



Optimization modeling of plant root architecture for water and phosphorus acquisition

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Abstract

An optimization model is presented that examines the relationship between root architecture and multiple resource acquisition, specifically water and phosphorus in spatially heterogeneous environments. The basal root growth angle of an individual common bean plant, which determines the orientation and localization of the bulk of the root system, was modeled as the decision variable. The total payoff to the plant, the benefit obtained from water and phosphorus acquisition, minus the costs of spatial competition between roots, is given as a function of the (x, y) coordinates of the basal root in two-dimensional Cartesian space. We obtained a general solution and applied it to four unique environmental cases which are as follows: (1) the case of uniformly distributed water and phosphorus; (2) the case of localized shallow phosphorus; (3) the case of localized deep water; and (4) the case of shallow phosphorus and deep water. The general solution states that the optimal basal root growth angle will occur at the point where the total rate of change in the value of the resources acquired equals the total rate of change in cost that results from locating the root deeper in the soil. An optimizing plant locates its roots deeper in the soil profile until the marginal benefit exactly equals the marginal cost. The model predicts that the basal root angle of an optimizing plant will be shallower for Case 2 and deeper for Case 3, relative to the basal root angle obtained in the case of uniformly distributed water and phosphorus. The optimal basal root angle for Case 4 will depend on the marginal rate of substitution of water availability for phosphorus availability that occurs with depth. Empirical observations of bean root architecture in the greenhouse and in the field confirm model results and are discussed. In addition, the potential importance of phenotypic plasticity and phenotypic variation are discussed in relation to optimization of traits and adaptation to spatially heterogeneous environments.

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1. Introduction

1.1. The problem of multiple resource acquisition: the importance of root architecture

Plant productivity is limited by water and phosphorus availability in most terrestrial ecosystems. The ability to acquire soil resources determines the reproductive success of individuals and/or species in ecological and agricultural communities (Aerts et al., 1991; Aerts,

1999). Root architecture, the spatial configuration of a root system in the soil, can vary between and among species (Fig. 1) and plays an important role in below-ground resource acquisition (Fitter, 1987; Lynch, 1995). The importance of root architecture for plant productivity stems from the fact that many soil resources are unevenly distributed in space and time and are often subject to localized depletion (Robinson, 1994). Spatial deployment of the root system thus determines the ability of a plant to exploit heterogeneous soil resources (Pregitzer et al., 1993; Robinson, 1996; Lynch and Brown, 2001). For example, drought tolerance in common bean has been associated with depth of rooting (Markhart, 1985; Sponchiado et al., 1989; Sanders and Markhart, 1992), while greater nutrient acquisition has been associated with increased soil exploration by roots

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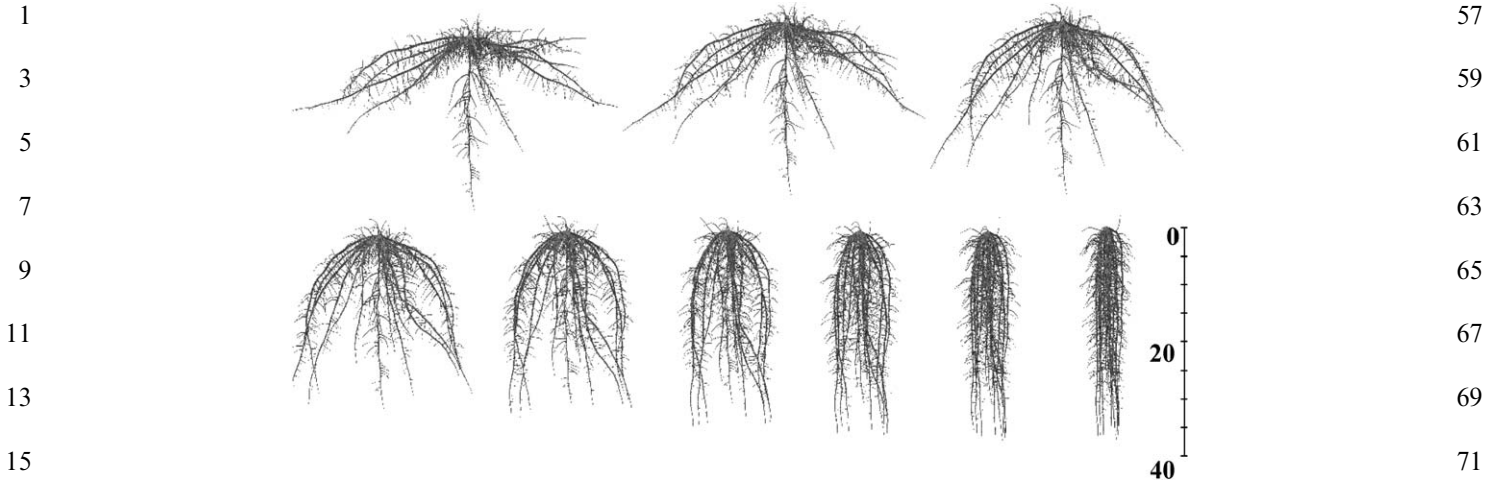


Fig. 1. Geometric simulation modeling of bean root systems that vary in basal root angle, but are otherwise identical in length and branching. Scale is given in centimeter. The variation shown here is present among different genotypes of common bean and has been shown to be regulated by P availability (Ge et al., 2000).

in surface layers, especially in the case of immobile nutrients such as phosphorus (Lynch and Beebe, 1995; Bonser et al., 1996; Lynch and Brown, 2001).

