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Modelling nutrient uptake: a possible indicator of phosphorus deficiency

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Abstract

An understanding of the processes controlling soil nutrient supply and plant uptake has led to process-based models that can predict nutrient uptake and the concentration gradient that develops at the root surface. By using this information, it may be possible to develop an indicator of soil phosphorus status based on the predicted uptake and/or concentration of phosphorus (P) at the root surface. To identify the potential for such a test, the relationships between model output and observed plant growth were examined using data from a published experiment. The experiment was initially designed to investigate the relationship between common indices of soil-available P and the growth of maize (*Zea mays*) in 26 surface soils from Queensland. There was a high correlation between observed and predicted P uptake, and between relative dry matter yield and predicted P uptake. The predicted concentration of P at the root surface was also highly correlated with P uptake and dry weight increase. It is hypothesised that the short growth period (25 days) was responsible for the high correlation between P uptake and measured soil solution P. The hypothesis that a predicted concentration of P at the root surface or predicted P uptake may be valuable indicators of P deficiency in the longer term still remains to be tested.

Additional keywords: soil solution, phosphorus, phosphorus uptake, phosphorus testing.

Introduction

A widely applicable test for determining soil phosphorus (P) status (i.e. for any given combination of soil type and plant species) has been long sought, because plant growth is often limited by low P availability. Phosphorus availability is commonly assessed by extracting dry soil with alkaline or acid solutions, e.g. the Colwell (1963) and Bray (Bray and Kurtz 1945) analyses for ‘available P’, but these analyses are sometimes not well correlated with the extent of P deficiency experienced by a crop (Holford 1983; Moody *et al*. 1988; Cox 1994). A possible reason for this lack of correlation is that P availability is usually limited by transport to the root rather than ‘available’ amounts (Nye and Tinker 1977).

An approach to developing a widely applicable soil test is to include information about several important mechanisms of P supply and uptake. Transport of P to the root surface is controlled by the gradient of P concentration that exists

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between the bulk soil solution and the solution at the root surface. This gradient is generated and maintained by a combination of the uptake ability of the roots and the ability of the soil to supply P to the root surface. Hence, soil supply factors and properties of the roots in question determine the nutrient status of the plant. In the case of P particularly, the relationship between common soil P availability indicators and plant growth is dependent on interactions among the soil, plants, and the environment (Cox 1994).

The concentration of P in solution is an important factor in determining plant growth. It appears that in a highly buffered situation, the optimum solution P concentration for growth is specific to the plant species in question (Asher and Loneragan 1967; Fox 1980; Moody and Standley 1980; Skinner and Attiwill 1981; Fohse *et al.* 1988). For example, Fox (1980) showed that the P concentration in soil solution required for 95% of maximum yield ranged between about $0 \cdot 005$ and $0 \cdot 3$ μg/mL for 9 plant species. Sorption curves have been found to be very useful for describing the partitioning of P between solid and solution phases in the soil and its relation to plant uptake (Fox and Kamprath 1970; Fox 1980; Dear *et al.* 1992) because they indicate the extent to which soil solution P is buffered. Sorption characteristics affect the shape and width of the concentration gradients that develop near root surfaces. These principles of nutrient supply and uptake have made it possible to model the effect that these factors have on the concentration profile in the zone of depletion. Hence, we can predict the concentration of P at the root surface ($\mathrm{P}_{\mathrm{root}}$), and consequently P uptake (Nye and Tinker 1977; Silberbush and Barber 1983; Smethurst and Comerford 1993). By using a model of this type it may be possible to determine mechanistically whether a plant is likely to receive optimal nutrition under any given set of conditions.

We used the model of Smethurst and Comerford (1993) because it had significantly more power and flexibility than the widely accepted model of Barber and Cushman (1981), which was also described by Oates and Barber (1987). The Smethurst–Comerford model is more flexible than the Barber–Cushman model because the former takes into account variable buffer powers, does not fix root length density, and provides a more comprehensive output. The 2 models also use different mathematical methods for determining the concentration at the root surface. The Smethurst–Comerford model uses an analytical method to derive the nutrient concentration at the root surface, while the Barber–Cushman model uses a more accurate numerical method.

