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CO_2 ENRICHMENT AND MYCORRHIZAL EFFECTS ON CUTTING GROWTH AND SOME PHYSIOLOGICAL TRAITS OF CUTTINGS DURING ROOTING

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Abstract. Propagation conditions of bedding plants can eliminate or reduce the possibility of AMF inoculation of the root system during greenhouse production. Due to the ability of AMF to increase plant growth the effects of AMF and CO_2 enrichment on rooting and some physiological traits of geranium and osteospermum cuttings were investigated. AMF and CO_2 enrichment increased leaf number and fresh and dry weights of osteospermum shoots. Mycorrhization also significantly increased the length and fresh and dry weights of osteospermum roots formed in CO_2 enriched atmosphere but it did not affect root system developed in ambient atmosphere. AMF increased the length and fresh weight of geranium roots, irrespectively of CO_2 concentration, and dry weight of roots in CO_2 enriched atmosphere. Transpiration and stomatal conductance values were higher in inoculated osteospermum at higher CO_2 concentration. Mycorrhization and CO_2 enrichment increased photosynthetic activity of garden geranium leaves and this effect was connected with the increased ratio of variable to maximum chlorophyll fluorescence (F_v/F_m).

Key words: osteospermum, garden geranium, transpiration, stomatal conductivity, assimilation rate

INTRODUCTION

Arbuscular mycorrhizal fungi (AMF) are one of type of mycorrhizal fungi that are commonly associated with the roots of horticultural crops. Plants with mycorrrhizae are potentially more effective at nutrient and water acquisition and outperform non-mycorrhizal plants in stress conditions, such as drought stress and low soil fertility [Al-Karaki 2000, Koide 1991]. Since the fungi are dependent on host photosynthesis, substantial amount of assimilates allocated to the roots is required for growth of fungus [Jakobsen and Rosendahl 1990]. Carbohydrate limitation may inhibit growth rate of

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host plants [Fitter 1991]. On the other hand, AM symbiosis is known to induce and/or to influence the changes in photosynthesis and carbohydrate metabolism in host plants to compensate the higher demand [Black et al. 2000]. In greenhouses the rate of photosynthesis can be also increased by CO_2 enrichment.

The technique employed for bedding plant propagation by cuttings does not allow the formation of mycorrhizae, because rooting substrates are usually sterilized or devoid of AM fungi. Inoculation of cuttings during rooting in greenhouses may be beneficial for further growth of bedding plants in outdoor conditions. The benefit from root colonization by AMF are thought to be highest when colonization occurs as early as possible during plant growth [Scagel et al. 2003].

These studies were designed to test the ability of *Glomus* species to colonize the root system of two commonly cultivated bedding plants: osteospermum and geranium during rooting, and to evaluate the effect of CO_2 enrichment and mycorrhization on growth of cuttings, transpiration and photosynthetic activity.

MATERIALS AND METHODS

Plant material, inoculation procedure, and recording of percentage infection. Unrooted cuttings of osteospermum (*Osteospermum ecklonis* (DC.) Norl. 'Denebola') and garden geranium (*Pelargonium hortorum* L.H. Bailey 'Tango Orange') were treated with rooting powder containing: 0.2% NAA, 0.1% Benomyl, and 1% Kaptan for rooting stimulation, and than planted into sphagnum peat + perlite substrate (3 : 1, v/v), pH 5.8. The substrate was inoculated with mycorrhizal fungi by adding 1-liter mixture of root pieces and substrate inoculated earlier with Endorize – TA AMF inoculum (Biorize Sarl, France) to 10 liters of fresh peat + perlite substrate. Inoculum consisted of a mixture of *Glomus* species. Control plants were rooted in fresh substrate, prepared without the mixture of inoculated roots and substrate. The substrates were not sterilized. The peat used in this experiment was devoid of AM fungi as confirmed by the absence of colonization with the non-inoculated treatments.

