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Interactions of arboreal yeast endophytes: an unexplored discipline

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ABSTRACT

The value of healthy forest ecosystems is well known and trees in these systems form symbioses with a variety of living organisms. This review focuses on literature pertaining to the potential interactions of arboreal yeast endophytes with trees and their associated insects. Although very little is known about the symbioses of arboreal yeast endophytes, indications are that some of these unicellular fungi produce plant-growth promoting phytohormones, while others are antagonistic towards phytopathogens or are capable of producing pheromones that affect the behavior of insect herbivores. However, more research needs to be conducted to fully understand the role of arboreal yeast endophytes in ecosystem processes.

1. Introduction

It is known that healthy forest ecosystems are invaluable to the planet and all of its inhabitants, including humans (Krieger, 2001; Farber et al., 2002). Such forests are described as complex (Bengtsson et al., 2000; Franklin et al., 2002) and may include a wide diversity of trees that may form symbioses with many different living organisms (Carroll, 1988). These associations may be classified as either ecto- or endophytic, depending on whether the symbionts occur on the plant surface (phylloplane and rhizoplane) or whether they are associated with the internal tissues of plants (Rodriguez et al., 2004, 2009). Endophytic microorganisms are viewed as those that refrain from causing disease in their host (Wilson, 1995; Porras-Alfaro and Bayman, 2011), while often playing a pivotal role in plant survival. Studies aimed at revealing the role of these microorganisms have mainly focused on bacteria and filamentous fungi, thus often neglecting a ubiquitous group of unicellular fungi – yeasts (Schulz et al., 1993; Wearn et al., 2012).

Yeasts are a polyphyletic group of fungi that primarily proliferate via asexual budding or cell fission (Kurtzman and Fell, 1998). However, some yeasts are also able to reproduce sexually by forming meiospores that are carried either on a basidium or within an ascus. These meiosporangia, in contrast to those of macrofungi, are never enclosed within fruiting bodies. The unicellular nature of yeasts is viewed as an adaptation to growth in aqueous environments, where yeasts may either reproduce in suspension or as part of a biofilm attached to various submersed surfaces, including the walls of xylem vessels, as depicted in Fig. 1 (Decho, 1990; Lachance and Starmer, 1998; Brányik et al., 2004; Joubert et al., 2006; Gai et al., 2009).

It is well known that yeasts may associate with both the phylloplane and rhizoplane, where they interact with a variety of organisms and their physiochemical environment (Lindow and Brandl, 2003; Fonseca and Inácio, 2006; Botha, 2011; Starmer and Lachance, 2011). However, little is known about the interactions and roles of endophytic yeasts, especially those associated with trees. Since knowledge of plant-microbe symbioses is an important prerequisite for sustainable management of terrestrial ecosystems (Requena et al., 2001; Finlay, 2008), the overall objective of this study was to review the current state of knowledge on the ecology of arboreal yeast endophytes. The role of these yeasts within their natural habitat will be explored, including some of their potential interactions with trees and arboreal insects. Furthermore, future directions in the field of arboreal endophytic yeast ecology will be discussed.

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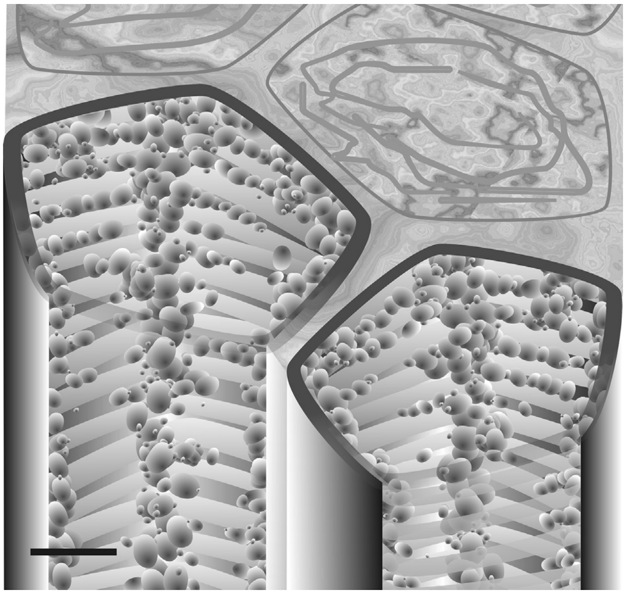

Fig. 1. An illustration of yeasts colonizing xylem vessels. Some yeasts occurring in these vessels (Gai et al., 2009; Khan et al., 2012) can utilize a wide diversity of simple nutrients (Kurtzman and Fell, 1998), such as amino acids, nitrate, carbohydrates and organic acids, thereby potentially altering the chemical composition of xylem sap. Additionally, the yeasts might produce phytohormones, such as indole-3-acetic acid and polyamines (Reyes-Becerril et al., 2011; Waqas et al., 2012), which are subsequently secreted into the sap. Bar = *ca.*10 μm.

