韓國林學會誌 86(4) : 466 - 475. 1997
Jour. Korean For. Soc. 86(4) : 466 - 475. 1997

Arbuscular Mycorrhizal Fungus Inoculation Effect on Korean Ash Tree Seedlings Differs Depending upon Fungal Species and Soil Conditions[1]

Chang-Duck Koo[2]

아버스쿨 菌根菌 接種이 菌種과 土壤狀態에 따라 물푸레나무 苗木의 生長에 미치는 影響[1]

具 昌 德[2]

ABSTRACT

I examined arbuscular mycorrhizal(AM) fungus inoculation effects on the seedling growth of Korean ash tree(*Fraxinus rhynchophylla* Hance), which distributes in fertile mesic soils, under a seven-day watering cycle of water stress and compost-added fertile conditions. Three Korea-native AM fungi were inoculated : an unidentified *Glomus* species, *Gigaspora margarita* Becker & Hall and *Scutellospora heterogama*(Nicol. & Gerd) Walker & Sanders from disturbed forest soils. The effect of AM fungus inoculation on the seedling varied depending upon fungal species and soil conditions. AM formation was 27 to 65% by the *Glomus* without forming spores, 47 to 74% with about 10 spores per 20g soil by *G. margarita* and about 65% with 35 spores by *S. heterogama*. The soil conditions did not affect either AM or spore formation. The *Glomus* inoculation increased shoot N and P concentrations, but did not affect seedling growth. *G. margarita* increased shoot N and P, irrespective of soil conditions, in general, but *S. heterogama* increased N under water stress and P in the control soil only. These two fungi significantly increased seedling growth in both control and water stress soils. Compost addition increased the growth of non-mycorrhizal seedlings and offset AM fungus inoculation effects. The relative field mycorrhizal dependency(RFMD) of the seedlings was significant only in control and water stress soils by over 40% in *G. margarita* or *S. heterogama* AM plants. Under water stress RFMD was the most evident in *S. heterogama* AM plants. I conclude that some AM fungi such as *G. margarita* and *S. heterogama* can broaden the niche of Korean ash seedlings to a water stress or nutrient poor site but less likely to more fertile sites.

Key words : Glomus, Gigaspora margarita, Scutellospora heterogama, *water stress, compost addition, ecological specificity*

要 約

아버스쿨 菌根菌(arbuscular mycorrhiza)이 물푸레나무(*Fraxinus rhynchophylla* Hance) 苗木의 生長에 미치는 영향을 對照區, 7일 週期의 水分缺乏 및 堆肥를 倍加시킨 비옥한 土壤條件에서 비교하였다. 接種菌으로는 훼손된 산림토양에서 채취한 미동정 *Glomus, Gigaspora margarita, Scutellospora margarita* 菌根菌을 사용하였다.

[1] 接受 1997年 8月 25日 Received on August 25, 1997.
[2] 임업연구원 서울시 동대문구 청량리동 207번지 Korean Forestry Research Institute 207 Cheongryangri-dong Dongdaemun-gu, Seoul, Korea
Present address : 36 Pensacola Cres. Christchurch 8004. New Zealand

아버스큘 菌根菌의 接種效果는 菌種과 토양상태에 따라 달라졌다. *Glomus* 菌은 菌根을 27~65% 형성하였으나 胞子는 형성하지 않았으며, *G. margarita* 菌은 47~74% 菌根형성과 함께 토양 20g당 약 10개의 胞子를, *S. heterogama* 菌은 약 65% 菌根형성율에 약 35개의 胞子를 형성하였다. 水分缺乏토양이나 肥沃한 토양이 菌根과 胞子형성에는 영향을 미치지 못하였다. *Glomus*菌은 식물체내 N과 P의 농도를 증가시켰지만 苗木生長에는 영향을 주지 않았다. *G. margarita*菌은 대체로 토양상태에 관계없이 식물체내 N과 P를, *S. heterogama* 菌은 水分缺乏土壤에서만 N를, 對照土壤에서는 P를 증가시켰다. 위 두 菌根菌은 對照土壤과 水分缺乏土壤에서 苗木의 생장을 촉진시켰다. 水分缺乏으로 *Glomus* 菌根植物과 *G. margarita* 菌根植物의 생장이 감소하였으나, *S. heterogama* 菌根植物은 N 농도가 증가하면서 생장에는 영향을 받지 않았다. 堆肥倍加 처리는 오직 非菌根 苗木만의 생장을 촉진시켰고, 菌根植物의 생장에는 영향을 미치지 않았다. 물푸레나무의 相對的인 菌根依存度(RFMD)는 對照土壤과 水分缺乏土壤에서 *G. margarita*와 *S. heterogama* 菌에 대해서만 40% 이상으로 유의하였고, 특히 水分缺乏 時에는 *S. heterogama* 菌에 대해서 더욱 뚜렷하였다. 따라서, *G. margarita*나 *S. heterogama* 같은 몇가지 菌根菌은 물푸레나무 苗木의 適地를 土壤水分과 養分이 부족한 곳으로 넓힐 수 있으나, 肥沃한 土壤에서는 效果가 없다고 결론짓는다.

