Optimizing reproductive phenology in a two-resource world: a dynamic allocation model of plant growth predicts later reproduction in phosphorus-limited plants

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INTRODUCTION

The timing of reproduction is a key life-history trait that is regulated by resource availability. Delayed reproduction in soils with low phosphorus availability is common among annuals, in contrast to the accelerated reproduction typical of other low-nutrient environments. It is hypothesized that this anomalous response arises from the high marginal value of additional allocation to root growth caused by the low mobility of phosphorus in soils.

Methods To better understand the benefits and costs of such delayed reproduction, a two-resource dynamic allocation model of plant growth and reproduction is presented. The model incorporates growth, respiration, and carbon and phosphorus acquisition of both root and shoot tissue, and considers the reallocation of resources from senescent leaves. The model is parameterized with data from Arabidopsis and the optimal reproductive phenology is explored in a range of environments.

Key Results The model predicts delayed reproduction in low-phosphorus environments. Reproductive timing in low-phosphorus environments is quite sensitive to phosphorus mobility, but is less sensitive to the temporal distribution of mortality risks. In low-phosphorus environments, the relative metabolic cost of roots was greater, and reproductive allocation reduced, compared with high-phosphorus conditions. The model suggests that delayed reproduction in response to low phosphorus availability may be reduced in plants adapted to environments where phosphorus mobility is greater.

Conclusions Delayed reproduction in low-phosphorus soils can be a beneficial response allowing for increased acquisition and utilization of phosphorus. This finding has implications both for efforts to breed crops for low-phosphorus soils, and for efforts to understand how climate change may impact plant growth and productivity in low-phosphorus environments.

Key words: Dynamic allocation budget, optimization, Arabidopsis thaliana, flowering phenology, root–shoot partitioning, phosphorus availability.

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diffusion is the primary mode of phosphorus transport to roots. Mechanistic models estimate that over 90% of phosphorus acquired by roots is acquired by diffusion (Barber, 1995). Phosphorus uptake via diffusion is maximized by increasing root exploration of virgin soil (which reduces the distance over which phosphorus must diffuse to reach a root), and by increasing time during which diffusion may occur. The reduction in vegetative (and hence root) growth that accompanies the transition to reproductive growth has the potential to limit phosphorus acquisition, and delaying reproduction might be disproportionately beneficial for phosphorus acquisition.

Annual plants in stressful conditions generally flower and mature earlier than plants in benign conditions (Pigliucci and Schlichting, 1995; Gungula et al., 2003; Callahan and Pigliucci, 2005). Several models of plant phenology predict this response (Cohen, 1976; Amir and Cohen, 1990). In contrast, low phosphorus availability typically delays plant phenology (Rossiter, 1978; Shepherd et al., 1987; Ma et al., 2002). Nord and Lynch (2008) showed that delayed phenology may be an adaptive response to low phosphorus availability in Arabidopsis thaliana, by allowing more time for phosphorus acquisition and utilization.

The degree to which nutrients in vegetative tissue can later be reallocated to reproduction is important in determining how nutrient allocation to vegetative growth affects subsequent reproduction. Nutrients are typically reallocated from leaves as part of the leaf senescence programme. Both nitrogen and phosphorus resorption from leaves can be highly efficient with reported values of up to 90% (Aerts et al., 1992; Aerts, 1996; Aerts and Chapin, 2000). The high rates of reproductive tissue growth in annuals should mean that sink strength would be high, potentially increasing resorption efficiency. Just how this reallocation is affected by phosphorus availability is unclear. In one study with common bean, leaf phosphorus remobilization occurred earlier under phosphorus deficiency (Snapp and Lynch, 1996).

It appears that root nutrients are not reallocated, or are reallocated with very low efficiency. Aerts seeds (Snapp and Lynch, 1996), and do not exhibit pro-co-ordinated growth of root and shoot, although they do not include the transition to reproductive growth.

Although several models have addressed the optimal phenology of reproduction in plants, we are aware of none that have addressed the optimization of reproductive phenology while considering the mobility and uptake dynamics of soil resources. Such a model would be a useful tool for understanding the importance of phenological delays in response to low-phosphorus environments. The consequences of low phosphorus for optimization of reproductive phenology could be quite different than those of water or nitrogen limitation because the mobility of phosphorus in soil differs markedly from those of water and nitrogen. In addition, because phosphorus remobilized from leaves to seeds represents an important source of seed nutrients (potentially at a cost of reduced photosynthetic capacity), the timing of leaf senescence may be important in attempting to understand the observed phenological responses to low phosphorus availability. Here, a model of plant growth and resource allocation is presented, which considers phosphorus acquisition by roots, carbon acquisition by shoots, reproductive growth and seed production, and leaf senescence. The model is quite general, and should be applicable to many monocarpic plants. This model is used to test the hypothesis that delayed reproduction in low-phosphorus environments can be a beneficial response to limitation of growth by a low-mobility soil nutrient, based on a case study of Arabidopsis thaliana. We also use the model to consider under what conditions low phosphorus availability may favour later reproduction.

METHODS

A dynamic energy budget framework (Kooijman, 2000) is used to model the optimal timing of reproduction when roots acquire a low-mobility soil resource and shoots acquire carbon. This modelling framework is very flexible and has been used to model acquisition and utilization of multiple resources (Cordes et al., 2003, 2005). The model is a discrete time model that tracks daily changes in carbon and phosphorus in each of five organ categories: root, stem, leaves, reproductive tissue (excluding mature seeds) and (mature) seeds (Fig. 1). Roots acquire phosphorus, stem and leaves acquire carbon, and all tissues require both carbon and phosphorus for growth and carbon for respiration. It is assumed that the ratio of carbon and phosphorus is fixed for each organ category, and that growth of each organ category is limited either by the pool of acquired carbon or by phosphorus available for growth. The processes in the model for simulation of resource acquisition, resource allocation, organ growth, survival, and senescence are presented here.

Table 1 summarizes the assumptions upon which the model is based, Table 2 lists the variables in the model, and Table 3 lists the parameters the model requires, and the values used in the simulations. Note that the model requires a large number of variables and parameters so compound symbols are required to represent them. The parameters are generally either easily measured, or estimable from easily obtained data. The model was implemented and optimized in R (version 2.6; R Development Core Team, 2008).
Resource acquisition

Phosphorus acquisition at each time step \( P_{\text{up}(t)} \) is modelled as a function of maximal phosphorus uptake rate per unit of root carbon, the rate of decline in phosphorus uptake with root age, and the size and age distribution of the root carbon pool.

\[
P_{\text{up}(t)} = P_{\text{max}}(p \cdot c)
\]
Where $P_{\text{max}}$ is the maximum phosphorus uptake rate, $p$ is the vector of efficiency of root phosphorus uptake for root segment ages 1 to $t$, and $c$ is the vector of allocation of carbon to the roots from time $t$ to 1.

