

Endophytic mediation of reactive oxygen species and antioxidant activity in plants: a review

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Abstract Reactive oxygen species are in all types of organisms from microbes to higher plants and animals. They are by-products of normal metabolism, such as photosynthesis and respiration, and are responsive to abiotic and biotic stress. Accumulating evidence suggests reactive oxygen species play a vital role in programmed cell death, stress responses, plant defense against pathogens and systemic stress signaling in conjunction with antioxidant production. Here, we propose that reactive oxygen species and antioxidants, as both universal and evolutionarily conserved, are likely to play important role(s) in symbiotic interactions. To support this hypothesis we review the root and foliar fungal endophyte literature specific to fungal-plant symbiotum production of reactive oxygen species and antioxidants in response to stress. These asymptomatic fungi can produce antioxidants in response to both biotic and abiotic stress when grown in culture as well as *in planta*. In addition, there is a growing but nascent literature reporting a significant impact of endophyte colonization on the antioxidant activity of colonized (E+) hosts when compared to uncolonized (E-) hosts, especially when exposed to stress. Here we summarize general patterns emerging from the growing literature specific to antioxidant activity of endophytes in

colonized hosts and bring up possible future research questions and approaches. The consequences of changes in reactive oxygen species production and increased antioxidant activity in the symbiotum appear to be beneficial in many instances; but costs are also indicated. Unexplored questions are: 1) to what extent do antioxidants originating from the fungal endophyte mediate host metabolism, and thereby control host responses to endophyte colonization; (2) what role do fungal, plant, or symbiotum produced reactive oxygen species and antioxidants have in determining symbiotic outcome between extremes of pathogenicity and mutualism; and (3) what role if any, do the production of reactive oxygen species and their antioxidant counterparts play in the symbiotum's ability to respond to changing selection pressures? If as the literature suggests, such endophyte imposed mediation can be utilized to foster increases in plant production in resource limited habitats then the utilization of fungal endophytes may prove useful in agronomic and conservation settings.

Keywords Endophyte · Symbiosis · Neotyphodium · Epichloë · Mutualism · Dark septate endophytes · Antagonism · Stress · Pathogen

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Introduction

Symbioses in general are complex interactions with the ecological context and evolutionary framework within which they exist capable of leading to different outcomes at population and community levels (Bronstein 1994). Research investigating genetic and physiological mechanism(s) responsible for differences in symbiotic outcomes is necessary to develop a robust understanding of the ecological and coevolutionary origins, consequences, and trajectories of

symbiotic interactions. Recent research suggests oxidative balance plays a crucial role in modulating plant-fungus interactions (Rodríguez and Redman 2005 and 2008; Nanda et al. 2010; White and Torres 2010; Redman et al. 2011). Part of the complex plant immune system is driven by biphasic reactive oxygen species bursts mediating first, recognition of invading fungi, and then the establishment of defense responses in the plant (Mittler 2002; Overmyer et al. 2003; Box 1 and Fig. 1). Virulent pathogens appear able to suppress the second burst of reactive oxygen species (Torres et al. 2006; Torres 2010; Eaton et al. 2011). Similarly, a suppressed second burst is suggested to inactivate plant defense responses against symbiotic fungi (Gechev et al. 2006; Tanaka et al. 2006; Lohar et al. 2007; Torres 2010; Eaton et al. 2011; Fig. 1).

Box 1. Glossary

Symbiosis: Symbioses are close ecological relationships between two or more, inter-specific individuals. Symbiosis does not indicate the outcome of the inter-specific interaction, only the degree of interaction ranging from obligate to facultative (Smith 1979). As such, a symbiotic interaction can be positive (mutualism), negative (pathogenesis or parasitism), or neutral for one or both of the partners (commensalism).

Endophytism: An endophyte is an asymptomatic life stage of a symbiotic microorganism (Wilson 1995). The stage may last part, or the entire life cycle of the organism and is typified as asymptomatic at least throughout some portion of colonization. Endophytes may be maternally transmitted (vertical) or horizontally transmitted passively or via vectors (Wilson 1995).

