Root system plasticity as a factor in crop breeding for improved nutrient uptake

J.B. Reid[1], Y. Tan[1], W.B. Griffin[2] and D. Goulden[2]
[1]The New Zealand Institute for Plant & Food Research Limited, Hastings, P.O. Box 8285, Havelock North 4157, New Zealand
[2]The New Zealand Institute for Plant & Food Research Limited, Private Bag 4704, Christchurch 8140, New Zealand

Abstract

Root architecture may reflect uneven distribution of soil water and nutrients. It is not clear however, if plant breeders should screen for such plasticity when breeding plants for improved nutrient uptake. A mechanistic model was used to forecast how such plasticity affects nutrient uptake and growth of peas (*Pisum sativum*), concentrating on a putative *+P plasticity* trait (the ability to partition root dry matter preferentially to regions where P uptake is greatest. Calculations were made for crops grown for 60 days in a silt loam, with no limitations due to supply of water or nutrients except P. Five soil P treatments (P10, P25, P50, P75 and P100) were chosen. For each the initial P distributions that were either uniform with depth or patchy with a peak at 0.1-0.15 m depth were compared. The *+P* plasticity trait affected root distribution least at P10 and most at P100. It did not increase total root production, and it increased total P uptake only slightly. For P25, P50 and P75 the trait increased simulated biomass yields up to 9%, but it gave no yield benefits at P10 or P100. The trait increased the apparent efficiency of P uptake (ε_P, in g P kg^{-1} roots) by 10% on average, with most benefit at P50 and P75. However, ε_P varied more between P supply treatments, and is not a good selection characteristic for breeding. Although these results need to be confirmed by direct experimentation, it seems that, for peas at least, breeders need not concentrate on root system plasticity to localised P supply.

Additional keywords: growth rules, modelling, pea, *Pisum sativum*, phosphate, root architecture

Introduction

Crop breeding programmes that concentrate on root system properties offer a way of improving the cost-effectiveness and sustainability of fertiliser use. However, breeding for improved root performance is a challenging pursuit. Root systems are difficult to access and measure unless grown in artificial substrates - and then they may grow and function quite differently than in field soils (Bengough and Mullins, 1990; Tinker and Nye, 2000; Gregory *et al.*, 2009; Wojciechowski *et al.*, 2009). Furthermore, root system architecture is an aggregate characteristic that results from several distinct and simultaneous processes in the roots (Lynch, 1995) - and is influenced by the sufficiency of resources

(light, mineral nutrients, water) for shoot activities (Huck and Hillel, 1983; Huck *et al*., 1983; Husain *et al*., 1990).

There can be substantial and stable differences between species and varieties in the patterns of dry matter allocation to roots and in root system architecture (Fitter, 1985; Fitter *et al*., 1988; de Dorlodot *et al*., 2007). Under some conditions these differences can be clearly related to crop performance (Ho *et al*., 2005; Manschadi *et al*., 2006; Botwright Acuña *et al*., 2007; Manschadi *et al*., 2008). The reliability of these differences from season to season and site to site indicates that they result from different inherited strategies of root growth. For example, one particular variety or species will try to allocate more of its dry matter to growth of deep roots whereas another may give more priority to producing an extensive but shallow root system. Lines with such traits can be selected fairly readily in breeding programs (Lynch, 1995; de Dorlodot *et al*., 2007). In many cases the genetic aspect of these differences has been known for many years, as in the case of certain mutants (Zobel, 1991).

Root systems may also respond tactically to local or transitory conditions, displaying much morphological plasticity. Genetically identical lines grown in different environments may produce greatly different root systems. For example, substantially enhanced growth of roots may occur in soil zones with increased supply of some inorganic nutrients (Drew, 1975; Anghinoni and Barber, 1980; Strasser and Wener, 1995; Forde and Lorenzo, 2001) or water (Beukes, 1984).

Another type of root system plasticity has some of the characteristics of both tactics and strategy. Strategically a crop may adapt to water shortage by increasing the allocation of dry matter to the root system at the expense of new leaf growth (Husain *et al*., 1990; Rengasamy and Reid, 1993a; Vogt *et al*., 1993). That extra dry matter may be allocated in such a way that does not greatly distort the root distribution through the soil (Rengasamy and Reid, 1993b). Alternatively, it might be more tactically allocated to growth in soil zones where water is most readily available (Rengasamy and Reid, 1993b), which does distort root system architecture. In some species such changes can be rapid, presumably as a means of drought avoidance (Reidenbach and Horst, 1997).