One limitation of the Smethurst–Comerford model was that it had the potential to underestimate significantly uptake for moderately to highly buffered solutes (i.e. buffer power >7; Smethurst and Comerford 1993) compared with the Barber–Cushman model. The Smethurst–Comerford model includes a comparison of the concentration predicted at the root surface ($\mathrm{P}_{\mathrm{root}}$) and the concentration below which there is no net uptake (i.e. $C_{\min}$). If the difference between $\mathrm{P}_{\mathrm{root}}$ and $C_{\min}$ is $<10^{-5}$ mM, it is assumed there is no uptake. This type of comparison was necessary to avoid computational errors with very small values on some computers. We hypothesised that by decreasing the value of this difference, the predicted uptake would be significantly increased at low concentrations which typically develop for highly buffered solutes. In this study we evaluated a modification of the Smethurst–Comerford model (modified to improve its prediction of uptake in highly buffered soils) by comparing predicted uptake using this modified model with that predicted using the Barber–Cushman model for soils with a range of P buffer powers. We then investigated the potential for using the modified Smethurst–Comerford model to predict P deficiency, using data from an experiment comparing several soil P availability indicators and the growth and P uptake of maize (*Zea mays*) in 26 Queensland soils (Moody *et al.* 1988).

Methods

Model comparison

The tolerance for uptake, i.e. the difference between $\mathrm{P_{root}}$ and C_{min} was changed from 10^{-5} to 10^{-11} mM in the modified Smethurst–Comerford model. An impedance factor (f) for sand was originally coded into the model, but this was replaced with a more general impedance factor of $f = \theta^{0\cdot5}$, where θ is the volumetric water content (Nye and Tinker 1977). Both the modified and original versions of the Smethurst–Comerford model were compared with the Barber–Cushman model. To facilitate the running of the Barber–Cushman simulations, a modification was used that allowed multiple inputs (K. C. J. Van Rees, pers. comm.).

Because root growth and soil volume are handled very differently by the contrasting models, exact comparisons of predicted uptake could only be made for a fixed root length in a fixed volume of soil. To ensure that buffer power was constant during a simulation in the Smethurst–Comerford model (as it is in the Barber–Cushman model), the Freundlich n parameter was set to 1, and the Freundlich a parameter was set to the appropriate constant of the solid–liquid partition coefficient (K_{d}) required for each soil (Table 1). The K_{d} value is the slope, i.e. the first derivative, of the Freundlich isotherm at a given solution concentration and equals a if $n = 1$. The desired buffer power (b) is then given by

$$b = \theta + \rho K_{\mathrm{d}}$$

where ρ is soil bulk density (Van Rees *et al.* 1990). Buffer power in this data set ranged from 10·7 to 4807 (Table 1). Other soil-based inputs to the model (i.e. soil bulk density, water content, and P concentration in solution) were measured (Moody *et al.* 1988; Table 2).

Table 1. Freundlich parameters and resultant buffer power used in simulations to compare the Smethurst–Comerford and modified Smethurst–Comerford models with the Barber–Cushman model

Freundlich equation: $y = ax^{1/n}$, where y is the solid phase P (μg/g) and x is the liquid phase P (μg/mL). The value of n was set to 1 for all soils

Soil no.	Buffer power	Freundlich *a* parameter	Soil no.	Buffer power	Freundlich *a* parameter
1	1299·41	877·74	14	115·25	81·01
2	3300·46	2558·25	15	799·42	823·66
3	4807·05	3641·48	16	387·13	317·10
4	302·54	228·96	17	197·86	170·36
5	3319·46	2593·05	18	46·21	39·60
6	707·42	516·18	19	35·20	29·12
7	471·31	351·53	20	232·58	200·28
8	492·11	279·50	21	74·81	64·28
9	805·41	649·28	22	493·90	498·44
10	1098·36	773·34	23	381·53	388·86
11	718·07	531·73	24	69·99	55·73
12	17·30	16·62	25	10·74	8·55
13	964·13	1189·91	26	281·83	207·05

Table 2. Values of parameters and assumed root growth

BD, bulk density; MC, moisture content at 10^4 Pa; DW, dry weight; RG, root growth. Freundlich equation: $y = ax^{1/n}$, where y is solid phase P (μg/g), x is liquid phase P (μg/mL), and a and n are fitted parameters