Common bean (*Phaseolus vulgaris* L.) has been used as a model system for understanding the importance of root architecture for soil resource acquisition (Bonser et al., 1996; Liao et al., 2001; Rubio et al., 2003). Common bean is the most important food legume on earth, providing essential nutrients for over 500 million people in developing nations (FAO, 1991; CIAT, 2001). Drought and soil infertility, especially phosphorus deficiency often co-occur, and are primary constraints to crop production in many developing countries, affecting over 80% of bean production regions in the world (Wortmann and Allen, 1994; CIAT, 2001).

Experiments in the greenhouse and field have demonstrated that phosphorus availability regulates the growth angle of basal roots (Bonser et al., 1996; Liao et al., 2001) and the production of adventitious roots (Miller et al., 1998) in responsive genotypes, resulting in greater topsoil exploration. Phosphorus efficient bean genotypes may also exhibit more root architectural plasticity in response to phosphorus availability, whereby they become more shallow under low-phosphorus availability (Bonser et al., 1996). In addition, genetic variation for these traits has been shown to exist in common bean (Lynch and van Beem, 1993, 1995; Bonser et al., 1996). In most soils, phosphorus availability is greatest at the surface and decreases with depth (Chu and Chang, 1966). Thus, a shallow root system is likely to be advantageous under low-phosphorus conditions because it enhances root exploration of soil surface horizons, which results in increased phosphorus uptake and plant productivity (Lynch and Brown, 2001).

Although root architectures that exploit topsoil resources efficiently may be advantageous in low-phosphorus soils, this may inadvertently result in reduced water acquisition, since water availability typically increases with soil depth in a terminal drought environment. In fact, recent evaluation of phosphorus-efficient germplasm in the tropics suggests that genotypes selected for adaptation to low-phosphorus soils may be sensitive to drought (S. Beebe, pers. comm). Thus, there may be a trade-off in the optimization of root architecture for shallow immobile resources such as phosphorus, and deep mobile resources such as water.

In recent years, optimization theory and game theory have been widely employed to analyse evolutionary adaptation (Maynard Smith, 1982; Parker and Maynard Smith, 1990; Schmid-Hempel, 1990; Orzack and Sober, 1994; Seger and Stubblefield, 1996; Abrams, 2001; Halama and Reznick, 2001). Originally constructed for use in economics, these powerful and elegant models are used to address adaptive evolution in terms of phenotypes and selective forces (Schlichting and Pigliucci, 1998). The overall objectives of optimization modeling are to understand specific examples of adaptation in terms of natural selection and the historical and developmental constraints operating on them (Parker and Maynard Smith, 1990). The optimization approach assumes that variation in a trait reflects variation in fitness of the individuals. Application of these types of economic models has increased the precision and scope of understanding about the existence of phenotypic variation and its relationship to environmental adaptation. The basic guiding principles of optimality modeling are: (1) that traits associated with fitness should be maximized by selection (Parker and Maynard Smith, 1990), and (2) that there are inherent trade-offs and constraints between components of fitness, which serve

to limit the possible set of trait combinations (Seger and Stubblefield, 1996). Explicit optimization models are developed for specific cases and predictions are the result of the model assumptions. Thus, a model is only as valid and appropriate as the assumptions on which it is based. If the predictions of the model match biological observations, then we can infer that correct assumptions have been made about the nature of adaptation.

This paper presents an optimization model that addresses the relationship between root architecture and the acquisition of water and phosphorus. The primary objective of our model is to examine the trade-offs of a given root architecture strategy (shallow vs. deep) for resource acquisition under different environmental scenarios. The basal root angle of an individual common bean plant is the decision variable that is optimized, as the basal root angle determines the orientation and localization of the bulk of the root system. Adventitious and tap roots are modeled as fixed at 0° and 90° relative to the soil surface, respectively. The model specifically examines the conditions of sub-optimal water and phosphorus availability, two principal soil constraints to plant growth that typically co-occur in terrestrial environments. Water and phosphorus are interesting since they represent extremes of contrasting resource availability in time and space. Water is ephemeral and usually localized deep upon depletion, whereas phosphorus is stable and typically localized shallow. Architectural strategies that optimize phosphorus acquisition would also be beneficial for the acquisition of other immobile resources such as the micronutrient metals, whereas traits optimizing water acquisition would also be beneficial for the acquisition of soluble mobile resources such as nitrate. Therefore, architectural strategies that co-optimize the acquisition of both water and phosphorus should also encompass the majority of belowground material resources. The regulation of root architecture by resource availability has important implications for a number of ecological and agricultural issues, including the evolutionary and ecological role of root architecture in plant adaptation to different soil environments, competition for localized soil resources within and between root systems, and the development of resource acquisition efficient crops and cropping systems.

In this model, the total payoff to the plant, the benefit obtained from water and phosphorus acquisition, minus the costs of spatial competition between roots, is given as a function of the (x, y) coordinates of the basal root in two-dimensional Cartesian space. The general optimization solution of the model states that the optimal basal root angle will occur at the point where the total rate of change in the value of the resources acquired equals the total rate of change in cost that results from locating the root deeper in the soil. In other words, an optimizing plant locates its roots deeper until the marginal benefit

exactly equals the marginal cost, a basic and common attribute of optimization modeling. The general solution of the model is applied to four unique environmental cases, where phosphorus and water are localized at different spatial locations: (1) the case of uniformly distributed water and phosphorus; (2) the case of shallow phosphorus; (3) the case of deep water; and (4) the case of shallow phosphorus and deep water.

2. The model

We use a decision-theoretic approach to consider a single optimizing plant's root architecture under different environmental conditions. Let the basal root be represented by a straight line of fixed length, L , located in the positive quadrant of a two-dimensional Cartesian coordinate system, and anchored at the origin as depicted in Fig. 2. The basal root can then be represented by the set of points (x, y) . The plant's "decision" is to choose the depth at which the basal roots will grow.

