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Can fungal endophytes fast-track plant adaptations to climate change?

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ABSTRACT

Rapid climate change threatens plant communities. While many studies address the impact of climate change on plants and mechanisms of their resilience to climate stressors, the role of the plant microbiome in aiding plants' adaptation to climate change has been less investigated. We argue here that fungal endophytes, an important constituent of the plant microbiome, may be key to the ability of plants to adapt to climatic stressors. The rapid adaptive response of endophytes coupled with their ability to 'transfer' resistance to their hosts may fast-track plants' adaptation to climate change. We briefly review the importance of Class 3 fungal endophytes of terrestrial plants and discuss how they may accelerate adaptations to climate change in crops and natural plant communities and call for efforts directed at improving the understanding of fungal endophyte-facilitated plant health. Such information could aid in devising improved strategies for mitigating climate change effects on plant communities.

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1. Introduction

The Earth is experiencing a general warming attributed mostly to anthropogenic greenhouse gas emissions, especially to CO₂, which has currently risen to an atmospheric concentration of over 400 ppm – its highest in the past 800,000 y (Ritchie and Roser, 2020). According to the Intergovernmental Panel on Climate Change, if the current rate of global warming continues, it will significantly elevate risks to 'health, livelihoods, food security, water supply, human security, and economic growth' (IPCC, 2018). Global warming is predicted to affect many facets of biodiversity including species distribution, trophic interrelations and ecosystem functioning (Kelly and Goulden, 2008; Grimm et al., 2013; Suggitt et al., 2019) culminating in the extinction of numerous species that possibly equates to a sixth mass extinction event (Barnosky et al., 2011). Due to their core position in many food webs and the various ecosystem services they provide, land plants have been a major focus of climate change studies (Cleland et al., 2007). Climate change is predicted to perturb plant communities by impacting on their distribution (Thuiller et al., 2008), flower, nectar, and pollen production (Scaven and Rafferty, 2013), photosynthesis (Kirschbaum, 2004), and carbon partitioning to the roots

(Thompson et al., 2017).

2. Fungal endophytes - neglected facet of plant microbiome

The effect of climate change on microbial communities in general, and their feedback response to this phenomenon has not been addressed adequately (Cavicchioli et al., 2019; Rodriguez and Durán, 2020). Climate change is predicted to affect the diversity, distribution and function of microbes associated with plants, which in turn feeds back on plant productivity and climate change itself (e.g., increased greenhouse gas emissions) (Cavicchioli et al., 2019). It is increasingly being realised that plants interact selectively with their surrounding microbiome which aids in enhancing their stress tolerance (Rodriguez and Durán, 2020). This has galvanised the idea of microbiome engineering leading to the possible use of microbes to alleviate climate change-induced abiotic stress of plants (Hacquard et al., 2017; Bennett and Classen, 2020; Jansson and Hofmockel, 2020; Rodriguez and Durán, 2020). The results of a few studies on plant growth promoting bacteria and rhizosphere fungi show that plants exposed to stress recruit rhizosphere microbes to protect them from the stress (Yi et al., 2011). Such a stress-induced selection of microbes by plants could result in a firm association between the two partners such that these microbes would become an integral facet of the phenotype of the plant. While considering microbiome-mediated alleviation of stress, a

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significant omission is the probable role of fungal endophytes in aiding plant adaptation to climate change.

Endophytes are bacteria and fungi which are mutualists or commensals and reside inside the living tissues of plants. The fungal component of these non-disease causing microbes are termed fungal endophytes and they are constant associates of the plant microbiome. Four distinct types of fungal endophytes are recognized based primarily on the tissue they infect and their mode of transmission (Rodríguez et al., 2009). The Clavicipitaceous endophytes belong to Class 1 endophytes and grow systemically in the above ground tissues of some cool season grasses and are transmitted vertically through seeds. The Class 2 endophytes encompass fungi which grow internally in the roots, stems and leaves and are spread through seed coats and rhizomes. The Class 4 endophytes infect only the roots and above ground tissues of plants. Although endophytes of this Class occur in the leaves, stems, barks and flowers (Kumar and Hyde 2004; Murali et al., 2013), due to the availability of more information, we have chosen the leaf endophytes as a model to cogitate on the possible role of endophytes in moderating climate change effects on their plant hosts. The leaf endophytes are hyperdiverse, ubiquitous, and transmitted horizontally; they are commensals, mutualists, latent pathogens, or temporary residents in plants. These fungi exhibit a broad host and geographic range and infect plants of all lineages growing in different parts of the world. They have been isolated from most terrestrial and aquatic plants studied to date (Venkatachalam et al., 2015; Suryanarayanan et al., 2018a).

