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ORIGINAL ARTICLES

Influence of root and stem exudates of tomatoes infected by different *Glomus* species on germination of *Phelipanche ramosa* L. Pomel in vitro

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ABSTRACT

A series of laboratory experiments were carried out in order to investigate the influence of root and stem exudates of tomatoes infected by arbuscular mycorrhizal fungi (AMF) on germination of *P. ramosa.* Three tomato varieties commonly grown in Sudan were inoculated with three *Glomus* species at two inoculum densities. Root exudates were collected 21 or 42 days after transplanting (DAT) and stem exudates 42 DAT and tested for their effects on germination of *P. ramosa* seeds in vitro. At the higher inoculum density AMF colonization of tomato roots 42 DAT depended on crop cultivar and mycorrhizal species with no interaction between the two factors. Germination of *P. ramosa* was significantly lower in response to root exudates and stem diffusates from mycorrhizal than from non-mycorrhizal tomato plants. Plant roots harvested at 21 DAT had slightly lower rates of mycorrhiza infection (17.1%) compared to roots of 42 day old plants (21%), albeit not significantly different. Nevertheless, germination of *P. ramosa* was consistently higher in the presence of root exudates from 21 day old plants than from 42 day old plants. No correlation between amount of root colonization and *P. ramosa* germination suppression could be found. The lack of difference between the germination in response to root exudates from plants inoculated with different rates of AMF inoculum (250 and 500 spores per plant) is a promising result from a practical and economical point of view particularly for field application of mycorrhiza.

Key word: *P. ramosa*, germination stimulants, *Glomus* species, inoculum levels

Introduction

Several members of the genera *Phelipanche* and *Orobanche* are root parasitic weeds on economically important dicotyledonous crops across the world (Parker and Riches, 1993). *P. ramosa* (L.) Pomel (syn. *O. ramosa*), a root parasitic weed predominant in the Mediterranean region, is distributed globally. Its host range is very wide, including members of the families Alliaceae, Cannabidaceae, Asteraceae, Brassicaceae, Solanaceae, Cucurbitaceae and Umbelliferae (Parker and Riches, 1993). Among *P. ramosa* hosts tomatoes (*Solanum lycopersicon* (L.)) are the most susceptible and the most important on a global scale (Joel *et al*., 2007).

P. ramosa was first reported in Sudan in 1948 as a minor pest on horticultural crops and common weeds in Wadi Halfa on the southern borders of Egypt (Andrews, 1956). Andrews (1956) documented a wide distribution and identified the parasite as a threat to agriculture in the northern region of Sudan. Repeated importation of contaminated seeds, poor production practices including continuous monocropping of host plants, lack of awareness among farmers of the importance of the parasite, its invasive nature and difficulties to control once established have led to wide dispersal of the parasite and make it a weed of national importance. Severe infestation by the parasite was reported to inflict over 80% losses in tomato yield (Babiker *et al*., 2007).

The infection process by *P. ramosa*, as with other obligate root parasitic plants entails a defined sequence of tightly regulated developmental events. These include host–induced germination of seeds, directed growth of the radicle towards the host roots, and development of a haustorium, the attachment organ, that eventually penetrates the host roots and forms a physiological bridge that ensures transport of nutrients, water and carbon compounds from the host to the parasite (Watling and Press, 2001). The pre-infection processes are controlled by environmental factors, endogenous, and host-derived signals (Bouwmeester *et al*., 2007).

Strigolactones, a group of apocarotenoids that are exuded by roots of host and non-host plants in extremely low concentrations stimulate seed germination of the parasitic genera *Striga*, *Orobanche* and *Phelipanche* (Matusova *et al*., 2005). At the same time, however, strigolactones play an important role in the interaction

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between plants and arbuscular mycorrhizal fungi (AMF) (Akiyama *et al*., 2005; Besserer *et al*., 2006). AMF are root symbionts of most terrestrial plants and are known to facilitate the uptake of water and inorganic nutrients, particularly phosphorus (P) and nitrogen by their host plants. In return, they obtain photosynthetic products (Smith and Read, 2008).

