

# Functional trait and life-history variation of arbuscular mycorrhizal fungi during secondary succession

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## **Abstract**

Composition of plant communities during secondary succession are, to a great extent, determined by their arbuscular mycorrhizal (AM) symbionts. However, the role of AM fungi in driving secondary succession of plant communities is still the subject of extensive research. In recent years, efforts have been made to classify plants and AM fungi according to their life history traits. The mutualistic interactions between a plant and an AM fungal species with matching life history traits are very stable over time. In contrast, mutualism is weak between plants and AM fungi with non-complementary strategies. Plants and fungi maximising each other's fitness preferentially interact at the same successional stage. Moreover, there is compelling evidence for AM fungi driving plant-soil feedbacks. While altering feedback dynamics, AM fungi play a significant role in driving secondary succession towards climax stages by changing the composition of plant communities and recruiting more competitive or stress-tolerant species during intermediate successional stages. Consequently, community composition and change along successional gradients can be only fully understood when accounting for one of its major determinants: the AM fungi residing below ground.



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## Introduction

During the development of an ecosystem, plant and soil communities undergo successional shifts from stages dominated by ruderals and opportunists to a climax community, mostly dominated by competitive species. This climax state persists until stress increases or a new disturbance takes place and starts the process over again. Many biotic and abiotic factors are involved in secondary succession to gradually transform the composition of plant communities (e.g. Grime, 1977). Symbiotic interactions between plants and other organisms, particularly those residing below-ground, are vital for the progress of succession. The highly-specialised symbiosis of plants and arbuscular mycorrhizal (AM) fungi is of special interest in this context, because it is crucial to the survival of most land plants. Vegetation of all kinds benefits from mycorrhizae in terms of, for example, enhanced acquisition of soil-derived nutrients, facilitation, or protection against pathogens (Finlay, 2004).

Arbuscular mycorrhizal plants are found in ecosystems worldwide and it is estimated that approximately 75% of all angiosperms live in symbiosis with AM fungi (Brundrett, 2002). Arbuscular mycorrhizal fungi are important determinants for the assembly of plant communities, and they influence the diversity, distribution, and relative abundance of plant species (van der Heijden et al., 1998). Plants may differ to the degree on which they depend on mycorrhizal fungi (van der Heijden et al., 1998), and these responses could be related to certain plant life history traits (Grime, 2001). This variation in mycorrhizal dependency between plants relying on different life history strategies and range of possible responses may be one of the major mediators of species coexistence in plant communities, hence also a significant determinant for the assemblage and changes of plant communities during secondary succession (Chagnon et al., 2013). The triangular model of plant strategies developed by Grime (1977) will be used to classify both plant and fungal communities according to their life history traits during secondary succession. The gradual change from an early coloniser community mainly consisting of ruderal species, through seral communities, towards a climax vegetation dominated by com-

petitors or stress-tolerators shall be explained from a myco-centric perspective. How are the interactions between plants and AM fungi altered during the change from a ruderal to a competitive system, and to what extent is the successional transformation of these plant communities propelled by AM fungi? Which fungal life strategies are under selection along typical successional trajectories and do they resemble the strategies selected for in above-ground plants? This article will briefly summarise Grime's classification of ruderal, competitive, and stress-tolerant strategies from a plant perspective and apply this classification to explain the different strategies of AM fungi to explore their interactions with plants during secondary succession. Then, the CSR-framework will be applied to explain the different strategies of AM fungi in relation to their functional traits. Lastly, the role of arbuscular mycorrhizae as determinants of successional dynamics is outlined and discussed in relation to whether and to what extent AM symbionts drive secondary succession in plants.

