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Plant-endophyte communication: Scaling from molecular mechanisms to ecological outcomes

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ABSTRACT

Diverse communities of fungal endophytes reside in plant tissues, where they affect and are affected by plant physiology and ecology. For these intimate interactions to form and persist, endophytes and their host plants engage in intricate systems of communication. The conversation between fungal endophytes and plant hosts ultimately dictates endophyte community composition and function and has cascading effects on plant health and plant interactions. In this review, we synthesize our current knowledge on the mechanisms and strategies of communication used by endophytic fungi and their plant hosts. We discuss the molecular mechanisms of communication that lead to organ specificity of endophytic communities and distinguish endophytes, pathogens, and saprotrophs. We conclude by offering emerging perspectives on the relevance of plant-endophyte communication to microbial community ecology and plant health and function.

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INTRODUCTION

Endophytic fungi are asymptomatic inhabitants of most, if not all, plant species (Rodriguez et al. 2009). They can form diverse communities in both aboveground and belowground plant organs (David et al. 2016; De Souza et al. 2016; Fonseca-García et al. 2016; Kandalepas et al. 2015; Wagner et al. 2016; Wearn et al. 2012; Zarraonaindia et al. 2015) and show affinity for particular plant taxa (Dastogeer et al. 2018; Gange et al. 2007; Vincent et al. 2016; Wang et al. 2019; Wearn et al. 2012) as well as plant organ habitats (Durand et al. 2017; Hamonts et al. 2018). For the past three decades, researchers have been documenting the composition of fungal endophyte communities (e.g., Arnold et al. 2007; Faeth and Hammon 1997; Whitaker et al. 2021; Zimmerman and Vitousek 2012), and increasingly it has been shown that sometimes endophytes can play important functional roles for their hosts. Endophytic fungi in both leaves and roots can improve plant growth (Ahmad et al. 2020; Chen et al. 2022; Kleczewski et al. 2012), protect plants from pathogen and herbivore enemies (Arnold et al. 2003; Estrada et al. 2015), and help plants cope with abiotic stress (Barberis et al. 2021; Morsy et al. 2020). However, endophytes do not always benefit their host—they typically form commensal relationships with plants (May 2016) and can also operate as latent pathogens or saprotrophs that switch their functional guild in response to cues from their host or the environment (Zanne et al. 2020). From an ecologist's

perspective, the outcomes of plant-endophyte interactions are extremely flexible and context dependent, but the molecular mechanisms that drive these interactions are often classified as a “black box” (Compant et al. 2016; Franco et al. 2022).

At the same time, plant pathologists, molecular biologists, and geneticists have built detailed maps of how fungi interact with plants (Rai and Agarkar 2016; Zeilinger et al. 2016). This knowledge has been particularly well developed for plant-pathogen interactions (Bi et al. 2021; Bolton et al. 2008; Darino et al. 2021; Dutra et al. 2020; Gawehts et al. 2014; Kohmoto 1993; Kombrink and Thomma 2013; Lanubile et al. 2015; Lo Presti et al. 2015; Meena and Samal 2019; Palma-Guerrero et al. 2008; Pradhan et al. 2021; Rep et al. 2004; Rocafort et al. 2020) and has been used as a fulcrum for understanding how endophytes bypass or manipulate the plant immune system to engage in long-lasting relationships that can benefit both partners (e.g., Freeman and Rodriguez 1993). Such molecular mechanisms of communication give rise to the ecological consequences that ecologists have documented. To better understand and predict the functional outcomes of plant-endophyte communication, it is important to integrate molecular and ecological approaches.

The goal of this review is to scale from the molecular mechanisms to the ecological implications of plant-endophyte communication. First, we outline the general molecular mechanisms by which fungal endophytes

may establish and persist within plant tissues, and the strategies that plants use to respond to endophyte presence. We draw from literature on plant interactions with fungal pathogens and mycorrhizal mutualists, as mechanistic studies of endophyte communication are limited. We then discuss more specialized communication strategies, including those used by endophytes specializing on different plant organs and by fungi that operate on endophyte-pathogen and endophyte-saprotroph spectra. In these sections we provide, where known, a portrait of molecular mechanisms used on the fungal and plant sides of the conversation. Finally, we scale up to discuss how plant-endophyte communication affects plant and fungal community ecology more broadly.

INITIATING THE CONVERSATION

We take communication for granted because we do it so frequently, but it's actually a complex process.

—Joseph Sommerville

Plant-fungal communication begins belowground via fungal perception of secreted plant cues, or aboveground via perception of volatile compounds or following establishment of physical contact. Such perceptions influence first the process of establishment, followed by persistence (or lack thereof) (FIG. 1).

Establishment.—Communication comprises both the sending and receiving of signals. Although fungi benefit from a quiet entry into plant tissues, plants are always listening for cues that warn them of an intruder and are prepared to mount the first layer of their inducible immune response: pattern-triggered immunity (PTI) (Bigeard et al. 2015). Fungi and other microbes bear microbe- or pathogen-associated molecular patterns (MAMPs or PAMPs, respectively) (Ausubel 2005), essential, conserved structures including chitin, chitosan, peptidoglycans, glycoproteins, lipopolysaccharides, or any number of secreted components (Chagas et al. 2018). Plant chitinases and glucanases cause the release of chitin and β -glucan oligomers from fungal cell walls, and these metabolites are often recognized as MAMPs (Wawra et al. 2016). Plants recognize MAMPs and PAMPs through pattern recognition receptors (PRRs) found on the surface of plant cells and consequently trigger a first line of defense in the plant immune response (Newman et al. 2013). This rapid response includes the accumulation of reactive oxygen intermediates, activation of ion channels, activation of specific, defense-related mitogen-activated protein kinase

(MAPK) cascades, and extensive transcriptional reprogramming of the host (Lo Presti et al. 2015). Collectively, these changes lead to an accumulation of antimicrobial compounds that damage fungi, as well as enzyme inhibitors that target molecules produced by the fungi (Lo Presti et al. 2015; Pradhan et al. 2021).

There is no communication that is so simple that it cannot be misunderstood.

—Luigina Sgarro

Fungi, in turn, have evolved mechanisms to evade or bypass pattern-triggered immunity. Most of these mechanisms have been described in fungal pathogens, which have historically been considered to be distinct from endophytes. However, recent research suggests that endophytes and pathogens exist as a continuum (see “Specialized communication styles for specialized lifestyles” below), so mechanisms underlying plant-pathogen interactions may be more broadly applicable to communication between plants and fungal endophytes. For example, sucrose is the normal currency of the plant, but fungi can break down sucrose to provide glucose sources. Glucose can therefore trigger host defenses, but some fungi bypass this problem by having a high-affinity sucrose transporter that directly takes up sucrose, which is then digested internally (Wahl et al. 2010). Curiously, although chitosan, a derivative of chitin, can trigger host immune response and also has antifungal properties, some fungal pathogens generate this derivative of chitin as a way of evading the immune response because it is a less effective MAMP than chitin (Sánchez-Vallet et al. 2015).

Additionally, it has long been known that pathogenic fungi have evolved the ability to deploy effector proteins to evade pattern-triggered immunity (TABLE 1; for comprehensive and excellent reviews, see Lo Presti et al. 2015; Pradhan et al. 2021). One example is production of small secreted proteins (SSPs). Often associated with virulence, these proteins are typically up-regulated during infection, but many of their functions cannot be assessed simply through bioinformatic means. This is because most lack conserved functional domains (Lo Presti et al. 2015). Their functional analysis often requires additional experimental approaches. Specific effectors may function in the apoplastic space between plant cells, whereas others perform their functions within host cells (TABLE 1). The former are often cysteine (Cys)-rich proteins, whereas the latter usually have few Cys residues (Dutra et al. 2020). Cys-rich (usually even numbers) effectors can form disulfide bonds between Cys residues, leading to greater stability of the protein in the generally oxidative environment of

