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Plant growth-promoting traits in soil yeasts from Brazilian natural ecosystems

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INFO

Keyworks
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ABSTRACT

Soil yeasts are known to be abundant and diverse inhabitants in natural ecosystems and may also play a role as plant growth promoters. To the best of our knowledge, the use of soil yeasts from natural ecosystems as plant growth-promoting agents has yet to be extensively investigated in South America. This study aimed to analyze the plant growth-promoting traits in soil yeasts from natural and revegetated ecosystems. Indole acetic acid production was evaluated in a DF medium using L-tryptophan as a precursor and quantified by Salkowski's method. Siderophore production was assessed using the Chrome Azurol S method. Phosphate solubilization was evaluated on Pikovskaya agar containing aluminum and tricalcium phosphates. The biocontrol activity of phytopathogenic fungi was evaluated by pairing cultures in PDA. In total, 52 isolates presented positive results, representing 17 yeast species. *Rhodotorula* spp. were the best Indole-3-acetic acid producers and showed siderophore-producing capacity. *Wickerhamomyces anomalus* and *Meyerozyma guilliermondii* strains exhibited phosphate solubilizing activity. Eight species exhibited antagonistic effects against *Fusarium oxysporum*. The *Candida insectorum*, *W. anomalus* and *Rh. mucilaginosa* strains proved to be promising for future investigations. Our study results highlight the potential use of soil yeasts as potential plant growth-promoting agents.

Palavras-chaves
ácido indol-3-acético
bioinsumos
fungos unicelulares
solubilização de fosfato
biocontrole

RESUMO

Características de promoção do crescimento das plantas em leveduras do solo de ecossistemas naturais brasileiros

As leveduras do solo são conhecidas por serem habitantes abundantes e diversas nos ecossistemas naturais e também podem desempenhar um papel como promotores do crescimento das plantas. Até onde sabemos, o uso de leveduras de solo de ecossistemas naturais como agentes promotores de crescimento de plantas não foi extensivamente investigado na América do Sul. O objetivo deste estudo foi analisar características de promoção do crescimento vegetal em leveduras de solo de ecossistemas naturais e revegetados. Produção de ácido indol-3-acético foi avaliado em DF meio utilizando L-triptofano como precursor e quantificado pelo método Salkowski. Produção de sideróforos foi avaliada pelo Chrome Azurol S método. Solubilização de fosfato foi avaliada em Pikovskaya agar contendo fosfatos de alumínio e tricálcico. Atividade de biocontrole de fungos fitopatogênicos foi avaliada pelo pareamento de culturas em PDA. No total, 52 isolados apresentaram resultados positivos, representando 17 espécies de leveduras. *Rhodotorula* spp. foram os melhores produtores de ácido indol-3-acético e capacidade de produção de sideróforos. As espécies *Wickerhamomyces anomalus* e *Meyerozyma guilliermondii* apresentaram atividade solubilizadora de fosfato. Oito espécies exibiram efeitos antagônicos contra *Fusarium oxysporum*. A *Candida insectorum*, *W. anomalus* e *Rh. mucilaginosa* mostraram-se promissoras para investigações futuras. Os resultados do nosso estudo destacam o uso potencial de leveduras do solo como potenciais agentes para produção de bioinsumos visando a produção vegetal.

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INTRODUCTION

Anthropogenic activities such as agricultural practices, mining, and metal processing are major sources of soil contamination. Those activities lead to the loss of natural vegetation and change the chemical, physical, and biological characteristics of soils (Gastauer et al., 2018; Santos et al., 2016; Silva et al., 2018; Quadros et al., 2015; Moreira & Vale 2018; Moreira & Vale 2020; Moreira et al., 2020; Chen et al., 2022, He et al. 2022. Sustainable approaches to remediate the impact of anthropogenic activities are emerging. Amongst them, microbial agents that may promote plant growth (Targino et al., 2022) and reduce environmental degradation have been proposed (Syed and Prasad, 2019; de-Bashan et al., 2012).

Plant growth-promoting microorganisms (PGPMs) promote plant growth by direct and indirect mechanisms. Direct plant growth-promoting includes nutritional supplementation, nitrogen fixation, and phytochemical production of hormones. Instead, microorganisms can promote plant growth by producing siderophores and anti-fungal activity. The indirect mechanism leads to plant growth by reducing the activity of pathogens or deleterious microorganisms (El-Tarabily and Sivasithamparam, 2006; Nutaratat et al., 2014; Berg, 2009; Liu et al., 2020; Millan et al., 2020; Bright et al. 2022, Manici et al., 2023). PGPMs represent a wide diversity of bacteria (Dell'Amico et al., 2006, May et al., 2023), including bacteria (El-Mehalawy et al., 2004), filamentous fungi (Shah et al., 2018; Liu et al., 2020, Manici et al., 2023), and yeasts (Amprayn et al., 2012, Fu et al., 2016; Kumla et al., 2020, Millan et al., 2020, Bright et al., 2022, Targino et al., 2022).