Dark septate endophytes (DSE): DSE are a miscellaneous group of ascomycetous anamorphic fungi that colonize root tissues intra- and inter-cellularly (Jumpponen 2001). Evidence suggests a role for DSE as a mycorrhizal substitute especially in habitats exposed to recurrent stress (Read and Haselwandter 1981; Cázares et al. 2005; Postma et al. 2007) leading to the suggestion DSE functionally replace mycorrhizae in hosts living at latitudes beyond the reach of mycorrhizal symbiosis (Jumpponen 2001; Newsham et al. 2009). Thus, mycorrhizal hosts may rely on root endophytes to navigate the vicissitudes of extreme environments or even stable but stressful ones (Johnson et al. 1997; Jumpponen 1999; Jumpponen and Trappe 1998; Jumpponen and Jones 2010; Mandyam and Jumpponen 2012).

Reactive oxygen species: Reactive oxygen species (ROS) are multifunctional metabolites resulting from aerobic metabolism found in all living organisms. When light absorption by photosynthetic cells exceeds utilization, free radicals in the form of different ROS are produced (Logan 2006; Gill and Tuteja 2010). This is a phenomenon of the electron transport system and the oxygen molecule's ability to readily accept electrons (Foyer and Noctor 2000). Additionally, plants exposed to pathogens and herbivores produce ROS via oxidative bursts (Apel and Hirt 2004; Jaspers and Kangasjärvi 2010; Fig. 1). These bursts result in the production of molecules, which can be employed to create physical barriers to hyphal growth and have direct detrimental effects to the cells of invading entities (Overmyer et al. 2003; De Gara et al. 2010).

The role of ROS in plant abiotic stress response has undergone an important reevaluation with accumulating research supporting the beneficial role of ROS in priming the plant response to abiotic stresses (Foyer and Noctor 2000 and 2005; Foyer and Shigeoka 2011). In this role various singlet oxygen species are induced by the plant, travel long distances within plant tissues and produce systemic

signaling throughout the plant (Mittler 2002; Apel and Hirt 2004; Foyer and Noctor 2005 and 2011; Fig. 1). Activation of plant stress response includes production of an arsenal of antioxidants which then mediate the level of ROS accumulation in plants cells thereby reducing cell damage and death (Jaspers and Kangasjärvi 2010; Fig. 1).

Antioxidants: Antioxidants are the means by which reactive oxygen species (ROS) are mediated and regulated so as to avoid or reduce cell damage and death (Gechev et al. 2006; Foyer and Noctor 2011). Antioxidant enzymes responsive to ROS production are numerous and include ascorbate peroxidase (APX), catalase (CAT), glutathione reductase (GR), glutathione peroxidase (GPX), MAPK kinases (MAPK), and superoxide dismutase (SOD), to name a few. Antioxidants vary in terms of quantity within plant tissues as well as in terms of the specific ROS scavenged (Fig. 2).

Increases in various antioxidants have been repeatedly shown to correlate with increased plant tolerance to multiple stresses (Smith et al. 1989; Sharma and Dubey 2005; Gaber et al. 2006; Simon-Sarkadi et al. 2006; Agarwal 2007; Hoque et al. 2007; Molinari et al. 2007; Zhang and Nan 2007; Shao et al. 2008; Yan et al. 2008; Rodríguez and Redman 2008; Kumar et al. 2009; Shittu et al. 2009; Pang and Wang 2010; Srinivasan et al. 2010) including salt, drought, metals, and pathogens (Gill and Tuteja 2010). As a result of their protective roles antioxidants are critical to plant survival and fitness and presumably selection has resulted in both redundant and highly specific pathways to address ROS production and mediate stress.

In this paper we focus on asymptomatic fungal endophytes in plant roots and shoots. Despite abundant research attempting to label these symbioses, many studies have shown plant-fungal symbioses to be labile and readily qualified as antagonistic, neutral, or mutualistic depending on host and fungus life stage, genotype, as well as abiotic and biotic environmental conditions (Clay 1993; Bronstein 1994; Saikkonen et al. 1998; Ahlholm et al. 2000; Lehtonen et al. 2005; Saikkonen et al. 2004; Gundel et al.