Not surprisingly, plant breeders have paid most attention to selecting lines that differ in strategic approaches to root system growth and architecture (Ho *et al*., 2005; de Dorlodot *et al*., 2007; Manschadi *et al*., 2008; Hammer *et al*., 2009). Typically, this involves selecting genotypes that have root systems with reliable characteristics like coarse, greatly branched, deep and narrow, or shallow and wide.

However, even genotypes that have clearly defined architectural types like these might also exhibit considerable plasticity if conditions warrant it (Lynch, 1995). Root system plasticity has been implicated in causing genotype x environment interactions (MacMillan *et al*., 2006). Where such plasticity is significant, but ignored, it could cause a number of different genotype x environment interactions that could confound comparisons between breeding lines late in the breeding process.

It would be difficult to include plasticity to factors such as localised P supply in breeding programmes. Before embarking on such an exercise breeders need confidence that expression of such plasticity would benefit sufficiently the yields or quality of

crops under conditions the crops are expected to experience. Direct experimental evidence of this is lacking, and could be expensive and difficult to obtain.

The aim of this paper is to identify whether breeding programmes could expect to improve the efficiency of fertiliser P use by selecting lines that show morphological plasticity in response to soil phosphate concentrations. A model of crop growth and nutrient uptake is used to calculate the benefits of a putative *+P* plasticity trait.

Materials and methods

Model

A full description of the mathematical model is beyond the scope of this paper, but the key features are given below.

The growing period is divided into a series of time steps (from 1 to 10 min) during which environmental conditions are assumed constant. Air temperature and incident radiation are assumed to vary sinusoidally during the day. The soil is divided into 20 horizontal layers, each 0.05 m thick.

Crop dry matter production is taken to be a simple function of light interception by the leaves (Monteith, 1977). The dry matter is allocated to plant organs using simple rules. Reproductive growth is not considered. Under unstressed conditions the allocations to leaves, stems and the root system are taken from time series measurements made for pea (*Pisum sativum* L. cultivar `Sonata') grown in the glasshouse. Leaf specific area (m^2 kg^{-1}) is assumed constant. For each type of plant organ there is a minimum amount of P per kg of growth that must be supplied from a labile nutrient pool in the crop. If the amount available is insufficient then the dry matter is diverted to another organ using the priority scheme root system > leaves > stem. If the leaf water potential falls below a critical value then the dry matter that would have gone to the leaves is diverted to the roots. Dry matter that cannot be allocated to leaves or roots due to nutrient or water limitations is allocated to the stems.

For each type of plant organ there is a maximum concentration of P that can be tolerated before growth ceases. Any plant phosphate in excess of these maxima is stored in the stem and can be remobilised later. For each time interval the labile pool of P consists of uptake by the root system plus mobilisation from the seed, and remobilisation of a constant fraction of the amount present above the minimum required in leaves, stems and roots.

The process of nutrient uptake is regulated by both the physiological state of the plant and the rates of supply from the soil. Diffusive and mass flow movement of nutrients through the rhizosphere is described using a steady-state assumption (Baldwin *et al*., 1973; Yanai, 1994) modified so that the radial distance each root section has for exclusive use is the minimum of (a) the average distance between roots (assuming they are parallel), and (b) the radial distance of the depletion zone if movement was purely by diffusion. Uptake at the root surfaces is described using Michaelis-Menten kinetics (Yanai, 1994; Tinker and Nye, 2000), but with an important addition. Feedback control of the final uptake is exerted by the overall concentration of P in the plant, along the lines described previously for K (Greenwood and Karpinets, 1997).

Water uptake, transpiration, soil surface evaporation and water movement within the soil are described using the model of Reid (1990).

