

Optimum resource allocation in the plant–fungus symbiosis for an exponentially growing system

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ABSTRACT

Question: What is the optimal allocation of carbon by a plant to its mycorrhizal fungus, and what is the optimal allocation of phosphorus by the mycorrhizal fungus to the plant?

Method: We examined the level of resource allocation by both a plant and fungus (hereafter, ‘players’) that achieved the most rapid growth within the overall system during the exponential growth phase. We assumed resource acquisition rates of the Cobb-Douglas type. We also analysed the dynamic optimization condition (singular subarc) for each player to maximize its own fitness given its partner’s growth schedule.

Results: Each player should allocate more to its partner when the resource provided by the partner is more important to its own resource acquisition. The ESS resource allocation by each player is equivalent to that which achieves the cooperative optimum.

Keywords: allocation of resources, exponential growth, plant–fungus interaction.

INTRODUCTION

Mutualism with soil fungi is prevalent in terrestrial plants. Most terrestrial plants develop root systems called mycorrhiza by interacting with soil fungi (i.e. mycorrhizal fungi). The plant produces carbohydrates from atmospheric CO₂ by photosynthesis and transfers a proportion of these to the fungal symbiont. The fungus, on the other hand, takes up soil nutrients such as phosphates and provides a fraction of these to the host plant.

Many theoretical studies have examined the resource exchange between host and symbiont. Schwartz and Hoeksema (Schwartz and Hoeksema, 1998; Hoeksema and Schwartz, 2003) applied biological market theory to the plant–mycorrhiza system. If the cost of acquiring ambient resources differs between two species, each species benefits by specializing towards acquisition of one resource and trading the other resource with its partner species.

De Mazancourt and Schwartz (2010) demonstrated that organisms could use resources more efficiently by trading resources. They considered two species that require two resources and whose resource acquisition abilities differ. If one species can use both resources more efficiently than the other species, the latter species goes extinct. However, if one species can

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use one resource more efficiently and the other species can use the other resource more efficiently, the two species can co-exist. In addition, if growth is limited by the less abundant resource among the two, there exists a surplus of the second resource that the species cannot use efficiently. Then, by trading the resource surpluses of the two species, they can both use the resource more efficiently than is the case without trading.

In their theoretical model, Grman *et al.* (2012) combined the cooperative game model used for the plant–rhizobia system by Akçay and Roughgarden (2007) and the biological market theory developed by Schwartz and Hoeksema (1998). If the growth of organisms is dependent on two resources, two symbiotic conditions can exist. In the first set of conditions, both the plant and fungus specialize in taking up one resource. They obtain the other resource by trading: the plant makes carbohydrate by photosynthesis but does not take up phosphorus from the soil, while the fungus takes up only phosphorus from the soil. These conditions are optimal if light availability is low and phosphorus levels in the soil are moderate. In the second set of conditions, one organism takes up both resources and the other organism can only take up one. For example, when soil is rich in phosphorus, the plant specializes in taking up carbon, but the fungus takes up both carbon and phosphorus from the soil. However, neither Grman *et al.* (2012) nor De Mazancourt and Schwartz (2010) considered the dynamic aspects of the plant–fungus interaction.

Both the host plant and symbiotic fungus change their behaviour in response to the environment. For example, the presence of fungi would enhance plant growth when soil nutrients are scarce, whereas fungi could deter plant growth when soil nutrients are abundant (Johnson *et al.*, 1997). In response to such shifts in the relative benefit of the symbiosis, plants can decrease carbon allocation to symbiotic fungi, leading to a reduced size of mycorrhiza (Bever *et al.*, 2009). In addition, plants can engage in partner choice: when a plant harbours many symbiotic fungi in its roots, it can selectively decrease allocation to those fungi that do not allocate very much phosphorus (Bever *et al.*, 2009; Kiers *et al.*, 2011). In turn, fungi can also control resource allocation to the host plant: when the fungus interacts with many roots, it can allocate more phosphorus to roots that provide more carbohydrate (Kiers *et al.*, 2011). Changing resource allocation is sometimes considered a form of ‘punishment’ that stabilizes the mutualism (Kiers *et al.*, 2011). However, this situation provides an opportunity for cheaters, such as mycoheterotrophic plants, which do not have chloroplasts and do not produce carbohydrate via photosynthesis (Leake, 1994). Thus, fungi can allocate not only nutrients from the soil, but also carbohydrates that are allocated by other plants (Leake, 1994).