Older root segments acquire phosphorus at a reduced rate because of depletion of available phosphorus in the rhizosphere, which results in the formation of depletion zones around the roots. The maximal phosphorus uptake rate, and the root age-related decline in phosphorus acquisition at a given concentration of soil phosphorus is estimated using the Barber–Cushman model (Barber, 1995; see the Appendix for the parameters used in the model). The Barber–Cushman model integrates Michaelis–Menten transport kinetics with water flux and nutrient diffusion processes in the soil to estimate the nutrient uptake by a segment of root over time. To avoid repeatedly re-running the Barber–Cushman model, the decline in root efficiency was approximated over time (as predicted by the Barber–Cushman model) with an exponential decline function, scaled to approach a minimum value within a given time ($t_{\text{Pmin}}$). The fractional phosphorus uptake rate for a root segment of given age $[P(t)]$ is given by:

$$P(t) = P_{\text{min}} + (1 - P_{\text{min}})^{0.01 \times P_{\text{min}} \left(1 - \frac{t}{t_{\text{Pmin}}}\right)}$$

where $P_{\text{min}}$ is the minimum acquisition rate of old tissue (as a fraction of $P_{\text{max}}$), and $t_{\text{Pmin}}$ is the time at which $P$ is within 1 %

Table 3. Description of parameters in the model, the values used in simulation, and the sources of the parameters

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>HP</th>
<th>LP</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>$Z_{stm}$</td>
<td>Stem C : P ratio</td>
<td>60</td>
<td>130</td>
<td></td>
</tr>
<tr>
<td>$Z_{lf}$</td>
<td>Leaf C : P ratio</td>
<td>60</td>
<td>130</td>
<td></td>
</tr>
<tr>
<td>$Z_{rep}$</td>
<td>Reproductive C : P ratio</td>
<td>60</td>
<td>90</td>
<td></td>
</tr>
<tr>
<td>$Z_{stem}$</td>
<td>Seed C : P ratio</td>
<td>70</td>
<td>80</td>
<td></td>
</tr>
<tr>
<td>$f_{stem}$</td>
<td>Fraction of shoot biomass in stem (fraction)</td>
<td>0.05</td>
<td>0.05</td>
<td></td>
</tr>
<tr>
<td>$P_{\text{max}}$</td>
<td>Max phosphorus-uptake rate (mg P mg Rtc$^{-1}$ d$^{-1}$)</td>
<td>0.0235</td>
<td>0.00366</td>
<td></td>
</tr>
<tr>
<td>$P_{\text{min}}$</td>
<td>Min phosphorus-uptake rate (fraction of max)</td>
<td>0.985</td>
<td>0.80</td>
<td></td>
</tr>
<tr>
<td>$t_{\text{Pmin}}$</td>
<td>Time of min phosphorus uptake (d)</td>
<td>15</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>$A_{\text{max}}$</td>
<td>Max C assimilation (mg C mg leaf C$^{-1}$ d$^{-1}$)</td>
<td>0.463</td>
<td>0.463</td>
<td></td>
</tr>
<tr>
<td>$A_{\text{min}}$</td>
<td>Min C assimilation (fraction of max)</td>
<td>0.01</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td>$g_{A}$</td>
<td>Steepness of C assimilation decline</td>
<td>0.3</td>
<td>0.3</td>
<td></td>
</tr>
<tr>
<td>$k_{A}$</td>
<td>C assimilation half-max (d)</td>
<td>20</td>
<td>20</td>
<td></td>
</tr>
<tr>
<td>$A_{\text{rep}}$</td>
<td>C assimilation of reproductive organs (fraction of A)</td>
<td>0.15</td>
<td>0.15</td>
<td></td>
</tr>
<tr>
<td>$R_{rt}$</td>
<td>Root maintenance resp.</td>
<td>0.0643</td>
<td>0.0643</td>
<td></td>
</tr>
<tr>
<td>$R_{stm}$</td>
<td>Stem maint. resp.</td>
<td>0.0643</td>
<td>0.0643</td>
<td></td>
</tr>
<tr>
<td>$R_{lf}$</td>
<td>Leaf maint. resp.</td>
<td>0.0643</td>
<td>0.0643</td>
<td></td>
</tr>
<tr>
<td>$R_{rep}$</td>
<td>Reprod. maint. resp.</td>
<td>0.0964</td>
<td>0.0964</td>
<td></td>
</tr>
<tr>
<td>$R_{g}$</td>
<td>Growth respiration</td>
<td>0.1932</td>
<td>0.1932</td>
<td></td>
</tr>
<tr>
<td>$R_{old}$</td>
<td>Respiration rate for old leaf tissue (fraction)</td>
<td>0.3</td>
<td>0.3</td>
<td></td>
</tr>
<tr>
<td>$T_{ad}$</td>
<td>Time lag to mature seed (d)</td>
<td>10</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>$f_{ad}$</td>
<td>Fraction of reproductive resources in seeds (fraction)</td>
<td>0.39</td>
<td>0.42</td>
<td></td>
</tr>
<tr>
<td>$g_{S}$</td>
<td>Steepness of decline in survival</td>
<td>0.1</td>
<td>0.1</td>
<td></td>
</tr>
<tr>
<td>$k_{S}$</td>
<td>Survival half-max (d)</td>
<td>79</td>
<td>79</td>
<td></td>
</tr>
<tr>
<td>$f_{sx}$</td>
<td>Fixed leaf cost (fraction)</td>
<td>0.65</td>
<td>0.42</td>
<td></td>
</tr>
<tr>
<td>$D$</td>
<td>Initial rate of resource remobilization (d$^{-1}$)</td>
<td>0.1</td>
<td>0.1</td>
<td></td>
</tr>
<tr>
<td>$D_{\text{max}}$</td>
<td>Max rate of resource remobilization (d$^{-1}$)</td>
<td>0.3</td>
<td>0.3</td>
<td></td>
</tr>
<tr>
<td>$G_{\text{max}}$</td>
<td>Max shoot growth rate (mg C d$^{-1}$)</td>
<td>28</td>
<td>14</td>
<td></td>
</tr>
<tr>
<td>$r_{\text{max}}$</td>
<td>Max canopy radius (cm)</td>
<td>6</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>$L_{\text{max}}$</td>
<td>Max leaf area index (LAI)</td>
<td>4</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td>$T_{D}$</td>
<td>Max reproductive transition length (d)</td>
<td>10</td>
<td>10</td>
<td></td>
</tr>
<tr>
<td>$K$</td>
<td>Light extinction by one layer of leaf tissue (fraction)</td>
<td>0.65</td>
<td>0.65</td>
<td></td>
</tr>
<tr>
<td>$C_{\text{den}}$</td>
<td>Carbon density of leaf tissue on an area basis (mg C cm$^{-2}$)</td>
<td>1.31</td>
<td>1.31</td>
<td>Empirical data from Nord and Lynch (2008).</td>
</tr>
</tbody>
</table>
of \( P_{\text{maint}} \). This use of the Barber–Cushman model to estimate the decline in phosphorus uptake as roots deplete the phosphorus in the rhizosphere soil provides a relatively simple way to estimate the decline in phosphorus uptake caused by depletion, and a way to estimate phosphorus-uptake parameters that represent known soil characteristics. Note that individual roots are not explicitly modelled – instead the size and age distribution of the pool of root carbon is modelled.

