How changing root system architecture can help tackle a reduction in soil phosphate (P) levels for better plant P acquisition

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Abstract

The readily available global rock phosphate (P) reserves may run out within the next 50-130 years, causing soils to have a reduced P concentration which will affect plant P uptake. Using a combination of mathematical modelling and experimental data we investigated potential plant-based options for optimising crop P uptake in reduced soil P environments.

By varying the P concentration within a well-mixed agricultural soil, for high and low P (35.5 to 12.5 mg l^{-1} respectively, using Olsen's P index), we investigated branching distributions within a wheat root system that maximise P uptake.

Changing the root branching distribution from linear (evenly spaced branches) to strongly exponential (a greater number of branches at the top of the soil), improves P uptake by 142% for low P soils when root mass is kept constant between simulations. This causes the roots to emerge earlier and mimics topsoil foraging. Manipulating root branching patterns, to maximise P uptake, is not enough on its own to overcome the drop in soil P from high to low P. Further mechanisms have to be considered to fully understand the impact of P reduction on plant development.

Keyword index: modelling, plant nutrient uptake, rhizosphere, root architecture, *Triticum aestivum*

Introduction

Fertiliser prices are continuing to increase, following a dramatic rise and fall in 2008. The increased volatility in the price of nutrients is linked to the price of oil, and doubt about the limitation of rock P availability in the medium term, maybe outweighed by limitations in energy and sulphur to process rock phosphate. Further, there have been repeated and increasing warnings stating that the readily available global rock phosphate (P) reserves will become exhausted within the next 50-130 years (Déry & Anderson, 2007; Cordell, Drangert & White, 2009). Therefore careful use of this finite resource in agricultural systems is clearly warranted (Vaccari, 2009). This need to reduce our reliance on rock P may also become exacerbated by political control as the remaining reserves are highly spatially localised, being mainly owned by China, Morocco and the US, who together control 85% of the known global phosphorus reserves (Elser & Bennett, 2011).

P is typically applied in large quantities in most productive cropping systems (>20 kg P ha^{-1}), however, it is often used inefficiently with a large proportion of the added P subsequently becoming unavailable for plant P uptake or lost altogether. To achieve greater sustainability within agriculture requires new strategies that will either reduce the P demand of the crop or promote greater root recovery of the added P such that less fertiliser is required (Withers et al., 2014). This would reduce the negative aspects of P use in agriculture (e.g. eutrophication) as well as yielding greater economic returns for farmers. Repeated fertilisation over many decades can lead agricultural soils close to, or at, P saturated levels (Borda *et al*., 2011). While this increases organic and readily available P in the soil it also stimulates vertical loss down the soil profile and allows P to be readily released from particles when surface runoff enters freshwaters (Hartikainen, Rasa & Withers, 2010; Stutter et *al*., 2012). One mitigation strategy is therefore to "run down" soil P reserves by reducing P inputs relative to the amount of P offtake in the crop. To maintain yields, however,

necessitates that P is used more efficiently by the crop. It is therefore important to assess how crops will cope under a reduced P environment, and if that is not plausible, determine what plant-based options are available, for adapting to these conditions.

There are many potential strategies to help tackle the reduced P scenario, from changing the plant traits by targeted plant breeding (e.g. reduced seed P content, changes in root architecture), to altering the properties of the soil (Vance, Uhde-Stone & Allan, 2003; Lynch, 2007). Plants are estimated to take up less than 15% of the P added in the soil, and therefore an alternative method involves manipulating the chemistry and biology of the rhizosphere to make more of the added P available to plants (Qiu, 2010). As P is often highly immobile in soil, one method could be to adapt the root system architecture to obtain P more efficiently (Williamson *et al*., 2001; Ho *et al*., 2005).

Simulating P uptake by a growing root system using mathematical models enables us to capture a multitude of scenarios in less time and at significantly lower costs than via experimentation. However, the experimentation is essential to provide validation and parameters for the model. In this paper experimental data and model simulations are brought together to further advance the understanding of P uptake by plant root systems. Optimisation algorithms are used to further synthesise new knowledge from the models and to get the most out of the collected data. Although previous models have been developed to investigate the influence of root architecture on plant P acquisition (Ge, Rubio & Lynch, 2000; Lynch & Brown, 2001; Grant & Robertson, 1997), these studies followed a pseudo 3 dimensional approach (Lynch *et al*., 1997) that presents computational problems in up-scaling to the field level (Roose & Schnepf, 2008). A review of the current 3 dimensional models is well described in Dunbabin *et al*. (2013) providing strengths and weaknesses of each approach. Here we present an alternative approach to modelling P uptake: using an adaptation of the more efficient root system model of Roose et *al*. (2001) to simulate P uptake of a crop on a

field scale. This model is comparable to other density based root models (Dupuy, Gregory and Bengough, 2010). Roose *et al*. (2001) capture the nutrient depletion zone along all roots and scale up an analytical solution for a single ordered root to produce an accurate estimate for plant P uptake per soil surface area; extrapolating surface area to produce field scale results.