In this paper, we examine the optimal resource allocation of a plant and fungus to their partner when the entire system grows exponentially. Rapid growth is critical for the survival of seedlings, and phosphorus provided by the fungus is key to seedling establishment (Smith and Read, 2008). Under these conditions, the exponential growth rate for the whole system is a natural measure of overall success. The rates of resource acquisition (photosynthesis by the plant and phosphorus absorption by the fungus) increase with increases in both carbon and phosphorus within the body of each player. Assuming Cobb–Douglas production functions, we show that given the optimal rate of resource allocation, each player should allocate more to its partner when the resource provided by the partner is more important to its own resource acquisition. Second, we show that the growth trajectory corresponding to the optimal allocation fractions satisfies the conditions for the singular control subarc for dynamical optimization when each player maximizes its own fitness given its partner’s growth schedule. Hence, the ESS resource allocation by two players in a

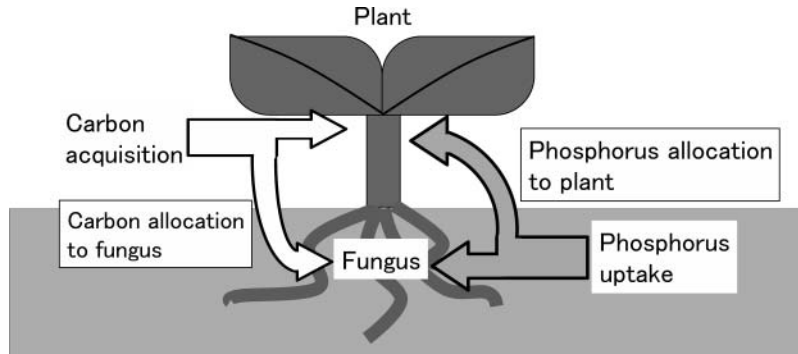


Fig. 1. Scheme of the model. One plant and one mycorrhizal fungus interact with each other. The plant obtains carbon by photosynthesis and controls the allocation of carbon to the fungus. The fungus takes up phosphorus from the soil and controls the allocation of phosphorus to the plant. By allocating resource, they can help the growth of the partner, and the partner may allocate more resources in the future.

non-cooperative game is equivalent to the cooperative optimum of resource allocation during the exponential growth phase.

MODEL

Consider two players: a plant and its symbiotic fungus in soil (Fig. 1). The plant performs photosynthesis and obtains carbon in its aboveground parts, while the fungus takes up nutrients, such as phosphorus, from the soil. The plant needs phosphorus supplied by the fungus to function properly. Hence, the plant allocates some fraction of its carbon to the soil fungus, which may in turn supply phosphorus to the plant in the future. In contrast, the fungus needs carbon supplied by the plant; thus, it allocates some phosphorus to the plant to secure future carbon. As a result, both players – plant and fungus – allocate some fraction of its acquired resource to its partner to secure future resources that are otherwise difficult to obtain directly. Here, we focus on a small, young plant individual (or seedling) and its soil fungus, in the state in which both grow exponentially through time.

We distinguish quantities of plant and fungi by $i = 1$ and $i = 2$, respectively. For simplicity, we assume that the soil fungus interacting with an individual plant exists as a large number of bundles or sheets of hyphae composed of genetically identical cells. Let C_i be the amount of carbon and P_i the amount of phosphorus contained in the plant ($i = 1$) and in the fungus ($i = 2$). Let $f(C_1, P_1)$ be the rate of carbon acquisition by the plant, and $g(C_2, P_2)$ be the rate of phosphorus acquisition by the fungus. These resource acquisition rates are increasing functions of both carbon and phosphorus. We consider the following dynamics:

$$\frac{dC_1}{dt} = (1 - u_1)f(C_1, P_1), \quad (1a)$$

$$\frac{dP_1}{dt} = u_2\xi_2g(C_2, P_2), \quad (1b)$$

$$\frac{dC_2}{dt} = u_1\xi_1f(C_1, P_1), \quad (1c)$$

$$\frac{dP_2}{dt} = (1 - u_2)g(C_2, P_2), \quad (1d)$$

where u_1 is the fraction of carbon obtained by the plant that will be allocated to the fungus (it satisfies $0 \leq u_1 \leq 1$). The plant can choose this value. In contrast, u_2 is the fraction of phosphorus sequestered by the fungus that will be allocated to the plant ($0 \leq u_2 \leq 1$). We consider that some loss occurs during this allocation process; hence, we consider the fractions lost, ξ_1 and ξ_2 , to be factors smaller than 1 ($\xi_1 < 1$ and $\xi_2 < 1$).

