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Mycorrhizal symbiosis increases growth, reproduction and recruitment of *Abutilon theophrasti* Medic. in the field

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Abstract. We examined in the field the effect of the vesicular-arbuscular (VA) mycorrhizal symbiosis on the reproductive success of *Abutilon theophrasti* Medic., an early successional annual member of the Malvaceae. Mycorrhizal infection greatly enhanced vegetative growth, and flower, fruit and seed production, *resulting in significantly greater recruitment the following year*. In addition, the seeds produced by mycorrhizal plants were significantly larger and contained significantly more phosphorus than seeds from non-mycorrhizal plants, an effect which may improve offspring vigor. Infection by mycorrhizal fungi may thus contribute to the overall fitness of a host plant and strongly influence long-term plant population dynamics.

Key words: Mycorrhiza – *Abutilon theophrasti* – Fitness – Seed quality – Recruitment

Vesicular-arbuscular mycorrhizal (VAM) fungi form symbioses with the vast majority of terrestrial plant species (Gerdemann 1968). They may play important roles in the ecology of their hosts by influencing long term plant population dynamics. For example, mycorrhizal infections have been shown to increase both fecundity and offspring vigor of host plants (Lewis and Koide 1990; Lu and Koide 1991; Carey et al. 1992; Koide and Lu 1992). Despite this potentially very important effect of mycorrhizal fungi, little effort has been directed toward understanding their role in controlling the population dynamics of their hosts.

Stimulation of plant growth and reproduction due to mycorrhizal infection has been relatively well documented from greenhouse experiments. There are far fewer published studies concerning the effects of VAM in the field and the results from these are extremely variable (see McGonigle 1988). Moreover, many of these investigations were performed on cultivated plant species for which population dynamics were not of interest (notable exceptions include the works of Carey et al. 1992 and Gange et al. 1990). In order to better understand the ecological significance of mycorrhizal fungi, field experiments with wild host species are clearly necessary. The purpose of this study was to investigate, in the field, vegetative and reproductive responses to mycorrhizal infection and their consequences for host plant population dynamics. The host plant employed was *Abutilon theophrasti* Medic., an early successional annual member of the Malvaceae that is naturalized in much of the eastern and midwestern portions of the United States.

Materials and methods

The experiment was conducted in field #82 of the Horticulture Farm at the Russell E. Larson Agricultural Research Center of the Pennsylvania State University in Centre County, Pennsylvania. The soil was a Hagerstown silty clay loam, with a moderately low level of available phosphorus (bicarbonate extractable P was approximately 10 μg P g^{-1}). On 9 May 1991, 0.40 ha of the field (the entire experimental area) was injection-fumigated with a mixture of methylbromide (67%) and chloropicrin (33%) at the rate of 560 kg ha^{-1} to kill indigenous mycorrhizal fungi in the soil. Prior to fumigation, the same portion of the field was fertilized with nitrogen in the form of NH_4NO_3 at a rate of 147 kg N ha^{-1}.

The field was divided into five blocks, the length of each running perpendicular to a gentle slope. Each block contained 16 square plots. Plots were each 2 × 2 m and there were 2 m between plots. On 30 May 1991, eight plots in each block were inoculated with 0.68 kg of inoculum containing spores of *Glomus intraradix* Schenck and Smith (approximately 2000 spores g^{-1} inoculum) in a dry clay-based carrier (NPI, Salt Lake City, Utah, USA). The inoculum was mixed into the soil to a depth of 15 cm by hoe. Soil in non-mycorrhizal plots was also mixed by hoe but no inoculum was incorporated. Previous tests indicated that the clay-based carrier had no independent effects on *Abutilon* growth or reproduction (Koide unpublished). No effort was made to add other microbes present in the inoculum, if any, to the non-mycorrhizal

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plots. Seeds of *Abutilon theophrasti* (Valley Seed Service, Fresno, CA, USA) were then evenly distributed, 600 per plot, on all 80 plots and lightly raked into the soil. On 13 June 1991, phosphorus was applied to all contiguous plots in one half of each block (300 kg superphosphate ha^{-1}, equivalent to 6 g P m^{-2}), resulting in a split-plot design (phosphorus treatment assigned to the main plot and mycorrhizal treatment assigned to the subplot). Thus, mycorrhizal inoculation and phosphorus amendments created four treatments within each block: mycorrhizal, no P amendment (MPO); non-mycorrhizal, no P amendment (NMPO); mycorrhizal, plus P (MP1); non-mycorrhizal, plus P (NMP1) and there were four 4-m^2 replicate plots for each treatment combination in each block.