INTRODUCTION

Over the last decade, mycorrhizal symbiosis has been increasingly appreciated as an important component of forest ecosystem structure (Varma, 1995) and function(Molina et al., 1992 ; Sanders et al., 1996 ; Douglas, 1995). In terrestrial ecosystem the symbiosis is a significant structural component, because the roots of most plant species associate with mycorrhizal fungi (Trappe, 1987 ; Brundrett, 1991). Molina et al (1992) estimated that some 6000 species, about 10% of soil fungus species, are mycorrhizal. Of them only about 300 species are arbuscular mycorrhizal(AM) fungi, but they form mycorrhizas in the roots of an enormously wide variety of host plants(Smith and Read, 1997). One mycorrhizal plant can form mycorrhizae with numerous AM fungal species and one AM fungus can associate with a number of plants. The mycorrhizas are so diverse that even different genera of AM fungi commonly coexist in a root segment(Sanders et al., 1996).

Mycorrhizas are significantly involved in ecosystem function, such as C-, N- and P-cycling(George et al., 1992 ; Cui and Caldwell, 1996 ; Lapointe and Molard, 1997), soil stability(Tisdall, 1991), host plant survival(Trappe, 1987), plant succession(Barea and Jeffries, 1995) and plant competition(Hartnett et al., 1993). Mycorrhizal fungi are also an important component of the food web through their fruiting body eaten by animals(Pegler et al., 1993 ; Maser and Trappe, 1984) and even a precious income source i.e. truffles and matsutake(Hall et al., 1994). Thus, mycorrhizal function in forest ecosystems should also be considered for sustainable forest resource management(Barea and Jeffries, 1995).

Molina et al.(1992) addressed ecological specificity phenomena in mycorrhizal association : all environmental biotic and abiotic factors influence the ability of host plants to form functional mycorrhizas with particular fungi in natural soils. Although most mycorrhizal fungi have broad host ranges, not all fungi significantly affect their host growth(Wilson and Tommerup, 1992). A mycorrhizal fungus known as effective one does not always improve its host growth(Haselwandter and Bowen, 1996). After observing that AM plant species associated with different fungal species across its range, Allen et al.(1995) argued that AM fungi respond to the environment directly without doing so individually via the host. That is, AM fungus diversity is regulated by genetics of the fungi themselves along with their responses to the host and the environment. For example, *Gigaspora margarita*, an AM fungus, improved sweet gum seedling growth only at low P and acidic soils(Yawney et al., 1982)

By using AM fungi tolerant to certain soil

conditions, we foresters may be able to broaden the ecological niche of plants through changes in the availability of nutrients and water(Varma, 1995). The host-plant niche broadening mediated by mycorrhizal fungi may not be limited to plant survival under harsh conditions but may extend to plant thriving under a fertile mesic environment.

In this study I tested the hypothesis that the niche of host plants can be broadened by mycorrhizal fungus inoculation under water stressed or fertile soil conditions. For this experiment, I inoculated the seedling of Korean ash tree(*Fraxinus rhynchophylla* Hance) with three native AM fungi collected from disturbed forest soils. The ash tree with its high economic value species is distributed in fertile mesic soils in Korean forests (Korean Forestry Research Institute, 1993).

MATERIALS AND METHODS

Organisms

Korean ash tree seeds were collected late autumn and stored under -18℃ until they were used. Three AM fungal species were an unidentified *Glomus* species, *Gigaspora margarita* Becker and Hall and *Scutellospora heterogama* (Nicol. & Gerd) Walker and Sanders. Spores of *G. margarita* and *S. heterogama* were collected by wet-sieving loamy sand soils under *Kummerocallis, Cassia* and *Calix* grass species near Cheongju Teacher's College in Chung-buk province in Korea. *G. margarita* spore is white and usually larger than 300(μm. *S. hetrogama* spore is brown and had a germination shield with closely crowded warts on the spore surface. These two species were clearly identified according to the INVAM description(Schenck and Perez et al., 1987). The unidentified *Glomus* species inoculum had been potcultured with the soil from an abandoned coal mine area in Kyung-buk province in Korea. This fungus formed hyaline spores, about 40(μm diameter, inside sorghum roots.