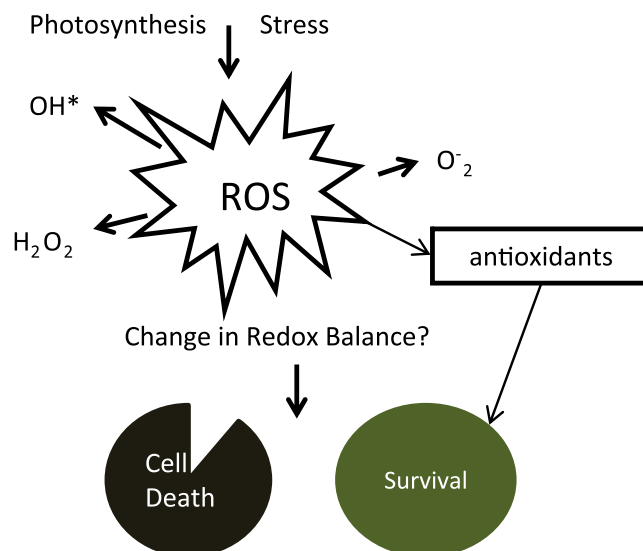


Fig. 1 Reactive oxygen species produced from various types of stress as well as basic metabolic processes elicit antioxidants to scavenge reactive oxygen species and thus avoid cell death

2006, 2010, 2011; Sullivan and Faeth 2008; Cheplick and Faeth 2009; Hamilton et al. 2009 and 2010; Rodriguez et al. 2004 and 2009; Rudgers et al. 2009; Johnson et al. 2010; Saikkonen et al. 2010; Mouhamadou et al. 2011; Purahong and Hyde 2011; Tejesvi et al. 2011; Vesterlund et al. 2011). The benefit of endophytic fungi to a diverse group of host plants has commonly been observed in nutrient poor environments and when plants are under stress such as drought, flooding, plant competition, herbivory, and pathogen attacks (Hesse et al. 2003; Rodriguez et al. 2004; Clarke et al. 2006; Schardl et al. 2004; Saikkonen et al. 2006; Morse et al. 2007; Hahn et al. 2008; Saikkonen et al. 2010; Gundel et al. 2012; Torres et al. 2012). These fungi include root associated dark septate endophytes as well as obligate and facultative, asymptomatic endophytes residing within above-ground plant parts of the hosts throughout the fungal life cycle (systemic and vertically transmitted endophytes; e. g. *Neotyphodium*; Box 1). In addition, all plants host a diverse community of horizontally transmitted endophytic fungi which are often close relatives to pathogens (e.g. *Trichoderma* spp., *Colletotrichum* spp., *Cladosporium* spp., *Phomopsis* spp., *Phyllosticta* spp., and *Fusarium* spp. (Saikkonen 2007; Ghimire et al. 2011; González and Tello 2011; Rocha et al. 2011; Udayanga et al. 2011; Wikee et al. 2011).

Tanaka et al. (2006 and 2008) demonstrated reactive oxygen species bursts originating from a mutualistic endophyte are required to inactivate plant defense responses against the fungus thereby maintaining the mutualism. Whether the suppression of plant defense is the result of fungal, plant, or symbiotum metabolism is poorly understood (Fig. 2). Because reactive oxygen species play a mechanistic role in programmed cell death, general stress responses and systemic signaling, they can have multifarious effects on the success of fungal infection or endophyte colonization and the plant responses, i.e. resistance, acceptance, or sanctioning. Moreover, antioxidants can serve to transmit stress signals through the oxidant-antioxidant interaction (CH Foyer, pers. comm.; Box 1). This may facilitate the chemical communication between a host and an avirulent pathogen or asymptomatic endophyte enabling the host to react quickly to pathogenesis and differentiate a pathogen from a mutualist (Fig. 2). A sophisticated mammalian immune recognition system, called the ‘innate immune system’ has evolved to distinguish invading microbes (Medzhitov and Janeway 1997). Future studies are needed to reveal if such a system exists in plants. Despite the nascent stages of research, there is evidence to indicate fungi both produce antioxidants *in vitro* and also alter the activity level of antioxidants *in planta* (Pang and Wang 2010; Harman 2011; Figs. 1 and 2).