Within the root system two main types of roots are distinguished. *Pioneer roots* (a constant number per plant) are the first to emerge from the seed and penetrate vertically. Their rate of depth penetration is determined by the overall production rate of dry matter (dictated by light interception), the fraction of the available dry matter assigned for pioneer roots, the effects of soil strength (see below), and a constant root length per unit mass. The *bulk roots* can have a different length per unit mass, and their overall growth rate is dictated by dry matter production in the leaves. The partitioning of bulk root growth between the soil layers depends on simple rules. First, bulk roots can grow in a soil layer only after it has been entered by pioneer roots. Second, the extension rate in each layer is adjusted for the effects of soil strength (itself a function of dry bulk density and water content), using empirical relationships (Bengough and Mullins, 1991). Third, the fraction of the total dry matter available for bulk root growth that is allocated to each layer is adjusted using a plasticity rule.

Here two plasticity rules are considered. Both imply teleonomic behaviour of the plant. The first is that partitioning between layers varies with the fraction of the total water uptake provided by each layer. This rule has been used elsewhere as a key assumption of mechanistic soil-plant system models (Huck and Hillel, 1983; Hoogenboom, 1999), and is consistent with much observational evidence (Huck, 1977; Huck *et al*., 1983; Reid and Renquist, 1997). Below this rule is regarded as a baseline or control. The second rule arises from a putative *+P* plasticity trait - partitioning varies directly with the fraction of total P uptake that each layer provides. Although preferential root growth in zones of increased P availability and uptake has been described (Drew and Saker, 1975a; 1975b; Anghinoni and Barber, 1980; Strasser and Wener, 1995) we are not aware of any quantitative analysis of dry matter partitioning along these lines. The form assumed here is intended as an illustrative, extreme case of root system responsiveness to spatial variability in P uptake rates.

These two rules can be implemented independently or in combination. To combine them the fractional contributions to water and P uptake are first multiplied for each layer. Each product is then expressed as the fraction of the sum of the products.

The calculations

Exploratory calculations were carried out for pea cultivar `Sonata') with and without the putative *+P* plasticity trait and with a range of amounts and distributions of available P in the soil.

Weather conditions and planting date were chosen to give a good combination of minimal water stress and rapid growth. Weather data were taken from the records for Whakatu (39° 36' 39.60" S, 176° 54' 43.2" E) for a crop planted on 1 October 1997. Two overnight irrigations of 10 mm were also included at 31 and 53 DAS. The assumed plant population was 100 plants m^{-2}.

Plants were assumed to be grown in the sort of large containers that breeders might use when assessing performance of breeding lines. Normally under those conditions care is taken to ensure uniformity of the soil. The soil was 1 m deep with uniform initial distributions of water content and dry bulk density. Supply of all mineral nutrients except P was assumed to be non-limiting. Soil physical properties were chosen for the topsoil of a Templeton silt loam (Reid and Hutchison, 1986).

The availability of P in a given volume of soil depends on the initial concentration in the soil solution, the volumetric soil water content, and the diffusion coefficient for P in the soil, which in turn depends on the soil P buffer power and the soil water content (Tinker and Nye, 2000). Ten treatments were imposed with different initial P availabilities. This range was achieved by varying both the initial concentration of P in the soil solution and the buffer power (Table 1). There were two main categories of P treatments - Uniform and Patchy - and within each there were 5 different levels of P availability (P10, P25, P50, P75 and P100, where the numbers refer to relative sizes of the P concentrations and buffer power). These treatments were contrived to give a roughly three-fold range in yields. The initial total amount of P in solution was the same for the uniform and patchy distributions at the same P availability levels. The patchy distributions had an enhanced P concentration in soil layer 3 (0.1-0.15 m), with a corresponding reduction in concentration in the rest of the soil profile. In separate calculations it was established that for both uniform and patchy P distributions the biomass yields were not increased by supplying more P than that in the P100 treatments.

For each of the above 10 treatments the performance of two different types of plants was calculated: those with only the water plasticity trait (Control treatment), and those with the water plasticity and *+P* plasticity traits (*+P* plasticity treatment).

Table 1: Initial soil phosphate (P) distributions used for the calculations. Soil P buffer power did not vary with depth although it varied between treatments.