Plots were thinned on 16 June 1991 (17 days after sowing) so that each plot contained between 45 and 50 plants. Thinning was random with respect to plant size but resulted in an even spatial distribution of plants throughout each plot. Weeds were removed from the plots by hand as necessary to maintain a monospecific stand of *Abutilon theophrasti*. In the local area, we have observed that *Abutilon* often occurs in rather dense monospecific stands following soil disturbance.

Sprinkler irrigation was occasionally necessary due to the unusually low rainfall. A total of 25 cm of rain fell during the months of May, June, July, and August, approximately 15 cm below the mean rainfall from 1983 to 1990 during these months. Care was taken when setting out the irrigation pipes to prevent inadvertent inoculation of plots with mycorrhizal fungi from other plots.

On 24 June 1991 (25 days after sowing), three randomly selected plants in each plot were tagged. All reproductive data (quantities of flowers and capsules) and the quantity of branches were collected from these representative plants (240 total). The representative plants were chosen by marking a spot on the ground within the plots 0.6 m in from three corners of the plot (compass directions SW, SE, NE). The points of orientation were initially chosen at random. The plants closest to the marks were selected.

The average height of the plants in each plot was recorded on 30 July 1991, 61 days after sowing. The quantities of flowers and capsules on each representative plant were recorded on 6, 10, 16, and 23 August 1991 (68, 72, 78, and 85 days after sowing). Pods containing mature seeds were harvested from one of the representative plants of each plot on either 6 September 1991 or 13 September 1991 (99 or 106 days after sowing). Seeds were removed from the capsules in the laboratory. One seed from each plot was randomly selected and the seeds were pooled according to treatment combination and block. They were then acid-digested prior to colorimetric analysis for total phosphorus (molybdo-phosphate method, Watanabe and Olsen 1965) and for total nitrogen (Nessler method, Jensen 1962).

Two additional plants (not the representative plants) from each plot were randomly selected and harvested on 19 July 1991 (50 days after sowing). The shoots were oven-dried in an oven at 70° C to constant weight. Shoots were ground and acid-digested prior to colorimetric analyses for total P and for total N using the methods described above. The fine roots were collected to a depth of about 20 cm, rinsed in distilled water to remove soil, and preserved in a formaldehyde-acetic acid-ethanol (FAA) solution. Roots were stained with trypan blue and the percent colonization was calculated using the methods previously described (Koide and Mooney 1987). On 12 August 1991 (74 days after sowing), one plant from each plot was randomly selected and analyzed for P and N in the manner previously described. On 24 September 1991 (117 days after sowing), one plant was randomly selected from half of the plots and percent colonization was measured as described above.

On 1 October 1991, the seeds that had fallen to the ground within each plot were counted. A metal ring (20 cm diam) was placed in three locations within each plot on a diagonal line from the southwest to the northeast corner of the plot. All seeds within the rings were counted and used to calculate the density of seeds on the ground. The soil was left undisturbed at the end of the growing season of 1991 so that natural recruitment could occur in 1992.

In the Spring of 1992, permanent wire rings (36 cm diam) were randomly placed into each of the 80 plots to document offspring seedling establishment. On several occasions throughout this second growing season, the number of seedlings within the rings were counted to determine the effect of the treatments of the previous generation of plants on recruitment in the following generation. Sampling dates were 7 May, 21 May, 4 June, 18 June, 2 July, 16 July, 29 July and 13 August.

The effects of phosphorus and mycorrhizal infection on height of plants, number of flowers per plant, number of capsules per plant, number of branches per plant, seed weight, total seed P, total seed N, shoot weight, total shoot P, total shoot N, percentage of root colonized by VAM fungi, seeds m^{-2} on the ground, and offspring seedling recruitment were analyzed using a split-plot analysis of variance (STSC, 1991). Because there were four 4-m^2 experimental plots for each treatment combination in each block, replication mean values of the various measured and calculated variables were computed and used in the split-plot analysis of variance. All standard errors reported are pooled and do not reflect variability among blocks. Mean separations were accomplished using Fisher's protected Least Significant Difference method for the split-plot analysis of variance (Gomez and Gomez 1984). In all analyses we used 0.05 as the level of significance.