It appears that plants release strigolactones to 'announce' their presence and position to their beneficial fungal symbionts (Paszkowski, 2006) and it has been shown that the secretion of strigolactones is increased by P deficiency in red clover (Yoneyama, *et al*., 2007) and tomato (López-Ráez *et al*., 2008). Strigolactones have also been shown to act as endogenous inhibitors of axillary bud outgrowth, but their biosynthesis and mechanism of action are poorly understood (Gomez-Roldan, *et al*., 2008; Umehara *et al*., 2008). It is thought that a part of the total pool of strigolactones pool is synthesized in the roots and that they are either exuded into the rhizosphere or transported to the shoot where they affect shoot branching. Parasitic plants appear to have co-opted the strigolactone based signals to recognize and locate host roots (Bouwmeester *et al*., 2007).

Enhanced colonization with AMF can reduce *Striga* infection in maize and sorghum (Gworgwor and Weber, 2003; Lendzemo *et al*., 2007). This is due to a reduction of the production of strigolactones upon AMF infection. Lendzemo *et al*. (2009) found that down-regulation of the *Striga* seed-germination activity occurs not only in root exudates upon root colonization by different AM fungi but also in the compounds produced by stems. It is unknown, however, if infection by AMF also results in reduced germination of *P. ramosa.*

To elucidate changes in the effect of root and stem exudates on *P. ramosa* seed germination through AMF infection the following questions were addressed in this study: 1) Is the germination stimulation of *P. ramosa* by root and stem exudates of tomatoes influenced by AMF genera and tomato genotypes? 2) Do different AMF inoculum rates influence the stimulation pattern? and 3) Do changes in germination stimulation depend on host age? Three tomato varieties commonly grown in Sudan were inoculated with three *Glomus* species at two inoculum densities. Root exudates were collected 21or 42 days after transplanting (DAT) and stem exudates 42 DAT and tested for their effects on germination of *P. ramosa* seeds in vitro.

Materials And Methods

2.1 Plant materials and growing conditions:

Experiments were conducted at the University of Kassel, Germany during January to July, 2010. Seeds of the tomato cultivars '*Strain B*', '*Peto 86*', and '*Castle rock'*, all commonly grown in Sudan, were surface sterilized for 5 min with a 3% solution of NaOCl containing two drops of 0.02% Tween 20 per 50 ml and thoroughly washed with sterilized distilled water (H_2O dist). Seeds were sown in peat and allowed to grow for 10 days prior to transfer to 1 1 plastic pots filled with autoclaved sand. Average day and night temperatures in the greenhouse were adjusted to 16h /24°C and 8 h /19°C, respectively. Day light was supplemented by 1000 lux light intensity supplied by Philips-Son 400 W sodium high pressure lamps and relative humidity was kept at 50-60%. The plants were watered twice a week with tap water. Fertilization was done every two weeks with 50 ml of Flory 2 , Euflor GmbH, Munich, Germany (N: P: K, 0.038: 0.006: 0.062/ L).

2.2 Experimental design and inoculation:

Experiment 1 was two factorial with five replications. The pots were randomized once a week to minimize positional effects. Factor one was the AMF species *GIomus intraradices*, *Glomus mosseae* and Glomus Sprint. The latter is a ready-made mix of three *Glomus* species (*G. etunicatum*, *G. intraradices* and *G. claroideum*) obtained from INOQ GmbH Germany. Factor two was the three tomato cultivars. At transplanting, each plant was inoculated with approximately 500 AMF propagules administered as 50 g soil-sand- based inoculum into the planting hole. Control plants received 50 g autoclaved inoculum. Plants were kept in the greenhouse for 42 days.

In experiment 2, each treatment was replicated six times. Three of the replicates were harvested after 21 days and three after 42 days. Each plant received 25 g soil-sand- based inoculum of the three arbuscular mycorrhizal fungi prepared and applied as previously described. The control pots received 25 g of autoclaved inoculum.

2.3 Root exudate collection and assessment of mycorrhizal infection:

Root exudates were collected as described by Stevenson *et al*. (1995) and Pinior *et al*. (1999). Roots of inoculated and control plants were gently washed free of sand and the plants transferred to conical flasks containing 100 ml H_2O dist in which the roots were completely submerged. The flasks were covered with aluminum foil to exclude light. In experiment 1, the flasks were placed for 72 h, in experiment 2 for 24 h in the greenhouse with temperature, light and relative humidity set as previously described. Subsequently, the fresh

weight of the roots was determined and samples taken for estimation of mycorrhizal infection. The exudate solution was adjusted with H_2O dist to 1 g root fresh weight per 100-ml or 20ml (w/v) in experiment 1 and 2, respectively. Exudate solutions were immediately frozen and stored at –20°C until use.