	Soil P buffer	Soil solution P (mols m^{-3})	
Treatment	power	0.1-0.15 m	Rest of profile
Uniform P10	0.6	0.0050	
Uniform P25	1.1	0.0125	
Uniform P50	1.8	0.0250	
Uniform P75	2.6	0.0375	
Uniform P100	3.3	0.0500	
Patchy P10	0.6	0.0240	0.0040
Patchy P25	1.1	0.0600	0.0100
Patchy P50	1.8	0.1200	0.0200
Patchy P75	2.6	0.1800	0.0300
Patchy P100	3.3	0.2400	0.0400

Results

When the initial P distribution was uniform, the simulated biomass yields on the five P supply treatments increased from 3.6 t ha^{-1} for P10 to 13.6 t ha^{-1} for P100 (Table 2). The yields were slightly larger when the initial P distribution was patchy, except at the P100 level.

For the intermediate P supply treatments (P25, P50 and P75) the *+P* plasticity trait allowed simulated yields that were up to 9% greater than the controls (Table 2). However, at the smallest (P10) and largest (P100) rates of P supply the *+P* plasticity trait gave no yield benefits. Nevertheless the *+P* plasticity trait affected root distribution in all of the P supply treatments, with the size of the effect increasing with P supply from P10 to P100. For initially uniform P distributions the *+P* plasticity trait resulted in a more even distribution of roots down the profile (Figure 1). The same trend was apparent for the patchy initial P distributions, except that there were many more roots on the *+P* plasticity treatment at 0.1-0.15 m depths (where initially there was an enhanced concentration of soil solution P).

Table 2: Biomass yields (t ha^{-1}) of the simulated crops 60 DAS.

Treatment	Control	*+P* plasticity	*+P* plasticity (% of control)
Uniform P10	3.6	3.6	100
Uniform P25	5.6	6.1	108
Uniform P50	10.5	11.5	109
Uniform P75	13.1	13.3	102
Uniform P100	13.6	13.6	100
Patchy P10	3.8	3.7	99
Patchy P25	6.0	6.4	107
Patchy P50	10.9	11.4	105
Patchy P75	13.2	13.4	101
Patchy P100	13.6	13.6	100