Experimental design

The experiment had three soil conditions and four mycorrhizal fungus treatments within each soil condition. The three soil conditions were control, water stress and compost addition. The control soil had the basic pot medium, the water stress soil received water to a field capacity once a week and the compost addition soil was doubled in the amount of compost. The four AM fungus treatments were non-inoculation, unidentified *Glomus*, *G. margarita* and *S. heterogama* inoculations. Each combination of the compost addition and fungus inoculation had nine replicated pots. Each combination of the other two soils and fungus inoculations had 15 replicated pots.

Inoculation

The spore collections of *G. margarita* and *S. heterogama* were diluted with fine vermiculite. Ten ml of vermiculite spore mixture was inoculated into each plastic pot(400ml) and the spore density was 30 spores/pot for *G. margarita* and 16 spores/pot for *S. heterogama*. The *Glomus* species inoculum was about 10g of air-dried sorghum roots and included about 10 spores per cm root length. Those fungal inocula were mixed into 5cm deep and no inoculation pots received 10g of autoclaved pot-cultured sorghum roots.

Growing conditions

The basic rooting medium was 1 : 1 : 0.5(v/v) mixture of peatmoss, perlite and forestry compost. Nutrient contents of the compost were 35.5% organic matter, 1.43% total N, 810ppm P, 5.6me/100g K_2O, 0.6% CaO, 1.27% MgO and pH6.6. The components of the medium were autoclaved separately for one hour. Ash tree seeds were planted on 400ml plastic pots after 24 hours cold-soaking. In seven weeks the germinated seedlings were thinned to three per pot. The seedlings were irrigated with chlorinated tap water and grown in the greenhouse covered with clear plastic from April to September for 5 months.

Measurement and statistical analysis

Percentage mycorrhizal formation was estimated by the grid line intersection method(Giovan-

netti and Mosse, 1980) after staining the root with trypan blue in lacto-glycerine solution after cleaning in 10% KOH solution(Phillips and Hayman, 1970). Spores in the pot were counted per 20g of the air-dried potting medium. Height, root collar diameter and dry weight of shoot and root were also measured. For shoot N and P analyses, four pots per treatment were randomly sub-sampled and analyzed at the Soil and plant tissue analysis laboratory at the Korean Forestry Research Institute. N was determined after Kjeldahl digestion and P was by acid digestion and molybdovanado-phosphoric acid colorimetry. Statistical data analysis was done with GLM procedures in SAS(SAS Institute Inc. Cary, NC, USA, 1990). ANOVA was done within each soil condition or each fungus inoculation and then the means were compared by Tukey's test. Relative Field Mycorrhizal Dependency(RFMD) was calculated as Bagyaraj(1992) : RFMD(%)=((dry weight of mycorrhizal plant - dry weight of non-mycorrhizal plant)/dry weight of non-mycorrhizal plant) * 100

RESULTS

Arbuscular mycorrhiza(AM) and spore formation

The AM and spore formation of ash tree seedlings significantly differed depending upon AM fungus species and soil conditions(Table 1). The unidentified *Glomus* formed mycorrhizas from 27 to 65% but did not form spores either outside or inside of the roots. AM formation by the *Glomus* was significantly decreased by water stress but not by compost addition. *G. margarita* formed AM by 47% to 74% and 4 to 18 spores per 20g of potting medium. *S. heterogama* also formed AM by 64 to 71% and about 35 spores. The soil treatments did not affect the formation of AM and spores in either *G. margarita* or *S. heterogama* inoculated seedlings. On the other hand, AM formation by *S. heterogama* was significantly higher than that by the *Glomus* species both in control and water stress soils. AM formation by *G. margarita* was higher than that by the *Glomus* only in the control soil. In the compost addition soil, AM formation did not differ among the fungus inoculation treatments.

Seedling growth

In non-mycorrhizal ash tree seedlings, the 7-day water stress cycle did not affect diameter and total shoot dry weight, but the compost addition significantly increased the growth parameters(Table 1). On the other hand, AM fungus inoculations, with *G. margarita* and *S. heterogama* significantly increased the growth parameters in the control and water stress soils. The *Glomus* species significantly increased only diameter in the control and water stress soils. The *Glomus* is less effective than the other two fungi for the seedling growth.