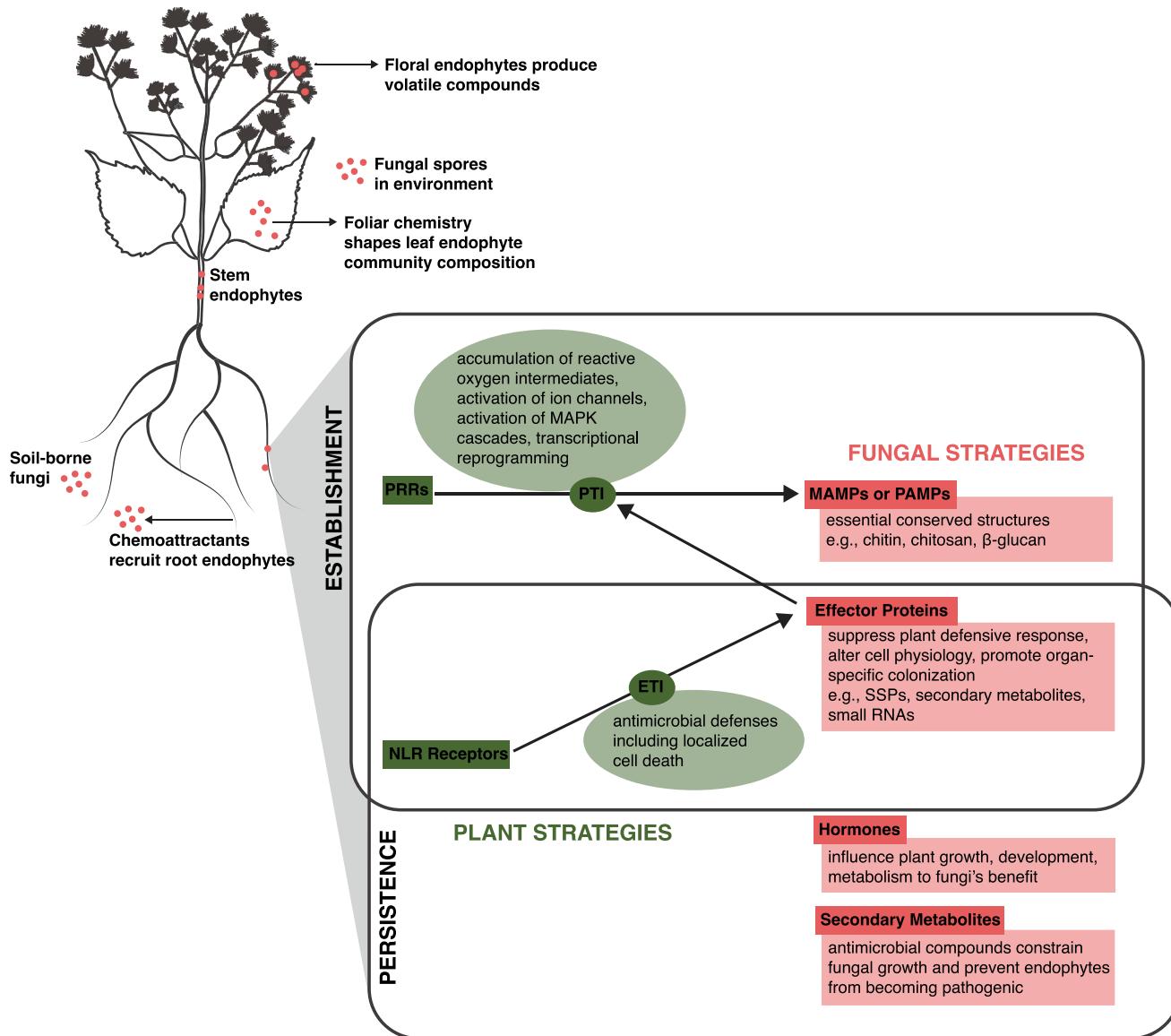


Figure 1. Fungal and plant communication/interaction strategies that may lead to establishment and persistence of endophyte communities. PRR = pattern recognition receptor; MAPK = mitogen-activated protein kinase; PTI = pattern-triggered immunity; MAMPs = microbe-associated molecular patterns; PAMPs = pathogen-associated molecular patterns; NLR = nucleotide-binding/leucine-rich repeat; ETI = effector-triggered immunity; SSPs = small secreted proteins.

the apoplast. Not limited to pathogens, even symbiotic fungi, such as the mycorrhizal *Glomus intraradices*, secrete effectors such as SP7 to inhibit transcription of defense-related genes in root cells (Kloppholz et al. 2011). Some effectors promote successful infection but may subsequently trigger a second layer of the plant inducible immune response: effector-triggered immunity (ETI). During effector-triggered immunity, a family of polymorphic intracellular nucleotide-binding/leucine-rich repeat (NLR) receptors bind to fungal effectors. Subsequently, plants can activate signaling pathways (Chagas et al. 2018), including localized cell

death, to stop pathogen growth (Cui et al. 2015; Jones and Dangl 2006). Plants and fungi are thus engaged in a coevolutionary arms race, and due to the selection pressure by fungal pathogens, *NLR* genes are the most rapidly evolving of plant genes (Cui et al. 2015).

Other types of microbially secreted molecules, such as secondary metabolites and small RNAs (Wang et al. 2016a), can function as effectors. Interestingly, homologous molecules are employed not only by pathogens, but also by other types of symbiotic organisms, such as endophytes, mutualists, and even saprotrophs (Rovenich et al. 2014) (TABLE 1). For example,

effectors containing LysM domains are encoded by both pathogenic and endophytic fungi (Suarez-Fernandez et al. 2021). These effectors can bind chitin and chitin oligomers, limiting pattern-triggered immunity responses (Desaki et al. 2018) and protecting fungi from plant chitinases (Sánchez-Vallet et al. 2020). Chitin derivatives (e.g., Myc and Nod factors) act as symbiotic signaling compounds for mycorrhizae and rhizobia bacteria (Genre and Russo 2016). LysM effectors also act to suppress plant immunity by manipulating plant hormone signaling associated with plant defense (Le et al. 2014). Effectors can also be considered more generally to be microbially secreted molecules that contribute to niche colonization (Rovenich et al. 2014). However, effectors in endophytes are far less studied compared with those of pathogens (TABLE 1). Although small secreted proteins have been bioinformatically predicted to be effectors in nonpathogenic endophytes, functional analyses are still needed to identify the potential roles of these “effector-like” proteins (Feldman et al. 2020) and to determine how they affect the organism’s ecology. Moreover, future research investigating how plants differentially mount effector-triggered immune responses to pathogenic vs. nonpathogenic endophytes will help inform our understanding of fungal endophyte community assembly.

Persistence.—Despite the intricately evolved plant immune systems outlined above, pattern-triggered immunity and effector-triggered immunity clearly do not exclude all fungi from colonizing plant hosts, as diverse communities of fungal endophytes accumulate and persist within plant tissues. Indeed, endophytes can establish compatible interactions with hosts and subsequently proliferate, engage in interactions with other colonizers, and induce changes to plant ecology and physiology. To do any of this, they must avoid eliciting MAMP-triggered immunity, or cope with it, or suppress it. For example, fungal effector molecules (including SSPs and some secondary metabolites; Brader et al. 2017) suppress plant defense responses and alter plant cell physiology, ultimately protecting the fungal colonizer by ensuring a hospitable environment. Chitin deacetylases from endophytic *Pestalotiopsis* spp. generate chitosan oligomers that, unlike chitin, no longer elicit plant immunity (Cord-Landwehr et al. 2016). Moreover, some biocontrol fungi can degrade chitosan and use it as a nutrient source (Palma-Guerrero et al. 2008).

Plant hormones are also important chemical signals that facilitate endophyte persistence. Not only do they

regulate internal processes, including defense and growth and development, but they are also critical to communication between plants and their associated microbial communities (Eichmann et al. 2021). Fungi can also produce compounds that act similarly to plant hormones, including auxins, cytokinins (CKs), gibberellic acids (GAs), ethylene (ET), abscisic acid (ABA), jasmonic acid (JA), and salicylic acid (SA) (Chanclud and Morel 2016). For example, the plant hormone indole-3-acetic acid (IAA) plays a role in the communication between host plants and endophytes or pathogens (Jahn et al. 2021). IAA is an auxin that plays a role in plant growth and development and is involved in most plant processes, including cell growth, root initiation, tropism, fruit ripening, and senescence. Fungal colonizers that can regulate IAA can influence plant metabolism to their benefit. For example, endophytes can increase root growth, which benefits both the endophyte and the plant by increasing nutrient uptake and tolerance to environmental stresses (Jahn et al. 2021). Chitosan is a known modulator of plant hormones and associated development (Lopez-Moya et al. 2019). High doses can block root development, causing modification of root cell division, polarity, and architecture (Lopez-Moya et al. 2017). These effects are due in part to repression of the main gene involved in IAA translocation, with auxin buildup in roots. Additional targets include GA, SA, and JA expression in roots (Lopez-Moya et al. 2017).