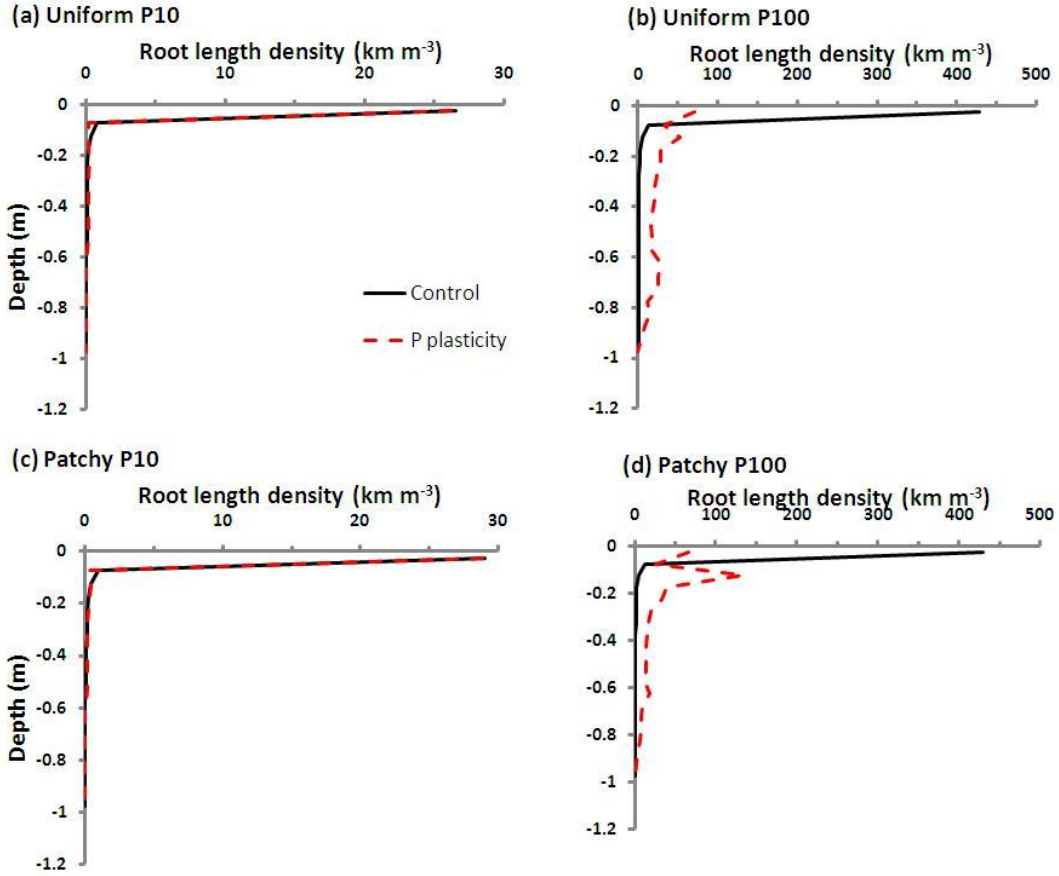

Figure 1: Effects of the +P plasticity trait on simulated root distributions for the extreme P treatments (P10 and P100). For the P25, P50 and P75 treatments the effects of the +P plasticity trait were between the extremes shown here. Note that if less well-watered conditions had been chosen, then the plasticity rules chosen for the model would have resulted in much less dominance of the top 0.05 m in the root distributions.

Although root distribution was markedly affected by the *+P* plasticity treatment, total root length or mass was not increased (Table 3). In the P25, P50 and P75 treatments where plant biomass was increased by the *+P* plasticity trait (Table 2), total root length and mass were decreased (Table 3).

Uptake of P was strongly affected by the P supply treatments, increasing from P10 through to P100, and it tended to be slightly greater in the patchy than in the uniform distributions (Table 4). Compared with the controls, the *+P* plasticity treatment increased calculated P uptake slightly – the average increase was 0.3 kg P ha^{-1} or 4%. Given that P uptake was increased slightly and total root mass was decreased by the plasticity trait, we calculated ε_P, the apparent P uptake efficiency of the root systems, as the mass of P taken up per unit mass of roots. The *+P* plasticity trait increased ε_P on average by 10%, but the benefit was greatest (about 20%) for the P50 and P75 treatments.

Table 3: Effects of the *+P* plasticity trait on total root production for the simulated crops at 60 DAS.

`	Total root length (km m^{-2})		Total root mass (t ha^{-1})	
	Control	*+P* plasticity	Control	*+P* plasticity
Uniform P10	1.4	1.4	0.45	0.46
Uniform P25	5.1	5.0	1.2	1.2
Uniform P50	13.2	11.1	2.7	2.3
Uniform P75	19.9	17.2	3.9	3.4
Uniform P100	23.2	23.3	4.5	4.5
Patchy P10	1.6	1.6	0.47	0.49
Patchy P25	5.2	5.0	1.2	1.2
Patchy P50	13.0	11.6	2.7	2.4
Patchy P75	20.0	17.2	3.9	3.4
Patchy P100	23.3	23.3	4.5	4.5

Table 4: P uptake and apparent P uptake efficiency (εP) of the simulated crops from sowing to 60 DAS.

	P uptake (kg ha^{-1})		ε_P (g P uptake kg^{-1} root)	
Treatment	Control	*+P* plasticity	Control	*+P* plasticity
Uniform P10	0.19	0.20	0.42	0.44
Uniform P25	1.28	1.31	1.04	1.08
Uniform P50	4.27	4.42	1.59	1.92
Uniform P75	8.78	9.23	2.25	2.71
Uniform P100	13.97	14.89	3.11	3.31
Patchy P10	0.22	0.23	0.47	0.48
Patchy P25	1.31	1.34	1.05	1.10
Patchy P50	4.37	4.47	1.65	1.86
Patchy P75	9.07	9.42	2.32	2.76
Patchy P100	14.25	15.20	3.17	3.38

Discussion

The patterns of yield differences between the P supply and distribution treatments confirm that the conditions chosen provided a good test for the likely effectiveness of the +P plasticity treatment. The slightly larger yields on the patchy rather than uniform P distribution treatments suggest that a greater amount of soil solution P was accessible early in crop growth when the roots were able to exploit layer 3.

