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REVIEW

A potentially important resource: endophytic yeasts

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Abstract

Recent advancements in the research on endophytes isolated from plants and crops have greatly broadened its application in various fields. Endophytic bacteria and endophytic fungi are known to promote the growth of various plants. Besides, the secondary metabolites such as alcohol and xylitol secreted by the endophytic yeast also help their hosts to resist microbial invasion. This makes them a potential substitute for chemical-based control methods. Moreover, the plant hosts can also provide nutrients for the growth of endophytic yeasts. To achieve the symbiotic relationship, yeasts must colonize most parts of the plant tissues, including intercellular spaces, cytoplasm, stomata of seeds, roots, stems, leaves, and fruits as well. Conventionally, isolation of endophytic yeasts from different plant tissues and understanding their interior plants colonization mechanism have remainedkey strategies to exploit their key potentials. In this review, we will elaborate on the diversity, characteristics of colonization, and the factors that influence the distribution of endophytic yeasts. This review also lays a theoretical foundation for the application of endophytic yeasts in various industrial and agricultural practices.

Keywords Endophytic yeasts · Diversity · Applications · Yeast community

Introduction

Endophytes are endosymbionts that reside in plant tissues without causing any apparent harm to the host. Most common endophytes have been identified as filamentous fungi and unicellular bacteria (Schulz and Boyle 2005). Yeast, on the other hand, inhibits a unique niche along with filamentous fungi and endophytic bacteria in forest trees and agricultural plants (Doty 2013). However, the same plant species harbor far less the number and diversity of endophytic yeasts compared to the endophytic bacteria (Cui et al. 2012; Knoth et al. 2014). In general, endophytes maintain a symbiotic relationship to enhance the growth of the host plant, assist nutrient acquisition, and also improve their ability to tolerate abiotic stresses (Saikkonen et al. 2004). The diversity and quantity of endophytic yeasts are affected by many factors, such as cultivation methods for crops and atmospheric conditions (Camatti-Sartori et al. 2005). Most of the endophytic yeasts are classified in genera *Rhodotorula*, *Pichia*, *Candida,* and *Debaryomyces.* Phytologists have been immensely interested in the ecological effects and application of endophytes. Interestingly, endophytes directly or indirectly promote the growth and also help host plants to resist pests and diseases by secreting active metabolites. In particular, endophytic yeasts serve additional functions that include secretion of inhibitors, namely xylose and ethanol (Doty 2013; Vajzovic et al. 2012). Being encouraged by the importance of endophytic yeasts applications in industrial and agricultural fields, we review the current status of research progress and future application potential of endophytic yeasts in the present article.

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Diversity of endophytic yeasts

Endophytic yeasts have been identified in many perineal trees and crops. Moreover, different tissue parts of the same plant harbor different species of endophytic yeasts. In the following sections, we will elaborate on the distribution and influencing factors of endophytic yeasts.

Endophytic yeasts diversity in different plants

In recent years, there have been growing interests in research about the diversity of endophytic yeasts in different plants and crops. *Cryptococcus, Debaryomyces, Sporobolomyces, and Rhodotorula* are relatively common and well-studied endophytic yeast genera (Doty 2013). With the elevated interest of the scientific community in the endophytic yeasts and their diversity, many new endophytic yeast genera have been recently discovered. Lorenzini et al. (2018) discovered *Candida railenensis*, *Candida cylindracea*, *Hanseniaspora pseudoguilliermondii* and *Metschnikowia sinensis,* the first time in apple juice. Remarkably, some researchers have studied the diversity of endophytic yeasts in Thailand's economically important crops: rice, corn, and sugar cane (Khunnamwong et al. 2018). They reported that the number of basidiomycetes is more than that of the ascomycetes among the endophytic yeasts isolated from the leaves of these crops. The report was also confirmed by other research groups (Into et al. 2020; Peng et al. 2018; Tantirungkij et al. 2015). In contrast, the ascomycetes isolated from *Malus domestica* and *Pyrus communis* were more diverse than basidiomycetes inside the fruits. Moreover, the number of ascomycetes yeasts increased as the fruits matured (Glushakova and Kachalkin 2017b). In addition, Peng et al. (2018) isolated 62 yeast strains from the pulp, 72 strains from the peel, and 152 strains from leaves of Nanfeng mandarin (*Citrus reticulata* cv.). Evidently, the number of yeasts isolated in citrus leaves was much higher than that of citrus peel and citrus pulp. The same group also reported that 12 species of yeasts including *Candida metapsilosis*, *Symmetrospora* spp., *Candida cf. azyma,* and *P. kluyveri* were exclusively found in citrus leaves but not in other parts of the plant. Interestingly, *Aureobasidium pullulans* and *Hanseniaspora opuntiae* were the dominant yeast species in the citrus leaves, while *Hanseniaspora opuntiae* and *Meyerozyma guilliermondii* were dominantly present in the citrus peels and pulps respectively. The above reports suggest that plant species harbor a set of dominant yeast species, and the quantity, as well as the diversity of endophytic yeast, differing from parts of the same plant.