Soil yeast has received attention due to its ability to enhance plant growth. The ability to produce plant growth regulators such as Indole Acetic Acid (IAA) was detected in soil yeast species such as *Candida tropicalis* (Amprayn et al., 2012), *C. pseudointermedia* and *Torulaspora globosa* (Bispo et al., 2023). Plant-growth regulators, such as indole-3-acetic acid (IAA) and indole-3-pyruvic acid (IPYA), were observed in the endophytic maize roots yeast *Williopsis saturnus* (Nassar et al., 2005). Rhizosphere yeasts, *Cryptococcus flavus*, and *Candida railenensis*, improved maize shoot phosphorus (P) content through phosphate solubilization in association with arbuscular mycorrhizal (AM) fungi (Sarabia et al., 2017). Indirect mechanisms such as antagonism to fungal plant pathogens and production of antifungal compounds were exhibited in *Torulaspora globosa* strains (Nutaratat et al., 2014; Bispo et al., 2023), *Torulaspora asahii* (Bispo et al., 2023) and *Saccharomyces cerevisiae* (Natarajan et al., 2022). Siderophore production was detected in *Rhodosporidium paludigenum* (Nutaratat et al., 2014). Induction of resistance through the production of enzymes such as peroxidase and catalase was the mechanism of action used by *Bullera sinensis* for the disease control of damping-off and stem rot caused by *Rhizoctonia solani* on cowpea plants (Tenório et al., 2019). The yeasts *Candida valida*, *Rhodotorula glutinis* and *Trichosporum asahii* were demonstrated to be effective against *R. solani* diseases of sugar beet, resulting in disease suppression and a significant increase in the dry weight of roots and shoots compared with the untreated control (El-Tarabily, 2004).

Yeasts that present those plant growth-promoting traits can be inoculated in plants, increasing the growth of roots and shoots. The co-cultivation of *Nicotiana benthamiana* with yeast isolates that have PGP (plant growth-promoting) traits enhanced plant growth by the development of lateral roots, formation of root hairs, and elongation of primary roots, indicating a potential yeast-plant interaction (Fu et al., 2016). Additionally, microorganisms that have PGP traits can also be used in the recovery of degraded or impacted areas (Syed and Prasad, 2019; Rafi et al., 2019; Ahmed and Holmström, 2014). However, few studies have reported the plant growth promotion traits of soil yeasts from natural ecosystems, especially in Brazil.

Plant growth-promoting (PGP) traits play an essential role in the ecology of soils and have the potential for biotechnology applications, especially in agricultural systems. In this context, this study aimed to evaluate a) the indole-3-acetic acid-producing abilities, b) aluminum- and tricalcium-phosphates solubilizing abilities, c) production of siderophores and d) performance as pathogen control agents by the yeasts isolated from the soil of natural and revegetated ecosystems.

MATERIALS AND METHODS

The yeasts evaluated in this study were obtained from the Yeast Culture Collection of the Department of Plant Pathology at the University of Brasilia (UnB), Brasilia, Brazil. The screening for plant growth-promoting traits was conducted for 379 isolates belonging to 48 species. The yeast strains were obtained from soil samples from an iron-mining site in natural and revegetated ecosystems in Minas Gerais state and protected areas of the Brazilian Atlantic Forest in Rio de Janeiro state. All the isolates tested were previously cultured in YPD medium (yeast extract 1%, peptone 2%, dextrose 2% w/v) to verify the cultures' purity and obtain metabolically active cells.

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IAA production was investigated using the method described in Amprayn et al. (2012). Briefly, to quantify the IAA produced, the strains were grown overnight in YPD medium and transferred to Dworkin and Foster (DF) salt minimal medium (Dworkin and Foster, 1958) amended with or without 0.1 % (w/v) L-tryptophan (L-Trp). The cultures were incubated on a shaker at 28 °C and 150 rpm for seven days. One milliliter of the isolate was centrifuged at 10,000 rpm for 10 minutes, and 100 µL of the supernatant was mixed with 100 µL of Salkowski's reagent (1 mL of 0.5 M $FeCl_3 \cdot 6H_2O$ in 50 mL of 35% $HClO_4$) (Gordon and Weber, 1951), and incubated in the dark for 30 minutes. The change in color was quantified using a spectrophotometer (SpectraMAX® 190, Molecular Devices, USA) at 450 nm. Finally, the concentration of IAA produced by yeast strains was calculated from a standard curve obtained with known concentrations of a commercial IAA solution in the range of 0 – 100 µg/mL.

Siderophore production was investigated using the method described by Ribeiro et al. (2012). The strains were cultivated in a KB liquid medium (pH 7) for seven days at 28 °C under agitation. After this period, 1 mL of the cultures was centrifuged at 10,000 rpm for five minutes, and 100 µL of the supernatant was mixed with 100 µL of Chrome Azurol S reagent (CAS) (Alexander and Zuberer, 1991). After 30 min of incubation in the dark, the plates were qualitatively evaluated for changes in color from blue to orange. Orange or yellow staining of the samples indicates the production of siderophores by yeast. The KB medium without yeast inoculum was used as a negative control.

The phosphate-solubilizing activity of yeasts was determined according to Fu et al. (2016). The strains were grown overnight in YPD medium, and then 3 µL were spotted onto Pikovskaya's agar containing aluminum- and tricalcium-phosphates (5 g L^{-1} each). The plates were incubated at 28 °C for five days and observed for the appearance of a clearing zone around the colonies caused by the solubilization of inorganic phosphate. The solubilization index (SI) was calculated by subtracting the colony diameter from the total diameter of the solubilization halo.

Antagonism tests were conducted in vitro against isolates of soil-borne phytopathogenic fungi *Fusarium oxysporum* and *Macrophomina phaseolina* to select the most promising yeast isolates as biocontrol agents. The isolates of soil-borne phytopathogenic fungi were obtained from the Department of Plant Pathology of the University of Brasilia. The yeasts and soil-borne phytopathogenic fungi were co-cultured, as described by Sperandio et al. (2015). Briefly, the tested phytopathogenic fungi and yeast strains were paired in Petri dishes containing a PDA culture medium. Plates receiving only the inoculum of the pathogen were used as controls. The plates were incubated at 28 °C, and the growth inhibition was evaluated when the whole control medium was covered by fungal growth. Mycelial growth inhibition (% inhibition) was calculated in relation to the control treatment without any yeast isolate.