Results

Both phosphorus (P) treatment and mycorrhizal (M) treatment increased ($p \leq 0.05$) the height of the plants by day 61 (Fig. 1). There was no significant interaction between P and M treatments.

By 68, 72, 78, and 85 days after sowing, M treatment increased ($p \leq 0.05$) the number of flowers per plant (Fig. 2A). There were no significant effects of P treatment on the number of flowers per plant for those days, nor were there any significant interactions between P and M treatments. By 68, 72, 78, and 85 days after sowing, M treatment increased ($p \leq 0.05$) the number of capsules per plant (Fig. 2B). There were no significant effects of P treatment for those days, nor were there any significant interactions between P and M treatments.

By day 50, P treatment increased shoot weight ($p \leq 0.05$, Fig. 3A). In contrast, M treatment did not significantly affect shoot weight. By day 74, however, P treatment no longer significantly affected shoot weight (Fig. 3B), but M treatment did increase shoot weight ($p \leq 0.05$). There were no interactions between M and P treatments for either day 50 or day 74.

By day 50, M treatment increased ($p \leq 0.05$) shoot P and N concentrations (Table 1). Addition of P did not

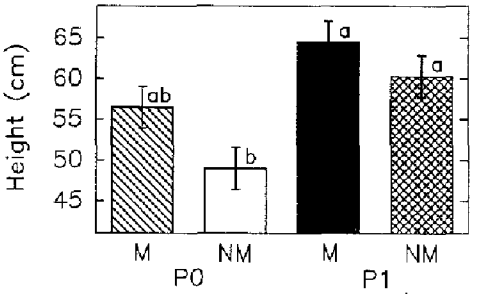

Fig. 1. Mean height of plants 61 d after sowing. Vertical error bars are ±1 SE. *M*=mycorrhizal; *NM*=non-mycorrhizal; *P0*=no P amendment; *P1*=plus P. Analysis of variance results given in Results section. $n=5$ blocks

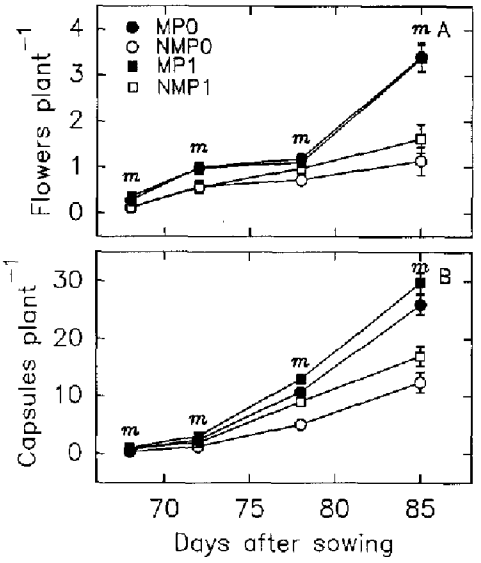

Fig. 2. **A** Mean number of flowers per plant. **B** Mean number of capsules per plant. Data were collected 68, 72, 78, and 85 d after sowing. Vertical error bars and abbreviations as in Fig. 1. According to the analysis of variance, there was never a significant interaction between P treatment and M treatment, and P treatment was never significant. m=significant ($p \leq 0.05$) effect of maternal mycorrhizal infection. $n=5$ blocks

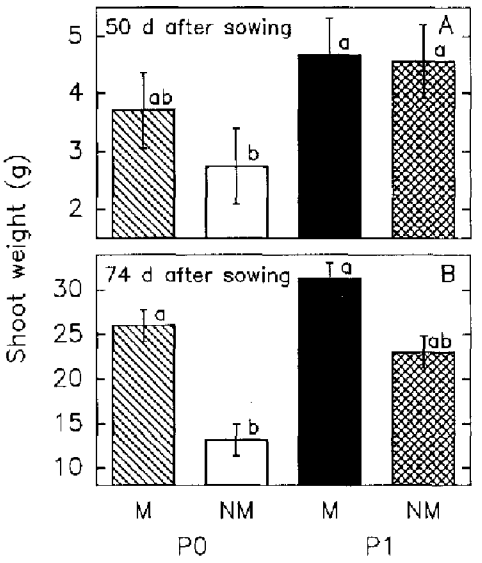

Fig. 3. **A** Mean shoot dry weight, 50 d after sowing. **B** Mean shoot dry weight, 74 d after sowing. Vertical error bars and abbreviations as in Fig. 1. Analysis of variance results given in Results section. $n=5$ blocks