2. Functional roles of arboreal yeast endophytes

Yeasts are known for their ability to produce a variety of metabolites, for example vitamins (Ruiz-Barba and Jiménez-Díaz, 1995; Leathers and Gupta, 1997), enzymes (Table 1) and hormones (Table 2). These metabolites may play a pivotal role in the interactions of yeast endophytes (Fig. 2) with other organisms. Recently, the knowledge of the diversity of endophytic yeasts was extensively reviewed (Doty, 2013), and the vast untapped biotechnological potential of these unicellular fungi was emphasized. In addition, the author highlighted endophytic yeast diversity of tree aerial organs, which was found to represent a wide diversity of ascomycetous and basidiomycetous yeasts belonging to the genera *Candida*, *Cryptococcus*, *Cystofilobasidium*, *Debaryomyces*, *Filobasidium*, *Guehomyces*, *Meyerozyma*, *Rhodotorula*, *Sporobolomyces* and *Sporidiobolus*. In more recent literature (Scholtysik et al., 2013; Solis et al., 2015) the endophytic status of some yeast species was corroborated, while it was revealed that other yeast species can also exist as tree endophytes (Table 1).

To date, arboreal yeast endophyte research has primarily focused on the assessment of diversity, with a dearth of information on the functional role of these unicellular fungi in their host's biology. In contrast, bacterial and filamentous fungal endophytes are more researched, with most knowledge on the functional roles of endophytes stemming from research conducted on filamentous fungal endophytes of grasses (Porras-Alfaro and Bayman, 2011) and bacterial root endophytes (Pirttilä, 2011). Nevertheless, the functional roles of bacterial and filamentous fungal endophytes in leaves and stems of trees have been elucidated in some studies (Brooks et al., 1994; Taghavi et al., 2009; Pirttilä, 2011). Considering the evidence for convergent evolution between bacteria and yeasts (Bork et al., 1993; Brazhnik and Tyson, 2006), as well as between filamentous fungi and yeasts (Berbee and Taylor, 1992), the potential roles of arboreal yeast endophytes (Table 2) can be inferred from literature on bacterial and filamentous fungal tree endophytes.

It is known that endophytes can positively benefit their hosts through production of plant-growth promoting hormones (Pirttilä, 2011) and through antagonism against phytopathogens (Mengoni et al., 2003). Bacterial endophytes can mediate tree growth through the production of phytohormones, such as giberellins, cytokinins and auxins (Pirttilä, 2011). For example, Taghavi et al. (2009) demonstrated that bacterial endophytes, originating from a poplar hybrid (*Populus trichocarpa* × *Populus deltoides*) could improve the growth of another poplar hybrid (*P. deltoides* × *Populus nigra*) and ascribed this to the production of the auxin, indole-acetic acid (IAA), by the bacteria. However, representatives of some yeast species are also able to produce IAA *in vitro* (Table 2), and it was demonstrated that plant growth was improved when some of these yeasts, i.e. *Cryptococcus laurentii* (Cloete et al., 2009, 2010) and *Rhodotorula glutinis* (El-Tarabily, 2004), were applied exogenously to the rhizosphere. Considering these aspects, it seems likely that some endophytic yeasts might be able to improve their host tree's growth. However, it must be noted that phytohormone production levels may differ among endophytic yeasts, since intraspecific variation exists among yeasts with regard to the production of IAA (Moller et al., unpublished). This phenomenon should, therefore, be taken into account when the effect of these yeasts on tree physiology is studied in future.

As mentioned, endophytes may also positively benefit their host through biological control of phytopathogens (Mengoni et al., 2003). In the study conducted by Brooks et al. (1994), it was found that *Ceratocystis fagacearum*-related crown loss and deaths of Spanish oak (*Quercus texana*) were reduced when endophytic bacteria, originating from aboveground organs of live oak (*Quercus fusiformis*), were inoculated into the stems of the trees. Furthermore, these authors demonstrated that the bacterial endophytes could inhibit growth of *C. fagacearum in vitro,* either through the production of antimicrobial compounds under nutrient-rich conditions or through the production of siderophore-like molecules under iron-limiting conditions. However, bacteria are not the only siderophore-producing microorganisms. It is well known that some yeast species belonging to the genera *Rhodotorula* and *Sporobolomyces* can produce the siderophore rhodotorulic acid (Table 2), which has been linked to their antagonistic relationship with various phytopathogens of crop plants and fruits (Calvente et al., 2001a, 2001b; Sansone et al., 2005). In addition, the antagonism of some yeasts towards bacteria, filamentous fungi and other yeast species has been ascribed to the production of killer toxins by these unicellular fungi (Polonelli and Morace, 1986). Interestingly, it was demonstrated that the killer toxin producing yeast *Debaryomyces hansenii* (Table 2) can inhibit the growth of *Ophiostoma piceae* and *Ophiostoma piliferum* on *Pinus sylvestris* timber (Payne and Bruce, 2001). Yet, the mode of antagonism was not elucidated by the authors. Considering these aspects, it seems plausible that arboreal yeast endophytes might benefit their host by inhibiting phytopathogen growth; various yeast species need to be tested *in planta* to determine whether this is a common occurrence. From the above it appears that arboreal yeast endophytes may play a vital role in the biology of their host trees, yet these interactions are not always confined to dual symbioses between yeasts and trees. In some instances multipartite interactions may occur, especially where insects are involved.

3. Potential multipartite interactions involving insects, trees and yeasts

It is known that yeasts are associated with insects and a vast body of information exists on this topic (Reviewed by Suh and Blackwell, 2005; Vega and Dowd, 2005; Ganter, 2006). It is thus

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