Climatic factors such as temperature, precipitation, and humidity affect the diversity and performance of symbiotic fungus in an area (Giauque et. al. 2013). In parallel with this study, Gai et al. reported that the numbers and types of endophytic yeasts found in the NF (Nanfeng) area were more than that of NC (Nancheng) area. Reportedly, the diversity of endophytic yeast was not significantly different in sweet orange trees studied in four sampling sites. *Rhodotorula mucilaginosa*, *Pichia guilliermondii,* and *Cryptococcus flavescens* were found most commonly and remained distributed mainly in the stomata and xylem of the plants (Gai et al. 2009). Based on the latest research, yeasts can also invade from fruit epidermis and colonize internal tissues of fruits (Solis et al. 2015). Moreover, other groups of researchers also proposed that the yeasts in citrus plants can migrate from roots to the leaves using the vasculature system of the plants (Gai et al. 2009). Table 1 lists important endophytic yeasts isolated from some forest trees and crops.

Factors affecting plant endophytic yeasts community

Natural environmental factors including anthropogenic impacts and plant internal environment are the key factors that affect the quantity and species composition of endophytic yeasts. As outlined in the previous section, environmental factors such as seasonal variations of pH, nutrients, temperature, humidity, solar radiation, plant exudates, and rainfall significantly affect the yeast abundance and species composition in the plants of that area (Solis et al. 2015). In support of this finding, it has been observed that the number of endophytic yeasts isolated from wine grapes in autumn and spring were 41.67% and 25% respectively (Cui et al. 2012). It further proves that seasonal changes have a great impact on the quantity and community of endophytic yeasts. In a separate study conducted in Moscow about the endophytic relationship of yeast with *Malus domestica* and *Pyrus communis*, the number of ascomycetous yeasts continued to increase as the fruit matured (Glushakova and Kachalkin 2017b). Strikingly, the factors affecting yeast abundance were mainly depended on the type of study sample and sampling date, rather than the tree species and sampling location. More recently, it has been found that agrochemicals had negative effects on yeast abundance and their community composition. The treatment of winter wheat with strong fungicides (fenpropimorph, a commercial mixture of pyraclostrobin, epoxiconazole and thiophanate-methyl), led to a significant decrease in the number of yeast colonies down to 85% (Wachowska et al. 2018). The endophytic yeasts isolated from winter wheat (*Aureobasidium pullulans* and *Rhodotorula glutinis*) were severely affected by fungicides. The fungicidal effect was relatively less severe for *Metschnikowia pulcherrima*, *Debaryomyces hansenii*, *Candida albicans,* and *Candida sake*. Internal factors such