A simple linear regression analysis was conducted to assess the relationships between plant growth-promoting traits and various factors, including (i) IAA production with and without L-tryptophan, (ii) the effect of siderophore production on biocontrol capability, and (iii) the influence of substrates on phosphate solubilization. The analysis was performed using the R software, and the results were visualized with the ggplot2 package.

RESULTS

This study revealed that 52 isolates (13.7% of the total) presented positive results to many recognized plant growth-promoting traits, including IAA production with and without L-tryptophan, phosphate solubilization, siderophore production, and antagonism in solid medium (Table 1).

Table 1 - Soil yeasts that presented positive results for at least one plant growth promoter trait, soil source and locality

Species	Strains	Soil source	Locality
Phylum Ascomycota			
Candida parapsilosis	CA116	Revegetated area	Brumadinho, MG
Candida parapsilosis	CA414	Revegetated area	Brumadinho, MG
Candida parapsilosis	CA824	Revegetated area	Brumadinho, MG
Candida parapsilosis	CR75	Iron outcrops	Nova Lima, MG
Candida parapsilosis	CR817	Iron outcrops	Nova Lima, MG
Candida parapsilosis	CR31	Iron outcrops	Nova Lima, MG

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Table 1 - Soil yeasts that presented positive results for at least one plant growth promoter trait, soil source and locality

Species	Strains	Soil source	Locality
Candida parapsilosis	CR818	Iron outcrops	Nova Lima, MG
Candida parapsilosis	CR819	Iron outcrops	Nova Lima, MG
Candida parapsilosis	F46	Atlantic Forest	Brumadinho, MG
Candida insectorum	CR96	Iron outcrops	Nova Lima, MG
Candida sanyaensis	F117	Atlantic Forest	Brumadinho, MG
Candida neerlandica	F29	Atlantic Forest	Brumadinho, MG
Candida maltosa	F31	Atlantic Forest	Brumadinho, MG
Candida maltosa	CA117	Revegetated area	Brumadinho, MG
Candida maltosa	CA215	Revegetated area	Brumadinho, MG
Candida maltosa	CA216	Revegetated area	Brumadinho, MG
Candida maltosa	CA910	Revegetated area	Brumadinho, MG
Candida maltosa	CA48	Revegetated area	Brumadinho, MG
Candida maltosa	CA64	Revegetated area	Brumadinho, MG
Schwanniomyces vanrijiae	CA18	Revegetated area	Brumadinho, MG
Wickerhamomyces anomalus	F112	Atlantic Forest	Brumadinho, MG
Meyerozyma guilliermondii	F27	Atlantic Forest	Brumadinho, MG
Meyerozyma guilliermondii	CR72	Iron outcrops	Nova Lima, MG
Meyerozyma guilliermondii	CA87	Revegetated area	Brumadinho, MG
Meyerozyma guilliermondii	CR64	Iron outcrops	Nova Lima, MG
Meyerozyma guilliermondii	A416	Atlantic Forest	Teresopólis, RJ
Meyerozyma sp.	CR74	Iron outcrops	Nova Lima, MG
Torulaspora sp.	CA1010	Revegetated area	Brumadinho, MG
Hanseniaspora uvarum	CA310	Revegetated area	Brumadinho, MG
Hanseniaspora uvarum	CA311	Revegetated area	Brumadinho, MG
Candida glabrata	CA323	Revegetated area	Brumadinho, MG
Phylum Basidiomycota			
Saitozyma podzolica	A122	Atlantic Forest	Teresopólis, RJ
Saitozyma podzolica	A146	Atlantic Forest	Teresopólis, RJ
Rhodotorula toruloides	CR13	Iron outcrops	Nova Lima, MG
Rhodotorula toruloides	CA312	Revegetated area	Brumadinho, MG
Rhodotorula mucilaginosa	CA322	Revegetated area	Brumadinho, MG
Rhodotorula mucilaginosa	CA610	Revegetated area	Brumadinho, MG
Rhodotorula mucilaginosa	CA314	Revegetated area	Brumadinho, MG
Rhodotorula mucilaginosa	CE33	Neotropical Savanna	Nova Lima, MG
Rhodotorula mucilaginosa	CE83	Neotropical Savanna	Nova Lima, MG
Rhodotorula mucilaginosa	F76	Atlantic Forest	Brumadinho, MG
Rhodotorula mucilaginosa	CA313	Revegetated area	Brumadinho, MG
Rhodotorula mucilaginosa	CA46	Revegetated area	Brumadinho, MG
Rhodotorula mucilaginosa	CR53	Iron outcrops	Nova Lima, MG
Rhodotorula mucilaginosa	F811	Atlantic Forest	Brumadinho, MG
Rhodotorula mucilaginosa	CA317	Revegetated area	Brumadinho, MG
Rhodotorula mucilaginosa	CA319	Revegetated area	Brumadinho, MG
Rhodotorula mucilaginosa	CA712	Revegetated area	Brumadinho, MG
Rhodotorula sp.	CA521	Revegetated area	Brumadinho, MG
Papiliotrema laurentii	CA99	Revegetated area	Brumadinho, MG
Papiliotrema laurentii	CA52	Revegetated area	Brumadinho, MG
Papiliotrema laurentii	CA522	Revegetated area	Brumadinho, MG

MG: Minas Gerais. RJ: Rio de Janeiro

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In this study, 37 strains (9.8%) were IAA producers, belonging to 11 species (Table 2).

