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Influence of salinity on biomass production by Australian *Pisolithus* spp. isolates

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Abstract Eighteen isolates, comprising three putative *Pisolithus* species from eastern and central Australia, were screened for resistance to NaCl during growth in axenic culture. Biomass yield for most isolates showed a decline with increasing NaCl up to 200 mM; however, only five isolates reached an EC_{50} point (effective concentration inhibiting growth by 50%) below 200 mM NaCl. Most *Pisolithus* isolates were thus found to be resistant to NaCl at concentrations found in very saline soils. Of five isolates screened for Na_2SO_4 resistance, none reached an EC_{50} point below 100 mM. While intraspecific variation was evident in the resistance of isolates to both salts, no obvious patterns of interspecific variation were observed. The data thus indicate that isolates of the three Australian *Pisolithus* species are broadly resistant to salinity and may represent useful ectomycorrhizal inoculants for outplanting of compatible, salt-resistant host trees at saline sites.

Keywords Ectomycorrhizal fungi · *Pisolithus* · Salinity · Sodium salts

Introduction

Soil salinity is regarded as one of the most significant environmental problems and can often render soil of little or no value for agriculture, horticulture or silviculture (Chen et al. 1998; Bell 1999; Grattan and Grieve 1999; Kozlowski 2000). The extent of saline soils is increasing worldwide and there is great international interest in ways by which saline soils can be remediated and returned to practical use.

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Tree planting is regarded as a leading solution in controlling salinity (Dunn et al. 1994; Ghassemi et al. 1995). It is thought, for example, that hydrological imbalances may be considerably restored by replacement of shallow agricultural grass species with deep-rooted trees (Hussain and Gul 1991; Sun and Dickinson 1995), thereby reversing the causal process of salinisation. A number of studies in the field have investigated reclamation of areas using certain tree species (e.g. Pepper and Craig 1986; Eastham et al. 1993; Dunn et al. 1994; Sun and Dickinson 1995). Although the results are somewhat variable, in general it seems that selected provenances of certain tree taxa may be successfully established at some sites (see Pepper and Craig 1986; Luangjame 1990; Marcar et al. 1995; Niknam and McComb 2000).

Ectomycorrhizal (ECM) associations are known to enhance the mineral nutrition of trees (Read 1991) and to aid tree establishment at sites subject to a range of edaphic stresses, including high concentrations of toxic metals and/or drought (see Colpaert and van Assche 1987; Lamhamedi et al. 1992a, b; Brundrett et al. 1996). There is considerable evidence that arbuscular mycorrhizal fungi can enhance plant growth and vigour under salt stress conditions (Pond et al. 1984; Kim and Weber 1985; Pfeiffer and Bloss 1988; Dixon et al. 1993; Juniper and Abbott 1993; Tsang and Maun 1999). By contrast, we currently know little about salt resistance of ECM fungi or their potential use in facilitating tree establishment on saline sites.

Hutchison (1990) reported that isolates of a broad taxonomic range of ECM fungi continued growth at 171 mM NaCl, although at a lower rate than in the absence of salt. While clearly suggesting a degree of salt resistance in many ECM fungi, these data, derived by comparing growth at a single salt concentration with a no-salt control, do not indicate the relative salt resistances of the different isolates. Comparative toxicity testing requires data for growth over a range of concentrations to allow construction of dose response curves and estimation of EC_{50} values (effective concentration inhibiting growth by 50%). In such an experiment, Saleh-Rastin

(1976) estimated an EC_{50} value for growth of ca. 135 mM NaCl for an isolate of *Cenococcum geophilum* (Sow.) Ferd., with growth inhibited completely at concentrations above ca. 190 mM. In similar experiments (Dixon et al. 1993), radial growth of some isolates of five ECM fungal taxa was significantly reduced with increasing NaCl concentration up to 120 mM, but the growth of only one isolate (*Thelephora terrestris* Ehrh.: Fr.) was reduced by 50% in this concentration range. When toxicity was assessed by relative biomass production in liquid media, which is regarded as a more accurate measure of toxicity effects than radial growth in agar (Hartley et al. 1997), the *T. terrestris* isolate also showed no growth decrease up to 120 mM NaCl (Dixon et al. 1993). Thus, while slight inter- and intraspecific differences were identified among the isolates screened (1–3 isolates per taxon), all appeared broadly resistant to concentrations of NaCl considered toxic to all but the most resistant trees. Although a maximum of three isolates of each taxon was studied by Dixon et al. (1993), their data suggested that intraspecific differences exist in ECM fungi with regard to salt resistance. ECM fungi display much intraspecific physiological variation (Cairney 1999) but, to date, no detailed screening of a large number of isolates of any ECM fungal taxon for salt resistance has been undertaken.