Soil conditions differently affected the growth of AM seedlings depending upon fungal species. In the *Glomus* AM seedlings water stress significantly decreased diameter and total dry weight, but the compost addition did not affect the growth. In *G. margarita* AM seedlings, while water stress did not affect diameter but reduced total dry weight, compost addition significantly increased diameter but did not affect total dry weight. In *S. heterogama* inoculated seedlings, water stress significantly reduced diameter growth but the compost addition affected neither diameter nor dry weight. Only *S. heterogama* significantly increased shoot to root ratio of ash tree seedlings in the control and water stress soils.

Relative field mycorrhizal dependency (RFMD)

The RFMD of ash tree seedlings also varied depending upon AM fungal species and soil conditions(Fig. 1). RFMD was significant only in *G. margarita* or *S. heterogama* inoculated seedlings in the control and water stress soils, as shown in the total dry weight in Table 1. The RFMD of *Glomus* AM seedlings was 24% in the control soil, but almost zero under water stress and about 10% in the compost addition. The RFMD of *G. margarita* AM seedlings was 45% in the control soil, but decreased to around 30% in the water stress and compost addition

Table 1. The effect of arbuscular mycorrhizal(AM) fungus inoculation and soil conditions on the mycorrhiza formation, growth and shoot N and P concentration of five-month-old Korean ash tree seedlings.

AM fungus	Soil	Mycorrhiza (%)	No. Spore /20g soil	Diameter (㎜)	Total dry weight(g)	Shoot-root ratio	Shoot N (%)	Shoot P (%)
Noinoculation								
	Control	0 a* A*	0 a A	2.5 a A	1.04 a A	1.14 a AB	1.12 a A	0.27 a A
	Water stress	0 a A	0 a A	2.3 a A	0.88 a A	1.13 a A	1.61 a A	0.29 a A
	Compost addition	0 a A	0 a A	2.8 b A	1.38 b A	1.20 a A	1.57 a A	0.28 a A
Glomus unidentified								
	Control	41 ab B	0 a A	2.8 a B	1.29 a AB	1.07 a A	3.11 a B	0.55 a B
	Water stress	27 a B	0 a A	2.6 b B	0.90 b AB	1.10 a A	2.73 a B	0.49 a B
	Compost addition	65 b B	0 a A	3.1 a A	1.56 a A	1.16 a A	2.80 a B	0.49 a B
Gigaspora margarita								
	Control	71 a C	4 a A	2.9 a B	1.51 a B	1.11 a A	2.06 a AB	0.51 a B
	Water stress	47 a BC	12 a B	2.7 a B	1.13 b BC	1.30 a AB	2.45 a B	0.47 a AB
	Compost addition	74 a B	18 a B	3.4 b B	1.79 a A	1.18 a A	2.66 a B	0.52 a B
Scutellospora heterogama								
	Control	70 a C	35 a B	3.0 a B	1.50 a B	1.34 a B	1.57 a A	0.42 a B
	Water stress	71 a C	40 a C	2.7 b B	1.26 a C	1.47 a B	2.48 b B	0.40 a AB
	Compost addition	64 a B	34 a B	3.0 a A	1.42 a A	1.23 a A	1.57 a A	0.34 a A

a* : Means followed by the same lower case letter are not different between soil treatments within each AM fungus inoculation by Tukey's test at $p<0.05$.

A* : Means followed by the same upper case letter are not different between AM fungus inoculation within each soil treatments by Tukey's test at $p<0.05$.

