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Effect of Arbuscular Mycorrhizal Fungi on Tree Growth and Nutrient Uptake of *Sclerocarya birrea* under Water Stress, Salt Stress and Flooding

Benard Oula Muok* and Takaaki Ishii

Graduate School of Agriculture, Kyoto Prefectural University, Shimogamohangi, Sakyo, Kyoto 606–8522, Japan

A greenhouse experiment was conducted to determine the influence of arbuscular mycorrhizal (AM) fungus inoculation on water stress, salt stress and flooding tolerance of three subspecies of *Scleocarya birrea* (A. Rich.) Hochst. *Gigaspora margarita* Baker and Hall was used for the inoculation. All the three subspecies of *S. birrea* had high tolerance both to water stress and flooding even without *G. margarita* inoculation. All flooded seedlings developed lenticels and survived three months of flooding. Non-mycorrhizal seedlings of *S. birrea* subsp. *multifoliolata* survived even under electric conductivity of up to 7.1 $dS \cdot m^{-1}$. Root colonization by *G. margarita* markedly improved tolerance of *S. birrea* seedlings to water stress, salt stress and flooding. In particular, *S. birrea* subsp. *caffra* under water stress and flooding conditions showed the highest response to inoculation. Mycorrhizal *S. birrea* subsp. *multifoliolata* recorded enhanced uptake of N, P, Ca and Mg at 7.1 $dS \cdot m^{-1}$. These results demonstrate that even though *S. birrea* has natural tolerance to water stress, salt stress and flooding, AM fungus is very effective in strengthening the tolerance of *S. birrea* grown in arid and semi arid areas.

Key Words: arbuscular mycorrhizae, flooding, salt stress, *Sclerocarya birrea*, water stress.

Introduction

Sclerocarya birrea (marula) is one of the indigenous fruit tree species which is fast gaining recognition in Africa (Muok et al., 2000; Nerd and Mizrahi, 1993, 1996). It is native to Africa, occurring on dry and rocky hills sites with barely any soil. Fruits are eaten fresh or fermented to make alcoholic drinks and reported to have high content of vitamin C (Thiongo and Jaenicke, 2000). The kernels are eaten directly or oil extracted from them. Leaves are browsed by livestock and have a variety of medicinal uses, as does the bark (Kokwaro, 1976). In addition, Muok et al. (2000) reported that the tree is appropriate for introduction in the dryland agroforestry systems and highly valued by local communities for its potential for domestication and commercialization.

It is also found along riverbanks as riverine vegetation in drylands (Dale and Greenway, 1961; Maundu et al., 1999; Peters, 1988). In these arid and semi arid areas, low and erratic rainfall and high temperature often lead to low soil moisture and salt accumulation in the rhizosphere. Therefore, plants growing in these areas have to overcome severe water and salt stresses, which are the major limiting factors to tree planting. In addition, because many plants in arid and semi arid are riverine vegetations, which are prone to occasional flooding during rainy seasons, such plants need to have tolerance to flooding.

High variation of *S. birrea* was been reported within different provenances in terms of morphological characteristics (Maundu et al., 1999). Muok et al. (in press) suggested the classification of *S. birrea* in Kenya into three subspecies. However, it is not known if these variations could also be reflected in its tolerance to different environmental stresses such as low soil moisture, high soil salinity and occasional flooding.

The beneficial effects of arbuscular mycorrhizae in improving tolerance to environmental stress conditions such as water stress (Cruz et al., 2000; Dell'Amico et al., 2002; Ming et al., 1999; Stahl et al., 1998), flooding (Osundina, 1998; Rutto et al., 2002) and high soil salinity (Aboulkhair and El-Sokkary, 1994; Jindal et al., 1993; Katembe et al., 1998; Sengupta and Chaunduri, 1990), in some plant species are widely reported. The mechanisms of the improved tolerance includes increased nutrient uptake, especially for P and Zn (Al-Karaki, 2000; Miller and Sharitz, 2000; Osonubi et al., 1991; Rutto et al., 2002; Solaiman and Hirata, 1995). Formation of mycorrhizal roots enables plants to obtain more moisture from the surrounding soil than non-mycorrhizal plants (Stahl et al., 1998).