Table 1 The endophytic yeasts extracted from some forest trees and crops

Host plant	Vernacular name	Tissue	Yeast genus	References
Populus trichocarpa × P. deltoids	Poplar	Stems	*Rhizobium tropici*	(Doty et al. 2005)
Morinda citrifoli L	Wild Noni	Seeds	*Eremothecium, Kodamaea*	(Bai et al. 2014)
Vitis vinifera L	Wine grape	Roots, Stems, Leaves, Pericarp	*Pytiros sp.*	(Cui et al. 2012)
Vitis vinifera L	Wine grape	Roots, Pericarp	*Kleckera sp.*	(Cui et al. 2012)
Triticum aestivum L	Winter wheat	Grains	*Aureobasidium pullulans, Candida albicans, Candida sake, Debaryomyces hansenii, Metschnikowia pulcherrima, Rhodotorula glutinis*	(Wachowska et al. 2018)
Malus domestica	Apple	Fruits	*Candida parapsilosis, F. wieringae, F.magnum, Hanseniaspora uvarum, Pichia kluyveri, Rh. glutinis, and R. colostri*	(Glushakova and Kachalkin 2017b)
Pyrus communis	Pear	Fruits	*Candida parapsilosis, F. wieringae, F.magnum, Hanseniaspora uvarum, Kwoniella sp., Pichia kluyveri, Rh. glutinis, and R. colostri*	(Glushakova and Kachalkin 2017b)
Citrus sinensis	Sweet orange	leaves	*Aureobasidium pullulans, Candida parapsilosis, Cryptococcus flavescens, C. laurentii, Pichia guilliermondii, Rhodotorula mucilaginosa, R. dairenensis*	(Gai et al. 2009)
Oryza Sativa	Rice	Leaves	*Candida sp., Cryptococcus sp., Debaryomyces sp., Debaryomyces sp., Meyerozyma sp., Pseudozyma sp., Trichosporon sp.*	(Tantirungkij et al. 2015)
Populus trichocarpa	Wild Cottonwood	Stems	*Rhodotorula sp.*	(Xin et al. 2009)
P. trichocarpa × Populus deltoids	Hybrid Poplar	Stems	*Rhodotorula mucilaginosa*	(Xin et al. 2009)
Salix fragilis L	Willow	Galls	*Candida fructus, Candida railenensis, Filobasidium magnum, Filobasidium wieringae, Hanseniaspora uvarum, Metschnikowia henanensis, Metschnikowia pulcherrima, Papiliotrema flavescens, Pichia fermentans, Rhodotorula mucilaginosa*	(Glushakova and Kachalkin 2017a)
Salix caprea	Willow	Galls	*Candida fructus, Candida railenensis, Filobasidium magnum, Filobasidium wieringae, Hanseniaspora uvarum, Metschnikowia henanensis, Metschnikowia pulcherrima, Papiliotrema flavescens, Pichia fermentans, Rhodotorula mucilaginosa, Vishniacozyma carnescens*	(Glushakova and Kachalkin 2017a)
Quercus robur	Oak	Galls	*Candida railenensis, Dioszegia changbaiensis, Dothiora cannabinae, Filobasidium magnum, Filobasidium wieringae, Rhodotorula mucilaginosa, Vishniacozyma victoria,*	(Glushakova and Kachalkin 2017a)

Table 1 (continued)

Host plant	Vernacular name	Tissue	Yeast genus	References
Tilia cordata Mill	Tilia cordata	Galls	*Candida railenensis, Filobasidium magnum, Filobasidium wieringae, Hanseniaspora uvarum, Metschnikowia pulcherrima, Papiliotrema flavescens, Rhodotorula mucilaginosa, Vishniacozyma carnescens, Vishniacozyma victoriae*	(Glushakova and Kachalkin 2017a)
Ulmus laevis Pall	Ulmus laevis	Galls	*Filobasidium magnum, Filobasidium wieringae, Hanseniaspora uvarum, Metschnikowia pulcherrima, Papiliotrema flavescens, Rhodotorula mucilaginosa, Vishniacozyma carnescens, Vishniacozyma victoriae*	(Glushakova and Kachalkin 2017a)
Saccharum officinarum	Sugar Cane	Leaves	*Wickerhamiella sp.*	(Khunnamwong et al. 2014)
Populus euphratica	Populus euphratica	Stems	*Rhodotorula sp.*	(Zumrat et al. 2012)
Quercus robur	English Oak	Fruits	*Candida railenensis*	(Isaeva et al. 2009)
Oryza sativa	Rice	Leaves	*Papiliotrema, Rhodotorula, Saitozyma, Sporobolomyces, Sakaguchia oryzae, Toruloides,*	(Khunnamwong et al. 2018)
Saccharum officinarum	Sugarcane	Leaves	*Cystobasidium, Dioszegia takashimae, Flava, Hannaella, Kwoniella, Mangaliensis, Papiliotrema, Rhodotorula, Saitozyma aff., Sporobolomyces, Trichosporon*	(Khunnamwong et al. 2018)
Zea mays	Corn	Leaves	*Cryptococcus, Hannaella Kwoniella, Naganishia, Papiliotrema, Rhodotorula, Rhodosporidiobolus, Saitozyma, Sporobolomyces*	(Khunnamwong et al. 2018)
Malus domestica	Apple	Leaves	*Cryptococcus laurentii, Candida spp, Sporobolomyces roseus, Sporodiobolus pararoseus, Rhodotorula mucilaginosa, Debaryomyces hansenii,*	(Camatti-Sartori et al. 2005)
Malus domestica	Apple	Flowers	*Cryptococcus laurentii, Debaryomyces hansenii,*	(Camatti-Sartori et al. 2005)
Malus domestica	Apple	Fruits	*Candida spp, Cryptococcus sp.*, *Pichia sp.*	(Camatti-Sartori et al. 2005)
Solanum lycopersicum	Tomato	Fruits	*Candida guilliermondii*	(Infante et al. 2012)
Ficus	Ficus	Leaves	*Cryptococcus sp., Rhodotorula sp.*	(Solis et al. 2015)
Ficus carica	Ficus	Fruits	*Saccharomyces cerevisia*	(Yachen et al. 2014)
Citrus reticulate Blanco	Tangerine	Peels	*Hanseniaspora sp., Meyerozyma guilliermondii,Pichia kluyveri*	(Ling et al. 2019)

