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Significance of Arbuscular Mycorrhizal Fungi in Re-Vegetation Process in Nitrogen-Limited Degraded Ecosystems

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Abstract

It is well documented that arbuscular mycorrhizal (AM) fungi absorb phosphorus (P) from soil and supply P to host plant in exchange for carbon (C) from plants. Currently it is also recognized that AM fungi absorb nitrogen (N) from soil and supply it to plants. We examined possible roles of AM fungi in terms of N acquisition and establishment of plants under N-limited conditions. First, we used a split compartment system composed of root and hyphal compartments. By using the system, we successfully showed that growth of Welsh onion inoculated with AM fungi was increased by supplying N through AM fungi, when movement of soil mineral N to plant roots was limited. Secondly, we investigated how AM fungi were functioning through primary development of vegetation occurring in the lahar (mud flow of volcanic deposit) area of Mt. Pinatubo, Philippines. Pioneer plants in this area were a few gramineous plants, especially *Saccharum spontaneum*. Secondary plant species were wild leguminous plants, such as *Calopogonium muconoides*, which were characterized by co-existence of the gramineous plants. The growth of the gramineous plants was greatly enhanced due to N_2 fixation of leguminous plants. Laboratory inoculation experiments with AM fungi showed that some of the pioneer gramineous species responded to added N only when these were mycorrhizal. These suggest that AM fungi might help their host plants to acquire N efficiently in N-limited soil environments.

Introduction

Arbuscular mycorrhiza (AM) is a sophisticated symbiotic system composed of arbuscular mycorrhizal (AM) fungi and plant roots. It is well documented that AM fungi absorb phosphorus (P) from soil and supply P to host plant in exchange for carbon (C) from plants (Saito 1997). Since 1980's, it has been recognized that AM fungi also absorb nitrogen (N) from soil and supply it to plant (Ames et al. 1983). A main form of mineral nitrogen in soil is nitrate-N under aerobic conditions. In contrast to phosphate, nitrate-N in soil is not adsorbed with soil particles and moves easily along with mass flow of water. Therefore, unlike P, N supply through AM fungi to plant roots may not be critical for plant growth. It is now recognized that AM fungi may not increase plant growth under usual arable conditions (Reynolds et al. 2005). Although metabolic process of N transfer from AM fungi to plant has been clarified (Govindarajulu et al. 2005, Guether et al. 2009), it is still uncertain if N transfer from AM fungi to plant is important under natural conditions.

In this manuscript, first, we examine if AM fungi can enhance plant growth through their N supply to plant using a model system. Secondly, the significance of AM fungi in nitrogen-limited degraded soils is discussed with emphasis on re-vegetation process.

Can AM fungi enhance plant growth by supplying N through their hyphae?

Various compartment systems have been used to study nutrient transfer from AM fungi to plant. In most systems, the roots compartment is separated with fine nylon mesh from extraradical hyphal compartment. In the case of P, such mesh is effective to prevent P transfer between the compartments because of extreme slow mobility of phosphate in soil. Unlike phosphate, mineral N moves easily across the mesh. So it is difficult to quantitatively evaluate the effect of

AM fungi on N transfer. We modified a two-compartment system having roots and hyphal compartments (Tanaka and Yano 2005). In the system, the compartments were separated with fine nylon mesh and air gap so that neither movement of mineral nitrogen nor roots elongation between the compartments occurred. Washed river sand was used as a medium in both plant and hyphal compartments (Fig. 1). A 30 days seedling of Welsh onion, "Naga-Negi" in Japanese, (*Allium fistulos* CV. Motokura) was transplanted and inoculated with *Glomus* sp. R10 (Idemitsu Kosan Co.) in the root compartment (RC). After transplanting, ^{15}N labeled ammonium nitrate was added either RC or hyphal compartment (HC). The treatment was combination of N addition to HC or RC; A) No N, B) N to only HC, C) N to only RC, and D) N to both RC and HC. After 3 weeks, the system was dismantled. Plant growth and fungal growth parameters were measured. Polyphosphate which is a main P storage substance in AM fungi was also determined (Takanishi et al. 2009).

ANOVA analyses showed that "N to RC" treatment increased almost all plant and fungal growth parameters (plant dry weights, N and P concentrations, N uptake, colonization). "N to HC" treatment increased plant dry weight, shoot N and root ^{15}N concentrations, and P uptake. These indicate that AM fungi can enhance plant growth by supplying N under nitrogen-limited conditions (Fig. 2). Interestingly, P uptake and polyphosphate concentration in roots were also significantly increased by "N to HC" treatment. These further suggest that P transfer through AM fungi may be regulated by soil N availability.

Roles of AM fungi in re-vegetation process in nitrogen-deficit volcanic deposit

Secondly, we investigated how AM fungi were functioning through primary development of vegetation occurring in the lahar (mud flow of volcanic deposit) area of Mt. Pinatubo, Philippines (Saito et al. 2002; Oba et al. 2004). Because the lahar is comprised of newly erupted volcanic materials, it contains little organic matter and nutrients available for plants. Most of the area was sparsely vegetated with only a few gramineous plants, especially *Saccharum spontaneum*. However, some densely vegetated areas could be found in patch. These patches were characterized by co-existence of the gramineous plants and leguminous plants such as *Calopogonium muconoides* and *Centrosema pubescens*, which were well nodulated. Growth of the gramineous plants in these patches was greatly favored.

The δ^{15}N values in wild legumes in densely vegetated (DV) sites were near to atmospheric δ^{15}N (0 ‰), suggesting that these legumes actively fixed atmospheric nitrogen. *S. spontaneum* in sparsely vegetated (SV) sites showed much lower δ^{15}N values, probably because it absorbed N from a small amount of N in precipitation and/or in the soil extremely poor in organic N. On the other hand, the same plants in DV sites showed the medium values between the two formers, suggesting that *S. spontaneum* in DV sites used the N fixed by the legumes and its supported its vigorous growth in DV sites.