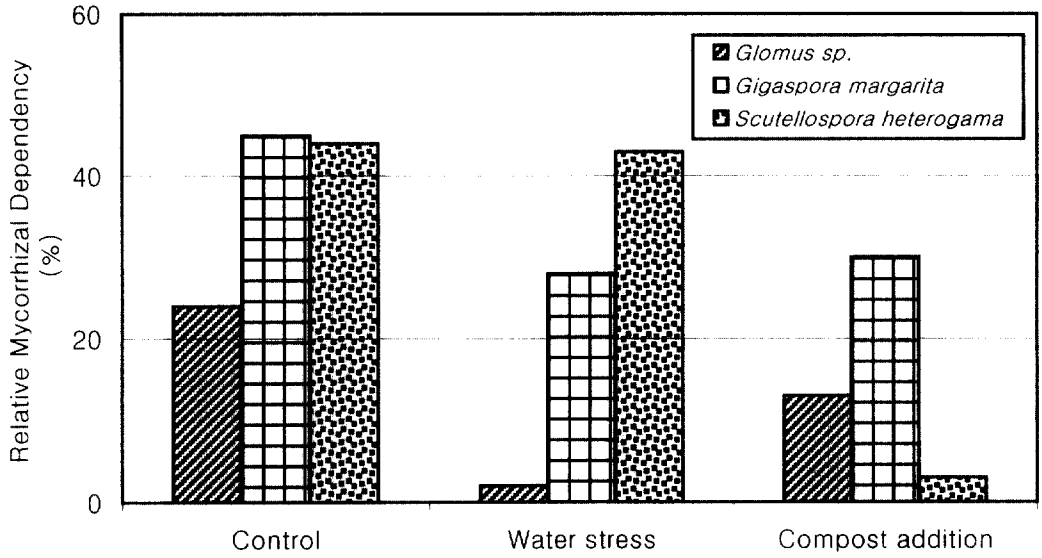

Fig. 1. Relative field mycorrhizal dependency(RFMD) of arbuscular mycorrhizal ash tree seedlings under different soil conditions. RFMD was calculated with the total dry weight in Table 1.

soils. The RFMD of *S. heterogama* AM plant was 43% in both control and water stress soils, but almost zero in the compost addition soil.

Shoot N and P concentration

The *Glomus* or *G. margarita* inoculations significantly increased shoot N concentration in all the three soils(Table 1). However, *S. heterogama* increased the N concentration only in the water stress soil. On the other hand, soil condition did not affect the N concentration except that water stress significantly increased the N concentration in *S. heterogama* AM seedlings.

Soil conditions did not affect shoot P concentration, but AM fungi differently affected it (Table 1). While the *Glomus* species increased the P concentration in all the soil conditions, *G. margarita* increased the P in the control and compost addition soils, and *S. heterogama* increased the P only in the control soil. Generally, the *Glomus* inoculation increased shoot N and P concentrations irrespective of soil conditons, while the effect of the other two fungi on the N and P varied with soil conditions.

DISCUSSION

The results strongly support AM benefit for nutrient uptake and growth of plants in a great many reports(Smith and Read, 1997). However, a growth enhancement by only *G. margarita* and *S. heterogama* under water stress and nutrient poor conditions partly support the hypothesis that the niche of host plants can be broadened by AM fungus inoculation. That is, the unidentified *Glomus* did not affect plant growth in the water stress and all the AM fungi tested did not improve the growth in the fertile soil. *S. heterogama*, especially, was more effective than others under water stress. These differences between fungal species and soil conditions are also verified in many grass plants(Hetrick et al., 1985 ; Smith and Read, 1997 ; Noyd et al., 1995).

Whereas water stress did not significantly affect the growth of non-mycorrhizal plant, it affected the mycorrhizal plants of the *Glomus* or *G. margarita*. Because the water potential of the soils and plants were not measured, explanation is very limited. However, nonmycorrhizal plant may have been less stressed during the sevenday dry cycle due to its slower growth.

The AM plants were 30 to 50% higher in total dry weight.

Several possible mechanisms have been suggested about how mycorrhizas improve plant water relations. Subramanian et al.(1995) summarized as follows : by 1)improving hydraulic conductivity 2)increasing transpiration rate and lowering stomatal resistance 3)reducing leaf elasticity 4)increasing leaf water and turgor potentials 5)increasing rooting length and depth and 6)more rapid recovery from water stress. However, Smith and Read(1997) argued that mycorrhizal effects on the drought tolerance of the host would be rather due to the hyphal contribution to uptake of nutrients.

In the compost addition, i.e., a mesic and fertile soil, the RFMD of *S. heterogama* AM plants was very low despite the 64% AM formation. In the fertile condition AM plant was similar to the non-mycorrhizal plant in shoot to root ratio and total dry. The AM fungus seemed to form unidirectional symbiosis by depending on the carbohydrate of their host without either improving or reducing the host growth. Graham et al.(1997) found that mycorrhizal citrus grown at high P supply expended less carbon to acquire P than heavily colonized mycorrhizal plant at low P supply. They also found that at high P the more mycorrhizal dependent genotype had a higher starch concentration in their root tissues than did less mycorrhizal dependent genotypes, irrespective of mycorrhizal status. This means that carbohydrate allocation patterns in plants are characteristics of the host itself. Thus, it may be not necessarily true that at high P soil, AM fungi become parasitic to drain carbohydrate without benefiting the host. In this aspect ash tree seedlings may not be affected significantly by the carbohydrate drain to keep mycorrhizal symbiosis in fertile soils, but get full benefits during water and nutrient stress situations.

