

Modelling the optimal phosphate fertiliser and soil management strategy for crops

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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)

Aims Phosphorus (P) is an essential nutrient necessary for maintaining crop growth, however, it's often used inefficiently within agroecosystems, driving industry to find new ways to deliver P to crops sustainably. We consider a precision agriculture approach which aim to combines traditional soil and crop measurements with climate-driven mathematical models, that canto optimise the 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

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.

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

31 Introduction

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

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

We are interested in how crops grow and survive in low P environments and how fertiliser and soil cultivation methods are influencing crop performance. A number of studies have considered the response of adding different amounts and rates of fertiliser P; in some soils large effects are seen whereas no effect is seen in others (Bolland and Baker, 1998; Kuchenbuch and Buczko, 2011; Valkama et al., 2011). There are many ways one could apply P to soils; for example incorporating (also known as broadcasting, involves an even spreading of P on top of the soil), placing (also known 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 differences in soil cultivation methods on plant P uptake; for example, conventional plough versus 50 minimum tillage (also considering gene variation, George et al., 2011). The idea behind ploughing is 51 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 reduces crop establishment costs, but segregates P content with depth and can leave 30% of crop 55 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 and environmental impact of fertilisers. This is a complex problem due to varying climatic conditions, 59 60 an abundance of technological machines, and availability of more data concerning the states of fields than ever before. Precision agriculture is an emerging field involved with combining the 61 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. Mathematical models, supported by experimental data, are needed to help predict best decisions in 65 66 the short term, and also strategically, to optimise between possible future options. Whilst such models are seldom not always commercially usedemployed at present, their potential capabilities 67 are attractive, given that field-scale experiments are both costly and time-consuming, and 68 integration and dissemination of their empirical results is challenging (Selmants and Hart, 2010; 69 Jeuffroy et al., 2012; Sylvester-Bradley, 1991). 70

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 agrotechnology transfer (DSSAT) which focuses on average plant-environment interactions; and 76 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. We hope to address some of these problems by creating a model that links the above and below 88 ground processes in such a way that they rely on one another. Our whole crop model is based on a 89 90 below ground plant-soil interaction model (Roose and Fowler, 2004b; Heppell et al., 2015) coupled with an above ground leaf growth model based on the seminal work of Thornley (1995). 91

Here we describe a whole crop model that includes a below-ground root model and an aboveground leaf model and which is validated against experimental data on barley with a varying P fertiliser scenario analysis. The development of the model is seen as a step-change in our computational capability to help predict soil P supply, crop P uptake patterns and fertilizer 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 different growth stages (GS31, GS45 and GS91 for spring barley; GS39 and GS92 for winter barley). 100 101 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 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

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.

114 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 (ψ_1), branching angle (θ), 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 Formatted: Superscript

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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.

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

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

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, *u*, is given by Darcy's law,

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

130 In the above equations S is the relative water saturation given by $S = \phi_1/\phi$, ϕ_1 is the volumetric water content, and ϕ is the porosity of the soil. D_0 (cm² day⁻¹) and K_S (cm day⁻¹) are the parameters 131 132 for water 'diffusivity' and hydraulic conductivity, respectively (Van Genuchten, 1980). D(S) and K(S) characterize reduction in water 'diffusivity' and hydraulic conductivity in response to the 133 134 relative water saturation decrease, where the functional forms for partially saturated soil are given 135 by Van Genuchten (1980). \hat{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).

For the total P conservation (Eqn. 3), c is the P concentration in soil pore water, b is the soil buffer power characterising the amount of P bound to the soil particle surfaces, D_f is the P diffusivity in free water and d is an impedance factor; $1 \le d \le 3$ (Barber, 1984; Nye and Tinker, 1977). F(c, S, t)describes the rate of plant P uptake by a root branching structure (Roose *et al.*, 2001). Both F_w and F are affected by the spatially and temporally evolving root structure. Water is only taken up by the main order roots while P is taken up by all roots; see Roose and Fowler (2004b) for details of the derivation. The equation for F_w is given by,

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

where ψ_1 is the density of first order roots on the main order roots, a_1 is the first order root radius, *a* is the main order root radius, L_1 is the maximum length of the first order branches, θ is the angle between the main root and the first order branches, k_r is the root radial water conductivity parameter (m s⁻¹ Pa⁻¹), k_z is the root axial hydraulic conductivity calculated using Poiseuille law (m⁴ Pa⁻¹ s⁻¹), p_c (Pa) is a characteristic suction pressure determined from experimental data for different types of soil, $f(S) = (s^{-1/m} - 1)^{1-m}$, where *m* is the Van Genuchten soil suction parameter (where 0 < m < 1), and p_r is the root internal xylem pressure (Pa).

