



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

Heppell, J.; Payvandi, S.; Talboys, P.; Zygalkis, K. C.; Langton, D.; Sylvester-Bradley, R.; Edwards, A. C.; Walker, R.; Withers, P.; Jones, David; Roose, T.

Plant and Soil

DOI:

[10.1007/s11104-016-2883-4](https://doi.org/10.1007/s11104-016-2883-4)

Published: 01/09/2016

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):

Heppell, J., Payvandi, S., Talboys, P., Zygalkis, K. C., Langton, D., Sylvester-Bradley, R., ... Roose, T. (2016). Use of a coupled soil-root-leaf model to optimise phosphate fertiliser use efficiency in barley. *Plant and Soil*, 406(1-2), 341-357. <https://doi.org/10.1007/s11104-016-2883-4>

Hawliau Cyffredinol / General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

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

2 J. Heppell^{1,2,*}, S. Payvandi³, P. Talboys⁵, K. C. Zygalkis^{2,4}, D. Langton⁶, R. Sylvester-Bradley⁷, T.
3 Edwards⁸, R. Walker⁸, P. Withers⁵, D.L.Jones⁵ and T. Roose^{1,2}

4 ¹Faculty of Engineering and the Environment, University of Southampton, Southampton, SO17 1BJ,
5 UK. ²IFLS Crop Systems Engineering, University of Southampton, Southampton, SO17 1BJ, UK.
6 ³Syngenta, Cambridge, CB21 5XE, UK. ⁴School of Mathematics, University of Southampton,
7 Southampton, SO17 1BJ, UK. ⁵School of Environment, Natural Resources and Geography, University
8 of Bangor, Bangor 57 2UW, UK. ⁶Agrii, GL54 4LZ, UK. ⁷ADAS Boxworth, Cambridge CB23 4NN, UK.
9 ⁸Crop & Soil systems, Scotland's Rural College, Aberdeen, AB21 9YA.

10 *Corresponding Author: jph106@soton.ac.uk (J. Heppell)

11 **Abstract: (299200/200)**

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 give insight into~~
16 optimis~~ing~~ 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 ~~above ground dry leaf~~
19 mass. We let P-dependent photosynthesis estimate carbon (C) mass, which in conjunction with
20 temperature sets 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 [to be made](#).

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 [crop](#) yields sustainably by manipulating the existing environment in which crops
35 are 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, 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.

Formatted: Font: Italic

Formatted: Font: Italic

Formatted: Font: Italic

97 **Materials and Methods**

98 **Experimental data**

99 Two barley field trial data sets are used, consisting of [leaf mass above ground dry mass](#) and plant P
100 uptake values at different growth stages (GS31, GS45 and GS91 for spring barley; GS39 and GS92 for
101 winter barley). [The experimental data includes different rates of P application \(0, 5, 10, 20, 30, 60, 90](#)
102 [kg P ha⁻¹ for spring barley; 0, 15, 30, 60, 90, 120 kg P ha⁻¹ for winter barley\) and both sites were](#)
103 [classified with an Olsen P index 1 soil.](#) -The protocol for this is described in Heppell *et al.* (2015). In
104 addition, we use the climate data, from the UK Met office Integrated Data Archive System (MIDAS),
105 to accompany the spring barley (Inverurie, Scotland) and winter barley (Cambridge, England) data
106 sets for the specific fields in the trial. The climate data consists of daily values for mean temperature
107 (°C), rainfall (mm), 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 [leaf](#) model which estimates [above ground dry leaf](#)
111 mass (based on Thornley, 1995), to produce a whole crop model. We first describe the root-soil
112 model (hereafter called the root model), followed by the leaf model and then our coupling process
113 to create a whole 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

Formatted: Superscript

Formatted: Superscript

120 down as the root becomes longer. Following Heppell *et al.* (2015) we also let the root growth rate (r)
121 be dependent upon [air](#) temperature T , [we detained from the MIDAS database.](#)

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 (S) (Eqn. 2) and
125 P (Eqn. 3) concentration (c) 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

Formatted: Font: Italic

Formatted: Font: Italic

142 are affected by the spatially and temporally evolving root structure. Water is only taken up by the
 143 main order roots [and the small region of first order roots near the branch point](#) while P is taken up
 144 by all roots; see Roose and Fowler (2004b) for details of the derivation. The equation for F_w is given
 145 by,