Ishii (2000) reported that *S. birrea* forms an association with AM fungi in its natural habitat in Kenya. This survey showed that *Gigaspora margarita* was one of the

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* Corresponding author (E-mail: bmuok@yahoo.com).

mycorrhizal fungus species found to occur naturally in Kenyan soils. However, no attempt was made to determine the effect of AM fungi on growth improvement of *S. birrea* under water stress, salt stress and flooding. The aim of the present study was to investigate the tolerance of *S. birrea* to water stress, salt stress and flooding and evaluate the effect of mycorrhizal inoculation in improving the tolerance of water stress, salt stress and flooding on the subspecies of *S. birrea.*

Materials and Methods

Plant material and AM fungus inoculation

Seeds of *S. birrea* subsp. *multifoliolata*, *S. birrea* subsp. *birrea* and *S. birrea* subsp. *caffra* were collected from Nyanza, Baringo and Kwale in Kenya, respectively (Muok et al., submitted). The seeds were germinated in sterilized vermiculite. A month later, the seedlings of uniform size were transplanted to pots (18 cm in diameter, 15 cm in depth) containing vermiculite, perlite and zeolite (2:1:1 in volume) in a plastic greenhouse at Kyoto Prefectural University. A week after transplanting, each seedling was inoculated with approximately 250 spores of *G. margarita* (Central Glass Co. Ltd, Tokyo, Japan).

Water stress tolerance (Experiment 1)

1. *Effect of AM fungus inoculation and water stress on growth of S. birrea subsp. multifoliolata seedlings*

The experiment was layed-out in a randomized 2×2 factorial design consisting of water stressed seedlings inoculated with *G. margarita* or un-inoculated, and well-watered seedlings inoculated with *G. margarita* or un-inoculated (control). Only seedlings of *S. birrea* subsp. *multifoliolata* were used in this experiment. Three plants were used per treatment. Control seedlings were watered daily while water stressed seedlings were watered once a week.

2. *Relative performance of mycorrhizal and non-mycorrhizal seedlings of three S. birrea subspecies under water stress conditions*

Seedlings of *S. birrea* subsp. *multifoliolata*, *S. birrea* subsp. *birrea* and *S. birrea* subsp. *caffra* were used. The experiment was layed-out in a randomized 3×2 factorial design consisting of three subspecies and inoculated with *G. margarita* or un-inoculated. Three plants were used per treatment and watered once a week.

The experiments 1-1 and 1-2 were maintained for 93 days. Pre-dawn leaf water potentials were taken once using a pressure chamber (Meiwa Shoji Co. Ltd, Tokyo, Japan), just before harvesting, after the seedlings were denied water for a week.

Salt tolerance (Experiment 2)

The experiment was layed-out in a randomized 3×2 factorial design consisting of control (tap water, EC $1.4\ dS \cdot m^{-1}$), medium salt concentration (EC $4.9\ dS \cdot m^{-1}$) and high salt concentration (EC $7.1\ dS \cdot m^{-1}$) and either inoculated with *G. margarita* or un-inoculated. Only seedlings of *S. birrea* subsp. *multifoliolata* were used in this experiment. Three plants were used per treatment. The salt levels were achieved by addition of NaCl and $CaCl_2$ (1 M NaCl, 1 M $CaCl_2$) to the pot during watering to give saturation extract electric conductivity (EC) values $4.9\ dS \cdot m^{-1}$ (medium salt concentration) and $7.1\ dS \cdot m^{-1}$ (high salt concentration), respectively. Regular watering was done gently to avoid leaching. The experiment was maintained for 79 days.

Tolerance to flooding (Experiment 3)

The experiment was layed-out in a randomized 3×2 factorial design consisting of three subspecies and either inoculated with *G. margarita* or un-inoculated. Three plants were used per treatment and placed in a container filled with water to the root collar level.

Nutrient supply

Each seedling in the experiment was drenched once a week with Hoagland's nutrient solution (Millner and Kitt, 1992) modified by halving the concentrations of P and Zn at a rate of 100 mL per plant.