Wheat (*Triticum aestivum* L.) is a key crop for global food production, with total worldwide yields for 2012 estimated to be 652.17 Mt (USDA, 2013). In this study, the increasingly popular winter wheat cultivar variety 'Gallant' was used to provide the root parameters for the Roose *et al*. (2001) model. This model has been adapted so that different root structural patterns can be simulated and the optimal root branching structure that maximises P uptake determined. To check if a certain root structure will give adequate compensation, the effect of lowering the soil P concentration level will be assessed.

Materials and Methods

Experimental collection of plant parameters

Plant root growth

Given the variability of rooting within crop varieties (Středa *et al*., 2012), and the scarcity of studies quoting such basic root system characteristics, our own cultivar specific set of rooting parameters were produced (Table 1). In all experiments the soils were passed through a 5 mm sieve before use. All plants were grown in a greenhouse maintained at a minimum of 20°C, supplied with artificial lighting providing at least 16 hour days. Experiments were conducted in the UK winter, therefore the temperature and number of daylight hours rarely exceeded these values.

To measure the physical characteristics of the roots required by the model, seeds were planted to a depth of 1 cm in perspex rhizotrons (30 cm × 30 cm × 1 cm) filled with a Eutric

112 Cambisol sandy clay loam textured soil (Abergwyngregyn, UK) which had a high available P
113 content due to repeated long term fertilisation (Olsen P = 33 mg l^{-1} see Jones *et al*. (2004) for
114 further details of the soil). This soil was maintained at 80% water holding capacity by
115 watering three times a week. We used 2-dimensional rhizotrons as these have been shown to
116 be representative of basic root architecture for cereal plants growing unconstrained
117 (Hargreaves, Gregory & Bengough, 2009). The rhizotrons were tilted at a 30° angle to allow
118 visualisation of the root system and measurement of root attributes: root growth of roots
119 growing along the edge of the rhizotrons were measured by monitoring their progress with a
120 ruler, and visible branching angles were measured using a protractor. It should be noted,
121 however, the short length of the second order roots meant that measurement of their growth
122 rate was not possible using this approach. At 21 days after emergence the plants were
123 harvested. The roots were washed thoroughly by hand in distilled water, floated out on water
124 in transparent plastic trays, and scanned using a flatbed scanner (Epson Perfection 4990
125 Photo). The diameter of each root order was then determined, using WinRhizo® software
126 (Regent Instruments Inc., Canada). The inter branch distances, non-branching zone lengths
127 and maximum root lengths were then measured manually for each root system using a ruler.
128 To estimate root hair density and average lengths, 1 cm samples from the centre of each of
129 these washed roots were mounted on slides in 50% glycerol and observed using a light
130 microscope (Axioplan 2; Carl Zeiss Ltd, Cambridge, UK). The number of hairs protruding
131 from each cm section of root as seen when mounted on microscope the microscope slide was
132 doubled to account for half the root not being visible, and then used to define the root hair
133 density for each root order. The length of the root hairs in these sections was measured using
134 the microscope's eyepiece graticule, and then the average for each root order was then used
135 to define the root hair lengths in the model.
136

137 **Rooting responses to P**

138 A key component of the plant physiological response to P is the variation of root production
139 (Drew, 1975). To ensure this would be factored into the model, an experiment was designed
140 to measure the difference in rooting characteristics in low and high P soils. Seeds were
141 incubated in aerated de-ionised water overnight at room temperature and then grown on moist
142 tissue paper until the roots reached ≈5 cm. This represents the start time in the model. These
143 seedlings were then planted in 50 ml centrifuge tubes each containing 55 g of either Morfa
144 Cambisol (low P, Olsen P = 12.6 mg l^{-1}) or Eutric Cambisol (high P, Olsen P = 33.0 mg l^{-1})
145 soils (both Abergwyngregyn, UK), maintained at 80 % water holding capacity, and kept in a
146 greenhouse (as previously described) for 10 days. Despite this being a small mass of soil, the
147 plant available P supply remains significantly greater than the plant's total P demand over
148 such a limited timeframe (Table 2). As the model assumes the relationship of soil solution P
149 to sorped P is at equilibrium, it was decided that using a soil high in native P that was already
150 at equilibrium would provide better high-P model fits than applying soluble P fertiliser to a
151 low-P soil, which would then perturb the sorption equilibrium. After 10 days the plants were
152 harvested and the root systems were washed in water to remove the soil, excised from the
153 remainder of the plant, dried to remove surface water with tissue paper and weighed to assess
154 the differences in root mass between low and high P soil environments (Table 3). The same
155 cultivation method was also used to produce plants with which to measure the impact upon
156 inter-branch distance of order 1 branches in low and high P soils (Table 3): the inter-branch
157 distance measured by scanning each root system using the flatbed scanner (Epson Perfection
158 4990 Photo) and then using the resulting images to measure the distance between each order
159 1 root branch on the seminal roots of each plant.

