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Plant growth promoting characteristics of soil yeast (*Candida tropicalis* HY) and its effectiveness for promoting rice growth

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Compared with bacteria and mycorrhizal fungi, the potential to use yeasts as plant growth promoting agents has been under-exploited. We investigated the ability of the soil yeast *Candida tropicalis* HY (CtHY) to stimulate rice seedling growth and some of the possible mechanisms by which plant interaction may occur. Laboratory culture experiments found that CtHY produces small quantities of indole acetic acid (IAA), but grows rapidly on aminocyclopropane-1-carboxylate (ACC) as a sole source of nitrogen, indicative of high ACC deaminase activity. The strain also tested positive for polyamine and phytase production, and mobilized phosphate from insoluble tri-calcium phosphate. CtHY rapidly colonized the roots of rice seedlings and maintained high numbers for at least 3 weeks, increasing the dry weight of inoculated roots by 16–35% compared to non-inoculated control seedlings. These results validate the inclusion of CtHY in the commercial biofertiliser product BioGro, which has previously been demonstrated to increase the nutrition, growth and yield of paddy rice.

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1. Introduction

The rhizosphere of plants is home to a huge diversity of microbial species, many of which interact mutualistically with plant roots. There has been significant interest recently is exploiting these beneficial microorganisms for the purpose of more sustainable crop production. The documented benefits of plant inoculation with beneficial microorganisms include reduced pathogen infection, improved fertiliser use efficiency and improved resistance to abiotic stresses such as drought, mineral deficiency and salinity (Yang et al., 2009; Martinez-Viveros et al., 2010; Kim et al., 2011). Much of this research has focused on the use of particular bacterial species, commonly referred to as plant-growth promoting rhizobacteria (PGPR) (Vessey, 2003), or mycorrhizal fungi (Johansson et al., 2004); the role of other microbial species, including yeasts, has received less attention (Nassar et al., 2005).

Yeasts are unicellular fungi that proliferate primarily through asexual means and grow rapidly on simple carbohydrates, often through fermentative as well as respiratory pathways (Botha, 2011). As a consequence of their nutritional preference, yeast populations are generally an order of magnitude higher in the rhizosphere as opposed to the bulk soil (Cloete et al., 2009; Botha, 2011). A diverse range of yeasts exhibit plant growth promoting characteristics, including pathogen inhibition (El-Tarabily, 2004; El-Tarabily and Sivasithamparam, 2006; Sansone et al., 2005); phytohormone production (Nassar et al., 2005); phosphate solubilisation (Falih and Wainwright, 1995; Mirabal Alonso et al., 2008); N and S oxidation (Falih and Wainwright, 1995); siderophore production (Sansone et al., 2005) and stimulation of mycorrhizal-root colonization (Vassileva et al., 2000; Mirabal Alonso et al., 2008).

CtHY is a soil yeast that was isolated from the rhizosphere of rice and is included in a commercial biofertiliser product called BioGro (Kecskés et al., 2008). Field experiments have demonstrated that inoculation of rice with BioGro improves paddy rice growth and N nutrition (Cong et al., 2009), but the plant-growth promoting characteristics of CtHY have not yet been described. The aim of this investigation was therefore to identify potential mechanisms of plant growth promotion exhibited by CtHY and to test the hypothesis that it enhances rice seedling growth without co-inoculation with other PGPR.

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2. Materials and methods

2.1. PGP characteristics of CtHY

CtHY obtained from Prof Hien Thanh Nguyen, BARC Hanoi, Vietnam, was revived in modified nutrient broth (mNB) for 24 h and was subsequently kept in glycerol medium at −80 °C for all experiments. Strains of BioGro inoculant biofertiliser selected at the Hanoi University of Science were identified at the University of Sydney using a number of different techniques, including morphological, biochemical and genetic methods (Kecskés et al., 2008). Subsequently, the identity of the strains was also confirmed at the laboratories of the German Culture Collection of Microbes (DSMZ), Braunschweig, Germany. The strains comprising BioGro were identified as strains of *Pseudomonas fluorescens*, *Candida tropicalis*, *Bacillus subtilis* and *B. amyloliquefaciens*.