### Grime's triangular model of plant strategies

According to British ecologist John Philip Grime, the growth of plants is restricted solely due to two factors, stress and disturbance. Stress is defined as abiotic phenomena that reduce plant primary production, like shading, water, mineral shortage, and climatic harshness (Grime, 1977, 2001). In contrast, the term disturbance addresses everything that leads to partial or total destruction of the vegetation in a given habitat, like herbivory, human activity, perturbations, or fires. The interplay of disturbance and stress gives rise to three possible plant strategies. Plant species that predominate habitats characterised by low stress and low disturbance are suggested to be good competitors (C), species colonising environments with high stress and low disturbance are predicted to be stress-tolerant (S), and ruderals (R) are predicted to thrive under highly disturbed conditions with little stress (Figure 1). Grime defines secondary succession as a gradual change in plant composition from weedy and easily outcompeted ruderals to more competitive and long-lived perennial herbs which can persist alongside other more long-lived plants (Grime, 1977, 2001). If stress increases due to shortage

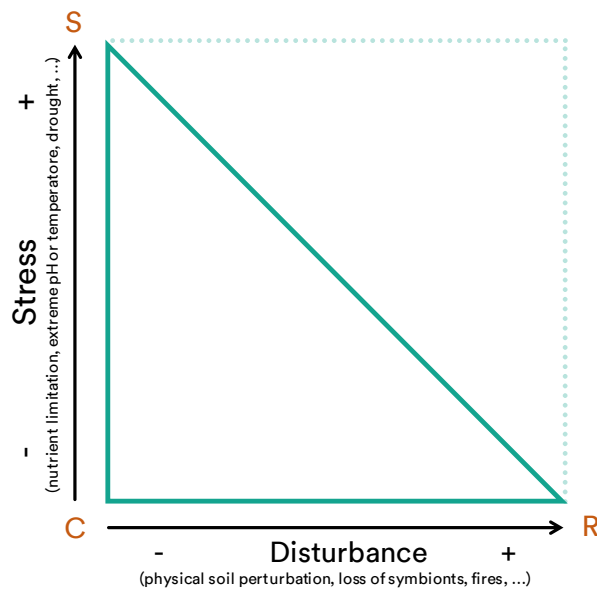


Figure 1. The triangular arrangement of life-histories consisting of competitive (C), stress-tolerant (S), and ruderal (R) strategies (adopted from Grime, 1977 and Chagnon et al., 2013) along increasing gradients of stress and disturbance. Note that there are no strategies adapted to high levels of both, disturbance and stress (dotted line).

of nutrients, water, or other resources such as light, competitive seral species may eventually become replaced by more stress-tolerant and even more persistent plants like woody shrubs or trees. The CSR model is a well-established theory, not only in plant ecology. Several efforts have been made to extend it to the community assemblage of different groups of organisms, such as in phytoplankton (Smayda & Reynolds, 2001), bryophytes (Grime et al., 1990), lichens (Grime, 1977), and mycorrhizal fungi (Chagnon et al., 2013).

#### Variation of life history traits and strategies in AM fungi

Because every plant has a limited energy budget, different strategies of allocating resources have evolved in order to cope with different environments. Species of AM fungi differ not only in their ability to translocate soil-derived nutrients to their host (Pearson & Jakobsen, 1993), but also in species-specific patterns of carbon storage and resource allocation to different reproductive and vegetative structures (Hart & Reader, 2002). These differences make it possible to classify fungal life history strategies based on functional traits, revealing how and to what

extent mycorrhizal communities are assembled along environmental and thus also successional gradients. Mycorrhizal fungi are highly dependent on their plant symbionts, which rely on different life history strategies, meaning that the fungi likely have life-histories similar, or at least compatible, to the strategies of their hosts. Therefore, it is possible to use the same theoretical approach for fungi as for plants. Classifying mycorrhizal fungi according to the three primary life history strategies in plants as defined by Grime (1977) seems thus to be a reasonable approach because it makes use of a thorough and well-established framework.

Grime defines competitiveness as the ability to take up and store limiting resources in a more efficient way than a potential neighbour (Grime, 1977). Given that AM fungi are efficient foragers of mineral nutrients and water, but at the same time dependent on organic nutrients originating from primary production, the availability of plant-derived carbon eventually limits the growth of mycorrhizal hyphae. Because the amount of carbohydrates fungi obtained from their symbionts is proportional to the amount of soil-derived nutrients delivered to the plant (Kiers et al., 2011), competitive mycorrhizal fungi

use most of their resources to produce absorptive hyphae that maximise foraging in the soil and delivery of nutrients to the plant (van der Heijden & Scheublin, 2007). Using most of the carbohydrates retrieved from the plant host to grow a network of fungal hyphae (mycelium) implies that less carbon can be allocated to storage organs or production of spores. Potential trade-offs may therefore limit reproduction rates and stress tolerance.

