



Imaging the interaction of roots and phosphate fertiliser granules using 4D X-ray tomography

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1 **Use of a coupled soil-root-leaf model to optimise phosphate fertiliser use efficiency in barley**

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11 **Abstract: (200192/200)**

12 *Aims* Phosphorus (P) is an essential nutrient necessary for maintaining crop growth, however, it's
13 often used inefficiently within agroecosystems, driving industry to find new ways to deliver P to
14 crops sustainably. We ~~consider a precision agriculture approach which aim to~~ combine traditional
15 soil and crop measurements with climate-driven mathematical models, ~~that can to~~ optimise the
16 timing and placement of fertiliser applications.

17 *Methods* The whole plant crop model combines an above-ground leaf model with an existing
18 spatially explicit below-ground root-soil model to estimate plant P uptake and leaf mass. We let P-
19 dependent photosynthesis estimate carbon (C) mass, which in conjunction with temperature sets
20 the root-growth-rate.

21 *Results* The addition of the leaf model achieved a better estimate of two sets of barley field trial data
22 for ~~leaf mass and~~ plant P uptake, compared with just the root-soil model alone. Furthermore,

23 discrete fertiliser placement increases plant P uptake by up to 10% in comparison to incorporating
24 fertiliser.

25 *Conclusions* By capturing essential plant processes we are able to accurately simulate P and C use
26 and water and P movement during a cropping season. The powerful combination of mechanistic
27 modelling and experimental data allows physiological processes to be quantified accurately and
28 useful agricultural predictions for site specific locations.

29 **Keywords** Mathematical modelling, phosphate, phosphorus, fertiliser strategy, barley field study,
30 above and below ground

31 **Introduction**

32 The world-wide production of food has increased due to the demands of an ever expanding global
33 human population (Brown, 2012). Due to the lack of land available for agricultural expansion, there
34 is a need to increase yields sustainably by manipulating the existing environment in which crops are
35 grown, and breeding more resource efficient crops. Resource management for arable farming
36 systems is critical to the survival of the human population and large amounts of money and time are
37 needed to elicit the appropriate improvements (Conway and Barbier, 1990).

38 Phosphorus (P) is one of the essential nutrients required for plant growth and plays an important
39 role in photosynthesis, respiration, and seed and fruit production.

40 We are interested in how crops grow and survive in low P environments and how fertiliser and soil
41 cultivation methods are influencing crop performance. A number of studies have considered the
42 response of adding different amounts and rates of fertiliser P; in some soils large effects are seen
43 whereas no effect is seen in others (Bolland and Baker, 1998; Kuchenbuch and Buczko, 2011;
44 Valkama et al., 2011). There are many ways one could apply P to soils; for example incorporating
45 (also known as broadcasting, involves an even spreading of P on top of the soil), placing (also known
46 as banding, involves injecting P into the soil nearer the rooting zone either in row or between rows)

47 or as a coating on seeds. Studies have shown that injecting fertiliser into the soil nearer to the root
48 zone (placing) increases plant P uptake compared to incorporated P (Randall and Hoeft, 1988; Lohry,
49 1998; Owusu-Gyimah *et al.*, 2013). In addition, studies have been conducted to estimate the
50 differences in soil cultivation methods on plant P uptake; for example, conventional plough *versus*
51 minimum tillage (also considering gene variation, George *et al.*, 2011). The idea behind ploughing is
52 to turn over or mix the top 25 cm of soil to loosen the soil for seeding, bury any existing crop
53 residues or weeds, and to provide a good distribution of nutrients for the coming crop. This is in
54 contrast to minimum tillage which enhances topsoil stability against erosion, retains moisture and
55 reduces crop establishment costs, but segregates P content with depth and can leave 30% of crop
56 residue on the soil surface.

57 Due to the rising cost of fertilisers and agricultural machinery, crop production has become a multi-
58 objective optimisation problem to minimise multiple costs while trying to maximise the crop yield
59 and environmental impact of fertilisers. This is a complex problem due to varying climatic conditions,
60 an abundance of technological machines, and availability of more data concerning the states of
61 fields than ever before. Precision agriculture is an emerging field involved with combining the
62 newest technologies to the farming industry, ranging from unmanned drone maps of fields to
63 computer-assisted tractors (Blackmore, 2014). This new technology is enabling automated real time
64 decision making, applying the most effective treatment to crops at the best time for the best price.
65 Mathematical models, supported by experimental data, are needed to help predict best decisions in
66 the short term, and also strategically, to optimise between possible future options. Whilst such
67 models are ~~seldom-not always commercially usedemployed at present~~, their potential capabilities
68 are attractive, given that field-scale experiments are both costly and time-consuming, and
69 integration and dissemination of their empirical results is challenging (Selmants and Hart, 2010;
70 Jeuffroy *et al.*, 2012; Sylvester-Bradley, 1991).