Soil no.	Freundlich parameters		BD (g/cm^3)	MC	P concn^A (μM)	DW increase^B (g)	RG parameters^C		P uptake^B (mmol/pot)
	a	n					c	f	
1	261·74	2·88	1·48	0·350	1·00	2·50	1·28	1·11	0·160
2	265·04	2·83	1·29	0·315	0·19	1·49	1·11	1·09	0·089
3	304·82	2·69	1·32	0·302	0·13	0·56	3·06	1·04	0·057
4	443·35	3·57	1·32	0·314	13·82	5·28	0·61	1·17	0·428
5	429·66	3·00	1·28	0·358	0·42	1·73	1·48	1·09	0·104
6	161·69	2·02	1·37	0·255	0·81	0·95	1·89	1·06	0·067
7	83·93	1·87	1·34	0·258	0·38	0·80	1·81	1·06	0·061
8	51·83	1·95	1·76	0·196	0·26	0·95	1·77	1·06	0·066
9	117·27	2·78	1·24	0·297	0·45	2·57	0·89	1·12	0·159
10	141·66	1·97	1·42	0·220	0·26	0·89	1·81	1·06	0·061
11	172·01	1·80	1·35	0·238	0·68	0·88	1·95	1·06	0·072
12	116·46	4·10	1·02	0·346	65·68	7·98	0·95	1·16	0·899
13	139·87	2·26	0·81	0·305	0·16	1·30	2·19	1·07	0·093
14	131·69	6·30	1·42	0·210	6·46	5·12	1·40	1·13	0·349
15	221·94	2·11	0·97	0·465	0·65	1·90	1·82	1·08	0·153
16	72·93	2·53	1·22	0·263	0·61	1·84	1·22	1·10	0·104
17	92·69	2·87	1·16	0·239	2·52	3·67	1·75	1·11	0·216
18	127·68	3·68	1·16	0·271	27·00	8·38	1·31	1·15	0·749
19	118·36	3·55	1·20	0·254	39·01	8·07	1·13	1·16	0·760
20	84·73	2·89	1·16	0·255	1·71	3·36	1·93	1·10	0·208
21	102·69	3·57	1·16	0·247	10·59	6·72	1·24	1·15	0·436
22	130·04	2·37	0·99	0·440	0·71	1·01	1·91	1·06	0·079
23	130·99	2·77	0·98	0·444	1·19	1·98	1·67	1·09	0·150
24	48·68	1·97	1·25	0·321	6·20	2·03	1·31	1·10	0·115
25	98·89	4·00	1·22	0·305	133·19	8·99	0·84	1·17	1·194
26	108·25	3·92	1·36	0·241	2·16	2·74	1·53	1·10	0·170

[A] In soil solution.

[B] 15–25 days.

[C] Root growth equation: $y = cf^x$, where y is root-length density (cm/cm^3), x is time (days), and c and f are fitted parameters.

Other inputs to the model that were assumed and maintained at set levels for each of the 26 soils were root radius (0·15 mm; Oates and Barber 1987), Michaelis–Menten kinetic parameters for P uptake by maize ($I_{\max} = 7{\cdot}9{\times}10^{-6}$ μmol/cm$^2\cdot$s, $K_{\rm m} = 2{\cdot}45$ μM, $C_{\min} = 0$; Nye and Tinker 1977; Jungk *et al.* 1990), and water flux to the root ($6{\times}10^{-7}$ cm^3/cm$^2\cdot$s, which is typical of values found in literature). A $C_{\min}$ of zero was used because this value is not well defined in the literature, and because this provided the widest range of predicted uptake values. A sensitivity analysis of the model for water flux to the root showed that this assumption had very little effect on root surface concentrations of P or P uptake rates (see **Discussion**).

Observed growth and P uptake in relation to model predictions

A full description of the materials and methods used to collect and assess the soils and grow the plants was provided in Moody *et al.* (1988). In summary, 26 surface soils of different types were collected from Queensland and analysed for a number of recognised soil P availability indices, including buffer capacity, sorption indices, and concentration of P in soil solution. To determine the growth response to different levels of phosphate addition in each soil, maize was grown in each of the soils in a glasshouse experiment. Data from the growth of maize in the unamended soils were analysed in the current study. Relative dry matter yield was defined as the percentage growth that occurred in the unamended soil, when compared with the maximum growth when P was added (i.e. 100% relative dry matter yield occurred where there was no response to added fertiliser). Measurements of shoot dry weights were made on the maize at 15 days and at 25 days. Uptake was simulated using the Smethurst–Comerford model over the entire 25-day growing period, but to minimise the effect of the contribution of seed P on measured P uptake, changes during only the last 10 days of the growth period were used to compare observed and predicted values.

Root lengths were not recorded in the original experiment, but these were inferred from shoot weights by assuming a constant root : shoot ratio of 1, a root tissue density of 1 g/cm^3, and an average root radius of 0·15 mm. Root-length density was assumed to increase exponentially by assuming zero root density at planting and estimated values from the shoot measurements at 15 and 25 days. The coefficients derived from this relationship were used in the simulations.