160

161 **Plant P demand**

To estimate plant P demand, wheat seeds were germinated on moist tissue paper until the roots had reached approximately 5 cm after which the seedlings were transferred to pots containing the high P Eutric Cambisol soil (150 g). Over the next 10 d, plants were sequentially harvested, washed to remove the soil, and dried at 85°C overnight. The plants were then dry-ashed (550°C, 16 h), the residue dissolved in 0.5 M HCl and then their P content determined according to the ascorbate/molybdate blue method of Murphy & Riley (1962).

Soil tests

The relationship between P in solution (c, mol/l) and P held on the solid phase of soil particles (c_s, mol/kg) is described by the soil buffer power (b),

Eqn. 1 $$b = dc_{tot} / dc,$$

for

Eqn. 2 $$c_{tot} = (c \cdot \phi) + (c_s \cdot \rho_b),$$

where ϕ is the soil's volumetric water content ($dm^3\ dm^{-3}$), and ρ_b is the soil bulk density (kg dm^{-3}).

To determine b (a constant used within the mathematical model), c_s and c a sorption isotherm was measured (Barber, 1984). Using varying initial solution concentrations of ^{33}P-labelled KH_2PO_4 (0 to 1 mM; 1 kBq ml^{-1}, American Radiolabeled Chemicals Inc., USA), 5 ml of P solution was added to 1 g air-dry soil, shaken (200 rev min^{-1}, 24 h), centrifuged (16,000 g, 15 min), the supernatant solution mixed with the liquid scintilant Optiphase 'Hisafe' 3 (Perkin-Elmer, Boston, MA, USA), and ^{33}P concentration (c) measured using a Wallac 1404 a liquid scintillation counter (Perkin-Elmer, Boston, MA, USA). The amount of P sorbed to the solid phase (c_s) was calculated by difference. A Langmuir isotherm was then fitted to the experimental data using SigmaPlot v11 (Systat Software Inc., San Jose, CA) to

enable calculation of c, c_s and b for each soil. This was done by using the middle of each Olsen P index band from DEFRA (2010) (Table 4) as the total P (c_{tot}) value for high and low P soils. The corresponding c, c_s and b values for that c_{tot} on the Langmuir isotherm were used as the initial conditions in the model, with b remaining fixed throughout the duration of the experiments.

Statistics applied to experimental data

To test whether means from experimental data are significantly different to each other a two tailed t-test was performed, where $p<0.05$ would yield a positive significance. For two means, x_1 and x_2, with corresponding standard deviations, s_1 and s_2, and sample numbers, n_1 and n_2, equation 3 calculates the value of t,

Eqn. 3

$$t = \frac{\bar{x}_1 - \bar{x}_2}{\sqrt{\left(\frac{(n_1-1)s_1^2 + (n_2-1)s_2^2}{n_1+n_2-2}\right)\left(\frac{1}{n_1}+\frac{1}{n_2}\right)}}.$$

The following assumptions are made; there are two independent samples, the data is normally distributed and the samples have the same variance. Once t is known the degrees of freedom (calculated from $(n_1 - 1) + (n_2 - 1)$) is needed to produce a p value which is then compared to the confidence interval, 0.05 for 5%. If $p < 0.05$ then the means are significantly difference.

Phosphate uptake model

Nye and Tinker (1977) and Barber (1984) have previously modelled nutrient uptake for a single cylindrical root surrounded by an infinite extent of soil, where the nutrient concentration is equal to the farfield nutrient concentration away from the root. Due to nonlinearity in the root nutrient uptake boundary condition, Nye and Tinker (1977) and Barber (1984) were forced to solve the model numerically, which meant that adapting a

single root model to a more realistic root system was computationally expensive. Roose *et al*. (2001) and Roose & Kirk (2009) provide a fully explicit "approximate" analytical solution to the Nye-Tinker-Barber model which enabled a more realistic model that utilises a more complex root branching structure. In all four previous studies (Nye & Tinker, 1977; Barber, 1984; Roose *et al*., 2001; Roose & Kirk, 2009) the uptake of P by roots is represented by Michaelis-Menten uptake kinetics and a convection-diffusion model containing a linear diffusion equation with a nonlinear root surface uptake condition. The rate of convective transport of nutrients is assumed to be negligible relative to diffusion (Jungk & Classen, 1997; Roose *et al*., 2001; Roose & Kirk, 2009). For a complete solution of the convection-diffusion equations for P transport to plant roots see Roose & Kirk (2009). Roose *et al*. (2001) calculate the total uptake of nutrients given an initial set of parameters, which represent the nutrient concentration, water saturation and root parameters, such as length and radius. The analytical solution for the flux of nutrients $F_D(t\ ;\ a)$ into a root of radius a by Roose *et al*. (2001) is given by,