In the study of Dixon et al. (1993), two isolates of *Pisolithus tinctorius* (Pers.) Coker and Couch were little affected by NaCl up to 120 mM. *Pisolithus* has a global distribution and has been used successfully to inoculate plantation stock of several tree taxa, including *Acacia*, *Eucalyptus* and *Pinus*. This has proven particularly successful for outplanting in soils subject to a variety of edaphic stresses (see Chambers and Cairney 1999), making it a potentially strong candidate for use in tree plantation in saline soils. However, it is clear from recent molecular studies that several *Pisolithus* species with different host specificities and geographical origins exist worldwide (Anderson et al. 1998; Junghans et al. 1998; Martin et al. 1998). At least three *Pisolithus* species are thought to exist in Australia (Cairney et al. 1999; Chambers and Cairney 1999). Despite the widespread occurrence of salinised soils on the Australian continent (Isbell et al. 1983; Niknam and McComb 2000), we know nothing about the salt resistance of the Australian *Pisolithus* spp. The aim of the present investigation was to screen isolates of Australian *Pisolithus* spp. for salt resistance with a view to identifying isolates to be used in plantation trials in saline soils with hosts such as *Acacia* spp., *Casuarina* spp. and *Eucalyptus* spp.

Materials and methods

Fungal isolates

Eighteen isolates of eastern and central Australian *Pisolithus* spp. (Table 1) were maintained on Modified Melin Norkrans (MMN) agar medium (Marx and Bryan 1975) at 23° C in the dark, subculturing every 4 weeks. Previous RFLP analyses of rDNA ITS regions and ITS sequence comparisons indicate that the isolates represent three putative *Pisolithus* species (I, II and III) (Anderson et al. 1998, 1999; Cairney et al. 1999). While most isolates have been in culture for less than 2 years, isolates BM01 and NSW1 have been maintained in culture for over 10 years.

Influence of salinity on biomass production

The influence of NaCl on biomass yield was determined by growing the isolates in a basal medium amended with NaCl at different concentrations (0, 25, 50, 100, 125, 150, 200 mM) or with Na_2SO_4 (0, 12.5, 25, 37.5, 50, 62.5, 75, 100 mM). The NaCl concentration range was based on prior experimentation with rhizosphere organisms (Reddell et al. 1986; Marcar et al. 1991) and field assessments of soil salinity (Allen et al. 1994; Niknam and McComb 2000). Na_2SO_4 concentrations were selected to provide equimolar concentrations of Na^+ in the NaCl and Na_2SO_4 treatments. Five isolates of *Pisolithus* I (WH01, R15, R08, NT07, R01) were randomly screened for Na_2SO_4 resistance (Table 1). The basal medium was a modified version of MMN containing per litre

Table 1 *Pisolithus* isolates included in the study, with details of their origin and species classification, and estimated EC_{50} values (mM) for growth in NaCl and Na_2SO_4. The isolates were classified as putative *Pisolithus* species based on rDNA ITS sequence comparison (see Anderson et al. 1998) (*nd* not determined)

Isolate	Geographical origin	*Pisolithus* species	EC_{50}	
			NaCl	Na_2SO_4
BM01	Blue Mountains National Park, NSW	I	125	nd
NSW1	NSW	I	>200	nd
NT07	Northern Territory	I	>200	>100
QLD02	Queensland	I	>200	nd
R01	Royal National Park, NSW	I	>200	>100
R02	Royal National Park, NSW	I	>200	nd
R08	Royal National Park, NSW	I	>200	>100
R15	Royal National Park, NSW	I	>200	>100
W14	N. Wilberforce, NSW	I	>200	nd
W17	N. Wilberforce, NSW	I	170	nd
W43	N. Wilberforce, NSW	I	>200	nd
W48	N. Wilberforce, NSW	I	140	nd
WH01	N. Wilberforce, NSW	I	140	>100
BW03	Brisbane Water National Park, NSW	II	>200	nd
LJ08	N. Turramurra, NSW	II	>200	nd
W34	N. Wilberforce, NSW	II	170	nd
WM02	Westmead, NSW	II	>200	nd
LJ30	N. Turramurra, NSW	III	>200	nd