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

147 where ψ_1 is the density of first order roots on the main order roots, a_1 is the first order root radius,
 148 a is the main order root radius, L_1 is the maximum length of the first order branches, θ is the angle
 149 between the main root and the first order branches, k_r is the root radial water conductivity
 150 parameter ($\text{m s}^{-1} \text{Pa}^{-1}$), k_z is the root axial hydraulic conductivity calculated using Poiseuille law (m^4
 151 $\text{Pa}^{-1} \text{s}^{-1}$), p_c (Pa) is a characteristic suction pressure determined from experimental data for different
 152 types of soil, $f(S) = (s^{-1/m} - 1)^{1-m}$, where m is the Van Genuchten soil suction parameter (where
 153 $0 < m < 1$), and p_r is the root internal xylem pressure (Pa).

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

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

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

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

160 Eqn. 8
$$p_r = P \text{ at } z = 0,$$

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

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

164 The rate of plant P uptake is given by,

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

166 where F_0 and F_1 are the uptake rates for zero and first order roots; [see derived in](#) Roose *et al.*
167 (2004b) [for derivation](#).

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

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

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

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

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

175 In addition, we have a [zero flux](#) boundary condition for the concentration of P (c) at the soil surface,

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

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

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

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

180 The initial state of P concentration and water saturation in the soil is given, where possible, by the
181 initial soil data for the spring and winter barley experimental sites. A uniform water saturation
182 profile is initially set at $S = 0.3$ for the two experimental sites; however for the initial P

183 concentration ($c_0(z)$) we consider two different cases; (1) a uniform concentration and (2) an
184 exponentially decaying concentration:

185 Eqn. 16

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

186 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
187 the strength of the decay in the concentration of P (0.345). The initial P concentration values (C_A ,
188 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
189 Olsen P index 1 soil (Defra, 2010). To reflect the different fertiliser scenarios being used at each field
190 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
191 at a set depth below the soil (D_1) (P placement).

192 Eqn. 17

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

193 [With the soil P profile initialised \(Equations 16 and 17\) we are able to estimate \(belowground only\)](#)
194 [the water and P concentrations in the soil by solving Equations 1-15, as in Heppell *et al.*, 2014.](#)

Formatted: Font: Italic

195 Leaf growth model

196 We have altered a compartmental model developed by Thornley (1995) to describe leaf mass [\(a](#)
197 [proxy for above ground dry mass\)](#) M_L (kgL), leaf C M_C (kgC) and leaf P M_P (kgP) as well as the
198 concentration of free C [C] = M_C/M_L (kgC kgL⁻¹) and free P [P] = M_P/M_L (kgP kgL⁻¹) dynamics
199 within the leaves. The leaf model takes into account non-linear dynamics of formation of leaf litter
200 and leaf self-shading. Additionally we have made photosynthesis dependent upon P content in the
201 plant (Foyer and Spencer, 1986, Wissuwa *et al.*, 2005) and we have altered the leaf growth term, G_{sh} ,
202 [which was dependent on \[C\] and \[P\]](#), to also depend upon ~~the~~ air temperature (A_T), ~~for the~~ winter
203 [barley, but not for spring barley](#)), as well as ~~[C] and [P]~~. [We do not let air temperature affect spring](#)
204 [barley as the growing season is much shorter compared to winter barley and it appeared not to be](#)

205 [needed for a good fit to the experimental data.](#) The governing equations are given below and are
 206 represented in a flow diagram on Figure 1, i.e., we have

207 Eqn. 18
$$\frac{\partial M_L}{\partial t} = \overbrace{\widehat{G}_{sh}}^{\text{Leaf growth rate}} - \overbrace{\frac{K_{litt}}{1 + \frac{K_{litt}}{M_L}} M_L}_{\text{Leaf metabolism/litter}},$$

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

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

210 where,

211 Eqn. 21
$$\widehat{G}_{sh} = k_G M_L [C] [P] \frac{A_T^{s_1}}{s_2^{s_1} + A_T^{s_1}},$$

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

213 where k_g is the leaf growth rate, K_{litt} is the litter rate, K_{mlitt} is the litter Michaelis-Menten constant,
 214 K_C is the photosynthesis rate, k_M is the constant accounting for the leaf self-shading, J_C is the C
 215 product inhibition constant, f_c is the fraction of total C used for leaf growth, f_p is the fraction of total
 216 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
 217 photosynthesis, β_c is the rate of C output from the xylem to the phloem, β_p is the rate of P output to
 218 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
 219 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
 220 respectively.