Eqn. 4
$$F_D = \frac{2F_m c}{K_m + c + L + (4cK_m + (K_m - c + L)^2)^{1/2}},$$

with,

Eqn. 5
$$L = \frac{F_m a}{2\phi D} \ln\left(1 + 4e^{-\gamma} \frac{\phi D}{(\phi + b)a^2} t_D\right),$$

where F_m represents the maximum rate of P uptake (μmol cm^{-2} s^{-1}), c is the far field concentration of P in pore water (μmol cm^{-3}), K_m is the Michaelis constant (μmol cm^{-3}), $\gamma \approx 0.5772$ is Euler's constant, ϕ is the water saturation (dm^3 solution dm^{-3} soil), D is the diffusion coefficient of nutrient in pore water (cm^2 s^{-1}), b is the soil buffer power (dimensionless) and t_D represents time (days). The values of these parameters, taken from Roose et *al*. (2001), are presented in Table 5 and it is assumed that the farfield concentration of P is constant within the soil. The model calculates the uptake of P for one zero order root

(as in equation 3.13 in Roose et *al*. 2001), and this is extrapolated to five to account for the number of primary root axes in a developing wheat root system.

To capture the effect of root hairs on nutrient uptake, we will apply the method of Leitner *et al*. (2010b) where 3 different models for nutrient uptake were considered. A dimensionless parameter α is calculated and depending on the morphological and physiological properties of the root hairs 3 scenarios occur. For $\alpha \sim 1$, a concentration gradient dynamically develops within the root hair zone, for $\alpha > 1$, the uptake by root hairs is negligibly small and for $\alpha < 1$, P in the root hair zone is taken up instantaneously. The dimensionless parameter α is given by,

Eqn. 6
$$\alpha = \log_e\left(\frac{dl_{ni}}{DK_m}F_m\right) / \log_e\left(\frac{l_{ni}}{K_i}\right),$$

where d is dimensionless factor that distinguishes between solution culture and soil systems (in the soil culture d=1; in soil d=1/(ϕ +b)), l_{ni} is the distance between two root hairs on the i_{th} order root (cm) and K_i is the i_{th} order root length (cm).

The value of α for zero, first and second order roots is 0.466, 0.703 and 1.477, respectively. For zero and first order roots $\alpha < 1$, which means root hairs effectively extend the root radius by the root hair length. For second order roots $\alpha > 1$, which means the roots hairs have a small uptake compared to the roots and are neglected. Experimental data showed root hairs appearing everywhere on all ordered roots and as a result, increased root radius occurred over the entire root length.

Equation (4) is used to construct a model for the nutrient uptake of a plant root system. The root system consists of a distribution of roots of radius a and length l. Figure 1 shows the layout of the root structure where the top section of the root is labelled l_b and the bottom section l_a, which are the non-branching zones. The main root is called 0 order, side branches of this are called 1st order and so forth. The root system branches by creating smaller side

253 roots between the non-branching zones l_b and l_a, and this starts commencing when the
254 original root reaches the length l_b+l_a. Given a root of length l, there are $[(l-l_a-l_b)/l_n]_+$ branches,
255 where l_n is the interval for each branching root.
256 Different order growing roots will have different radii a_i, and will grow at different rates $L_i(t)$.
257 The elongation of roots of order i decreases with age and is described by,

Eqn. 7
$$\frac{dl}{dt} = L_i = r_i\left(1 - \frac{l}{K_i}\right),$$

258 where l is the length of the root (cm), r_i is the initial rate of growth (cm d^{-1}) and K_i is the i_{th}
259 order root length (cm).

260 The Roose *et al*. (2001) model uses a constant branching rate to define root
261 architecture, thereby creating an even branching distribution. To change the root architecture
262 we replace the constant value by a root branching distribution parameter, which interpolates
263 between an even branching distribution and one which exponentially decreases in root length
264 density down the soil profile. An exponential branching distribution is used where the same
265 final volume of roots is grown; however, it creates a root system where top soil foraging is
266 maximised (Varney *et al*., 1991). This also matches observations of root proliferation in top
267 soils (0-30 cm) when fertilisers are strategically placed (McConnell, Sander & Peterson,
268 1985). The exponential branching distribution (G, the number of roots per cm) is described
269 by,

Eqn. 8
$$G = Ae^{-Bl},$$

270 where two variables define the branching structure, A (cm^{-1}) denotes the maximum density
271 distribution (i.e. the maximum number per cm) and B (cm^{-1}) denotes how density decays
272 towards the tip of the main root l. For example, at a linear branching rate of 0.7 cm we set
273 A=1/0.7 cm^{-1} and B=0 cm^{-1}.

The branching points are calculated by first varying l between 0 and d, where d is the length of the final branching zone along the main root. Secondly, the total area created by the curve in equation (8) from l=0 to l=d is calculated. Thirdly, a point l such that the area covered by the curve from l=0 to l=l_1 is calculated to be equal to the total area divided by the number of branching roots. The next point l_2 is chosen such that the area created between the two points l_1 and l_2 is the same as between 0 and l_1. Finally, continuing this approach will generate an equal number of branching roots, but the distribution will be exponential rather than linear.