2.1.1. IAA production

IAA production was investigated by the modified method of Gordon and Weber (1951), using *Azospirillum brasilense* sp245 as a reference strain (Ona et al., 2005). The strains were grown overnight in Dworkin and Foster (DF) salt minimal medium (Dworkin and Foster, 1958) and transferred to fresh DF medium amended with 0.1% L-tryptophan. The cultures were incubated for 7 days at 28 °C, and then centrifuged at 15,000 × *g* for 10 min. One millilitre of the supernatant was mixed with 2 mL of Fe-H_2SO_4 solution (1 mL of 0.5 M $FeCl_3{\cdot}6H_2O$ in 75 mL of 6.13 M H_2SO_4) and incubated in the dark for 45 min. The concentration of IAA was calculated from a standard curve of IAA obtained in the range of 0.5–10.0 $\mu g\,mL^{-1}$ by measuring the absorbance of samples and standards at 450 nm.

2.1.2. ACC deaminase activity

The presence of ACC deaminase activity was determined as described by Dell'Amico et al. (2005), using *Pseudomonas putida* S-313 as a reference strain (Penrose and Glick, 2003). The strains were first cultured in enriched medium (Modified Nutrient Broth or mNB contains 3.0 g beef extract, 5.0 g peptone, 5.0 g yeast extract, 0.5 g glucose, and 0.5 g sucrose in 1 L of distilled water) for 16 h and then transferred to N-free DF medium supplemented with 3.0 mM (filter sterilized) ACC as sole nitrogen source. After inoculation, the cultures were grown at 28 °C with continuous shaking and optical density at 600 nm was read for 8 days. Growth indicates the potential for the microorganism to use ACC as a N-source through deamination.

2.1.3. P-solubilisation

Modified Pikovskaya medium was used for all experiments unless otherwise stated, containing ($g\,L^{-1}$ in distilled water) glucose 10.0, $(NH_4)_2SO_4$ 0.5, NaCl 0.2, $MgSO_4{\cdot}7H_2O$ 0.1, KCl 0.2, yeast extract 0.1, $MnSO_4$ trace amount, $FeSO_4{\cdot}7H_2O$ trace amount. The pH was adjusted to 6.8 for all experiments before autoclaving. Phosphate (PO_4^{3-}) was added at 3.0 $g\,L^{-1}$ as tri-calcium phosphate $Ca_3(PO_4)_2$. Flasks were inoculated 10^5 ($\pm 5 \times 10^5$) cells of either CtHY or the reference strain, *Klebsiella pneumoniae* 4P (Ahmed, 2006). All experiments were conducted with triplicate sample flasks for each time sample, with each flask containing 25 mL of liquid growth media. Flasks were incubated aerobically with shaking (100 rpm) for 10 days at 30 °C. At each sample time 100 μL of culture suspension was taken and serially diluted for plate counting. The remainder of the sample was centrifuged at 5000 × *g* for 15 min and the pH and soluble P in the supernatant were analysed. The pH was measured with a PHM210 meter (Radiometer Analytical, France). Soluble P was measured using the ascorbic acid method (Olsen et al., 1954).

2.1.4. Polyamine production

Polyamine production was detected by streaking on Long Ashton Decarboxylase (LAD) agar containing NH_4NO_3 0.16 g, $Na_2HPO_4{\cdot}12H_2O$ 0.021 g, $CaCl_2{\cdot}2H_2O$ 0.111 g, K_2SO_4 0.174 g, $MgSO_4{\cdot}7H_2O$ 0.185 g, H_3BO_3 0.4 mg, $MnSO_4{\cdot}4H_2O$ 0.2 mg, $ZnSO_4{\cdot}7H_2O$ 0.03 mg, $CuSO_4{\cdot}5H_2O$ 0.04 mg, $NaMoO_4{\cdot}2H_2O$ 0.003 mg, $CoSO_4{\cdot}7H_2O$ 0.003 mg, FeNaEDTA 0.021 g, glucose 10.0 g, L-arginine monohydrochloride 2.0 g, phenol red 0.02 g in 1 L of distilled water, and pH was adjusted to 5.5 (Cloete et al., 2009). Inoculated LAD plates were incubated in the dark at 28 °C for 7 days. Red halos on yellow background indicated arginine decarboxylation by the strain.

