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Research Paper

Impact of water potential on growth and germination of *Fusarium solani* soilborne pathogen of peanut

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Abstract

Studies were conducted to determine the effect of osmotic and matric stress on germination and growth of two *Fusarium solani* strains, the etiological agent responsible of peanut brown root rot. Both strains had similar osmotic and matric potential ranges that allowed growth, being the latter one narrower. *F. solani* showed the ability to grow down to -14 MPa at 25 °C in non-ionic modified osmotic medium, while under matric stress this was limited to -8.4 MPa at 25 °C. However, both strains were seen to respond differently to decreasing osmotic and matric potentials, during early stages of germination. One strain (RC 338) showed to be more sensitive to matric than osmotic (non ionic) and the other one (RC 386) showed to be more sensitive to osmotic than matric imposed water stress. After 24 h of incubation, both isolates behaved similarly. The minimum water potential for germination was -8.4 MPa on glycerol amended media and -5.6 MPa for NaCl and PEG amended media, respectively. The knowledge of the water potential range which allow mycelia growth and spore germination of *F. solani* provides an inside to the likely behaviour of this devastating soilborne plant pathogen in nature and has important practical implications.

Key words: *Fusarium solani*, germination, growth, matric potential, osmotic potential, peanut brown root rot, soilborne pathogen.

Introduction

Argentina is a major peanut producing country. During the 2010/11 season, peanut production reached 701,535 tons with approximately 98% of the crop produced in the Córdoba Province. Most of the peanut production is exported to the European Union and the USA, and a smaller percentage is consumed within Argentina. Peanut seeds are used for direct human consumption and as raw material for the production of animal feed and oil (MAGyP, 2012).

Diseases caused by soilborne pathogen fungi limit peanut production, and can result in fields being taken completely out of peanut production (Busso *et al.*, 2004). Peanut brown root rot (PBRR) was first discovered in Cordoba province in 1992 (March and Marinelli 1998) and is now widespread in Argentina peanut-growing regions. Since 1992, PBRR has been of epidemic proportions in Cordoba province. The pathogen infects adult plants resulting in large economic losses. In seasons with long drought stress periods, this disease represents the most important disease of peanut and may reach 95% disease incidence in some fields (March and Marinelli 2005). The etiological agent responsible for the disease in Argentina was first reported as *Fusarium solani* (Mart.) Appel. and Wollenw. Snyd. and Hans. The *F. solani* species complex contains approximately 50 phylogenetic species many of which could be distinct species (Nalim *et al.*, 2011). Studies on the genetic characterization of this pathogen are in progress and specific primers have been developed to detect the pathogenic strains (Casasnovas *et al.*, 2013).

The disease has also been reported in Indonesia, Pakistan, Egypt and Australia (Semangun, 1993; Saleh, 1997; Elsayed Abdalla and Abdel-Fattah, 2000; Fuhlbohm *et al.*,

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2007; Widodo and Budiarti, 2009; Ahmed *et al.*, 2012; Zaman and Ahmed, 2012).

March *et al.* (2005) considered that soil and crop debris infected with *F. solani* serve as the main reservoir of inoculum. In most cases, inoculum takes form of conidia, chlamydospores or hyphal fragments. It has also been found a positive correlation between the level of inoculum present and the occurrence of the disease (Oddino *et al.*, 2008).

One important environmental factor, with major effects on fungal activity, is water availability. Water potential is a measure of how much energy is required to extract water from a substrate. Total soil water potential is the sum of many components including matric, pressure, and gravitational potentials (Cook and Duniway, 1980). With regard to soil systems, the most important ones are those governing water flow and availability for physiological process which are osmotic and matric potentials. Osmotic potential is due to the presence of solutes in soil water and it is important in saline soils or soils amended with fertilizers and organic waste. Matric potential includes both adsorption and capillary effects and it is the most important factor affecting fungal growth in soil or on root surfaces (Tan, 2011).

Water potential has been shown to have significant effects on fungal plant pathogens such as *Sclerotinia sclerotiorum* and *S. minor* (Hao *et al.*, 2003), *Rhizotocnia solani* (Ritchie *et al.*, 2006), *Fusarium graminearum* (Ramirez *et al.*, 2004), *Fusarium pseudograminearum* (Singh *et al.*, 2009) and *Macrophamina phaseoli* (Cervantes-García *et al.*, 2003). However, there is not information available on the response of *F. solani* to osmotic and matric potentials with regard to the different growth phases, which is relevant to colonization of natural substrate such as crop residue and soil.