The two parameter family in equation (8) can be reduced to a single parameter if the total final length of the root system is kept the same. This simplifies the fitting process, discussed in section 'Model validation and optimisation', as fewer parameters reduce the search space and thus the computational time of the model. The method is described in the set of equations below, which begins with the total number of roots N_i, which are in the length range $(0,d_i)$ for root order i.

Eqn. 9
$$\int_0^{d_i} Ae^{-Bl}\,dl = N_i.$$

Simplifying and solving equation (9) for A produces,

Eqn. 10
$$A = -\frac{N_i B}{e^{-Bd_i} - 1},$$

which generates the root branching distribution G that conserves the final size of the root system, just in terms of the new variable B.

Eqn. 11
$$G = \frac{N_i B}{1 - e^{Bd_i}} e^{-Bl}.$$

The values of d_i are prescribed to be equal to 100 cm and 7.9 cm for the main root and order 1 root, respectively, and N_i equal to the number of roots for each given order calculated from the experimental data presented in Table 1. The chosen variable B will be bounded, such that at its minimum, 0 cm^{-1}, the root branching is linear and at its maximum, 10 cm^{-1}, the root

295 branching is exponential and almost all the side roots branch at the top of the branching zone.
296 Figure 2 shows the root structure (with only 50 side roots for simplification) for the cases
297 where B is 0, 5 and 10 cm^{-1} and the different initial branching scenarios can be clearly seen
298 between Figure 2a (B=0 cm^{-1}) and 2c (B=10 cm^{-1}). The minimum branching distance
299 measured from the experimental data (0.067 cm) was also set as the minimum branching
300 distance in the model, i.e. at the upper bound when B=10 cm^{-1}. As we assume there is a
301 constant P concentration within the soil, every root is therefore given their own depletion
302 zone which does not overlap with others within the time frame.

303 For modelling purposes the growth angles of the roots in our experiments are not used,
304 all other values in Table 1 are used in the model. This is due to the fact that the initial P
305 concentration in the soil is constant, and roots will achieve the same uptake from any position;
306 it is therefore sufficient to just calculate the time at which a root started growing. This
307 simplification in the root system is justified by the comparison made in Leitner (2010a),
308 where the P uptake from the roots in the Roose *et al*. (2001) model was shown to be
309 comparable to the one of a 3D plant root system.

310 The second order roots are experimentally shown to grow where the density of root
311 mass is greatest rather than in a linear or exponential distribution. The greatest density of
312 second order roots on a first order branch was experimentally calculated to be 1.153 second
313 order roots per mm. Therefore the second order roots were modelled such that there were a
314 greater number of branches at higher density areas with the greatest density capped at 1.153
315 roots per mm. This distribution can be seen in Figure 3 where the position of the second order
316 roots is affected by the exponential distribution of the first order roots. In the linear branching
317 distribution case all of the root branches are constant whereas for the exponential branching
318 distribution case, the majority of second order roots appear nearer the top of the plant as there
319 is a greater density of roots there.

Results

Model parameterisation

The experimentally derived values for wheat root characteristics for 0, 1st and 2nd order roots are summarised in Table 1. Significant differences were apparent for all characteristics for the different root types, except for 'root angle on lower ordered root'. We used these values to parameterise the model to estimate the P uptake for different root branching distributions in soil possessing two contrasting P contents, 35.5 mg l^{-1} (high P) and 12.5 mg l^{-1} (low P)(Table 4).

Experimental analysis showed that the biomass of roots grown in a low P soil was reduced on average by 45% in 10 day-old plants compared to those grown in a high P soil, and yielded a significant difference ($P < 0.05$; *Table* 3). However, the inter-branch distance for the emergence of first order roots was not significantly greater when the roots were grown in a high P environment ($P > 0.05$; Table 3). To capture this P-induced change in root architecture within the model, the simulation scenarios for the low P soil had the maximum root length for all order roots capped to match the experimental data. To determine the impact of this capping, simulations were undertaken with both reduced and constant root mass. The effects of a reduced root mass could present problems with current plant nutrition strategies, and perhaps placement of nutrients could produce greater yields (Randall and Hoeft, 1988).

Model simulations

Figure 4 shows the model predictions of plant P uptake across a range of P concentrations within the soil for the different root branching distributions. For a given line of constant branching distribution, there is a linear relationship between P concentration and P uptake (R^2

344 = 1 due to the model being deterministic). However, for the line of constant P concentration,
345 there is non-linear relationship between branching distribution and P uptake.

346 Three scenarios in particular were studied; a linear branching distribution in a low and
347 high P soil and an exponential branching distribution in a low P soil. For each of these
348 scenarios our model estimated the amount of P uptake by the whole root system (Fig. 5). In
349 the high P soil, the model predicted that the plant would acquire 183% more P than a plant
350 grown in the low P soil. When the root branching distribution was changed from a linear to
351 an exponential pattern the model predicted that this improved plant P uptake by 142% in the
352 low P soil. This represents a reduction of 14.5% in comparison with plants grown in a high P
353 soil with a linear branching pattern.