The rate of photosynthesis increases with carbon C_1 and phosphorus P_1 . In addition, the rate increases in proportion to plant size, if the ratio of carbon to phosphorus is kept constant. This last assumption is plausible for a young, small plant (or seedling) growing exponentially together with its symbiotic fungus. More specifically, we assume that the carbon acquisition rate of the plant and the phosphorus acquisition rate of the soil fungus satisfy the following relationships:

$$f(KC_1, KP_1) = Kf(C_1, P_1) \quad \text{for any positive } K, \quad (2a)$$

$$g(KC_2, KP_2) = Kg(C_2, P_2) \quad \text{for any positive } K. \quad (2b)$$

Equation (2a) implies that if both C_1 and P_1 are multiplied by factor K , $f(C_1, P_1)$ is also multiplied by the same factor K . Hence, the rate of carbon acquisition increases in proportion to plant size, if the size by which the plant increases with the ratio of carbon and phosphorus is kept constant. In a similar manner, equation (2b) indicates that if both C_2 and P_2 are multiplied by factor K , $g(C_2, P_2)$ is also multiplied by the same factor K .

Optimal application to own partner

As a simple example of production functions satisfying equation (2), we assume that the photosynthetic rate is the power function of two resources: $f(C_1, P_1) \equiv f_0 C_1^{1-\alpha} P_1^\alpha$, where α indicates the relative importance of phosphorus ($0 < \alpha < 1$), and f_0 indicates the basic rate of carbon acquisition. In economics, $f(C_1, P_1)$ is called the ‘Cobb-Douglas production function’ (see Fig. 2). In a similar manner, the rate of phosphorus sequestering by the fungus is $g(C_2, P_2) \equiv g_0 C_2^\beta P_2^{1-\beta}$, which increases with both carbon and phosphorus levels of the fungus. Here, β indicates the relative importance of carbon in this function ($0 < \beta < 1$), and g_0 indicates the basic rate of phosphorus acquisition. Again, if both C_2 and P_2 are multiplied by factor K , $g(C_2, P_2)$ is also multiplied by the same factor K .

Now, we focus on the exponential growth solution for this system. Assume that $C_1 = c_{10}e^{rt}$, $P_1 = p_{10}e^{rt}$, $C_2 = c_{20}e^{rt}$, and $P_2 = p_{20}e^{rt}$, where r is the exponential rate of growth. Then, equation (1) becomes:

$$rc_{10} = (1 - u_1)f_0 c_{10}^{1-\alpha} p_{10}^\alpha, \quad (3a)$$

$$rp_{10} = u_2 \xi_2 g_0 c_{20}^\beta p_{20}^{1-\beta}, \quad (3b)$$

$$rc_{20} = u_1 \xi_1 f_0 c_{10}^{1-\alpha} p_{10}^\alpha, \quad (3c)$$

$$rp_{20} = (1 - u_2)g_0 c_{20}^\beta p_{20}^{1-\beta}. \quad (3d)$$

After some arithmetic (see evolutionary-ecology.com/data/2941Appendix.pdf, part A), we have:

$$r^{\frac{1}{\beta} + \frac{1}{\alpha}} = u_1 (1 - u_1)^{\frac{1-\alpha}{\alpha}} u_2 (1 - u_2)^{\frac{1-\beta}{\beta}} g_0^{\frac{1}{\beta}} f_0^{\frac{1}{\alpha}} \xi_1 \xi_2. \quad (4)$$