Mycorrhizal root colonization was assessed using 1 g of the fine roots. The roots, cleared by heating in 10% KOH at 90 °C for 30 min, acidified with 1% HCl for five min at room temperature, were stained with Trypan blue (Phillips and Haymann, 1979) at 90°C for 60 min using a water bath. Colonization was quantified as percentage with a dissecting microscope (40 x magnification) using the grid-line intersect method (Giovannetti and Mosse, 1980).

2.4 Conditioning of P. ramosa seeds:

P. ramosa seeds, collected from *P. ramosa* growing under tomato plants in Gezira state in 2006 were supplied by Dr. K. Idris of the Plant Protection Centre, Agricultural Research Corporation, Sudan (ARC). For cleaning the seeds were placed in a beaker (1000 ml) containing tap water, and agitated for five min. Floating materials containing debris and immature light seeds were discarded. The process was repeated several times. The seeds were surface sterilized by soaking for 3 min in 70% ethanol, followed by three min in 3% solution of NaOCl containing two drops of 0.02% Tween 20 per 50 ml. After this, the seeds were thoroughly washed with H_2O dist, dried on filter paper in a laminar flow hood, and stored in sterile glass vials at room temperature until use. Approximately 75-100 surface-sterilized seeds were placed separately onto discs of 1 cm diameter glass fiber filter paper (GFFP) discs. Discs were transferred to 9 cm Petri dishes (five discs per Petri dish) lined with two layers of filter paper wetted with 3 ml of H_2O dist. The Petri dishes were sealed with Parafilm, wrapped in aluminum foil, and incubated at 21°C in the dark for seven days.

2.5 Germination assays:

Discs containing preconditioned seeds were blotted dry on tissue paper for 30 min in a laminar flow hood and transferred to new Petri dishes (five discs, each) lined with a filter paper ring. Three ml of the respective root exudate solution were added to each Petri dish. GR_{24} a synthetic germination stimulant provided by Prof. Zwanenburg from the University of Nijmegen, The Netherlands (10 mg/l solution) or distilled water were included as controls for comparison. The Petri dishes were sealed with Parafilm, wrapped in aluminum foil and incubated as above for seven days. The seeds were subsequently examined for germination under a dissecting microscope. Seeds were considered germinated if the radicle protruded from the seed coat.

2.6 Stem cut assay:

In both experiments, stems of 42 old tomato plants were cut into approximately 0.5 cm-fragments. Aluminum foil wells, approximately 1.5 cm deep and 3 cm in diameter, with perforations at the bottom were placed in the centre of a 9-cm Petri dish lid lined with two layers of filter paper (Whatman, No.2). The filter papers were moistened with 3 ml of H_2O dist. A 1 g sample of cut stem was placed in each well. Similar arrangements of aluminum foil wells without stem fragments were made to serve as controls for comparison. Three 1-cm GFFP discs containing conditioned *P. ramosa* seeds were placed in a triangular fashion close to each well and 350µl H_2O dist was pipetted onto the stem fragments. In the control wells, 350 µl of either 10 mg/l GR_{24}, or distilled water were applied. Assessments were made as described above.

2.7 Statistical analysis:

Prior to analysis of variance (ANOVA), data were checked for normality using Shapiro-Wilks-W-Test. Data on percentage germination of *P. ramosa* seeds and mycorrhiza infestation were arcsine square root transformed to fulfill ANOVA requirements. No mycorrhizal colonization was detected in the control plants; data from G0 treatments were not included in the analysis of variance of percentage of root length bearing mycorrhizal colonization. The data were subsequently subjected to ANOVA using SAS 9.1 statistical package (SAS Ins., North Carolina, USA). Mean separations were made by Tukey honestly significance difference test at P> 5%.

Results:

As intended, the tomato plants suffered of nutrient deficiency in the experiments. Fresh weight of plants 42 DAT varied from 2.3 to 3.8 g/ plant with no significant effects of any of the treatments (Data not shown)

In experiment one mycorrhizal colonization of tomato roots depended on crop cultivar and mycorrhizal species with no interaction between the two factors. Roots from '*Peto 86*' (40%) had the highest colonization by

AMF followed by '*Castle Rock*' (29.7%) and '*Strain B'* (26.2%). Inoculation with *G. intraradices* (31.1%) and *G. mosseae* (32.6%) resulted in significantly higher colonization than with G. Sprint (26.3%) (Table 1).