The earliest endophytic association of a fungus with its plant host was reported to have been about 400 million y ago (Krings et al., 2007); endophyte association could have assisted plants in the colonization of the terrestrial environment (Field et al., 2015). The leaf endophytes have been recorded from the Carboniferous period (359.2–299 million y ago) (Krings et al., 2009). According to Schulz and Boyle (2005), the endophyte-plant host interactions comprise a balance of antagonism where the endophyte shows controlled virulence, while the host restricts the incitement of disease by the endophyte. In view of such a long and constant association with plants, it is reasonable to expect that the mutualistic fungal endophytes contribute to the ecological fitness of their plant hosts to respond to climate change.

It is known that fungal endophytes may modulate phenotypic plasticity of some plant traits and enhance their host plant's tolerance to heat, drought and salinity (Rodríguez et al., 2008; Ali et al., 2018), metals (Yamaji et al., 2016) and insect pests (Raman and Suryanarayanan, 2017; White et al., 2019) and pathogens (Busby et al., 2016a). This ability to modify the traits of their host plants, their universal occurrence, broad host range and the non-pathogenic nature of many of the fungal endophytes provide a strong reason for employing endophytes for stress alleviation in plants. Before the successful use of endophytes for this purpose, it is essential to understand the mechanisms by which they impart or increase stress tolerance to their host plants. This may not be a straightforward exercise, since in nature more than one kind of stress operates simultaneously and each stress could affect the plant at various levels. For instance, drought alone as stressor causes reduction in leaf area, stem length, leaf water potential, stomatal conductance, net photosynthetic rate and productivity in plants (Rodríguez and Durán, 2020). More information is available for bacterial endophytes on the mechanisms enhancing stress tolerance of plants (Khare et al., 2018). Although the exact mechanism of the fungal endophyte-induced abiotic stress tolerance is not clear, a few studies point to certain possibilities. Leaf endophytic yeasts of Antarctic plants such as *Cryptococcus victorialis*, *Cystobasidium laryngis*, *Rhodotorula mucilaginosa*, *Sporidiobolus ruineniae*, and *Leucosporidium* aff. *golubevii* increase their plant

host's fitness to survive in a stressful environment by elaborating certain metabolites (Santiago et al., 2017). The root endophyte *Piriformospora indica* increases the salt tolerance capacity of a salt-sensitive barley cultivar by increasing the antioxidant enzymes including ascorbate peroxidase (APX) and catalase (CAT) which are associated with salt tolerance of plants (Baltruschat et al., 2008). Root endophyte-enhanced heat and drought tolerance in wheat is thought to involve an epigenetic mechanism (Hubbard et al., 2014). In another study, fungal endophytes increased drought and salinity tolerance of rice by altering the levels of abscisic acid, jasmonic acid and salicylic acid (Waqas et al., 2012). Fungal endophytes regulate the content of salicylic acid, jasmonate, indole-3-acetate and ABA in shoot tissues of the Antarctic plant *Colobanthus quitensis* thus increasing its tolerance to UV-B radiation (Ramos et al., 2018).

The biotic stress posed by insect pests and pathogens is also expected to be influenced by climate change. There is not enough base-line information to enable a reasonably sound prediction of the effect of climate change on biotic stressors (Velásquez et al., 2018); however, it is expected that climate change will affect losses due to plant diseases and the geographical distribution of plant diseases (Chakraborty et al., 2000) as well as pathogen development and survival and host susceptibility (Elad and Pertot, 2014). Fungal endophytes could be employed to counter such stress as they increase tolerance of host plants to biotic stress. *Colletotrichum tropicale*, a foliar fungal endophyte upregulates many defense-related genes in *Theobroma cacao* (Mejía et al., 2014) thus increasing its resistance to the pathogen *Phytophthora palmivora* (Arnold et al., 2003). Leaf fungal endophyte densities in plants can have a negative effect on insect pests (Van Bael et al., 2009; Estrada et al., 2015). With such an overarching influence, it is logical that fungal endophytes would aid in plants' resilience to the stresses induced by a rapidly changing climate.