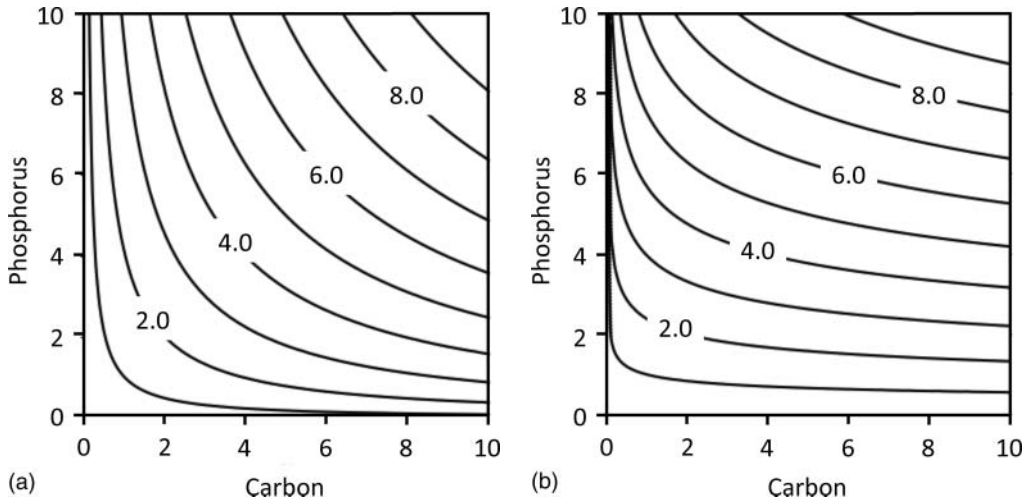


Fig. 2. Functional form of the Cobb-Douglas production function. Contour plots of the Cobb-Douglas production function for photosynthesis: (a) when both carbon and phosphorus are equally important ($\alpha = 0.5$), (b) when phosphorus is more important than carbon ($\alpha = 0.8$). The other parameter, $f_0 = 1.0$.

The optimum carbon allocation for the plant to the partner is the value of u_1 that maximizes the exponential rate of growth (equation 4). By calculating the partial derivative of equation (4) by u_1 and then setting it to 0, we have

$$u_1^* = \alpha. \quad (5a)$$

In a similar manner, the optimal rate of phosphorus allocation for the fungus to the plant that achieves the maximum exponential growth rate r is:

$$u_2^* = \beta. \quad (5b)$$

(For derivations, see [2941Appendix.pdf](#), part A.)

Power α is a coefficient for the dependence of the rate of photosynthesis on the amount of phosphorus that is supplied by the fungus. If α is close to 0, the photosynthetic rate is almost independent of P ; if instead α is close to 1, it is proportional to P and is almost independent of C . The plant should allocate more to the fungus if the resource supplied by the fungus is more important for its own function (i.e. larger α). Equation (5b) is a similar result for optimal resource allocation for the fungus. If the phosphorous acquisition rate by the fungus is strongly dependent on its carbon rather than phosphorus level (large β), then the fungus should allocate a larger fraction of newly acquired phosphorus to the plant, rather than for its own use.

Figure 3a illustrates a contour plot of the optimal allocation ratio by the plant to the fungus, where the horizontal axis is α , and the vertical axis is β . Figure 3b depicts a similar contour plot of the optimal allocation ratio by the fungus to the plant.

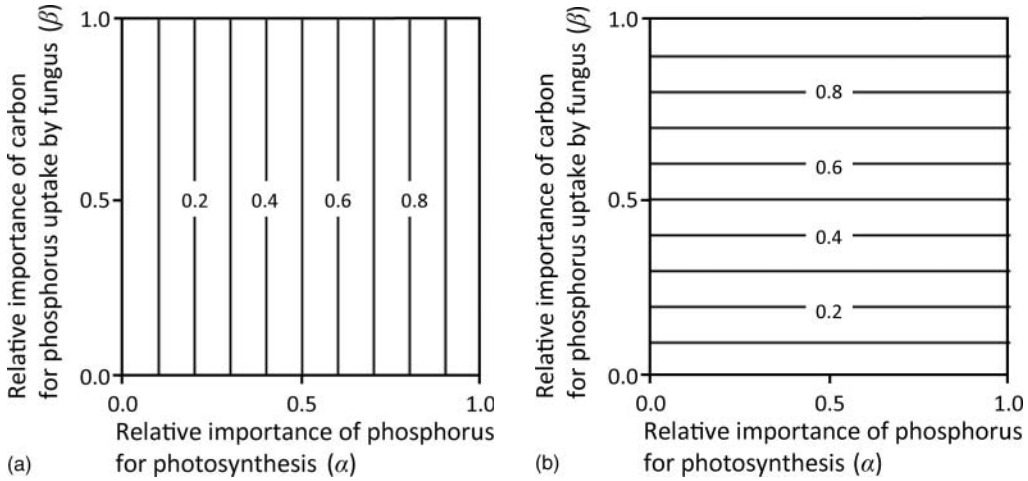


Fig. 3. The optimal reaction of plant and fungus. (a) Contour plot of u_1^* , the optimal allocation ratio by the plant to the fungus. (b) Contour plot of u_2^* , the optimal allocation ratio of the fungus to the plant. The horizontal axis is α , the relative importance of phosphorus to photosynthesis by the plant. The vertical axis is β , the relative importance of carbon for phosphorus uptake by the fungus.