Rooting conditions and CO_2 enrichment. Cuttings were rooted in glass chambers (0.75 × 0.50 × 0.45 cm) covered with plexiglass, at 50 μmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD) and 12/12 h photoperiod. Ambient constant temperature was maintained during rooting at 25ºC, and humidity near saturation point. The cuttings were grown at two CO_2 concentrations (350 and 1000 μmol mol^{-1}). The CO_2 concentration within chambers was monitored with gas monitor (ADC 2000, Analytical Development Company Limited, (England). Carbon dioxide was added from a compressed supply of pure gas.

Measurements. All measurements were conducted at the end of experiment, osteospermum after 8 weeks of rooting, geranium after 5 weeks of rooting. Twenty plants from each treatment were used for the measurements. A single plant was treated as a replication. Plant height, leaf number, fresh and dry weights of upper part and roots were determined.

The transpiration and stomatal conductance (g_s) were determined on first fully developed leaf of each cutting using portable porometer (LICOR, 1600M, Nebraska,

USA). Net CO_2 assimilation rates were measured using a portable LCA-3 infrared CO_2 analyzer and the Parkinson Broad Leaf Chamber PLC-3B (ADC, England) on first fully developed garden geranium leaf only, because osteospermum leaves are too small for Parkinson Broad Leaf Chamber PLC-3B.

Chlorophyll fluorescence was measured on the *ad axial* surface of the attached leaves using a fluorescence measurement system (PEA, Hansatech Instruments, LTD., England). The leaves were covered with clips, darkened for 20 min, and then illuminated with red light emitting diodes (peak at 650 nm, maximum irradiance at leaf surface 3000 μmol m^{-2} s^{-1}, 40% of full light intensity). The samples were characterized by F_o, F_m and T_{fm}, where F_o – initial fluorescence, corresponding to all PSII reaction centers in the open configuration, F_m – maximal fluorescence, corresponding to all PSII reaction centers in the closed state, T_{fm} rise time from F_o to F_m. The following expressions were also calculated: F_v – variable fluorescence, ($F_m - F_o$), F_v/F_m – an indicator of the rate of photochemical reactions.

Root colonization by mycorrhizal fungi was recorded using slide method [Giovanetti and Mosse 1980] after staining the roots with trypan blue [Phillips and Hayman 1970].

The experiment was conducted twice. Owing to the similarity of results obtained in the two trials, the data presented in the tables are arithmetical means. The treatments were statistically analyzed by analysis of variance and means were compared with Duncan's multiple range test at P = 0.05.

RESULTS AND DISCUSSION

Successful rooting depends on cutting quality and environmental conditions during root formation. Both bedding plants used in this experiment are commonly propagated by cuttings. Geranium cuttings are considered very easy to root, after about 4 weeks of rooting they develop adequate amount of roots for transplanting. Osteospermum cuttings takes 2–4 weeks longer to root, especially during winter time. The amount and quality of rooted cuttings is very important for propagation profitability. Today CO_2 enrichment is commonly used in greenhouses for plant growth stimulation and reduction of production time. In many species CO_2 enrichment enhances root development of cuttings and their subsequent growth [Davis and Potter 1983]. At elevated CO_2 concentration increase in percentage of fine roots colonized by AM fungi was frequently observed [Olesniewicz and Thomas 1999]. In some studies no responses or even decreases in percent infection of AMF with high CO_2 have been reported [Staddon and Fitter 1999]. In this experiment CO_2 enrichment had no effect on mycorrhizal colonization of osteospermum cuttings. The percentage of root colonization of inoculated osteospermum cuttings grown in ambient and CO_2 enriched atmosphere was similar – about 30 % (tab. 1). The un-inoculated plants had no root infection. The infection of roots of inoculated geranium cuttings grown in CO_2 enriched atmosphere was recorded as about 97 % (tab. 3). The infection of inoculated geranium cuttings grown in ambient CO_2 atmosphere ranged from 45–53%. The effect of elevated CO_2 on mycorrhizal colonization can be indirect and dependent on stimulatory effect of CO_2 on plant growth [Staddon et al. 1999 a, b]. It was also earlier found that elevated CO_2 concentration enhances

the effectivity of flavonols responsible for chemotactic action on AM fungi [Bécard et al. 1992]. The exudates can stimulate hyphal growth, root colonization or both [Bécard and Piché 1989].