In experiment 2, when inoculum rate was half mean infection rates (24.5%) were lower than in experiment 1 (30%). Plant roots harvested at 21 days had lower rates of mycorrhiza infection (17.1%) compared to 42 day old plants (21%), albeit not significantly different. For both harvesting times, differences in mycorrhizal colonization among tomato genotypes and mycorrhizal species were not statistically significant.

In both experiments, germination of *Phelipanche* seeds in the water controls was negligible (data not shown). GR_{24} induced 40-42% germination and the root exudates collected from non-mycorrhizal tomato plants after 42 days stimulated 24.3 and 25.6% germination of *P. ramosa* in experiment 1 and 2, respectively. Germination in response to exudates from 42 day old mycorrhizal plants was significantly reduced in comparison to non-mycorrhizal controls. The relative reduction in the germination stimulatory activity of the exudates from roots of 42 day old plants colonized by the three *Glomus* species ranged from 32 to 41% (Table 2 a, b). The magnitude of reduction was similar for all mycorrhiza species and tomato varieties with no significant interaction between the factors.

Germination of *P. ramosa* in response to root exudates from 21 day old plants was consistently higher than for 42 day-old plants ($F=121.6$; $P<0.01$). There was an interaction between mycorrhiza and tomato varieties ($F=4.5$; $P=0.01$). While germination was consistently reduced in all cultivar-mycorrhiza combinations, these reductions were not always statistically significant (Table 2 c). There was no discernible correlation between percentage of mycorrhizal infection and *P. ramosa* germination (Fig 1).

P. ramosa germination in response to stem diffusates from non-mycorrhizal plants was 16% in experiment 1 and 29% in experiment 2. In both experiments, stem diffusates from non-mycorrhizal plants invariably elicited higher germination than diffusates from the corresponding mycorrhizal ones and differences were mostly statistically significant. In the first experiment, mycorrhiza infection reduced germination in response to root exudates of '*Castle Rock*', '*Peto 86*' and '*Strain B*' by 29, 22 and 39%, respectively. In contrast, in the second experiment, the respective reductions in germination were 16, 19 and 24% (Table 3 a, b). The absolute reductions in germination rates in response to AMF infection were very similar in the two experiments, however. In experiment 1 the difference was 6.4%, in exp 2 it was 7.7% (Table 3.3). When taking into account the different levels of germination inhibition by stem diffusates of the control plants in the two experiments no correlation between amount of root colonization and *P. ramosa* germination suppression could be found (Fig 2).

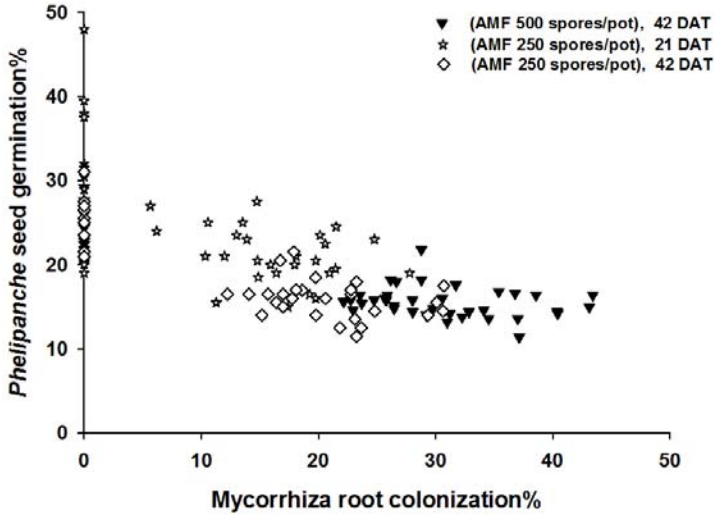

Fig. 1: Influence of arbuscular mycorrhizal colonization on the stimulation of *P. ramosa* seed germination by root exudates of tomatoes

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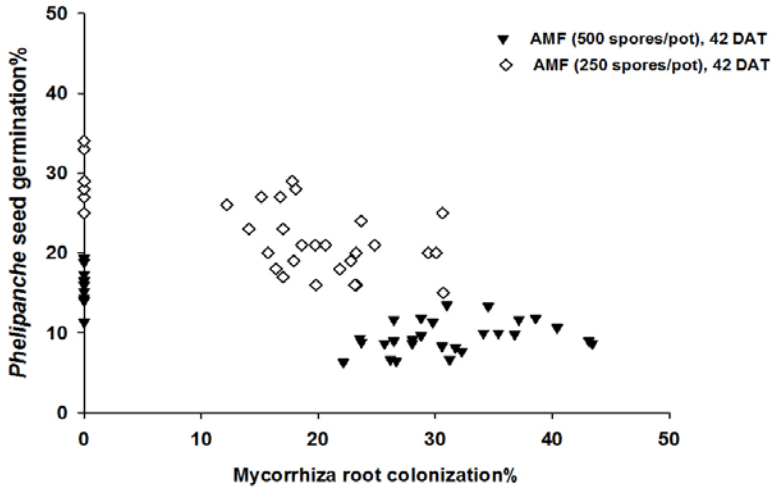