DYNAMIC OPTIMIZATION OF EACH PLAYER

Equations (5a) and (5b) are the allocation values for two players given that they are constant over time. Here, we show that even if the allocation fraction is allowed to depend on time, these constant solutions are the optimal control for the respective players. This can be shown by the use of dynamic optimization. By fixing phosphorus allocation by the fungus at a constant value $u_2(t) = \beta$, we search for the optimal control schedule of the plant $u_1(t)$, and show that the optimal solution is a constant $u_1(t) = \alpha$. The allocation ratio affects the dynamics linearly, and this solution is an intermediate value $0 < u_1(t) < 1$, which is called a ‘singular control subarc’ (Intriligator, 1971). In a similar manner, we also show that the optimal control problem for the fungus is a constant solution $u_2(t) = \beta$, which maximizes the performance of the fungus under the condition of $u_1(t) = \alpha$.

We consider the optimal allocation schedule for the plant (player $i = 1$), denoted by $0 \leq u_1(t) \leq 1$ ($0 < t < T_f$), which maximizes $f(C_1(T_f), P_1(T_f))$, the rate of photosynthesis of the plant at time T_f . In calculating this dynamic optimization problem, we treat the behaviour of the fungus as given. This is a typical problem of optimal control and can be solved using Pontryagin’s maximum principle (Pontryagin *et al.*, 1962). The Hamiltonian of this dynamic optimization model for the plant (the first player) is defined as:

$$\begin{aligned}
 H = & \lambda_{C_1}(1 - u_1)f_0C_1^{1-a}P_1^a + \lambda_{P_1}u_2^*\zeta_2g_0C_2^\beta P_2^{1-\beta} \\
 & + \lambda_{C_2}u_1\zeta_1f_0C_1^{1-a}P_1^a + \lambda_{P_2}(1 - u_2^*)g_0C_2^\beta P_2^{1-\beta}.
 \end{aligned}
 \tag{6a}$$

λ_{C_1} , λ_{P_1} , λ_{C_2} , and λ_{P_2} are costate variables, corresponding to C_1 , P_1 , C_2 , and P_2 respectively. These variables indicate the ‘marginal effect of a small unit increase in the corresponding variable toward enhancing fitness’ (Intriligator, 1971; Iwasa and Roughgarden, 1984). They change with time following the differential equations below:

$$\frac{d\lambda_{C_1}}{dt} = -\frac{\partial H_1}{\partial C_1} = -(\lambda_{C_1}(1-u_1) + \lambda_{C_2}u_1\xi_1)(1-\alpha)f_0C_1^{-\alpha}P_1^\alpha, \quad (6b)$$

$$\frac{d\lambda_{P_1}}{dt} = -\frac{\partial H_1}{\partial P_1} = -(\lambda_{C_1}(1-u_1) + \lambda_{C_2}u_1\xi_1)\alpha f_0C_1^{1-\alpha}P_1^{-1+\alpha}, \quad (6c)$$

$$\frac{d\lambda_{C_2}}{dt} = \frac{\partial H_1}{\partial C_2} = -(\lambda_{P_1}u_2^*\xi_2 + \lambda_{P_2}(1-u_2^*))\beta g_0C_2^{-1+\beta}P_2^{1-\beta}, \quad (6d)$$

$$\frac{d\lambda_{P_2}}{dt} = \frac{\partial H_1}{\partial P_2} = -(\lambda_{P_1}u_2^*\xi_2 + \lambda_{P_2}(1-u_2^*))(1-\beta)g_0C_2^\beta P_2^{-\beta}. \quad (6e)$$