Given the effect of water potential on mycelia growth and spore germination for other soil borne pathogens, it will be very interesting to study the effect of osmotic and matric potentials in order to understand the biology and epidemiology of this economical important pathogen. Thus, the objectives of this study were to compare the effect of osmotic and matric potential stress on (i) growth and (ii) germination, in two *F. solani* strains.

Materials and Methods

Fungal isolates

F. solani RC 386 and RC 338 were isolated from peanut plants exhibiting symptoms of peanut brown root rot. The isolates were previously confirmed as peanut pathogens following Koch`s postulates (Casasnovas *et al.*, 2009). DNA sequence data generated for these isolates causing PBRR belonging to *Fusarium solani* species group (FSSC) have been deposited in GenBank under accession numbers GQ121877-GQ121891 (ITS region), GQ121892-GQ121906 (β-tubulin gene), and GQ121907-GQ121921 (TEF-1α gene). The strains were stored as lyophilized cultures or in 15% glycerol at -80 °C in the culture collection at the Department of Microbiology and Immunology, Universidad Nacional de Río Cuarto, Cordoba, Argentina.

Media

A soil extract medium was used in this study. This medium was prepared with a sandy loam soil from Chucul, Cordoba Argentina, containing 46% sand, 39.2% silt, 10.6 clay, 1.37% organic matter, 0.13% total nitrogen, and pH of 6.07 (INTA, 1991). Soil extract was prepared by using 200 g of untreated field-moist soil in 400 mL of tap water. The soil/water mixture was autoclaved for 30 min, centrifuged at 2400 *g* for 20 min and filtered through filter paper (Whatman N^{o} 1), using a vacuum pump.

The water potential of the basic medium (soil extract) was modified osmotically by the addition of the ionic solute NaCl (Lang, 1967) or the non-ionic solute glycerol (Dallyn and Fox, 1980) to -0.7, -1.4, -2.8, -5.6, -8.4, -11.2 and -14.0 MPa (0.995, 0.99, 0.98, 0.96, 0.94, 0.92 and 0.90 water activity, respectively). Soil extract was a liquid broth, for solid medium experiments technical agar No. 1 (2%) was added to the liquid medium. For modification of the matric potential, the agar was omitted and known amounts of PEG 8000 were used (Michel and Kaufmann, 1973; Magan 1988), resulting in matric potentials of -0.7, -1.4, -2.8, -5.6 and -8.4 MPa. It has previously been shown that the water potential generated by PEG 8000 is predominant (99%) due to matric forces (Steuter *et al.*, 1981). Sterile disks of capillary matting (8.5 cm diam, 1.5 mm thick, Gardman, Spalding, Lincolnshire, U.K.) were placed in sterile 9 cm Petri dishes to which approx. 15 mL of the cooled medium was added. The matting was overlaid with sterile disk of black polyester lining cloth (0.15 mm thick) and then a cellophane disk (P400, Cannings Ltd, Bristol, U.K.).

The water potential of representative samples of media were checked with an Aqualab Series 3 water activity meter (Decagon devices, Inc., WA, USA) and converted to water potential.

Inoculation, incubation, and growth assessment

For each treatment Petri plates were inoculated centrally with 3 mm diameter agar plug from the margin of 7 d old colonies on 2% synthetic nutrient agar (SNA) (Gerlach and Nirenberg, 1982). Inoculated plates of the same water potential were sealed in polyethylene bags. Triplicate sets of each treatment (solute x water potential) were incubated at 18 and 25 °C for 20 days and all experiments repeated twice.

Two perpendicular diameters of the growing colonies were measured daily until the colony reached the edge of the plate. The radii of the colonies were plotted against time

for each replicate, and linear regression was applied to obtain the growth rate (mm/day) as the slope of the line.

