



Using hybrid automata modelling to study phenotypic plasticity and allocation strategies in the plant mycorrhizal mutualism



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ABSTRACT

Plants are exemplified by high plasticity in resource allocation strategies which allows them to maximize their fitness under changing resource conditions. In many plant species, obtaining resources involves mutualistic interactions with arbuscular mycorrhizal fungi (AMF), where plants provide the AMF with sugars in exchange for soil nutrients like phosphorus (P). These nutrient exchange rates have high context dependency, influenced by both the cooperative level of the AMF species involved (a qualitative trait) and the ambient nutrient concentrations in the soil (a quantitative value). Because this context dependency arises from a mix of both quantitative and qualitative factors, standard ordinary differential equation (ODE) modeling methods often complicate the representation of resource allocation strategies. Here, we explore the utility of a hybrid automata modeling framework that can intuitively combine the qualitative AMF traits and quantitative nutrient concentrations. This allows for a better analysis and understanding of phenotypic plasticity in resource allocation in the plant–AMF, and other nutrient exchange mutualisms. We consider a focal strategy in which nutrients are allocated to growth at times of nutrient limitations, and to storage otherwise and ask how this changes plant allocation to growth vs. storage. We first model this system dynamically to show how the plant responds to different environmental conditions and interacts with AMF and show that our hybrid automata model can replicate experimental data from the plant–AMF system. From our work, novel perceptions into the well-studied plant–AMF symbiosis and testable hypotheses can be underlined: (1) leaf biomass does not increase proportionally with the level of AMF cooperation; (2) in the context of multiple AMF simultaneously colonizing a host–plant, a narrow variance of response is observed and explained by an auction-like mechanism of the AMF to acquire C from the plant.

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1. Introduction

Phenotypic plasticity is the ability of an organism to change its phenotype based on environmental conditions such as nutrient availability and temperature (West-Eberhard, 1989). For example, in plants, high phenotypic plasticity in root growth is observed related to resource distributions or neighbor interactions (e.g. Hodge, 2004; Hutchings and de Kroon, 1994). As a result of this plasticity, plants can balance their carbon (C) investment to plant shoots and roots depending on the growth conditions.

Plant–phenotypic plasticity can also result from the symbiosis between plants and arbuscular mycorrhizal fungi (AMF) (Streitwolf-Engel et al., 1997). Because 80% of land plants are involved in AMF symbiosis (Smith and Read, 2008), the impact of this interaction on plant trait plasticity is likely substantial, yet has not been extensively studied. In this nutrient-exchange symbiosis, the plant is a facultative mutualist that provides photosynthetically-derived sugars to its obligate mutualist partner, AMF, in exchange for soil nutrients like phosphorus (P). Our aim is to examine the allocation strategies, i.e. the phenotypic plasticity such as root and leaf growth, of the plant depending on changes with its fungal partner. In general, a plant has different allocation strategies based on the environmental conditions, namely it allocates resources to growth vs. storage depending on the value of limiting nutrients (Poorter et al., 2012; Schachtman et al., 1998). For example, a low atmospheric C concentration induces investment in the

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growth of leaf biomass to increase the uptake of C, whereas shading of the host plant can result in changes in the amount of C the host allocates to the root and fungal partner (Fellbaum et al., 2014 and references therein).

A mathematical model of these dynamic processes is of great interest to explore how the environment influences the potential phenotypes of the organism formally by means of functions and variables. However, accurately representing the switching between qualitative phenotypes (e.g. discrete allocation strategies) and quantitative concentrations (e.g. changes in nutrients in the environment) can be difficult and complex if using standard modeling approaches such as ordinary differential equation (ODE) modeling methods (Zhai et al., 2014; Suzuki and Arita, 2013; Thornley and Parsons, 2014). In particular, dynamical equations often remain difficult to parametrize and are unable to capture both qualitative and quantitative features of available experiments. Rather than to model the details of these strategies in terms of specific chemical reactions and processes (Meyer et al., 2012), we use hybrid automata to describe the strategies, namely allocating resources to growth or storage, qualitatively, while basing these strategies on quantitative concentrations.