71 A plethora of models exist that describe the processes involved in plant growth and the behaviour of
72 nutrients and water in the soil. Each model has its own unique assumptions and is generally targeted
73 at specific scientific problems within the area of agriculture. For example, Greenwood *et al.* (2001)
74 developed a dynamic model (PHOSMOD) for the effects of soil P and fertiliser P on crop growth, P
75 uptake and soil P in arable cropping;- Jones *et al.* (2003) describe a decision support system for
76 agrotechnology transfer (DSSAT) which focuses on average plant-environment interactions; and
77 Keating *et al.* (2003) review an agricultural production systems simulation (APSIM) developed in
78 CISRO, Australia which deals with water, N, P, pH, erosion and management issues. At the beginning
79 of the 21st century, modelling 3D architectures of plant roots (RootBox, ROOTMAP, SimRoot,
80 RootTyp, SPACSYS, R-SWMS) has become popular (Dunbabin *et al.*, 2013). In addition, two research
81 groups that model above ground 3D plant structures, Prunskiewicz Algorithmic Botany group at
82 the University of Calgary and the Andrieu group (ADEL-wheat model), both use L systems to simulate
83 the above ground structure of wheat plants. L systems, introduced by Lindenmayer in 1968,
84 represent a string of production rules that are used to create geometric structures, ideal for plant
85 development. However all these models do not describe the root-soil interaction explicitly and do
86 not fully integrate functions that occur above ground with ones that occur below ground. Therefore
87 plants of the same genotype are represented alike and phenotypic differences cannot be observed.
88 We hope to address some of these problems by creating a model that links the above and below
89 ground processes in such a way that they rely on one another. Our whole crop model is based on a
90 below ground plant-soil interaction model (Roose and Fowler, 2004b; Heppell *et al.*, 2015) coupled
91 with an above ground leaf growth model based on the seminal work of Thornley (1995).

92 Here we describe a whole crop model that includes a below-ground root model and an above-
93 ground leaf model and which is validated against experimental data on barley with a varying P
94 fertiliser scenario analysis. The development of the model is seen as a step-change in our
95 computational capability to help predict soil P supply, crop P uptake patterns and fertilizer
96 requirements.

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97 **Materials and Methods**

98 **Experimental data**

99 Two barley field trial data sets are used, consisting of leaf mass and plant P uptake values at
100 different growth stages (GS31, GS45 and GS91 for spring barley; GS39 and GS92 for winter barley).

101 The experimental data includes different rates of P application (0, 5, 10, 20, 30, 60, 90 kg P ha⁻¹ for
102 spring barley; 0, 15, 30, 60, 90, 120 kg P ha⁻¹ for winter barley) and both sites were classified with an

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103 Olsen P index 1 soil. -The protocol for this is described in Heppell *et al.* (2015). In addition, we use
104 the climate data, from the UK Met office Integrated Data Archive System (MIDAS), to accompany the
105 spring barley (Inverurie, Scotland) and winter barley (Cambridge, England) data sets for the specific
106 fields in the trial. The climate data consists of daily values for mean temperature (°C), rainfall (mm),
107 wind speed (m s⁻¹) and humidity (%).

108 **Modelling the whole crop**

109 In this paper we extend a root-soil model (Roose and Fowler, 2004b; Heppell *et al.*, 2015) which
110 estimates plant P uptake, with an above ground model which estimates leaf mass (based on
111 Thornley, 1995), to produce a whole crop model. We first describe the root-soil model (hereafter
112 called the root model), followed by the leaf model and then our coupling process to create a whole
113 crop model.

114 **Root and soil model**

115 To model the root system we follow the same approach as described in Roose *et al.* (2004b) and
116 Heppell *et al.* (2015) by modelling two orders of root branches only (main and first order branches).
117 First order roots branch off the main order roots at a given density (ψ_1), branching angle (θ), and
118 each order of roots has a given maximum length and radius (L_0, L_1 and a, a_1 for main and first order
119 roots, respectively). As in Roose *et al.* (2004b) and Heppell *et al.* (2015) we let the root growth slow

120 down as the root becomes longer. Following Heppell *et al.* (2015) we also let the root growth rate (r)
121 be dependent upon temperature T ,

122 Eqn. 1
$$\frac{\partial l_i}{\partial t} = r(T(t)) \left(1 - \frac{l_i}{L_i}\right),$$

123 where l_i is the current length of an order i root and L_i is the maximum length of an order i root.

124 The root-soil model is described by the following two equations for water saturation (Eqn. 2) and P
125 (Eqn. 3) concentration respectively,

126 Eqn. 2
$$\phi \frac{\partial S}{\partial t} = \nabla \cdot [D_0 D(S) \nabla S - K_S k(S) \hat{\mathbf{k}}] - F_w(S, z, t),$$

127 Eqn. 3
$$\frac{\partial}{\partial t} [(b + \phi S)c] + \nabla \cdot [c\mathbf{u}] = \nabla \cdot [D_f \phi^d S^d \nabla c] - F(c, z, t),$$

128 where the water flux in the soil, \mathbf{u} , is given by Darcy's law,

129 Eqn. 4
$$\mathbf{u} = -D_0 D(S) \nabla S + K_S k(S) \hat{\mathbf{k}}.$$

130 In the above equations S is the relative water saturation given by $S = \phi_1 / \phi$, ϕ_1 is the volumetric
131 water content, and ϕ is the porosity of the soil. D_0 ($\text{cm}^2 \text{day}^{-1}$) and K_S (cm day^{-1}) are the parameters
132 for water 'diffusivity' and hydraulic conductivity, respectively (Van Genuchten, 1980). $D(S)$ and
133 $K(S)$ characterize reduction in water 'diffusivity' and hydraulic conductivity in response to the
134 relative water saturation decrease, where the functional forms for partially saturated soil are given
135 by Van Genuchten (1980). $\hat{\mathbf{k}}$ is the vector pointing vertically downwards from the soil surface and F_w
136 is the water uptake by the plant root system per unit volume of soil as given by Roose and Fowler
137 (2004a).