Spore germination studies

Fusarium solani strains were grown on SNA 14 days, resulting in heavily sporulating cultures, which were flooded with 10 mL sterile water, and the spores dislodged by gently rubbing the surface with a sterile glass spreader. Stock spore suspension (1 mL) was added to 25 mL Universal bottles containing 9 mL sterile water amended to the appropriate osmotic or matric potential (-0.7 to -14.0 MPa) with glycerol, NaCl or PEG 8000. The final concentration of spores was in the range of 1-5 x 10^5 per mL.

A 100 µL spore suspension in osmotic solutions (glycerol and NaCl) was pipetted onto 2% soil extract-agar plates of the same osmotic potential, spread with a glass spreader and incubated at 25 °C in polyethylene bags for 24-48 h. Experiments were carried out with three replicates per treatment and repeated twice.

The system for testing the effect of matric potential on germination consisted of a 9 cm Petri dish containing sterile capillary matting. Loops of spore suspensions made up in appropriate PEG solutions were streaked across the surface of 13 mm membrane filters (Nucleopore, polycarbonate 0.2 mm membranes), which were placed carefully on the capillary matting previously soaked with about 15 mL of 2% soil extract suspension amended with PEG 8000 solution of the same matric potential. Three replicate membrane filters were used for each matric potential, and the experiments were repeated twice. Petri dishes were sealed in polyethylene bags and incubated at 25 °C.

Three agar plugs from each replicate (osmotic potential medium) were aseptically removed every hour from each treatment plate using a cork borer (10 mm diam) and placed on a slide. Replicate membrane filters from the matric potential plates were removed with forceps and placed on labelled slides. The agar plugs and membrane filters were stained with cotton blue/lactophenol and examined microscopically. A total of 50 spores per agar plug or membrane filters (150 per replicate plate, 450 per treatment) were counted. Spores were considered germinated when the germ-tube length was equal to or longer than the diameter of the spore.

Statistical treatment of the results

The linear regression of increase in radius against time (in days) was used to obtain the growth rates (mm/day) under each set of treatment conditions. The germination percentage after 8 and 24 h of incubation at different water potential values were logit (log x[x/(100 - x)]) transformed to homogenize variance before analyzing variance (ANOVA). The growth rates and percentage of germination were evaluated by ANOVA for each experiment to determine the effect of water potential, solute, isolate and two and three-way interactions.

When the analysis was statistically significant, the Tukey's multiple-comparison procedure test was used for separation of the means. Statistical significance was determined at the level $p < 0.05$. All the studies (ANOVA and correlation) were made by using SigmaStat for Windows version 2.03 (SPSS Inc.).

Results

Effects of osmotic and matric potentials on growth

In general, the lag phase length increases as the water potential and temperature decrease for both strains assayed. Also, both strains behave similarly at a given temperature and water potential (Table 1).

Figure 1 shows the effect of osmotic and matric stress on relative growth rates at 25 and 18 °C. Maximum growth rates were obtained at -0.7 MPa and 25 °C on osmotically (ionic and non-ionic) amended medium. On the matrically modified media, maximum growth rates were also obtained at -0.7 MP at 25 °C, but were lower than those obtained on osmotically modified media. Similar behaviour was observed at 18 °C.

Table 1 - Effect of water potential modified with glycerol, NaCl, and PEG 8000 on the mean lag phase (h) of *Fusarium solani* RC 386 and RC 338 at 25 and 18 °C.

Type of water potencial		Lag phase (h)			
		Strain RC 386		Strain RC 338	
	(-MPa)	18 °C	25 °C	18 °C	25 °C
Glycerol	-14	450	174	429	139
	-11.2	225	56	220	63
	-8.4	99	33	133	30
	-5.6	50	10	96	16
	-2.8	28	11	47	11
	-1.4	23	12	41	12
	-0.7	15	14	43	5
NaCl	-14	> 480	> 480	> 480	> 480
	-11.2	> 480	> 480	> 480	> 480
	-8.4	400	129	396	389
	-5.6	277	18	294	41
	-2.8	82	10	144	13
	-1.4	59	8	71	11
	-0.7	57	5	55	8
PEG 8000	-8.4	> 480	61	> 480	44
	-5.6	252	11	264	23
	-2.8	92	10	70	16
	-1.4	48	9	54	10
	-0.7	32	7	52	11