Using these functions, Pontryagin's maximum principle states that the optimal schedule is the one that maximizes the Hamiltonian H with respect to control variable u_1 , given state variables and costate variables. This condition gives the following:

$$\begin{aligned} u_1^* &= 0 & \text{if } \lambda_{C_1} > \lambda_{C_2}\xi_1 \\ u_1^* &= 1 & \text{if } \lambda_{C_1} < \lambda_{C_2}\xi_1 \\ 0 < u_1^* < 1 & \text{if } \lambda_{C_1} = \lambda_{C_2}\xi_1. \end{aligned} \quad (7)$$

The costate variables satisfy the following differential equations:

$$\frac{d\lambda_{C_1}}{dt} = -\frac{\partial H_1}{\partial C_1} = -\max[\lambda_{C_1}, \lambda_{C_2}\xi_1](1-\alpha)f_0C_1^{-\alpha}P_1^\alpha, \quad (8a)$$

$$\frac{d\lambda_{P_1}}{dt} = -\frac{\partial H_1}{\partial P_1} = -\max[\lambda_{C_1}, \lambda_{C_2}\xi_1]\alpha f_0C_1^{1-\alpha}P_1^{-1+\alpha}, \quad (8b)$$

$$\frac{d\lambda_{C_2}}{dt} = \frac{\partial H_1}{\partial C_2} = -(\lambda_{P_1}u_2^*\xi_2 + \lambda_{P_2}(1-u_2^*))\beta g_0C_2^{-1+\beta}P_2^{1-\beta}, \quad (8c)$$

$$\frac{d\lambda_{P_2}}{dt} = \frac{\partial H_1}{\partial P_2} = -(\lambda_{P_1}u_2^*\xi_2 + \lambda_{P_2}(1-u_2^*))(1-\beta)g_0C_2^\beta P_2^{-\beta}. \quad (8d)$$

The optimal control problem would typically be composed of the intervals in which the allocation ratio takes on terminal values (0 or 1) as well as an interval in which the allocation is an intermediate value (between 0 and 1). If the latter lasts for an interval of a positive length, it is called a 'singular subarc' (Intriligator, 1971). In the singular subarc, $\lambda_{C_1} = \lambda_{C_2}\xi_1$ holds for some time interval with a positive length, which generates additional equations and allows us to derive the solution (2941Appendix.pdf, part B).

Based on the other optimal growth schedule, the optimal solution is composed of three parts: (1) the initial phase in which allocation is either 0 or 1, which produces the most rapid convergence to the singular subarc; (2) a singular subarc in which both players receive a supply of carbon; and (3) the final period in which the plant stops supplying carbon to the fungus and uses all carbon income for itself. If the entire period of growth is sufficiently long (i.e. T_f is large), the singular subarc should comprise a large portion of the growth schedule.

We also consider the optimal allocation schedule for the fungus (the second player, $i = 2$), which is given by $0 \leq u_2(t) \leq 1$ ($0 < t < T_f$), which maximizes $g(C_2(T_f), P_2(T_f))$, the rate of photosynthesis of the plant at time T_f . In calculating this optimization, we treat the

behaviour of the plant as given. This can also be analysed using Pontryagin's maximum principle.

If both players (plant and fungus) adopt intermediate allocation ratios, the growth path needs to be a singular subarc in the two optimal control problems. Along this exponential growth solution, the conditions required by Pontryagin's maximum principle are satisfied for two dynamic optimization problems (optimization of $u_1(\bullet)$ by the plant, and optimization of $u_2(\bullet)$ by the fungus). By combining these two conditions, the same solution results as in the previous section: $u_1 = \alpha$ and $u_2 = \beta$ (derivations given in [2941Appendix.pdf](#), part B).

We note that there are two differences between the calculation in the present section and the arguments in the previous section. First, the calculation in the present section is the dynamic optimization, while that in the previous section was parametric optimization. The second, more important difference is a potential conflict of interest. In the present section, we discuss the solution in which each player maximizes its own objective function that differs between players, and the solution obtained is the evolutionarily stable strategy (Maynard Smith and Price, 1973; Maynard Smith, 1982) or the Nash equilibrium (Nash, 1951). The evolutionarily stable dynamic allocation turned out to be the same as the solution for the cooperative optimum, which is the solution that achieves maximization of the common target, i.e. the most rapid growth rate r of the whole system.

DISCUSSION

In this paper, we have analysed the optimal allocation between a terrestrial plant and a soil fungus. The plant acquires carbon by photosynthesis, and the soil fungus sequesters phosphorus from the soil. Because both players require both resources, both parties might profit by allocating some fraction of its resource to the other player. We focused on the situation for which both the plant and fungus grow exponentially through time and determined the optimal fraction of resources allocated to the other player.

