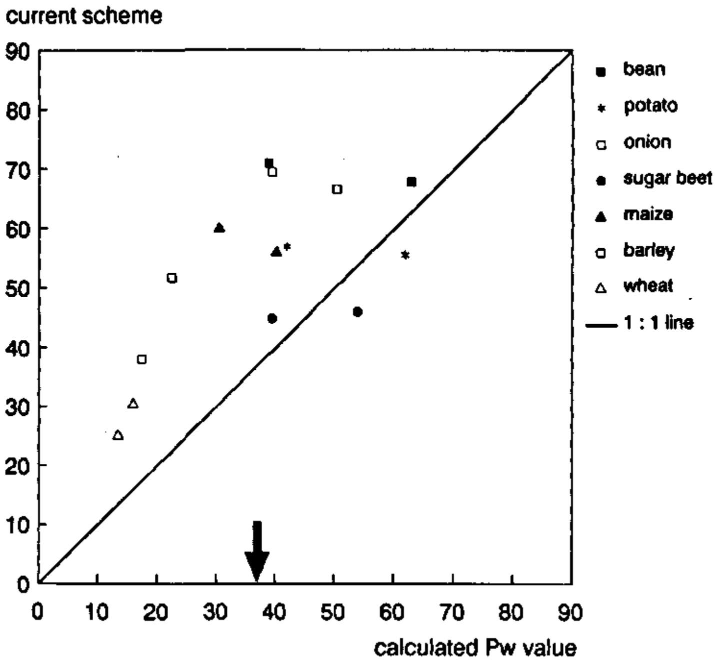

Fig. 5. Comparison of the required Pw value calculated with our simple model and the Pw value resulting from recommended P application at the apparent equilibrium point of the P-recommendation scheme; values are averages for the two classes of soils in the recommendation scheme; the arrow indicates a Pw value for sandy soils where the concentration in the soil solution is in agreement with environmental standards for the upper meter of groundwater.

Pw value as an index of P availability

The required Pw values calculated with the same crop parameters for different soils show variation. The ratios of highest and lowest value range from 1.9 for wheat to 2.8 for beans. Although this ratio is much smaller than the ratios of highest and lowest K_a or sorption maximum among the soils, it suggests that, at least for certain crops, fertilizer recommendations cannot be based on a single parameter, such as the Pw value, but should also consider other information, related to the P-adsorption isotherm. A classification by soil types may help to a certain extent, but the two calculations for Haren sand, based on adsorption isotherms for soils collected from adjacent fields, gave a 1.7-fold difference in Pw value required for beans. The performance of the Pw value technique as a compromise between a measurement of *intensity* of P supply (concentration in the soil solution, C) and its *capacity* (total amount of labile P, C_a) can be judged from our calculations. Required P levels vary more when expressed as capacity than when expressed as intensity. For a number of crops they vary less when expressed as a Pw value than when expressed as a concentration in the soil solution. Based on Equation 2 we calculated the Pw(V_w) values for different water-to-soil volume ratios V_w during the extraction,

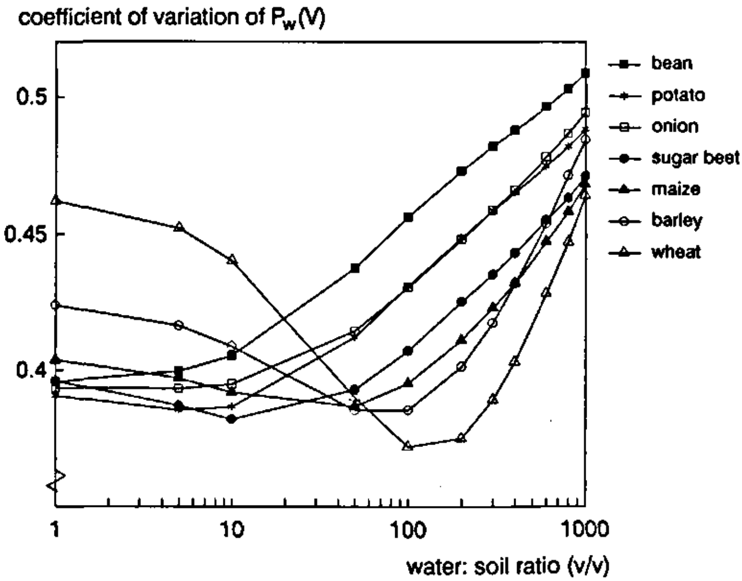

Fig. 6. Coefficient of variation (standard deviation divided by mean) of calculated P status on the various soils (Table 1), when the P status is expressed as Pw(V) value for different water-to-soil ratios V_w during the extraction.