The root uptake kinetic parameters and water flux to the root were the same as used in the model comparison. A constant pot volume of 1200 cm^3 was used. The other inputs that were measured and characteristic to each soil type are given in Table 2.

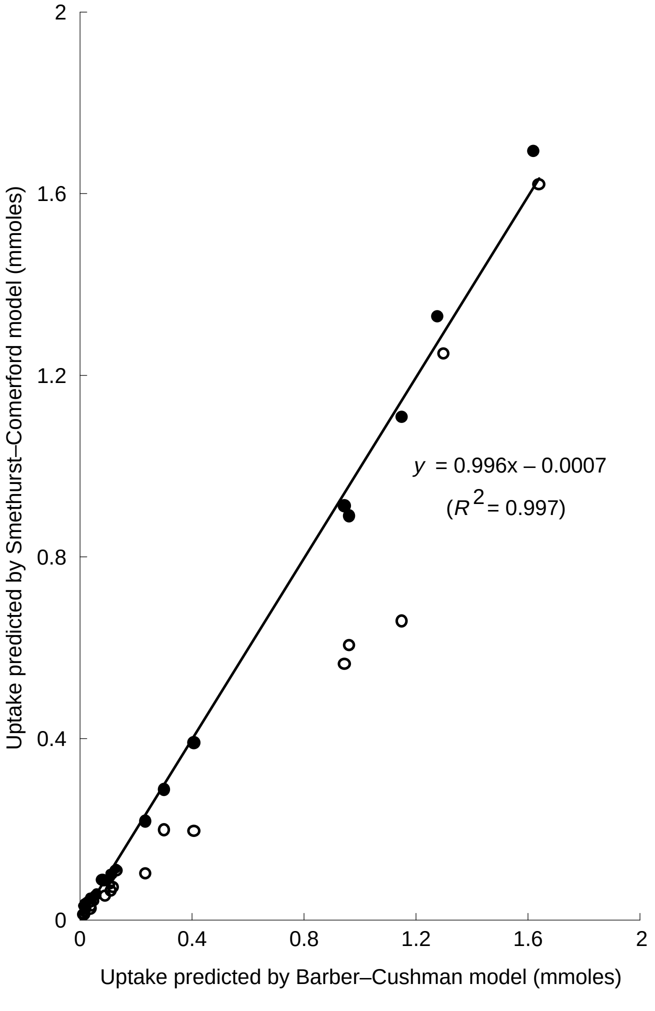

Fig. 1. Relationship between P uptake predicted by the Barber–Cushman model and the modified (●) and original (○) Smethurst–Comerford models.

A sensitivity analysis was conducted to assess the robustness of the Smethurst–Comerford model. To conduct this sensitivity analysis, the 'standard simulation' was defined as above, i.e. with soil-specific inputs of buffer power, bulk density, moisture content, and root growth (values supplied in Table 2), and constant inputs of Michaelis–Menten kinetic parameters, water influx to the root, and root radius (values supplied in text above). The factors that were changed included the liquid influx rate, C_{min}, root radius, and root growth. Each factor was altered individually, and the effect of that alteration on the uptake was averaged over the 26 soils, and recorded as an average percentage change. The root growth was variable in the standard simulation, but for the purposes of the sensitivity analysis, it was maintained at a constant level (low or high) for all of the soils. This was done to determine whether an accurate root growth estimate was required for each soil.

Results and discussion

Model comparison

When identical inputs were used in both the modified Smethurst–Comerford and Barber–Cushman models, a very high correlation was obtained between both estimates of uptake (Fig. 1). A linear regression fitted to these data gave an R^2 value of $0 \cdot 997$, and a slope not significantly different ($P > 0 \cdot 05$) from unity, and the intercept was not significantly different ($P > 0 \cdot 05$) from zero. Hence there