2.2. Assessment of plant growth promotion by CtHY

2.2.1. Inoculum preparation

CtHY was grown in mNB at 28 °C for 2 days. Yeast cells were harvested by centrifugation at 10,000 × *g* for 10 min, and the pellet was washed twice and resuspended in distilled water. The resulting suspension was diluted to ~10^6 cfu mL^{-1} prior to inoculation.

2.2.2. Seed surface sterilization

Rice seeds (*Oryza sativa* cv. Reiziq) were surface sterilized by soaking in 70% ethanol for 5 min and then in 0.5% mercuric chloride solution for 30 s. Once drained, the seeds were rinsed with sterile distilled water for five times (James et al., 2002).

2.2.3. Root elongation bioassay

Sterilized rice seeds were incubated with yeast suspension for 1 h with gentle agitation to allow the yeast to bind to the seed coat. Sterile distilled water was replaced in control seeds. Coated seeds were germinated on water agar in a growth chamber for 7 days at 25 °C. Shoot and root lengths were measured. The number of germinated seeds was recorded and seedling vigor index was calculated as given below (Jegathambigai et al., 2009). Ten plants of each water agar plate were averaged and considered as one replicate.

$$\text{Seedling vigor index} = \%\text{Germination} \times (\text{shoot length} + \text{root length})$$

2.2.4. Sand pot experiment

Propagation trays were filled with sterile washed river sand and soaked to semi-submerge level of moisture with a quarter strength of Hoagland's nutrient solution (Guimil et al., 2005). Surface sterilized rice seeds were pre-germinated on water agar for 4 days in dark and then sown into the moist sand. Each treatment was replicated with 10 plants. One hundred microlitre of the cell suspension was inoculated to each plantlet. Sterile distilled water was replaced in control plants. The pots were placed on cool-white fluorescent lighting shelf, and the plants were grown at room temperature (28 ± 2 °C) and were watered with sterile distilled water every day. A quarter strength Hoagland's nutrient solution was applied to the plants every week and the plants were grown for 3 weeks after sowing. Plants were sampled weekly and growth parameters including shoot and root length and shoot and root dry weight were measured. Total root length was measured using WinRhizo software. Percentage yeast-induced root growth response (%YGR) and specific root length (SRL) were calculated using the following formulas (Cloete et al., 2009):

$$\%\text{YGR} = \frac{\text{mean g DW (inoculated)} - \text{mean g DW (control)}}{\text{mean g DW (control)}} \times 100$$

$$\text{SRL} = \text{Root length (cm)/root DW (mg)}$$

Table 1
Plant growth promoting characteristics of *Candida tropicalis* HY. Values are means of three replicates ± standard errors (SE). Values in rows not followed by the same letter are significantly different according to Student's *t*-test ($P < 0.05$).

PGP characteristics	Unit	CtHY	Reference strain[a]
IAA production (maximum)	μg IAA mL^{-1}	2.6 ± 0.1 a	31.2 ± 0.5 b
P solubilisation (maximum)	μg P mL^{-1}	119 ± 10 a	74 ± 14 b
ACC deaminase activity	max. $OD_{600\ nm}$	0.48 ± 0.03 a	0.12 ± 0.01 b
Polyamines production	Yes/no	Yes	–
Phytase production	Yes/no	Yes	–

[a] See Section 2 for the identity of the reference strains.

Table 2
Influence of yeast on seed germination and rice plant growth and vigor. Values are means of three replicates (ten plants in each replicate) ± standard errors (SE). Values in columns not followed by the same letter are significantly different according to Student's *t*-test ($P < 0.05$).

Treatment	Germination (%)	Shoot length (cm)	Root length (cm)	Vigor index
Control	96 ± 2 a	2.44 ± 0.05 a	12.3 ± 0.5 a	1400 ± 80 a
CtHY	97 ± 1 a	2.89 ± 0.07 b	19.1 ± 0.7 b	2100 ± 100 b

2.2.5. Estimation of root colonization

At each sample time above, three plants were sampled, and the roots washed twice in pyrophosphate buffer pH 7. The roots were then transferred to McCartney bottles containing 10 mL of similar buffer with 10 glass beads and the yeast cells were detached by vortexing. The suspension was serial diluted and plated out on mNA supplemented with 100 $\mu g\,mL^{-1}$ tetracycline. The plates were incubated at 28 °C for 24 h before determining the cfu mL^{-1}.