Stress is the sum of all abiotic restrictions that limit the production of biomass (Grime, 1977). Fungi are stressed when experiencing environmental extremes such as high soil acidity, low temperatures, or general shortage of nutrients, including those derived from their hosts (Chagnon et al., 2013). Such stressors may select for fungi that are efficient at handling plant-derived carbon, preferentially allocating it to the growth of hardy, long-lived hyphae that withstand extreme stressors and reduce the need to sustain constant growth (Chagnon et al., 2013). Exposure to stress agents present in the soil may also be minimised by reducing the total hyphal surface area exposed to potential toxins (Chagnon et al., 2013). Potential trade-offs associated with these traits may be, due to low growth rates, a generally limited ability to compete with faster growing, competitive species, and poor resilience to disturbance that may disrupt the mycelial hyphae. This eventually selects for fast-growing species with better healing abilities.

Ruderal environments are shaped by forces that partially or totally destroy biomass. From a fungal perspective, this is equivalent to the breakage of hyphae and the subsequent disruption of the entire mycelium, such as perturbation of soil by tilling or removal of the roots the fungi are anchored in (Chagnon et al., 2013). Ruderal AM fungi should therefore have effective healing mechanisms, meaning that disrupted hyphae grow fast and fuse easily together, thereby increasing tolerance to disturbance (de la Providencia et al., 2005). The root system of the plant host does not necessarily tolerate equal amounts of disturbance as an AM symbiont relying on a ruderal strategy (Chagnon et al., 2013). Therefore, the colonisation of new hosts may be advantageous. This strategy is achieved by vegetative growth and asexual spores, which allows faster re-establishment of connections after a disturbance than sexual reproduction. High quantities of hyphae produced per individual fungus result in decreased hyphal quality, meaning that production of many short-lived hyphae may go to the expense of a long life-cycle and the ability to withstand stress by producing rigid and long-lived hyphae (Chagnon et al., 2013).

Before assessing the compatibility of competitive, stress-tolerant, and ruderal AM fungi to plants with corresponding strategies, one needs to clarify the evolutionary foundations that lead to the formation of mutualistic interactions between plant and arbuscular mycorrhizal fungi.



### Partner selection

Plant selection of mycorrhizal partners is trait-based, meaning that it is driven by phenotypical characteristics that impact the fitness of the individual and the respective symbiotic partner. According to evolutionary theory, plants and fungi seek to maximise their fitness by avoiding symbiotic interactions with non-cooperative and hence antagonistic or detrimental partners (Chagnon et al., 2015). This partnership is easy to picture when thinking of mycorrhizae as a simple interaction with two partners involved. However, most mycorrhizal plants and fungi usually form mycelial networks with multiple individual plants (e.g. Selosse et al., 2006). A potential evolutionary consequence of that may be the emergence of 'cheaters' that simply rely on the benefits provided by others and live merely exploitative (Johnson et al., 1997; Selosse et al., 2006). There are numerous examples of arbuscular mycorrhizal fungi being parasites on plants (Egger & Hibbett, 2004). On the other hand, there are also solely mycoheterotrophic plants that forage by linking themselves into existing mycorrhizal symbioses without providing any compensation (Bidartondo et al., 2002). These cases are, however, exceptions and even though such parasitic adaptations exist both among fungi and plants, the common case seems to be the formation of mutualistic relationships. Due to the sheer number of species forming arbuscular mycorrhizae, it seems puzzling that mutualism seldom evolves into merely exploitative relationships, indicating evolutionary stability of AM symbiosis. What are the mechanisms behind the selection of the mutualistic partners?

In a series of experiments, Kiers et al. (2011) show that plant roots as well as fungal hyphae remunerate the most beneficial host. When the plants and the fungi are interconnected with several partners, the most cooperative mutualists are selected for. This strategy was recently also confirmed for networks with living plants (Fellbaum et al., 2014), where fungi enhanced the allocation of nitrogen (N) and phosphorus (P) to plants with the greatest photosynthetic activity, but retained hyphal connection to suboptimal hosts when high-quality symbionts were absent. Plants therefore compete for the best fungal partners by maximising pho-

tosynthetic activity above ground and disposing carbohydrates through the roots (Bever et al., 2009).