Changes in host production of antioxidants (Box 1) resulting from endophyte colonization of host tissues have

been found in numerous studies. Huang et al. (2007) explored 292 endophyte morphotypes isolated from 29 plant species representing numerous plant families. They measured antioxidant and phenolic production finding all the endophytes could produce antioxidants and/or phenolics (see also Phongpaichit et al. 2007; Debbab et al. 2011). Although the variation in the level of production was high across endophyte species, 65% of the endophytes showed relatively high activity levels. Antioxidants involved in antifungal responses have been identified in a putative fungal endophyte, *Pestalotiopsis microspora* (Strobel and Daisy 2003). Srinivasan et al. (2010) reported high antioxidant activities when *Phyllosticta* sp. cultures were exposed to reactive oxygen species. In the interplay between endophytic fungi and host plant, the production of both reactive oxygen species and antioxidants may be the mechanism by which the host’s hypersensitive and systemic acquired resistance responses are mediated (Tanaka et al. 2006; Fig. 2). Multiple studies have documented a role for MAP kinase (MAPK) genes produced by the symbiotum in mutualistic interactions (Eaton et al. 2008 and 2011; Matsouri et al. 2010). The MAP kinase pathway is integral to the production of reactive oxygen species (Box 1) and thus its role in the proliferation of fungal growth within the host, development of innate immunity due to microbial invasion, and abiotic stress signaling within plants (Asai et al. 2002; Kawasaki et al. 2002; Eaton et al. 2008). Thus, the interplay among reactive oxygen species, various signaling pathways, and antioxidant activity is critical to successful endophyte colonization and may define the symbiotic outcome (Tanaka et al. 2006; Torres 2010; Eaton et al. 2011).

In this paper, we review the literature on interactions between plants and fungal endophytes as an attempt to increase understanding of the role of reactive oxygen species and antioxidants in inter-specific interactions, as well as to examine whether these molecules are causal to putatively mutualistic outcomes. Though several outstanding reviews have focused on endophyte impacts on host physiology in response to stress (Rodriguez and Redman 2005 and 2008; Rouhier and Jacquot 2008; White and Torres 2010; Shores et al. 2010) this review provides hypotheses for future empirical and theoretical studies, and aims to increase dialogue between physiologists, ecologist, and evolutionary biologists to increase understanding of fungus-plant symbioses.

Literature survey

We reviewed the published experimental studies in order to identify the strength of support for or against the hypothesis that endophyte colonization can be mutualistic via increased production of antioxidants. The following combinations of

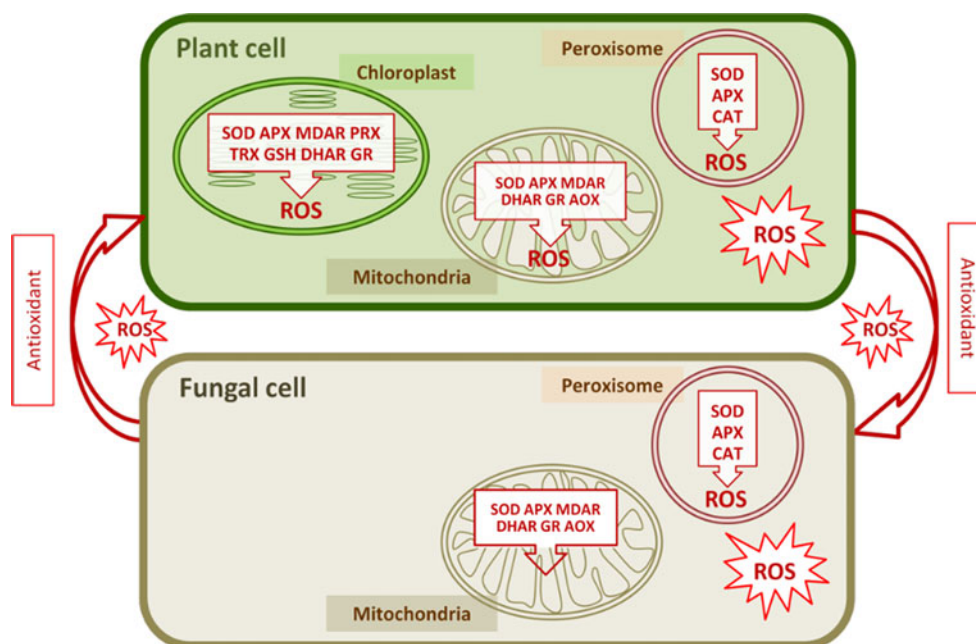


Fig. 2 Reactive oxygen species production occurs in various organelles and the cellular matrix of both plants and fungi. To mediate damage by reactive oxygen species, organisms produce a variety of antioxidants (AOX—alternative oxidase; APX—ascorbate peroxidase; CAT—catalase; DHAR—dehydroascorbate reductase; GR—glutathione reductase; GSH—glutathione reduced; MDAR—monodehydroascorbate reductase; PRX—peroxidoredoxin; SOD—superoxide