221 Whole crop model

222 In order to provide feedback between the root model and leaf model, we allow C mass to affect the
 223 root growth rate. Increasing C mass will increase root growth which in turn will increase plant P

224 uptake. Through the process of photosynthesis, increasing plant P uptake will also increase C mass,
225 thus creating a positive feedback loop.

226 The order i root growth rate is now dependent on C as well as temperature, therefore we replace
227 Eqn. 1 with,

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

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

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

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

233 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
234 C effect and A is a fitting parameter determining the strength of temperature dependence on root
235 growth rate. Below critical temperature (5°C) there is no root growth and this reflects cold periods
236 over the winter (Sylvester-Bradley *et al.*, 2008).

237 [Fitting process Calibration](#)

238 The parameter list for the models above is given in Table 1. A subset of these parameters are fitted
239 to the experimental data and their values can be seen in Table 2. To begin the [fitting](#)
240 [procedure calibration process](#), the leaf model is first fit against the experimental [leaf-above ground](#)
241 [dry](#) mass data, by changing 4-6 parameters (β_c, k_1, f_c, f_p for spring barley and in addition s_1 and s_2
242 for winter barley). In the leaf model only, we set the rate of P entry from the xylem ($F(c, z, t)$, Eqn.
243 10) proportional to the experimental plant P uptake to simulate a representative plant P root uptake.
244 We then combine the models, i.e. let the rate of P entry from the xylem be estimated from the root
245 model, and fit for the remaining parameters (γ_c and α_c).

246 During the [fitting process calibration step](#) we minimise the sum of squares value between the
247 plant P uptake and [leaf above ground dry](#) mass values against the experimental data values for ~~each~~
248 [control and maximum](#) applied P scenario (0 and 90/120 kg P ha⁻¹ respectively). [With the fitted](#)
249 [parameters we then run the model for all applied P scenarios.](#)

250 The differences between modelling spring barley and winter barley are the time they are grown for
251 (151 and 313 days, respectively), the initial P profile in the soil (20 mg P l⁻¹ decay profile and 16 mg P
252 l⁻¹ constant profile, respectively) and leaf growth dependence (also depending upon air temperature
253 for winter barley).

254 **Results**

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

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

268 When considering plant P uptake in winter barley, the coupled model behaves similarly to the root
269 model (Figure 3). At GS92, both models under-predict plant P uptake for the same reasons as stated

270 in Heppell *et al.* (2015); the P profile is depleted which limits the amount of P available for uptake,
271 and perhaps the total amount of P in the soil was different to that estimated by the one soil test for
272 the whole site (Olsen P index 1). The effect of slow release P pools in the soil was not taken into
273 consideration due to the fact experimental data for this phenomenon was not available.

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

287 The leaf model component allows us to estimate P (Figure 6) and C mass (Figure 7) in the above
288 ground tissue over the growing period of the crop. The estimated P mass is higher in the leaf model
289 compared to the coupled model for both spring and winter barley. The estimated C mass is higher in
290 the leaf model compared to the coupled model for winter barley, but the other way around for
291 spring barley. In the winter barley case, the increased C and P masses in the leaf model are due to
292 higher plant P uptake values (Figure 3 compared to Figure 2) resulting in a larger end [above ground](#)
293 [dry](#)leaf mass. For spring barley, C mass in the coupled model begins lower and ends higher
294 compared to the leaf model because plant P uptake by the root system also begins lower and ends

295 higher (P uptake remains constant in the leaf model). The sudden decrease in C and P mass, for
296 winter barley, around the 250 day mark is due to the enforced halting of the root growth rate.