The IAA concentration ranged from 18.9 to 137 µg mL^{-1} when cultured on a DF medium with Trp as the biochemical precursor. The concentration of IAA produced was strain-dependent, and strains of the *Rhodotorula* genus are among the best producers of IAA. The *Rhodotorula toruloides* (CR13) and *R. mucilaginosa* (CA610) strains produced high concentrations of IAA, ranging from 116.8 to 127.5 µg mL^{-1}. The strains evaluated produced only basal amounts of IAA, with only three strains reaching a maximum of 20 µg mL^{-1} when cultured in DF medium without Trp. The yeast isolates in our study produced significantly high amounts of IAA in the presence of exogenous Trp and basal amounts of IAA in the absence of exogenous Trp.

Table 2 - Indole-3-acetic acid (IAA) production by yeast species in medium with and without tryptophan

SpeciesSpecies/ Strains	**IAA production (µg mL^{-1}) in DF with Trp**	**IAA production (µg mL^{-1}) in DF w/o Trp**
Candida parapsilosis CA116	63.5	8.85
Candida parapsilosis CA414	35.3	8.2
Candida parapsilosis CA824	36.6	11.1
Candida parapsilosis CR75	36.8	9.14
Candida parapsilosis CR817	35.9	9.74
Candida parapsilosis CR31	26.6	8.7
Candida parapsilosis CR818	20.7	9.44
Candida parapsilosis CR819	20.6	8.65
Candida parapsilosis F46	28.4	ND
Candida insectorum CR96	56.1	1.18
Candida sanyaensis F117	40.8	9.69
Candida neerlandica F29	41.1	ND
Candida maltosa F31	32.8	10.1
Candida maltosa CA117	46.6	13
Candida maltosa CA215	47	ND
Candida maltosa CA216	46.4	2.48
Candida maltosa CA910	54	ND
Candida maltosa CA48	55.7	ND
Candida maltosa CA64	36.1	5.56
Schwanniomyces vanrijiae CA18	59.7	19.2
Torulaspora sp. CA1010	ND	3.2
Candida glabrata CA323	ND	1.54
Saitozyma podzolica A146	40.7	8.25
Rhodotorula toruloides CR13	127.5	9.5
Rhodotorula mucilaginosa CA322	93.6	17
Rhodotorula mucilaginosa CA610	116.8	2.64
Rhodotorula mucilaginosa CA314	72.1	18.8
Rhodotorula mucilaginosa CE33	67.2	ND
Rhodotorula mucilaginosa CE83	42.2	9
Rhodotorula mucilaginosa F76	56.7	ND
Rhodotorula mucilaginosa CA313	27.1	9.19
Rhodotorula mucilaginosa CA46	24.9	12
Rhodotorula mucilaginosa CR53	18.9	9.8
Rhodotorula mucilaginosa F811	40.7	8.65
Rhodotorula mucilaginosa CA317	33.8	14
Rhodotorula mucilaginosa CA319	64.6	20
Rhodotorula mucilaginosa CA712	34	8.35
Rhodotorula sp. CA521	137	11.1
Papiliotrema laurentii CA99	50.3	8.95
Papiliotrema laurentii CA52	30.3	ND

ND: Not detected

We observed that 15 strains (4%) belonging to 11 species exhibited *in vitro* phosphate solubilizing ability for the two sources of phosphate (aluminum and calcium) (Table 3). Strains of *Meyerozyma*

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guilliermondii, *Hanseniaspora uvarum*, *Candida glabrata*, and *C. insectorum* exhibited the strongest solubilizing activity for aluminum- and tricalcium-phosphates, expressed using the solubilization index (SI) ranged from 1.31 to 3.37.

Table 3 - Phosphate solubilization by soil yeasts in aluminum- and tricalcium-phosphates as inorganic phosphate substrate

Species/ Strains	**Aluminum-phosphates solubilization (SI)**	**Tricalcium-phosphates solubilization (SI)**
Candida parapsilosis F46	1.67	ND
Candida insectorum CR96	ND	2.29
Wickerhamomyces anomalus F112	1.55	1.85
Meyerozyma guilliermondii F27	1.9	ND
Meyerozyma guilliermondii CR72	2.67	2.56
Meyerozyma guilliermondii CA87	3.37	2.72
Meyerozyma guilliermondii CR64	2	ND
Meyerozyma sp. CR74	1.6	ND
Torulaspora sp. CA1010	ND	1.42
Hanseniaspora uvarum CA310	ND	2.19
Hanseniaspora uvarum CA311	ND	2.12
Candida glabrata CA323	ND	2.4
Saitozyma podzolica A122	ND	1.31
Papiliotrema laurentii CA522	ND	1.37

ND: Not detected

Three strains, belonging to species *Wickerhamomyces anomalus* and *M. guilliermondii*, exhibited solubilizing activity for the two sources of phosphate (aluminum and calcium), and *M. guilliermondii* CA87 had the strongest solubilizing activity, with an SI unit of 3.37 and 2.72, for aluminum- and tricalcium-phosphates, respectively (Figure 1). The W. anomalus (F112) and *M. guilliermondii* (CR72 and CA87) strains showed solubilizing activity for the two sources of phosphate (aluminum and calcium). However, most of the strains that showed the ability to solubilize phosphate were driven by a specific source of phosphate, with 67% of the strains being able to solubilize phosphate from tricalcium-phosphate as a substrate.