dismutase; TRX—thioredoxin). Here we present a plausible model of interactions between fungal and plant cells as well as within the various organelles of the fungal cell. The feedback between fungal and plants cells via reactive oxygen species production and resultant signaling is known to occur but the details of the system and the consequences to both organisms are unknown. Plant cell adapted from Broshce et al. 2009

words were used as search criteria in Web of Science®: 1) endophyte antioxidant, 2) endophyte antioxidant pathogen, 3) endophyte reactive oxygen species, 4) endophyte reactive oxygen species pathogen, 5) dark septate endophyte reactive oxygen species, 6) dark septate endophyte reactive oxygen species pathogen, 7) dark septate antioxidant, 8) dark septate antioxidant pathogen, 9) endophyte metab*, 10) dark septate metab*, 11) fung* reactive oxygen species, and 12) fung* antioxidant. Among the 3077 papers resulting from this search, a subsequent screen excluded papers not involving plant and fungal endophytes. A third screening was performed to identify papers containing experimental manipulations of stress and measuring at least one antioxidant (enzymatic or non-enzymatic) or reactive oxygen species. The experimental papers were classified according to type of plant-fungus system, stress response, endophyte identity, stress treatment, experimental context, and fitness proxy (Table 1).

Empirical research included study plants from broad taxonomic groups, i.e. monocots, dicots as well as horizontally and vertically transmitted endophytes. A majority of the papers used plant seedlings. In 80% of the papers, the experiments were conducted in growth chambers or greenhouses, and only one was a field experiment. Only one paper included a fitness proxy variable in the experimental measures (Table 1).

Root endophytes

In terms of antioxidant and reactive oxygen species activity in root endophyte colonized plants (E+), there is limited research much of which indicates a mutualistic symbiosis (Table 1). Baltruschat et al. (2008) recorded increased activity of several antioxidants in E+hosts exposed to salt stress. Additional support documented increased antioxidant production in E+corn plant roots when the plants were exposed to pathogenic *Fusarium* spp. (Table 1). The increased antioxidant activity positively correlated with host biomass and root length but negatively with secondary root counts (Kumar et al. 2009; Table 1) compared to endophyte free (E-) plants. Similarly, Waller et al. (2005) found E+ wheat produced significantly more antioxidants and biomass when exposed to salt stress compared to E- wheat (Table 1).

Though not measuring antioxidant nor reactive oxygen species directly, Mandyam et al. (2010) documented production of polyphenol oxidases, which are known to scavenge reactive oxygen species, in E+but not E- hosts. For example, Grünig et al. (2003) reported enzymatic differentiation within *Phialocephala* spp. suggesting these root endophytes are able to produce various enzymatic metabolites which may positively impact host physiology. Bartholdy et al. (2001) quantified the production of hydroxamate siderophores

Table 1 Review of experimental literature specific to fungal endophyte effects on host plant production of reactive oxygen species (ROS) or antioxidant activity (A) levels in response to stress. See text for list of search terms used to identify papers fitting these criteria. Endophytes are either localized to root or shoot tissues or found in both. Fitness proxy refers to direct measures on seed and/or reproductive output. The symbols '+', '-', and '0' refer to positive, negative, and unknown or commensalistic effects (respectively; from host point of view) on host performance measures