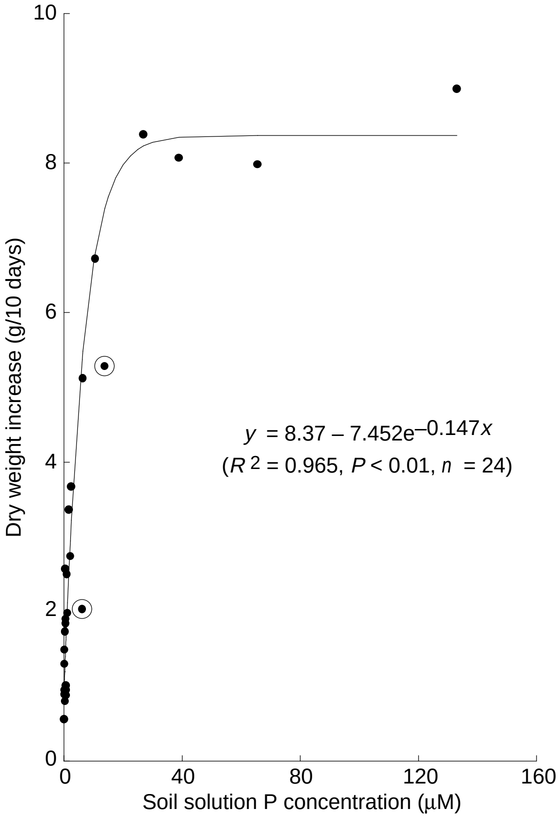

Fig. 2. Relationship between dry weight increase (15–25 days) of maize and initial concentration of P in soil solution (circled points were not included in the regression analysis).

was good quantitative agreement between the modified Smethurst–Comerford and the Barber–Cushman model. Output from the standard Smethurst–Comerford model followed a linear trend with uptake predicted by the Barber–Cushman model, but the uptake predicted by this model was less than that predicted by both the modified Smethurst–Comerford and the Barber–Cushman models. The only soils that did not follow this trend were the 2 soils with the highest soil solution concentrations (soils 12 and 25). These soils maintained a P_{root} $\gg 0$, and modifications to the Smethurst–Comerford model had little effect on predicted uptake. Hence, modifications made to the Smethurst–Comerford model increased predicted uptake values to those comparable with the widely accepted Barber–Cushman model.

Observed growth and P uptake in relation to model predictions

The initial measured concentration of P in soil solution explained 97% of the variation in dry weight increase for the unfertilised pots (Fig. 2). The long-term predictive value of this relationship, however, is probably minimal, because the plants were grown for only 25 days. During this period only a small proportion of solid-phase P would have been used. The dry weight increase reached a maximum value of approximately 8·5 g and was associated with soil solution P concentrations up to about 40 μM.

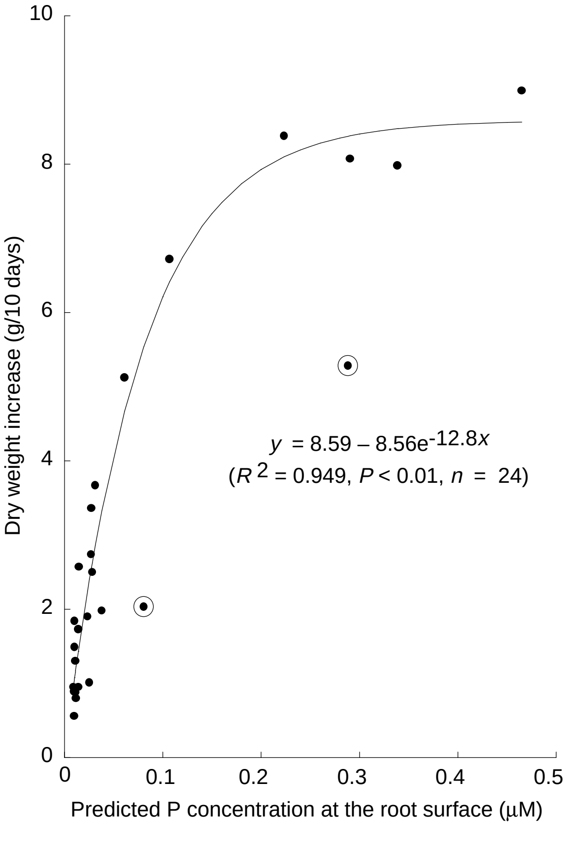

Fig. 3. Relationship between dry weight increase (15–25 days) of maize and the predicted P concentration at the root surface.

When P$_{\mathrm{root}}$ (i.e. predicted P concentration at the root surface) was related to the dry weight increase, a slightly lower R^2 value was observed ($0{\cdot}949$, see Fig. 3) than when soil solution P was used. In these regressions, 2 soils (nos 4 and 24, circled) that appear to be outliers were omitted. Plant growth in these soils was probably limited in some other way, but this could not be explained with the data that were available. Hence, qualitative prediction of a response to fertiliser was generally very good with the P$_{\mathrm{root}}$ parameter.