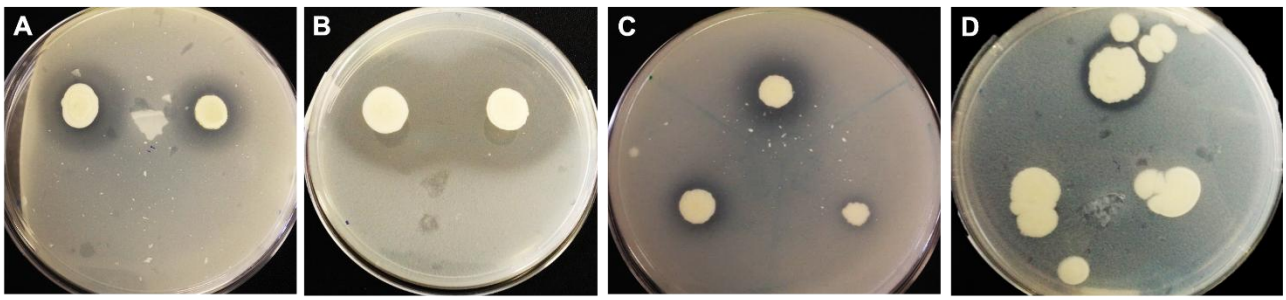

Figure 1 - Solubilization halos produced by yeasts on Pikovskaya's agar after spot inoculation and incubated at 28 °C for five days. Phosphate-solubilizing medium was prepared separately using (A and C) tricalcium-phosphates and (B and D) aluminum-phosphates as a source of insoluble inorganic phosphate. Strains of *Meyerozyma guilliermondii* (A-B) and *Wickerhamomyces anomalus* (C-D)

Production of siderophores was detected in 16 strains (4.2%), representing five species (Table 4). Our investigation of siderophore production revealed that strains of the *Rhodotorula* genus showed the best siderophore-producing capacity.

Table 4 - Siderophore production and antagonism against the soil-borne plant pathogens

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Species/ Strains	Siderophore production	Antagonism in solid medium (% inhibition)	
		F. oxysporum	*M. phaseolina*
Candida parapsilosis CA414	ND	25	ND
Candida parapsilosis CA824	ND	44	35
Candida parapsilosis CR75	ND	30	ND
Candida parapsilosis CR817	ND	37.5	ND
Candida parapsilosis CR818	ND	46	ND
Candida insectorum CR96	ND	32.5	ND
Candida maltosa CA215	ND	44	32
Candida maltosa CA216	ND	33	ND
Candida maltosa CA910	ND	50	ND
Candida maltosa CA48	ND	22	ND
Candida maltosa CA64	ND	44	ND
Wickerhamomyces anomalus F112	ND	56	41
Meyerozyma guilliermondii A416	(+)	ND	ND
Meyerozyma sp. CR74	ND	34	ND
Candida glabrata CA323	ND	37.5	ND
Rhodotorula toruloides CR13	(+)	ND	ND
Rhodotorula toruloides CA312	(+)	ND	ND
Rhodotorula mucilaginosa CA322	(+)	ND	ND
Rhodotorula mucilaginosa CA610	(+)	ND	ND
Rhodotorula mucilaginosa CA314	(+)	ND	ND
Rhodotorula mucilaginosa CE33	(+)	ND	ND
Rhodotorula mucilaginosa CA313	(+)	ND	ND
Rhodotorula mucilaginosa CA46	(+)	ND	ND
Rhodotorula mucilaginosa CR53	(+)	ND	ND
Rhodotorula mucilaginosa F811	(+)	ND	ND
Rhodotorula mucilaginosa CA317	(+)	30	ND
Rhodotorula mucilaginosa CA319	(+)	40	40
Rhodotorula mucilaginosa CA712	(+)	37.5	ND
Rhodotorula sp. CA521	(+)	ND	ND
Papiliotrema laurentii CA99	(+)	ND	ND
Papiliotrema laurentii CA522	ND	40	ND

ND: Not detected

The yeast isolates were investigated for their antagonistic activity against the soil-borne fungal pathogens, and 18 strains (4.7%) exhibited antagonistic effects against the two fungi tested on PDA agar plates (Table 4, Figures 2 and 3). The antagonistic activity was more prominent against *Fusarium oxysporum*, with 18 strains exhibiting antagonistic effects (Table 4 and Figure 2), belonging to species *C. parapsilosis, C. insectorum, C. maltosa, C. glabrata, W. anomalus, Meyerozyma* sp., *R. toruloides, R. mucilaginosa,* and *Papiliotrema laurentii.*