354 The results for cumulative P uptake for the 3 root branching scenarios over a 90 d
355 crop growth period are shown in Figure 5a. The end time of 90 d was chosen as it gave
356 suitable long term behaviour for wheat growth. For the majority of the time period, up to
357 around 65 d, the exponential branching distribution in a low P soil (green-dashed) possessed
358 the greatest P uptake even when compared with the linear branching distribution in a high P
359 soil (red-solid). This is due to the fact that the side roots emerge earlier and therefore there is
360 a greater surface area to enable earlier P uptake. After 65 d, the linear branching distribution
361 in a high P soil catches up with and overtakes the exponential branching distribution in a low
362 P soil and can take advantage of the rich P environment. The shape of the P uptake curve is
363 defined by the branching distribution. In both linear root branching examples (red-solid and
364 blue-dotted) there is smooth hinge shape curve, however in the exponential root branching
365 example (green-dashed) a saturation growth curve is observed, which is expected as the root
366 system grows to its full length.

367 With the negative effect of reduced root mass in the low P soil (Fig. 5b), the
368 difference between the low and high P soil was magnified. Plant P uptake for the exponential

branching distribution in a low P soil (green-dashed) fell by 74% compared to when the root system growth was not capped (Fig. 5a) and matches a linear exponential branching distribution with an effective Olsen P index of 3.7 (39 mg l^{-1}). Changing from a linear to an exponential branching distribution improves P uptake by 151% in the low P soil, but this is a large decrease of 78% when compared with a high P soil using a linear branching pattern; which is expected given the large reduction in root mass.

Model validation and optimisation

The estimated P uptake from our model was compared with the experimental data collected for a root system grown in a high and low P environment (Table 2, Fig. 6). The parameter for the root branching structure, B, was fit to minimise the sum of squares difference between our model and the experimental data. The estimated total plant P uptake fits well with experimental data within the initial 10 d of growth; for the comparisons, high P with B=1.5 cm^{-1} and high P data, and low P with B=7 cm^{-1} and low P data. The scenario for a low P soil with B=7 cm^{-1} is not enough to capture the effects of the experimental high P uptake, because it is difficult to overcome the 45% reduced root mass and beyond the 10 day mark this difference is amplified.

Discussion

The important question that needs addressing is how alteration of root system architecture could (by breeding or genetic manipulation) produce greater P uptake. To that end, the model by Roose *et al*. (2001) has been adapted by introducing a parameter that changes the root branching distribution. Our model has two parameters that we will directly manipulate, the nutrient concentration in the soil c and the root branching distribution parameter B. By

393 looking at the effect of changing the P level against the root branching distribution, by
394 altering *c* (Table 4) and *B*, the P uptake is estimated.

395 Our study estimated the P uptake using our experimental soil and plant parameters
396 found in Table 1. Our model is adapted from Roose *et al*. (2001) such that the branching
397 density distribution is allowed to change from linear to exponential, to see the effects that
398 root structure with different P concentrations in the soil, has on P uptake. Three scenarios
399 were considered, a high and low P concentration level with a linear branching distribution
400 and a low P concentration with an exponential branching distribution. In these scenarios the
401 effect of reduced root mass in low P soils is considered, as seen in our experimental results.
402 The experimental P uptake (Table 2, Fig. 6) fits best with a weak exponential root branching
403 distribution for P3 data, which can be seen for certain crops. A shift towards increased early
404 lateral rooting has previously been shown experimentally to increase P uptake efficiency
405 (Zhu & Lynch, 2004), and this scenario is successfully captured in the model. The strong
406 exponential branching modelled here is however more aggressive than our data suggests and
407 is currently seen within wheat root developmental plasticity. Perhaps breeding varieties to
408 adopt this rooting strategy would be limited by carbon availability from photosynthesis.
409 Although our model simulates a uniform soil P profile, that top soil foraging has been shown
410 to be an essential component of plant P acquisition (Zhu, Kaeppler & Lynch, 2005), provides
411 further emphasis upon the need to produce lateral roots early in the plant's growth; helping to
412 improve root-foraging strategies (Richardson *et al*., 2011). By modelling a non-uniform soil
413 P profile (Roose and Fowler, 2004) a better fit to the data could be achieved, given necessary
414 depth dependent data of available soil P. This is the subject of our follow on work which will
415 be published separately.

416 Our model shows that changing the root structure of the plant, to produce more lateral
417 roots earlier, has a positive effect on the uptake and can help plants survive in lower

phosphate environments. This is corroborated by previous experimental approaches (Zhu & Lynch, 2004). On average a 147% increase in P uptake is achieved from having a highly exponential root branching distribution over a linear one. However this positive increase is not enough to completely overcome the difference between a high and low P soil environment. Therefore, although increasing early lateral root production will enhance P uptake, other plant and fertiliser based strategies would be required to produce the required yields at low soil P levels. For example, an increase to all root lengths of all orders in combination with the exponential root branching distribution is sufficient, as only an 8% improvement is needed to match an exponential branching distribution in a low P soil, with a linear branching distribution in a high P soil (without accounting for the reduced root mass in a low P soil).