The relationship between solution P concentration and P uptake was described by a Mitscherlich function (Fig. 4; $r^2 = 0{\cdot}965$, $P < 0{\cdot}01$, $n = 26$), whereas a linear function was adequate for the relationship between P$_{\mathrm{root}}$ and P uptake (Fig. 5; $r^2 = 0{\cdot}971$, $P < 0{\cdot}01$, $n = 24$). Hence, roots took up P in direct relation to the P concentration at their surface. This is because uptake approaches linearity at P concentrations between the C_{min} and K_{m} values. This suggests that adequate P supply was achieved well before the uptake mechanism for phosphate was saturated. The equation in Fig. 5 suggests a y intercept at $81{\cdot}4$ μmol/pot, which was probably the contribution of seed P at 15 days. Hence the seed P contribution was minimal compared with the uptake for the 15–25-day period. Comparison of Figs 3 and 5 indicates that, at concentrations greater than about

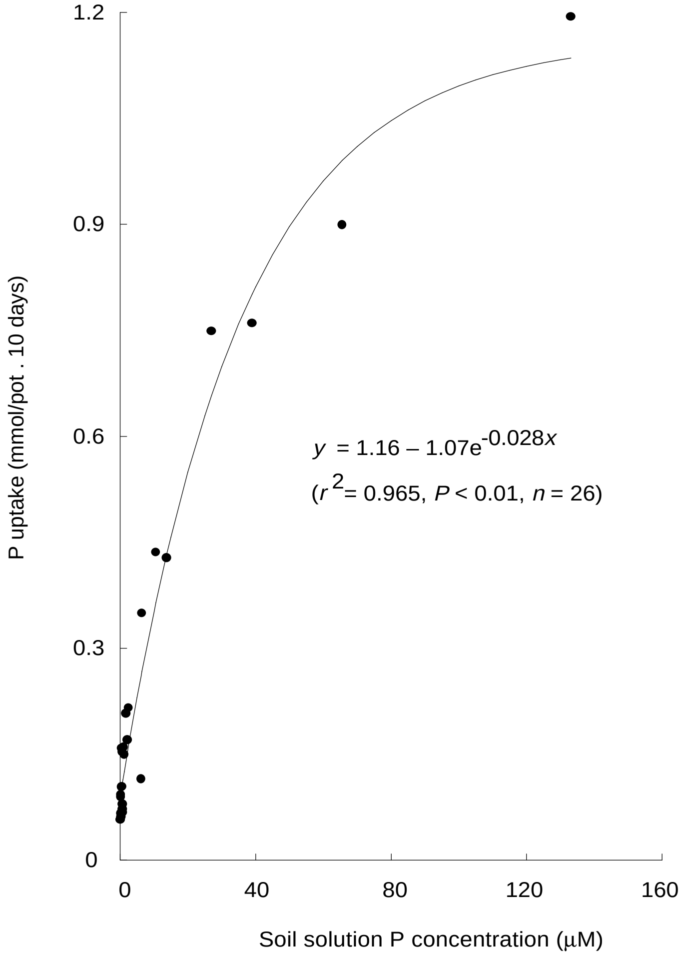

Fig. 4. Relationship between P uptake (15–25 days) and the concentration of P measured in the soil solution of the unamended soils.