138 For the total P conservation (Eqn. 3), c is the P concentration in soil pore water, b is the soil buffer
139 power characterising the amount of P bound to the soil particle surfaces, D_f is the P diffusivity in
140 free water and d is an impedance factor; $1 \leq d \leq 3$ (Barber, 1984; Nye and Tinker, 1977). $F(c, S, t)$
141 describes the rate of plant P uptake by a root branching structure (Roose *et al.*, 2001). Both F_w and F

142 are affected by the spatially and temporally evolving root structure. Water is only taken up by the
 143 main order roots while P is taken up by all roots; see Roose and Fowler (2004b) for details of the
 144 derivation. The equation for F_W is given by,

145 Eqn. 5
$$F_W = \frac{2\pi a_1 k_r + (2\pi a_1 k_r k_z)^{\frac{1}{2}} \psi_1(z)}{\pi(a+L_1 \cos\theta)^2} [-p_c f(S) - p_r],$$

146 where ψ_1 is the density of first order roots on the main order roots, a_1 is the first order root radius,
 147 a is the main order root radius, L_1 is the maximum length of the first order branches, θ is the angle
 148 between the main root and the first order branches, k_r is the root radial water conductivity
 149 parameter ($\text{m s}^{-1} \text{Pa}^{-1}$), k_z is the root axial hydraulic conductivity calculated using Poiseuille law (m^4
 150 $\text{Pa}^{-1} \text{s}^{-1}$), p_c (Pa) is a characteristic suction pressure determined from experimental data for different
 151 types of soil, $f(S) = (s^{-1/m} - 1)^{1-m}$, where m is the Van Genuchten soil suction parameter (where
 152 $0 < m < 1$), and p_r is the root internal xylem pressure (Pa).

153 Root internal xylem pressure (p_r) is calculated by balancing radial and axial fluid fluxes inside the
 154 root, i.e. after Roose and Fowler (2004a) we have,

155 Eqn. 6
$$2\pi a k_r (-p_c f(S) - p_r) = -k_z \frac{\partial^2 p_r}{\partial x^2},$$

156 with two boundary conditions; an impermeable root tip (Eqn. 7) and a root internal pressure (P) at
 157 the base of the zero order root (Eqn. 8),

158 Eqn. 7
$$\frac{\partial p_r}{\partial x} = 0 \text{ at } x = L,$$

159 Eqn. 8
$$p_r = P \text{ at } x = 0,$$

160 where P is a function of temperature (T), humidity (H) and a base line pressure (p_r^0) for fitting
 161 parameters λ_1 , λ_2 and λ_3 (see Heppell *et al.*, 2014 for the procedure to estimate them), i.e.

162 Eqn. 9
$$P = (p_r^0 + \lambda_3) + \lambda_1 T + \lambda_2 H.$$

163 The rate of plant P uptake is given by,

164 Eqn. 10
$$F(c, z, t) = \frac{F_0 + F_1}{\pi(a + L_1 \cos \theta)^2},$$

165 where F_0 and F_1 are the uptake rates for zero and first order roots derived in Roose *et al.* (2004b).

166 The boundary conditions to accompany Equations 1 and 2 include a soil surface boundary condition
167 for water,

168 Eqn. 11
$$-D_o D(S) \frac{\partial S}{\partial z} + K_S k(S) = W_{dim} \text{ at } z = 0.$$

169 W_{dim} (the flux of water into the soil) is dependent upon rainfall (R), humidity (H), temperature (T),
170 wind speed (WS) and a constant (E) which sets a base line flux i.e.

171 Eqn. 12
$$W_{dim} = \delta R + \alpha H + \beta T + \gamma WS + E,$$

172 for fitting parameters δ , α , β and γ (see Heppell *et al.*, 2014 for how these values were estimated).