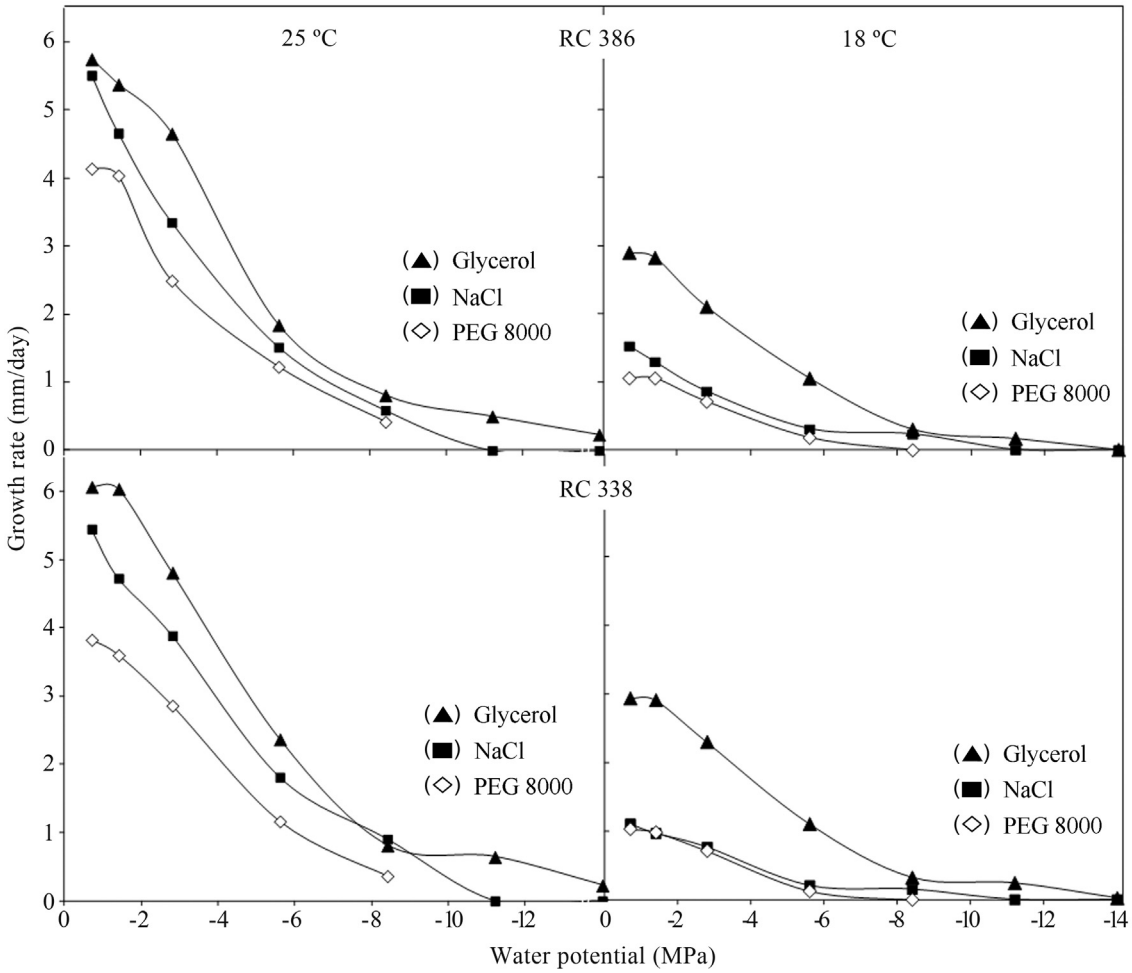

Figure 1 - Comparison of the effect of water potential modified with glycerol, NaCl and PEG 8000 on growth rates of *Fusarium solani* RC 386 and RC 338 at 25 and 18 °C.

On the osmotically (ionic and non ionic) modified media, growth rates for both strains were faster at -0.7 MPa and generally declined with decreasing osmotic potential. The maximum growth rate was at -0.7 MPa at 25 °C on osmotically amended media with glycerol.

Both isolates were able to grow at all water potentials tested on osmotically modified media amended with glycerol at 25 and 18 °C, respectively. However, complete inhibition of mycelial growth occurred at -11.2 MPa on osmotically modified media amended with NaCl at 25 and 18 °C, respectively.