297 The root growth rate is affected by C mass (spring barley) and also temperature (winter barley);
298 therefore different final root lengths can be observed between model simulations (Figure 8). The
299 leaf model created a longer root length compared to the coupled model in the winter barley
300 scenario due to the early differences in C mass. For spring barley, the early C mass values for the
301 coupled and leaf model were similar resulting in almost identical root growth rates and hence final
302 root lengths. As C mass increases above a certain value any differences are masked when affecting
303 the root growth rate. There was little difference in root length between the two different fertiliser
304 applications (0 and 90/120 kg P ha⁻¹), the largest being between the coupled model for winter barley
305 GS92. Due to the small increase in plant P uptake between scenarios (0 and 120 kg P ha⁻¹) there was
306 little effect on increasing root length via the slow feedback loop created by the addition of the leaf
307 model. Chemotropism effects from adding large amounts of P fertiliser could perhaps explain any
308 differences between plant P uptake values at early growth stages. In the winter barley scenario, as
309 root growth rate was dependent upon temperature, we see periods of no root growth matching
310 periods of low temperature, as expected.

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

320 **Discussion**

321 In order to obtain a more accurate representation of the growth of barley throughout a crop life
322 cycle we have combined a below ground root-soil model with an above ground leaf model. By
323 combining the two models we are able to let an above ground process (photosynthesis) affect a
324 below ground process (root growth) and vice versa. C is created via photosynthesis in the leaf model
325 (dependent upon [above ground dry leaf mass](#) and P) and stimulates root growth; increased root
326 growth increases plant P uptake and hence [above ground dry leaf mass](#). This positive feedback effect
327 could explain why crops with early plant P uptake levels grow more vigorously and can produce
328 higher yields (Brenchley, 1929; Boatwright and Viets, 1966; Green *et al.*, 1973; Grant *et al.*, 2001).
329 Due to possible unfavourable (e.g. dry) weather conditions, maximising early plant P uptake through
330 greater root proliferation is also a good strategy to help ensure continuing capture of soil resources
331 at later stages of growth.

332 From the modelling work conducted we can postulate that the whole crop model accurately
333 estimates [above ground dry mass leaf mass](#) at all growth stages given it has accurate estimates of
334 plant P uptake (an average difference of 4.6% for the whole crop model for [above ground dry leaf](#)
335 mass, compared to 15.8% when using values one standard deviation away from the experimental
336 data). Using the calibrated whole crop model we found the optimal fertiliser and cultivation scenario
337 is to use a plough and place the P fertiliser. The largest increase in plant P uptake when placing
338 fertiliser over incorporating fertiliser was 9.6% (plough, dry climate). The difference between
339 incorporating and placing has been long studied and depends upon a range of criteria such as soil P
340 concentration, soil temperature, crop species and price (Devine *et al.*, 1964; Mahler, 2001). Owusu-
341 Gyimah *et al.* (2013) found that applying fertiliser at a depth of 10 cm and 20 cm away from the
342 plant (placed P) gave the best outcome for maize growing under tropical conditions. By placing
343 fertiliser instead of incorporating it throughout the soil the available P is being put where the root
344 system is going to grow hoping to ensure early plant P uptake and a more successful crop. Hence

345 Wager et al. (1986) found that P fertilizer application rates could be halved by placing fertiliser
346 instead of incorporation because the applied P was more efficiently used. However, optimal fertiliser
347 and cultivation methods depend on the initial soil P condition/distribution (Randall and Hoeft, 1988);
348 this includes at the depth at which existing P is initially available within the soil (Heppell *et al.*, 2015).

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

371 better optimised treatments through targeting P use (Yang *et al.*, 2013; Withers *et al.*, 2014).
372 Furthermore, since crop and fertiliser management have long-term effects on topsoil and subsoil P
373 availability (Bolland and Baker, 1998), it will be important to validate the model over several years if
374 it is to improve on current simpler approaches to decision making. Additional model features would
375 be needed, such as effects between cropping seasons, but would make for a more overall
376 accomplished model. We note that the model would have to be calibrated separately for different
377 crops.