173 In addition, we have a boundary condition for the concentration of P (c) at the soil surface,

174 Eqn. 13
$$-D_f \phi^d S^d \frac{\partial c}{\partial z} + W_{dim} c = 0 \text{ at } z = 0, \text{ for } t > 0.$$

175 We set a zero flux at the bottom of the soil (l_w) for both P and water,

176 Eqn. 14
$$-D_o D(S) \frac{\partial S}{\partial z} + K_S k(S) = 0 \text{ at } z = l_w,$$

177 Eqn. 15
$$-D_f \phi^d S^d \frac{\partial c}{\partial z} = 0 \text{ at } z = l_w.$$

178 The initial state of P concentration and water saturation in the soil is given where possible by the
179 initial soil data for the spring and winter barley experimental sites. A uniform water saturation
180 profile is initially set at $S = 0.3$ for the two experimental sites; however for the initial P
181 concentration ($c_0(z)$) we consider two different cases; (1) a uniform concentration and (2) an
182 exponentially decaying concentration:

183 Eqn. 16

$$\begin{aligned} (1) \quad c_0(z) &= c_A \quad \text{at } t = 0, \forall z \\ (2) \quad c_0(z) &= A_1 e^{-B_1 z} \quad \text{at } t = 0, \forall z' \end{aligned}$$

184 where c_A is set to 16 mg P l⁻¹, A_1 is the P concentration at the top of the soil (23 mg P l⁻¹) and B_1 is
 185 the strength of the decay in the concentration of P (0.345). The initial P concentration values (C_A ,
 186 A_1 and B_1) come from a best fit to the data sets in Heppell et al., (2015) and are both classified as an
 187 Olsen P index 1 soil (Defra, 2010). To reflect the different fertiliser scenarios being used at each field
 188 site a set amount of P (P_1) (0-120 kg P ha⁻¹) was either applied at the surface ($z = 0$) (P broadcast) or
 189 at a set depth below the soil (D_1) (P placement).

190 Eqn. 17

$$\begin{aligned} &c = c_0(z) + H(z), \\ (\text{broadcast}) \quad H(z) &= P_1 \quad \text{at } t = 0, \quad z = 0 \\ (\text{placement}) \quad H(z) &= P_1 \quad \text{at } t = 0, \quad z = D_1 \\ (\text{else}) \quad H(z) &= 0 \quad \text{at } t = 0 \quad \forall z \end{aligned}$$

191 **Leaf growth model**

192 We have altered a compartmental model developed by Thornley (1995) to describe leaf mass M_L
 193 (kgL), leaf C M_C (kgC) and leaf P M_P (kgP) as well as the concentration of free C [C] = M_C/M_L (kgC
 194 kgL⁻¹) and free P [P] = M_P/M_L (kgP kgL⁻¹) dynamics within the leaves. The leaf model takes into
 195 account non-linear dynamics of formation of leaf litter and leaf self-shading. Additionally we have
 196 made photosynthesis dependent upon P content in the plant (Foyer and Spencer, 1986, Wissuwa *et*
 197 *al.*, 2005) and we have altered the leaf growth term, G_{sh} , which was dependent on [C] and [P], to
 198 also depend upon ~~the~~ air temperature (A_T), ~~for the~~ winter barley but not spring barley, ~~as well as [C]~~
 199 and [P]. We don't let air temperature affect spring barley as the growing season is much shorter
 200 compared to winter barley and it is not needed for a good fit to the experimental data. The
 201 governing equations are given below and are represented in a flow diagram on Figure 1, i.e., we
 202 have

203 Eqn. 18

$$\frac{\partial M_L}{\partial t} = \overbrace{G_{sh}}^{\text{Leaf growth rate}} - \overbrace{\frac{K_{litt}}{1 + \frac{K_{mlitt}}{M_L}} M_L}_{\text{Leaf metabolism/litter}},$$

204 Eqn. 19
$$\frac{\partial M_C}{\partial t} = \overbrace{\varepsilon k_1 [P]}^{\text{Production of C from photosynthesis}} - \overbrace{f_c G_{sh}}^{\text{Use of C for L growth}} - \overbrace{\beta_c [C]}^{\text{Output of C to phloem}},$$

205 Eqn. 20
$$\frac{\partial M_P}{\partial t} = \overbrace{-f_p G_{sh}}^{\text{Use of P for L growth}} + \overbrace{F(c, z, t)}^{\text{Input of P from xylem}} - \overbrace{\beta_p [P]}^{\text{Output of P to phloem}} - \overbrace{k_p \varepsilon [P] k_1}^{\text{Use of P to produce C}},$$

206 where,

207 Eqn. 21
$$G_{sh} = k_G M_L [C] [P] \frac{A_T^{s_1}}{s_2^{s_1} + A_T^{s_1}},$$

208 Eqn. 22
$$\varepsilon = \frac{k_C M_L}{\left(1 + \frac{M_L}{k_M}\right) \left(1 + \frac{[C]}{J_C}\right)},$$

209 where k_g is the leaf growth rate, K_{litt} is the litter rate, K_{mlitt} is the litter Michaelis-Menten constant,
 210 K_C is the photosynthesis rate, k_M is the constant accounting for the leaf self-shading, J_C is the C
 211 product inhibition constant, f_c is the fraction of total C used for leaf growth, f_p is the fraction of total
 212 P used for leaf growth, k_1 is the amount of P used for photosynthesis, $k_p k_1$ is the P loss due to
 213 photosynthesis, β_c is the rate of C output from the xylem to the phloem, β_p is the rate of P output to
 214 the phloem, $F(c, z, t)$ is the rate of P entry from the xylem (Eqn. 10) and s_1 and s_2 are fitting
 215 parameters. Initial values for the leaf (M_L), C (M_C) and P (M_P) mass are 1×10^{-4} , 0 and 1×10^{-7} kg
 216 respectively.