There exist two resources that the basal root must acquire, water and phosphorus. Let $w(x', y')$ and $p(x', y')$ denote the value of the water and phosphorus the plant acquires by having the root pass through point (x', y') . The total benefit obtained by the plant at (x', y') is the sum $w(x', y') + p(x', y')$. Each plant has other types of roots, namely tap and adventitious. It is assumed that the taproot grows perpendicular to the soil surface along the y -axis and the adventitious roots grow parallel to the soil surface along the x -axis (Fig. 2). A root depletes resources from the surrounding soil. When multiple roots are located in the same area, inefficiencies arise

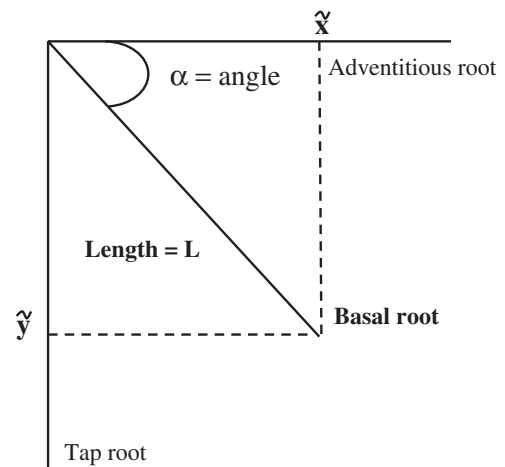


Fig. 2. Two-dimensional representation of basal root optimization model, where the taproot and adventitious roots are fixed along the y -axis and x -axis, respectively. The basal root is the ray with the endpoint (\tilde{x}, \tilde{y}) , and the basal root angle is modeled as the decision variable.

1 due to competition among roots for the same resources.
 2 Let $c(x', y')$ denote the cost of competition if the basal
 3 root is located at the point (x', y') . Therefore, the payoff
 4 to the plant by locating the basal root at a particular
 5 point (x', y') is as follows:

$$6 \pi(x', y') = w(x', y') + p(x', y') - c(x', y'). \quad (1)$$

7 Let (\tilde{x}, \tilde{y}) denote the endpoint of the basal root.
 8 Integrating (1) over the ranges of x and y gives the
 9 following payoff function for the entire root.

$$11 \Pi(\tilde{x}, \tilde{y}) = W(\tilde{x}, \tilde{y}) + P(\tilde{x}, \tilde{y}) - C(\tilde{x}, \tilde{y}). \quad (2)$$

13 Here, $W(\tilde{x}, \tilde{y})$ is the total value of water acquired, $P(\tilde{x}, \tilde{y})$
 14 is the total value from phosphorus acquisition, and
 15 $C(\tilde{x}, \tilde{y})$ is the total cost due to competition.¹ It is
 16 assumed that competition costs are minimized when
 17 roots are farthest away from all other roots, which
 18 occurs when the basal root is closer to the 45-degree
 19 line.²

20 Since the basal root is of a fixed length, it follows from
 21 the Pythagorean theorem that $\tilde{x}^2 + \tilde{y}^2 = L^2$. Thus, there
 22 exists an exact relationship between \tilde{x} and \tilde{y} , $\tilde{x}(\tilde{y})$. We
 23 can substitute this relationship into the payoff function
 24 to obtain an unconstrained payoff function, $\Pi(\tilde{x}(\tilde{y}), \tilde{y})$.
 25 In other words, the plant chooses its depth, \tilde{y} , to
 26 maximize the payoff to the plant. An elaboration on the
 27 payoff function and a discussion of the existence of an
 28 interior solution is in the appendix. To maximize the
 29 payoff function, we simply set the derivative to zero.
 30 Thus, the general solution to this problem is

$$31 \frac{dW}{d\tilde{y}} + \frac{dP}{d\tilde{y}} = \frac{dC}{d\tilde{y}}. \quad (3)$$

33 Each term in (3) represents the total derivative, that is,
 34 the total change as depth changes. Each term can be
 35 represented as the sum of its partial derivatives³ and is
 36 discussed in greater detail in the appendix.

37 The general solution, (3), states that the plant will
 38 locate its roots at a soil depth where the marginal benefit
 39 of water and phosphorus acquisition will exactly equal
 40 the marginal cost of interroot competition. If the
 41 marginal benefit exceeds the marginal cost, then locating
 42 roots deeper gives a greater payoff. If the marginal
 43 benefit falls short of the marginal cost then the roots will

44 ¹ $W(\tilde{x}, \tilde{y}) = \int \int w(x, y) \partial x \partial y$, $P(\tilde{x}, \tilde{y}) = \int \int p(x, y) \partial x \partial y$, and $C(\tilde{x}, \tilde{y}) =$
 45 $\int \int c(x, y) \partial x \partial y$.

46 ² Specifically, we assume that the cost function takes on a U-shape
 47 where the minimum occurs at the point where $x = y$, or rather, when
 48 the basal root locates along the 45-degree line. This implies that the
 49 partial derivatives decrease toward the minimum and increase beyond;
 50 $C_1 < 0$ for $x < y$ and $C_2 > 0$ for $x > y$, as well as, $C_1 > 0$ for $y < x$ and
 51 $C_2 < 0$ for $y > x$.