Carbon acquisition at each time step is a function of maximal carbon fixation rate, leaf mass, leaf age distribution, and the decline of leaf carbon fixation efficiency with age, analogous to eqn (1). The principal difference is that there are pools of ‘old’ leaf carbon and phosphorus (leaf carbon or phosphorus enter the ‘old’ pool when carbon uptake is less than maintenance cost). The fractional carbon assimilation rate of leaf tissue of a given age \( A_{(i)} \) was modelled with a scaled sigmoidal curve:

\[
A_{(i)} = A_{\text{min}} + (1 - A_{\text{min}}) \left( \frac{\exp[-g_A(t - k_A)]}{1 + \exp[-g_A(t - k_A)]} \right)
\]

where \( A_{\text{min}} \) is the minimum efficiency of oldest leaves, \( g_A \) is the steepness of the efficiency decline, \( k_A \) is the age at 50 % of efficiency decline, and \( t \) is age at leaf efficiency = 1 (we take \( t = 1 \) to be 1). This function was chosen for its smooth transitions (as compared with a step function), and for its general agreement with available data on temporal decline in leaf-level photosynthesis (Hensel et al., 1993; Stessman et al., 2002).

There is an upper limit on daily carbon fixation in the model imposed by the maximum effective leaf carbon. Maximum effective leaf carbon represents the limitation on light interception imposed by shoot architecture. Maximum effective leaf carbon \( C_{l\text{fmax}} \) is the carbon equivalent of the leaf area corresponding to the product of the maximum canopy radius, maximum leaf area index, and the sum of the light incident on the canopy layers:

\[
C_{l\text{fmax}} = \pi r_{\text{max}}^2 C_{\text{den}} \sum_{l=1}^{L_{\text{m}}} (1 - K)^{(l-1)}
\]

where \( C_{\text{den}} \) is leaf carbon per unit area (leaf carbon concentration per leaf area per unit leaf mass), \( L_{\text{m}} \) is maximum leaf area index, \( K \) is the light extinction coefficient, and \( r_{\text{max}} \) is maximum canopy radius. Note that individual leaves are not explicitly modelled – rather, the total size and age distribution of the pool of leaf carbon is modelled.

It is assumed that acquisition of carbon and phosphorus per unit carbon in the acquiring organ changes only as a result of phosphorus depletion and tissue ageing, and the parameters that govern these processes in the model are calculated on the basis of specific leaf area (SLA) and specific root length (SRL), which are assumed to be constant. This assumption is made for the sake of simplicity and because no data showing changes of both SRL and SLA in Arabidopsis are available.

**Resource allocation**

The carbon required for maintenance respiration is removed from the pool of acquired carbon before carbon is allocated for other processes. Maintenance respiration for each organ class is the product of the carbon pool and maintenance respiration rate of that organ class. The only exception to this rule is maintenance respiration for leaves, which is calculated in an analogous fashion to carbon acquisition, scaling \( A_{(i)} \) between the leaf maintenance respiration \( R_{\text{lf}} \) and the ‘old’ leaf maintenance respiration, given by the product of \( R_{\text{lf}} \) and the fractional rate for ‘old’ leaf organs \( R_{\text{oldlf}} \).

Allocation to reproduction is zero until time of initiation of reproductive growth \( (T_1) \), and increases in a linear fashion to reach unity at the time vegetative growth terminates \( (T_2) \). While allocation to reproduction is less than unity, the remainder is allocated to vegetative growth as described below. The time between \( T_1 \) and \( T_2 \) was also limited to a set value, \( T_{1p} \). Small values of \( T_D \) \( (T_D \leq 20) \) force a rapid and complete switch to reproductive growth, while large values of \( T_D \) \( (T_D \geq 40) \) permit (but do not force) an extended period of both reproductive and vegetative growth.

The partitioning of resources between root and shoot growth is broadly similar to the model of Reynolds and Thornley (1982). At each time step, newly acquired carbon is pooled with any carbon that was not utilized in growth or metabolism in the previous time step, and the carbon required for maintenance metabolism is removed from this pool. The newly acquired phosphorus is similarly pooled with any unused phosphorus remaining from the previous time step. The ratio of available carbon to available phosphorus, normalized by the phosphorus and carbon allocation to growth in the previous time step (referred to here as the internal resource ratio, \( Z_{\text{int}} \)) determines the ratio of allocation to root and shoot.

\[
Z_{\text{int}} = \frac{C_{\text{int}} P_{\text{a}}(t-1)}{P_{\text{int}} C_{\text{int}}(t-1)}
\]

\( C_i \) is the pool of internally available carbon, \( P_i \) is the pool of internally available phosphorus, \( C_{\text{int}}(t-1) \) and \( P_{\text{int}}(t-1) \) are the carbon and phosphorus allocation to growth in the previous time step. The fraction of resources allocated to roots \( (f_r) \) is given by:

\[
f_r = (1 - f_{\text{rep}}) \frac{Z_{\text{int}}}{Z_{\text{int}} + (1/Z_{\text{int}})}
\]

where \( f_{\text{rep}} \) is the allocation fraction to reproductive organs, and \( Z_{\text{int}} \) is given by eqn (5). The fraction of resources allocated to stems and leaves is similar to eqn (6), but \( Z_{\text{int}} \) in the numerator is replaced by the inverse of \( Z_{\text{int}} \). For \( Z_{\text{int}} > 1 \), available carbon is in excess, growth is limited by phosphorus, and root growth is favoured. For \( Z_{\text{int}} < 1 \), available phosphorus is in excess, growth is limited by carbon, and stem and leaf growth are favoured.