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

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

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

- 158 Eqn. 7 $\frac{\partial p_r}{\partial x} = 0$ at x = L,
- 159 Eqn. 8 $p_r = P \text{ at } x = 0,$

where *P* is a function of temperature (*T*), humidity (*H*) and a base line pressure (p_r^0) for fitting 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
$$F(c, z, t) = \frac{F_0 + F_1}{\pi (a + L_1 \cos \theta)^2},$$

where F_0 and F_1 are the uptake rates for zero and first order roots derived in Roose *et al.* (2004b). The boundary conditions to accompany Equations 1 and 2 include a soil surface boundary condition

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
$$-D_f \phi^d S^d \frac{\partial c}{\partial z} = 0 \text{ at } z = l_W.$$

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

183 Eqn. 16
(1)
$$c_0(z) = c_A$$
 at $t = 0, \forall z$
(2) $c_0(z) = A_1 e^{-B_1 z}$ at $t = 0, \forall z'$

where c_A is set to 16 mg P \vdash^1 , A_1 is the P concentration at the top of the soil (23 mg P \perp^{-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

$$c = c_0(z) + H(z),$$
(broadcast) $H(z) = P_1$ at $t = 0$, $z = 0$
(placement) $H(z) = P_1$ at $t = 0$, $z = D_1$
(else) $H(z) = 0$ at $t = 0$ $\forall z$

191 Leaf growth model

192 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 193 194 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 $(A_T)_{T}$ 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
$$\frac{\partial M_L}{\partial t} = \widetilde{G_{sh}} - \frac{\int_{t=1}^{t=1} \frac{dt}{dt} \frac{dt}{dt}}{\frac{K_{titt}}{M_L}} M_L,$$

Production of C from photosynthesis Use of C for L growth Output of C to phloem
204 Eqn. 19
$$\frac{\partial M_C}{\partial t} = \widetilde{\varepsilon k_1[P]} - \widetilde{f_c G_{sh}} - \widetilde{\beta_c[C]},$$
205 Eqn. 20
$$\frac{\partial M_P}{\partial t} = -\widetilde{f_p G_{sh}} + \widetilde{F(c, z, t)} - \widetilde{\beta_p[P]} - \widetilde{k_p \varepsilon[P] k_1}$$

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 photosynthesis, β_c is the rate of C output from the xylem to the phloem, β_p is the rate of P output to 213 214 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 parameters. Initial values for the leaf (M_L), C (M_C) and P (M_P) mass are 1x10⁻⁴, 0 and 1x10⁻⁷ kg 215 216 respectively.

217 Whole crop model

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

The order *i* root growth rate is now dependent on C as well as temperature, therefore we replaceEqn. 1 with,

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

where the rate of growth r(T, C) is given by a function of temperature multiplied by a function of C (r(T, C) = f(C)g(T)),

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

228 Eqn. 25
$$g(T) = \begin{cases} 0 & T \le 5^{o}C \\ A(T-5) & T > 5^{o}C' \end{cases}$$

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 C effect and A is a fitting parameter determining the strength of temperature dependence on root growth rate. Below critical temperature (5°C) there is no root growth and this reflects cold periods over the winter (Sylvester-Bradley *et al.*, 2008).

233 Fitting processCalibration

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 procedurecalibration 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 <u>fitting processcalibration step</u> 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 <u>each-the control and maximum</u> applied P scenario <u>(0 and 90/120 kg P ha⁻¹ respectively)</u>. With the 245 <u>fitted parameters we then run the model for all applied P scenarios</u>.