significantly affect shoot N or P concentrations or shoot P contents by day 50, but it did increase ($p \leq 0.05$) shoot N content. M treatment increased shoot P content ($p \leq 0.05$), but did not significantly affect shoot N content. There were no significant interactions between M and P treatments on day 50 for shoot N concentration and content or shoot P concentration and content.

By day 74, M treatment increased ($p \leq 0.05$) shoot N concentration and N content (Table 1) and increased ($p \leq 0.05$) shoot P concentration and P content. P treatment decreased ($p \leq 0.05$) shoot N and P concentrations (Table 1), but did not significantly affect shoot N and P contents on day 74. There were no significant interactions between M and P treatments on day 74 for shoot N concentration and content or shoot P concentration and content.

M treatment significantly increased ($p \leq 0.05$) the mean weight of an individual seed (Fig. 4A). P treatment did not significantly affect individual seed weight, and there was no significant interaction between P and M treatments.

M treatment increased ($p \leq 0.05$) seed P concentration and seed P content (Fig. 4B, C), but P treatment did not. There were no significant interactions between P and M treatments on seed P concentration or content.

Neither M treatment nor P treatment significantly affected seed nitrogen concentration (Fig. 4D). There was no significant interaction between P and M treatments on N concentration. While seeds from M plants had a slightly higher nitrogen content than seeds from NM plants (Fig. 4E), the effect of M treatment was not significant. P treatment also did not significantly affect

Table 1. Means of shoot N and P contents and concentrations. Data were collected on 19 July 1991 (50 d after sowing) and on 12 August 1991 (74 d after sowing). Different letters within rows indicate significant differences among treatment means according to Fisher's protected LSD method. "M"=mycorrhizal; "NM"=non-mycorrhizal; "P0"=no P amendment; "P1"=plus P. $n=5$ blocks

	Treatments means			
	P0		P1	
	M	NM	M	NM
50 d after sowing				
Shoot N, %	3.90a	3.54ab	3.72ab	3.45b
Shoot N, mg plant^{-1}	69.5ab	47.1b	87.0a	77.0ab
Shoot P, %	0.22a	0.16b	0.22a	0.16b
Shoot P, mg plant^{-1}	4.02ab	2.21b	4.99a	3.71ab
74 d after sowing				
Shoot N, %	2.83a	2.52ab	2.62ab	2.29b
Shoot N, mg plant^{-1}	733a	324b	809a	506ab
Shoot P, %	0.20a	0.11b	0.17a	0.11b
Shoot P, mg plant^{-1}	52.5a	15.0b	55.2a	25.8b

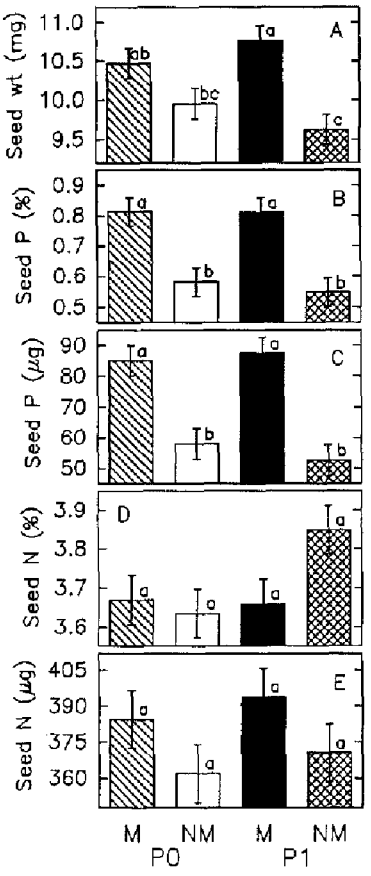

Fig. 4. A Mean seed weight for each treatment combination. B Mean seed phosphorus concentration. C Mean seed phosphorus content. D Mean seed nitrogen concentration. E Mean seed nitrogen content. Vertical error bars and abbreviations as in Fig. 1. Analysis of variance results given in Results section. $n=5$ blocks