**Organ growth**

The carbon and phosphorus allocated to each organ class (root, stem, leaf, reproductive tissue and seeds) is incorporated into new tissue of each type on the basis of the C : P ratio and the carbon requirement for growth respiration of that organ.
class. The growth of the root carbon pool \( \left[ C_{\text{rln}(t)} \right] \) is given by:

\[
C_{\text{rln}(t)} = f_{\text{rt}} \times \min\left( \frac{C_{\text{r}(t)}}{(1 + R_g)}, P_{\text{r}(t)} \times Z_{\text{rt}} \right)
\]  

(7)

where \( R_g \) is the growth respiration rate, \( Z_{\text{rt}} \) is the root C : P ratio. Growth of other organs is analogous, but growth of stems and leaves is controlled by the allocation fraction to stems and leaves (\( f_{\text{sln}} \)) which is further divided between the fraction to stem (\( f_{\text{stn}} \)) and the fraction to leaves (\( 1 - f_{\text{stn}} \)). Since carbon and phosphorus allocation to the organ classes is based on the ratio of overall carbon and phosphorus allocation in the previous time step, and the incorporation of carbon and phosphorus into each organ class depends on the C : P ratio of that organ class, there may be excess carbon or phosphorus that is not incorporated into new growth. In addition, there is a maximum rate of leaf growth, above which any carbon or phosphorus allocated to leaf growth is considered to be in excess. Any excess carbon or phosphorus resulting from these factors is stored until the next time step, when it is included in the \( C_i \) or \( P_i \) terms in the calculation of \( Z_{\text{rt}} \).

A fixed proportion of resources allocated to reproduction are converted into mature seed (\( f_{\text{sd}} \)), after a time delay (\( T_{\text{sd}} \)) representing the time required for floral growth, pollination, and seed maturation. Viable seed is the cumulative sum of the product of allocation to seed and the probability of surviving at each time step.

**Survival**

Survival was modelled by considering mortality to be a sigmoidal function with half-maximum and steepness parameters, normalized by mortality at 120 d:

\[
S(t) = 1 - \left[ \frac{\exp[g_s(t - k_S)]}{1 + \exp[g_s(t - k_S)]} \right] \left[ 1 + \frac{\exp[g_s(t_0 - k_S)]}{\exp[g_s(t_0 - k_S)]} \right]^{-1}
\]  

(8)

where \( g_s \) is a steepness parameter, \( k_S \) is the half-minimum, and \( t_0 \) is the time at which survival = 0. In effect, the first 100 d of a logistic curve that could be longer than 100 d is considered. For this reason the half-maximum parameter for the sigmoidal mortality function (\( k_S \)) may not correspond to 50 % survival. Three survival scenarios, with \( k_S \) values of 69, 79 and 89, which corresponded to 50 % survival to 68, 76 and 84 d were considered (see Fig. 2). These scenarios are referred to as S68, S76 and S84.

**Senescence**

There are two processes in the model for senescence and reallocation of resources in the leaf organ category. The model considers two pools in the leaf organ category: ‘new’ leaf organs, for which the carbon fixation rate exceeds the respiration rate, and ‘old’ leaf organs, for which the respiration rate exceeds the carbon fixation rate. The senescence of these pools is distinct. In both cases, there is a pool of leaf resources that cannot be reallocated (the fixed leaf fraction, \( f_{\text{fix}} \)), and leaf resources in excess of the fixed leaf fraction are reallocated at a specified rate (\( D \)). Carbon and phosphorus in the ‘old’ leaf pool are subject to reallocation (controlled by the above-mentioned rules) as leaf resources enter this pool. Conceptually, this mimics the ageing and senescence of individual leaves. Senescence of the ‘new’ leaf organ category mimics the programmed senescence of the entire canopy. This process begins at a specified time (\( T_3 \)) and proceeds at the specified rate of senescence. Removal of carbon and phosphorus from the two leaf organ pools caused by reallocation from senescent tissue is accounted for in later time steps in the calculation of carbon acquisition and maintenance metabolism of the leaf organ class. It is assumed that programmed senescence does not begin until after initiation of reproductive growth (\( T_3 \geq T_1 \)).

Senescence of both leaf pools can also be altered by metabolic demand. If the carbon demand for maintenance exceeds the available carbon, the rate of senescence of the ‘old’ leaf organ category is increased to free enough carbon to meet the respiratory demand (up to a specified maximum rate, \( D_{\text{max}} \)). If increasing the rate of senescence of the ‘old’ leaf pool is insufficient to meet respiration demands, the ‘new’ leaf organ category senescence rate is increased, even before \( T_3 \), up to the specified maximum. Carbon and phosphorus are reallocated from these pools at each time step after senescence begins at a fixed rate, so that the reallocation of carbon and phosphorus from leaves decays in an exponential fashion. Note that all senescence processes deal with reallocation of resources, but do not consider abscission of organs – it is assumed that all organs are retained.

**Optimization**

The model was optimized over the three phenology parameters that control initiation of reproduction (\( T_1 \)), termination of vegetative growth (\( T_3 \)) and initiation of programmed senescence (\( T_3 \)), to find the phenology that resulted in the maximum size of the pool of realized (surviving to seed maturity) seed carbon, \( Y \), which was used as a measure of yield:

\[
Y = \sum_{t=1}^{100} C_{\text{alsd}(t)} S_t
\]  

(9)
were tested using a coarse step of 9 d. For each combination
16-d window centred on the maximum seed carbon value
range of possible values followed by testing all values in a
determined using the coarse step of 9 d to cover the entire
cases (Fig. 3). These both showed a pronounced main peak
phenology parameters, all possible values of the three par-
tational load of testing all possible combinations of
were wished to optimize for integer values. To avoid the compu-
routines would be appropriate for this model, given that we
limits discussed above ($T_3 \geq T_1, T_2 \geq T_1, T_2 \geq T_1 + T_3$).
To characterize the response of seed carbon ($Y$) to the
phenology parameters, all possible values of the three param-
ters were tested for the base high- and low-phosphorus
cases (Fig. 3). These both showed a pronounced main peak
with several local optima on the main peak, but in neither
case were there isolated local optima apart from the main
peak. We were not confident that standard optimization
routines would be appropriate for this model, given that we
wished to optimize for integer values. To avoid the computa-
tional load of testing all possible combinations of $T_1$, $T_2$
and $T_3$ (>100,000 combinations), all other cases were opti-
imized using a two-step optimization process, with the first
step designed to find the main peak, and the second step to
find the true maximum.