Mycorrhizal infection did not contribute to height of osteospermum shoots, irrespectively of CO_2 concentration, but increased leaf number, fresh weight of shoots in CO_2 enriched atmosphere, and dry weight of shoots in both ambient and CO_2 enriched atmospheres (tab. 1). The effects of mycorrhization and CO_2 enrichment on growth of geranium shoots were negligible (tab. 2). This difference is probably due to shorter time of rooting of geranium cuttings.

Adding AMF inoculum to rooting substrate significantly increased the length and fresh and dry weights of osteospermum root system formed in CO_2 enriched atmosphere but it did not affect root system development in ambient CO_2 atmosphere. Mycorrhizal inoculation increased the length and fresh weight of geranium roots, irrespectively of

Table 1. Effects of CO_2 enrichment and mycorrhizal inoculation on percentage of root colonization and growth of osteospermum cuttings (*Osteospermum ecklonis* (DC.) Norl. 'Denebola')

Growth characteristics	CO_2 concentration (μmol mol^{-1})			
	350		1000	
	mycorrhizal inoculation			
	-	+	-	+
Root colonization by AMF (%)	0	31.0	0	27.2
Length of shoot (cm)	7.20a	7.25a	7.15a	7.95a
Leaf number	8.70ab	8.95ab	8.45a	9.85b
FW of shoot (g)	2.11a	2.31ab	2.53a	3.03b
DW of shoot (g)	0.34a	0.41b	0.44b	0.56c
Length of roots (cm)	11.55a	12.60a	12.45a	16.45b
FW of root system (g)	0.33a	0.37a	0.41ab	0.63b
DW of root system (g)	0.03a	0.04a	0.05b	0.06c

a–c – Means followed by the same letter(s) in a row are not significantly different at 5% level according to the Duncan's multiple range test

Table 2. Effects of CO_2 enrichment and mycorrhizal inoculation on some physiological parameters of osteospermum cuttings (*Osteospermum ecklonis* (DC.) Norl. 'Denebola')

Physiological parameters	CO_2 concentration (μmol mol^{-1})			
	350		1000	
	mycorrhizal inoculation			
	-	+	-	+
F_v/F_m	0.80a	0.81a	0.79a	0.84b
Transpiration (mmol H_2O m^{-2} s^{-1})	0.54b	0.71bc	0.33a	0.77c
Stomatal conductance (mmol H_2O m^{-2} s^{-1})	46.19b	56.30b	28.42a	61.95b

Explanation as in Table 1. F_v/F_m – an indicator of the rate of photochemical reactions, F_m – maximal fluorescence, F_v – variable fluorescence

CO_2 concentration, and dry weight of roots in CO_2 enriched atmosphere. Enhanced rooting of geranium cuttings in CO_2 enriched atmosphere and no effect of CO_2 on cutting growth were earlier reported by Davis and Potter [1983]. The addition of AM fungi into rooting substrate during cutting propagation increased rooting in many woody plants [Scagel 2001, Scagel et al. 2003]. Scagel [2001] reported increased rooting of rose cuttings in response to AMF inoculation on cuttings from cultivars that do not respond to rooting hormone application but no effect on rooting of cuttings from cultivars that responded to hormone application. Both, osteospermum and geranium cuttings respond to rooting hormone application. In this experiment all cuttings were treated with rooting powder. For both species, cuttings treated with the combination of hormone application, AMF inoculum and CO_2 enrichment had the most root growth when compared to cuttings from other treatments.