Fig. 2: Influence of arbuscular mycorrhizal colonization on the stimulation of *P. ramosa* seed germination by stem diffusates of tomatoes

Table 1: Percent colonization of tomato roots with AMF 42 days after transplanting as influenced by host genotype and mycorrhiza species[1] at an inoculum rate of 500 spores / plant.

Variety[2]	GI	GM	GS	Mean[3]
'Castle rock'	32.3 (±2.6)[2]	31.2 (±1.8)	25.7 (±2.1)	29.7b
'Peto 86'	36.7 (±3.1)	37.2 (±1.6)	28.1 (±1.4)	40.0a
'Strain B'	24.3 (±0.8)	29.3 (±1.7)	25.1 (±1.3)	26.2c
Mean[3]	31.1a	32.6a	26.3b	

[1]GI= Glomus intraradices, GM; Glomus mosseae; GS: Glomus sprint (a ready-made mix of three *Glomus* species (*G. etunicatum*, *G. intraradices* and *G. claroideum*).
[2]Data between parentheses are standard errors of the mean.
[3]Means followed by different letters are significantly different at P<0.05 (Tukey test). Data were arcsine transformed for analysis; non-transformed means are presented.

Table 2: Percentage seed germination of *P. ramosa* exposed to tomato root exudates as influenced by genotype, mycorrhiza species and inoculum level, and time of sampling (21 and 42 days after inoculation (DAT)[1]

a : inoculation= 50g AMF, sampling 42 DAT								
Variety	Control	GI	GM	GS	Mean[3]	+AMF	-AMF	Red%
Castle rock	22.1(±3.3)[2]	14.7(±1.2)	14.9(±1.8)	14.2(±1.9)	16.4a	15.1	24.3	37.9
Peto 86	25.9(±2.5)	17.9(±2.9)	16.6(±2.0)	14.4(±0.8)	19.1a			
Strain B	25.0(±2.7)	16.3(±1.8)	14.4(±0.8)	15.1(±1.0)	17.7a			
Mean[3]	24.3a	16.3b	15.3b	15.1b				
b : inoculation= 25g AMF, sampling 42 DAT								
Variety	Control	GI	GM	GS	Mean	+AMF	-AMF	Red%
Castle rock	25.4(±0.9)	15.5(±0.8)	19.0(±0.8)	17.0(±0.3)	19.2a	16.1	25.6	37.1
Peto 86	26.0(±1.5)	14.3(±0.6)	15.8(±0.3)	16.1(±0.9)	18.0a			
Strain B	25.6(±0.6)	14.4(±1.0)	15.5(±0.6)	17.0(±0.3)	18.1a			
Mean	25.6a	14.7b	16.8b	16.7b				
c : inoculation= 25g AMF, sampling 21 DAT								
Variety	Control	GI	GM	GS	Mean	+AMF	-AMF	Red%
Castle rock	33.1(±1.2)ab	17.6(±0.9)c	20.9(±0.8)bc	22.3(±0.8)bc	23.5	21.2	34.5	38.6
Peto 86	40.6(±1.8)a	20.8(±1.0)bc	22.8(±1.8)bc	21.5(±0.5)bc	26.4			
Strain B	29.6(±0.6)abc	21.9(±1.1)bc	23.4(±1.1)bc	19.5(±0.7)c	24.0			
Mean	34.5	20.1	22.3	21.1				

[1]Germination in the presence of GR24 (10 mg/l): *P. ramosa* (40-42%).
[2]Data between parentheses are standard error of mean.
[3]Variety means or AMF means followed by different letters are significantly different at P<0.05 (Tukey test). Data were arcsine transformed for analysis; non- transformed means are presented.