Harvesting and determination of root colonization, chlorophyll and nutrients, and data analysis

At the termination of the experiments, height and diameter were measured; shoots were severed from the roots and fresh weights of shoots and roots recorded. Roots were rinsed and samples taken for estimation of root colonization according to Ishii and Kadoya (1994). Leaf chlorophyll was extracted with 80% acetone and concentration analyzed using a spectrophotometer (Shimadzu UV-120-02, Shimadzu Corporation, Kyoto, Japan) at 645 nm and 663 nm for chlorophyll a and b, respectively (Kirk, 1968). Oven dried leaf samples were used for nutrient analysis. Concentrations of leaf N and P were determined by the indophenol method (Harwood and Huysen, 1970) and the vanado-molybdate method (Gericke and Kurmies, 1952), respectively. Concentrations of K, Ca and Mg were determined using an atomic absorption spectrometer (Hitachi 170-30, Hitachi Co. Ltd, Tokyo, Japan). Means of the data collected were tabulated and standard error (SE) of the means was calculated and significance was determined at $P<0.05$ by *t*-test. Root samples for scanning electron microscopy (SEM) were prepared according to Ishii and Kadoya (1984) and observed by a SEM (Nihon Denshi JXA-840, JEOL, Tokyo, Japan).

Results

Water stress tolerance

No significant difference was observed between un-inoculated seedlings growing under control and those under water stress, in terms of total biomass production, leaf chlorophyll content and uptake of P, K, Ca and Mg

(Table 1). Leaf chlorophyll concentration and uptake of N and P in mycorrhizal seedlings were increased significantly under both water stress and control treatments (Table 1).

Under water stress condition, non-mycorrhizal seedlings of the three subspecies showed no significant differences in terms of total biomass, leaf chlorophyll content and uptake of P, K, Ca and Mg, but subsp. *caffra* recorded higher N uptake (Table 2). All inoculated seedlings became mycorrhizal under water stressed conditions with no significant difference observed in root colonization rate among the three subspecies (Table 2). Response to root colonization by *G. margarita* varied with each subspecies. *S. birrea* subsp. *birrea* recorded as much as 49.4% increase in total biomass production due to *G. margarita* inoculation compared 25.9% in *S. birrea* subsp. *caffra* and 8.3% in *S. birrea* subsp. *multifoliolata*. Leaf P content in the three subspecies and leaf N in both subsp. *birrea* and *multifoliolata* were significantly increased by the inoculation. However, there were no significant differences in leaf water potential, chlorophyll content and uptake of K, Ca and Mg due to AM fungus inoculation or kind of subspecies (Table 2).

Salt tolerance

Although all *S. birrea* subsp. *multifoliolata* seedlings survived through the experiment duration in all the salt concentrations including the highest concentration (EC 7.1 $dS{\cdot}m^{-1}$) even without AM fungus inoculation, root colonization by *G. margarita* enhanced total biomass production at this value of EC. Furthermore, leaf N, P, Ca and Mg contents in mycorrhizal seedlings at 7.1 $dS{\cdot}m^{-1}$ were high compared to non-mycorrhizal ones. Increase of P and Mg in mycorrhizal seedlings was 170% and 225%, respectively of non-mycorrhizal ones at 7.1 $dS{\cdot}m^{-1}$ (Table 3).

Tolerance to flooding

All the seedlings of the three subspecies of *S. birrea* survived three months of flooding and formed lenticels on the roots (Fig. 1). When the effect of AM fungus inoculation on the three subspecies was compared, there was no significant difference between the three in total biomass, chlorophyll concentration and uptake of K (Table 4). Root colonization by *G. margarita*, however, significantly increased uptake of N and P under flooding in all the three subspecies, and uptake of Ca and Mg in subsp. *caffra*. In particular, subsp. *caffra* recorded the higher response in uptake of P, K, Ca and Mg compared to the other two subspecies (Table 4). No significant difference was observed on the infection rate between the subspecies (Table 4). All inoculated seedlings of the three subspecies became mycorrhizal even under flooding (Fig. 2).

Table 1. Effect of AM fungus inoculation and water stress on total biomass, root colonization, leaf chlorophyll concentration and leaf mineral content of *Sclerocarya birrea* subsp. *multifoliolata* seedlings.