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

392 Potentially, new ways to improve efficiency use of P can now be developed by combining recent
393 advances in application technology, sensing technology, geo-spatial information and modelling so as
394 to apply P where it is needed and importantly not apply it where it is not needed. Precision farming
395 equipment is being widely adopted; now, its effective deployment depends on whether the vast

396 amount of data available about a given plot of land can be interpreted to improve the precision and
397 decrease the risks compared to current decision making (Sylvester-Bradley *et al.*, 1999). For example,
398 soil nutrient maps, past yield maps, soil and canopy sensors and climate predictions may provide
399 input data for integrated crop models to output quantitative predictions of fertiliser requirements so
400 that application as sowing can be adjusted in real time. However, the more immediate and
401 preliminary prospect is of using simulation models to compare scenarios of possible treatments, to
402 help guide future soil and fertiliser management strategies, and to accompany continuing field
403 testing.

404 **Acknowledgements**

405 We would like to thank the BBSRC and DEFRA (BB/I024283/1) for funding S.P. and The Royal Society
406 University Research Fellowship for funding T.R. K.C.Z. was partially funded by Award No. KUK-C1-13-
407 04 of the King Abdullah University of Science and Technology (KAUST); J.H. by EPSRC Postdoctoral
408 Prize Fellowship; and S.P., P.T., D.L., R.S-B., R.W., D.L.J. and T.R. by DEFRA, BBSRC, Scottish
409 Government, AHDB, and other industry partners through Sustainable Arable LINK Project LK09136.

410 **References**

- 411 **Barber S (1984)** Soil nutrient bioavailability: a mechanistic approach. Wiley-Interscience.
- 412 **Bhadoria P, Kaselowsky J, Claassen N, Jungk A (1991)** Soil Phosphate Diffusion Coefficients: Their
413 Dependence on Phosphorus Concentration and Buffer Power. *Soil Science of America Journal*
414 **55(1):56-60.**
- 415 **Blackmore S (2014)** Address to the Oxford Farming Conference. 8 January 2014. See
416 <http://www.ofc.org.uk/videos/2014/vision-farming-robots-2050> last accessed 07/09/2015.
- 417 **Boatwright G, Viets F (1966)** Phosphorus absorption during various growth stages of spring wheat
418 and intermediate wheatgrass. *Agronomy Journal* **58:185–188.**

419 **Bolland M, Baker M (1998)** Phosphate applied to soil increases the effectiveness of subsequent
420 applications of phosphate for growing wheat shoots. *Australian Journal of Experimental*
421 *Agriculture* **38(8)**:865-869.

422 **Brenchley W (1929)** The phosphate requirement of Barley at different periods of growth. *Annals of*
423 *Botany* **43**:89–112.

424 **Brown L (2012)** Outgrowing the Earth: The Food Security Challenge in an Age of Falling Water Tables
425 and Rising Temperatures. Taylor & Francis. ISBN 1-84407-185-5.

426 **Conway G, Barbier E (1990)** After the Green Revolution: Sustainable Agriculture for Development.
427 Earthscan, London, UK. ISBN: 978-1-84971-930-8.

428 **Cordell D, Drangert J, White S (2009)** The story of phosphorus: Global food security and food for
429 thought. *Global Environmental Change* **19**:292-305.

430 **Defra (2010)** Fertiliser Manual (RB209), 8th Edition. The Stationary Office, London.

431 **De Luca T, Glanville H, Harris M, Emmett B, Pingree M, De Sosa L, Morena C, Jones D (2015)** A novel
432 rhizosphere trait-based approach to evaluating soil phosphorus availability across complex
433 landscapes. *Soil Biology and Biochemistry* **88**:110-119.

434 **Déry P, Anderson B (2007)** Peak phosphorus. In: Energy Bulletin, 08/13/2007. Post Carbon Institute.
435 Available: energybulletin.net/node/33164.

436 **Devine JJ, Gilkes R, Holmes MRJ (1964)** Field experiments on the phosphate requirements of Spring
437 wheat and barley. *Experimental Husbandry* **11**:88-97.

438 **Drew MC (1975)** Comparison of the effects of a localised supply of phosphate, nitrate, ammonium
439 and potassium on the growth of the seminal root system, and the shoot in Barley. *New*
440 *Phytologist* **75**:479-490.