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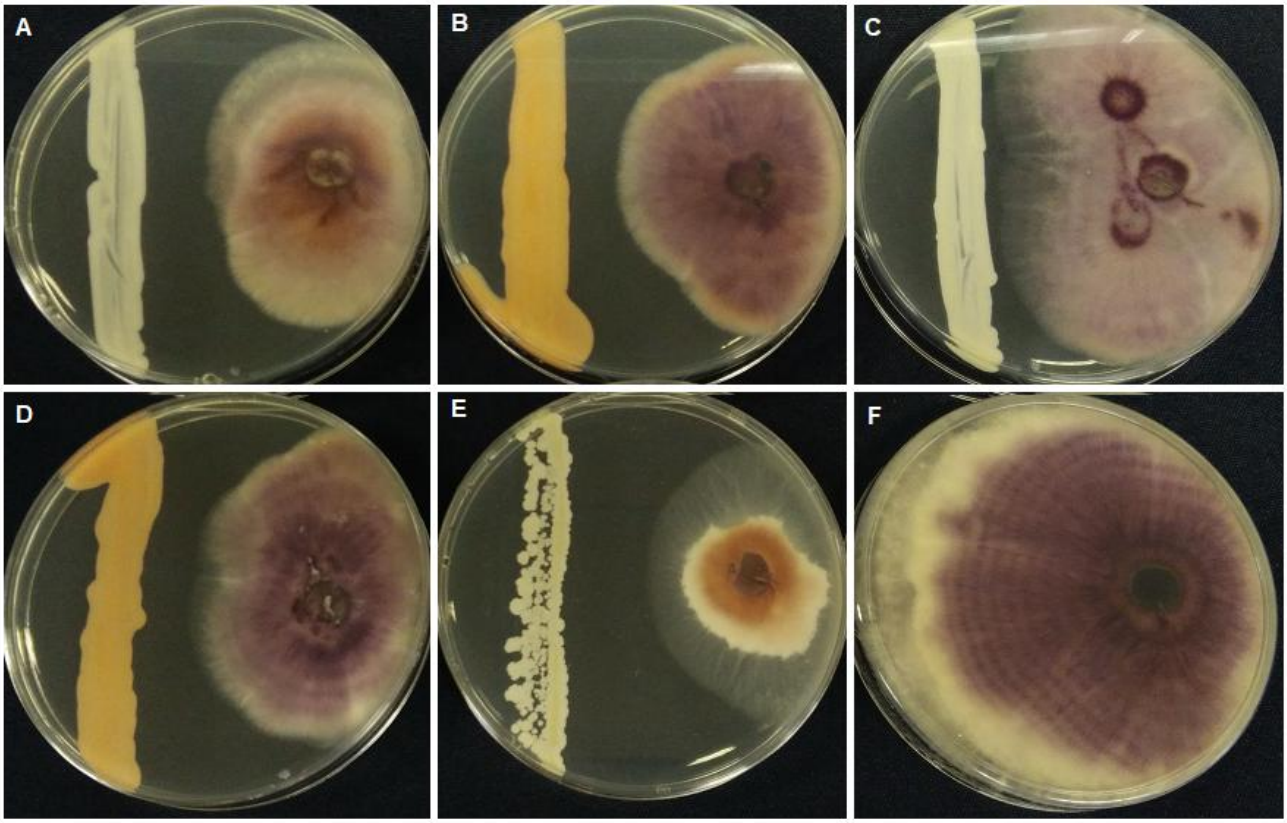
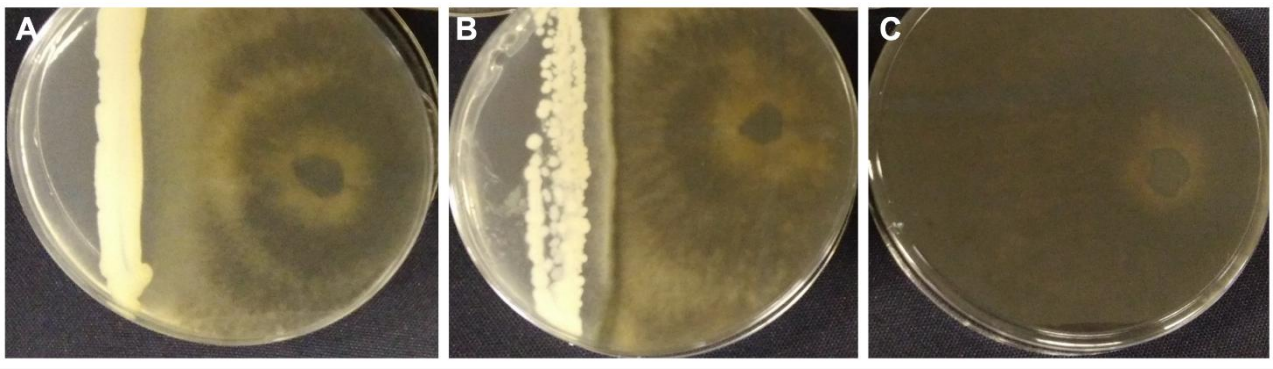


Legend: A: *Candida glabrata*, B and D: *Rhodotorula mucilaginosa*, C: *C. maltosa*, E: *Wickerhamomyces anomalus*, F: *F. oxysporum* without paired yeast as the control group.

Figure 2 - *In vitro* evaluation of antagonism by yeasts against the phytopathogenic fungus *Fusarium oxysporum*, after seven days of fungi growth

The antagonistic activity was not so evident against *Macrophomina phaseolina*, with small zones of inhibition of fungal growth (Table 4 and Figure 3). Only four strains exhibited antagonistic effects belonging to species *C. parapsilosis, C. maltosa*, *W. anomalus*, and *R. mucilaginosa.*



Legend: A: *Candida parapsilosis*, B: *Wickerhamomyces anomalus*, C: *M. phaseolina* without paired yeast as the control group.

Figure 3 - Evaluation of *in vitro* antagonism in a solid medium by yeasts against the phytopathogenic fungus *Macrophomina phaseolina*

The results for the linear regression fitting are shown in Figure 4. The effect of precursor on IAA production was statistically significant ($p < 0.05$), indicating an increase in production level when L-tryptophan is present. On the other hand, the sub-