Ultimately, endophytes that persist in plant tissues must navigate complex plant immune system responses. Proposed in 1999, the “balanced antagonism” hypothesis addressed why endophytic infections are asymptomatic, despite the production of secondary metabolites by both fungal and plant partners (Schulz et al. 1999). Schulz and colleagues proposed that if fungal virulence and plant defense are balanced, the association remains apparently asymptomatic (Schulz et al. 1999). More recent work highlighted that asymptomatic colonization of plants by diverse communities of endophytic fungi is extremely complex, given the network of interactions between endophytic fungi (and bacteria) that has direct and indirect effects on the plant host. The chemical landscape of the plant changes as plants respond to colonization by endophytic fungi, but also because fungi secrete their own metabolites in response to both the plant immune system and other microbial competitors. In a test of the antimicrobial capabilities of fungal endophyte culture extracts, 60% of extracts inhibited growth of other fungal endophytes in vitro (Schulz et al. 2015). The concentration of these metabolites in situ may constrain the growth of fungal competitors, potentially preventing some endophytic fungi from

Table 1. Fungal/oomycete effectors for different lifestyles.

Lifestyle	Species	Effector	Characteristics/activity	Localization in host	Host target/effect	References
PATHOGEN Necrotroph	<i>Alternaria alternata</i>	AM toxin		Chloroplasts, plasma membrane		Park et al. (1981)
		AAL toxin, ACR toxin, AT toxin		Mitochondria	Asc-1; ACRS	Brandwagt et al. (2000); Meena and Samal (2019)
		ACT toxin, AF toxin, AK toxin		Plasma membrane	AB5r	Kohmoto et al. (1993); Tsuge et al. (2013); Meena and Samal (2019)
		SsCP1		Apoplast		Yang et al. (2018)
	<i>Sclerotinia sclerotiorum</i>	SsNep1, SsNep2		Chloroplast		Dallal Bashi et al. (2010)
		SS1TL		Mitochondria		Zhu et al. (2013)
		SSSSVP1				Lyu et al. (2016)
		SSV263				Liang et al. (2013)
		Sspp1d		Plasma membrane		Wang et al. (2009)
					Cytotoxic	Zhu et al. (2022)
	<i>Botrytis cinerea</i>	BcSSP2	Cys-rich; acts late in infection	Cytoplasm	Cell death	Bi et al. (2021)
		Crh1		Cytoplasm	Corresponding host R proteins: e.g., Rpi-Smir2, R1, R2, etc.	Oh et al. (2009); Rietman et al. (2012)
		AvrSmira2, PexRD2		Nucleus		Vleeshouwers et al. (2008); Chen et al. (2012); Rietman et al. (2012); Boevink et al. (2016)
		IPI-O, AvrSmira1, Avrib1b1, Pj04314, Avr3a, Avrnt1, Pj04089		Nucleus, cytoplasm		Armstrong et al. (2005); Wang et al. (2015); Pais et al. (2018)
		Avr1		Nucleus, cytoplasm, peroxisomes		Balvora et al. (2002)
				Nucleus, cytoplasm, microtubules		
				Endoplasmic reticulum		
				Plasma membrane		
	<i>Hemibiotroph</i>	<i>Phytophthora infestans</i> ^c	Transglycosylase			Van Poppel et al. (2008)
		Crh1				
		AvrSmira2, PexRD2				
		IPI-O, AvrSmira1, Avrib1b1, Pj04314, Avr3a, Avrnt1, Pj04089				
		Avr1				
	<i>PiAvr4</i>					
	<i>Pi03192</i>					
	<i>Avr2</i>					
	<i>P. sojae</i>	Avr1b-1	RXLR effector, but function not known	Cytoplasm	Soybean Rps1b	Song et al. (2013)
	<i>Magnaporthe oryzae</i>	Avr-Pita, Avr-Pita3, Avr1-CO39, Avr-Piz-t, AVR-Pik, AVR-Pia, BAS2		R proteins: e.g., Pi-ta, Pi-CO39(t), Rmg7, etc.		Orbach et al. (2000); Farman et al. (2002); Chang et al. (2008); Li et al. (2009); Mosquera et al. (2009); Yoshida et al. (2009); Okuyama et al. (2011)
		AvrPib				Zhang et al. (2015)
		BAS1				Mosquera et al. (2009)
	<i>BAS3, SLP1</i>					Mosquera et al. (2009); Mentak et al. (2012)

Table 1. (Continued).

Lifestyle	Species	Effector	Characteristics/activity	Localization in host	Host target/effect	References
		AvrP154, MSP1 Avr-Pita2, MC69, AvrP19, SPD1- 11, AVR-Rhng8 MoCDIP1-5		B1C, cytoplasm Apoplast		Ray et al. (2016; Wang et al. 2016b Chang et al. (2008; Saitoh et al. (2012; Wu et al. (2015; Sharpee et al. (2017; Anh et al. (2018; Chen et al. (2013)
		IUG6, IUG9, IUG18 AVR1 ^b		Apoplast, cytoplasm Appressorium (of fungus)		Dong et al. (2015)
	<i>Fusarium</i> <i>oxysporum</i> f. sp. <i>lycopersici</i>	AVR2 ^b AVR3 ^b Avr7 F5176-SIX4 SIX5 SIX2 SIX6 Mgl1LysM	Interacts with SIX5 Not known, but not suppressed by SIX4 Interacts with SIX3 Binds chitin Binds chitin	Xylem Xylem Xylem Xylem Xylem Xylem	I-7 (receptor-like protein, RLP)	Houterman et al. (2009) Rep et al. (2004) Gonzalez-Cendales et al. (2016) Thatcher et al. (2012) Ma et al. (2015)
	<i>Zymoseptoria</i> <i>tritici</i>	Mgl3LysM	Binds chitin Phytotoxic and antimicrobial	Apoplast	Protects fungal hyphae from host chitinases; suppresses chitin-induced ROS Modulates host microbiome POX12, maize peroxidase; blocks ROS generation	Houterman et al. (2007) Gawehns et al. (2014) Sánchez-Vallet et al. (2020)
Biotroph	<i>Ustilago</i> <i>maydis</i>	Mgx1LysM Zf6 Pep1 Pit2	Chitosanase Blocks phosphorylation of MAPK target Stabilizes protein kinase ZmTTK1 Binds active site of targeted proteases; autophagy repressor	Apoplast	Maize Cys proteases; Pit2 action blocks SA-mediated plant defense	Tian et al. (2021) Kettles et al. (2018) Lo Presti et al. (2015)
		Cmu1 See1 Tim1 Tim2 Tim3	Chorismate mutase Blocks phosphorylation of MAPK target Stabilizes protein kinase ZmTTK1 Binds active site of targeted proteases; autophagy repressor	Cytoplasm Cytoplasm Cytosol Apoplastic interaction zone Cytoplasm	Reduces chorismate, a precursor of SA Maize SG1; stimulation cell division in leaves Suppression of basal host immunity Maize ZmTTK1; promotes anthocyanin production, prevents lignification Maize Mir3 (& closely related) secreted cysteine proteases involved in defense response	Lo Presti et al. (2015) Lo Presti et al. (2015) Redkar et al. (2015) Brefort et al. (2014) Lo Presti et al. (2015)
		Jsi1	Suppressor of hormonal signaling; has an EAR (ethylene-responsive element binding-factor- associated = amphiphilic repression) motif, which resembles EAR motifs from plant ERF-TFs Adhesin for hyphal aggregation in tumors Suppresses apical dominance	Cytoplasm	ERF (ethylene-response factor) pathway via TOPLESS (TPL)/TOPLESS-related (TPR) corepressors	Darino et al. (2021)
	<i>Sporisorium</i> <i>reilianum</i>	Lep1 Sad1 Vag2	Down-regulation of SA-induced genes (see Cmu1, above)	Cytoplasm	Ubiquitination, signaling, and nuclear processes	Fukada et al. (2021) Ghareeb et al. (2015)
	<i>Cladosporium</i> <i>fulvum^a</i>	sr1641 Avr2	Inhibits the apoplastic proteases PIP1 and Rcr3	Apoplast	ZmCM2, cytoplasmic chorismate mutase Suppresses INF-1-induced cell death R proteins: Cf-2, Cf-4, etc.	Zhao et al. (2022) Dutra et al. (2020) Lo Presti et al. (2015; Pradhan et al. (2021)

(Continued)

Table 1. (Continued).