Plant	Endophyte + Effect (ROS (R) measure, Antioxidant (A) measure)	Root endophyte, Foliar (shoot) endophyte	Stress	Plant Age and Experimental Context	Fitness Proxy?	Reference
<i>Theobroma cacao</i>	<i>Trichoderma hamatum</i> (A)	Root	drought	seedlings; growth chamber	no	Bae et al. 2009
<i>Hordeum vulgare</i>	<i>Piriformospora indica</i> (A)	Root	salt	seedlings, plants; growth chamber	no	Baltruschat et al. 2008
<i>Vitis vinifera</i>	<i>T. viride</i> (A)	Root	none	cell culture	no	Calderón et al. 1993
<i>Nicotiana benthamiana</i> , <i>Lycopersicon esculentum</i>	<i>T. harzianum</i> (R)	Root	none	seedlings, plants; growth chamber, hydroponics	no	Chacón et al. 2007
<i>Festuca</i> spp.	<i>Neotyphodium</i> spp (A)	Shoot	drought	seedlings; growth chamber	no	Hamilton and Bauerle 2012
<i>Schedonorus phoenix</i>	<i>N. coenophialum</i> (A)	Shoot	nutrient	plants; greenhouse	no	Lyons et al. 1990
<i>Lolium perenne</i>	<i>N. lolii</i> (A)	Shoot	drought	plants; greenhouse	no	Hahn et al. 2008
Various plant species	various DSE endophytes (A)	Root	none	greenhouse	no	Mandym et al. 2010
<i>Dichanthelium lanuginosum</i>	<i>Curvularia prouderata</i> (R)	Root Shoot	heat	seedlings, plants; growth chamber, greenhouse	no	Márquez et al. 2007
<i>L. esculentum</i>	<i>T. harzianum</i> (R&A)	Root	cold, heat, salt	seedlings, plants; greenhouse, growth chamber	no	Matsouri et al. 2010
<i>Oryza sativa</i>	<i>Curvularia prouderata</i> , <i>Fusarium culmorum</i> (R&A)	Root Shoot	cold, drought, salt	seedlings; greenhouse, growth chamber	yes	Redman et al. 2011
<i>Dichanthelium lanuginosum</i> , <i>Leymus mollis</i> , <i>O. sativa</i> , <i>L. esculentum</i>	<i>Colletotrichum magna</i> , <i>F. culmorum</i> (R)	Root Shoot	drought, heat, salt	seedlings, plants; growth chamber, field	no	Rodriguez et al. 2008
<i>Arabidopsis</i> sp.	<i>P. indica</i> (R&A)	Root	drought	seedlings; growth chamber, greenhouse	no	Sheraneti et al. 2008
<i>Guazuma tomentosa</i>	<i>Phyllosticta</i> sp. (A)	Shoot	none	in vitro	no	Srinivasan et al. 2010
<i>Brassica campestris</i>	<i>P. indica</i> (A)	Root	drought	seedlings; growth chamber, greenhouse	no	Sun et al. 2010
<i>Lolium perenne</i>	<i>Epichloë festucae</i> (R)	Shoot	none	seedlings; greenhouse	no	Tanaka et al. 2006 and 2008
<i>Hordeum vulgare</i>	<i>P. indica</i> (A)	Root	salt	seedlings; growth chamber	no	Waller et al. 2005
Plant Species	Endophyte - Effect (ROS (R) measure, Antioxidant (A) measure)	Root endophyte (root), Foliar endophyte (F)	Stress	Experiment	Fitness Proxy?	Reference
<i>L. perenne</i>	<i>N. lolii</i> (A)	Shoot	drought	plants; greenhouse	no	Hahn et al. 2008
<i>Zea mays</i>	<i>P. indica</i> (R)	Root	pathogen	plants; greenhouse	no	Kumar et al. 2009
<i>Elymus dahuricus</i>	<i>Neotyphodium</i> sp. (A)	Shoot	drought	plants; greenhouse	no	Zhang and Nan 2007
Plant Species	Endophyte 0 or Unknown Effect	Root endophyte (root), Foliar endophyte (F)	Stress	Experiment	Fitness Proxy?	Reference
<i>L. perenne</i>	<i>N. lolii</i> (A)	Shoot	zinc	plants; greenhouse	no	Bonnet et al. 2000
<i>L. perenne</i>	<i>Neotyphodium</i> sp. (A)	Shoot	drought	plants; greenhouse	no	Hahn et al. 2008
<i>E. dahuricus</i>	<i>Neotyphodium</i> sp. (A)	Shoot	drought	plants; greenhouse	no	Zhang and Nan 2007

by *Phialocephala fortinii* at different pH values. Siderophores chelate iron thereby increasing iron uptake in iron-poor habitats. Production of siderophores suggests a potential currency for endophyte-plant mutualism. However research is needed to determine if siderophore production by the fungus occurs in situ and if it positively correlates with plant performance.