$(NH_4)_2HPO_4$ 500 mg, KH_2PO_4 300 mg, glucose 10 g, $MgSO_4.7H_2O$ 140 mg, $CaCl_2$ 50 mg, NaCl 25 mg, $ZnSO_4$ 3 mg, thiamine 0.133 mg, and ferric EDTA 12.5 mg. Media were adjusted to pH 5–5.5 prior to the addition of the ferric EDTA and autoclaving. Discs of inoculum (5 mm diameter) were cut from the leading edge of actively growing colonies on MMN agar plates and one disc for each isolate was inoculated into 9-cm-diameter Petri dishes containing 25 ml liquid medium. Cultures were incubated at 23°C in the dark for 14–28 days (depending on the rate of growth of each isolate) and each treatment was replicated five times. Mycelial mats were then removed from the liquid media, dried overnight at 80°C and the biomass determined gravimetrically. Data for each isolate and each salt were analysed by one-way ANOVA and significant differences determined by Fishers PLSD. EC_{50} concentrations were estimated from dose response curves, with data converted to percentage growth relative to growth in the absence of salt for each isolate.

Results and discussion

Biomass yield by the majority of isolates showed an apparent general decline with increasing NaCl concentration, but the decline was not significant (P 0.005) in all cases (Fig. 1a–c, e). For some isolates this decline approximated an exponential decay function (Fig. 1a). Several isolates, including BM01, NSW and W34, showed significant peaks in relative biomass yield at low concentrations of NaCl (25–50 mM) relative to the zero NaCl treatment (Fig. 1a, e). Other isolates (NT07, R02, R08 and Qld02) showed significant peaks in relative biomass yield at around 100 mM NaCl (Fig. 1d). Over the NaCl concentration range utilised, EC_{50} values could be estimated for only five isolates (Table 1). Of these, the lowest EC_{50} value was 125 mM for BM01. The EC_{50} values for most isolates appear to be in excess of the highest NaCl concentration used (200 mM). For some isolates, such as LJ08, W43 and WM02, biomass yield at 200 mM was not significantly reduced compared with growth at zero NaCl, suggesting EC_{50} values for these isolates well in excess of 200 mM.

Isolates WH01 and R08 showed an apparent general decline in biomass yield with increasing Na_2SO_4 concentration, although the decline was not significant (P 0.05) (Fig. 1h). EC_{50} values lay outside of the concentration range tested (Table 1). While isolates R15 and R01 were not significantly affected by Na_2SO_4 up to 100 mM, biomass of NT07 showed a general increase with increasing Na_2SO_4 concentration. NT07 biomass was significantly higher (P 0.001) than in the zero Na_2SO_4 treatment at all Na_2SO_4 concentrations above 20 mM (Fig. 1g).

Selection of the salt concentration ranges used in the present study was based on field measurements of soil salinity (Barrett-Lennard et al. 1986; Allen et al. 1994; Niknam and McComb 2000) and the results of previous experiments with rhizosphere organisms (Reddell et al. 1986; Marcar et al. 1991). Our data indicate that isolates of the three Australian *Pisolithus* species are broadly resistant to NaCl at concentrations encountered in saline soils (Peck 1993). No obvious interspecific patterns were observed with respect to NaCl resistance, with all isolates producing measurable biomass at the highest concentration tested (200 mM). Growth of four isolates of species I and one of species II was reduced by 50% within the concentration range tested, while all other isolates failed to reach EC_{50} concentrations in the range up to 200 mM NaCl. This indicates intraspecific variation with respect to NaCl resistance, but further screening at concentrations above 200 mM are required to ascertain the full extent of this variation. Nevertheless, for none of these isolates was biomass production significantly reduced at concentrations of NaCl regarded as typical of very saline soils (<160 mM) (Marschner 1995).