First, the entire range of possible values for initiation of
reproduction ($T_1$) and termination of vegetative growth ($T_2$)
were tested using a coarse step of 9 d. For each combina-
tion of $T_1$ and $T_2$, the optimal initiation of senescence ($T_3$) was
determined using the coarse step of 9 d to cover the entire
range of possible values followed by testing all values in a
16-d window centred on the maximum seed carbon value
from the coarse step test. The optimal $T_1$ and $T_2$ values were
similarly found using a second testing of all possible $T_1$ and
$T_2$ values in a 16-d window centred on the maximum seed
carbon value from the coarse step testing of $T_1$ and $T_2
values. In practice, this procedure required about 6000–8000
iterations of the model (a 12- to 14-fold reduction from all
possible combinations) to find the optimal phenology.

The sensitivity of the model to input parameters was ana-
ysed in several ways. Since the major cost to delayed repro-
duction was expected to be increased risk of mortality,
optimal phenology was compared in two environments, high
phosphorus (20 μm) and low phosphorus (1 μm), and for
three survival scenarios with phosphorus-uptake parameters
(maximum uptake rate – $P_{\text{max}}$, minimum uptake rate – $P_{\text{min}}$, and
time of minimal uptake – $t_{\text{pmin}}$), corresponding to five
values of effective diffusion rate ($D_e$) of phosphorus in soil
(see the Appendix). The survival scenarios ranged from
50% survival at 84 d to 68 d (Fig. 2), and the phosphorus-uptake parameters corresponded to $D_e$ from $1 \times 10^{-5}$ to $1 \times 10^{-3}$ cm$^2$ s$^{-1}$ ($8.64 \times 10^4$ to $8.64 \times 10^6$ μm$^2$
d$^{-1}$), the range reported by Schenk and Barber (1979).

To determine sensitivity of plant growth and allocation simu-
lated by the model to the parameters used, each parameter was
varied by 10% above and below the base value, and the
optimal phenology and yield were determined for that scenario.

To estimate the relative importance of the various differ-
ces between plants from high- and low-phosphorus environ-
ments the parameters that differed between the high- and
low-phosphorus scenarios were examined. Ten parameters
differed between high- and low-phosphorus scenarios, two of
which were parameters of phosphorus availability ($P_{\text{max}}$ and
$P_{\text{min}}$), and the remaining eight were plant physiological par-
eters ($Z_{\text{eff}}, Z_{\text{atm}}, Z_{\text{fix}}, Z_{\text{rep}}, Z_{\text{abs}}, f_{\text{abs}}, f_{\text{fix}}, G_{\text{max}}$; for definitions,
see Table 3). To understand the impact of the differing
parameters of plant physiology on simulated growth in the
high- and low-phosphorus scenarios, both the high- and
low-phosphorus scenario values of each in a scenario were tested
with intermediate values for the other four differing para-
eters. The mean of the high- and low-phosphorus values of a
parameter were used for the intermediate value, which
corresponded to differences of 20–37% from the original
values (Table 4). First the model was optimized with the com-
bination of all eight intermediate values for the physiology
parameters for the high- and low-phosphorus scenarios. Then
each of the eight parameters was altered singly to its corre-
sponding high- and low-phosphorus values, and the model
optimized for the high- and low-phosphorus scenarios. The
effects of the phosphorus availability parameters were tested
in a similar manner, by optimizing with each parameter at the
corresponding high- or low-phosphorus scenario value
while the other was set at a central value. The intermediate
values used for the phosphorus availability parameters
represented an increase or decrease of 11% (for low- or
high-phosphorus environments, respectively). For $P_{\text{min}}$, the

Fig. 3. The effect of reproductive phenology on seed production (seed carbon) of simulated Arabidopsis in high-phosphorus (A) and low-phosphorus (B) conditions. Increasing seed production is shown as increasing lightness, and the contour interval is 25 mg. Optimal phenology (indicated by *) occurred on a relatively smooth peak, which was later and lower in low phosphorus than in high. Termination of vegetative growth was constrained to be within 10 d of initiation of reproduction.
minimum phosphorus-uptake parameter, the 11% difference corresponded to a value intermediate between the high- and low-phosphorus values. Since the maximum phosphorus uptake rate ($P_{\text{max}}$) differed by nearly an order of magnitude (Table 3), a single intermediate value for this parameter was not used, but rather the parameter value was increased (for low phosphorus) or decreased (for high phosphorus) by 11% to facilitate comparison between parameters.

Parameterization

In principle, this model should be widely applicable to monocarpic annuals. Here a parameterization of the model for *Arabidopsis thaliana* is presented. Most of the necessary parameters were estimated from published reports (see Table 3), and several were calculated from data collected in an earlier experiment (Nord and Lynch, 2008).

Validation

The model predictions were validated against two sets of experimental results for *A. thaliana* grown in high- and low-phosphorus soils (Table 4). The first set was from an earlier experiment (Nord and Lynch, 2008), and the second set was from an unpublished experiment in which *A. thaliana* was grown with high or low phosphorus in elevated or ambient CO$_2$; here only the ambient CO$_2$ results are considered. The code for this model, along with an example input file, is available at: http://roots.psu.edu/phenology.

RESULTS

The model results were generally consistent with experimental data, predicting that low phosphorus availability delays flowering and reduces yield (Table 4). In general, the model predicted longer delay in flowering than was observed (16 d vs. 3–6 d). However, the range of age at flowering in the experimental data (35–44 d for low, and 40–47 d for high phosphorus) nearly overlapped with the model predictions (34 d and 50 d for low and high phosphorus), so that simulated phenology was slightly earlier than that observed in high-phosphorus and slightly later than that observed in low-phosphorus soils (Table 4).

Patterns of plant growth and partitioning predicted by the model were consistent with experimental observations. The sigmoidal carbon accumulation curves generated by the model (Fig. 4A, B) resemble plant growth curves. Simulated

---

**Table 4. Main model predictions were generally similar to observed data for Arabidopsis**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>High phosphorus</th>
<th>Low phosphorus</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T_1$ (d)</td>
<td>34</td>
<td>50</td>
</tr>
<tr>
<td>$T_2$ (d)</td>
<td>41</td>
<td>60</td>
</tr>
<tr>
<td>Yield (mg C)</td>
<td>218-6</td>
<td>155-1</td>
</tr>
<tr>
<td>Total carbon (mg)</td>
<td>1050</td>
<td>1150</td>
</tr>
</tbody>
</table>

(A) Model results

Base parameters

<table>
<thead>
<tr>
<th>Parameter</th>
<th>High phosphorus</th>
<th>Low phosphorus</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T_1$ (d)</td>
<td>34</td>
<td>50</td>
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</tr>
<tr>
<td>Total carbon (mg)</td>
<td>1050</td>
<td>1150</td>
</tr>
</tbody>
</table>