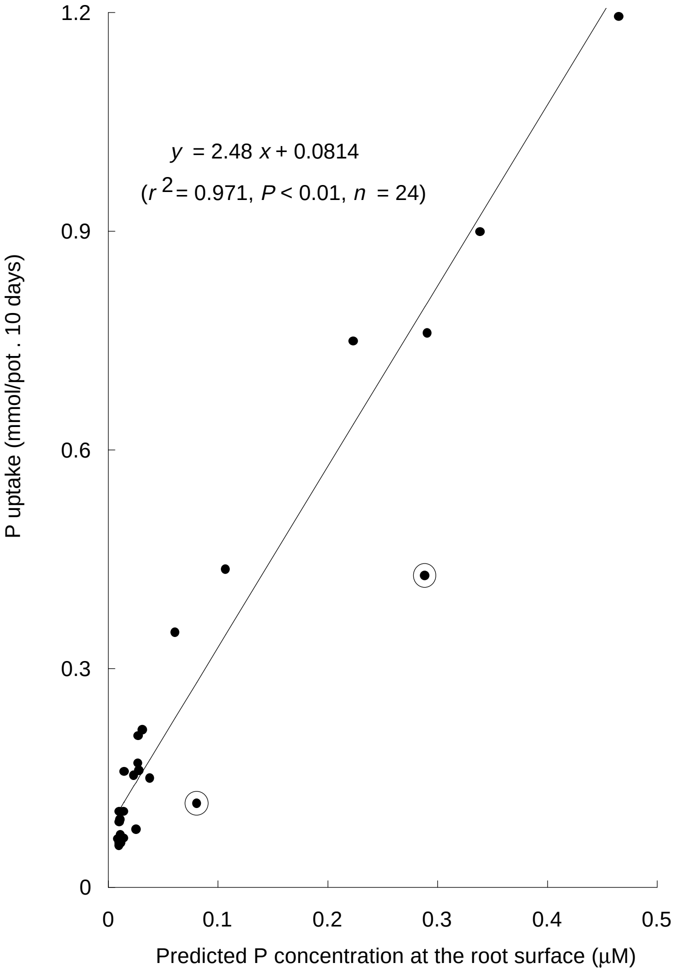

Fig. 5. Relationship between P uptake (15–25 days) and predicted concentration of P at the root surface for the unamended soils.

$0{\cdot}2\ \mu\text{M}$ at the root surface, the plants had attained maximum yield and were taking up P superfluous to their needs (i.e. luxury uptake).

Predicted and observed uptake were highly correlated (linear relationship, $r^2 = 0{\cdot}945$; Fig. 6), but predicted uptake was about twice that observed. A number of errors in the assumption of parameter values were examined as potential causes of this discrepancy, i.e. liquid influx rate, C_{min}, root radius, and root growth. A sensitivity analysis of these inputs (Table 3) showed that the liquid influx rate was unlikely to have caused an error of this magnitude. However, errors in assumed values of either C_{min} or root growth could account for this discrepancy. As an indicator of P deficiency, a high level of accuracy in predicted uptake may not be needed, but merely a strong correlation. If this is the case, it may be adequate to assume 'typical' values for many of the soil and plant parameters that are difficult to measure, e.g. root growth and uptake kinetics.

Relative dry matter yield was also highly correlated with predicted P uptake across all soils ($r^2 = 92{\cdot}8\%$; Fig. 7). There was a noticeable point of inflection at about 70% relative dry matter yield, or a predicted uptake of approximately $0{\cdot}4$ mmol. A relationship of similar form was observed when relative dry matter

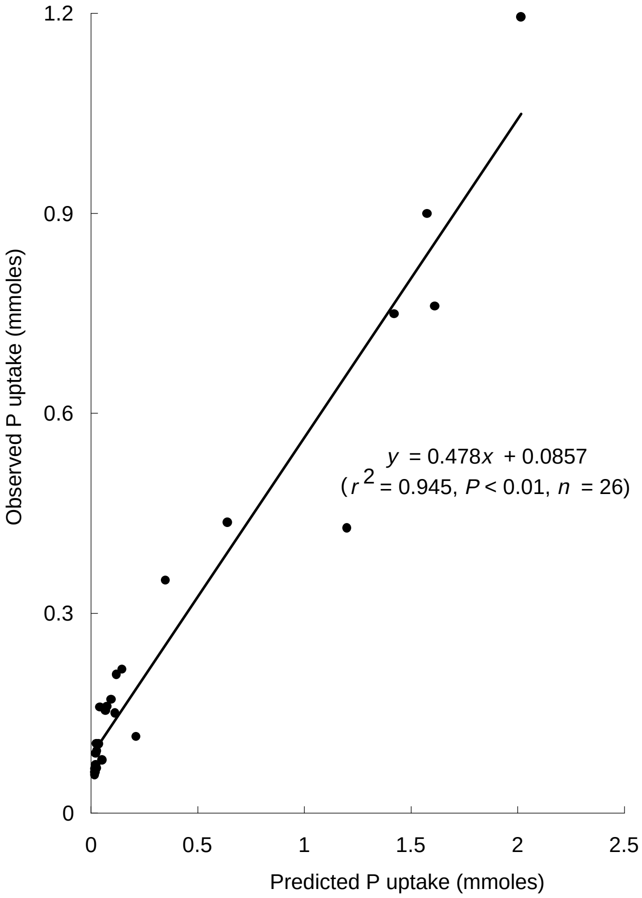

Fig. 6. Comparison of predicted and observed P uptake for the 26 soils (15–25 days).

yield was plotted against P_{root} ($r^2 = 87{\cdot}8\%$), where the point of inflection occurred at around 0·05 μM (data not presented). Hence, predicted P uptake, or predicted concentration at the root surface, was a useful indicator of relative dry matter yield (or conversely, deficiency) in this range of soils.