52 ³ For example, $dC/d\tilde{y} = C_2 + C_1(\partial\tilde{x}/\partial\tilde{y})$, where C_2 is the partial
 53 derivative with respect to the second argument, y , ($\partial C/\partial\tilde{y}$) and C_1 is
 54 the partial derivative with respect to the first argument, x , ($\partial C/\partial\tilde{x}$).
 55 This is equivalent to assuming that cost is a function of the basal root
 angle, and that cost is minimized at an angle of 45°.

be shallower. We now use the derived general solution to
 solve four interesting scenarios.

2.1. Case 1: uniform distribution of resources

The case of uniform soil implies that both water and
 phosphorus are uniformly distributed throughout the
 soil profile and do not vary with depth. The acquisition
 of soil resources is not spatially dependent. As a result,
 the value of the resources obtained is constant through-
 out. Thus, assume that $W(x', y') = w$ and $P(x', y') = p$
 for all (x', y') where w and p are positive numbers.
 Consequently, the derivatives of the two benefit terms
 on the left side of Eq. (3) equal zero. Thus, the general
 solution reduces to $dC/d\tilde{y} = 0$. From the given assump-
 tions on the cost function, this occurs when the basal
 root is located at 45°, where $\tilde{x} = \tilde{y}$.

Notice that the utility maximization problem reduces
 to a cost minimization problem. When nutrients are
 located uniformly throughout the soil, there is no
 difference in the amount of nutrients received with
 different root configurations. Thus, the only considera-
 tion left is to minimize the competition among roots for
 these resources.

2.2. Case 2: the case of shallow phosphorus

In most soils, phosphorus availability is greatest in the
 topsoil or near surface horizons. A simple way to model
 this is to assume that the deeper the root grows the less
 phosphorus it obtains, or rather, $P_2 < 0$ (Recall that P_2
 and P_1 are the partial derivatives with respect to the y
 and x arguments, respectively. See footnote 3 and
 appendix for clarification.) We maintain the assumption
 that water is distributed uniformly and the amount of
 phosphorus available in the soil surface horizon is
 uniform, simply $dW/d\tilde{y} = P_1 = 0$. The general solution
 (3) reduces to

$$P_2 = C_2 + C_1 \left(\frac{d\tilde{x}}{d\tilde{y}} \right).$$

Since $P_2 < 0$, the term $dC/d\tilde{y}$ must also take on a value
 less than zero. Since $\tilde{x} = \sqrt{L^2 - \tilde{y}^2}$, it follows that

$$\frac{d\tilde{x}}{d\tilde{y}} = -\frac{\tilde{y}}{\sqrt{L^2 - \tilde{y}^2}} < 0.$$

From the assumptions on the cost function, if x and y
 do not equal then C_1 and C_2 have opposite signs. Thus,
 the solution to this case must have $C_1 > 0$ and $C_2 < 0$.
 This occurs when $\tilde{x} > \tilde{y}$ and the basal roots are shallow.
 This occurs because the scarcity of phosphorus reduces
 the marginal benefit. As a result, along the 45-degree
 line the marginal cost is greater than the marginal
 benefit and the roots are too deep.

From (3), a more negative P_2 results in a more
 positive C_1 and a more negative C_2 , which will result in a

basal root angle that is even shallower than 45° . In other words, the greater the rate of change in phosphorus availability with depth, the shallower the basal root.

2.3. Case 3: the case of scarce water

Another common occurrence is for a plant to exist in environments where water is scarce and localized deep, as in the case of a terminal drought environment. Because water availability increases with soil depth, roots must subsequently grow deeper in order to reach the reservoir of water. To model such a situation we will assume that the deeper the basal root grows, the more water is gained, $W_2 > 0$. Again, we continue with the assumptions that phosphorus is evenly distributed throughout the soil. Under these assumptions, the optimal root position solves the following reduced expression of (3)

$$W_2 = C_2 + C_1 \left(\frac{d\tilde{x}}{d\tilde{y}} \right).$$

Since $W_2 > 0$ the equality holds only if $C_2 > 0$ and $C_1 < 0$. This occurs if $\tilde{x} < \tilde{y}$ and the basal root grows deeper than the first case where water is uniform throughout the soil. As in Case 2, the depth of the basal root depends on just how quickly the amount of water available increases with depth. In other words, the larger the slope of W , the deeper the root.

2.4. Case 4: the case of multiple constraints

In the previous two cases one resource was assumed to have heterogeneous spatial distribution, while the other resource was distributed uniformly. Now we consider the scenario where both resources are scarce and localized in different parts of the soil profile. Specifically, assume that phosphorus tends to be more abundant near the surface of the soil while water tends to be more abundant deeper in the soil. Using the assumptions previously discussed, $W_1 = P_1 = 0$, $W_2 > 0$ and $P_2 < 0$. The optimization solution, (3), reduces to

$$W_2 + P_2 = C_2 + C_1 \left(\frac{d\tilde{x}}{d\tilde{y}} \right).$$

If $W_2 + P_2 > 0$, where water scarcity has a greater impact on the plant, then the optimal solution has $\tilde{x} < \tilde{y}$ and the basal root grows at an angle greater than 45° . Instead, if $W_2 + P_2 < 0$ then, as shown in the phosphorus constrained case, the optimal solution has $\tilde{x} > \tilde{y}$ and the basal root grows shallower than the 45-degree angle under uniformly dispersed nutrients.

As stated previously, $|W_2|$ and $|P_2|$ denote the marginal rate of change of water and phosphorus availability with depth, respectively. Recall that the marginal rate of change of water availability increases, while the marginal rate of change of phosphorus

decreases with an incremental increase in the depth of the basal root. If we consider the ratio of the two, $|W_2|/|P_2|$, we can see that this ratio increases the deeper the root grows. If $|W_2|/|P_2|$ is less than one, then $|W_2|$ is less than $|P_2|$ and the difference between the two is negative. Thus, the optimal root angle would be less than 45° , as in Case 3. If the ratio is greater than one, then the angle is greater than 45° as in Case 2. This ratio is equivalent to the marginal rate of substitution of one resource for the other. It is this ratio that ultimately determines the optimal root orientation.