Dixon et al. (1993) reported that Na_2SO_4 was more toxic to some ECM fungi than NaCl. In these experiments, however, the salts were applied in equimolar concentrations, making it difficult to ascertain whether the salt per se was more toxic, or whether the results simply reflect the fact that twice as much Na^+ was added in the Na_2SO_4 treatment. In our experiments, the concentrations of the two salts were adjusted so that equimolar Na^+ concentrations were applied. In the case of isolates R08 and WH01, EC_{50} Na_2SO_4 appeared to be lower than that for NaCl. While further comparisons of the isolates are required in order to confirm this, the results suggest that SO_4^{2-} is more toxic to these isolates at the cellular level than Cl^-. This certainly appears to be the case for some higher plants (Datta et al. 1995a, b).

Some isolates showed clear peaks in biomass yield at concentrations in the range 25–100 mM NaCl. While some marine fungi require Na^+ for growth, terrestrial fungi such as filamentous basidiomycetes appear to have no such requirement (Blomberg and Adler 1993; Jennings 1995). The observed peaks thus seem more likely to reflect responses to lowered external water potential generated by NaCl in the medium. This is supported by the observation of similar peaks in experiments in which growth of ECM or other fungi was measured at different external water potentials (generated by organic osmotica such as polyethylene glycol) (Mexal and Read 1973; Jennings 1995).

Although considered in general as less salt-resistant than other fungal groups, isolates of some basidiomycetes can grow at NaCl concentrations in excess of those used in the present work (Tresner and Haynes 1971). In common with other fungi, basidiomycetes including ECM taxa such as *Pisolithus* are known to accumulate compounds, such as polyols, that play a role in regulating the internal osmotic environment of hyphae (Jennings and Burke 1990; Cairney and Alexander 1992; Hocking 1993; Koide et al. 2000). Such an ability may explain the observed growth of ECM fungi under conditions of extreme external osmotic stress (Mexal and Reid 1973) and may in part explain the resistance to salt that we have identified in Australian *Pisolithus*. Isolates of *Pisolithus* are known to enhance host drought resistance (Lamhamedi et al. 1992a, b) and are regarded as adapted ecologically to relatively dry soil conditions (see Chambers and Cairney 1999). While naturally occurring sodic soils (when the exchangeable sodium is high enough to impair the soils physical properties) are com-