3. Results

3.1. PGP characteristics of the yeast

CtHY tested positive to a number of recognized PGP traits including the production of IAA, ACC deaminase, phytase and polyamines, along with the ability to solubilise tricalcium phosphate (Table 1).

The overall production of IAA increased with time, but the highest IAA accumulation (2.57 $\mu g\,mL^{-1}$) remained 12 fold less than the maximum amount produced by the reference strain, *A. brasilense*. In contrast, ACC deaminase activity and P solubilisation activity were both significantly higher in CtHY than the corresponding literature reference strains.

3.2. Effects of yeast inoculation on the growth of rice plants

3.2.1. Root elongation bioassay

Seed treatment with CtHY noticeably enhanced seedling growth (Fig. 1), equating to significantly ($P < 0.05$) higher seedling vigor index compared to untreated controls (Table 2). Shoot and root length, but not germination percentage, were significantly ($P < 0.05$) higher in inoculated seedlings compared to un-inoculated controls (Table 2).

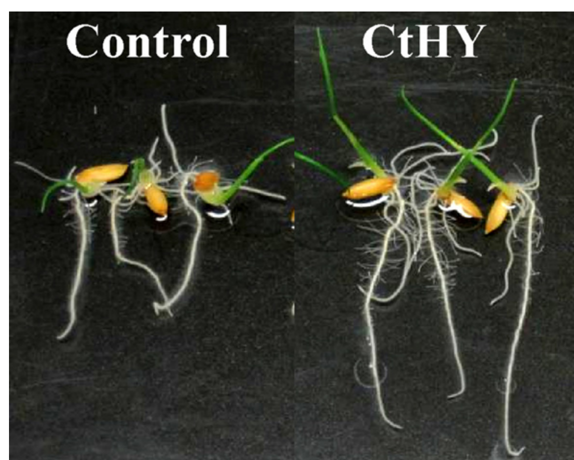

Fig. 1. Growth of rice seedlings (7 days after inoculation) from coated and non-coated seeds with *Candida tropicalis* HY.

3.2.2. Time course sand pot experiments

The inoculation of seedlings with CtHY did not significantly affect shoot dry weights, but resulted in significantly ($P < 0.05$) higher root dry weights than non-inoculated controls. Over the 3 week period, this equated to a CtHY-induced growth response of between 16% and 35%. CtHY also significantly ($P < 0.05$) affected the root morphology of rice plants as evidenced by the lower SRL compared with control plants (Table 3). The SRL is a frequently used measure of fine roots since the length of roots occasionally does not represent better growth when correlated with dry weight. SRL

Table 3
The colonization of *Candida tropicalis* HY on rice seedlings and its effect on dry weight and root morphology. Values are means of ten replicates ± standard errors (SE).

Time (days)	Treatment	Shoot dry weight (mg)	Root dry weight (mg)	SRL (cm mg^{-1})	%Yeast-induced growth response	Root colonization (10^4 cfu $plant^{-1}$)[a]
7	Control	14 ± 1	7.1 ± 0.3	12.5 ± 0.2	(0)	(0)
	CtHY	14 ± 1	9 ± 1*	11.3 ± 0.5	29	2.4 ± 0.5
14	Control	29 ± 2	10 ± 1	13.2 ± 0.9	(0)	(0)
	CtHY	30 ± 1	14 ± 0.8*	10.2 ± 0.2*	35	9.4 ± 0.8
21	Control	37 ± 3	16 ± 1	9.0 ± 0.3	(0)	(0)
	CtHY	41 ± 3	19 ± 1*	8.4 ± 0.2	16	3.5 ± 1.1
ANOVA	Time	<0.001	<0.001	<0.001	–	–
P-value	Treatment	0.242	0.01	<0.001	–	–
	T × *T*	0.742	0.656	0.048	–	–

[a] Initial target inoculation was 3.75×10^3 cfu $plant^{-1}$.
* Significant difference between treatment and control by pairwise multiple comparison using Holm-Sidak method at $P = 0.05$.

is believed to be indicative of environmental changes. CtHY rapidly colonized the roots of rice seedlings, increasing from an initial inoculation density of 3.75×10^3 cfu plant^{-1} to nearly 10^5 cfu plant^{-1} 2 weeks later. Although numbers declined to 3.5×10^4 cfu plant^{-1} after an additional week, the total number of cells remained higher than the initial inoculation.