Lifestyle	Species	Effector	Characteristics/activity	Localization in host	Host target/effect	References
		Avr4	Binds chitin in fungal cell wall, protects fungus from plant chitinases	Fungal cell wall		Lo Presti et al. (2015; Pradhan et al. (2021)
		Ep6	Evolutionarily conserved across a variety of phytopathogenic fungi; contains 3 LysM domains. Sequesters chitin oligosaccharides released from cell walls of invading hyphae		Chitin-triggered host immunity	Bolton et al. (2008; Lo Presti et al. (2015; Pradhan et al. (2021)
		Tom1	Tomatinase that degrades α -tomatinine into the less toxic compounds: β -tomatinine, tomatidine	Apoplast		Pareja-Jaime et al. (2008)
		AvrL567			Flax L5-L7	Petre et al. (2014; Wu et al. (2019)
<i>Melampsora</i> <i>lini</i>		AvrP4 AvrP123 RTP1	Small Cys-rich protein Small Cys-rich protein, protease inhibitor Structural/stabilizing role in host cell by forming amyloid-like filamentous structures		Flax P4 Flax P123	Petre et al. (2014; Wu et al. (2019) Petre et al. (2014; Wu et al. (2019) Kemen et al. (2005)
<i>Uromyces</i> <i>viciae-</i> <i>fabae</i> / <i>Uromyces</i> <i>striatus</i>						
ENDOPHYTE	Multiple				Multifunctional effectors targeting host and microbes	Snelders et al. (2018)
	Multiple				Microbe-targeting effectors	Snelders et al. (2018)
	<i>Glomus</i>	SP7	Blocks expression of several <i>Medicago truncatula</i> defense-related genes		ERF19, ethylene-responsive TF that regulates defense-related genes	Kloppholz et al. (2011; Lo Presti et al. (2015)
	<i>Intraradices</i>				PtJAZ6, negative regulator of JA-induced gene regulation in <i>Populus trichocarpa</i> . JA-induced genes, e.g., those with predicted function in cell wall modification; could facilitate hyphal entry into root and establishment of Hartig net	Lo Presti et al. (2015; Daguere et al. (2020)
	<i>Laccaria</i> <i>bicolor</i>	MISSP7	Prevents jasmonic acid (JA)-dependent degradation of PtJAZ6 repressor, resulting in repression of JA-induced genes. Differs from strategy of AMF and biotrophic pathogens that induce JA responses during host colonization.	Nucleus		
SAPROTROPH	<i>Trichoderma</i> <i>atroviride</i>				Possible role in control of hyphal growth	Seidl-Seiboth et al. (2013)

^aSee Pradhan et al. (2021) for a more complete list.^bAVR1, also known as (aka) SiX4; AVR2, aka SiX3; AVR3, aka SiX1.

becoming pathogenic (FIG. 2) (Schulz et al. 2015), but this remains to be tested. More generally (including in human systems; Manor et al. 2020), diverse microbiomes can be disease suppressive (Garbeva et al. 2006). In plants, the chemical warfare between plants and fungi and among fungal endophytes may reinforce the persistent nature of these symbioses.

Future research on mechanisms of communication will help to inform how plant-endophyte interactions both establish and persist. Using knowledge from interactions between plants and their fungal pathogens, we can generate hypotheses about the key regulatory pathways (both fungal and plant) that are activated or suppressed during endophyte colonization. Examining

transcriptomic and metabolomic changes through time could also help tease apart the mechanisms responsible for endophyte establishment and maintenance.

SPECIALIZED COMMUNICATION STYLES FOR SPECIALIZED LIFESTYLES

Like pathogens, endophytic fungal communities show affinity for different plant organs. Within hosts there are fundamental differences in microbial community structure and composition in leaves compared with roots (Durand et al. 2017; Fonseca-García et al. 2016; Hamonts et al. 2018), and these distinctions have been attributed to differences in ecological processes that

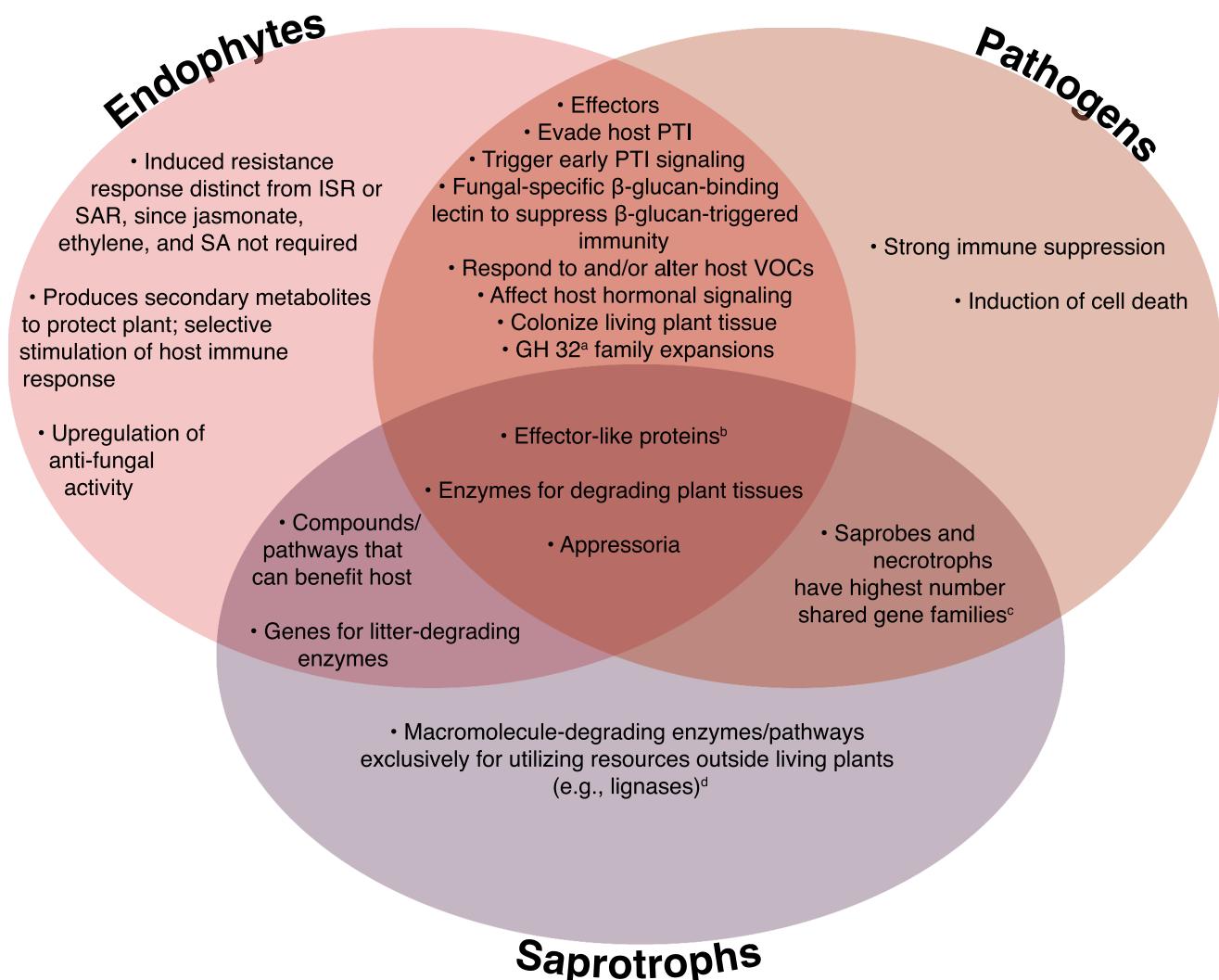


Figure 2. Venn diagram comparing and contrasting endophyte, pathogen, and saprotroph communication. This figure shows characteristics found in common between or unique to the three types of fungi. If a trait is found in a particular area of the diagram, this means that it has been observed for at least some fungi; its presence does not necessarily indicate that a particular trait is found in all fungi for a particular classification. ^aGlycoside hydrolase family 32 enzymes (GH 32) (Parrent et al. 2009). ^bEffect-like proteins (Feldman et al. 2020). ^cPandaranayaka et al. (2019). ^dExamples of lignases present in specific saprotrophic species, with references: *Phanerochaete chrysosporium*, *Schizophyllum commune*, *Dichomitus squalens*, *Trametes versicolor*, and *Trichoderma harzianum* (Asemoloye et al. 2020; Benoliel et al. 2005).