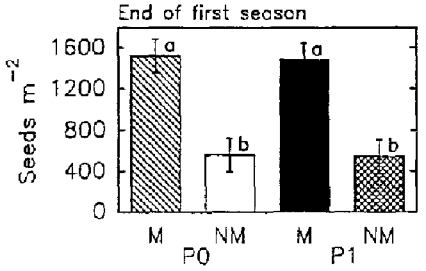

Fig. 5. The density of seeds on the ground within the plots measured at the end of the growing season (1 October 1991). Vertical error bars and abbreviations as in Fig. 1. Analysis of variance results given in Results section. $n=5$ blocks

seed nitrogen content and there was no significant interaction between P and M treatments.

The mean percent colonization of roots by VAM fungi on 19 July 1991 (50 d after sowing) for MP0, NMP0, MP1, NMP1 treatment combinations were 62a, 0.2b, 56a, 0.8b, respectively. Different letters indicate significant differences among treatment combination means by the Least Significant Difference method. On 24 September 1991 (117 d after sowing), the means for MP0, NMP0, MP1, NMP1 were 87a, 2.6b, 89a, and 4.8b,

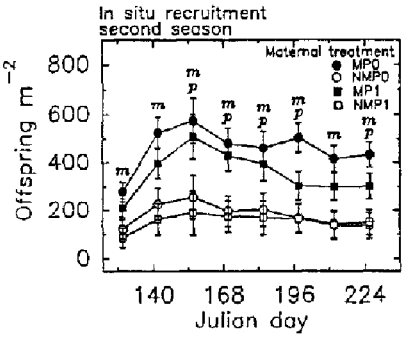

Fig. 6. Recruitment of offspring plants in the second growing season as measured by the number of offspring per square meter within the plots over time. Vertical error bars and abbreviations as in Fig. 1. According to the analysis of variance, there were never significant interactions between maternal P treatment and maternal mycorrhizal treatment. m = significant ($p \leq 0.05$) effect of maternal mycorrhizal infection. p = significant ($p \leq 0.05$) effect of maternal P application. $n=5$ blocks

respectively. M treatment was significant ($p \leq 0.05$) at both sample times. There were no significant P treatment effects on day 50 or on day 117, nor were there significant interactions between P and M treatments.

At the end of the first growing season (1 October 1991) the quantity of seeds on the ground within the plots (Fig. 5) was significantly increased by M treatment ($p \leq 0.05$), but not by P treatment. There was no significant interaction between M and P treatments.

Recruitment in the second growing season within the plots was increased ($p \leq 0.05$) by both maternal plant M and P treatments (Fig. 6). In general, M plots had significantly greater recruitment than NM plots, and P0 plots had greater recruitment than P1 plots. In no case was there a significant interaction between maternal plant M and P treatments.

Discussion

Mycorrhizal infection by *Glomus intraradix* Schenck and Smith greatly enhanced the vegetative growth and reproduction of *Abutilon theophrasti* in the field. Nearly every character measured on plants grown in fumigated soil was significantly increased by mycorrhizal (M) infection: height, shoot weight, branching, shoot nutrient contents, the number of flowers and capsules, seed weight, the nutrient content of seeds and seed density on the ground. Numerous studies document stimulation of growth due to mycorrhizal infection (Harley and Smith 1983), but few have investigated mycorrhizal effects on plant reproduction (Daft and Okusanya 1973; Bagyaraj and Sreeramulu 1982; Jensen 1982; Dodd et al. 1983; Koide et al. 1988; Bryla and Koide 1990; Carey et al. 1992). Still fewer of these studies have been performed in the field. As a result we know relatively little of the consequences of mycorrhizal infections on host population dynamics in natural communities despite the fact that mycorrhizal fungi are nearly ubiquitous.

In the current field study, mycorrhizal (M) plants produced significantly more flowers and capsules than non-

mycorrhizal (NM) plants. This can be largely attributed to a significant increase in the branching of M plants. By 89 d after sowing, M plants had over 2.5 times the number of branches of NM plants (data not shown). Branching has been shown to be increased by enhanced plant P status (Lynch et al. 1991). The effect of M treatment on branching in this study is thus likely to be mediated by plant P status.