The *+P* plasticity trait had substantial effects on the simulated root distributions, which might be expected to have substantial impacts on total P uptake, particularly for the patchy initial P distributions. Although the *+P* plasticity trait increased rooting density up to 25 fold where initial soil P was enhanced (at 0.1 to 0.15 m depth), these local clumps of roots did not dominate the total P uptake of the root system. The *+P* plasticity trait increased total P uptake by 2-19%, with the maximum in the Patchy P25 treatment (where yield was increased by only 7%). The size of these

improvements is surprising given that in experiments with beans and soybeans, differences in root architecture are often associated with much larger differences in P uptake and yield (Lynch, 1995; Ao *et al*., 2010). It must be pointed out that contrary to many accounts in the published literature, here the plants were not confined to small volumes of soil, so roots often encountered fresh soil where uptake rates initially at least can be quite large.

We have not established if there is a threshold percentage of the root system or root zone that needs to be exposed to enhanced P concentrations for the *+P* plasticity trait to substantially improve crop performance. Here 5% of the available root zone had soil solution P concentrations enhanced by a factor of 6 times. In agricultural practice, P fertiliser placement would probably cause larger initial differences in soil solution concentrations but for a smaller percentage of the possible root zone (Tinker and Nye, 2000).

When breeding plants to improve the efficiency of P fertiliser use it is tempting to focus on measures of root system efficiency - the amount or rate of P uptake per unit mass or length of the roots grown. There is good evidence, for instance, that "specific uptake rate" (g P taken up per unit time per unit mass of root) varies considerably between lines selected for root architectural differences (Crush *et al*., 2008; Ao *et al*., 2010; Zhu *et al*., 2010). However, such measures must be interpreted very carefully. In this paper the apparent uptake efficiency (ε_P, in g P kg^{-1} roots) has been calculated, with the word "apparent" chosen to avoid the implication that ε_P is a physiological characteristic of the root system largely under genetic control. ε_P was increased by 2-21% by the *+P* plasticity trait, but the values were dominated by the initial amounts of P in the soil, with ε_P varying by a factor of almost 8 between the P10 and P100 treatments. Values of ε_P would have varied even more between soil layers of the same root system, reflecting factors such as initial soil phosphate concentrations and time since roots entered the layer. That measured values of ε_P could have a genetic component is not disputed. However, the variations due to environmental conditions are potentially so large that it would be risky to base selection processes on P uptake efficiencies calculated from multiple experiments that differed in environmental conditions. Our results suggest that even within a single experiment, differences in ε_P may not be detectable at high or low rates of P supply (Table 4, P10, P25 and P100 treatments).

General Discussion

It is important to consider the limitations of this preliminary study. A mathematical model designed to replace difficult or impossible experiments with calculations and, subsequently, to make predictions that *can* be empirically tested has been relied on. The model integrates a great deal of our current understanding of crop growth and soil-plant processes, but necessarily it contains many simplifications. For example, for the process of P uptake the possible improvement due to vesicular-arbuscular mycorrhizas at low availability of soil P (Tinker and Nye 2000; Zhu *et al*., 2005) is ignored. Experimental evidence that these would have favoured the *+P* plasticity treatment above the controls, and they are unlikely to substantially affect root production in peas (Gavito *et al*., 2001) could not be found, so it seems unlikely that their omission would affect our conclusions.

There is much evidence that crop root systems may divert dry matter to soil zones

that are enriched with N, and particularly where N and P are locally more available than in the bulk soil (Drew, 1975; Strasser and Wener, 1995). Here interactions between plasticity in response to P and N supply rates have not been considered. Given the very different mobility of phosphate and nitrate in the soil (Tinker and Nye, 2000), calculations to explore these interactions are beyond the scope of this paper. Even so, it is difficult to envisage that the extra competition for dry matter between soil regions that would be introduced by *+N* plasticity would *increase* the likely importance of *+P* plasticity and invalidate our conclusions.

The model ignores the possibility that roots could release chemicals that increase the solubility of P in the rhizosphere. There is no doubt that such effects can occur (Tinker and Nye, 2000), but we are unaware of any evidence that such processes would be affected by the presence or absence of a *+P* plasticity trait. Release of such chemicals by both the control and *+P* plasticity treatments would have raised P uptake rates on the P10-P75 treatments, reducing the scope for the *+P* plasticity trait to improve crop performance.