217 **Whole crop model**

218 In order to provide feedback between the root model and leaf model, we allow C mass to affect the
 219 root growth rate. Increasing C mass will increase root growth which in turn will increase plant P
 220 uptake. Through the process of photosynthesis, increasing plant P uptake will also increase C mass,
 221 thus creating a positive feedback loop.

222 The order i root growth rate is now dependent on C as well as temperature, therefore we replace

223 Eqn. 1 with,

224 Eqn. 23
$$\frac{\partial I_i}{\partial t} = r(T, C) \left(1 - \frac{I_i}{L_i}\right),$$

225 where the rate of growth $r(T, C)$ is given by a function of temperature multiplied by a function of C

226 $(r(T, C) = f(C)g(T)),$

227 Eqn. 24
$$f(C) = \frac{\alpha_c M_c}{\gamma_c + M_c},$$

228 Eqn. 25
$$g(T) = \begin{cases} 0 & T \leq 5^\circ C \\ A(T - 5) & T > 5^\circ C \end{cases}$$

229 where γ_c is the mass of C when the root system is at half its maximum size, α_c is the strength of the
230 C effect and A is a fitting parameter determining the strength of temperature dependence on root
231 growth rate. Below critical temperature ($5^\circ C$) there is no root growth and this reflects cold periods
232 over the winter (Sylvester-Bradley *et al.*, 2008).

233 Fitting process Calibration

234 The parameter list for the models above is given in Table 1. A subset of these parameters are fitted
235 to the experimental data and their values can be seen in Table 2. To begin the fitting
236 procedure calibration process, the leaf model is first fit against the experimental leaf mass data, by
237 6 parameters (β_c, k_1, f_c, f_p for spring barley and in addition s_1 and s_2 for winter barley). In the leaf
238 model only, we set the rate of P entry from the xylem ($F(c, z, t)$, Eqn. 10) proportional to the
239 experimental plant P uptake to simulate a representative plant P root uptake. We then combine the
240 models, i.e. let the rate of P entry from the xylem be estimated from the root model, and fit for the
241 remaining parameters (γ_c and α_c).

242 During the fitting process calibration step we minimise the sum of squares value between the
243 model's output for plant P uptake and leaf mass values against the experimental data values for
244 each the control and maximum applied P scenario (0 and 90/120 kg P ha⁻¹ respectively). With the
245 fitted parameters we then run the model for all applied P scenarios.

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246 The differences between modelling spring barley and winter barley are the time they are grown for
247 (151 and 313 days, respectively), the initial P profile in the soil (20 mg P l⁻¹ decay profile and 16 mg P
248 l⁻¹ constant profile, respectively) and leaf growth dependence (also depending upon air temperature
249 for winter barley).

250 **Results**

251 We compare two sets of barley field experimental data against the coupled model, the leaf model
252 (where plant P uptake is given by experimental data) and the root model. The aim is to address the
253 differences between the models and how well they fit the experimental field data for barley.

254 First we compare the values for plant P uptake between the root and coupled model for spring
255 barley at three different growth stages, GS31, GS45 and GS91 for seven applied P rates (0, 5, 10, 20,
256 30, 60 and 90 kg P ha⁻¹; Figure 2). The coupled model estimates higher plant P uptake compared to
257 the root model, better fitting the experimental data; staying within one standard deviation except at
258 high applied P rates (30, 60 and 90 kg P ha⁻¹ at GS31, 20, 60 and 90 kg P ha⁻¹ at GS45 and 30 and 60
259 kg P ha⁻¹ at GS91). The feedback effect within the coupled model enables the root structure to
260 become larger than in the root model and therefore the roots explore more of the soil and hence
261 achieve an increased plant P uptake (Figure 8). The final model estimate (GS91) is more accurate
262 than the earliest (GS31) due to not capturing the effects of possible lateral root proliferation due to
263 higher applied P rates (Drew, 1975). Early differences are averaged out as the root system grows.

264 When considering plant P uptake in winter barley, the coupled model behaves similarly to the root
265 model (Figure 3). At GS92, both models under-predict plant P uptake for the same reasons as stated
266 in Heppell *et al.* (2015); the P profile is depleted which limits the amount of P available for uptake,
267 and perhaps the total amount of P in the soil was different to that estimated by the one soil test for
268 the whole site (Olsen P index 1). The effect of slow release P pools in the soil was not taken into
269 consideration due to the fact experimental data for this phenomenon was not available.