Increases in root initiation and root growth on cuttings rooted in medium containing AMF inoculum were not always associated with increased levels of root colonization [Scagel 2001]. In this experiment, better growth of osteospermum cuttings inoculated with AM fungi and rooted in CO_2 enriched atmosphere was also not associated with higher percent of root colonization (tab. 1). The opposite was found for geranium, better root growth of geranium cuttings inoculated with AM fungi and rooted in CO_2 enriched atmosphere was associated with higher percent of root colonization (tab. 3). It is also possible that some early changes in root initiation and growth resulting from AMF inoculation could be stimulated by bacteria living in peat + perlite substrate used as AMF inoculum. The relationship between rhizobacteria enhancing plant growth and mycorrhizal fungi has been earlier documented [Germida and Walley 1996].

Table 3. Effects of CO_2 enrichment and mycorrhizal inoculation on percentage of root colonization and growth of geranium cuttings (*Pelargonium hortorum* L.H. Bailey 'Tango Orange')

Growth characteristics	CO_2 concentration (μmol mol^{-1})			
	350		1000	
	mycorrhizal inoculation			
	-	+	-	+
Root colonization by AMF (%)	0	49,2	0	97,4
Length of shoot (cm)	15.60a	15.50a	14.25a	14.65a
Leaf number	6,70ab	7.05ab	6.30a	7.40b
FW of shoot (g)	10.93a	11.10a	10.26a	11.60a
DW of shoot (g)	1.27ab	1.15a	1.25ab	1.60b
Length of roots (cm)	5.30a	10.65b	7.30a	14.60c
FW of root system (g)	0.77a	1.03b	1.13b	1.51c
DW of root system (g)	0.08a	0.10a	0.16b	0.19c

Explanation as in Table 1

Root growth and functioning during rooting of cuttings are dependent mainly on carbohydrates originating from current photosynthesis. After inoculation the fungus competes for assimilates with developing root system, particularly in conditions of low

irradiation during rooting of cuttings. It is very well known, that the mycorrhizal plants can compensate the higher carbohydrate demand by increase in rate of photosynthesis [Black et al. 2000]. However, despite of this beneficial effect on photosynthesis, in mycorrhizal plants root growth is less stimulated or even depressed [Mosse 1973]. Mycorrhization and CO_2 enrichment increased photosynthetic activity of osteospermum and geranium cuttings and this effect was connected with increased ratio of variable to maximum chlorophyll fluorescence (Fv/Fm), which is directly proportional to the maximum yield of primary photochemistry of PS II [Lichtenthaler et al. 1986] (tabs 2 and 4). During rooting photosynthesis rate can rather be regulated by sink strength, because development of root system and fungus development take place at the same time creating high carbon demand. The increase in sink strength of root system of mycorrhizal *Trifolium repens* was suggested to be the cause of increased photosynthesis over non mycorrhizal plants [Wright et al. 1998]. Increase in the rate of photosynthesis in mycorrhizal plants can be also mediated by increased by P nutrition [Black et al. 2000]. Low level of Pi led to starch accumulation in chloroplasts and decrease in photosynthesis rate [Black et al. 2000]. In this experiment rooted cuttings were not fertilized during rooting and in non mycorrhizal plants low P can limit photosynthesis.

Table 4. Effects of CO_2 enrichment and mycorrhizal inoculation on some physiological parameters of geranium cuttings (*Pelargonium hortorum* L.H. Bailey 'Tango Orange')

Physiological parameters	CO_2 concentration (μmol mol^{-1})			
	350		1000	
	mycorrhizal inoculation			
	-	+	-	+
Fv/Fm	0.79a	0.79a	0.80a	0.85b
CO_2 assimilation rate (μmol CO_2 m^{-2} s^{-1})	2.10a	2.28b	2.36b	2.59c
Transpiration (mmol H_2O m^{-2} s^{-1})	1.69a	2.04a	2.10a	1.96a
Stomatal conductance (mmol H_2O m^{-2} s^{-1})	83.39a	99.87a	112.82a	107.59a