Treatment	Total biomass (gFW)	Root colonization (%)	Chlorophyll concn. (mg per cm^2)	Leaf mineral content (%)				
				N	P	K	Ca	Mg
C + AM	115.5 ± 8.8[z]	48.5 ± 1.6	0.022 ± 0.001	2.93 ± 0.01	0.22 ± 0.01	0.83 ± 0.06	2.09 ± 0.44	0.39 ± 0.06
C − AM	92.7 ± 13.6	0	0.018 ± 0.001	2.65 ± 0.03	0.16 ± 0.02	0.80 ± 0.14	1.80 ± 0.38	0.38 ± 0.12
WS + AM	84.6 ± 7.4	39.4 ± 1.6	0.023 ± 0.001	2.63 ± 0.03	0.21 ± 0.02	0.75 ± 0.02	1.93 ± 0.00	0.52 ± 0.09
WS − AM	78.0 ± 4.5	0	0.015 ± 0.003	2.20 ± 0.06	0.16 ± 0.01	0.74 ± 0.03	1.71 ± 0.22	0.48 ± 0.04

Gigaspora margarita was used for inoculation. C + AM: inoculated control, C − AM: un-inoculated control, WS + AM: inoculated and water stressed, WS − AM: un-inoculated and water stressed.
[z] Means ± SE (n = 3).

Table 2. Effect of AM fungus inoculation on total biomass, root colonization, leaf chlorophyll concentration and leaf mineral content of three subspecies of *S. birrea* seedlings under water stress conditions.

Treatment	Total biomass (gFW)	Root colonization (%)	Leaf water potential (-MPa)	Chlorophyll concn. (mg per cm^2)	Leaf mineral content (%)				
					N	P	K	Ca	Mg
SBM + AM	84.5 ± 7.4[z]	39.4 ± 1.6	1.83 ± 0.07	0.023 ± 0.001	2.63 ± 0.03	0.21 ± 0.02	0.75 ± 0.06	1.93 ± 0.00	0.52 ± 0.09
SBM − AM	78.0 ± 4.5	0	2.03 ± 0.09	0.015 ± 0.003	2.20 ± 0.06	0.16 ± 0.01	0.74 ± 0.03	1.71 ± 0.22	0.48 ± 0.04
SBB + AM	108.0 ± 3.3	41.3 ± 3.5	1.67 ± 0.07	0.022 ± 0.003	2.39 ± 0.14	0.24 ± 0.02	1.08 ± 0.09	2.48 ± 0.22	0.55 ± 0.06
SBB − AM	72.3 ± 4.9	0	1.77 ± 0.08	0.015 ± 0.003	1.91 ± 0.06	0.20 ± 0.01	0.99 ± 0.06	2.04 ± 0.30	0.54 ± 0.10
SBC + AM	109.4 ± 4.8	42.2 ± 0.9	1.83 ± 0.15	0.018 ± 0.000	2.84 ± 0.04	0.20 ± 0.00	0.95 ± 0.16	2.34 ± 0.11	0.45 ± 0.06
SBC − AM	86.9 ± 8.9	0	2.07 ± 0.03	0.017 ± 0.004	2.67 ± 0.05	0.15 ± 0.01	0.77 ± 0.08	1.71 ± 0.22	0.44 ± 0.00

G. margarita was used for inoculation. +AM: inoculated, −AM: un-inoculated, SBM: *S. birrea* subsp. *multifoliolata*, SBB: *S. birrea* subsp. *birrea*, SBC: *S. birrea* subsp. *caffra*.
[z] Means ± SE (n = 3).

Table 3. Effect of AM fungus inoculation and salt stress on total biomass, root colonization, leaf chlorophyll concentration and leaf mineral content of *S. birrea* subsp. *multifoliolata* seedlings.

Treatment ($dS \cdot m^{-1}$)	Total biomass (gFW)	Root colonization (%)	Chlorophyll concn. (mg per cm^2)	Leaf mineral content (%)				
				N	P	K	Ca	Mg
C + AM	90.3 ± 6.2[z]	39.7 ± 9.7	0.021 ± 0.000	2.45 ± 0.04	0.22 ± 0.01	0.86 ± 0.04	1.07 ± 0.27	0.45 ± 0.02
C − AM	76.7 ± 9.3	0	0.020 ± 0.000	2.25 ± 0.10	0.19 ± 0.01	0.77 ± 0.10	0.78 ± 0.19	0.38 ± 0.03
4.9 + AM	82.4 ± 10.9	23.8 ± 5.3	0.020 ± 0.001	2.24 ± 0.05	0.17 ± 0.01	0.99 ± 0.11	1.98 ± 0.77	0.23 ± 0.07
4.9 − AM	63.1 ± 5.7	0	0.018 ± 0.000	2.20 ± 0.04	0.13 ± 0.02	0.70 ± 0.13	1.50 ± 0.40	0.20 ± 0.06
7.1 + AM	62.4 ± 9.3	12.7 ± 1.4	0.018 ± 0.001	2.16 ± 0.04	0.17 ± 0.01	0.96 ± 0.10	2.70 ± 0.20	0.27 ± 0.06
7.1 − AM	41.8 ± 8.1	0	0.017 ± 0.000	1.76 ± 0.04	0.10 ± 0.00	0.86 ± 0.04	1.70 ± 0.28	0.12 ± 0.01