On the matrically modified media, growth rates for both isolates were faster at -0.7 MPa and generally declined with decreasing matric potential. Complete inhibition of mycelial growth occurred at -8.4 MPa at 18 °C on matrically imposes stress.

Although maximum growth rates were obtained at the same water potential on osmotically and matrically amended media, those obtained on matrically modified media were lower than those obtained on osmotically modified media.

ANOVA showed that the effects of water potential, type of water potential, and two- and three-way interactions with the strains were statistically significant at both incubation times ($p \leq 0.001$), being water potential the most important factor (Table 2).

Comparison between effects of osmotic and matric potentials on germination

The effect of osmotic and matric potentials on macroconidial germination of two *F. solani* strains (8 and 24 h of incubation) are shown in Figure 2. Both strains of *F. solani* were seen to respond differently to decreasing osmotic (ionic and non ionic) and matric potentials shown by the significant ($p \leq 0.001$) interaction between strain and water potential effect on germination. The isolate RC 338, showed to be more sensitive to matric than osmotic (non ionic) potential from -0.7 to -2.8 MPa after 8 h of incubation. However, at the same conditions the isolate RC 386

Table 2 - Analysis of variance on the effects of water potential (ψ), type of water potential (Ψ type), and different strains and their interactions on growth at 18 and 25 °C.

		18 °C		25 °C	
Source of variation	df[a]	MS[b]	F [c]	MS [b]	F[c]
Strain	1	0.00791	3.239	0.722	39.215
Ψ	5	9.651	951.706*	82.691	4493.271*
Ψ type	2	15.421	6314.234*	14.096	765.972*
Strain x ψ	5	0.0118	4.826*	0.0577	3.138*
Strain x Ψ type	2	0.0388	15.881*	0.196	10.624*
Y x Ψ type	8	1.081	442.594*	0.852	46.311*
Strain x ψ x Ψ type	8	0.0223	9.123*	0.0843	4.579*

Strains: RC 386 and RC 338, ψ (-0.7 to -14 MPa), Ψ type (osmotic: ionic and non-ionic and matric). *p < 0.001, [a]Degrees of freedom, [b]Mean square, [c]Snedecor-F.