at the soil P status calculated to be required for each crop. For infinitely high V_w a Pw(V_w) value constitutes a measurement of capacity, for V_w of about 0.3 it is a measurement of intensity. Figure 6 shows the coefficient of variation of calculated Pw(V_w) values as a function of V_w, with a minimum indicating an optimum value of V_w for each crop. The higher the required uptake per unit root length, the more important intensity becomes and the lower V_w should be to obtain an optimum basis for a P-recommendation scheme independent of soil type.

Long-term P balance of arable soils

Figure 7 shows Pw values measured during a period of 16 years in two long-term P fertilization trials, at various rates of annual P application. Each year the P balance was estimated as the difference (positive or negative) of P added as water-soluble phosphate and P removed in harvested products. In the two graphs, solid lines designate calculated changes in Pw value if only fertilization and crop uptake would influence the amount of labile P in the soil. The long-term behaviour of the soil differs in two important respects from these calculations: at high P application rates the increase in Pw value is much smaller, and without P application the decrease in Pw value is much smaller. In fact, the Pw value tends to an equilibrium value of about 7 for the sandy loam and about 10 for the Wijster sand. Raats et al. (1982) described P transport in the soil assuming an irreversible fixation process to remove P from the labile pool. Maximum fixation capacity was assumed to be

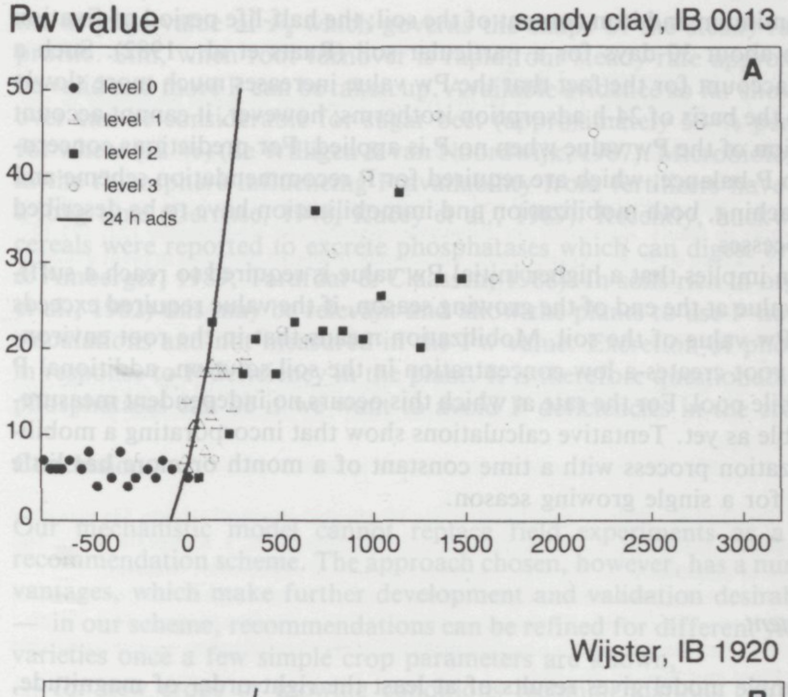

Fig. 7. Pw measurements during a period of 16 years as a function of the P balance of two experimental fields (inputs as water soluble P minus outputs in harvested products). (A) a sandy clay soil in the Noordoostpolder (Lovinkhoeve, IB 0013); (B) sandy soil in Wijster (IB 1920) at five levels of superphosphate; at four levels of TSP (triple superphosphate). The solid lines were calculated on the basis of 24 h adsorption isotherms.

related to the aluminium and iron content of the soil; the half-life period of fixation was found to be about 30 days for a particular soil (Raats et al., 1982). Such a description may account for the fact that the Pw value increases much more slowly than expected on the basis of 24-h adsorption isotherms; however, it cannot account for the stabilization of the Pw value when no P is applied. For predictions concerning the long-term P balance, which are required for P recommendation scheme and predictions of leaching, both mobilization and immobilization have to be described as reversible processes.