As promoted in Systems Biology for studying single cell molecular systems, hybrid automata is an alternative modeling method (Henzinger, 1996; Henzinger et al., 1996) that we advocate for studying organisms displaying phenotypic plasticity. Hybrid methods are hybrid because they are able to combine qualitative (e.g. discrete allocation strategies) with quantitative (e.g. fluctuations in concentrations) behaviors. A hybrid automaton is a hybrid method that switches between allocation strategies via the transitions, which are triggered when conditions on variables are satisfied. In that sense, any system displaying phenotypic plasticity could be modeled using hybrid automata. For example, an organism that changes behavior with respect to the seasons can be intuitively modeled using hybrid automata. Hybrid automata are implemented in systems biology (Siebert and Bockmayr, 2008; Ahmad et al., 2009, 2008), where the qualitative feature provides a convenient representation of the system when detailed or quantitative knowledge is lacking. In this paper, we show the potential of the hybrid automata modeling approach by considering a system that exhibits phenotypic plasticity. Although automata and hybrid methods have been individually applied to other systems such as cells and economies (Gronewold and Sonnenschein, 1998; Liu et al., 2014), hybrid automata have not yet been applied to an ecological system, such as a symbiotic relationship.

Using an ecological example of the plant–AMF symbiosis, hybrid automata are able to describe the fluctuation of carbon (C) and phosphorus (P) concentrations over time with changing allocation strategies. For example, allocation of storage could decrease the concentration of C and in turn, decreasing C concentration could switch resource allocation from storage to leaf growth (Fig. 1). In other words, representing the system as a hybrid automata intuitively combines the quantitative change in concentrations with the qualitative change in allocation strategies.

Our dedicated hybrid automata model accurately represents the plant–AMF C–P exchange system in order to investigate the plant's behavior of altering resource allocation to growth vs. storage according to which nutrients are limiting. In particular, we aim to determine when the switching between different strategies occurs. The challenge arises in coordinating the strategies of above- and belowground structures with the C and P that they both depend on.

We simulate scenarios where a host plant is exchanging nutrients with a fungal partner. We observe different strengths of symbiosis, i.e., rates of nutrient exchange between organisms, based on data from empirical work (Kiers et al., 2011). The formal construction of the model allows us to examine the link between

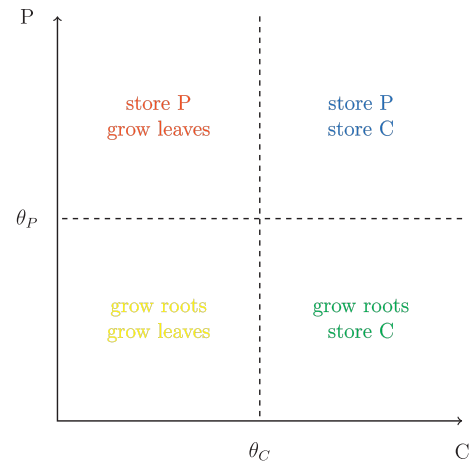


Fig. 1. The allocation strategies (phenotypes) of the plant based on the free carbon (C) and phosphorus (P) concentrations in the plant. Each quadrant is labeled with the corresponding allocation strategy. The threshold θ_C (and θ_P) determines the concentration of C (and P) at which the allocation strategy changes from growth to storage and vice versa. Intuitively, switching from one strategy to another is a result of C and P concentration changing over their respective thresholds. The red, yellow and green strategies belong to the growth phase and blue strategy to the storage phase as described in Section 4. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

data from experimental set-ups and the processes of resource allocation and exchange with AMF. Since the differential behavioral types for both the plant and AMF is completely lacking (Cahill and McNickle, 2011), this work looks to bridge the gap between the behaviors of the organism and their underlying allocation strategies.

2. Methods

2.1. Variables

The variables used in our model (Table 1) are associated with the plants allocation strategies with AMF symbiosis, namely obtaining C and P and allocating the nutrients in the processes of growth, storage and exchange. We assume that each variable can only take positive finite values due to physical restrictions of the plant.

C_p and P_p are used by the plant for general maintenance, growth, and exchange. St_C and St_P are the forms of carbon and phosphorus that are not available for use in maintenance, growth or exchange (e.g. starches). Qualitatively, we distinguish low and high values of C_p and P_p using the thresholds, θ_C and θ_P respectively (Fig. 1). The variables B_l and B_r are assumed to be proportional to the biomass of above and belowground structures respectively.

The C in the air, C_a , and the P in the soil, P_s , do not decrease in this model because the carbon in the air is assumed to be readily available and the P in the soil is thought to be replenished by the decay of other organic matter. Although we assume the very strong assumption that P in the soil is uniformly distributed due to the P

Table 1

Each variable in our model with description and units.

Variable	Definition	Value	Unit
C_p	Concentration of freely available carbon	1	mmol g ⁻¹
P_p	Concentration of freely available phosphorus	1	mmol g ⁻¹
B_l	Biomass of aboveground structures	10	g
B_r	Biomass of belowground structures	10	g
St_C	Stored carbon	0	mmol g ⁻¹
St_P	Stored phosphorus	0	mmol g ⁻¹
θ_C	Threshold of carbon	30	mmol g ⁻¹
θ_P	Threshold of phosphorus	30	mmol g ⁻¹

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