It is thus reasonable to think of partner selection as a competitive process where fungi and plants compete for symbiotic partners that increase their own fitness. Recently, Chagnon et al. (2015) confirmed that partners with similar strategies of resource allocation are more likely to form mutualistic interactions than plants and fungi with different life history traits – in line with earlier predictions (Chagnon et al., 2013). However, plant species may differ in their ability to sanction parasitic fungi by adjusting the allocation of photosynthates to their symbionts (Grman, 2012), allowing cheaters to persist in small numbers. This restriction creates room for extensive discussion concerning the complementary nature of plant life-histories and the strategies of their AM symbionts.

### Are plant and fungal strategies complementary?

Plants that rely on different strategies vary considerably in terms of their preferential symbiotic interactions with AM fungi. The degree of dependence on fungal symbionts varies from obligate, facultative, to non-mycorrhizal species (Francis & Read, 1994), and seems to be correlated with certain life history traits in plants (van der Heijden et al., 1998). This variation raises the question whether the complementary fungal strategies follow the same successional pattern as their hosts, and whether plants and AM fungi betting on the same tactic preferentially interact with each other.

Ruderal plants typically dominate during the earliest stages of succession, when environments feature a high degree of disturbance. They are often small, short-lived herbs with high growth rates as well as low production of total leaf and root biomass. Ruderals use resources to reproduce quickly and in the greatest numbers possible (Grime, 2001). Therefore, many monocarpic big-bang reproducers that flower early in their life cycle at the expense of a constitutive defense are considered ruderals. Habitats occupied by ruderals are often perishable and change rapidly, not only due to edaphic, meaning soil-related, shifts such as decreasing

availability of nutrients (Gorham et al., 1979), but also due to colonisation by more competitive species. Disturbance entails erosion that mobilises mineral nutrients in the soil and decomposition of the former vegetation will often additionally increase the availability of P and N on that site (Gorham et al., 1979). Accordingly, ruderal plants have high shoot to root biomass ratios and their root system is typical for plants with a resource-acquisitive strategy (Reich, 2014). Specific root length in ruderals is high (i.e., short roots but with a high root dry mass) and the roots are typically highly branched to increase surface area for nutrient uptake (Reich, 2014). Investment in terms of carbon is low, meaning that ruderal plant roots are fine and have a short life-span (Roumet et al., 2006). In order to overcome the constant loss of symbiotic interface, rates of colonisation by AM fungi must be higher in habitats dominated by annual ruderals than on sites with more competitive, bi- and perennial species that produce more long-lived roots (Navas et al., 2010; Roumet et al., 2006). Enhanced colonisation rates are in accordance with an AM fungal strategy adapted to disturbance predicted by Chagnon et al. (2013), suggesting that the need to steadily colonise new hosts to secure access to carbon may select for ruderal traits.

Fast-growing pioneer plants rapidly deplete the soil of P and N, which eventually become limiting agents. Consequently, selection for plant strategies that increase the uptake of nutrients unevenly distributed in the soil intensifies (Grime, 1977), meaning that the assemblage of the plant community will be adjusted towards more competitive species that invest in more persistent root biomass (Roumet et al., 2006). The root system of competitive plants will therefore be coarser and less branched compared to ruderals (Lambers et al., 2008). From a fungal perspective, the limiting resource, carbon, becomes more sparsely dispersed and concentrated in a smaller number of roots during the successional shift from ruderal to more competitive plants. This change eventually leads to selection of fungal functional traits that maximise carbon storage and uptake from the plant and increase competitiveness (Hart et al., 2001; Maherali, 2014). As mentioned before, the most

stable evolutionary strategy to maintain maximum carbon gain from the plant host is to maximise delivery of soil-derived nutrients (Kiers et al., 2011). AM fungi investing in absorptive hyphae are most prevalent during seral stages of secondary succession dominated by competitive plants (Chagnon et al., 2013), supporting the hypothesis that competitive plants and AM fungi preferentially interact with each other. Nevertheless, many mid-successional, competitive plant species are reported to be facultative mycorrhizal, which means they forage through producing root-bearing stolons, tillers, and ramets rather than investing carbon in mycorrhizal symbiosis (Hempel et al., 2013). However, in a study conducted on a ramet producing clover species (Du et al., 2009), switching to a mycorrhizal strategy was shown to bring greater benefit under increased nutrient stress. This discovery may illustrate that competitors invest in vegetative spread if the net benefit is positive, and increase allocation of carbon to AM fungi when nutrient concentrations drop below levels the plant can forage on.