G. margarita was used for inoculation. +AM: inoculated, −AM: un-inoculated, C: control (tap water; EC 1.4 $dS \cdot m^{-1}$).
[z] Means ± SE (n = 3).

Fig. 1. Scanning electron micrographs of *S. birrea* roots. A: Lenticels formed on flooded roots (×70), B: Normal roots under non-flooded roots (×70).

Table 4. Effect of AM fungus inoculation on total biomass, root colonization, leaf chlorophyll concentration and leaf mineral content of three subspecies of *S. birrea* seedlings under flooding.

Treatment	Total biomass (gFW)	Root colonization (%)	Chlorophyll concn. (mg per cm^2)	Leaf mineral content (%)				
				N	P	K	Ca	Mg
SBM + AM	90.1 ± 19.5[z]	50.4 ± 7.6	0.017 ± 0.001	1.80 ± 0.12	0.13 ± 0.00	0.84 ± 0.14	0.86 ± 0.37	0.26 ± 0.05
SBM − AM	69.9 ± 3.0	0	0.016 ± 0.001	1.07 ± 0.12	0.10 ± 0.00	0.63 ± 0.10	0.73 ± 0.09	0.23 ± 0.02
SBB + AM	106.9 ± 22.6	47.2 ± 3.0	0.019 ± 0.003	2.85 ± 0.03	0.20 ± 0.00	1.30 ± 0.23	0.81 ± 0.02	0.25 ± 0.02
SBB − AM	91.5 ± 1.9	0	0.016 ± 0.002	1.63 ± 0.01	0.14 ± 0.00	1.00 ± 0.06	0.79 ± 0.12	0.25 ± 0.02
SBC + AM	74.6 ± 10.5	47.4 ± 4.2	0.018 ± 0.002	1.79 ± 0.04	0.15 ± 0.01	0.90 ± 0.05	0.87 ± 0.22	0.21 ± 0.00
SBC − AM	42.8 ± 10.4	0	0.015 ± 0.001	1.16 ± 0.06	0.10 ± 0.00	0.59 ± 0.06	0.37 ± 0.01	0.14 ± 0.00

G. margarita was used for inoculation. +AM: inoculated, −AM: un-inoculated, SBM: *S. birrea* subsp. *multifoliolata*, SBB: *S. birrea* subsp. *birrea*, SBC: *S. birrea* subsp. *caffra*.
[z] Means ± SE (n = 3).

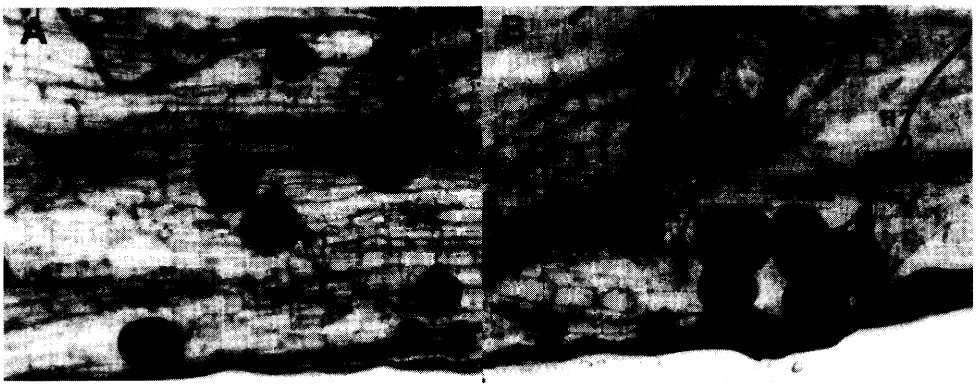

Fig. 2. Arbuscular mycorrhizae in flooded roots (A, ×150) and non-flooded roots (B, ×150) of *S. birrea*. S: Spore, H: Hypha.