as genotype of the plant, its growth phase, and the tissue type severely influenced the growth of endophytic yeasts (Xu et al. 2019). A seminal study with the acorns revealed that the number of *Candida railenensis* in the cotyledons reached up to 10^7 CUF/g before its germination. It was the largest number reported in the possible life span of an acorn. The simple sugars released during the breakdown of starch in the germinating acorn apparently provide nutrients to stimulate the rapid growth of the yeasts (Isaeva et al. 2009). Human activities also affect the symbiotic relationship of endophytic yeasts population with plants. An opportunistic species *Candida parapsilosis*, known to be harmful to humans, existed within every stage of fruit development under anthropogenic impact in Moscow (Russia) city (Glushakova and Kachalkin 2017b). Besides, yeasts are found more commonly in sweet fruits such as wine grape Cabernet Sauvignon (Liu et al. 2016), *Malus domestica* and *Pyrus communis* fruits (Glushakova and Kachalkin 2017b) and *Citrus sinensis* (Gai et al. 2009); and storage tissues of *Ficus carica* L. (Yachen et al. 2014), *Saccharum officinarum* leaves (Khunnamwong et al. 2014), *Solanum lycopersicum L.* (Infante et al. 2012) and winter *Triticum aestivum* L. (Wachowska et al. 2018).

Application of endophytic yeasts

Owing to its antibacterial, antifungal, antiviral, anti-inflammatory, and anti-tumor effects, endophytic yeasts have great application prospects in agriculture, medicine, and industries (Jalgaonwala and Mahajan 2014). Although research on endophytic yeasts as biological agents has gained momentum only in recent years, endophytic yeasts present great potential in inhibiting a wide spectrum of plant pathogens. For instance, two endophytic yeasts, *Wickerhamomyces anomalus* and *Kodamaea ohmeri*, can be isolated from rice, corn or sugarcane leaves significantly inhibit the growth of phytopathogenic fungi *Curvularia lunata* (causes dirty panicle disease in rice) and *Fusarium moniliforme* (causes bakanae disease in rice) respectively (Khunnamwong et al. 2019). In addition, among 73 endophytic yeasts isolated from orange, *Metschnikowia* sp. can significantly inhibit *Penicillium digitatum* on oranges (Liu et al. 2017). Some endophytic yeasts, known to secrete the biological agents, not only suppressed the damage to fruits and vegetables caused by certain pathogens, but also promoted the growth of crops to a certain extent (Jamal 2019). One remarkable example is the endophytic yeast strain, isolating, fholds strong inhibitory effect against mycelial growth of *Fusarium solani*, *F. oxysporum* and *Macrophomina phaseolina* which can prevent sunflower root rot, and also enhances plant growth at the same time (Fareed et al. 2019). In addition to the above-stated functions, endophytic yeasts can produce extracellular polysaccharides on the surface of fruits. Thus, they compete with pathogens for nutrients and spaces, the pathogens' growth can be subsequently limited (Luna 2017). These features also qualify endophytic yeasts to be a promising non-chemical agent to control postharvest diseases.