Lapointe and Molard(1997) argued that benefit from the presence of mycorrhizas varied during the life cycle of the host. They found that in trout lily, a spring ephemeral of Canadian maple forests, mycorrhizal plants used more corm carbohydrate reserves by about 15% before the host developed stems and leaves. That is the cost that the spring ephemeral paid. Nature cycles with the regimes of light, water and temperature. During those cycles plants may have benefit by keeping the symbiosis without sacrificing their growth. At their harvesting, mycorrhizal plants produced 44% higher corm biomass than the fungicide-treated plants. That is the profit. Thus, investing the extra carbohydrate in keeping mycorrhizal symbiosis can be highly profitable.

Recently DNA based molecular techniques have shown that different genera of AM fungi coexist in plant roots and that this is a common occurrence(Sanders et al., 1996). However, not all of them are equally effective at improving nutrient uptake(Wilson and Tommerup, 1992). Allen et al.(1995) observed that different species of AM fungi were also active during different times of the growing season on the same host. Competitive interactions would favor these species which rapidly colonize an uninfected root and can subsequently exclude infection by other species (Sanders et al., 1995). From this study it is very limited to predict the dynamics of AM fungal communities within a root system, such as the interactions among AM fungal species in forming mycorrhizas under the various soil conditions. However, it is possible for *S. heterogama* mycorrhizas to become dominant as roots turnover during water stress seasons, because while the *Glomus* mycorrhizas decrease, *S. heterogama* mycorrhizas and spore formations are not affected by the water stress. On the other hand, it is still impossible to predict how AM community changes in fertile soils, because all the three fungi formed mycorrhizas by similarly high percentage.

Ecology of *G. margarita* has been known relatively in detail compared with the other two species. It widely spreads from agricultural fields to virgin marine sand dunes, and is present throughout the year(Becker and Hall, 1976 ; Rose, 1980). *G. margarita* formed mycorrhiza better at moderately acid conditions(i.e. pH5.5), and improved sweet gum seedling growth at low soil P (Yawney et al, 1982). The fungus can form my-

corrhizas even in aquatic plants, such as Ranunculus(Khan and Belik, 1995). These diverse habitat characteristics of *G. margarita* may explain its resilient response to the water stress and compost addition in this study.

Nitrogen uptake by AM fungi has been inconclusive(Smith and Read, 1997), in contrast to P uptake that has been clearly approved in many sophisticated experiments(Cui and Caldwell, 1996). *Glomus mosseae* improved both NH_4^+ and NO_3^- uptake(George et al., 1992) but un-known *Glomus* species did not improve NO_3^- uptake(Cui and Caldwell, 1996). In this study N concentrations in *S. heterogama* mycorrhizal seedling tissues were significantly lower than those of the other two mycorrhizal plants in both control and compost addition soils. The shoot N of *S. heterogama* AM plants was significantly higher than that of non-mycorrhizal plants only under water stress. This experiment is very limited in explaining N uptake, because NO_3^- and NH_4^+ were not measured. However, N uptake by the AM plant can be discussed in relation to water stress.

Tobar et al.(1994a) found that in a ^{15}N-labelled NO_3^- study NO_3^- uptake did not differ between non-mycorrhizal and AM plant inocu-lated with *Glomus fasciculatum* and well-watered conditions. However, in dry soils the NO_3^- uptake of the AM plants was four times higher than that of the non-mycorrhizal. In another study(Tobar et al., 1994b) showed that when a trace amount of $^{15}NH_4^+$ was applied to lettuce, AM fungi greatly increased ^{15}N enrichment of plant tissues, whereas the ^{15}N was negligible in non-mycorrhizal control plants. Smith and Read(1997) argued that AM fungi would not be effective for the uptake of NO_3^-, which is mobile in moist soils, but the fungi might increase NH_4^+ which is adsorbed and relatively non-mobile. Thus, I infer that *S. heterogama* may become active in NO_3^- uptake under water stress. The significantly higher shoot to root ratio of *S. heterogama* seedlings in the water stress soil may support this prediction.

