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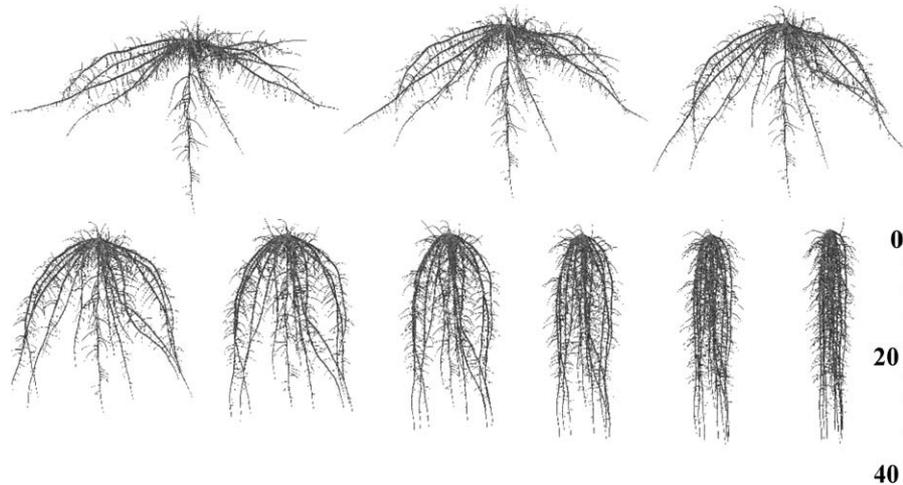
Fig. 1. Geometric simulation modeling of bean root systems that vary in basal root angle, but are otherwise identical in length and branching. Scale is given in centimeter. The variation shown here is present among different genotypes of common bean and has been shown to be regulated by *P* availability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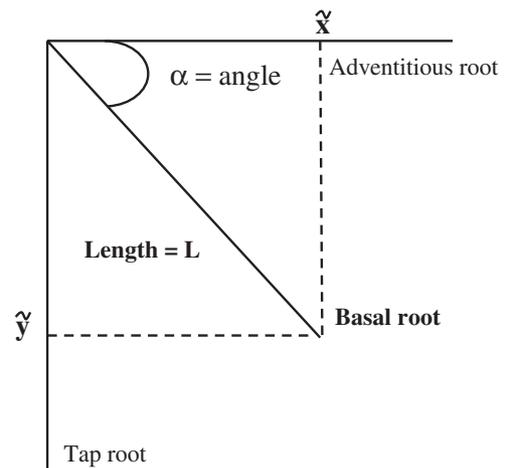

Fig. 2. Two-dimensional representation of basal root optimization model, where the taproot and adventitious roots are fixed along the y-axis and x-axis, respectively. The basal root is the ray with the endpoint $(\tilde{x}, \tilde{y})$, and the basal root angle is modeled as the decision variable.

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

$$\pi(x', y') = w(x', y') + p(x', y') - c(x', y'). \tag{1}$$

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

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

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

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

$$\frac{dW}{d\tilde{y}} + \frac{dP}{d\tilde{y}} = \frac{dC}{d\tilde{y}}. \tag{3}$$

Each term in (3) represents the total derivative, that is, the total change as depth changes. Each term can be represented as the sum of its partial derivatives[3] and is discussed in greater detail in the appendix.

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

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[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 $C(\tilde{x}, \tilde{y}) = \int\int c(x, y)\partial x\partial y$.

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

[3] For example, $dC/d\tilde{y} = C_2 + C_1(\partial\tilde{x}/\partial\tilde{y})$, where C_2 is the partial derivative with respect to the second argument, y, $(\partial C/\partial\tilde{y})$ and C_1 is the partial derivative with respect to the first argument, x, $(\partial C/\partial\tilde{x})$. 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 throughout. 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 assumptions 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 consideration 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)

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

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

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

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 $\mathrm{d}W/\mathrm{d}\tilde{y}$ and $\mathrm{d}P/\mathrm{d}\tilde{y}$ 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