drive microbial community composition. For instance, in a coastal dune ecosystem, host species and geographic distance were the primary drivers of fungal leaf endophyte communities, whereas root endophytes were structured by environmental filtering (David et al. 2016). Plant-endophyte communication may also govern organ specificity of endophyte communities. The “habitats” (i.e., plant organs) encountered by different fungi might be expected to inform the evolution of different forms of communication, or at least the need for different subsets of molecules and their perception, depending on the plant organ where a fungus may need to develop in its host. Endophytes of roots and leaves have been most extensively studied to date, but a growing number of studies of both stem and floral fungal endophytes are proving to be fruitful as well (Martins et al. 2021; Qian et al. 2014; Skaltsas et al. 2019). Moreover, within different plant organs, fungi can operate on an endophyte-pathogen or an endophyte-saprotroph spectrum (Zanne et al. 2020). Endophytes exist asymptotically inside plants and may provide benefits, such as protecting plants from abiotic stresses and/or pathogens (Busby et al. 2016). However, in some cases, endophytes may facilitate pathogens (Busby et al. 2016). Pathogens include parasites, which tend to reduce host fitness but rarely kill the host; these are typically biotrophic fungi. Other pathogens do lead to host death, with necrotrophic fungi inducing tissue death to provide fungal nutrient acquisition (Shao et al. 2021). Saprotrophs derive nutrients from decayed plant (and other) species. Some fungi can shift between these functional guilds on ecological or evolutionary timescales to increase fitness (Zanne et al. 2020). This leads to changes in communication strategies employed by fungi, and the mechanisms used by plants to respond (or not). Not surprisingly, there are strategies that are both unique to and also shared among fungal guilds (FIG. 2). Here we present aspects of communication for such organ-specific endophytic interactions and explore possible differences among endophytes and pathogens or saprotrophs.

Organ-specific communication of fungal endophytes.—Belowground, plant roots secrete various compounds that act as chemoattractants to root-colonizing microbes in the soil, initiating plant-fungal communication prior to physical contact that actively shapes the composition of the fungal community (Lombardi et al. 2018). Arbuscular mycorrhizal fungi (AMF) are crucial endophytes of plants that provide multiple fitness benefits to their host species (Delavaux

et al. 2017). Their association and entry into plant roots elicits a plant response that includes initiating the common symbiosis pathway (CSP), altering gene expression and root morphology (Lu et al. 2021). Their escape of early plant defense responses is due, in large part, to transcriptional reprogramming of the plant hormone defense signal, followed by a transient repression of plant immune responses. The initial transient stress induced by chemical mediators released by the fungus can transition to the eventual symbiotic response after endophyte and host initiate contact (Vahabi et al. 2015). Other root-specific endophytes such as *Serendipita indica* employ genes encoding a fungal-specific β -glucan-binding lectin to efficiently suppress β -glucan-triggered immunity in different plant hosts. This process is mediated by altering fungal cell wall composition or properties (Lu et al. 2021). During colonization by *S. indica*, extracellular ATP accumulates in the apoplast at early symbiotic stages. Additionally, fungal-derived enzymes, i.e., ecto-5'-nucleotidases, can modify plant-derived apoplastic nucleotide levels in a way that prevents the plant from mounting an immune response against this beneficial root endophyte (Nizam et al. 2019).

Leaves, like roots, produce chemical compounds that can be sensed and utilized by other organisms in the environment. For example, volatile organic compounds (VOCs) are particularly important for communication with other plants and insects (Pieterse and Dicke 2007). Foliar VOCs can also play a significant role in determining the characteristics of leaf-associated microbial communities through antimicrobial effects and by serving as a carbon source (Farré-Armengol et al. 2016). But in contrast to the rhizosphere, before plant-fungal communication can begin in leaves, there must be a physical encounter between the leaves and fungi that arrive on their surfaces. Leaf-associated endophytes originate in diverse environmental sources, including the leaf litter, soil, rain, air, and neighboring plants (Herre et al. 2007), and possibly via pollinators, although this may be more limited to floral endophytes (Cullen et al. 2021). Once present on the leaf surface as germinated spores or hyphal fragments, fungi grow in an undirected fashion until they encounter and enter stomata or leaf lesions (Huang et al. 2018). There is some suggestion that appressoria may also provide a mechanism of entry for some endophytes directly through the leaf cuticle (FIG. 2) (Thilini Chethana et al. 2021).

Some endophytes may be acquired from the environment, whereas others are inherited vertically, from the parental plant (Becker et al. 2016; Card et al. 2021). Clavicipitaceous fungi, most notably in the genus *Epichloë*, are ascomycete endophytic species on grass

hosts (Clay and Schardl 2002), primarily found in leaf primordia and leaf sheaths (Liu et al. 2017). Whereas sexual *Epichloë* species may reduce host fitness by suppressing seed production, asexual species are symptomless, and their transmission is vertical via the host seeds (Chung and Schardl 1997). The relationship between host and endophyte has many possible benefits for grasses, including protection from mammalian and invertebrate herbivores via production of secondary metabolites, such as alkaloids (Clay 1988). *Epichloë* colonization can also cause dramatic restructuring of the plant microbiome, although the outcomes in previous work vary for bacterial vs. fungal microbiomes as well as aboveground vs. belowground communities (Mack and Rudgers 2008; Nissinen et al. 2019; Novas et al. 2005; Zabalgogeazcoa et al. 2013). It is well known that *Epichloë* can inhibit important phytopathogenic fungi (Xia et al. 2018). Apparently, this effect is not restricted to one type of pathogen, since both biotrophic (e.g., *Blumeria graminis*; Kou et al. 2021) and necrotrophic (Pérez et al. 2020) fungi are inhibited. This property may be due to the production of antifungal compounds, stimulation of the plant immune response (involving up-regulation of specific hormonal pathways used in defense), or physical exclusion of pathogenic fungi (Card et al. 2021). In the case of biotrophs (e.g., *B. graminis*), in addition to activation of plant defense SA signaling pathways, incremental changes in SA levels were observed, as well as increased expression of genes associated with antifungal activity, i.e., β -1,3-glucanase and callose synthase (Kou et al. 2021).

Fungal endophytes have also been identified and characterized to some extent in stem and floral tissues (Martins et al. 2021; Qian et al. 2014; Skaltsas et al. 2019). The fungal endophytic community in stem tissue of some Amazonian hardwood tree genera was relatively recently explored and correlated with host developmental stages (Skaltsas et al. 2019). The dominant community members found in adult stem (i.e., inner bark) tissues were potentially saprotrophic species (e.g., *Trichoderma* spp., *Penicillium* spp., and *Tolypocladium* spp.), whereas seedling stem tissue was more highly populated with pathogenic species (e.g., *Diaporthe* spp.). Some members of the filamentous pathogenic *Diaporthe* genus have the capability of transforming the infection-inhibiting factors (+)-catechin and (−)-epicatechin into the 3,4-*cis*-dihydroxyflavan derivatives (Shibuya et al. 2005). However, the molecular mechanisms responsible for the observed differential dominance by one taxonomic group in one or other developmental stages of these tree species remains to be determined. Even fewer examples have been published on floral endophytes. Qian et al. (2014) identified

from mistletoe (*Viscum coloratum*) a floral endophytic fungus, *Lasiodiplodia* sp. ME4-2, most related taxonomically to *L. pseudotheobromae* (Qian et al. 2014). Of particular interest, this isolate was found to produce a variety of aromatic compounds, including two indole-containing compounds, indole-3-carboxylic acid (ICA) and indole-3-carbaldehyde, both of which are valuable for pharmaceutical and agricultural industries (Qian et al. 2014). Additionally, the study found high levels of 2-phenylethanol, a common component of essential oils derived from flowers. Such compounds may not only influence the communication between host plant and endophyte but may have additional impacts on the ecology of microbe-plant-pollinator communities (see “Ecological implications of plant-endophyte communication,” below).

Organ specificity of fungal endophytes could be attributed in part to the arsenal of fungal effectors, as has been shown to occur in some plant-pathogen interactions. For example, *Ustilago maydis*, the causative agent of galls on maize, can infect all aboveground plant organs. The ability to infect such diverse plant tissues requires organ-specific effectors, whose expression is differentially regulated depending on the tissue spores come in contact with (Reviewed in Lanver et al. 2017). Thus, an effector such as See1 is expressed in seedlings, but not in tassels, where it is not required for virulence. Conversely, there are effectors required for virulence in tassels (e.g., Um03046, Um03650, and Um05439). The *um03046*, *um03650*, and *um05439* genes are barely expressed—nor are they required for virulence—in seedlings (Schilling et al. 2014). Although detailed analyses of endophyte “effectors” have yet to materialize, they are increasingly being investigated in different host tissues. Examining possible roles of effectors in organ or host specificity of endophytes would be valuable for microbial community ecologists who frequently face a high degree of unexplained variation in endophyte community composition (Christian et al. 2020).