Immobilization implies that a higher initial Pw value is required to reach a sufficiently high Pw value at the end of the growing season, if the value required exceeds the equilibrium Pw value of the soil. Mobilization means that in the root environment, where the root creates a low concentration in the soil solution, additional P appears in the labile pool. For the rate at which this occurs no independent measurements are available as yet. Tentative calculations show that incorporating a mobilization/immobilization process with a time constant of a month or more has little effect on results for a single growing season.

Discussion

Model improvement

Although our simple model gives results of at least the right order of magnitude, a number of discrepancies exist between calculations and empirical results. These may indicate that the simple model needs refinements, e.g. inclusion of the role of root hairs, mycorrhiza, phosphatase activity in the rhizosphere or pH changes induced by the root. The empirical basis for the P recommendations for crops other than potato is rather weak, however, and the between-years variation in P response on each site is considerable. Hence, refutation of the simple model and incorporation of refinements should be based on individual field experiments where the parameters necessary for a rigorous test are known.

Our calculated P requirements for soils at field capacity are slightly below empirical values; under drier conditions our model would calculate higher values because of lower effective diffusion constants. Parameter values such as root length densities where chosen in the range documented in the literature; in specific experiments, both higher and lower root length densities are possible; present data are inadequate to establish reliable ranges of values for each crop under field conditions. The role of root hairs was neglected in our calculation, but we assumed complete soil-root contact, which is realistic only if roots form sufficient root hairs when they grow in a gap or channel larger than their own diameter. The role of mycorrhizal hyphae as an extension of roots was neglected so far: the P levels required by mycorrhizal crops may be considerably lower. P uptake from the soil below the plough layer was neglected; it will be usually low as soil P levels as well as root length density in deeper layers will be considerably lower than those in the plough layer, but exceptions exist. Root turnover, simultaneous new root growth and root death in the same soil layer, will have no effect on the possible P uptake in our model, as it does not affect the average value of F_a which governs the shape of the steady-rate concentration profile. Still, when root turnover is rapid, our steady-rate approximation will not be valid and more P can be taken up. Available evidence so far shows that root turnover can be considerable for sugar beet (approximately 50 % per season) but not for wheat (12 %) (de Willigen & van Noordwijk, 1987). Microbiological interactions in the rhizosphere influencing P availability from fertilizers have been known for a long time (Gerritse, 1948; Kucey et al., 1989). Recently, buckwheat, clover and cereals were reported to excrete phosphatases which can digest organic P (Amann & Amberger, 1989; Tarafdar & Claassen, 1988). In soils rich in organic P (Gerritse et al., 1982) this may be relevant and allow the plants to use P not included in our calculations and not measured in the Pw value. Excretion of phosphatases occurs in response to P deficiency in the plant. It is therefore questionable how important phosphatases can be if we want to avoid P deficiencies in the crop.

Conclusion

Our mechanistic model cannot replace field experiments as a basis for a P-recommendation scheme. The approach chosen, however, has a number of clear advantages, which make further development and validation desirable:
— in our scheme, recommendations can be refined for different yield levels or crop varieties once a few simple crop parameters are known,
— for new crops or growing conditions recommendations can be made with a reduced research effort (a few intensively quantified rather than many extensively quantified field experiments), especially when the parameters required are known from other research,
— effects of modifications in the water balance of the soil can be predicted from our scheme to give recommendations that are more site-specific,
— field experiments can be used for rigorous testing of quantitative hypotheses rather than for parameter estimation as a basis of ad hoc adaptations of a qualitative theory about plant-soil fertility interactions.

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