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The differences between modelling spring barley and winter barley are the time they are grown for (151 and 313 days, respectively), the initial P profile in the soil (20 mg P l⁻¹ decay profile and 16 mg P l⁻¹ constant profile, respectively) and leaf growth dependence (also depending upon air temperature 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, especially at later growth stages (the experimental differences are not statically significant). In 276 277 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 r²=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);
- 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, placing fertiliser rather than incorporating achieves a higher plant P uptake estimate and under a 311 312 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 <i>et al.,</i> 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 most appropriate way to overcome the problems of site specificity in soil P supply that confound 348 349 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 requirement, or mis-interpretation of soil P supply through inappropriate tests leads not only to 362 363 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 availability (Bolland and Baker, 1998), it will be important to validate the model over several years if 368 369 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

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 et al., 2001). However, if the measured 'low' P soil was an underestimation for the total amount of 378 available P in the soil then this could explain the lack of response at harvest observed in the field. In 379 380 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 equipment is being widely adopted; now, its effective deployment depends on whether the vast 390 391 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

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

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- 550 Figure 3: Winter barley plant P uptake experimental data values for different applied P rates (0, 15,
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Parameter	Definition	Value	Units			
Leaf Model (Values from Thornley, J. H., 1995)						
k _G	Leaf growth rate constant	1000	$\left(\frac{\mathrm{kg}\mathrm{C}}{\mathrm{kg}\mathrm{Leaf}}\frac{\mathrm{kg}\mathrm{P}}{\mathrm{kg}\mathrm{Leaf}}\mathrm{day}\right)^{-1}$			
k _{litt}	Leaf litter rate constant	0.05	day ⁻¹			
k _{mlitt}	Leaf litter Michealis-Menten	0.5	kg Leaf			
	constant					
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	kg C kg Leaf			
f_c	Fraction of C used for leaf growth	(fitted)	kg C kg Leaf			
f _p	Fraction of P used for leaf growth	(fitted)	kg P kg Leaf			
<i>k</i> ₁	P used for photosynthesis	(fitted)	kg Leaf kg P			
k _p	P:C ratio for photosynthesis production	0.005-0.05	kg P kg C			
β_p	Rate of P output to phloem	0	kg Leaf day			
F	Rate of P entry from xylem	Taken from barley experimental data or root model output	kgP day			
A _T	Air temperature	Taken from Local	°C			

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

		Met office MIDAS	
		stations	
β _c	Rate of C output to phloem	(fitted)	kgL day
<i>s</i> ₁	Air temperature slope constant	(fitted)	-
s ₂	Air temperature transition constant	(fitted)	°C
	Root-Soil Model (values fr	om Heppell <i>et al.,</i> 2015)
D ₀	Water diffusivity	10 ³	cm ² day ⁻¹
K _s	Water hydraulic conductivity	5	cm ² day ⁻¹
D_f	P diffusivity in free water	10 ⁻⁵	cm ² day ⁻¹
d	Impedance factor	2	-
а	Main order root radius	0.085	cm
<i>a</i> ₁	first order root radius	0.060	cm
k _r	Root radial water conductivity	7.85*10 ⁻⁶	$m^2s^{-1}MPa^{-1}$
k _z	Root axial hydraulic conductivity	1.198*10 ⁻²	$m^4 Pa^{-1}s^{-1}$
ψ_1	Density of first order roots	2.33	cm ⁻¹
p_r	Root internal xylem pressure	1	Ра
p _c	Characteristic suction pressure	0.0232	МРа
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- <i>L</i> ₀	cm
b	Buffer power	23.28	-
θ	Angle between the main root and	60	degrees
	first order branches		
φ	Porosity of soil	0.3	-
p_r^0	Initial root internal xylem pressure	1	Ра

λ1	Root internal xylem pressure	2.7*10 ⁻³	Pa/ degC
	parameter		
λ ₂	Root internal xylem pressure	8.46*10-4	Pa/% humidity
	parameter		
λ_3	Root internal xylem pressure	7.9*10 ⁻²	Ра
	parameter		
δ	Flux of water parameter	2.69*10 ⁻²	-
α	Flux of water parameter	1.2*10 ⁻⁶	m s ⁻¹ of water
β	Flux of water parameter	2.22*10 ⁻⁶	m s ^{−1} of water/degC
γ	Flux of water parameter	5.35*10-4	m s ⁻¹ of water/ m s ⁻¹ of
			air
Е	Flux of water parameter	5*10-4	m s ⁻¹ of water
l _w	Bottom of the soil	200	cm
	Coupled	Model	
Υс	Root carbon growth parameter	(fitted)	-
α _c	Strength of carbon effect on root	(fitted)	-
	growth		
A	Strength of temperature	0.0780	-
	dependence on root growth rate		

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

	k1	100	859
	f _c	0.5	0.5
	fp	7*10 ⁻⁴	1.6*10 ⁻³
	<i>s</i> ₁	n/a	20.78
	<i>s</i> ₂	n/a	-1.446
Coupled model	Ŷc	1.30*10 ⁻⁵	1.31*10-4
	α _c	1	1.982