How endophytes differ from pathogens: the mutualist-to-pathogen spectrum, differences in communication and response.—Much of what we have learned or hypothesized about mechanisms of plant-endophyte communication has built upon studies of plant-pathogen interactions. Given the shared evolutionary history of some endophyte and pathogen lineages (e.g., Spatafora et al. 2007; Wheeler et al. 2019), it is perhaps not surprising that pathogens and endophytes share many communication strategies in

common (FIG. 2). Fungi also have the flexibility to exhibit different lifestyles (e.g., endophytic or pathogenic) depending on genotype, environmental condition, and potential host. *Fusarium oxysporum* is one such ubiquitous soil-borne fungus, with specific isolates responsible for wilt on a wide range of host plants, including tomato, tobacco, banana, legumes, cucurbits, and even herbaceous plants (Joshi 2018). Both pathogenic and nonpathogenic *forma speciales* can be found persistently in soils (potentially for years), even absent of wilt for a particular host species, demonstrating their saprotrophic capabilities as well (Park 1959). Among these, some isolates behave as endophytes that colonize plant roots without causing disease symptoms. This suggests that in addition to communication strategies shared by pathogens, they also have unique ways of communicating with plant hosts. They appear to lack pathogenicity chromosomes present in known pathogenic *forma speciales*, which typically encode virulence proteins or effectors (De Lamio and Takken 2020). Yet, like other endophytes, endophytic *F. oxysporum* must have some way of suppressing or evading host responses that would otherwise hinder their proliferation or eliminate them from a potential host plant (FIG. 2) (Gadkar et al. 2001; Jacobs et al. 2011). Some clues about the basis for endophyte avoidance of plant immune responses come from co-inoculation studies. For instance, when nonpathogenic *F. oxysporum* and a *forma specialis* specific for asparagus were inoculated together in asparagus plants, there was a reduction in disease prevalence. This phenomenon has been termed endophyte-mediated resistance (EMR; De Lamio and Takken 2020). Moreover, the nonpathogenic *F. oxysporum* induced approximately 10% cell death observed in roots, a phenotype absent with only inoculation of the pathogenic *forma specialis* (He et al. 2002). Comparative transcriptome profiles from analogous studies in soybean roots discovered up-regulation of several MAPKs at a relatively late infection stage (72 hours post infection), whereas the endophytic strain induced zero MAPKs (Lanubile et al. 2015). Thus, pathogenic strains seem to trigger stronger immune suppression of host, even though both pathogenic and endophytic strains trigger early pattern-triggered immunity signaling (FIG. 2). De Lamio et al. (2018) identified two Pathogenesis-Related (PR) proteins (NP24, a PR-5; and a β -glucanase) that were altered in a biocontrol experiment where endophytic and pathogenic *F. oxysporum* were used to co-infect tomato. The *F. oxysporum*-induced resistance response in tomato was distinct from induced systemic resistance (ISR) or systemic acquired resistance (SAR), since jasmonate,

ethylene, and SA were not required (FIG. 2). Thus, some additional, as-yet-unexplained plant defense response appears to have been triggered by the endophyte that differentially affects its survival relative to that of the pathogenic isolates. *F. oxysporum* as a root endophyte can also lead to reduced disease caused by other vascular pathogens (e.g., *Verticillium dahliae*, *Pythium ultimum*) (Ishimoto et al. 2004). This protection does not extend to aboveground pathogens (e.g., *Botrytis cinerea*, *Phytophthora caprici*) (De Lamio and Takken 2020).

In some cases, the difference between a pathogen and an endophyte can be as simple as a single gene. Freeman and Rodriguez (1993) isolated a mutant of *Colletotrichum magna*, the causative agent of anthracnose on cucurbits. The path-1 mutant, whose mutation mapped to a single genetic locus, was nonpathogenic. However, it retained the ability to infect the same host range as wild type, as well as properties of spore adhesion to plants, spore germination, and appressoria formation. Moreover, the path-1 mutant grew as an endophyte that, remarkably, protected host plants from superinfection by other phytopathogenic fungi, including wild-type *C. magna*, *C. orbiculare*, and *F. oxysporum* (Freeman and Rodriguez 1993). Mutants such as path-1 demonstrate that the underlying bases of host specificity and pathogenicity can be distinct and, therefore, teased apart through the isolation of such mutants. Further dissection of the mechanism(s) whereby path-1 acts as both endophyte and protector indicated that protection was tissue specific (mediated in stems, but not cotyledons) and correlated with a more rapid induction of plant defense response in path-1-colonized plants compared with those inoculated only with wild type (Redman et al. 1999). Since a very important component of host resistance is the timing and activation of the defense response following recognition of the pathogen, a working model proposed by Redman et al. (1999) posits that path-1 either activates plant defenses to very low levels or primes the defense system without activation. If a threshold level of fungal metabolites is required for a full plant response, path-1 may expose the plant to concentrations of fungal metabolites slightly below threshold levels, thus preventing defense system activation. However, when a pathogen is also present, the virulent fungus adds to the levels of metabolites, yielding threshold levels necessary for defense system activation. What this model does not explain, however, is how the endophyte eludes and survives the plant response, once activated.

Recently, Almeida De Menezes et al. (2023) completed sequence analysis of the genome for

Ophiocordyceps australis. *O. australis* is an entomopathogenic fungus that parasitizes ants (Hymenoptera, Ponerinae, Ponerini), leading to their behavior as “zombies” that facilitate fungal spore dispersal (De Menezes et al. 2023). Its inventory of CAZymes (plant cell wall-degrading Carbohydrate-Active enZymes) includes 28 related to degrading cellulose, hemicellulose (xylan, xyloglucan, and galactomannan), pectin, starch, and inulin and is predicted to support a full endophytic stage (De Menezes et al. 2023). Such findings support earlier reports of this fungus existing as an endophyte (Lei et al. 2015). Moreover, genes encoding Mad2 and GHs (glycosyl hydrolases) in *O. australis* may add to our understanding of the infection process in plants and the interkingdom colonization exhibited by such a fungus.

Given the continuum that exists between pathogenic and endophytic fungi that colonize plants, more work is needed to understand how plants recognize “pathogens” and “endophytes” and how these fungi differentially respond to mounted plant defenses. Of particular interest are latent pathogens—fungi that colonize and exist as asymptomatic endophytes for some period of time before switching to a pathogenic lifestyle. What fungal genomic machinery underlies this functional lability, and how does the plant response change in response to a fungal guild shift?

Saprotry and communication leading to endophytism or pathogenic lifestyles.—Saprotrhops are generally defined as fungi that consume dead plant material, whereas endophytes live asymptotically inside living plants. An additional way to distinguish saprotrhops from endophytes is by comparing the ways in which these fungi may provide benefits to plants. Some fungi can act in both capacities. For example, dark septate endophytes, a diverse, ubiquitous group of fungal generalists, can behave as saprotrhops, by mineralizing complex soil substrate, often leading to improved plant nutrition and physiology (Malicka et al. 2022). In contrast, they also have broad niches in host plants. As endophytes of roots, they colonize plant hosts in stressful environments, including those with high salinity, heavy metals, or drought. In this capacity, they can provide protection from heavy metals by reducing uptake and sequestering heavy metals in root cell walls as insoluble compounds, blocking transport to shoots (Malicka et al. 2022). They have evolved melanin-dependent and melanin-independent mechanisms to detoxify heavy metals and can also scavenge reactive oxygen species (Malicka et al. 2022). The key to such functional flexibility is in the fungal genome. *Laccaria*

bicolor, an ectomycorrhizal fungus, was the first mycorrhizal fungus to have its complete genome sequenced (Martin et al. 2008), an accomplishment that revealed the genomic basis for its dual lifestyle as a plant root colonizer and decomposer of organic matter (Martin and Selosse 2008). Similar flexibility has been found for root fungal endophytes, including the nonmycorrhizal *Phomopsis liquidambari*, which has gene sets involved in lifestyle transition from saprophytism to endophytism (Zhou et al. 2018a). These genes include those involved in the broad processes of translation, ribosome biogenesis and MAPK signaling; several were up-regulated in the endophytic stage but not in the saprotrophic stage.