3. Discussion

A central concept of Darwinian evolution is that adaptation occurs as a result of natural selection (Darwin, 1859). The application of economic optimization theory and evolutionary game theory to biological systems has provided useful insights into adaptation and evolution (Maynard Smith, 1979, 1982; Parker and Maynard Smith, 1990; Orzack and Sober, 1994; Abrams, 2001; Brown, 2001). The processes of plant growth, resource allocation, and acquisition of multiple resources have many analogous principles to optimization theory in economics. We have developed an optimization model to predict the basal root angle of an individual plant. Our primary objectives were to examine the trade-offs of a given root architecture strategy for water and phosphorus acquisition, particularly in environments where these resources are heterogeneously localized. Quantification of the costs and benefits of particular root geometries is useful in analysing and comparing resource acquisition efficiencies among phenotypes.

Root systems that have optimal architectures should allocate carbon to root deployment patterns that are the most effective for acquisition of limiting soil resources, particularly when multiple resources are limiting such as water and nutrients (Bloom et al., 1985). Under uniform soil conditions, resource acquisition is not dependent upon the spatial configuration and growth angle of the basal roots. Essentially the $dW/d\tilde{y}$ and $dP/d\tilde{y}$ terms in Eq. (3) would equal zero and the problem reduces to a cost minimization problem. The orientation of the basal roots should be such that the costs of interroot competition are minimized. Thus, the optimal basal root angle is achieved when the basal roots grow at a 45-degree angle. We should note that in actual bean root systems, basal roots typically emerge from one of four poles around the hypocotyl. There are typically 8–12 basal roots for a single bean plant, all of which may be oriented at different angles relative to the soil surface. We do not mean to imply that all the basal roots of a given plant are each precisely oriented at 45-degree angles. This angle may represent an average distribution

1 of roots around the main axis, so that competition is
 2 minimized. Identifying an optimal basal root angle and
 3 root system configuration under uniform soil conditions
 4 serves as a good reference point for comparison to other
 5 environmental conditions. A particular plant may
 6 deviate from this configuration for several reasons, as
 7 we have seen from the results of the other environmental
 8 cases. An angle less than 45° essentially represents a root
 9 system that is shallower than the uniform case, as in the
 10 case of shallow phosphorus (Case 2). A solution where
 11 the angle is greater than 45° would represent a root
 12 system that is deeper than the uniform case, as in the
 13 case of deep water (Case 3).

14 Observations of real bean plants in the greenhouse
 15 and in the field confirm the results of our optimization
 16 model. Numerous studies have shown that genetic
 17 variation exists for the response of basal root angle to
 18 low phosphorus, as measured in a 5-day old pouch
 19 system (Bonser et al., 1996; Liao et al., 2001). As
 20 predicted by the model Case 2, the case of shallow
 21 phosphorus, plants that perform better in this environ-
 22 ment exhibit a shallower basal root angle. In addition,
 23 shallow basal root angle has been correlated with overall
 24 root system shallowness, total plant phosphorus acqui-
 25 sition and subsequent yield under low-phosphorus
 26 conditions in the field (Bonser et al., 1996; Liao et al.,
 27 2001). Genotypic differences in root shallowness also
 28 have implications for plant competition in low-phos-
 29 phorus environments. Both computer simulation studies
 30 (Ge et al., 2000) and field studies (Rubio et al., 2003)
 31 have shown that monogenetic stands of shallow bean
 32 genotypes have increased interroot competition. Simi-
 33 larly for the model Case 3 of deep water, deeper rooted
 34 genotypes perform better under terminal water stress
 35 conditions in greenhouse and field conditions (Mar-
 36 khart, 1985; Sponchiado et al., 1989). Experiments are
 37 currently being conducted in the greenhouse and field to
 38 examine implications of root architecture for tradeoffs
 39 in water and phosphorus acquisition when both
 40 resources are co-limiting.

41 3.1. Optimization and phenotypic variation

42 There is abundant evidence for major developmental
 43 changes in the structural and functional characteristics
 44 of individuals, as a consequence of exposure to
 45 particular environmental factors (Grime and Mackey,
 46 2002). Phenotypic plasticity is the property of a given
 47 genotype to produce different phenotypes in response to
 48 distinct environmental conditions (Pigliucci, 2001). The
 49 fundamental conceptual research tool in phenotypic
 50 plasticity is the idea of a reaction norm (Schlichting and
 51 Pigliucci, 1998). A reaction norm is the function that
 52 relates the environments to which a particular genotype
 53 is exposed and the phenotypes that can be produced by
 54 that genotype (Schlichting and Pigliucci, 1998). A

55 reaction norm is considered adaptive if it results in a
 56 higher mean fitness across environments than does a
 57 single phenotype. Phenotypic plasticity in the response
 58 of basal root angle to phosphorus availability has been
 59 shown to exist in some genotypes of common bean
 60 (Bonser et al., 1996). Whether plasticity is a trait that
 61 confers greater adaptation to environmental heteroge-
 62 neity and instability is of great ecological interest (Lortie
 63 and Aarssen, 1996; Halama and Reznick, 2001; Pigliuc-
 64 ci, 2001; Alpert and Simms, 2002; Grime and Mackey,
 65 2002). In this particular instance, basal root angle
 66 plasticity, the ability of a root system to alter its root
 67 angle in response to different environmental conditions,
 68 would be predicted by our model to allow a plant to
 69 optimize nutrient and water acquisition when grown in
 70 variable environments. But obviously there exists trade-
 71 offs to plasticity, as we have observed non-plastic plants
 72 to low-phosphorus availability in nature.