The exponential branching distribution however does provide greater early P uptake in low P soils when compared to linear branching root systems grown in high P (Figure 4a). Early growth, and yield size, have been shown to be most significantly correlated with early P uptake levels (Boatwright and Viets, 1966; Brenchley, 1929; Grant et *al*., 2001; Green et *al*., 1973), and greater early P uptake, and the corresponding early vigour seedlings display is also viewed by industry as insurance against problems which may occur in the growing period such as adverse weather conditions. Vigorous early growth also provides quicker soil surface cover, and therefor is useful in the reduction of soil erosion which can be a significant driver of environmental problems, and loss of P from agricultural systems (Pimentel et *al*. 1995). The diminished uptake that exponential branching in low P displays over linear branching in high P could still potentially impact final yields, where P-uptake from the environment is still required to augment grain filling (Boatwright and Hass, 1961; Grant et *al*., 2001; Mohamed and Marshall, 1979), and also to facilitate carbohydrate translocation into the ripening grain (Sutton et *al*., 1983). However, such a small difference in final P uptake

443 could potentially be met by a small targeted application of P late in the growing season,
444 whilst still allowing for significantly lower application rates of P fertiliser than in current
445 systems. The enhanced effectiveness of the exponential branching distribution provides an
446 insight into the potential benefits possible from crop breeding (Figure 4a). The extent of the
447 wheat root system already varies significantly between varieties (Středa *et al*., 2012), and
448 plant breeding efforts have been made to use plant breeding to produce cultivars with an
449 enhanced ability to acquire P (Gahoonia & Nielsen, 2004). Significant improvements in crop
450 growth and output have been demonstrated to be possible from targeted breeding to improve
451 varieties (Siddique et al., 1989), therefore a re-profiling of root branching distribution is
452 potentially possible, and could drive an increase in crop P-acquisition. Additional and more
453 rigorous experiments would need to be undertaken to properly validate possible improved
454 root structures and their effects in high and low P soil. Given the variations in root system
455 size present in commercially available wheat varieties (Středa *et al*., 2012), a targeted
456 breeding programme has the potential to provide a range of root architectural variations
457 which may prove to be more suited to low P soils. Furthermore, other parameters from Table
458 1, such as root hair dynamics, could be re-calculated to find possible differences between
459 high and low P soils.

460 Due to the root structure being diminished in a low P environment we implemented
461 the reduced root mass scenario. The difference between the high and low P soils generated a
462 substantial 45% root mass decrease after 10 days which heavily affected the P uptake values
463 in the low P environment. In a low P environment, targeting P close to early root growth
464 (seed dressing or placement of fertiliser in bands 5 cm down from seed) is emphasised as
465 even more essential due to the fact that the plant's ability to search out P in a low P soil is
466 severely limited by the smaller area of soil the root system can cover.

467 This paper provides modelling basics towards the development of whole plant
468 nutrient uptake models, by assessing what root structures are needed for given concentrations
469 of P in the soil to maximise plant P uptake.
470
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480
481
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606 **Tables**

607 **Table 1** Experimental values for nine wheat root characteristics for 0, 1st and 2nd order roots
608 used in the mathematical modelling. The only non-significant values are between the root
609 angles for 1st and 2nd order roots.

	Units	0 order root	1st order root	2nd order root
Growth rate	mm day^{-1}	15.83 ± 5.2^{a}	8.97 ± 2.6^{b}	4.00*
Inter-root branch distance	mm	n/a	3.64 ± 2.2^{a}	2.44 ± 1.3^{b}
Root diameter	mm	0.516 ± 0.090^{a}	0.229 ± 0.037^{b}	0.192 ± 0.049^{c}
Length of no branching zone	mm	43 ± 8^{a}	12.2 ± 3.4^{b}	n/a
Tip to root hair distance	mm	0.48 ± 0.15^{a}	0.0615 ± 0.037^{b}	0.376 ± 0.20^{c}
Root angle on lower ordered root	degrees	n/a	60.6 ± 9.0^{a}	63.8 ± 14.7^{a}
Number of root hairs on root	cm^{-1}	202 ± 52^{a}	250 ± 63^{b}	444 ± 120^{c}
Root hair length	mm	0.59 ± 0.25^{a}	0.49 ± 0.13^{b}	0.43 ± 0.11^{c}
Length of root	mm	1000**	79	2.8

610 Values represent means ± SD and those bearing the same alphabet are not significantly
611 different within a row. *Result estimated from experimental data which is consistent with
612 Pagès *et al*. (1989). **Result taken from Sylvester-Bradley *et al*. (1997).
613 **Placement:** Materials and Methods – Plant root growth – line 109.
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Table 2 Experimentally-derived average P uptake (μmol plant^{-1}) measured over the 10 day growth period after sowing, for high and low P soil environments. After 10 days the P uptake values become significantly different, for a two tailed test with $P<0.05$.