We assumed that the resource acquisition rates (photosynthesis by the plant and phosphorus uptake by the mycorrhizal fungus) were Cobb-Douglas type as a function of carbon and phosphorus content of the body. When we measure how a quantity Q depends on a parameter A , a widely used index for the sensitivity is 'elasticity', which is defined as follows: $A(\Delta Q)/Q(\Delta A) = \partial \ln Q / \partial \ln A$, which is non-dimensionalized. For Cobb-Douglas production functions, the elasticity of the resource acquisition rate to the amount of resource supplied by the partner is constant at α and β for the plant and fungus, respectively. Cobb-Douglas production functions are commonly assumed in economic theory. The optimal allocation fraction is determined by the importance of the resource that is supplied by the opponent. More specifically, the plant's optimal allocation fraction to the soil fungus is equal to the elasticity of the photosynthetic rate on phosphorus (α), and the optimal allocation fraction of the fungus to the plant is equal to the elasticity of the nutrient acquisition rate on carbon (β). These optimal allocation fractions are independent of the functional form of the resource acquisition rate for the opponent.

Cooperative optimum and non-cooperative equilibrium

Another interesting result is that the solution for the most rapid growth rate for both the plant and fungus satisfies the ESS condition for each player to maximize its own performance. This implies that there is no conflict of interest. Although the two players have

different objective functions, to attain high fitness they must realize the fastest rate of growth, which is achieved by the same resource allocation as the cooperative optimum.

Relationship between the results and past theoretical models

Our model shows that if resource acquisition follows the Cobb–Douglas production function, an organism will allocate more resource to its partner when the resource provided by the partner is more important to its survival. This is similar to previous studies that have assumed the plant and mycorrhizal fungus to be in a stationary state (e.g. De Mazancourt and Schwartz, 2010; Grman *et al.*, 2012). Grman *et al.* (2012) demonstrated that the plant allocates more carbon if the soil contains more phosphorus. Although this situation corresponds to a high basic rate of acquisition of phosphorus (g_0) in our model, the result is different. According to our analysis, optimally growing plants should allocate the same fraction of photosynthates to the soil fungus regardless of the rate of acquisition of phosphorus. Whether this difference is caused by the difference in the functional forms of resource acquisition rates or by the contrast between a dynamically growing system and a stationary system should be determined in future studies.

Generalization of functional forms

Under these conditions, we can show that the whole system grows exponentially through time. The exponential rate of growth r is the solution of the following equation (derivation given in [2941Appendix.pdf](#), part C):

$$\frac{u_1 u_2 \xi_1 \xi_2}{(1-u_1)(1-u_2)} = \varphi^{-1}\left(\frac{r}{1-u_1}\right) \psi^{-1}\left(\frac{r}{1-u_1}\right). \quad (9)$$

The optimal allocation ratios of both players that achieve the fastest growth rate can be determined numerically.

Future extensions

Several extensions of the current model should be explored in future theoretical studies. A plant may obtain phosphorus directly from the soil without the help of the fungus. Also, some mycorrhizal fungi, such as ectomycorrhizal fungi, can obtain carbon directly. Thus, we should consider conditions under which the plant–fungus symbiosis is more beneficial to the plant or the fungus than the case without symbiosis.

In this paper, we assume that a single plant individual interacts with a fungus composed of a single genotype. Given that the hyphae are produced by cell division, this is a plausible assumption. However, sometimes a single plant interacts with multiple strains of fungi, each of which might start from a separate cell that proliferates to produce an individual lineage. The plant may then undergo partner choice by preferentially supplying resources to a strain that provides a highly efficient supply of phosphorus. If this is possible, then the outcome of the plant–fungus interaction could be greatly modified. We can also consider partner choice by the fungus if a single hypha interacts with multiple plant individuals and preferentially supplies phosphorus to an individual plant that provides a larger supply of carbon. These modifications to the model warrant additional theoretical treatment.

ACKNOWLEDGEMENTS

This study was conducted with the support of a Grant-in-Aid for Scientific Research B 15H04423 from JSPS to Y.I. and a JSPS pre-doctoral fellowship to K.U. We also thank M. Nakamaru, H. Ohtsuki, Y. Tachiki, A. Telschow, and H. Toju for their very helpful comments.

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