Within a climax community, stress-tolerant plants are usually found in shaded, severely nutrient-depleted niches. Due to their generally low rate of carbon fixation, stress-tolerant plants are suboptimal hosts for fungi sustaining high growth rates and sinking great amounts of carbon, because mutualistic reward from photosynthates is restricted. Effects of, for example, light stress on AM fungi have been shown in a simple experiment conducted by Heinemeyer et al. (2004), who revealed a significant decrease in colonisation by AM fungi in patches of grassland that were shaded for one year. In the same study, however, community composition of AM fungi also changed towards more long-lived taxa that are resistant to carbon limitations (Hart & Reader, 2002). A selective shift towards more stress-tolerant fungi means that, in turn, also the composition of plant species in the study system is going to be altered (Heinemeyer et al., 2004).

These complementary life history traits indicate that plants and AM fungi with equivalent strategies preferentially interact with each other. Root traits and the ability to colonise new roots or maintain already established connec-



tions, play an important role in partner selection. Moreover, investigations on the evolutionary history of AM fungi, and their preferential interactions with plants, revealed that functional traits are phylogenetically conserved and are rooted deeply within their pedigree (Powell et al., 2009). Orders and families of AM fungi are likely to form mycorrhizal guilds sharing the same functional traits and life-histories (Maherali & Klironomos, 2012). Measuring behaviour and response under experimentally manipulated conditions may thus become obsolete. Instead, molecular approaches like pyrosequencing can be used to study the community ecology of AM fungi and assess fungal networks in the field (e.g. Błaalid et al., 2012).

The fact that plants and AM fungi relying on the same life history strategies preferentially form symbioses with each other, does not explain how succession is propelled, and to what extent it is determined by the trait-variation of AM fungi. It remains to be seen if changes in natural communities of AM fungi are a consequence or the cause of plant community dynamics during secondary succession (Hart et al., 2001).

### **Plant–fungus interactions determining secondary succession**

Assuming that AM fungi are passively affected by plant community changes implies that they must be host-specific. The presence or absence of certain plant species should therefore determine the ability of AM fungi to establish on a site. Yet AM fungi are known to have low host-specificity (Smith & Read, 1997), whereas plants seem to be pickier in choosing their fungal symbionts (van der Heijden et al., 1998), which indicates that arbuscular mycorrhizae must play a somehow determinative role during secondary succession. Experimental evidence has also shown that arbuscular mycorrhizae increase plant diversity and production (Klironomos et al., 2000). On the other hand, AM fungi are obligate symbionts and their fitness depends on the amount of carbohydrates retrieved from plants (Treseder, 2004), which weakens their role as active drivers due to their dependence on photosynthetic partners. One may view the dynamics of above- and below-ground secondary succession in the light

of the mechanisms underlying the feedbacks between plants and their mycorrhizal symbionts.

These feedbacks may either be positive or negative for both fungi and plants. A positive feedback loop is created when the presence of a certain fungal species increases the abundance of plants providing benefits to that AM fungus. In turn, the presence of a good host will feed back on the fungus' performance on that site, which again recruits more individuals of that specific plant into the system (Reynolds et al., 2003). Nevertheless, a negative feedback would be initiated when the fitness or survivorship of a given plant species is impaired by the presence of certain fungal species in the soil. This constraint will not only decrease the number of plants of a certain strategy on that site, but also alter diversity and abundance of soil organisms, such as AM fungi (Reynolds et al., 2003). Another type of negative feedback would be if the presence of a plant species increases the abundance of AM fungi that provide greater benefits to a second plant species. What is the relative importance of such positive and negative feedbacks during secondary succession, and to what extent are these feedbacks controlled by AM fungi?