Both seed size and seed nutrient contents may influence offspring vigor. Seed size has been shown to affect germination characteristics, seedling size, adult plant size, and competitive ability (see review, Roach and Wulff 1987). In the current field study, seed size and seed nutrient content were increased by M treatment. Koide and Lu (1992) and Lewis and Koide (1990) found that these traits were associated with more vigorous offspring plant growth and reproduction. The results of the present study therefore suggest that the seeds produced by mycorrhizal *Abutilon theophrasti* may result in more vigorous offspring, particularly if they grow in P-deficient soils.

We have shown that mycorrhizal infections are capable of influencing the recruitment of *Abutilon* offspring plants in the succeeding growth season. Thus, long-term population dynamics are likely to be affected by mycorrhizal infection. The ecological consequences of this may be quite large. Some members of the early successional old field plant community in our region, unlike *Abutilon*, are non-mycotrophic (for example, *Amaranthus retroflexus*). Others, although mycotrophic, appear to respond poorly to mycorrhizal infection (for example, *Setaria lutescens*, see Koide and Li 1991). Thus, mycorrhizal fungi may influence the population dynamics differently for different plant species and thereby may have important effects on plant community structure and succession. The density of seeds sampled on the ground at the end of the first growing season was not significantly affected by P treatment. The cause of greater recruitment in the P0 plots compared to the P1 plots is therefore puzzling. One possible explanation for this is that additional P resulted in greater seed parasitism by soil fungi. Another possibility is that seed dormancy was significantly affected by P treatment. Both hypotheses remain untested at this time.

In the current study, superphosphate was applied to one-half of the field plots to determine if P amendment would produce effects similar to those resulting from mycorrhizal treatment. In many cases, phosphorus applications to non-mycorrhizal plants have mimicked growth increases observed in mycorrhizal plants (Harley and Smith 1983). The results of this experiment show that P amendment did not eliminate the very large differences between M and NM plants. Significant P treatment effects were observed only in early vegetative growth and P treatment did not significantly affect any reproductive characters. There are several possible reasons why P treatment did not produce effects similar to those which resulted from M treatment. Perhaps the amount of superphosphate added (300 kg superphosphate ha^{-1}, equivalent to 6 g P m^{-2}) was not sufficient to eliminate the difference in P uptake between M and NM plants. The superphosphate was surface applied only once, 14 days after sowing. Multiple applications throughout the season might produce substantially different results. Moreover, less than normal rainfall during the growing season may have been a factor. Diffusion of phosphate is much reduced in dry soils (Nye and Tinker 1977). Another possibility, although less likely in our opinion, is that increased P uptake was not the major benefit obtained through infection by VAM. Many investigators have demonstrated an increased uptake in Zn and Cu in mycorrhizal plants, and translocation of sulfur and calcium may be important as well (Harley and Smith 1983).

Various biocides have been utilized in an attempt to eliminate or depress indigenous mycorrhizal fungi populations in the field. In the present study, the field was injection fumigated with a mixture of methyl-bromide (67%) and chloropicrin (33%). A previous experiment had shown that repeated applications of Benomyl to be ineffective on the same soil type (Li and Koide unpublished results). Methyl-bromide was extremely effective in this field study and at 117 days after sowing, the percent root colonization by VAM in uninoculated plants was only 3.7%. Studies which involve soil sterilization, however, should be interpreted cautiously. Soil fumigation can destroy indigenous mycorrhizal fungi but also eliminates other soil inhabitants. The results of the present experiment demonstrate a clear effect of mycorrhizal infection on *Abutilon theophrasti*. The functioning of VAM in a more natural ecosystem, however, may differ. For example, nematodes and collembola are suspected grazers of mycorrhizal fungi (McGonigle and Fitter 1988; Fitter and Sanders 1992) and may reduce the effects of the symbiosis on host performance.

In the current study, however, it was clearly shown that mycorrhizal fungi have the potential to significantly increase fecundity, seed quality and recruitment of their host plants in the field. In this manner, mycorrhizal fungi may contribute to the overall fitness of a host plant and may have strong effects on long-term population dynamics.

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