In conclusion the AM fungus inoculation effects or mycorrhizal dependence of ash tree seedlings varied depending upon both AM fungal species and soil conditions. *G. margarita* distributing in diverse habitats has a potential for broadening the host niche. *S. heterogama* that functions effectively under water stress and nutrient poor soils may also facilitate ash tree to expand from mesic to harsh sites. Therefore, recognizing the structure and function of mycorrhizas at both the species and ecosystem levels will greatly contribute to a sustainable management of forest ecosystems by possibly making the trees more resilient to environment changes. Further, diversity of mycorrhizas can be a significant indicator for the assessment of ecosystem viability in both disturbed and undisturbed forests.

Acknowledgement

The author thanks Mr. Jae-Myoung Jo, former General Director of the Korean Forestry Research Institute for funding this project and also Dr. Chang-Keun Lee at the Institute for encouraging me through the project. The author is greatly indebted to Mr. Gang-Hyun Ka for the collection and identification of the arbuscular mycorrhizal fungi used in this experiment, and Mr. Craig Penfold for revising English of this writing. This project was partly funded from the Korean Ministry of Science and Technology supporting the Special Strategic Projects.

LITERATURE CITED

1. Allen, E.B., Allen, M.F. Helm, D.J. Trappe, J.M., Molina, R. and Ricon, E. 1995. Patterns and regulation of mycorrhizal plant and fungal diversity. Plant and Soil 170 : 47-62.
2. Bagyaraj, J.J. 1992. Vesicular-arbuscular mycorrhiza : application in agriculture. *In* Methods in microbiology, vol.24 : techniques for the study of mycorrhiza. Edited by Norris, J.R., Read, D.J. and Varma, A.K. Academic Press. London. pp.359-373.
3. Barea, J.M. and Jeffries, P. 1995. Arbuscular mycorrhizas in sustainable soil-plant systems. *In* Mycorrhiza : structure, function, molecular biology and biotechnology. Edited

by A. Varma and B. Kock. Springer, Berlin. pp.521-560.

4. Becker, W.N. and Hall, I.R. 1976. *Gigaspora margarita*, a new species in the Endogonaceae. Mycotaxon Ⅳ : 155-160.
5. Brundrett, M. 1991. Mycorrhizas in natural ecosystems. Advances in Ecological Research 21 : 171-313.
6. Cui, M. and Caldwell, M.M. 1996. Facilitation of plant phosphate acquisition by arbuscular mycorrhizas from enriched soil patches. Ⅱ. Hyphae exploiting root-free soil. New Phytol. 133 : 461-467.
7. Douglas, A.E. 1995. The ecology of symbiotic microorganisms. Advances in Ecological Research 26 : 69-103.
8. George, E., Haussler, K.-U., Vetterlein, D., Gorgues, E. and Marschner, J. 1992. Water and nutrient translocation by hyphae of *Glomus mosseae*. Can. J. Bot. 70 : 2130-2137.
9. Giovannetti, M. and Mosse, B. 1980. An evaluation of techniques for measuring vesicular arbuscular mycorrhizal infection in roots. New Phytol. 84 : 489-500.
10. Graham, J.H., Duncan, L.W. and Eissenstat, D.M. 1997. Carbohydrate allocation patterns in citrus genotypes as affected by phosphorus nutrition, mycorrhizal colonization and mycorrhizal dependency. New Phytol. 135 : 335-343.
11. Hall, I.R., Brown, G. and Byars, J. 1994. The black truffles : its history, uses and cultivation. Crop and Food Research, Lincoln, New Zealand. p107.
12. Hartnett, D.C. Hetrick, B.A.D., Wilson, G.W.T. and Gibson, J.J. 1993. Mycorrhizal influence on intra- and interspecific neighbor interactions among co-occurring prairie grasses. Journal of Ecology. 81 : 787-795.
13. Haselwandter, K. and Bowen, G.D. 1996. Mycorrhizal relations in trees for agroforestry and land rehabilitation. Forest Ecology and Management 81 : 1-17.
14. Hetrick, B.A.D., Kitt, D.G. and Wilson, G.T. 1986. The influence of phosphorus fertilization, drought, fungal species, and non-sterile soil on mycorrhizal growth response in tall grass prairie plants. Can. J. Bot. 64 : 1199-1203.
15. Khan, A.G. and Belik, M. 1995. Occurrence and ecological significance of mycorrhizal symbiosis in aquatic plants. *In* Mycorrhiza : structure, function, molecular biology and biotechnology. Edited by A. Varma and B. Kock. Springer, Berlin. pp.627-666.
16. Korean Forestry Research Institute. 1992. Illustrated woody plants of Korea. 4th edition. Seoul. p562.
17. Lapointe, L. and Molard, J. 1997. Costs and benefits of mycorrhizal infection in a spring ephemeral, *Erythronium americanum*. New Phytol. 135 : 491-500.
18. Maser, C. and Trappe, J.M. 1984. The seen and unseen world of the fallen tree. Gen. Tech. Rep PNW-164. Portland, Oregon. USDA Forest Service. Pacific Northwest Forest and Range Experiment Station. p56.
19. Molina, R. Massicotte, H. and Trappe, J. M. 1992. Specificity phenomena in mycorrhizal symbioses : community-ecological consequences and practical implications. *In* Mycorrhizal functioning : an integrative plant-fungal process. Edited by M. Allen. Chapman & Hall, New York. pp.357-423.
20. Noyd, R.K., Pfleger, F.L. and Russelle, M.P. 1995. Interactions between native prairie grasses and indigenous arbuscular mycorrhizal fungi : implications for reclamation of taconite iron ore tailing. New Phytol. 129 : 651-660.
21. Pegler, D.N., Spooner, B.M. and Young, T.W.K. 1993. British truffles : a revision of British hypogeous fungi. Royal Botanic Gardens, Kew. P216.
22. Phillips, J.M. and Hayman, D.S. 1970. Improved procedures for clearing roots and staining parasitic and vesicular-arbuscular mycorrhizal fungi for rapid assessment of infection. Transaction of the British Mycological Society 55 : 158-160.
23. Rose, S.L. 1980. Mycorrhizal associations of some actinomycete nodulated nitrogen fixing