Leaf fungal endophytes are also increasingly being considered to be latent saprotrophs, due to their potential contributions to litter decomposition. When screened for enzymatic activity, many endophytes have been shown to produce litter-degrading enzymes such as cellulase, laccase, pectate transeliminase, pectinase, lipolytic enzymes, and proteolytic enzymes (Kumaresan and Suryanarayanan 2002; Suryanarayanan et al. 2012). Endophytes’ enzymatic machinery could facilitate colonization of living plant hosts, but it is also potentially useful if endophytic organisms can adopt a saprotrophic life stage as well (FIG. 2) (Guerreiro et al. 2018). This strategy could give leaf fungal endophytes priority access to labile resources of freshly fallen leaf litter, such as energy-rich and easily consumed sugars and peptides (Gołębiewski et al. 2019). In contrast, later-stage saprotrophs may produce different enzymes, such as lignases, that are used to decompose and assimilate more recalcitrant substances, such as lignin and holocellulose, outside of living plants (FIG. 2) (Osono and Hirose 2009). Identifying how fungal endophytes (and the enzymes their genomes code for) in living leaves persist in decaying tissue could be useful for predicting decomposition rates at both local and global scales.

Interestingly, some fungi are so functionally flexible that they can exhibit all three lifestyles: endophyte, pathogen, and saprotroph. For example, *Pochonia chlamydosporia* is a plant root inhabitant that is first known as a nematophagous fungus, parasitizing nematode species that infest roots and thereby serving as a biocontrol fungus in plant protection strategies (Suarez-Fernandez et al. 2021). In this capacity, it must also be a plant endophyte, colonizing plant roots and potentially inducing plant defense. Finally, it is a weak saprotroph, persisting in soil. The sequencing of its genome revealed an expansion of hydrolases (Larriba et al. 2014), which may reflect the multitrophic behavior of the fungus. For example, one subset of these enzymes encoded by *P. chlamydosporia* contains those for generating and

degrading chitosan, such as chitin deacetylases or chitosanases (Larriba et al. 2014). A further key to *P. chlamydosporia*'s capacity for diverse lifestyles is its repertoire of LysM-containing effectors. This not only protects fungal hyphae from plant chitinases but also alters plant hormone signaling, thus allowing fungal penetration of root cells (Suarez-Fernandez et al. 2021). The four putative LysM effectors in *P. chlamydosporia* have differing levels of homology to LysM effectors of different types of fungi, including entomopathogens (functionally endophytic biocontrol fungi), phytopathogens, and saprotrophs. The divergence observed in conserved residues among LysM proteins of different origin (e.g., the presence of three Cys residues in endophytic fungal LysM motifs) may be part of the common evolutionary strategy of shielding fungal chitin from plant immunity, for both endophytes and pathogens. In contrast, for saprotrophs (e.g., *Aspergillus niger*), few Cys residues were found in each motif (Suarez-Fernandez et al. 2021).

ECOLOGICAL IMPLICATIONS OF PLANT-ENDOPHYTE COMMUNICATION

So far, we have illustrated some of the mechanisms by which endophytes and plants communicate. From the plant perspective, we have discussed how such communication involves triggering defensive signaling pathways that alter the chemical landscape in plant hosts.

From the fungal perspective, we have explored how communication strategies impact (or are impacted by) the biology and functional roles of fungal symbionts. These changes to plant and endophyte can have subsequent effects on how plants and endophytes interact, not only with each other, but also with other microbes and macrobes in the community (FIG. 3).

Plant-endophyte communication affects other microbial and plant interactions.

Communication between plants and a colonizing endophyte can have cascading effects for the community ecology of the entire plant-associated microbiome. When new microbial players are introduced into a plant system, the induced chemical changes can alter the plant habitat in ways that change the ability of other microbes to colonize and persist. For example, Leopold and Busby (2020) inoculated *Populus trichocarpa* leaves with the same mock community of fungal endophytes but manipulated the arrival order of the component species. They found that immigration history not only altered the ultimate composition of the *P. trichocarpa* leaf microbiome, but that it also influenced subsequent disease susceptibility independent of microbial community composition. The influence of immigration history on plant disease susceptibility was also strongly influenced by plant genotype, suggesting an important role of plant-endophyte communication in

Communication with endophytes influences plant chemistry

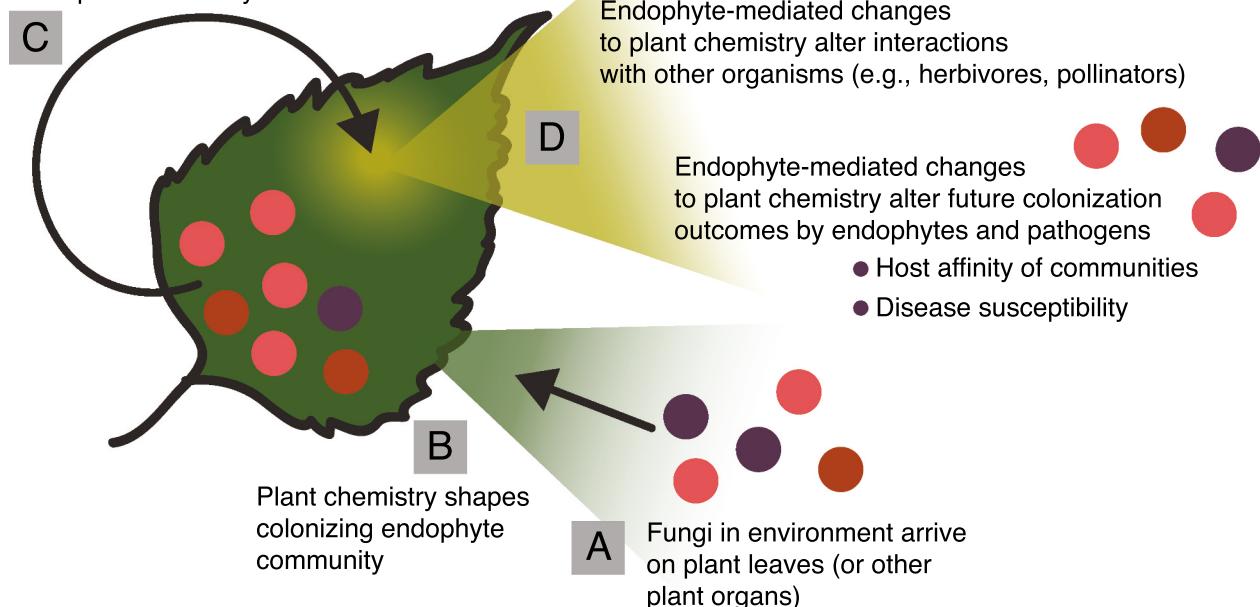


Figure 3. Plant-endophyte communication affects changes in plant chemistry that mediate future colonization outcomes by endophytes and pathogens, as well as affects interactions with macroorganisms (herbivores, pollinators).

microbiome composition and functional roles. For example, endophytes that arrive early can cause induced systemic resistance in their hosts, potentially changing physical and chemical traits that affect the establishment and persistence of endophytes or pathogens that arrive later (Leopold and Busby 2020). Moving forward, inoculation studies using tractable synthetic fungal communities can shed light on how endophyte-endophyte interactions affect both microbiome composition as well as the host itself. Pairing such manipulative studies with transcriptomic analyses would add insight into the fungal and plant mechanisms that underlie these impacts.

Ongoing communication between plants and fungal endophyte communities can also scale up to affect how plants interact with macroorganisms. For example, endophytes induce changes in chemical composition or other plant traits that affect plant-herbivore interactions. The classic example is the colonization of grasses by clavicipitaceous fungi. These fungi produce alkaloid toxins, which alter host physiology and ecology (Clay 1988). Consumption of these alkaloids by livestock, wild vertebrate herbivores, and insect herbivores can cause negative effects, and presence of the fungus can reduce herbivory pressure (Clay 1988). By reducing herbivory or altering other aspects of plant physiology (e.g., increasing plant biomass), colonization by clavicipitaceous endophytes can have cascading effects on co-occurring plant species, thus impacting plant population and community dynamics (Rudgers and Clay 2007). Communication between plants and horizontally transmitted endophytic fungi can also influence plant interactions. Leaf-cutter ants preferentially chose to cut leaves with lower abundances of leaf endophytes in their tissues (Estrada et al. 2013). Belowground, colonization by the root fungal endophyte *Serendipita indica* induced tolerance of rice plants to root herbivory by the rice water weevil, a major rice pest. Although colonization by *S. indica* did not directly affect herbivore survival or growth, it elicited gibberellin biosynthesis, resulting in compensatory regrowth of plant tissue (Cosme et al. 2016). Interestingly, because plant signaling can be systemic (e.g., root-to-shoot, shoot-to-root), the conversation between plants and their root or leaf endophytes can even translate to indirect effects on aboveground or belowground interactions, respectively. In the previous example, *S. indica* colonization of plant roots increased both root and shoot biomass (Cosme et al. 2016). Colonization by both vertically transmitted (Durden et al. 2019) and horizontally transmitted foliar endophytes (Zhou et al. 2018b) can reduce root-knot nematode infestation compared with endophyte-free individuals. Likewise, inoculation of maize with the root endophyte

Trichoderma atroviride decreased aboveground herbivory by *Spodoptera frugiperda* larvae (Contreras-Cornejo et al. 2018). These types of systemic effects have exciting potential for application in sustainable agriculture.