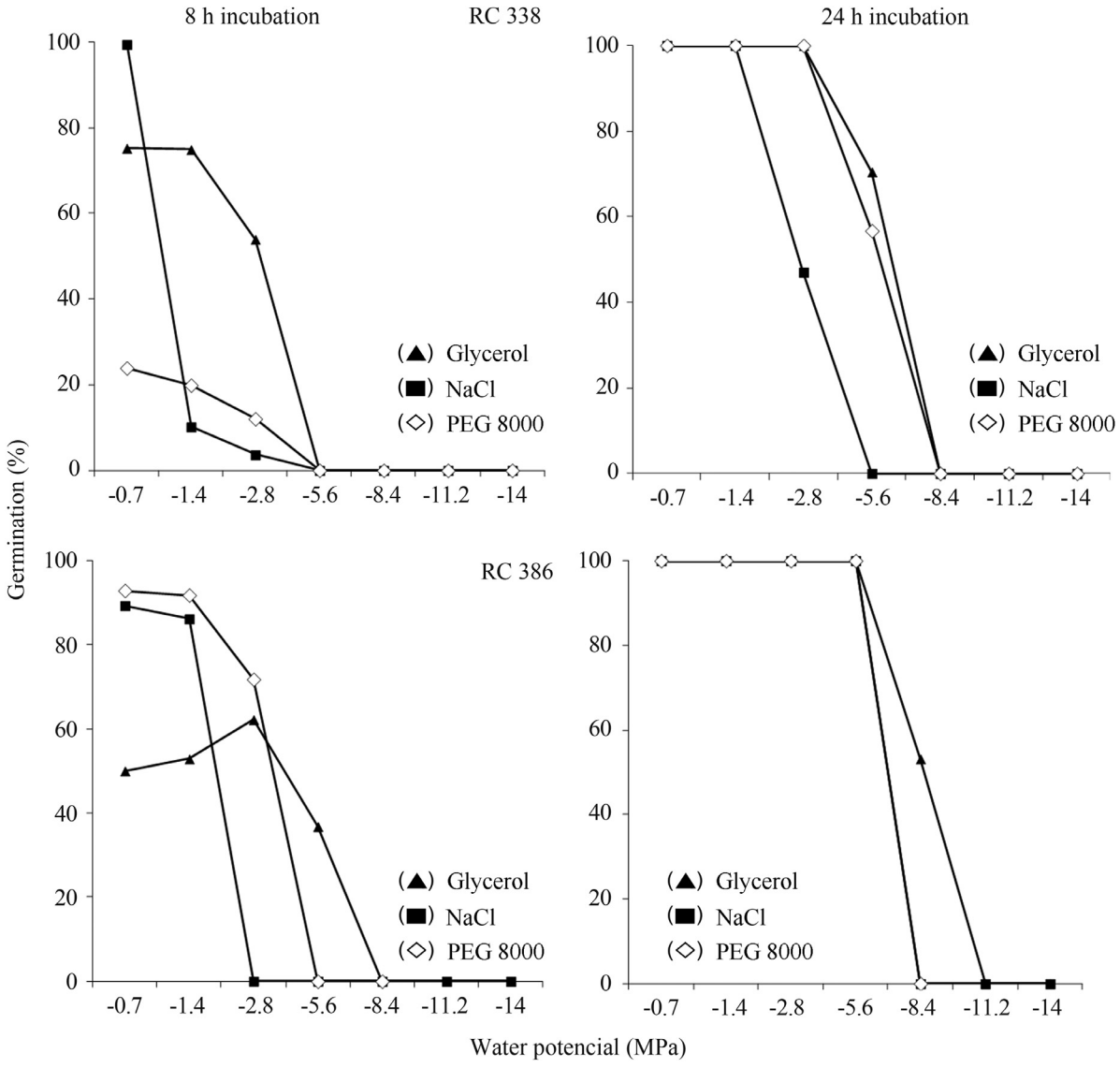

Figure 2 - Effect of water potential modified with glycerol, NaCl and PEG 8000 on germination of *Fusarium solani* spores after incubation at 25 °C.

showed more than 90% of germination on matric modified media in comparison with 89-86% and 50-52% on osmotic modified media amended with NaCl and glycerol, respectively. After 24 h of incubation, both isolates behaved similarly.

The minimum water potential for germination was -8.4 MPa on glycerol amended media and -5.6 MPa for NaCl and PEG amended media, respectively.

ANOVA showed that all single factors (strain, type of water potential, water potential) and two- and three-way interactions were statistically significant ($p \leq 0.001$) (Table 3).

Discussion

This study demonstrates that water potential and solute type have a significant effect on germination and growth rates of *F. solani,* the etiological agent of PBRR. Both strains had similar osmotic and matric potentials ranges that allowed growth, being the latter one narrower. *Fusarium solani* showed the ability to grow down to -14 MPa at 25 °C in non-ionic modified osmotic medium, while under matric stress this was limited to -8.4 MPa at 25 °C. This fungal pathogen seems to be more sensitive to matric than osmotic imposes stress.

Similar findings have been reported for other fungi with mycelial growth shown to be more sensitive to matric than osmotic stress (Magan 1988; Nesci *et al.*, 2004; Ritchie *et al.*, 2006; Jones *et al.*, 2011). However, for other fungal pathogen such as *F. graminearum,* responsible of *Fusarium* head blight in Argentina, Ramirez *et al.* (2004) have demonstrated that growth was more sensitive to osmotic than matric imposed stress.

When fungal cells are exposed to water stress, low molecular mass compounds are often synthesized or accumulated intracellularly to equilibrate the cytoplasm water potential with that of the surrounding environment. The decrease in total cellular water potential is necessary for the extraction of water from the substrate and its translocation to the growing mycelial front. This can be done effectively only by maintaining a water potential gradient from the substrate into the hyphal cells, which also facilitates the functioning of enzyme systems (Jennings 1995). It is interesting to note that Griffin (1981) suggested that matric imposed water stress is more difficult to overcome due to limited diffusion and motility of nutrients, which may restrict the ability of fungi to synthesize and accumulate osmolyte compounds.