441 **Dunbabin V, Postma J, Schnepf A, Pagès L, Javaux M, Wu L, Leitner D, Chen Y, Rengel Z, Diggle A**
442 **(2013)** Modelling root-soil interactions using three-dimensional models of root growth,
443 architecture and function. *Plant and soil* **372**:93-124.

444 **Foyer C, Spencer C (1986)** The relationship between phosphate status and photosynthesis in leaves.
445 *Planta* **167**(3):369-375.

446 **George T, Brown L, Newton A, Hallett P, Sun B, Thomas W, White P (2011)** Impact of soil tillage on
447 the robustness of genetic component of variation in phosphorus (P) use efficiency in barley
448 (*Hordeum vulgare* L.) *Plant and Soil* **339**:113-123.

449 **Grant C, Flaten D, Tomaszewicz D, Sheppard S (2001)** The importance of early season phosphorus
450 nutrition. *Canadian Journal of Plant Science* **81**:211–224.

451 **Green D, Ferguson W, Warder F (1973)** Accumulation of toxic levels of phosphorus in the leaves of
452 phosphorus-deficient barley. *Canadian Journal of Plant Science* **53**:241–246.

453 **Greenwood D, Karpinets T, Stone D (2001)** Dynamic Model for the Effects of Soil P and Fertilizer P
454 on Crop Growth, P Uptake and Soil P in Arable Cropping: Model Description. *Annals of Botany*
455 **88**:279-291.

456 **Heppell J, Payvandi S, Zygalkis K, Smethurst J, Fliege J, Roose T (2014)** Validation of a spatial-
457 temporal soil water movement and plant water uptake model. *Geotechnique* **64**(7):526–539.

458 **Heppell J, Payvandi S, Talboys P, Zygalkis K, Fliege J, Langton D, Sylvester-Bradley R, Walker R,**
459 **Jones DL, Roose T (2015)** Modelling the optimal phosphate fertiliser and soil management
460 strategy for crops. *Plant and Soil special edition PSP5*. DOI: 10.1007/s11104-015-2543-0.

461 **Hooda P, Truesdale V, Edwards A, Withers P, Aitken M, Miller A, Rendell A (2001)** Manuring and
462 fertilization effects on phosphorus accumulation in soils and potential environmental implications.
463 *Advances in Environmental Research* **5**(1):13-21.

464 **Jeuffroy M, Vocanson A, Roger-Estrade J, Meynard J (2012)** The use of models at field and farm
465 levels for the ex ante assessment of new pea genotypes. *European Journal of Agronomy* **42**:68-78.

466 **Jobbágy E, Jackson R (2001)** The distribution of soil nutrients with depth: Global patterns and the
467 imprints of plants. *Biogeochemistry* **53**(1):51-77.

468 [Jones J, Hoogenboom G, Porter C, Boote K, Batchelor W, Hunt L, Wilkens P, Singh U, Gijsman A,](#)
469 [Ritchie J \(2003\) The DSSAT cropping system model. *European Journal of Agronomy* **18**:235-265.](#)

470 **Jordan-Meille L, Rubæk G, Ehlert P, Genot V, Hofman G, Goulding K, Recknagel J, Provolò G,**
471 **Barraclough P (2012)** An overview of fertilizer – P recommendations in Europe: soil testing,
472 calibration and fertilizer recommendations. *Soil Use and Management* **28**(4):419-435.

473 [Keating B, Carberry P, Hammer G, Probert M, Robertson M, Holzworth D, Huth N, Hargreaves J,](#)
474 [Meinke H, Hochman Z, McLean G, Verburg K, Snow V, Dimes J, Silburn M, Wang E, Brown S,](#)
475 [Bristow K, Asseng S, Chapman S, McCown R, Freebairn D, Smith C \(2003\) An overview of APSIM,](#)
476 [a model designed for farming systems simulation. *European Journal of Agronomy* **18**\(3-4\):267-](#)
477 [288.](#)

478 **Kuchenbuch RO, Buczko U (2011)** Re-visiting potassium- and phosphate-fertilizer responses in field
479 experiments and soil-test interpretations by means of data mining. *Journal of Plant Nutrition and*
480 *Soil Science* **174**:171-185.

481 **Lohry R (1998)** Surface Banding superior To Broadcasting on Reduced-Till. *Fluid Journal* **22**:14-18.