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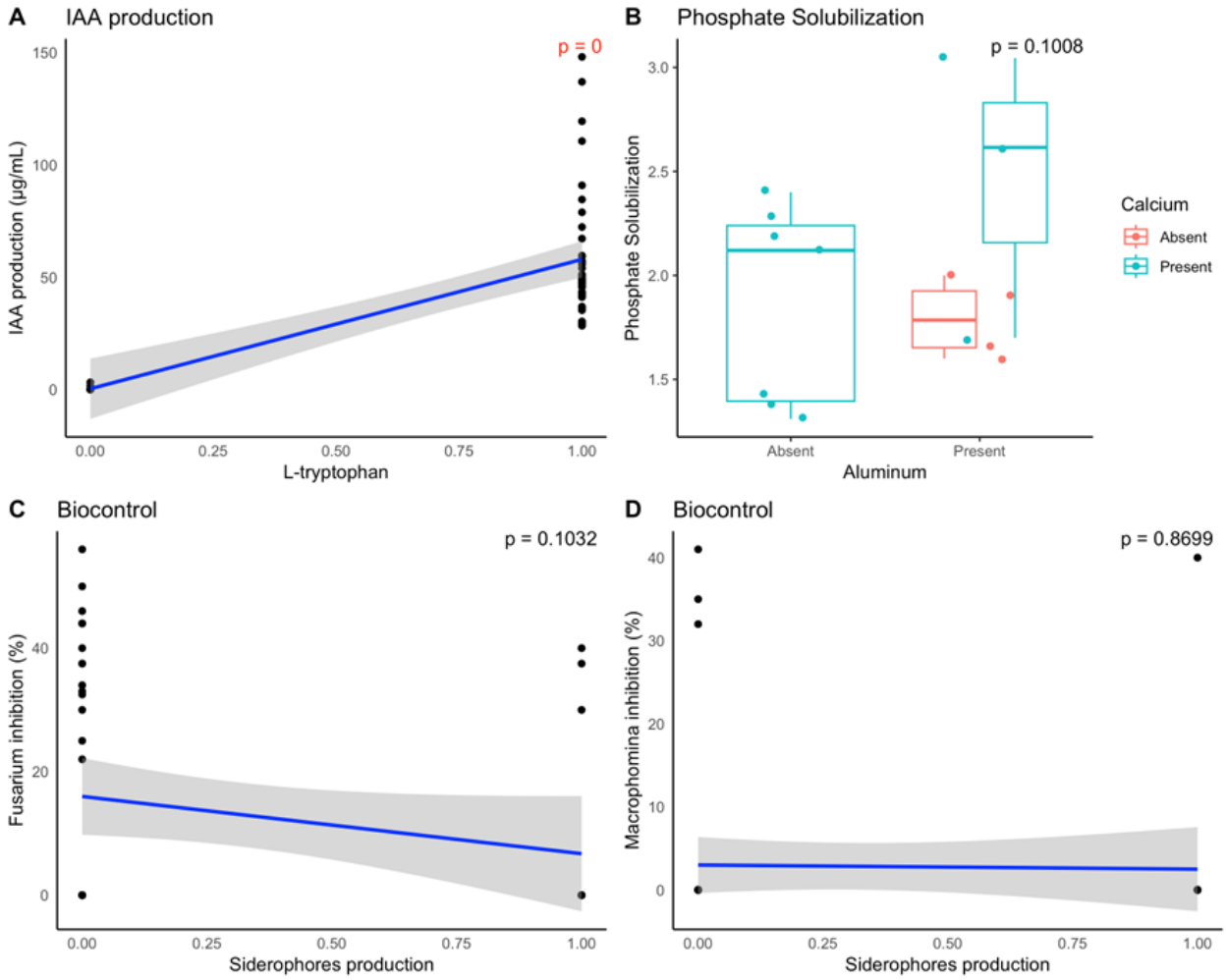
strate type was not statistically significant for phosphate solubilization ($p > 0.05$), even with higher SI values for solubilization of phosphate in the presence of tricalcium-phosphates. For antagonistic activity, the production of siderophores was not statistically significant ($p > 0.05$) in inhibiting the growth of *Fusarium oxysporum* and *Macrophomina phaseolina*.



Legend: A: IAA production as a function of presence (1) and absence (0) of L-tryptophan. B: Phosphate solubilization as a function of aluminum-phosphates as substrate, with boxplots colored according to calcium-phosphates as substrate. C: *Fusarium* inhibition (%) as a function of siderophore production. D: *Macrophomina* inhibition percentage as a function of siderophore production. In panels A, C, and D, the regression line is shown in blue, with the shaded area representing the 95% confidence interval. In all panels, dots represent individual data points. Statistical significance of the regression models is indicated by the p-values in black when not significant, and red when significant.

Figure 4 - Linear regression analysis of plant growth-promoting traits and their relationships with different factors

DISCUSSION

Soil microorganisms, whether associative or free-living, may contribute to plant nutrition and growth through a variety of mechanisms, including direct and indirect effects such as nutrient availability and root pathogen antagonists (Richardson et al., 2009; Natarajan et al., 2022). Yeasts are known to be abundant and diverse soil inhabitants in natural ecosystems (Yurkov, 2018; Moreira and Vale, 2018; Moreira and Vale, 2020; Moreira et al., 2020) and may also play a role as plant growth promoters and soil conditioners (Botha, 2011; Bispo et al., 2023). Plant hormones such as auxins play a critical role in plant development, and indole-3-acetic acid (IAA) is generally considered the most critical auxin.

The *Rhodotorula toruloides* (CR13) and *R. mucilaginosa* (CA610) strains produced high concentrations of IAA, ranging from 116.8 to 127.5 µg

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mL^{-1}. Species of the genus *Rhodotorula* have been reported to possess this PGP trait (Ignatova et al., 2015; Streletskii et al., 2016; Firrincieli et al., 2015; Silambarasan et al., 2019). To our knowledge, this is the first report on IAA production by *R. toruloides*.

Two major pathways for IAA biosynthesis have been proposed: using tryptophan as a precursor of the IAA (Trp-dependent) and the IAA synthesis without tryptophan (Trp-independent) (Bernales et al., 2019; Saharan and Nehra, 2011). A Trp-independent pathway was confirmed in a previous study for some yeast species with higher amounts of IAA produced (Sun et al., 2014), suggesting that yeast may have multiple pathways for IAA synthesis, one of which is not dependent on Trp (Rao et al., 2010).

Our results support the presence of a Trp-independent IAA biosynthetic pathway in yeasts. Moreover, adding Tryptophan, as a precursor for auxins, enhanced the production of IAA. Additionally, strains of one species exhibit different IAA-producing capabilities, revealing that the production was strain-dependent. These results are consistent with previous studies (Fu et al., 2016; Amprayn et al., 2012; Nassar et al., 2005; Nutaratat et al., 2014).