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

Observations of real bean plants in the greenhouse and in the field confirm the results of our optimization model. Numerous studies have shown that genetic variation exists for the response of basal root angle to low phosphorus, as measured in a 5-day old pouch system (Bonser et al., 1996; Liao et al., 2001). As predicted by the model Case 2, the case of shallow phosphorus, plants that perform better in this environment exhibit a shallower basal root angle. In addition, shallow basal root angle has been correlated with overall root system shallowness, total plant phosphorus acquisition and subsequent yield under low-phosphorus conditions in the field (Bonser et al., 1996; Liao et al., 2001). Genotypic differences in root shallowness also have implications for plant competition in low-phosphorus environments. Both computer simulation studies (Ge et al., 2000) and field studies (Rubio et al., 2003) have shown that monogenetic stands of shallow bean genotypes have increased interroot competition. Similarly for the model Case 3 of deep water, deeper rooted genotypes perform better under terminal water stress conditions in greenhouse and field conditions (Markhart, 1985; Sponchiado et al., 1989). Experiments are currently being conducted in the greenhouse and field to examine implications of root architecture for tradeoffs in water and phosphorus acquisition when both resources are co-limiting.

3.1. Optimization and phenotypic variation

There is abundant evidence for major developmental changes in the structural and functional characteristics of individuals, as a consequence of exposure to particular environmental factors (Grime and Mackey, 2002). Phenotypic plasticity is the property of a given genotype to produce different phenotypes in response to distinct environmental conditions (Pigliucci, 2001). The fundamental conceptual research tool in phenotypic plasticity is the idea of a reaction norm (Schlichting and Pigliucci, 1998). A reaction norm is the function that relates the environments to which a particular genotype is exposed and the phenotypes that can be produced by that genotype (Schlichting and Pigliucci, 1998). A reaction norm is considered adaptive if it results in a higher mean fitness across environments than does a single phenotype. Phenotypic plasticity in the response of basal root angle to phosphorus availability has been shown to exist in some genotypes of common bean (Bonser et al., 1996). Whether plasticity is a trait that confers greater adaptation to environmental heterogeneity and instability is of great ecological interest (Lortie and Aarssen, 1996; Halama and Reznick, 2001; Pigliucci, 2001; Alpert and Simms, 2002; Grime and Mackey, 2002). In this particular instance, basal root angle plasticity, the ability of a root system to alter its root angle in response to different environmental conditions, would be predicted by our model to allow a plant to optimize nutrient and water acquisition when grown in variable environments. But obviously there exists trade-offs to plasticity, as we have observed non-plastic plants to low-phosphorus availability in nature.

Phenotypic variation (multiple phenotypes) has been shown to exist in plant populations, where each phenotype is thought to be adapted to a subset of the environment the population occupies (Bazzaz, 1991; Lortie and Aarssen, 1996). Differences among individuals, whether discrete or continuous, may also arise through the actions of frequency- and density-dependent selection or through the evolution of genotypes that respond to specific cues in unpredictable environments (Gersani and Sachs, 1992; Gersani et al., 1998). It has been proposed that observed phenotypic variation among individuals and species has a functional basis that enhances the ability of a given organism to exploit specific environmental patches more efficiently than do other alternatives (Gersani and Sachs, 1992; Halama and Reznick, 2001; Grime and Mackey, 2002). While phenotypic plasticity of basal root angle in response to phosphorus availability may appear to be desirable, as predicted by our optimization model, there may be trade-offs and costs associated with plasticity (DeWitt et al., 1998; Alpert and Simms, 2002). In fact, non-plastic genotypes of common bean in response to low-phosphorus availability do exist in nature. Thus, we recognize that additional spatial and temporal environmental factors, other than those considered in this particular model, may also be important for optimization of root architecture for multiple resource acquisition. We cannot fail to note that an important limitation to the model presented in this paper is that it is not dynamic, it does not allow for frequency- or density-dependent optimization. In addition, this model could be expanded to include plasticity and the implications of plasticity for interplant competition. We intend to put forth a unique evolutionary game theory model to address these very interesting topics.

3.2. Theoretical implications of root architecture optimization model

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

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

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

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

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

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

plant under shallow phosphorus or deep water conditions, agrees with observations of adapted genotypes in the greenhouse and in the field. Common bean genotypes that are best adapted to low-phosphorus environments, where phosphorus is localized in the surface soil, tend to have a more shallow basal root angle. On the other hand, genotypes that are adapted to terminal drought environments have been shown to have deeper root systems. Optimization models are powerful tools to address plant physiological and ecological questions and have important implications on adaptationism and evolutionary biology. At the same time, we recognize the need to consider frequency- and density-dependent selection in optimization modeling, as well as other temporal and spatial factors such as phenotypic plasticity and the importance of interplant competition over time. We intend to address these interesting and exciting topics in an upcoming evolutionary game theory model.