482 **Lynch J (2007)** Roots of the second green revolution. *Australian Journal of Botany* **55**:493-512.

483 **Mahler R (2001)** Fertilizer Placement. CIS. Soil Scientist, Department of plant, Soil, and
484 Entomological Sciences, University of Idaho.

485 **Neyroud J, Lischer P (2002)** Do different methods used to estimate soil phosphorus availability
486 across Europe give comparable results? *Journal of Plant Nutrition Soil Science* **166**(4):422-431.

Formatted: Font: Not Bold

487 **Nye P, Tinker P (1977)** Solute movement in the soil-root system. Blackwell Science Publishers.

488 **Owusu-Gyimah V, Nyatuame M, Ampiaiw F, Ampadu P (2013)** Effect of depth and Placement
489 Distance of Fertilizer NPK 15-15-15 on the Performance and Yield of Maize Plant. *International*
490 *Journal of Agronomy and Plant Production*. **4**(12):3197-3204.

491 **Randall G, Hoelt R (1988)** Placement Methods for Improved Efficiency of P and K Fertilizers: A
492 Review. *Journal of Production Agriculture* **1**(1):70-79.

493 **Roose T, Fowler A, Darrah P (2001)** A mathematical model of plant nutrient uptake. *Mathematical*
494 *Biology* **42**(4):347-360.

495 **Roose T, Flower A (2004a)** A model for water uptake by plant roots. *Journal of Theoretical Biology*
496 **288**:155-171.

497 **Roose T, Fowler A (2004b)** A mathematical model for water and nutrient uptake by plant root 567
498 systems. *Journal of Theoretical Biology* **288**:173-184.

499 **Selmants P, Hart S (2010)** Phosphorus and soil development: Does the Walker and Syers model
500 apply to semiarid ecosystems? *Ecology* **91**(2):474-484.

501 **Sylvester-Bradley R (1991)** Modelling and mechanisms for the development of agriculture. Aspects
502 of Applied Biology 26, The Art and Craft of Modelling in Applied Biology, 55-67.

503 **Sylvester-Bradley R, Lord EI, Sparkes D, Scott RK, Wiltshire JJ, Orson JO (1999)** An analysis of
504 precision farming in Northern Europe. *Soil Use and Management* **15**:1-9.

505 **Sylvester-Bradley R, Berry P, Blake J, Kindred D, Spink J, Bingham I, McVittie J, Foulkes J (2008)** The
506 wheat growth guide, Spring 2008, 2nd edition. HGCA, London 30pp
507 <http://www.hgca.com/media/185687/g39-the-wheat-growth-guide.pdf>, last accessed
508 12/09/2014.

509 **Tandy S, Mundus S, Yngvesson J, de Bang T, Lombi E, Schjoerring J, Husted S (2011)** The use of DGT
510 for prediction of plant available copper, zinc and phosphorus in agricultural soils. *Plant and Soil*
511 **346**(1-2):167-180.

512 **Thornley JH (1995)** Shoot: root allocation with respect to C, N and P: an investigation and
513 comparison of resistance and teleonomic models. *Annals of Botany* **75**(4):391-405.

514 **Vaccari D (2009)** Phosphorus: a looming crisis. *Scientific American* **300**:54-49.

515 **Valkama E, Uusitalo R, Turtola E (2011)** Yield response models to phosphorus application: a
516 research synthesis of Finnish field trials to optimize fertilizer P use of cereals. *Nutrient Cycling in*
517 *Agroecosystems* **91**:1–15.

518 **Van Genuchten M (1980)** A closed-form equation for predicting the hydraulic conductivity of
519 unsaturated soil. *Soil Science Society of America Journal*, **44**(5):892-898.

520 **Van Rotterdam A, Temminghoff E, Schenkeveld W, Hiemstra T, Riemsdijk W (2009)** Phosphorus
521 removal from soil using Fe oxide-impregnated paper: Processes and applications. *Geoderma*
522 **151**(3-4):282-289.

523 **Van Rotterdam A, Bussink D, Reijneveld J (2014)** Improved Phosphorus Fertilisation Based on Better
524 Prediction of Availability in Soil. International Fertiliser Society, Proceeding 755, ISBN 978-0-
525 85310-392-9.