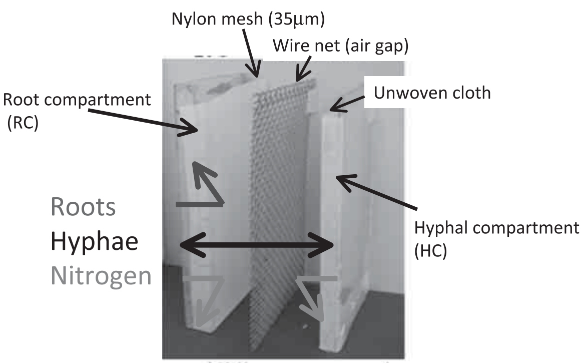

Fig. 1. Split compartment system for nitrogen addition experiment. Nitrogen was added to from the top of root compartment or hyphal compartment. Arrows indicate movement of nitrogen and elongation of roots and hyphae, respectively.

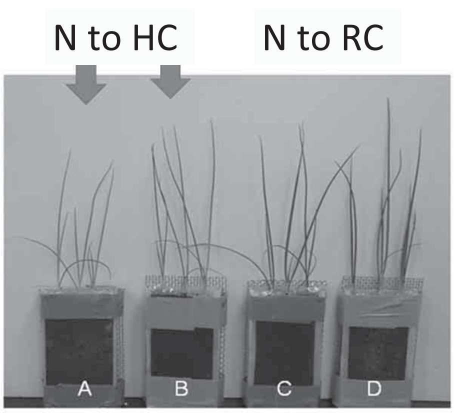

Fig. 2. Effect of nitrogen addition to different compartment on shoot growth of Welsh onion. A) No N, B) N to only HC, C) N to only RC, and D) N to both RC and HC.

The plant roots were colonized with AM fungi. The wild legumes such as *C. muconoides* were well colonized and the mycorrhiza was typical VA-type. *S. spontaneum* was less colonized, and the coiled hyphae were characteristics. In the dry season, the colonization, especially occurrence of arbuscule, was much less in both gramineous and leguminous plants than in the rainy season, suggesting the very weak activities of mycorrhiza in dry season.

The inoculation experiment indicated that *S. spontaneum* was not responsive to inoculation at least under nitrogen deficit conditions such as the lahar soils but increased the spore numbers of AM fungi. Some of other gramineous species responded to added N only when these were mycorrhizal (Fig. 3). This findings suggest that some gramineous plants may contribute to increase the population of AM fungi in soil although the AM fungi are not beneficial to the host plants, and further suggest that AM fungi might help their host plants to acquire N efficiently in N-limited soil environments.

The present study indicated that the re-vegetation process in the lahar area of Mt. Pinatubo involved the complex biological interaction among plants, microorganisms and environment. Based upon the results, we propose a picture of re-vegetation in the lahar soil. First, small seeds of the gramineous plants such as *S. spontaneum* are easily dispersed by wind from the area whose vegetation was not affected by volcanic activity, and they start to grow in the lahar. Secondly, spores of AM fungi are also dispersed by wind or flooding to the lahar area. The fungi colonize the gramineous plants, and host plants increase the fungal density. AM fungi might improve N nutrient of some gramineous species under such nitrogen-limited conditions, although we were not able to show direct evidence. Thirdly, seeds of legumes are dispersed into the lahar. The high population density of AM fungi supports the growth of the legumes, because leguminous plants are known to be highly mycorrhiza dependent (Crush,1974) and require higher P absorption for their nitrogen fixation. Vigorous growth of the legumes promotes the growth of associated gramineous plants through the supply of the fixed nitrogen. Then, once the vegetation is established, the erosion of the soil may be reduced so that organic matter starts to accumulate in the lahar soil, which will support the further growth of other plant species.

In conclusion, AM fungi have a potential to promote plant growth by supplying N to their host. Promoting effect of AM fungi on plants in a soil deficit of N was evident for some plant species when N was added to the soil. In re-vegetaion process in a volcanic deposit, AM fungi may have a role to facilitate vegetational succession.

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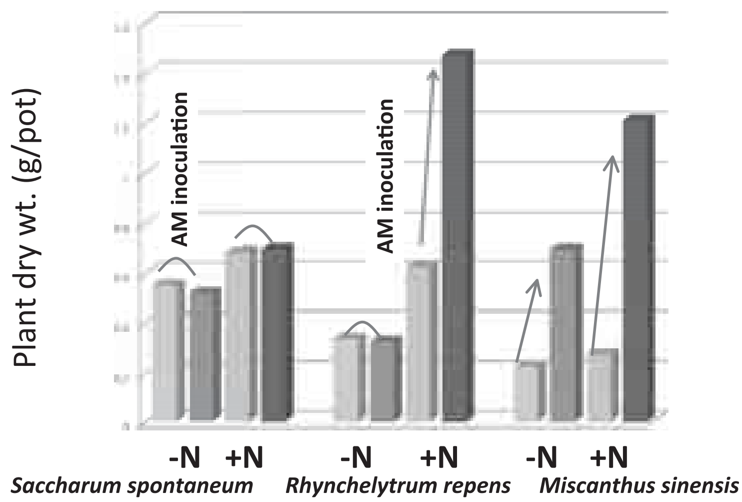

Fig. 3. Effect of AM fungal inoculation on wild gramineous plant species growing in a volcanic deposit deficit of nitrogen. Plants showing no-response with AM fungal inoculation were also colonized.

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