Table 3. Sensitivity analysis of the model

Input parameter	Values used	Av. uptake change[A]
Liquid influx rate ($cm^3/cm^2{\cdot}s$)[B]	6×10^{-9}, 6×10^{-5}	0%, +18%
C_{min} (μM)[C]	0·09, 0·24	−77%, −88%
Root radius (mm)	0·05, 0·25	−38%, +30%
Root growth[D]	Low, high	−27%, +71%

[A] Percentage change from the standard simulation (standard values are supplied in Table 2 and in the text).

[B] Liquid influx rate was varied by a factor of 100 from the standard simulation value of 6×10^{-7}.

[C] Low and high C_{min} and root radius values were chosen from the literature (Barber 1984; Nye and Tinker 1977; Jungk *et al.* 1990).

[D] Although root growth varied with soil type in the original input data, for the purposes of the sensitivity analysis, examples of the lowest and highest values from the data set were used, and these were set to the same value in all soil types.

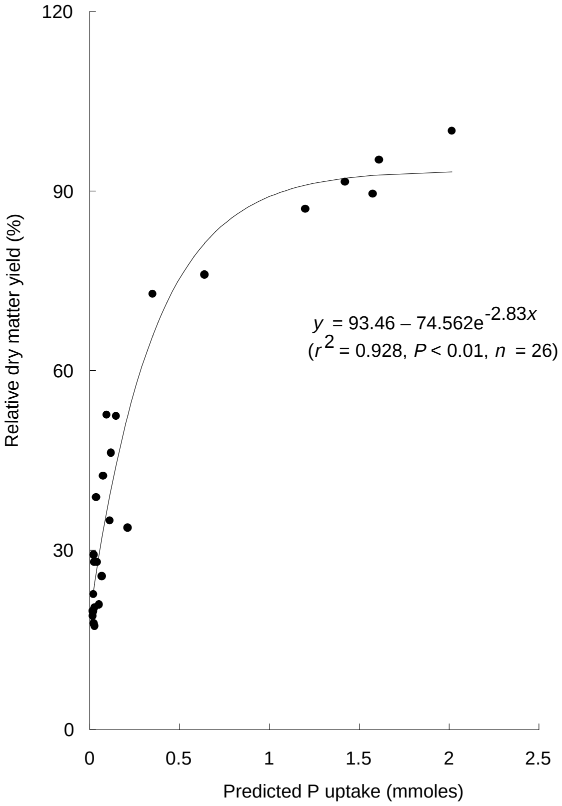

Fig. 7. Comparison of observed response to fertiliser and predicted P uptake for the 26 soils (15–25 days). Relative dry matter yield is growth in the unamended soil as a percentage of that with P fertiliser.

In the original analysis of these data, Moody *et al.* (1988) found that the soil factor which provided the highest correlation with plant growth was the equilibrium P concentration (EPC), with an r^2 value of 0·95. This high correlation was probably due to the brief nature of the experiment: the maize was harvested after only 25 days. During this short period, the amount taken up by the plants was several times more than that initially present in the soil solution, but the soil solution concentration is buffered by exchangeable pools. In longer term experiments with maize, soil solution P and EPC (which should be similar) have been poorer predictors of P deficiency than indicators which include a proportion of solid phase P (Holford and Mattingly 1976). Prediction of P deficiency by the modelling approach has the potential to be more widely applicable because it integrates P quantity and intensity factors and should require little empirical adjustment for soil type or plant type.

Conclusions

As a way of integrating our knowledge of the principles that affect P supply and uptake, a model was used to predict P concentration at the root surface and P uptake. The Smethurst–Comerford model was successfully modified to account better for soil types with a range of buffer powers. Uptake predicted by the modified version of the Smethurst–Comerford model was highly correlated with, and of the same magnitude as, that predicted by the widely accepted Barber–Cushman model under the same conditions.

When applied to an experimental set of data, the predictions of the model (P uptake and concentration at the root surface) were highly correlated with all measures of P deficiency (including dry matter yield, P uptake, and response to fertiliser) for a wide range of soil types.

Although the predicted concentration at the root surface during the 15–25 days for all soils was much less than that required for maximum uptake, P uptake was not the limiting factor to growth at the higher uptake rates. We conclude this because observed uptake followed a linear trend with P_{root} over the concentration range predicted, while dry matter accumulation had an asymptotic relationship (i.e. luxury consumption of P occurred past the point where it was the limiting factor to growth).

Even though some of the inputs were not measured, the model was still a very good indicator of P uptake and dry matter yield, or deficiency, over a wide range of soil types. Hence, this method shows some potential as a widely applicable test for P deficiency, and is worthy of a more rigorous investigation over a longer time-scale.

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