73 Phenotypic variation (multiple phenotypes) has been
 74 shown to exist in plant populations, where each
 75 phenotype is thought to be adapted to a subset of the
 76 environment the population occupies (Bazzaz, 1991;
 77 Lortie and Aarssen, 1996). Differences among indivi-
 78 duals, whether discrete or continuous, may also arise
 79 through the actions of frequency- and density-depen-
 80 dent selection or through the evolution of genotypes
 81 that respond to specific cues in unpredictable environ-
 82 ments (Gersani and Sachs, 1992; Gersani et al., 1998). It
 83 has been proposed that observed phenotypic variation
 84 among individuals and species has a functional basis
 85 that enhances the ability of a given organism to exploit
 86 specific environmental patches more efficiently than do
 87 other alternatives (Gersani and Sachs, 1992; Halama
 88 and Reznick, 2001; Grime and Mackey, 2002). While
 89 phenotypic plasticity of basal root angle in response to
 90 phosphorus availability may appear to be desirable, as
 91 predicted by our optimization model, there may be
 92 trade-offs and costs associated with plasticity (DeWitt
 93 et al., 1998; Alpert and Simms, 2002). In fact, non-
 94 plastic genotypes of common bean in response to low-
 95 phosphorus availability do exist in nature. Thus, we
 96 recognize that additional spatial and temporal environ-
 97 mental factors, other than those considered in this
 98 particular model, may also be important for optimiza-
 99 tion of root architecture for multiple resource acquisi-
 100 tion. We cannot fail to note that an important limitation
 101 to the model presented in this paper is that it is not
 102 dynamic, it does not allow for frequency- or density-
 103 dependent optimization. In addition, this model could
 104 be expanded to include plasticity and the implications of
 105 plasticity for interplant competition. We intend to put
 106 forth a unique evolutionary game theory model to
 107 address these very interesting topics.

1 3.2. Theoretical implications of root architecture 2 optimization model

3 The main theoretical point to be made from this
4 optimization model is that the most important factor
5 determining the depth of basal roots is the relative rates
6 of change with depth in the value of the availability of
7 resources. In other words, the marginal rate of
8 substitution of water for phosphorus is the primary
9 determining factor for predicting the distribution of
10 roots in the soil. This suggests that plants should adjust
11 allocation in a given environment so that all resources
12 equally limit growth. Though studies of allocation
13 qualitatively support this prediction, exchange ratios,
14 which should provide a broader perspective on a
15 resource balance by plants, have not been adequately
16 characterized in a more theoretical and quantitative
17 way.

18 Three important and immediate points can be made
19 based on this key conclusion. The first point is that the
20 optimal plant behavior is a function of the interplay of
21 multiple resources, in our case the availability of water
22 and phosphorus. Most studies of root deployment have
23 focused on the acquisition of one resource. This may not
24 be adequate, as the availability of a resource relative to
25 other resources is important. In the model presented, we
26 focus on the interaction of water and phosphorus. Our
27 purpose was to illustrate the need to study multiple
28 resources and not to argue that these are the only two
29 resources that are important. Water and phosphorus are
30 interesting resources to consider because they are both
31 primary limitations to plant growth in many ecosystems,
32 and since they represent extremes of resource avail-
33 ability, with water tending to be deep while phosphorus
34 tends to be shallow. The importance of relative rates of
35 change will continue to hold if additional resources are
36 included in the model.

37 The second point to be made is that the rate of change
38 is important rather than the total quantities. Because we
39 are interested in the behavior of an optimizing plant, the
40 solution will always occur at the point where marginal
41 benefits equal marginal costs. We can demonstrate the
42 subtle importance of this point in the following scenario,
43 where we will suppose that water is scarce in total
44 quantity but distributed uniformly, while phosphorus is
45 abundant throughout the soil profile but present in
46 higher concentrations closer to the soil surface. Since
47 water is scarce but phosphorus is plentiful, it may not
48 appear necessary for a plant to distribute basal roots
49 shallow. Because water is evenly distributed throughout
50 the profile, albeit scarce, the model predicts that plants
51 should grow shallower roots to take advantage of the
52 bounty of phosphorus, as the rate of change in the
53 availability of resources and not the absolute quantity or
54 availability of the resource is what is most important.
55 Roots would only go deeper at the point where water

availability in the surface was sufficiently depleted so 57
that the marginal value of water acquisition in deeper 58
layers outweighed the marginal value of additional 59
phosphorus acquisition in the surface. It is important to 60
note that in nature, plants have genetic programming, 61
which allows them to anticipate resource distribution in 62
their environment, regardless of actual resource dis- 63
tribution. For example, water stress triggers ABA 64
signaling that results in increased rooting depth (Davies 65
and Zhang, 1991; Spollen et al., 2000). Similarly, low- 66
phosphorus availability can result in ethylene responses 67
that increase root shallowness (Lynch and Brown, 68
1997). These hormonal triggers for changes in root 69
architecture in real plants are likely to serve as stress 70
signals that inform the plant of the internal requirement 71
for the resource.