Table 3: Percentage seed germination of *P. ramosa* exposed to tomato stem diffusates as influenced by genotype host, mycorrhiza species and inoculum level[1]

a : inoculation= 50g AMF, sampling 42 DAT [2]								
Variety	Control	GI	GM	GS	Mean[3]	+AMF	-AMF	Red%
Castle rock	14.0(±1.2)	9.4(±1.1)	9.1(±1.0)	7.1(±0.5)	9.9b	9.6	16.0	40.0
Peto 86	16.2(±1.2)	11.7(±0.6)	12.2(±1.0)	10.7(±0.4)	12.7a			

Strain B	17.8(±0.2)	7.6(±0.5)	9.0(±0.49	9.2(±0.5)	10.9b			
Mean[3]	16.0a	9.6b	10.1ab	9.0c				
b : inoculation= 25g AMF, sampling 42 DAT								
Variety	Control	GI	GM	GS	Mean	+AMF	-AMF	Red%
Castle rock	27.3(±1.2)	19.3(±1.7)	21.0(±3.5)	24.0(±3.6)	22.9ab	21.1	28.8	26.7
Peto 86	30.7(±1.7)	20.3(±0.3)	26.7(±0.9)	22.0(±1.0)	24.9a			
Strain B	28.3(±2.4)	18.0(±1.2)	19.7(±2.3)	18.7(±0.4)	21.6b			
Mean	28.7a	19.2b	22.4b	21.6b				

[1]Germination in the presence of GR24 (10 mg/l): *P. ramosa* (26.1 %).
[2]Data between parentheses are standard error of mean.
[3]Variety means or AMF means followed by different letters are significantly different at P<0.05 (Tukey test). Data were arcsine transformed for analysis; non- transformed means are presented.

Discussion:

Germination of *P. ramosa* was significantly lower in response to root exudates and stem diffusates from mycorrhizal than from non-mycorrhizal tomato plants. Germination of *P. ramosa* was also consistently higher in the presence of root exudates from 21 day old plants than from 42 day old plants. However, no correlation between amount of root colonization and *P. ramosa* germination suppression could be found and tomato plants harvested at 21 DAT had an equal degree of AMF colonization compared to those harvested at 42 DAT

The observed reduction in *P. ramosa* germination in the presence of root exudates from mycorrhizal tomato plants supports previous results (Lendzemo *et al*., 2007; López-Ráez *et al*., 2011). Mycorrhizal fungi increase uptake of nutrients mainly phosphorus and this is supposed to lead to a subsequent down-regulation of strigolactone production (Yoneyama, *et al*., 2007; López-Ráez *et al*., 2008, 2011). Similarly, Pinior *et al*. (1999) and García-Garrido *et al*. (2009) found that a modification in root exudates occurs once the AMF symbiosis is fully established that represses further mycorrhizal colonization and concomitantly germination of parasitic plants. This might imply changes in root exudation patterns with plant age. Alternatively, Mada and Bagyaraj (1993) suggested that this was due to a decrease in root membrane permeability. However, to the best of our knowledge, alterations in exudation patterns of strigolactones in response to AMF root colonization level have not been proven directly.

The lack of difference between the germination in response to root exudates from plants inoculated with varied rates of AMF inoculum (250 and 500 spores per plant) is a promising result from a practical and economical point of view particularly for field application of mycorrhiza.

Stem diffusates of control plants (non AMF inoculated) from experiment 2 elicited significantly higher *P. ramosa* germination than those from experiment 1. This could possibly be due to differences in light during these experiments. Experiment 1 took place during winter time (Jan-April), while experiment 2 was run from April-July. Possibly, plants grown under short-day conditions produce lower amounts of strigolactones resulting in lower germination stimulation. Mayzlish-Gati *et al*. (2010) provided first evidence on the role of strigolactones as positive regulators of light harvesting.

It has been reported that the culture conditions during the collection of exudates influence both the quantity and composition of exudates (Jones and Darrah, 1993). However, the mechanism of exudation of substances by plant roots is not yet fully understood. In this study the root exudates of tomato plants collected during 72 h in the first experiment and 24 h in the second experiment elicited similar germination rates of *P. ramosa.* Přikryl and Vančura (1980) suggested that an accumulation of high levels of organic substances in the vicinity of roots represses the release of more organic compounds resulting in a decrease of exudation rate by plants in hydroponic culture systems. This and a lack of aeration in the flasks used to collect exudates may have led to similar results with both extraction methods.

In conclusion, AMF infections do reduce germination stimulation of *P. ramosa* in response to root and stem exudates of tomatoes. There appear to be effects of light intensity on this interaction which deserve more detailed investigation.

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