3. Endophytes - ideal candidates for alleviation of climate change-induced stress

Two characteristics of fungal endophytes provide particular potential for enabling plants to respond to climate change. The first relates to genome size and generation time. Due to their relatively small genomes, short generation times, recombination and sexual reproduction processes (Grandaubert et al., 2019; de Vries et al., 2018), fungi are likely to support higher rates of evolution than plants and therefore adapt more rapidly to climate change. Scott et al. (2019), using arbuscular mycorrhizal fungi as a model, theorize that the genomic diversity allows modular organisms (including many filamentous fungi) to adapt to heterogeneous environments. Furthermore, filamentous fungi experiencing stressful environments show higher frequencies of new spontaneous mutations than those from less stressful environments (Lamb et al., 2008; Vallino et al., 2011). Hence, climate change events could drive relatively accelerated evolution, following which selection could act resulting in populations more equipped to survive better under stress conditions. The association of such fungi with plants as mycorrhizas or endophytes could modulate plant community response to climate change (Bunn et al., 2009), especially considering the fact that endophyte colonization of host plants could increase with increased CO₂ concentration in the environment (Compant et al., 2010). Many endophytes belong to the subphylum Pezizomycotina of Ascomycota (U'Ren et al., 2010) which exhibit a novel form of chromosomal evolution called mesosynteny where 'genes are conserved within homologous chromosomes, but with randomized orders and orientations' (Hane et al., 2011). Additionally, many genes governing pathogenesis of Dothideomycetes (of Pezizomycotina) are known to be present near repetitive sequences, thus aiding their rapid evolution (Ohm et al.,

2012). Furthermore, filamentous fungi experiencing stressful environments (harsher, drier, warmer) show higher frequencies of new spontaneous mutations than those from less stressful environments (Lamb et al., 2008; Vallino et al., 2011) resulting in more genetic variability among them which can drive evolutionary processes (Lamb et al., 2008). Although many such mutations could be deleterious, it can be expected that gradually, selection process would function resulting in populations better equipped to survive under stress conditions. These observations lead to a conclusion that climate change events could drive relatively accelerated evolution among fungi including endophytes. Although endophytes are shielded from stressful environments to a large extent due to their survival within the host, their ability to grow also as saprotrophs outside the plants (Prakash et al., 2015) exposes them to such environments.

The second characteristic of endophytes that may facilitate plant responses to climate change relates to their conferring enhanced abiotic and biotic stress resistance to their host plants. In this context, crop plants have been studied more rigorously than plants of the natural ecosystems. Such investigations aim ultimately to reduce the dependence on breeding and the use of agrochemicals to improve crop performance (Berg, 2009; Lata et al., 2018). In controlled greenhouse experiments, benefits can result from interactions of the plant microbiome with the plant host (Suryanarayanan et al., 2017; Rho et al., 2018). Evidence exists for fungal endophytes enhancing crop growth under conditions of drought (Hubbard et al., 2014), high salinity and nitrogen deficiency (Waller et al., 2005; Rho et al., 2018) and heat stress (Morsy et al., 2010) and for protecting plants against biotic stressors (Chadha et al., 2015). A few recent studies attempt to understand the molecular basis of endophyte-mediated alterations of plant gene expression that counter plant stress (Kord et al., 2019; Sampangi-Ramaiah et al., 2020; Ye et al., 2019). A moderately salt sensitive IR-64 rice enriched with a salt tolerant endophyte (a *Fusarium* sp.) from a salt tolerant Pokkali rice showed that there were 1348 up-regulated and 1078 down-regulated genes in plants colonized by the endophyte. These were mainly involved in the ion transporters, Ca²⁺ signalling pathway and serine/threonine protein kinases (Sampangi-Ramaiah et al., 2020). These authors also reported that under salinity stress, the endophyte reduced the overall alternative splicing events indicating its probable role in stress tolerance (Sampangi-Ramaiah et al., 2019). One study shows that foliar endophytes significantly increase nitrogen uptake by plants which could be diverted to increasing the production of defense related nitrogenous compounds (Christian et al., 2019). Furthermore, plants can acquire genes directly from their fungal endophytes, including genes that may enhance the plant's resistance to infection by fungal pathogens, via horizontal gene transfer (HGT) (Wang et al., 2020). For example, the *Fhb7* gene in *Thinopyrum elongatum* (wild relative of wheat) encodes for glutathione S-transferase and confers resistance against *Fusarium* head blight disease. Plants lack *Fhb7* homologs, and according to Wang et al. (2020), *T. elongatum* acquired this gene from an *Epichloë* sp. (Class1 endophyte) through HGT. Similarly, HGT of a Class1 endophyte nuclear gene encoding a β -1,6-glucanase enzyme to a cool season grass has been reported (Shinozuka et al., 2017). Although such HGT events have been rarely reported for the Class 3 endophytes, the above examples point to the possibility of HGT between a fungus and a plant. Furthermore, foliar fungal endophytes carry bacteria as non-obligate symbionts within their hyphae (endohyphal bacteria) which may significantly enhance IAA production by the endophyte (Hoffman et al., 2013). These studies substantiate endophyte-mediated plant responses to abiotic and biotic stresses that are relevant to mitigating the effects of climate change on cultivated crops. However, it is important to stress that owing to human interference, crops are not subjected to