4. Discussion

Candida tropicalis has previously been shown to promote plant growth when applied as a foliar spray on both potatoes and soybeans (Gomaa et al., 2005; Mekki and Ahmed, 2005). In both studies increases in dry matter and yield were apparent, along with a reduced incidence in white fly and thrips infestation on the potatoes. The strain CtHY comprises part of multi-strain biofertiliser (BioGro) previously shown to promote rice growth and yield in two seasonal field experiments in Vietnam (Cong et al., 2009). Here we demonstrated that CtHY exhibits a number of common plant growth promoting characteristics and is capable of enhancing rice seedling growth when inoculated alone, rather than as part of a multi-strain inoculant.

Yeasts require IAA to stimulate the growth of filaments (pseudohyphae) that assist in the infection/colonization of host plants (Martínez-Anaya et al., 2003; Xin et al., 2009; Rao et al., 2010), but isolates vary greatly in their efficiency for IAA production (Nassar et al., 2005). The relatively low capacity of CtHY to produce auxins is therefore not surprising, but suggests that this is not the main mechanism by which it affects rice seedling growth. Instead, the rapid and significant growth of CtHY on ACC, representative of high ACC deaminase activity, could indicate a major pathway for inducing morphological responses in plants. The function of ACC deaminase in plant-microbe systems, including those using the reference *Pseudomonas putida* strain, has been well studied and results in decreased ethylene production and consequent stimulation of plant root elongation (Glick et al., 2007; Yim et al., 2010). To our knowledge, high ACC deaminase activity has previously been reported in only two other yeast strains, *Hansenula saturnus* and *Issatchenkia occidentalis* (Palmer et al., 2007).

Further modification of root growth may also be induced by CtHY as a result of polyamine production. Polyamines (spermidine, spermine, putrecine) function in the spore germination of yeast (*Saccharomyces cereviase*) and are required for optimal growth (Brawley and Ferro, 1979). However, exogenous application of polyamines, such as spermidine and spermine, to plants also impacts root growth by increasing cell division (Tang and Newton, 2005). Indeed, inoculation of a slow-growing medicinal plant with the polyamine-producing yeast *Cryptococcus laurentii* significantly stimulated root growth (Cloete et al., 2009).

Aside from directly affecting root growth, CtHY also shows potential in contributing to the P nutrition of plants through its capacity to mobilize chemically incorporated organic P (e.g. phytate) and insoluble inorganic P. The ability of yeast to synthesise and excrete phytase in order to access organic P is well recognized, particularly under conditions where P is limiting (Nakamura et al., 2000); but the actual contribution of yeasts to increasing plant access to organic P remains, to our knowledge, unexplored. A number of other yeast strains have also been characterized for their ability to mobilize insoluble inorganic P sources, including calcium, iron and rock phosphates (Vassileva et al., 2000; Mirabal Alonso et al., 2008; Hesham and Mohamed, 2011). Some of these strains were also able to enhance the growth and P nutrition of associated organisms, including mycorrhizal fungi (Vassileva et al., 2000; Mirabal Alonso et al., 2008), tomato (Vassileva et al., 2000) and corn (Hesham and Mohamed, 2011). However, recent field studies involving inoculation of paddy rice with the CtHY-containing biofertiliser, BioGro, did not demonstrate improved P-nutrition, despite better overall growth.

Regardless, CtHY showed a strong ability to colonize roots by increasing in number after inoculation. The dynamics of colonization were similar to that of the endophytic PGP yeast *Williopsis saturnus*, which increased in number from about 5×10^2 cfu g^{-1} root fresh weight to 5×10^3 cfu g^{-1} root fresh weight within 3 weeks after inoculation onto maize roots (Nassar et al., 2005). That the colonization of CtHY resulted in 15–35% increases in root dry weights of rice seedlings clearly indicates its potential to promote plant growth and validates its inclusion and prospects for field use in the commercial BioGro biofertiliser product.

5. Conclusion

The soil yeast CtHY has the ability to produce IAA, grow on ACC as a sole N source, mobilize organic and inorganic phosphates, and synthesise polyamines. The application of CtHY on germinated seedlings resulted in better rice plant root growth and the colonization of CtHY was confirmed to persist on plant roots at least for 3 weeks. These results support ongoing prospecting of yeast isolates for inclusion into commercial PGP inoculants for sustainable agriculture.

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