270 By coupling the root model with the leaf model we are able to compare measured leaf mass values
271 against the coupled and leaf model only for both spring barley (Figure 4) and winter barley (Figure 5)
272 for different applied P rates. The coupled model accurately predicts leaf mass at GS91 for spring
273 barley, however it estimates a more average value for earlier growth stages; not distinguishing any
274 differences between applied P rates. The large errors bars in the experimental leaf mass data are
275 possibly due to field variation, making it hard to distinguish any differences between applied P rates,
276 especially at later growth stages (the experimental differences are not statically significant). In
277 addition, the variation in experimental plant P uptake values for GS31 is less than for GS91 (18% to
278 24%), implying little correlation between early and late plant P uptake (adjusted $r^2=0.4$). For winter
279 barley, the coupled model is able to match leaf mass at GS39, but vastly underestimates leaf mass at
280 GS92 due to underestimating plant P uptake as mentioned above. The leaf model fits well across all
281 scenarios for spring and winter barley as it takes the known plant P uptake from the experimental
282 data as an input.

283 The leaf model component allows us to estimate P (Figure 6) and C mass (Figure 7) in the above
284 ground tissue over the growing period of the crop. The estimated P mass is higher in the leaf model
285 compared to the coupled model for both spring and winter barley. The estimated C mass is higher in
286 the leaf model compared to the coupled model for winter barley, but the other way around for
287 spring barley. In the winter barley case, the increased C and P masses in the leaf model are due to
288 higher plant P uptake values (Figure 3 compared to Figure 2) resulting in a larger end leaf mass. For
289 spring barley, C mass in the coupled model begins lower and ends higher compared to the leaf
290 model because plant P uptake by the root system also begins lower and ends higher (P uptake
291 remains constant in the leaf model). The sudden decrease in C and P mass, for winter barley, around
292 the 250 day mark is due to the enforced halting of the root growth rate.

293 The root growth rate is affected by C mass (spring barley) and also temperature (winter barley);
294 therefore different final root lengths can be observed between model simulations (Figure 8). The

295 leaf model created a longer root length compared to the coupled model in the winter barley
296 scenario due to the early differences in C mass. For spring barley, the early C mass values for the
297 coupled and leaf model were similar resulting in almost identical root growth rates and hence final
298 root lengths. As C mass increases above a certain value any differences are masked when affecting
299 the root growth rate. There was little difference in root length between the two different fertiliser
300 applications (0 and 90/120 kg P ha⁻¹), the largest being between the coupled model for winter barley
301 GS92. Due to the small increase in plant P uptake between scenarios (0 and 120 kg P ha⁻¹) there was
302 little effect on increasing root length via the slow feedback loop created by the addition of the leaf
303 model. Chemotropism effects from adding large amounts of P fertiliser could perhaps explain any
304 differences between plant P uptake values at early growth stages. In the winter barley scenario, as
305 root growth rate was dependent upon temperature, we see periods of no root growth matching
306 periods of low temperature, as expected.

307 Heppell *et al.* (2015) considered the effects of discrete placing of fertiliser within the root zone
308 against incorporating fertiliser throughout the soil for a range of cultivation options (mix 25, 20 and
309 10 cm, inverted plough, minimum tillage and no cultivation) for winter barley at GS92. We do the
310 same in this paper for the new coupled model (Figure 9). We arrive at the same overall conclusion,
311 placing fertiliser rather than incorporating achieves a higher plant P uptake estimate and under a
312 wet climate ([x5 flux of water at soil surface](#)), such as in the UK, this difference decreases (9.9% to 0.3%
313 and 9.8% to 4.5%) over no cultivation for a dry and wet climate respectively. Ploughing was also the
314 best cultivation option moving top soil P to a lower depth, making it more accessible to a
315 comparatively larger root system.

316 Discussion

317 In order to obtain a more accurate representation of the growth of barley throughout a crop life
318 cycle we have combined a below ground root-soil model with an above ground leaf model. By
319 combining the two models we are able to let an above ground process (photosynthesis) affect a

320 below ground process (root growth) and vice versa. C is created via photosynthesis in the leaf model
321 (dependent upon leaf mass and P) and stimulates root growth; increased root growth increases
322 plant P uptake and hence leaf mass. This positive feedback effect could explain why crops with early
323 plant P uptake levels grow more vigorously and can produce higher yields (Brenchley, 1929;
324 Boatwright and Viets, 1966; Green *et al.*, 1973; Grant *et al.*, 2001). Due to possible unfavourable (e.g.
325 dry) weather conditions, maximising early plant P uptake through greater root proliferation is also a
326 good strategy to help ensure continuing capture of soil resources at later stages of growth.

327 From the modelling work conducted we can postulate that the whole crop model accurately
328 estimates leaf mass at all growth stages given it has accurate estimates of plant P uptake (an average
329 difference of 4.6% for the whole crop model for leaf mass, compared to 15.8% when using values
330 one standard deviation away from the experimental data). Using the calibrated whole crop model
331 we found the optimal fertiliser and cultivation scenario is to use a plough and place the P fertiliser.
332 The largest increase in plant P uptake when placing fertiliser over incorporating fertiliser was 9.6%
333 (plough, dry climate). The difference between incorporating and placing has been long studied and
334 depends upon a range of criteria such as soil P concentration, soil temperature, crop species and
335 price (Devine *et al.*, 1964; Mahler, 2001). Owusu-Gyimah *et al.* (2013) found that applying fertiliser
336 at a depth of 10 cm and 20 cm away from the plant (placed P) gave the best outcome for maize
337 growing under tropical conditions. By placing fertiliser instead of incorporating it throughout the soil
338 the available P is being put where the root system is going to grow hoping to ensure early plant P
339 uptake and a more successful crop. Hence Wager *et al.* (1986) found that P fertilizer application
340 rates could be halved by placing fertiliser instead of incorporation because the applied P was more
341 efficiently used. However, optimal fertiliser and cultivation methods depend on the initial soil P
342 condition/distribution (Randall and Hoefl, 1988); this includes at the depth at which existing P is
343 initially available within the soil (Heppell *et al.*, 2015).