526 **Vance C, Uhde-Stone C, Allan D (2003)** Phosphorus acquisition and use: critical adaptations by
527 plants for securing a non-renewable resource. *New Phytologist* **157**:423-447.

528 **Wager BI, Stewart JWB, Henry JL (1986)** Comparison of single large broadcast and small annual
529 seed-placed phosphorus treatments on yield and phosphorus and zinc contents of wheat on
530 Chernozemic soils. *Canadian Journal of Soil Science* **66**:237–248.

- 531 **Wissuwa M, Gamat G, Ismail AM (2005)** Is root growth under phosphorus deficiency affected by
532 source or sink limitations? *Journal of experimental botany* **56**(417):1943-1950.
- 533 **Withers PJA, Sylvester-Bradley R, Jones DL, Healey JR, Talboys PJ (2014)** Feed the crop not the soil:
534 rethinking phosphorus management in the food chain. *Environmental Science and Technology*
535 **48**:6523-6530.
- 536 **Withers PJA, van Dijk KC, Neset T-SS, Nesme T, Oenema O, Rubæk GH, Schoumans OF, Smit B,**
537 **Pellerin S (2015)** Stewardship to tackle global phosphorus inefficiency: The case of Europe.
538 *AMBIO* 44 (Suppl.):S193-S206.
- 539 **Yang X, Post W, Thornton P, Jain A (2013)** The distribution of soil phosphorus for global
540 biogeochemical modeling. *Biogeosciences Discussions* **9**(11):16347-16380.

541

542

543

544

545

546

547

548

549 **List of Figures**

550 **Figure 1:** A flow diagram for the leaf model which estimates phosphate, ~~leaf and~~ carbon and above
551 ground dry mass as mathematically described by Eqn. 18-22.

552 **Figure 2:** Spring barley plant P uptake experimental data values for different applied P rates (0, 5, 10,
553 20, 30, 60 and 90 kg P ha⁻¹) with standard deviation, compared against estimates from the coupled
554 model and root model at GS31, 45, 91.

555 **Figure 3:** Winter barley plant P uptake experimental data values for different applied P rates (0, 15,
556 30, 60, 90 and 120 kg P ha⁻¹) with standard deviation, compared against estimates from the couple
557 model and root model at GS39 and 92.

558 **Figure 4:** Spring barley [above ground dryleaf](#) mass experimental data values for different applied P
559 rates (0, 5, 10, 20, 30, 60 and 90 kg P ha⁻¹) with standard deviation, compared against estimates from
560 the coupled model and leaf model at GS31, 45, 91.

561 **Figure 5:** Winter barley [above ground dryleaf](#) mass experimental data values for different applied P
562 rates (0, 15, 30, 60, 90 and 120 kg P ha⁻¹) with standard deviation, compared against estimates from
563 the coupled model and leaf model at GS39 and 92.

564 **Figure 6:** Estimated [above ground](#) phosphate mass values from the coupled model and leaf model
565 for a) spring barley and b) winter barley at GS91, 92 respectively for 0 kg P ha⁻¹ and 90/120 kg P ha⁻¹.

566 **Figure 7:** Estimated [above ground](#) carbon mass values from the coupled model and leaf model for a)
567 spring barley and b) winter barley at GS91, 92 respectively for 0 kg P ha⁻¹ and 90/120 kg P ha⁻¹.

568 **Figure 8:** Estimated plant root length values from the root model, coupled model and leaf model for
569 a) spring barley and b) winter barley at GS91, 92 respectively for 0 kg P ha⁻¹ and 90/120 kg P ha⁻¹.

570 **Figure 9:** Estimated plant P uptake values for winter barley at GS92 for a set of fertiliser and soil
571 management strategies (mix 25, 20 and 10cm, inverted plough, minimum tillage and no cultivation,
572 and either no fertiliser, 90 kg P ha⁻¹ incorporated or 90 kg P ha⁻¹ placed) for a normal climate and a
573 wetter climate ([x5 flux of water at soil surface](#)).

574 **List of Tables**

575 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	°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	-

576

577 **Table 2: The fitted parameter set for the leaf and coupled models, for spring barley and winter**
578 **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