Means (s.e.) from sensitivity analysis

<table>
<thead>
<tr>
<th>Parameter</th>
<th>High phosphorus</th>
<th>Low phosphorus</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T_1$ (d)</td>
<td>34-1 (0-13)</td>
<td>49-7 (0-39)</td>
</tr>
<tr>
<td>$T_2$ (d)</td>
<td>41-3 (0-12)</td>
<td>59-7 (0-46)</td>
</tr>
<tr>
<td>Yield (mg C)</td>
<td>222 (3-02)</td>
<td>158 (2-37)</td>
</tr>
</tbody>
</table>

(B) Observed values (mean and s.e.)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>High phosphorus</th>
<th>Low phosphorus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bolting (d)</td>
<td>34-8 (1-3)</td>
<td>40-4 (1-6)</td>
</tr>
<tr>
<td>Total carbon (mg C)</td>
<td>1146 (71-7)</td>
<td>791 (64-4)</td>
</tr>
<tr>
<td>Yield (mg C)</td>
<td>175-7 (17-6)</td>
<td>131-4 (12-2)</td>
</tr>
</tbody>
</table>

E. A. Nord and J. P. Lynch (unpubl. res.)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>High phosphorus</th>
<th>Low phosphorus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bolting (d)</td>
<td>44-0 (2-3)</td>
<td>47-3 (2-0)</td>
</tr>
<tr>
<td>Total carbon (mg C)</td>
<td>1001 (176)</td>
<td>1126 (113)</td>
</tr>
</tbody>
</table>

Base parameters are reflected in Table 3.

The sensitivity analysis involved 116 scenarios in which individual parameters were increased or decreased by 10% while the others were held constant.

**Fig. 4. Allocation and growth as simulated by the model in two scenarios:** (A) 20 μM (high) phosphorus and (B) 1 μM (low) phosphorus. These are based on the standard parameters (Table 3), with $D_e = 1.0 \times 10^{-8}$ cm$^2$ s$^{-1}$, and optimal phenology. The dashed curve represents the probability of survival to a given age for scenario S76. The vertical dotted lines represent the initiation of reproduction and termination of vegetative growth from the optimal phenology. With high phosphorus the optimal phenology was: initiate reproduction at 34 d and terminate vegetative growth at 41 d. With low phosphorus these values were 50 and 60 d. Delaying reproduction in low phosphorus permitted enough additional phosphorus accumulation to offset the reduced probability of survival. Plants in low phosphorus can reach a similar size to those in high phosphorus, but are less likely to survive long enough to do so.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>High phosphorus</th>
<th>Low phosphorus</th>
</tr>
</thead>
<tbody>
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<td>175-7 (17-6)</td>
<td>131-4 (12-2)</td>
</tr>
</tbody>
</table>

Nord et al. — Phosphorus and reproductive phenology
Plant carbon accumulation (used as an analogue of biomass) was broadly similar to both experimental results for high phosphorus, but agreed better with the low-phosphorus results from the second experiment (Table 4). The model also predicted increased relative biomass allocation to roots in low phosphorus conditions (Fig. 4A, B), as expected. Model plants balanced acquisition of carbon and phosphorus during vegetative growth by allocating resources to acquisition of the limiting resource, and any excess of carbon or phosphorus that carried over from one time step to the next was very small (Figs 4 and 5). However, once reproductive growth began, model plants could no longer balance carbon and phosphorus acquisition effectively, since shoot and root growth became limited by reproductive growth. As a consequence, model plants in low phosphorus accumulated excess quantities of phosphorus during reproductive growth (Fig. 5B). Phosphorus availability, phosphorus mobility and probability of survival influenced model plant phenology and yield in different ways (Fig. 6). The optimal phenology under low phosphorus was consistently later than that for high phosphorus in all of the 15 combinations of survival probabilities and phosphorus mobility (effective diffusion coefficient, $D_e$) values simulated. This delay in reproduction under low phosphorus was sensitive to phosphorus mobility (Fig. 6A), with delays increasing from about 10 days with $D_e$ values of $3 \times 10^{-7}$ to nearly 40 days with $D_e$ values of $3 \times 10^{-9}$. The probability of survival barely affected the optimal timing of reproduction; only under low phosphorus with the lowest $D_e$ value ($3 \times 10^{-9}$) did probability of survival affect optimal phenology (Fig. 6A). Yield was more sensitive than phenology to probability of survival. Yield decreased when probability of survival declined earlier in the season (Fig. 6B). $D_e$ had little effect on yield under high phosphorus, but decreasing $D_e$ dramatically reduced yield under low phosphorus (Fig. 6B).

Optimal phenology and yield as simulated by the model were sensitive to several of the input parameters (Fig. 7). The sensitivity of a parameter in the model if a 10% change in that parameter yielded a change in response of >5% is reported. In general, yield responses were larger than phenology responses; no parameters produced changes of >17% in phenology, while three parameters affected yield by at least 20%. Increasing the maximal carbon assimilation rate ($A_{\text{max}}$) increased yield substantially (Fig. 7A, B). Increasing the conversion of reproductive organs into seed ($f_{\text{surv}}$), increasing the time to half-minimum for the decline in carbon assimilation with leaf age (increasing $k_A$) and increasing the carbon...
assimilation of reproductive tissue \( A_{\text{rep}} \) caused minor (5–10\%) increases in yield. Decreasing the respiration rate of reproductive tissue \( R_{\text{rep}} \) or the time lag required for seed to mature \( T_{\text{sd}} \) also caused minor (5–10\%) increases in yield. These are all factors which increase either resource acquisition or conversion of resources into yield. There was only one parameter to which both high- and low-phosphorus model plants were sensitive: increasing the maximum carbon assimilation rate \( A_{\max} \) accelerated reproduction in both cases.