344 For modelling across countries it will be important to measure soil available P levels consistently, by
345 either using a common method or a set of common descriptors. Although, an international 'standard'
346 soil extraction method is not necessarily needed; rather employing a basic soil property (e.g.
347 sorption/buffer capacity) would be better to calibrate fertiliser recommendations. Modelling is the
348 most appropriate way to overcome the problems of site specificity in soil P supply that confound
349 current soil P test methods which do not apply to all soil types, i.e. across countries. Countries
350 generally adopt a particular standard method for soil P tests; many different extractants are used.
351 However, these do not necessarily give correlated results, for example across European laboratories
352 (Neyroud and Lischer, 2002; Jordan-Meille *et al.*, 2012). It is possible that a more robust soil test will
353 be developed in the future, that more accurately reflects immediate P availability to roots across
354 different soil types. For example, using Diffusive Gradient in Thin films (DGT) based on soil P
355 diffusion rates (Van Rotterdam *et al.*, 2009; Tandy *et al.*, 2011) or a method that mimics root P
356 acquisition traits (De Luca *et al.*, 2015). The use of more mechanistic approaches to calculate soil
357 available P levels via a more standardised test, or a combination of tests, enhances their applicability
358 across a wider variety of soil types and may lead to more accurate assessment of fertiliser needs
359 (Van Rotterdam *et al.*, 2014). Also, given that patterns of P concentration with depth in soil profiles
360 vary between sites (Jobbágy and Jackson, 2001), it may also be important to assess surface
361 stratification in no-tilled soils or in subsoils. Over-fertilising soils due to inaccurate estimation of
362 requirement, or mis-interpretation of soil P supply through inappropriate tests leads not only to
363 waste of finite reserves of phosphate-rock but also increased risk of P loss to water causing
364 eutrophication (Hooda *et al.*, 2001). By using knowledge about the distribution of P within the soil
365 and by modelling its implications, it should be possible to save on fertiliser costs by implementing
366 better optimised treatments through targeting P use (Yang *et al.*, 2013; Withers *et al.*, 2014).
367 Furthermore, since crop and fertiliser management have long-term effects on topsoil and subsoil P
368 availability (Bolland and Baker, 1998), it will be important to validate the model over several years if
369 it is to improve on current simpler approaches to decision making. Additional model features would

370 be needed, such as effects between cropping seasons, but would make for a more overall
371 accomplished model. We note that the model would have to be calibrated separately for different
372 crops.

373 Although there was little response to P application observed in the field trial in terms of plant P
374 uptake at late growth stages (GS91 for spring barley and GS92 for winter barley), there was a
375 response at early growth stages (GS31 for spring barley and GS39 for winter barley). This early
376 response could imply that there were limiting environmental factors beyond nutritional inputs. Cold
377 and dry conditions in spring are known to inhibit the transport of P from the soil to the root (Grant
378 et al., 2001). However, if the measured 'low' P soil was an underestimation for the total amount of
379 available P in the soil then this could explain the lack of response at harvest observed in the field. In
380 addition, field variation could in part explain the early response to applied P; however as the root
381 system became larger during the latter growth stages any difference in plant P uptake and resulting
382 yield was evened out. Due to the complex nature of cereal physiology (Sylvester-Bradley *et al.*, 2008),
383 an early plant P uptake response does not necessarily indicate a higher final plant P uptake and yield;
384 because the plant compensates by taking up more P later on as temperatures warm up. The slow
385 feedback effect is a good explanation of the long term behaviour of the crop, and estimation of total
386 plant P uptake.

387 Potentially, new ways to improve efficiency use of P can now be developed by combining recent
388 advances in application technology, sensing technology, geo-spatial information and modelling so as
389 to apply P where it is needed and importantly not apply it where it is not needed. Precision farming
390 equipment is being widely adopted; now, its effective deployment depends on whether the vast
391 amount of data available about a given plot of land can be interpreted to improve the precision and
392 decrease the risks compared to current decision making (Sylvester-Bradley *et al.*, 1999). For example,
393 soil nutrient maps, past yield maps, soil and canopy sensors and climate predictions may provide
394 input data for integrated crop models to output quantitative predictions of fertiliser requirements so

395 that application as sowing can be adjusted in real time. However, the more immediate and
396 preliminary prospect is of using simulation models to compare scenarios of possible treatments, to
397 help guide future soil and fertiliser management strategies, and to accompany continuing field
398 testing.

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567 and either no fertiliser, 90 kg P ha⁻¹ incorporated or 90 kg P ha⁻¹ placed) for a normal climate and a
568 wetter climate [\(x5 flux of water at soil surface\)](#).