Explanation as in Table 2

Water status of cuttings during rooting process is very important for cutting survival and subsequent growth. Mycorrhizal symbiosis usually promotes transpiration and stomatal conductance [Augé 2001]. However, in some plants AMF colonization resulted in no effects [Syvertsen and Graham 1990] or even decrease in these parameter values [Mathur and Vyas 1995]. Rising CO_2 concentration usually reduces the transpiration of plants [Morison 1985]. Water consumption is thus significantly reduced by CO_2 enrichment. In this experiment transpiration and stomatal conductance were higher in inoculated osteospermum plants, at higher CO_2 concentration only (tab. 2). Elevated CO_2 decreased slightly these parameters in non-mycorrhizal osteospermum. Inoculation and CO_2 enrichment did not affect transpiration and stomatal conductance of geranium cuttings (tab. 4). It was earlier found that effect of mycorrhization on stomatal opening is closely linked to plant size [Ruiz-Lozano et al. 1995]. In AM osteospermum plants better growth of shoots in CO_2 enriched atmosphere was associated with higher transpi-

ration rate and stomatal conductance. In ambient CO_2 concentration such relation was not observed. Stomatal functioning of AM plants can be affected by leaf tissue mineral element content, especially phosphorus [Radin 1984]. Phosphorus deficiency in leaves can alter stomatal sensitivity to ABA – hormonal regulator of stomata. Regulation of stomatal opening in AM plants can be also related to greater root sink strength and photosynthetic activity of leaves. Low internal CO_2 concentration caused by increased photosynthetic rates of AM plants can stimulate opening of stomata, CO_2 enrichment can exert opposite effect [Jarvis and Davies 1998]. Mycorrhizal and CO_2 enrichment influence on plant water relations are species specific. In some plants CO_2-induced stomatal closure can be very helpful for maintaining water balance of cuttings after stucking before root development and colonization by AM fungi.

CONCLUSIONS

Both factors tested: mycorrhization and CO_2 enrichment significantly stimulate the growth of root systems of *Osteospermum* and *Pelargonium* cuttings. This stimulation is connected with higher photosynthetic activity of garden geranium leaves. The root colonization of bedding plants after inoculation with AMF resulted in a higher quality cuttings. It seems to be possible that AMF inoculated cuttings would be more resistant to transplanting stress and grow better during later stages of plant development than inoculated ones.

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WPŁYW MIKORYZACJI I DOKARMIANIA CO_2 NA WZROST SADZONEK I NIEKTÓRE PROCESY FIZJOLOGICZNE PODCZAS ICH UKORZENIANIA

Streszczenie. W czasie produkcji w szklarniach warunki rozmnażania roślin rabatowych mogą eliminować lub zmniejszać możliwość inokulacji korzeni przez grzyby wywołujące mikoryzę arbuskularną (AMF). Ponieważ mikoryzacja może wpływać korzystnie na wzrost roślin, badano wpływ inokulacji AMF i dokarmiania CO_2 na ukorzenianie i niektóre cechy fizjologiczne sadzonek pelargonii rabatowej i osteospermum. Inokulacja AMF i dokarmianie CO_2 powodowały wzrost liczby liści oraz świeżej i suchej masy części nadziemnej sadzonek. Mikoryzacja wpływała znacząco na długość oraz świeżą i suchą masę systemu korzeniowego osteospermum w warunkach podwyższonego stężenia CO_2 w atmosferze, ale nie wpływała na wzrost systemu korzeniowego sadzonek niedokarmianych CO_2. Mikoryzacja wpływała także korzystnie na długość i świeżą masę systemu korzeniowego pelargonii rabatowej niezależnie od stężenia CO_2 oraz na suchą masę korzeni pelargonii w warunkach podwyższonego stężenia CO_2. Transpiracja i przewodnictwo szparkowe były większe u inokulowanych sadzonek osteospermum niż u nieinokulowanych w większym stężeniu CO_2. Mikoryzacja i dokarmianie CO_2 powodowały wzrost intensywności fotosyntezy u pelargonii, co było związane ze wzrostem stosunku zmiennej do maksymalnej fluorescencji chlorofilu (F_v/F_m).

Słowa kluczowe: osteospermum, pelargonia rabatowa, transpiracja, przewodnictwo szparkowe, intensywność fotosyntezy

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