There were several differences between high- and low-phosphorus scenarios in sensitivity of yield to input parameters. The largest difference was that an increase in maximum canopy radius \( r_{\text{max}} \) caused larger yield increases under high phosphorus than under low phosphorus (approx. 30\% vs. < 10\%), reflecting the earlier optimal phenology in the high-phosphorus scenario. The eight plant parameters that differed between high- and low-phosphorus plants \( Z_{\text{rt}}, Z_{\text{stm}}, Z_{\text{lf}}, Z_{\text{rep}}, Z_{\text{sd}}, f_{\text{sd}}, f_{\text{fix}}, G_{\max} \) had important impacts on optimal phenology and yield when compared with a hypothetical plant with intermediate parameter values (Table 5). The effect of all plant parameter differences together was substantial, and was very favourable for plants in the low-phosphorus scenario, increasing yield by 58\%, but unfavourable for plants in the high-phosphorus scenario, causing a 17\% decrease in yield. The single parameters which most affected yield differed for the high- and the low-phosphorus scenarios. Under high phosphorus, the largest yield decrease was caused by the increase in the fraction of leaf carbon and phosphorus which was not available for reallocation \( f_{\text{fix}} \). Under low phosphorus, the two greatest increases in yield were caused by increases in the \( C : P \) ratio in leaves and roots \( Z_{\text{lf}}, Z_{\text{rt}} \). With high phosphorus, none of the
individual parameters caused changes of >5% in phenology, and all of them together only delayed the initiation of reproduction by 1 d (6-25%). With low phosphorus, several parameters caused changes in phenology of >5%, and all of them together accelerated phenology by 15%.

Differences in phosphorus availability caused larger differences in phenology and yield than differences in localized phosphorus depletion caused by reduced \( D_e \) (Table 5). A central value of 0.885 for the fraction of initial phosphorus uptake still available after 15 d increased yield by 12% and accelerated reproduction (\( T_1 \)) by 5% in the low-phosphorus scenario. A similar increase (11%) in initial phosphorus uptake (\( P \)) increased yield by 22% and accelerated reproduction (\( T_1 \)) by 10% under low phosphorus. However, similar decreases in these parameters had little effect under high phosphorus, with yield responses < 2%, and only one phenology response, which was <4%.

Low-phosphorus plants allocated relatively more resources to roots, and consequently root respiration was a greater fraction of total respiration (Fig. 8). Since the relative metabolic load of stems and leaves hardly differs between the low- and high-phosphorus scenarios, the greater respiratory cost of roots in low phosphorus reduces the ability of the plant to produce and support reproductive tissue. The metabolic load of roots and reproductive tissue was altered by phosphorus diffusivity in low phosphorus, with root metabolic costs increasing substantially for phosphorus diffusivity below 1.0 x 10^-8 (Fig. 8).

**DISCUSSION**

The model presented here captures many of the essential features of growth and partitioning of resources among root, shoot, and reproductive tissue in phosphorus-stressed plants. Simulated low-phosphorus plants were smaller in size than simulated high-phosphorus plants at any age, but with proportionally larger roots (Fig. 4). Simulated low-phosphorus plants consistently reproduced later than simulated high-phosphorus plants in 15 scenarios of survival probability and phosphorus mobility (Fig. 5). This highlights the trade-off faced by plants in low phosphorus; if the marginal decrease in survival is greater later in the season, the cost of delaying reproduction increases (Figs 2 and 4) later in the season.

The insensitivity of phenology and yield under high phosphorus to mobility of phosphorus in soil (\( D_e \)) is unsurprising – in high-phosphorus environments, growth should be
limited by carbon, not by phosphorus. The near-insensitivity of phenology in high phosphorus to probability of survival is somewhat surprising. Under high phosphorus, phenology is sufficiently early that even in the earliest risk scenario (S68), phenology is essentially unaffected (Fig. 6A). In contrast, because optimal phenology under low phosphorus is generally later than in high-phosphorus, it is slightly more sensitive to changes in probability of survival, especially at lower levels of $D_e$ (Fig. 6A). As a consequence, we hypothesize that plants adapted to soil environments in which phosphorus is less mobile should exhibit more phenological delay in response to low-phosphorus conditions than plants in more benign environments.

The extreme suppression of growth under low phosphorus with very low $D_e$ highlights the important role root metabolic costs play in the optimization of plant phenology (Figs 6B and 8). Under these conditions, simulated plants acquired about 2% of the resources they could acquire at higher $D_e$. Phosphorus availability was so low in these scenarios that a large fraction of plant resources was allocated to roots, and fewer resources to stem and leaves. This increased root respiration, and reduced resources available for reproductive growth. This is in agreement with other reports of the importance of root respiration, especially in low-phosphorus environments (Amthor, 1989; Fan et al., 2003; Lynch and Ho, 2005).

The plant parameter which most affected phenology was $A_{\text{max}}$, the maximum assimilation rate; increasing $A_{\text{max}}$ accelerated reproduction in our model. Increased leaf level photosynthesis, equivalent to $A_{\text{max}}$ in the model, generally increases in response to elevated CO$_2$ (Korner, 2006). Plant phenological responses to elevated CO$_2$ are somewhat variable (Nord and Lynch, 2009), but there are many reports of accelerated phenology, which would be consistent with the results of our model (Johnston and Reekie, 2008).

Substantial differences exist between the physiology of plants growing in high- and low-phosphorus conditions (Table 3). By varying each of these individually it was found that, of all the parameters that differed between these conditions, the leaf C:P ratio ($Z_P$) had the greatest effect on yield and phenology in low phosphorus (Table 4), increasing yield by nearly 30%. In general, the traits expressed in low phosphorus were beneficial in that environment when compared with a (hypothetical) phenotype intermediate to those of high and low phosphorus, increasing yield by over 58%. In contrast, the traits expressed in high phosphorus were not beneficial when compared with the intermediate phenotype, decreasing yield by nearly 17%. This suggests that plants might actually be better optimized for low phosphorus environments, which is consistent with the fact that low phosphorus availability is the primary constraint to plant growth in most terrestrial ecosystems (Lynch and Deikman, 1998).

Since metabolic costs influence yield (i.e. yield was sensitive to respiration rates of leaves and reproductive organs; Fig. 7A, B), the absence of leaf abscission in the model may be problematic, as a pool of old, inefficient leaf tissue continues to burden the plant. However, if this were the case, yield or phenology would be expected to respond to changing the fractional rate of respiration for old leaves ($R_{\text{shift}}$), which it did not. It is assumed that there is no remobilization of resources from roots, and root loss to herbivory or pathogens was not considered. Given the metabolic cost of maintaining roots and the reduced acquisition of phosphorus by older roots, root turnover could reduce the metabolic cost of root maintenance with little effect on phosphorus acquisition. Future extensions of this model could test the effect of root turnover on phosphorus acquisition, root respiration and reproductive phenology.

This model assumes that the C:P ratio of organs is fixed, though tissue phosphorus concentration varies with time (Nord and Lynch, 2008; Fig. 7). Furthermore, internal phosphorus redistribution is important in low-phosphorus environments (Wissuwa, 2003). These factors should permit greater growth in low-phosphorus conditions than the model predicts, since the sensitivity analysis (Fig 7) suggests that the C:P ratio of leaves influenced yield in low-phosphorus conditions. Future work with this model might involve testing the effect of allowing the C:P ratios to vary.