Days after sowing (initial root length was between 10 and 15cm over 3 roots)	0	1	2	4	6	8	10
Low P average uptake (μmol P plant^{-1})	0^{a}	0.058^{a}	0.14^{a}	0.37^{a}	0.79^{a}	1.3^{a}	2.1^{a}
Standard Deviation (μmol P plant^{-1})	n/a	0.19	0.35	0.34	0.37	0.54	0.49
High P average uptake (μmol P plant^{-1})	0^{a}	0^{a}	0.12^{a}	0.70^{a}	1.5^{a}	2.1^{a}	3.2^{b}
Standard Deviation (μmol P plant^{-1})	n/a	0.051	0.28	0.24	0.26	0.12	0.29

Means bearing the same alphabet are not significantly different within a column.

Placement: Materials and Methods – Rooting responses to P – line 160.

Table 3 The average inter-root branching distances of first order roots and masses of fresh weight roots for high and low P soil environments. The average root mass was significantly different between high and low P, whereas the average inter-root branching distance was not.

	Low P	High P
Average inter-root branching distance (mm)	4.2 ± 2.4 [a]	3.7 ± 1.7 [a]
Average root mass (mg per plant)	586 ± 141.7 [a]	313 ± 117.1 [b]

Values represent means ± SD and those bearing the same alphabet are not significantly different within a row.

Placement: Materials and Methods – Rooting responses to P – line 160.

662

663

664 **Table 4** Relationship between the DEFRA (2010) agronomic index values for available soil P
665 measured using the Olsen $NaHCO_3$ extract method and actual levels in the soil and soil
666 solution (P_{sol}).

667

DEFRA agronomic index value	P (mg l^{-1})	P (mmol l^{-1})	$P_{sol}=c$ (μmol l^{-1})
Index 0 (very low P)	0-9	0 – 0.2903	0 – 12.3
Index 1 (low P)	10-15	0.3226 – 0.4839	13.7– 20.5
Index 2 (moderate P)	16-25	0.5161 – 0.8065	21.9 – 34.2
Index 3 (high P)	26-45	0.8387 – 1.4516	35.6 – 61.6

668 P_{sol} is equivalent to the concentration of nutrients in pore water c and is dependent upon the
669 soil buffer power b and the water saturation (ϕ).

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671 **Placement:** Materials and Methods – Soil tests – line 190.

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Table 5 Soil and nutrient uptake parameters, with values and units.

Parameter	Description	Value	Unit
ϕ	Soil volumetric water content	0.3	L solution L soil^{-1}
D	P diffusion coefficient in pore water	0.3×10^{-5}	cm^2 s^{-1}
b	P buffer power in soil	239	-
F_m	Maximum rate of root P uptake	3.26×10^{-6}	μmol cm^{-2} s^{-1}
γ	Euler's constant	0.5772	-
K_m	Michaelis constant for root P uptake	5.8×10^{-3}	μmol cm^{-3}

Placement: Materials and Methods – Phosphate uptake model – line 232.

701 **Figure Legends**

702 **Figure 1** Branching structure of a root system, with non-branching zones l_a and l_b, and inter-
703 root branch distance l_n. The main root, order 0, branches order 1 roots which in turn branch
704 order 2 roots.

705

706 **Figure 2** The simulated root structure (with only 50 order 1 roots for simplification) for 3
707 different branching distributions; a) shows a linear branching distribution (B = 0 cm^{-1}), b)
708 shows a slight exponential distribution (B = 5 cm^{-1}), and c) shows a strong exponential
709 distribution (B = 10 cm^{-1}).

710

711 **Figure 3** The root distribution of order 2 roots; a) shows the distribution of order 2 roots for a
712 linear branching distribution of order 1 roots, and b) shows the distribution of order 2 roots
713 for an exponential distribution of order 1 roots. The greater the exponential distribution the
714 denser the order 2 roots become.

715

716 **Figure 4** Model estimates for whole plant P uptake (μmol P plant^{-1}) for different branching
717 distributions (B) and initial soil P concentrations. At B = 0 we have a uniform branching
718 distribution and for increasing values of B we have more concentrated branching at the top of
719 the soil profile.

720

721 **Figure 5** Predicted cumulative plant P acquisition for three root branching scenarios, a linear
722 branching distribution in a high and low P soil and an exponential branching distribution in a
723 low P soil; Panel (a) shows P uptake when the final volume of roots is conserved, while panel
724 (b) shows P uptake where there is a 45% reduced root biomass after 10 days for the low P
725 scenarios.

726

727 **Figure 6** Experimental and model values for the cumulative uptake of P by wheat seedlings
728 over a 10 d period when grown in high and low P soil for a range of root branching
729 distributions. The model values comprise of, a high P soil with a weak exponential
730 distribution (B = 1.5 cm^{-1}), and a low P with a strong exponential distribution (B = 7 cm^{-1}).