plants. Can. J. Bot. 58 : 1449-1454.

24. Sanders, I.R., Clapp, J.P. and Wiemken, A. 1996. The genetic diversity of arbuscular mycorrhizal fungi in natural ecosystems - a key to understanding the ecology and functioning of the mycorrhizal symbiosis. New Phytol. 133 : 123-134.
25. Sanders, I.R., Koide, R.T., Shumway, D. L. 1995. Community-level interactions between plants and vesicular-arbuscular mycorrhizal fungi. *In* Mycorrhiza : structure, function, molecular biology and biotechnology. Edited by A. Varma and B. Kock. Springer, Berlin. pp.607-625.
26. Schenck, N.C. and Perez, Y. 1987. Manual for the identification of VA mycorrhizal fungi. International culture collection of VA mycorrhizal symbiosis. 2nd ed. Academic Press. London. p605.
27. Smith, E.E. and Read, D.J. 1997. Mycorrhizal symbiosis. 2nd edition. Academic Press. New York. p605.
28. Subramanian, K.S., Charest, C., Dwyer, L.M. and Hamilton, R.I. 1995. Arbuscular mycorrhizas and water relations in maize under drought stress at tasselling. New Phytol. 129 : 643-650.
29. Tisdall, J.M. 1991. Fungal hyphae and structural stability of soil. Aust. J. Soil Res. 29 : 729-743.
30. Tobar, R., Azcon, R. and Barea, J.M. 1994a. Improved nitrogen uptake and transport from ^{15}N-labelled nitrate by external hyphae of arbuscular mycorrhiza under water-stressed conditions. New Phytol. 126 : 119-122.
31. Tobar, R., Azcon, R. and Barea, J.M. 1994b. Improvement of plant N acquisition from an ammonium-treated, drought-stressed soil by the fungal symbiont in arbuscular mycorrhizae. Mycorrhiza 4 : 105-108.
32. Trappe, J.M. 1987. Phylogenetic and ecologic aspects of mycotrophy in the Angiosperms from an evolutionary standpoint. *In* Ecophysiology of VA mycorrhizal plants. Edited by Safir, G.R. CRC Press, Boca Raton, Florida. pp.2-25.
33. Varma, A. 1995. Ecophysiology and application of arbuscular mycorrhizal fungi in arid soils. *In* Mycorrhiza : structure, function, molecular biology and biotechnology. Edited by A. Varma and B. Kock. Springer, Berlin. pp.561-591.
34. Wilson, J.M. and Tommerup, I.C. 1992. Interactions between fungal symbionts : VA mycorrhizae. *In* Mycorrhizal functioning : an integrative plant-fungal process. Edited by M.F. Allen. Champman and Hall. New York. pp.199-248.
35. Yawney, W.J., Schultz, R.C. and Kormanik, P.P. 1982. Soil phosphorus and pH influence the growth of mycorrhizal sweet gum. Soil Sci. Soc. Am. J. 46 : 1315-1320.