natural selection perhaps resulting in a static community of associated endophytes or even the loss of endophytes (Hemapriya et al., 2020).

4. Endophytes benefiting natural plant communities

Climate change models predict increased droughts and soil salinity affecting ecosystem stability (Dai, 2013). Even the limited studies on endophyte (*sensu lato*) symbioses with reference to climatic change underscore their importance in enhancing plant tolerance to these expected changes in climate. Bacterial endophytes provide benefits including stress tolerance to their host plants through increased availability of minerals, production of phytohormones, antioxidants (Khan et al., 2016) and 1-aminocyclopropane-1-carboxylate (ACC) deaminase (Yaish et al., 2015). Fungal endophytes protect *Colobanthus quitensis*, a plant native to Antarctica, from drought by lowering oxidative stress, increasing the production of osmoprotective molecules (Hereme et al., 2020). Although endophyte-mediated drought tolerance may not be significant in Antarctica due to climate change-induced increased water availability there (Hereme et al., 2020), such functional symbiosis would be beneficial to plants of warmer regions. Fungal endophytes from roots of Antarctic plants increase salt stress tolerance in cultivated plants hinting at their potential for increasing the fitness of their natural host plants (Molina-Montenegro et al., 2020). Root fungal endophytes increase solute accumulation which governs osmotic adjustments thus enhancing tolerance of their host plants to drought (Li et al., 2018). Inoculation of a mixture of bacteria and yeast endophytes reduced the damage caused by reactive oxygen species (ROS) in *Populus* sp. suggesting enhanced drought tolerance (Khan et al., 2016). The root fungal endophyte *Piriformospora indica* induced differential expression of barley genes governing carbohydrate metabolism, nitrogen metabolism, and the ethylene biosynthesis pathway providing systemic salt-tolerance in leaves (Ghaffari et al., 2016). Despite such findings revealing the potential of endophytes in enhancing abiotic stress tolerance in plants, unlike the plant growth-promoting rhizobacteria (PGPR) or mycorrhizas, there is a long road ahead before they can be commercialized (Lata et al., 2018).

A few studies attest to the ability of endophytes to increase the tolerance of their plant hosts to biotic stress. Fungal endophytes play a crucial role in altering the response of host plants to diseases (Busby et al., 2016a). An endophytic isolate of *Colletotrichum gloeosporioides* significantly reduced the incidence of black pod rot disease caused by *Phytophthora* spp. in *Theobroma cacao* (Mejía et al., 2008). Inoculation of *Populus trichocarpa* with endophytes affected positively or negatively the severity of the disease caused by *Melampsora* rust (Busby et al., 2016b). It is known that the environment plays a more critical role than the host factor in determining the endophyte assemblage of the leaf (Zimmerman et al., 2012) and that many endophytes exhibit habitat-mediated adaptations. Those isolated from trees of fire prone forests show extraordinary thermal tolerance of the spores (Suryanarayanan et al., 2011) and ability to use toxic furaldehydes which emanate from biomass burning (Govinda Rajulu et al., 2014); some fungal endophytes residing in plants of hypersaline and desert habitats are salt tolerant (Manasa et al., 2020; Sampangi-Ramaiah et al., 2020) and high temperature tolerant (Sangamesh et al., 2018), respectively. Such traits are habitat specific and not host plant species specific thus endorsing an environment mediated selection.

Warming causes alterations in microbial communities (Morrison et al., 2019) including alterations of fungal endophyte communities in leaves (Hashizume et al., 2010). With the broad host range of many of the endophytes (Suryanarayanan et al., 2018b), it is conceivable that a stress tolerant endophyte of a

plant growing in a stressed environment gets transmitted to a stress intolerant plant and confers tolerance (Redman et al., 2011; Sampangi-Ramaiah et al., 2020). Considering the holobiont (a plant and the all the microbes associated with it), it is possible that the taxonomy of the microbial species vary with conspecifics of the host; however, their functional diversity is less variable due to the occurrence of functionally similar (though taxonomically different) microbes (Doolittle and Booth, 2017). This and the loose host specificity of some leaf endophytes, as well as the herbivory-mediated increased spread of Class 3 endophytes (Saikkonen et al., 2007) could expand their geographical and host range favoured by climate change.