72 The final point of emphasis is the idea of value. When 73
empirically measuring resource availability in the soil it 74
is natural to consider absolute quantities. In the 75
proposed model, it is important to emphasize that the 76
functions $w(x,y)$ and $p(x,y)$ represent the value of the 77
resources to the plant and not necessarily the absolute 78
quantities. In other words, a point where $w(x,y) =$ 79
 $p(x,y)$ does not mean that the quantity of water is 80
equivalent to the quantity of phosphorus at the location 81
(x,y), but that the value of the quantities received is 82
equivalent for plant growth. This complicates the 83
empirical testability of the model but not the theoretical 84
points. The importance of the relative values of limiting 85
resources supports the theoretical predictions of Bloom 86
et al. (1985), who applied economic analogies to plant 87
resource allocation and/or acquisition. There are many 88
things that affect the relationship between quantity and 89
value, such as the overall scarcity of a given resource, 90
the demand for the resource, as well as other interacting 91
environmental and physiological factors. We recognize 92
that there may exist conditions where considering 93
relative values of distinct resources may not be entirely 94
valid, such as in conditions of extreme scarcity. In such 95
cases, co-optimization strategies may be overridden by 96
the need to acquire the most limiting resource (“the law 97
of the minimum”) as discussed in Rubio et al. (2003).

98 In conclusion, the optimization model presented 99
utilizes a simplified framework in which to evaluate 100
the relationship between root architecture and multiple 101
resource acquisition, particularly water and phosphorus. 102
The most important theoretical point that is brought out 103
by the general solution of the model is that the relative 104
rates of change with depth in the value of the availability 105
of resources matters most in determining the optimal 106
basal root angle. In other words, the marginal rate of 107
substitution of water for phosphorus is the primary 108
determining factor for predicting the distribution of 109
roots in the soil. Despite model limitations, namely that 110
it only considers a single plant and that it is not 111
dynamic, the predicted basal root angle of an optimizing

1 plant under shallow phosphorus or deep water condi- 57
 2 tions, agrees with observations of adapted genotypes in 59
 3 the greenhouse and in the field. Common bean 61
 4 genotypes that are best adapted to low-phosphorus 63
 5 environments, where phosphorus is localized in the 65
 6 surface soil, tend to have a more shallow basal root 67
 7 angle. On the other hand, genotypes that are adapted to 69
 8 terminal drought environments have been shown to 71
 9 have deeper root systems. Optimization models are 73
 10 powerful tools to address plant physiological and 75
 11 ecological questions and have important implications 77
 12 on adaptationism and evolutionary biology. At the same 79
 13 time, we recognize the need to consider frequency- and 81
 14 density-dependent selection in optimization modeling, 83
 15 as well as other temporal and spatial factors such as 85
 16 phenotypic plasticity and the importance of interplant 87
 17 competition over time. We intend to address these 89
 18 interesting and exciting topics in an upcoming evolu- 91
 19 tionary game theory model. 93
 20

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26 Appendix

27 The goal of the appendix is to elaborate on the 103
 28 mathematical assumptions that guarantee the solution 105
 29 described in the text. As described, the plant chooses 107
 30 the position of the basal root to maximize its payoff. 109
 31 The model assumed that the basal root, of fixed length L , 111
 32 took the form of a ray in the positive quadrant of the 113
 33 two-dimensional Cartesian coordinate system. Thus, 115
 34 equivalently, we can think of the plant choosing the 117
 35 endpoint of the line segment (\tilde{x}, \tilde{y}) so that the total 119
 36 payoff to the plant is (\tilde{x}, \tilde{y}) with the constraint that x and 121
 37 y are related according to the Pythagorean Theorem, 123
 38 $\tilde{x}^2 + \tilde{y}^2 = L^2$.

39 If we think of \tilde{y} as the depth of the basal root, the 125
 40 constraint gives a definitional relationship between the 127
 41 distance the endpoint is from the taproot and the depth, 129
 42 $\tilde{x}(\tilde{y}) = \sqrt{L^2 - \tilde{y}^2}$. Therefore, the solution to the con- 131
 43 strained problem is equivalent to the solution when we 133
 44 maximize the payoff function $\Pi(\tilde{x}(\tilde{y}), \tilde{y})$ without any 135
 45 constraints.

46 Notice the dual action of a change in depth. As \tilde{y} 137
 47 increases there is a direct effect on the plant's payoff. 139
 48 For example, the deeper the basal root grows the more 141
 49 water it acquires. In addition, there is also an indirect 143
 50 effect. Since the root is a ray of fixed length, growing 145
 51 deeper results in the basal root moving closer to the y -

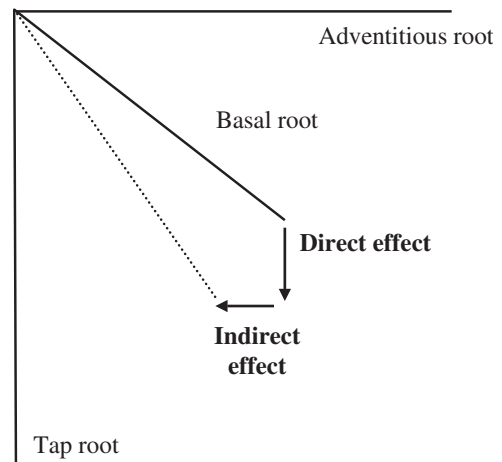


Fig. 3. Two-dimensional representation of the direct and indirect effects of increasing basal root angle depth on the payoff function of an individual plant.