Plant–soil feedback is strongly negative in early successional plant communities. Many, but not all, pioneer plants adapted to frequent and intense disturbance are non-mycorrhizal, which is not particularly surprising given that their habitats often contain easily accessible nutrients (e.g. Olsson & Tyler, 2004). Disturbance often entails soil horizon disturbance and erosion, leading to the mobilisation of mineral and organic nutrients. Moreover, the withered remains of the previous vegetation on that site will provide sufficient amounts of N to sustain a short-lived community of ruderal pioneers (Gange et al., 1990). Interacting with AM fungi is therefore often obsolete in habitats where nutrients are easy to access and may be foraged without the help of mutualists (Teste et al., 2014). Colonisation by AM fungi may in that case be detrimental for the plant, because the fungi act as additional carbon sinks and decrease plant growth and reproduction rates (Grime, 2001). But avoiding mycorrhizal symbiosis requires that non-mycorrhizal species within an early successional plant community select for

AM fungi recruiting other plant species into the system that leak greater amounts of photosynthates into the soil. In other words, competitive, mycorrhizal plants will gradually be able to establish themselves due to a prevalence of more 'generous' mycorrhizal species. Therefore, initially negative net feedback will reduce the dominance of 'greedy' pioneer species, leading to enhanced colonisation by plant species with greater competitive and cooperative abilities (Kardol et al., 2013). Total absence of AM fungi on a disturbed site significantly decreases plant productivity and recruitment of colonisers in the long run (Gange et al., 1990), meaning that mutualistic plants gain benefits from the presence of AM fungi on disturbed soils. Additionally, non-mycorrhizal plants do not profit from other advantageous functions AM fungi may provide, such as increased protection against pathogens (Finlay, 2004). In that way, selection for more resistant and mutualistic plants is strong and drives succession (terHorst & Zee, 2016). Due to the decreasing availability of soil nutrients from early to late successional stages, strength of mycorrhizal symbiosis increases within the plant community (Kardol et al., 2006; terHorst & Zee, 2016). Accordingly, abundance of competitive AM fungi will enhance diversity of plants providing greater reciprocal rewards and vice versa, meaning that the net feedback within a community turns positive when approaching successional climax.

A climax community can, however, be reset to an earlier successional state in the case that antagonists are selected. These may be parasitic fungi, mycoheterotrophic plants, or stress-tolerators that are suboptimal hosts to symbionts with mismatching strategies. In that case, the dominance of competitive species would cease due to the initiation of a negative feedback loop, thereby increasing disturbance, which subsequently starts secondary succession over again. However, shifts from climax back to early successional communities mainly occurs as a response to changes of abiotic parameters and stochastic events, such as availability of

water, radiation, or fires (Grime, 2001), rather than through alterations imposed by the fungal community.

### Concluding remarks

Fungal and plant life history traits are comparable within the same theoretical framework and resemble the same strategies when interpreted based on Grime's triangular model of life-strategies. However, it is not sufficient to solely contrast species located on the 'edges' of the CSR triangle to predict preferential interactions, mainly because the bulk of all fungi and plants will have intermediate strategies along these spectra. In order to get a more holistic view on how AM fungal communities change, it is necessary to integrate more than only preferential interactions between plants and AM fungi into the ecology of mycorrhizae. There are many other biotic and abiotic variables that determine the successional outcome, for example soil age and potential primary productivity. Especially in climax communities, interactions with other soil-dwelling organisms such as rhizobia and ectomycorrhizal fungi must be considered. Moreover, both AM and ectomycorrhizal fungi create common mycelial networks that mediate the translocation of nutrients (He et al., 2003; Walder et al., 2012), allelochemicals (Achatz et al., 2014), and other signalling molecules (e.g. Barto et al., 2012), altering the adaptive behaviour of both plants and fungi in a manner we are just beginning to understand (Gorzalak et al., 2015).

It is evident that arbuscular mycorrhizal fungi have an important role in adjusting plant communities from one successional stage to the next. They are important facilitators for plants dispersing into new locations and may hence alter community composition by the recruitment of new species. However, the ecological functioning and significance of plant-soil, and hence also plant-fungus, feedbacks are still poorly understood, and frameworks that integrate the relative roles of organisms across trophic levels in competition and facilitation are still under development (van der Putten et al., 2016).

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