Acknowledgements

Appendix

The goal of the appendix is to elaborate on the mathematical assumptions that guarantee the solution described in the text. As described, the plant chooses the position of the basal root to maximize its payoff. The model assumed that the basal root, of fixed length L, took the form of a ray in the positive quadrant of the two-dimensional Cartesian coordinate system. Thus, equivalently, we can think of the plant choosing the endpoint of the line segment $(\tilde{x}, \tilde{y})$ so that the total payoff to the plant is $(\tilde{x}, \tilde{y})$ with the constraint that x and y are related according to the Pythagorean Theorem, $\tilde{x}^2 + \tilde{y}^2 = L^2$.

If we think of $\tilde{y}$ as the depth of the basal root, the constraint gives a definitional relationship between the distance the endpoint is from the taproot and the depth, $\tilde{x}(\tilde{y}) = \sqrt{L^2 - \tilde{y}^2}$. Therefore, the solution to the constrained problem is equivalent to the solution when we maximize the payoff function $\Pi(\tilde{x}(\tilde{y}), \tilde{y})$ without any constraints.

Notice the dual action of a change in depth. As $\tilde{y}$ increases there is a direct effect on the plant's payoff. For example, the deeper the basal root grows the more water it acquires. In addition, there is also an indirect effect. Since the root is a ray of fixed length, growing deeper results in the basal root moving closer to the y-
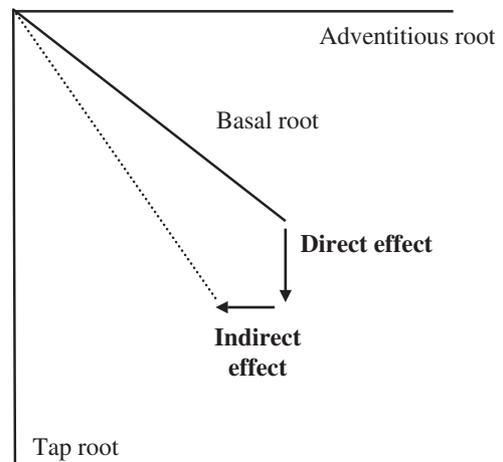
Fig. 3. Two-dimensional representation of the direct and indirect effects of increasing basal root angle depth on the payoff function of an individual plant.
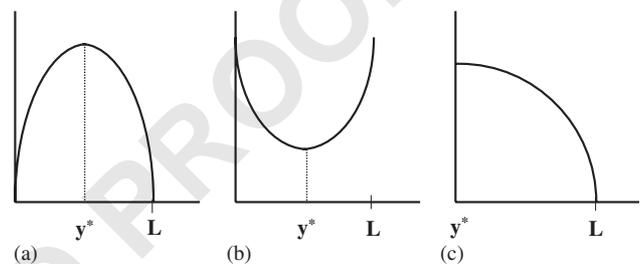
Fig. 4. Three potential model payoff functions. (a) Depicts the desirable concave function with a unique interior solution. (b) Depicts a convex function which has a minimum, rather than a maximum solution. (c) Depicts a concave function with a corner solution.

axis (the taproot) so that the value of $\tilde{x}$ must also change. Fig. 3 illustrates the direct effect of depth and the indirect effect of breadth on the overall payoff function of the plant. Following the previous example with localized deep water, as the plant grows deeper the direct effect on the payoff is always increasing. This assumes that the value of $\tilde{x}$ remains unchanged. The indirect effect is that the root becomes closer to the taproot and more competition costs are incurred. Both the direct and indirect effects are important, but the ultimate basal root angle choice is dependent upon the *total* change in the payoff function.

What does this mean mathematically? Fig. 4 illustrates three examples of a possible payoff function, $\Pi(\tilde{x}(\tilde{y}), \tilde{y})$. The different shape of each function has important implications for the model outcome and general solution. Fig. 4a is the desirable payoff function, in that a single peak, a distinct maximum, occurs at a depth between zero and L. Fig. 4b has the problem of a distinct minimum rather than a maximum. The depth y^* represents the worst root configuration, where the plant's payoff gets better as the basal root is located closer to the adventitious root ($\tilde{y} = 0$) or the taproot ($\tilde{y} = L$). Therefore, it is necessary to assume that

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

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

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

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

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

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

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

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

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

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