Discussion

All the three subspecies have shown tolerance to water stress and flooding even without root colonization by *G. margarita*. An important limiting factor to tree planting and agriculture in the arid and semi arid areas is the quantity and quantity of water available. Plants growing in these areas need to have tolerance to low soil moisture. The occurrence of *S. birrea* in arid and semi arid areas of Africa indicates that it has tolerance to drought (Maundu et al., 1999; Peters, 1988). The present investigation demonstrated that *S. birrea* subsp. *multifoliolata* has high tolerance to salt stress, surviving a high salt concentration of up to EC 7.1 $dS \cdot m^{-1}$. An experiment conducted in Negev desert, Israel, reported that *S. birrea* subsp. *caffra* survived soil salinity of EC 4.5 $dS \cdot m^{-1}$ (Nerd and Mizrahi, 1993). Except in the present study, little information is available on any of the subspecies of *S. birrea* surviving beyond EC 4.5 $dS \cdot m^{-1}$ level of salinity.

S. birrea is also known to occur along the riverbanks in arid and semi arid regions of Africa (Maundu et al., 1999; Peters, 1998). These areas are prone to flooding during the rainy seasons. Plants growing in such areas need to have tolerance to occasional flooding. The observation that all the seedlings also survived three months of continuous flooding even without inoculation shows that *S. birrea* is highly tolerant to flooding. In addition, the observed ability of *S. birrea* to form lenticels under flooding conditions is evidence of the species tolerance to flooding. Lenticels are spongy areas in the corky surface of plants that provide a pathway for gas exchange between the atmosphere and the inner layers of cells in plants. It has been reported in a study conducted on *Casuarina equisetifolia* that the plants which formed hypertrophied lenticels had better adaptation to flooding by showing increased oxygen availability (Osundina, 1998). The findings may explain why the adaptability of *S. birrea* to riverine vegetation in the arid and semi arid areas.

S. birrea has strong tolerance to water stress, salt stress and flooding even in non-mycorrhizal seedlings. Interestingly, inoculation of *S. birrea* seedlings with *G. margarita* remarkably improved their tolerances to the three environmental stresses. The response to inoculation, however, varied with the subspecies. Under water stress and flooding, *S. birrea* subsp. *caffra* showed the highest response to AM fungus inoculation compared to the other subspecies. There is very little data on the effect of AM fungi on the growth of *S. birrea* under water stress, salt stress or flooding. A related study on other arid and semi arid species has shown that AM fungi improved tolerance to plants under water stress (Stahl et al., 1998), salt stress (Sengupta and Chauduri, 1990) and flooding (Osundina, 1998).

The present study has demonstrated that even though *S. birrea* has tolerance to water stress, salt stress and flooding, AM fungi can be used to improve growth of *S. birrea* in arid and semi arid areas.

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アーバスキュラー菌根菌が水および塩類ストレス，並びに湛水条件下における *Sclerocarya birrea* の樹勢および養分吸収に及ぼす影響

Benard Oula Muok・石井孝昭

京都府立大学大学院農学研究科　606–8522　京都市左京区下鴨半木町

アーバスキュラー菌根（AM）菌が *Sclerocarya birrea* の耐乾性および耐塩性，並びに耐水性に及ぼす影響を温室内で調査した．AM 菌には *Gigaspora margarita* を用いた．その結果，菌根菌無接種でも，*S. birrea* の 3 亜種のいずれも強い水ストレスおよび湛水耐性を持っていた．また，湛水処理した実生はいずれも皮目が発達し，3 か月間の湛水に耐えた．さらに，無接種の *S. birrea* subsp. *multifoliolata* は高濃度塩類ストレス（EC 7.1 dS・m^{-1}）下でも生存した．*G. margarita* による菌根形成は *S. birrea* の耐乾性および耐塩性，並びに耐水性を著しく向上させた．特に，水ストレスおよび湛水条件下では 3 亜種の中で，*S. birrea* subsp. *caffra* が菌根菌接種に最もよく応答した．高濃度塩類ストレス下では，菌根菌接種は *S. birrea* subsp. *multifoliolata* の N, P, Ca および Mg の吸収量を増加させた．以上の結果，乾燥地・半乾燥地に生息する *S. birrea* は生来の耐乾性および耐塩性，並びに耐水性を有しているが，AM 菌の利用はその *S. birrea* においても環境耐性を強める上で非常に有効であることが示された．