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

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**Plant and Soil**

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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: (~~200~~192/200)**

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~~s~~ 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 used~~employed 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, Prunsinkiewicz 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.

**Materials and Methods**

**Experimental data**

Two barley field trial data sets are used, consisting of leaf mass and plant P uptake values at different growth stages (GS31, GS45 and GS91 for spring barley; GS39 and GS92 for winter barley). The experimental data includes different rates of P application (0, 5, 10, 20, 30, 60, 90 kg P ha$^{-1}$ for spring barley; 0 15, 30, 60, 90, 120 kg P ha$^{-1}$ for winter barley) and both sites were classified with an Olsen P index 1 soil. The protocol for this is described in Heppell *et al.* (2015). In addition, we use the climate data, from the UK Met office Integrated Data Archive System (MIDAS), to accompany the spring barley (Inverurie, Scotland) and winter barley (Cambridge, England) data sets for the specific fields in the trial. The climate data consists of daily values for mean temperature ($^{o}$C), rainfall (mm), wind speed (m s$^{-1}$) and humidity (%).

**Modelling the whole crop**

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

**Root and soil model**

To model the root system we follow the same approach as described in Roose *et al.* (2004b) and Heppell *et al.* (2015) by modelling two orders of root branches only (main and first order branches). First order roots branch off the main order roots at a given density ($\psi_1$), branching angle ($\theta$), and each order of roots has a given maximum length and radius ($L_0$, $L_1$ and $a$, $a_1$ for main and first order 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 $$\phi\frac{\partial S}{\partial t} = \nabla \cdot \left[D_0 D(S)\nabla S - K_S k(S)\widehat{\boldsymbol{k}}\right] - F_w(S, z, t) \,,$$

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

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

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

130    In the above equations $S$ is the relative water saturation given by $S = \phi_1/\phi$, $\phi_1$ is the volumetric

131    water content, and $\phi$ is the porosity of the soil. $D_0$ (cm$^2$ 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). $\widehat{\boldsymbol{k}}$ 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 $\psi_1$ 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, $\theta$ is the angle

148 between the main root and the first order branches, $k_r$ is the root radial water conductivity

149 parameter (m s$^{-1}$ Pa$^{-1}$), $k_z$ is the root axial hydraulic conductivity calculated using Poiseuille law (m$^4$

150 Pa$^{-1}$ s$^{-1}$), $p_c$ (Pa) is a characteristic suction pressure determined from experimental data for different

151 types of soil, $f(S) = \left(s^{-1/m} - 1\right)^{1-m}$, 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 $\lambda_1$, $\lambda_2$ and $\lambda_3$ (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 $\delta$, $\alpha$, $\beta$ and $\gamma$ (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 | $\begin{array}{lll} (1) & c_0(z) = & c_A & \text{at } t = 0, \forall z \\ (2) & c_0(z) = & A_1 e^{-B_1 z} & \text{at } t = 0, \forall z' \end{array}$ |

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 the strength of the decay in the concentration of P (0.345). The initial P concentration values ($C_A$, $A_1$ and $B_1$) come from a best fit to the data sets in Heppell et al., (2015) and are both classified as an Olsen P index 1 soil (Defra, 2010). To reflect the different fertiliser scenarios being used at each field 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 at a set depth below the soil ($D_1$) (P placement).

| 190 | Eqn. 17 | $\begin{array}{lll} c = c_0(z) + H(z), \\ \text{(broadcast)} & H(z) = P_1 & \text{at } t = 0, \quad z = 0 \\ \text{(placement)} & H(z) = P_1 & \text{at } t = 0, \quad z = D_1 \\ \text{(else)} & H(z) = 0 & \text{at } t = 0 \quad \forall z \end{array}$ |

**Leaf growth model**

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

| 203 | Eqn. 18 | $\dfrac{\partial M_L}{\partial t} = \overbrace{G_{sh}}^{\text{Leaf growth rate}} - \overbrace{\dfrac{K_{litt}}{1 + \dfrac{K_{mlitt}}{M_L}} M_L}^{\text{Leaf metabolism/litter}} \quad ,$ |

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, $\beta_c$ is the rate of C output from the xylem to the phloem, $\beta_p$ 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 1x10$^{-4}$, 0 and 1x10$^{-7}$ 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
$$\frac{\partial l_i}{\partial t} = r(T,C)\left(1 - \frac{l_i}{L_i}\right),$$

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
$$g(T) = \begin{cases} 0 & T \le 5^oC \\ A(T-5) & T > 5^oC' \end{cases}$$

229    where $\gamma_C$ is the mass of C when the root system is at half its maximum size, $\alpha_c$ 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°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 ($\beta_c$, $k_1$, $f_c$, $f_p$ 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 ($\gamma_c$ and $\alpha_c$).

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.

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 Hoeft, 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.

399  **Acknowledgements**

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548 20, 30, 60 and 90 kg P ha$^{-1}$) with standard deviation, compared against estimates from the coupled

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550 **Figure 3:** Winter barley plant P uptake experimental data values for different applied P rates (0, 15,

551 30, 60, 90 and 120 kg P ha$^{-1}$) with standard deviation, compared against estimates from the couple

552 model and root model at GS39 and 92.