As a caveat, it should be noted that climate change leading to global warming would enhance pathogen spread and virulence as well as their ability to infect plants and survive in natural environments (Bebber et al., 2013; Elad and Pertot, 2014). This could induce pathogenic fungi, which occur in plants as latent pathogens, to incite disease. Many of the common and dominant leaf endophytes including *Colletotrichum*, *Pestalotiopsis*, *Diaporthe* (*Phomopsis*), and *Xylaria* could include latent pathogenic forms. *Lasiodiplodia theobromae* usually exists as symptomless endophyte in plants but heat stress could enable it to cause disease (Paolinelli-Alfonso et al., 2016). While increased CO₂ has a positive influence on the abundance of arbuscular and ectomycorrhizal fungi, its effect on plant growth-promoting bacteria and endophytic fungi could be more variable (Compant et al., 2010). The interactions of fungal endophytes with co-occurring microbes in the host microbiome, the alterations in such interactions consequent to tissue-age related changes in the fungal endophyte community and the responses of plant-endophyte as a holobiont to changes in environment are hardly known (Suryanarayanan, 2013). Generally, older leaves have higher densities of endophyte colonization when compared with younger leaves; one study (Suryanarayanan and Thennarasan, 2004) revealed that there is a qualitative difference in the endophyte communities of young and old leaves of a plant perhaps reflecting differences in the physical and chemical status of leaves of different ages. A recent investigation revealed that an endophytic fungal association with roots of legumes is enabled by a common signalling pathway triggered by symbiotic rhizobia and arbuscular mycorrhiza (Skiada et al., 2020). This necessitates more rigorous studies on plant, endophyte and environment interactions such that reliable predictions can be made on endophyte-mediated plant adaptations to climate change. Unlike in agricultural plants where adaptation to rapid climate change can be countered to an extent by artificial inoculation of stress-tolerant endophytes sourced from diverse global environments, plants in natural communities are constrained by their native pool of endophytes. This is because the native endophytes may resist colonization of the tissue by alien endophytes (Mohandoss and Suryanarayanan, 2009) necessitating periodical reinoculation with the introduced endophyte to sustain it in the tissue (Suryanarayanan et al., 2018b). However, within this pool, it is likely that (a) over time, selection pressure would lead to skewing of endophytes towards those that are stress-tolerant and (b) that such endophytes would confer tolerance to host plants. Thus, natural selection of endophytes is expected to fast-track plants' adaptation in natural communities to climate change, although not at the same rate or scale as would be expected from human-assisted endophyte transfers in agricultural crops. To date, there are no explicit studies documenting such responses in the endophytic organisms of natural plant communities.

5. Conclusion

Although genetic engineering is a viable option to produce climate resilient plants (Saab, 2016), the current restrictions on the

use of transgenic plants in many countries could stand in the way of the success of this procedure (ISAAA, 2016). The appreciation that plant performance is a net result of interactions between the plant, its microbiome and the environment has shifted the focus on microbe-mediated trait alterations in plants to counter climate change effects. Although the ecological functions of the plant microbiome are little understood (Vandenkoornhuysen et al., 2015), there is experimental evidence supporting endophyte-mediated improvement of crop performance under various stressors. Although most studies on endophyte-mediated plant trait alterations are with reference to crops (Busby et al., 2016a), these results are of heuristic value while extending them to argue for the possible role of fungal endophytes in adaptations of non-crop plants to climate change. Hence, future investigations on resilience of plants to climate change should consider endophytes for their potential impacts which could aid in the development of models, policies, and solutions to mitigate climate change effects. For achieving this, it is imperative to study the holobiont (the plant and all its associated microbes) and not the endophytes in isolation (Suryanarayanan, 2020). This is further confounded by the fact that plant-associated microbes show overlapping functional diversities and lifestyles which may be environment dependent (Vandenkoornhuysen et al., 2015). The complex web of interactions between the (1) endophyte and co-occurring microbes in a plant (2) endophyte and its host plant (3) the environment and the endophyte-plant complex have to be discerned to fully realize the potential of endophytes (Schulz et al., 2015; Saikkonen et al., 2020; Suryanarayanan, 2020) in moderating the negative effects of climate change on plants.

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