569 **List of Tables**

570 Table 1: A list of the parameters used for the 3 models: leaf, root and coupled.

Parameter	Definition	Value	Units
Leaf Model (Values from Thornley, J. H., 1995)			
k_G	Leaf growth rate constant	1000	$\left(\frac{\text{kg C}}{\text{kg Leaf}} \frac{\text{kg P}}{\text{kg Leaf}} \text{day}\right)^{-1}$
k_{litt}	Leaf litter rate constant	0.05	day^{-1}
k_{mitt}	Leaf litter Michealis-Menten constant	0.5	kg Leaf
k_C	Photosynthesis constant	0.1	$\frac{\text{kg C}}{\text{kg Leaf}} \text{day}^{-1}$
k_M	Leaf self-shading constant	1	kg Leaf
J_C	Carbon product inhibition constant	0.1	$\frac{\text{kg C}}{\text{kg Leaf}}$
f_C	Fraction of C used for leaf growth	(fitted)	$\frac{\text{kg C}}{\text{kg Leaf}}$
f_P	Fraction of P used for leaf growth	(fitted)	$\frac{\text{kg P}}{\text{kg Leaf}}$
k_1	P used for photosynthesis	(fitted)	$\frac{\text{kg Leaf}}{\text{kg P}}$
k_p	P:C ratio for photosynthesis production	0.005-0.05	$\frac{\text{kg P}}{\text{kg C}}$
β_p	Rate of P output to phloem	0	$\frac{\text{kg Leaf}}{\text{day}}$
F	Rate of P entry from xylem	Taken from barley experimental data or root model output	$\frac{\text{kgP}}{\text{day}}$
A_T	Air temperature	Taken from Local	$^{\circ}\text{C}$

		Met office MIDAS stations	
β_c	Rate of C output to phloem	(fitted)	$\frac{\text{kgL}}{\text{day}}$
s_1	Air temperature slope constant	(fitted)	-
s_2	Air temperature transition constant	(fitted)	$^{\circ}\text{C}$
Root-Soil Model (values from Heppell <i>et al.</i>, 2015)			
D_0	Water diffusivity	10^3	$\text{cm}^2 \text{day}^{-1}$
K_s	Water hydraulic conductivity	5	$\text{cm}^2 \text{day}^{-1}$
D_f	P diffusivity in free water	10^{-5}	$\text{cm}^2 \text{day}^{-1}$
d	Impedance factor	2	-
a	Main order root radius	0.085	cm
a_1	first order root radius	0.060	cm
k_r	Root radial water conductivity	$7.85 \cdot 10^{-6}$	$\text{m}^2 \text{s}^{-1} \text{MPa}^{-1}$
k_z	Root axial hydraulic conductivity	$1.198 \cdot 10^{-2}$	$\text{m}^4 \text{Pa}^{-1} \text{s}^{-1}$
ψ_1	Density of first order roots	2.33	cm^{-1}
p_r	Root internal xylem pressure	1	Pa
p_c	Characteristic suction pressure	0.0232	MPa
L_0	Max length of main order root	150	cm
L_1	Max length of first order root	7.9	cm
L	Root tip position	$0-L_0$	cm
b	Buffer power	23.28	-
θ	Angle between the main root and first order branches	60	degrees
ϕ	Porosity of soil	0.3	-
p_r^0	Initial root internal xylem pressure	1	Pa

λ_1	Root internal xylem pressure parameter	$2.7 \cdot 10^{-3}$	Pa/ degC
λ_2	Root internal xylem pressure parameter	$8.46 \cdot 10^{-4}$	Pa/% humidity
λ_3	Root internal xylem pressure parameter	$7.9 \cdot 10^{-2}$	Pa
δ	Flux of water parameter	$2.69 \cdot 10^{-2}$	-
α	Flux of water parameter	$1.2 \cdot 10^{-6}$	m s^{-1} of water
β	Flux of water parameter	$2.22 \cdot 10^{-6}$	m s^{-1} of water/degC
γ	Flux of water parameter	$5.35 \cdot 10^{-4}$	m s^{-1} of water/ m s^{-1} of air
E	Flux of water parameter	$5 \cdot 10^{-4}$	m s^{-1} of water
l_w	Bottom of the soil	200	cm
Coupled Model			
γ_c	Root carbon growth parameter	(fitted)	-
α_c	Strength of carbon effect on root growth	(fitted)	-
A	Strength of temperature dependence on root growth rate	0.0780	-

571

572 **Table 2: The fitted parameter set for the leaf and coupled models, for spring barley and winter**
573 **barley.**

Parameter		Value for Spring barley	Value for winter barley
Leaf Model	β_c	0.0001	0.0001

	k_1	100	859
	f_c	0.5	0.5
	f_p	$7 \cdot 10^{-4}$	$1.6 \cdot 10^{-3}$
	s_1	n/a	20.78
	s_2	n/a	-1.446
Coupled model	γ_c	$1.30 \cdot 10^{-5}$	$1.31 \cdot 10^{-4}$
	α_c	1	1.982