It is widely accepted that the endophytic yeast has an excellent ability to promote plant growth that can be a boon for agricultural practices. This ability of the endophytic yeasts stems from their ability to secrete bioactive compounds such as indole-3-acetic acid (IAA), gibberellins, siderophores, and phosphate solubilizing or (1-Aminocyclopropane-1-Carboxylate) ACC (Joubert and Doty 2018). A very recent report suggested that *Candida* sp. strain isolated from rice seedings produced phytase, which promoted the growth of shoot, increased the fresh weight of shoot and roots by increasing phosphorus utilization (Zhu et al. 2019). In another study, filtrate culture treatment of *Vigna radiata* seeds with *Geotrichum candidum* strain isolated from the roots of mangrove plants readily promoted the germination rate (George et al. 2019). *Rhodotorula mucilaginosa* isolated from poplars and willows were capable of producing IAA that can also promote the growth of some important crops such as corn, tomato, pepper, squash, sunflower and grasses under nitrogen stress (Xin et al. 2009). Similarly, yeasts isolated from the roots of maize could also produce IAA and IPYA (Nassar et al. 2005). Besides the ability of endophytic yeasts in inhibiting pathogens and promoting plant growth, another endophytic yeast *Saccharomyces cerevisiae* is crucial in agriculture, baking, and alcohol industries (Vajzovic et al. 2012; Yachen et al. 2014).

It is well-established that both endophytic bacteria (Lodewyckx et al. 2002) and endophytic yeasts (Doty 2013) can promote the growth or protect plants from a wide variety of phytopathogenic microbes. Endophytic bacteria can also degrade complex organic metabolites of plant origin to sustain the management of agricultural wastes and control pollution (Afzal et al. 2014). The degraded components of the agricultural wastes help plants grow well in soil contaminated with heavy metals and organic matters (Germaine et al. 2009; Weyens et al. 2010). Although more emphasis has been given to the study of endophytic bacteria compared to endophytic yeasts, the latter is easier to cultivate, applicable to agricultural practices and has long-term storage (Joubert and Doty 2018). Moreover, endophytic yeasts have advantages over endophytic bacteria in resisting plant pathogens and promoting crop growth (Joubert and Doty 2018). The existing and growing body of literature substantiates the belief that endophytic yeasts have great potential to revolutionize agricultural and industrial outputs.

Conclusion

Research on endophytic yeasts is shifting focus from the understanding of the fundamental process to their applications. Despite its known applicability to be used as biocontrol and bio-based growth agent, extensive research over endophytic yeasts a required to optimize them for other applications. Endophytic yeasts have apparently better potential in the agriculture sector compared to endophytic bacteria. To exploit the economic potential, the diversity of endophytic yeast needs to be established more comprehensively. In addition, it is also imperative to understand the mechanism of endophytic yeast invasion and colonization to plant tissues. A thorough understanding of how yeasts colonize plants will help the scientific community develop a wider range of applications of endophytic yeasts. The applications of endophytic yeasts seem promising especially in academic research and industrial production that warrants further scientific attention.

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Compliance with ethical standards

Conflict of interest We would like to submit the attached manuscript entitled "A potentially important resource: endophytic yeasts", which we would like to consider for publication in this journal. There is no conflict of interest at the time of submission of this manuscript, and all authors had approved the publication of the manuscript.

Ethical Approval I certify that this manuscript is original and has not been published and will not be submitted elsewhere for publication while being considered by this journal. And the study is not split up into several parts to increase the quantity of submissions and submitted to various journals or to one journal over time. No data have been fabricated or manipulated (including images) to support our conclusions. No data, text, or theories by others are presented as if they were our own. The submission has been received explicitly from all coauthors. And authors whose names appear on the submission have contributed sufficiently to the scientific work and therefore share collective responsibility and accountability for the results.

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