Comparisons between E+ and E- plant hosts in terms of physiological phenotypes and stress have been investigated from the cell to whole plant level (Table 1). Cell cultures from wine cultivars colonized by *Trichoderma viride* had significantly reduced cell volumes after 48 h of exposure but significantly increased cell conductivity (Calderón et al. 1993). We hypothesize conductivity could conceivably increase the transmission of molecules across cell membrane surfaces, thereby enhancing signaling and associated response mechanisms. However, we acknowledge this is highly speculative and research on whole plants is necessary. Additional support for altered physiological phenotype of E+ plants comes from a specific strain of *Trichoderma harzianum*, T22, which is well documented to enhance host performance in a variety of contexts (Harman 2000 and 2006; Harman et al. 2004). Matsouri et al. (2010) looked for causal mechanisms and concluded that increased E+ host tolerance to salt and temperature stress resulted from changes in lipid peroxidation as well as ratios of reduced to oxidized forms of both glutathione and ascorbate. In addition, Bae et al. (2009) reported a significant increase in some amino acids and sugars in E+ hosts exposed to drought. Interestingly, in this case root symbiont did not produce significantly higher osmoprotectants, while drought exposed E- plants did. This suggests a complicated symbiotic outcome because increased amino acid and sugar production (both are indicators of increased osmolytic activity) are typical of plants possessing a drought tolerant phenotype (Shinozaki and Yamaguchi-Shinozaki 2007).

Some of the studies, however, indicate caveats to a generalized mutualistic outcome specific to endophyte effects on host physiological responses to stress. For example, though Andrade-Linares et al. (2011) did not measure antioxidant or reactive oxygen species production they reported a potential negative, life stage response of the host to endophyte colonization. In their study three dark septate endophyte species colonizing tomato (*Lycopersicon esculentum*) successfully decreased the negative effects of the fungal pathogen *Verticillium dahlia* but only when the pathogen was presented in low doses. At higher pathogen doses the endophyte effect on host biomass loss was not significantly different from controls. The same study found no significant difference in terms of reproductive output between E+ and E- plants except at the earliest harvest date. Fruit number and biomass at first harvest were significantly higher in E+ versus E- hosts. Thus positive impacts on host vegetative growth and reproductive output appear to be life stage

dependent, but whether they extend to increased host lifetime fitness has not been determined.

Shoot and whole plant endophytes

Several studies on various host species and their shoot associated fungal endophytes support increased host stress tolerance due to increased antioxidant production in E+ hosts (Table 1) compared to E- hosts. A comparison of cellular level reactive oxygen species scavenging activity in *Phyllosticta* colonized versus E- *Guazuma tomentosa* revealed significantly higher scavenging activity in the former (Srinivasan et al. 2010). *Neotyphodium*-endophyte colonized grasses showed significantly higher glutamine synthetase and total amino acid activity (Lyons et al. 1990) in response to nutrient treatments which positively correlated with host biomass. In response to temperature, drought, and salt stress, E+ hosts produced significantly more biomass than their E- counterparts (Redman et al. 2001 and 2002; Márquez et al. 2007; Rodríguez et al. 2008; Redman et al. 2011). Regardless of plant host or fungal endophyte genera, symbiosis resulted in increased plant biomass production and/or survival in response to all three stress treatments and the mechanism appeared to be increased antioxidant activity leading to higher reactive oxygen species scavenging rates and lower reactive oxygen species accumulation in E+ host tissues (Rodríguez et al. 2008). This leads to the general conclusion that habitat-specific stress tolerance can be effectively conferred via symbiotic interactions with fungal endophytes from diverse genera (Rodríguez et al. 2008). Additional studies reported a virus present in the endophyte *Curvularia protuberata* was needed for the endophyte to confer heat tolerance (Márquez et al. 2007). Both a monocot and dicot colonized by the virus-endophyte combination were able to successfully tolerate root zone temperatures of up to 65°C. Neither the E+ plant without the virus, nor *Curvularia protuberata* without its viral endosymbiont could survive temperatures above 38°C. Again the mechanism for enhanced symbiont tolerance was via reactive oxygen species which were reduced in endophyte-viral symbiont compared to E- hosts or E+ hosts without the viral endosymbiont (Márquez et al. 2007).