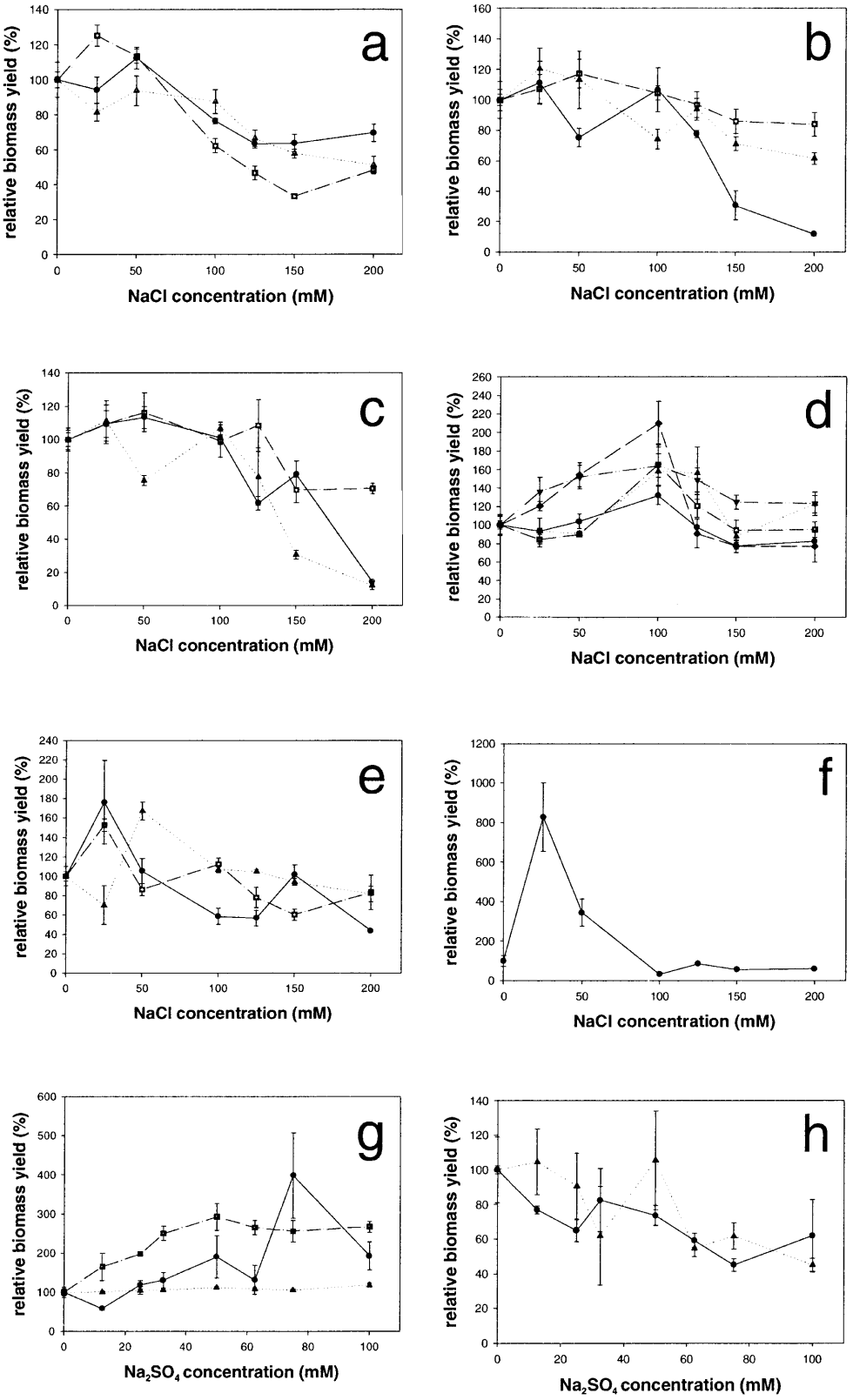

Fig. 1 Dose response curves for relative biomass yield of *Pisolithus* isolates in the presence of NaCl and Na_2SO_4 at a range of concentrations. Data are expressed as % of biomass produced at 0 mM NaCl for each isolate. For each point *n* 5, *bars* ±SE. **a** BM01* (■), LJ30* (▲), BW03* (●); **b** W43 (■), R15* (▲), W48* (●); **c** W14 (■), WH01* (▲), W17* (l); **d** NT07 (■), R02 (▲), R08 (●), WM02 (▼), Qld02 (◆); **e** NSW (■), LJ08 (▲), W34* (●); **f** R01 (●); **g** NT07* (■), R15 (▲), R01* (●); **h** WH01 (▲), R08 (●). * indicates significant differences ($P<0.05$) for each salt concentration determined by one-way ANOVA

mon in central and eastern Australia (Handreck and Black 1991), the isolates used in the present study were collected from sclerophyll forest sites where soils are not known to be specifically affected by salinity. Although, more specific salt resistance mechanisms, such as Na^+ efflux or vacuolar sequestration of Na^+ and Cl^- may to some extent underpin the observed salt resistance in Australian *Pisolithus* isolates (Blomberg and Adler 1993), the resistance may simply reflect a non-specific response to external osmotic stress induced under saline conditions.

Salt-resistant genotypes of a range of tree genera, including *Acacia*, *Casuarina* and *Eucalyptus*, have been identified from the many glasshouse and field trials conducted. These may have potential for establishment and remediation of salt-affected areas (Niknam and McComb 2000). The data from the present study suggest that many Australian *Pisolithus* species, which are known ECM partners of these tree taxa (Chambers and Cairney 1999), possess considerable resistance to salinity. Soil salinity can significantly reduce absorption of mineral nutrients such as phosphorus, nitrogen and potassium by plants (Marcar et al. 1995; Grattan and Grieve 1999). Under such circumstances, inoculation of trees for outplanting at saline sites with salt-resistant ECM fungi may significantly enhance survival and establishment. While the abilities of the salt-resistant *Pisolithus* isolates to survive under saline conditions during symbiosis with a host plant remain to be tested, they may form the basis of a useful inoculation programme for establishing trees on saline sites.

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