It has been assumed that the *+P* plasticity trait does not introduce fundamental physiological differences other than the dynamic diversion of dry matter to zones of greatest P uptake. It appears that root respiration rate interacts with P uptake by controlling the amounts of C available for root elongation, which is not inconsistent with the model used here. Measured respiration rates per unit root mass did not appear to vary between genotypes differing in P acquisition efficiency, although they did vary between different P supply treatments (Zhu *et al.*, 2010). It has been assumed that there was no appreciable root death in the first 60 days of crop growth. A short root lifespan would probably increase the need for *+P* plasticity to maintain uptake in the near surface layers (including the 0.1-0.15 m depth layer that had extra P in the patchy P distributions. The results of Gavito *et al.* (2001) suggest a longevity in excess of 28 days for pea roots. Although this might be expected to vary under stress conditions, this value is probably not so short that it invalidates our calculations given that by 60 DAS the vast majority of the root length was younger than 28 days. In future, the model should be adjusted to account for root longevity.

Our choice of environmental conditions for the calculations might also have prejudiced the outcome. In particular, the crops did not experience water stress. It is unlikely if this would have favoured the *+P* plasticity treatment, particularly for the P50, P75 and P100 treatments. Water stress would have reduced overall growth, reducing the responsiveness of yield to any extra P uptake that the *+P* plasticity trait might enable. With less rain, both the control and the *+P* plasticity treatments would have put proportionally less of their root resources into the 0-0.05 m depths that dominated these calculations and more into deeper layers. For the patchy P distributions even the controls would have invested more roots in the enriched 0.1-0.15 m zone.

All our calculations assumed that soil P buffer power did not vary down the soil profile. In the field this is unlikely to be the case, as soil mineralogy and fertility can vary with depth. Furthermore, soil P buffer power was assumed to be constant. This is common in nutrient uptake modelling (Anghinoni and Barber, 1980; Yanai 1994; Barber, 1995; Tinker and Nye, 2000). Inspection of buffer curves (Tinker and Nye, 2000) generally indicates that soil P

buffer power decreases as the concentration of P in the soil solution increases. However, when modelling nutrient uptake the assumption is normally made that buffer power is constant, as the range of soil solution concentrations involved is fairly small (Tinker and Nye, 2000). Nevertheless by assuming constant buffer power our calculations may overestimate the amounts of P that could be supplied from soil zones with initially enhanced P concentrations. This error would have favoured the *+P* plasticity trait. However, it is conceivable that a locally enriched zone might have a superior buffer power to the bulk soil if, for instance, it contains a readily mineralised source of organic P, or an unusually high concentration of moderately soluble P salts.

In the model, when a root penetrates fresh soil, the P uptake rate is dominated by the Michaelis-Menten parameters chosen for calculating uptake. Before long though the uptake rate becomes dominated by the speed of diffusion of the ions through the rhizosphere to the root surface (Yanai, 1994; Tinker and Nye, 2000). The diffusion coefficient for P varies with the soil buffer power, soil water content, and a correction for the tortuosity of the diffusion path. In our calculations a wide range of buffer power values were considered. As mentioned above, a range of Michaelis-Menten parameters nor soil water contents were not considered, and the sensitivity of the computer uptake rates to the tortuosity correction were not examined. However, there is no reason to expect that the chosen values of any of these parameters and variables would have preferentially affected P uptake by the +P plasticity or control treatments.

There remains a clear need to test the predictions of this model experimentally. This must be done opportunistically, if and when genetic material with a range of plasticity characteristics becomes available. In the meantime, there is no compelling reason to expect that our calculations are systematically biased against the *+P* plasticity treatment. The results suggest that it would be difficult and perhaps unnecessary for breeding programmes to directly target root system plasticity as a selection characteristic. They also suggest that the sorts of measures of P uptake efficiency that may be made readily in breeding programmes will not make good selection characteristics. Simple measures such as crop yield and total root length under conditions of low P supply will continue to be very useful, as will smaller scale morphological characters such as root specific length and branching patterns, which have already been used successfully (Lynch, 1995; Crush *et al*., 2008).

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