Additional examples of putative mutualistic endophyte-plant interactions include work by Zhang and Nan (2010). Seedling growth was enhanced by endophyte colonization of *Elymus* sp. and comparisons of this host across populations with different levels of aridity indicated a positive correlation between endophyte presence, drought, and antioxidant production. Zhang and Nan (2010) concluded the increased seedling growth in response to drought resulted at least in part from higher antioxidant activity. They found a positive effect of endophyte colonization on biomass, relative water content, and proline concentrations under low

water conditions and essentially no effect of endophyte under conditions of high water (Zhang and Nan 2007).

Few papers focused on a potential role of reactive oxygen species and/or antioxidant activity in endophyte mediated plant resistance to pathogens (Table 1). For example, when tomatoes susceptible to *Verticillium* wilt were simultaneously inoculated with a virulent and avirulent fungal strain the virulent strain was unable to produce as much biomass *in planta* but continued to successfully stunt the plant's growth (Shittu et al. 2009). When the avirulent strain was the only colonizer of the host, plant growth was significantly enhanced. Associated with this result was increased expression of signaling genes potentially responsible for increased reactive oxygen species activity and subsequent increases in antioxidant activity (Shittu et al. 2009).

As with the root endophytes, benefits from shoot endophyte colonization do not come without associated costs and disadvantages to the host plant (Ahlholm et al. 2000; Cheplick and Faeth 2009). For example, Hahn et al. 2008 evaluated E+ and E- host response to 26 days of drought and found only plant genotype significantly affected host physiological responses. Proline and alkaloid production was not significantly different in E+ plants exposed to drought versus adequate watering; however, there was a 30% increase in the baseline levels of proline in E+ compared with E- plants. It is important to note, increased proline did not correlate with increased plant biomass. Nonetheless, water uptake was significantly higher in E+ plants under both control and drought treatments. Whether this leads to increased host survival was not tested. Another example of low or no host response to endophyte colonization was reported by Bonnet et al. (2000). They looked at host vegetative growth and antioxidant activity in response to multiple levels of zinc, including toxic levels. Grasses colonized with *Neotyphodium lolii* did not produce significant differences in antioxidants nor biomass when compared to E- plants regardless of zinc treatment. Mannitol, which is produced by fungi has demonstrable antioxidant properties (Gessler et al. 2007) and is hypothesized to act as an osmoprotectant aiding drought tolerance of the host plant (Jennings et al. 1998). Mannitol is hypothesized to suppress reactive oxygen species mediated plant defenses against pathogens. Thus, reactive oxygen species suppression via mannitol production could increase the susceptibility of hosts to opportunistic pathogens.

Future research

Available literature suggests that oxidative balance of fungus-plant symbiosis is modulated during their coevolution from pathogenic to asymptomatic endophytism, and both root and shoot fungal endophytes may increase host

tolerance to various stresses via mechanisms involving reactive oxygen species and antioxidants. However, further experimental research is needed to confirm these mechanisms increase host lifetime fitness. To define the outcome of fungus-plant symbiosis as mutualistic requires measures of host plant fitness such as viable seed set, seedling germination success, and identification of long-term, population level endophyte colonization percentages. Finally, an evolutionary approach to identify selective mechanisms acting on reactive oxygen species and antioxidant metabolisms in the context of endophyte-host interactions is warranted. This would facilitate the type of research necessary to answer important questions such as:

1. Do most endophyte-host interactions begin as antagonisms and move to mutualisms from an arms race played at the physiological level?
2. What role does host sanctioning via different pathogen resistance systems play in the symbiotic outcome?
3. Are there distinct phylogenetic patterns visible in the evolution of pathogenic versus mutualistic reactive oxygen species (or antioxidant) systems suggesting divergence due to unique habitat level selective forces?
4. What role can cheaters play in a system involving horizontally transmitted endophytes capable of colonizing diverse host genera?

To answer these questions we look to the genomic era and novel approaches such as systems biology. We may be able to utilize the results from manipulative experiments to identify changes in gene and metabolite levels and protein functions (Scholes et al. 1994; Swarbrick et al. 2006; Chacón et al. 2007; Rasmussen et al. 2008 and 2009; Kogel et al. 2010) to develop theoretical models about functional groups of endophytes (Porrás-Alfaro and Bayman 2011). Using the predictions from such models we could test model predictions with gene knock-outs and functional genomics work.

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