During *F. solani* spore germination experiment both isolates seem to behave differently. Spore germination of the isolate RC 386, was more tolerant to matric than osmotic (non-ionic) stress after 8 h of incubation. However, we observed a wider range of osmotic potential over which germination occurred when the media was amended with glycerol, this may be partially due to accumulation of this solute in the spores. Tripling the incubation time (24 h) 100% of germination was observed on osmotically and matrically modified media between -0.7 and -5.6 MPa. Nevertheless, on osmotic amended media with glycerol around 50% of germination was observed at -8.4 MPa.

Spore germination of the isolate RC 338 was more tolerant to osmotic than matric imposed stress after 8 h of incubation. It was noticeable that the range of osmotic and matric potentials that allowed germination was the same, between -0.7 and -2.8 MPa. Tripling the incubation time (24 h) 100% of germination was observed on osmotically media amended with glycerol and matrically modified media between -0.7 and -2.8 MPa, it was also observed more than 50% of germination at -8.4 MPa at the same conditions. This isolate seemed to be more sensitive to osmotic potential adjusted with NaCl, because at this condition the range of osmotic potentials that allow germination was narrower, between -0.7 to -2.8 MPa.

Both strains used in this study were isolated from diseased root and, both have fulfilled the Kochs postulates.

Table 3 - Analysis of variance on the effects of water potential (ψ), type of water potential (Ψ type), and different strains and their interactions on germination at 25 °C at two incubation time 8 and 24 h.

		8 h		24 h	
Source of variation	df[a]	MS[b]	F [c]	MS [b]	F[c]
Strain	1	21.798	374.840*	53.622	1254.751*
Ψ	4	87.702	1508.129*	219.064	5126.056*
Ψ type	2	9.783	168.223*	23.059	539.583*
Strain x ψ	4	4.492	77.245 *	15.720	367.845*
Strain x Ψ type	2	7.473	128.512*	7.563	176.980*
Y x Ψ type	8	7.632	131.240*	7.633	178.613*
Strain x ψ x Ψ type	8	8.953	153.964*	11.507	269.263*

Strains: RC 386 and RC 338, ψ (-0.7 to -14 MPa), Ψ type (osmotic: ionic and non-ionic and matric). *$p < 0.001$, [a]Degrees of freedom, [b]Mean square, [c]Snedecor-F.

However, the isolated RC 386 seems to have an initial advantage in the first step of root infection due to the ability to germinate fast when water potential, under matrical stress, is imposed. This strain has also demonstrated to have high poligalacturonase (PGs) production, important enzymes in wall root degradation the-first step in root infection (Data no published).

We need to keep in mind that the most important factor for the disease development is days or weeks of drought in the middle of the growing peanut season. Drought stress limits water and in non-saline soil where matric potential is the dominant component, water availability decreases because water is held more tightly to the aggregate surface (Ilstedt *et al.*, 2000).

Another important factor in the main peanut production area of Argentina has been the increase in the salinity for the last 20 years due to deficient superficial and subterranean drainage and the ascent of the freatic layer (Cantero *et al.*, 1996). In this scenario the situation is more complicated due to the fact that osmotic potential is a function of matric potential. Osmotic potential decreases with decreasing matric potential as salt concentration increases in the remaining soil solution (Chowdhury *et al.*, 2011). According to our results *F. solani* seems to be adapted to grow and germinate in a broad range of osmotic and matric potentials, all these characteristics may contribute to its survival in the soil environment and improve potential for subsequent infection.

The range of water potential allowing mycelia growth and spore germination of isolates of *F. solani* provides an inside to the likely behaviour of the soil borne plant pathogen in nature and has important practical implications. The majority of agricultural soils are maintained naturally or artificially at water potential greater than the permanent wilting point of mesophytic higher plants, which is approximately -1.5 MPa (Slayter 1967). In the present study both mycelia growth and spore germination of *F. solani* occurred at lower water potential than this, down to -8.4 MPa. This indicates that isolates of this fungus are well adapted to proliferate over a range of soil water potentials well beyond the limits of their host. This must be one of the factors involved in its success as soil borne plant pathogen. Soil inoculum density and drought stress have previously been shown to affect the development of PBRR disease on peanuts, indicating that incidence and severity are partially determined a complex range of environmental factors.

Development of more effective integrated disease management strategies for PBRR could benefit from new knowledge on the factors that affect the biology of the host, the fungus, and their interaction.

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