The model also assumes static $A_{\text{max}}, P_{\text{max}}$ and respiration rates, but these are known to exhibit ontogenetic variability (Drouet et al., 2004). An alternate model was tested, in which specific root length (SRL) and, thus, $P_{\text{max}}$ was allowed to vary through time, and the basic results were broadly similar to those presented here, with delays of 3–8 d in phenology compared with the fixed SRL model (data not shown). The simpler model presented here is preferable because the data required for parameterization are more readily available and because the more complex model would require excessive time to optimize the phenology.

The root and shoot partitioning based on increasing the acquisition of the limiting nutrient, ‘balanced growth’ (Davidson, 1969), is a central assumption of this model. While this may be an oversimplification (Reich, 2002), it reproduces the essential features of the regulation of root and shoot partitioning by phosphorus availability. However, this approach seems preferable to some of the optimization-based partitioning models, as it is based only on current conditions (Reynolds and Chen, 1996). We note that this approach may not be applicable to nutrients other than phosphorus and nitrogen, which both regulate root and shoot partitioning (Marschner, 1995).

The prevalence of low-phosphorus soils globally, and the emerging evidence of the alteration of plant phenology in response to global climate change suggests that phenological responses of plants to low-phosphorus environments may be important for the adaptation of plants to a changing climate. Lengthened growing seasons resulting from global change may allow increased phenological delay, which could benefit plants in low-phosphorus soils. However, changes in patterns of precipitation are likely to increase the risk of drought in some areas, which may increase risk of mortality. Finally, we note that low phosphorus availability is a primary constraint to the productivity of low-input agroecosystems (Lynch, 2007). Understanding the role of phenology in adaptation to low-phosphorus soils may be beneficial in efforts to develop crop varieties suited to low-input agricultural systems and crop varieties that allow reduced loss of phosphorus from agricultural soils (Karpinet et al., 2004), as well as in the effort to understand the influence of global climate change on plant growth and productivity (Lynch and St Clair, 2004; Nord and Lynch, 2009).
In conclusion, it has been shown here that delayed reproduction, which has been observed in plants growing in low-phosphorus soil, can be understood as a beneficial response that allows for increased acquisition and utilization of phosphorus. However, the benefit a plant is able to derive from delaying reproduction in low-phosphorus conditions is limited by the mobility (effective diffusion coefficient) of phosphorus in the soil, and the temporal distribution of mortality risk.

ACKNOWLEDGEMENTS

We thank Johannes Postma for the many ideas and programming tips he contributed throughout the development of this model, and Andrew Stephenson and Kathleen Brown for their helpful suggestions. This work was supported by a grant from the McKnight Foundation Cooperative Crop Research Project to J.P.L.

LITERATURE CITED


APPENDIX: Parameters used in the Barber–Cushman model

The Barber–Cushman model was used to estimate phosphorus-uptake parameters for specific soil conditions. Phosphorus uptake was simulated over 15 d, and then the output used to calculate the maximal phosphorus-uptake rate (mg P mg root C⁻¹ d⁻¹) when a root grows into new soil, and the fractional phosphorus-uptake efficiency of roots at ages 2–15 d

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Units</th>
<th>Description and source</th>
</tr>
</thead>
<tbody>
<tr>
<td>( D_e )</td>
<td>( 1.0 \times 10^{-9} )</td>
<td>( 3.0 \times 10^{-9} )</td>
<td>( 1.0 \times 10^{-8} )</td>
</tr>
<tr>
<td>p.rteffmin</td>
<td>0.550</td>
<td>0.650</td>
<td>0.800</td>
</tr>
<tr>
<td>p.Pavail</td>
<td>2.09 × 10⁻³</td>
<td>2.83 × 10⁻³</td>
<td>3.66 × 10⁻³</td>
</tr>
<tr>
<td>p.treffminlime</td>
<td>15</td>
<td>15</td>
<td>15</td>
</tr>
</tbody>
</table>

High P (20 μm phosphorus)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Units</th>
<th>Description and source</th>
</tr>
</thead>
<tbody>
<tr>
<td>( D_e )</td>
<td>( 1.0 \times 10^{-9} )</td>
<td>( 3.0 \times 10^{-9} )</td>
<td>( 1.0 \times 10^{-8} )</td>
</tr>
<tr>
<td>p.rteffmin</td>
<td>0.700</td>
<td>0.903</td>
<td>0.968</td>
</tr>
<tr>
<td>p.Pavail</td>
<td>2.20 × 10⁻²</td>
<td>2.29 × 10⁻²</td>
<td>2.33 × 10⁻²</td>
</tr>
<tr>
<td>p.treffminlime</td>
<td>15</td>
<td>15</td>
<td>15</td>
</tr>
</tbody>
</table>

Derived by fitting an exponential decay curve to the output from the Barber–Cushman model using these inputs

<table>
<thead>
<tr>
<th>Name</th>
<th>Value</th>
<th>Units</th>
<th>Description and source</th>
</tr>
</thead>
<tbody>
<tr>
<td>( K_m )</td>
<td>( 5.25 \times 10^{-3} )</td>
<td>μM</td>
<td>From Narang et al. (2000)</td>
</tr>
<tr>
<td>( I_{max} )</td>
<td>( 5.25 \times 10^{-7} )</td>
<td>μmol cm⁻² s⁻¹</td>
<td>Initial root radius (Nord and Lynch, 2008)</td>
</tr>
<tr>
<td>( C_{min} )</td>
<td>9.60</td>
<td>nm</td>
<td>Half-distance between root axes, default value</td>
</tr>
<tr>
<td>( R_0 )</td>
<td>0.00865</td>
<td>cm</td>
<td>Initial phosphate concentration</td>
</tr>
<tr>
<td>( R_1 )</td>
<td>0.33</td>
<td>cm</td>
<td>Buffer power of the soil; lower values did not permit growth when phosphorus concentration was 1 μM; initial phosphate concentration</td>
</tr>
<tr>
<td>( V_0 )</td>
<td>( 5.00 \times 10^{-7} )</td>
<td>ml cm⁻³ s⁻¹</td>
<td>Max water flow rate, default value. Model sensitivity to this parameter is low for phosphorus (Barber, 1995).</td>
</tr>
<tr>
<td>( k )</td>
<td>0.00</td>
<td>cm s⁻¹</td>
<td>Root growth rate, zero because only depletion effects are required</td>
</tr>
</tbody>
</table>

Note: \( K_m \) and \( I_{max} \) differed for HP and LP, but the model is not particularly sensitive to them (Barber, 1995), so mean values were used.