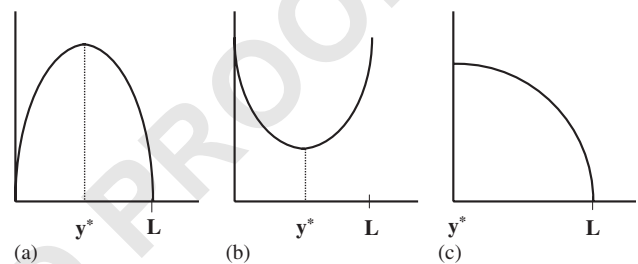


Fig. 4. Three potential model payoff functions. (a) Depicts the desirable concave function with a unique interior solution. (b) Depicts a convex function which has a minimum, rather than a maximum solution. (c) Depicts a concave function with a corner solution.

axis (the taproot) so that the value of \tilde{x} must also 89
 90 change. Fig. 3 illustrates the direct effect of depth and 91
 92 the indirect effect of breadth on the overall payoff 93
 94 function of the plant. Following the previous example 95
 96 with localized deep water, as the plant grows deeper the 97
 98 direct effect on the payoff is always increasing. This 99
 99 assumes that the value of \tilde{x} remains unchanged. The 101
 102 indirect effect is that the root becomes closer to the 103
 104 taproot and more competition costs are incurred. Both 105
 106 the direct and indirect effects are important, but the 107
 108 ultimate basal root angle choice is dependent upon the 109
 110 total change in the payoff function. 111

112 What does this mean mathematically? Fig. 4 illus- 101
 113 trates three examples of a possible payoff function, 103
 114 $\Pi(\tilde{x}(\tilde{y}), \tilde{y})$. The different shape of each function has 105
 115 important implications for the model outcome and 107
 116 general solution. Fig. 4a is the desirable payoff function, 109
 117 in that a single peak, a distinct maximum, occurs at a 111
 118 depth between zero and L . Fig. 4b has the problem of 113
 119 a distinct minimum rather than a maximum. The depth y^* 115
 120 represents the worst root configuration, where the 117
 121 plant's payoff gets better as the basal root is located 119
 122 closer to the adventitious root ($\tilde{y} = 0$) or the taproot 121
 123 ($\tilde{y} = L$). Therefore, it is necessary to assume that

1 $\Pi(\tilde{x}(\tilde{y}), \tilde{y})$ is a concave function that is smooth,
 2 continuous and differentiable. Finally, Fig. 4c depicts
 3 another potential problem with the shape of the payoff
 4 function. In Fig. 4c, the function achieves its maximum
 5 at a bound of the set of possible depths. Such a solution
 6 would imply that the basal root should locate *exactly*
 7 where either the taproot or adventitious roots grow. The
 8 solutions depicted in Fig. 4c are defined as corner
 9 solutions, while solutions depicted in Fig. 4a are defined
 10 as interior solutions. The function should be restricted
 11 so that corner solutions are eliminated. Because the cost
 12 of competition increases as the basal root grows closer
 13 to either the tap or adventitious root, a simple and
 14 sufficient assumption is that as \tilde{y} approaches zero and as
 15 \tilde{y} approaches L , the marginal cost of competition
 16 approaches infinity.

17 The important property of the peak to the payoff
 18 function is that the slope of the tangent line at that peak
 19 is zero. Therefore, mathematically, we need to only set
 20 the total derivative of the payoff function equal to zero.
 21 The depth that achieves this must then be the solution to
 22 the problem.

$$23 \frac{d\Pi}{d\tilde{y}} = 0.$$

24 As stated previously, the change in payoff with depth
 25 has a direct and indirect effect. The direct effect is the
 26 partial derivative of the payoff function, $\partial\Pi/\partial\tilde{y}$, which
 27 measures the change in total payoff when \tilde{y} changes,
 28 fixing \tilde{x} . The indirect effect is the product
 29 $(\partial\Pi/\partial\tilde{x}(\tilde{y}))(\partial\tilde{x}/\partial\tilde{y})$, which measures the change in total
 30 payoff with a change in \tilde{x} times the magnitude of the
 31 change in x with the change in \tilde{y} . Combining the effects,
 32

$$33 \frac{d\Pi}{d\tilde{y}} = \frac{\partial\Pi}{\partial\tilde{y}} + \frac{\partial\Pi}{\partial\tilde{x}(\tilde{y})} \left(\frac{\partial\tilde{x}}{\partial\tilde{y}} \right).$$

34 Also, we illustrated, in the text, that the total payoff to
 35 the plant was the sum of the value of water and the value
 36 of phosphorus obtained minus the cost of competition.
 37 Using this, the interior solution must be the following:

$$38 \frac{dW}{d\tilde{y}} + \frac{dP}{d\tilde{y}} - \frac{dC}{d\tilde{y}} = 0,$$

39 where each term is the total change with depth including
 40 the direct and indirect effects. For example, $dW/d\tilde{y}$
 41 equals $(\partial W/\partial\tilde{y} + \partial W/\partial\tilde{x}(\tilde{y}))(\partial\tilde{x}/\partial\tilde{y})$. Note that in the
 42 text we use the subscript notation for the partial
 43 derivatives to that $dW/d\tilde{y} = W_2 + W_1(\partial\tilde{x}/\partial\tilde{y})$.

44 In conclusion, in order to guarantee the existence of
 45 this solution, we assume that $\Pi(\tilde{x}(\tilde{y}), \tilde{y})$ is: (1) con-
 46 tinuously differentiable so that there are no jumps or
 47 breaks in the payoff and that the derivatives exist and
 48 are themselves continuous functions, and (2) strictly
 49 concave ($d^2C/d\tilde{y}^2 < 0$) so that a unique maximum exists,
 50 and (3) $\lim_{\tilde{y} \rightarrow 0} d\Pi/d\tilde{y} = \lim_{\tilde{y} \rightarrow L} d\Pi/d\tilde{y} = -\infty$ so that
 51 the solution is in fact an interior solution.

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