Endophyte-induced changes to plant volatile profiles could also feasibly affect plant-pollinator interactions, although direct evidence is scant (Cullen et al. 2021). Although floral microbes can have both endophytic and epiphytic habitats, most research on flower microbial communities has focused on epiphytic floral microbes and nectar microbes (Crowley-Gall et al. 2022; Morris et al. 2019; Rebolleda-Gómez et al. 2019). Floral microbes more generally have been shown to modify the chemical profiles of flowers directly and indirectly, and this has the potential to affect pollinator interactions with plants (Crowley-Gall et al. 2022; Martin et al. 2022). In some cases, fungal plant parasites, such as the anther smuts (*Microbotryum violaceum* complex), have also been shown to affect floral visitation by pollinator species (Gupta et al. 2012; Shykoff and Bucheli 1995). Given the effects on other aspects of plant chemistry and defense, it is tempting to speculate that communication between plants and their endophytes, not only in flowers but also in leaves and roots, plays roles in attraction of pollinator species. Additional studies are needed to test that hypothesis. In addition, given the role played by microbes in affecting pollinator behavior, it has been hypothesized that pollen receipt may be affected by pollen-transmitted endophytic microbes and their roles in pollen viability or tube growth (reviewed in Cullen et al. 2021).

Host affinity of endophytic communities.—Not only do distinct fungal communities form in different plant organs (see “Organ-specific communication of fungal endophytes”), but fungal endophyte communities can also show differential affinity for host species (Christian et al. 2020; Dastogeer et al. 2018; Gange et al. 2007; Vincent et al. 2016; Wang et al. 2019; Wearn et al. 2012; Whitaker et al. 2020; but see Higgins et al. 2014). It is not always clear why a host signature persists in endophyte communities, and ecological factors such as plant abundance may drive host specificity more than plant evolutionary history (Apigo and Oono 2022). However, even if host plant phylogenetic relatedness is an unreliable predictor of endophyte community composition (see Liu et al. 2019; Whitaker et al. 2020 for contrasting results), host affinity can be partly attributed to a variety of host structural and physical traits, including leaf mass per area, leaf punch strength, specific root length, or nutrient content (Deveautour et al. 2018;

Tellez et al. 2022). Plant chemical characteristics also play an important role in determining the composition of local endophyte communities. For instance, differences among *Psychotria*-associated endophyte communities in a common garden have been attributed to differences in host chemistry (Christian et al. 2020). Similarly, metabolomic differences in different horseradish (*Armoracia rusticana*) accessions explained about a third of the fungal endophyte community associated with those plants (Plaszko et al. 2022). Secondary metabolites may be antimicrobial or probiotic in nature, allowing the chemical composition of a plant to selectively promote or exclude various constituents of the endophytic community (Eichmann et al. 2021).

Interestingly, host plant chemistry is itself shaped by its communication with microbial consortia. For example, colonization by the endophyte *Chaetomium cochlioides* elicited a chemical response in its host, *Cirsium arvense*, that was similar to the response following wounding, herbivory, or pathogen invasion (Hartley et al. 2015). Similarly, inoculation of *Theobroma cacao* (cacao tree) with the endophyte *Colletotrichum tropicale* up-regulates plant defensive pathways such as the ethylene and jasmonic acid pathways (Mejía et al. 2014). The molecular mechanisms of plant-endophyte communication that we have highlighted throughout this paper are increasingly recognized for determining how endophytes modify plant disease (Busby et al. 2016). However, endophyte-induced changes to plant chemistry can also affect the community ecology of endophytic fungi by shaping future colonization or persistence of other endophytes. For example, field surveys have shown that the fungal endophyte *Colletotrichum tropicale* is a dominant member of the *T. cacao* leaf microbiome (Arnold et al. 2003). Experimental inoculations of cacao leaves with *C. tropicale* induce massive changes to the cacao metabolome that subsequently impair natural environmental colonization by other species of endophytes without inhibiting its own proliferation within leaf tissue (Christian et al. 2020). It appears that priority access to host tissues and subsequent plant-endophyte communication may help to reinforce species-affinity of these fungal communities (Christian et al. 2017a, 2020; Mejía et al. 2014, 2008).

Of course, endophytic fungi range from host specialists to host generalists (Christian et al. 2017b), and the fungal genome provides clues for ecological generalism. Recent research demonstrated that compared with specialist fungi, generalist Xylariaceae endophytes are under selection to diversify secondary metabolite gene clusters, via gene duplication, gene family expansion, and horizontal gene transfer. Fungi in the Xylariaceae

also occupy multiple functional guilds, so selection maintaining diverse genes for both endophytism and saprotrophy may explain their metabolic versatility (Franco et al. 2022). It remains unknown how the genomic signatures of specialist vs. generalist endophytes elicit different metabolomic responses in their plant hosts. This could be further investigated by pairing inoculation experiments with transcriptomic, metabolomic, and genome-wide association studies.

CONCLUSION

Fungal endophytes have evolved a variety of strategies to establish and persist in their host plants, all the while avoiding plant defense responses that would normally lead to their exclusion or, at least, hinder their persistence (FIG. 1). Chitosan, for example, in some fungal cell walls, may be a strategy to avoid host response (Sánchez-Vallet et al. 2015). It is important to note that many of the communication mechanisms we have identified as potentially facilitating the relationship between endophytes and their hosts were discovered in and primarily described for plant-fungal pathogen systems. Moving forward, confirming to what degree these mechanisms are conserved and/or modified for communication between plants and endophytic fungi will help inform what we know about when, why, and how these communities form and change. Endophytes are defined by their habitat, not their function, but unveiling the mechanisms that drive communication with their hosts can help inform their functional roles and ecology. For example, the number of Cys residues in fungal LysM proteins can provide clues to the functional guild of some fungi (Dutra et al. 2020; Suárez-Fernandez et al. 2021).

The question of what makes an endophyte act as an endophyte and not a pathogen or a saprotroph is also informed by the environmental and evolutionary constraints with which it is presented. Examples are becoming more prevalent even for necrotrophic fungi that can exist as endophytes, only becoming pathogenic to the host under new conditions (Van Kan et al. 2014). For example, *Botrytis deweyae* normally grows as an endophyte in ornamental daylilies (*Hemerocallis*) and elicits no stress responses or observable harm to its host but can show facultative pathogenic behavior (Grant-Downton et al. 2014; Van Kan et al. 2014). In this respect, plant-associated fungi resemble opportunistic fungal pathogens of animals and humans, e.g., *Candida albicans* or *Cryptococcus neoformans* (Pontón et al. 2000). Van Kan et al. (2014) proposed that the emergence of such endophytes “gone rogue” as

novel diseases may be due to increased inbreeding of hybrid lines and reduced host genetic diversity. Additional speculation envisions some aspects of endophytic behavior in plants as a milestone along a road to pathogenicity on insects (St. Leger and Wang 2020). As an example, consider *Epichloë*, among other endophytic *Hypocreales*, that synthesize peramine, a secondary metabolite that protects plants against herbivory and other fungi (FIG. 2).

Future experiments are needed to uncover the molecular biological bases, both proximal and distal, that favor the endophytic lifestyle, as well as the molecular, environmental, and evolutionary actors that lead to shifts between this phase and the other options available for evolutionary success. Furthermore, as climate change continues to alter existing ecosystems and species niches, fungi may increasingly shift along the endophyte-pathogen and endophyte-saprotroph spectra and engage in alternative functional roles. A better understanding of the molecular processes involved will also allow us to make new discoveries in endophyte and plant ecology (FIG. 3). For example, identifying factors that can trigger the breakdown of plant-endophyte communication and coexistence can help us predict plant disease epidemics or improve models of nutrient cycling. We encourage collaboration between ecologists and plant pathologists, molecular biologists, and geneticists, which will advance our understanding of how mechanisms of plant-endophyte communication scale up to affect the ecology of both plants and fungi.

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