Higher amounts of IAA were reported for rhizosphere and phylloplane yeasts, where the amount of Trp and other IAA precursors are present in larger quantities, unlike bulk soil, where the yeasts in this study were isolated. Compared with studies that used soil yeast (Amprayn et al., 2012; Ignatova et al., 2015), the *R. toruloides* (CR13) and *R. mucilaginosa* (CA610) strains are highly efficient in IAA production.

Yeasts also play an ecological role in solubilizing insoluble phosphates, making them bioavailable (Botha, 2011; Bright et al., 2022). The soil yeast *M. guilliermondii* has been shown to possess antifungal activities (Coda et al., 2013) and phosphate-solubilization ability (Nakayan et al., 2013). In another study, *M. guilliermondii* strains showed the highest phosphate-solubilizing capability for tricalcium-phosphate, but none exhibited aluminum-phosphate-solubilizing capabilities (Nakayan et al., 2013). However, our strain exhibited solubilizing activity for the two phosphate sources, with a high SI unit, becoming promising for future applications in agriculture.

Several other yeast species have also been characterized by their ability to solubilize phosphate (Hesham and Mohamed, 2011; Al-Falih, 2005; Sarabia et al., 2017; Mukherjee and Sen, 2014; Bright et al., 2022). We detected this activity in 11 species of soil yeast, corroborating that those yeasts could play a role in transforming organic materials and mineralizing phosphate in the soil.

Another activity detected in our isolates was the production of siderophores. Siderophores are organic molecules produced by microorganisms under iron-limiting conditions to increase the absorption of this nutrient. It is believed that siderophores can increase plant growth by increasing iron uptake (Saha et al., 2016; Targino et al., 2022) and still inhibit the growth of pathogens by sequestering iron from the environment.

Our investigation of siderophore production revealed that strains of the *Rhodotorula* genus showed the best siderophore-producing capacity. The relationship between a type of siderophores called rhodotorulic acid, produced by species of the genus *Rhodotorula* and the antagonistic activity against fruit pathogens has already been demonstrated (Calvente et al., 2001).

Interestingly, we did not detect a statistically significant relationship between the production of siderophores and the antagonistic activity against *F. oxysporum* and *M. phaseolina*, since only three isolates that produced siderophores showed antagonistic activity (Table 4 and Figure 4). The same result was reported by Fu et al. (2016), where yeasts that showed antifungal activity did not necessarily produce siderophores. This finding may relate to the type of siderophore that specific strains evaluated in this study produce. Unfortunately, the methodology used in this work does not allow the identification of the siderophore type, being necessary for future investigations.

The best results of inhibition of fungal growth were observed for the *W. anomalus* (F112) strain, inhibiting 56% of the mycelial growth of *F. oxysporum* and 41% of *M. phaseolina*. The *W. anomalus* species is already known for its potential as a biocontrol agent, mainly for producing killer toxins (Grzegorczyk et al., 2017; Fernández de Ullivarri et al., 2018).

The other three species, *C. parapsilosis* (CA824), *C. maltosa* (CA215) and *R. mucilaginosa* (CA319), exhibited antagonistic activity against the two soil-borne fungal pathogens. The *C. maltosa* inhibited fungal growth by producing antifungal metabolites (El-Mehalawy et al., 2004), but this study presented a small zone of inhibition for the tested fungi. However, *C. glabrata* and *R. mucilaginosa* strains showed a significant reduction in the growth of *F. oxysporum* (Figure 2). The ability to inhibit the growth of pathogens has already been demonstrated for these species (El-Mehalawy, 2004; Ignatova et al., 2015). The mechanism used by the yeasts to exert antagonistic activity was not evaluated. However, considering the methodology used here, which involved the direct co-inoculation of the pathogen with the yeast, it is probable that the inhibition occurred through the action of anti-

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fungal compounds diffused into the culture medium.

Three strains were highlighted because they present the best results for more than one PGP trait. The *C. insectorum* (CR96) was one of the best IAA producers, both with and without tryptophan. It also had a high tricalcium-phosphate solubilization and antagonistic activity against *F. oxysporum*. The *W. anomalus* (F112) strain showed an ability to solubilize the two sources of phosphate (aluminum and calcium) and exhibited antagonistic activity against both soil pathogens (*F. oxysporum* and *M. phaseolina*). Meanwhile, *R. mucilaginosa* (CA319) produced high concentrations of AIA, both with and without tryptophan, and showed one of the best siderophore-producing capacities. Additionally, it exhibited antagonistic activity against both pathogens used in this study.

Most isolates (28 out of 52) that showed positive PGP traits came from an iron-mining site in environmental recovery (Table 1). It is well known that soil microbial communities play an essential role in nutrient cycling, plant establishment, and soil formation, becoming essential for the successful recovery of impacted areas (Thavamani et al., 2017). The activity of microorganisms such as rhizobacteria and mycorrhizal fungi is already well known. This study highlights the ecological role of yeasts in the recovery of soil quality and re-establishment of the plant community.

CONCLUSIONS

Wickerhamomyces anomalus and *Meyerozyma guilliermondii* strains exhibited phosphate solubilizing activity. Eight species exhibited antagonistic effects against *Fusarium oxysporum*. The *Candida insectorum*, *W. anomalus* and *Rh. mucilaginosa* strains proved to be promising for future investigations.

Together, the three species have shown promise for future research on their potential to increase plant growth in vitro and in vivo. Our results support the prospecting of yeast isolates from natural ecosystems for future inclusion into commercial bio inputs for sustainable agriculture or their application to recover degraded areas, increasing plant growth.

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