553 **Figure 4:** Spring barley leaf mass experimental data values for different applied P rates (0, 5, 10, 20,

554 30, 60 and 90 kg P ha$^{-1}$) with standard deviation, compared against estimates from the coupled

555 model and leaf model at GS31, 45, 91.

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557 90 and 120 kg P ha$^{-1}$) with standard deviation, compared against estimates from the coupled model

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562 and b) winter barley at GS91, 92 respectively for 0 kg P ha$^{-1}$ and 90/120 kg P ha$^{-1}$.

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565 **Figure 9:** Estimated plant P uptake values for winter barley at GS92 for a set of fertiliser and soil

566 management strategies (mix 25, 20 and 10cm, inverted plough, minimum tillage and no cultivation,

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 | $\left(\dfrac{\text{kg C}}{\text{kg Leaf}}\dfrac{\text{kg P}}{\text{kg Leaf}}\text{day}\right)^{-1}$ |
| $k_{litt}$ | Leaf litter rate constant | 0.05 | $\text{day}^{-1}$ |
| $k_{mlitt}$ | Leaf litter Michealis-Menten constant | 0.5 | kg Leaf |
| $k_C$ | Photosynthesis constant | 0.1 | $\dfrac{\text{kg C}}{\text{kg Leaf}}\text{day}^{-1}$ |
| $k_M$ | Leaf self-shading constant | 1 | kg Leaf |
| $J_C$ | Carbon product inhibition constant | 0.1 | $\dfrac{\text{kg C}}{\text{kg Leaf}}$ |
| $f_c$ | Fraction of C used for leaf growth | (fitted) | $\dfrac{\text{kg C}}{\text{kg Leaf}}$ |
| $f_p$ | Fraction of P used for leaf growth | (fitted) | $\dfrac{\text{kg P}}{\text{kg Leaf}}$ |
| $k_1$ | P used for photosynthesis | (fitted) | $\dfrac{\text{kg Leaf}}{\text{kg P}}$ |
| $k_p$ | P:C ratio for photosynthesis production | 0.005-0.05 | $\dfrac{\text{kg P}}{\text{kg C}}$ |
| $\beta_p$ | Rate of P output to phloem | 0 | $\dfrac{\text{kg Leaf}}{\text{day}}$ |
| $F$ | Rate of P entry from xylem | Taken from barley experimental data or root model output | $\dfrac{\text{kgP}}{\text{day}}$ |
| $A_T$ | Air temperature | Taken from Local | $°C$ |

| | | Met office MIDAS stations | |
|---|---|---|---|
| $\beta_c$ | Rate of C output to phloem | (fitted) | $\dfrac{\text{kgL}}{\text{day}}$ |
| $s_1$ | Air temperature slope constant | (fitted) | - |
| $s_2$ | Air temperature transition constant | (fitted) | $°C$ |
| **Root-Soil Model (values from Heppell _et al.,_ 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 | $7.85*10^{-6}$ | $\text{m}^2\text{s}^{-1}\text{MPa}^{-1}$ |
| $k_z$ | Root axial hydraulic conductivity | $1.198*10^{-2}$ | $\text{m}^4\text{Pa}^{-1}\text{s}^{-1}$ |
| $\psi_1$ | Density of first order roots | 2.33 | $\text{cm}^{-1}$ |
| $p_r$ | 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 | $0\text{-}L_0$ | cm |
| $b$ | Buffer power | 23.28 | - |
| $\theta$ | Angle between the main root and first order branches | 60 | degrees |
| $\phi$ | Porosity of soil | 0.3 | - |
| $p_r^0$ | Initial root internal xylem pressure | 1 | Pa |

| | | | |
|---|---|---|---|
| $\lambda_1$ | Root internal xylem pressure parameter | $2.7*10^{-3}$ | Pa/ degC |
| $\lambda_2$ | Root internal xylem pressure parameter | $8.46*10^{-4}$ | Pa/% humidity |
| $\lambda_3$ | Root internal xylem pressure parameter | $7.9*10^{-2}$ | Pa |
| $\delta$ | Flux of water parameter | $2.69*10^{-2}$ | - |
| $\alpha$ | Flux of water parameter | $1.2*10^{-6}$ | m s$^{-1}$ of water |
| $\beta$ | Flux of water parameter | $2.22*10^{-6}$ | m s$^{-1}$ of water/degC |
| $\gamma$ | Flux of water parameter | $5.35*10^{-4}$ | m s$^{-1}$ of water/ m s$^{-1}$ of air |
| $E$ | Flux of water parameter | $5*10^{-4}$ | m s$^{-1}$ of water |
| $l_w$ | Bottom of the soil | 200 | cm |
| **Coupled Model** | | | |
| $\gamma_C$ | Root carbon growth parameter | (fitted) | - |
| $\alpha_c$ | 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 | $\beta_c$ | 0.0001 | 0.0001 |

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

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