ELSEVIER

Endophyte or parasite – what decides?

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Symbiosis between a fungus and a plant is a widespread phenomenon in nature. The outcome of such an interaction can vary in a seamless manner from mutualism to parasitism. In most cases, the host plant does not suffer, in fact it often gains an advantage from colonization by a fungus. This benefit is based on a fine-tuned balance between the demands of the invader and the plant response. If the interaction becomes unbalanced, disease symptoms appear or the fungus is excluded by induced host defence reactions. Symbioses of plants with beneficial or neutral endophytes share many common attributes with plant interactions with pathogens. Recent findings emerging from studies of compatible host–fungus interactions have enhanced our understanding of what determines whether the fungus behaves as an endophyte or a parasite and of how plants avoid exploitation by detrimental parasites but benefit from mutualistic endophytes.

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Introduction

Most, if not all, plants studied in natural ecosystems are infested by fungi that cause no disease symptoms. These fungi are called endophytes, in contrast to parasites, which lead to disease and reduce the fitness of their host plants. There are reports that endophytes can become parasites under certain conditions and *vice versa* [1,2•]. Hence, host–microbe interactions can range from mutualism through commensalism to parasitism in a continuous manner [3,4]. As disease is the exception in plant–microbe interactions, it can potentially be regarded as an unbalanced status of a symbiosis. The molecular and biochemical basis for the switch from endophyte to parasite is still to be elucidated, but recent findings in studies of compatible plant–microbe interactions have enhanced our understanding of what factors determine endophytic and parasitic lifestyles. Decoding the switches that lead to mutualistic symbiosis or disease will reveal new targets and strategies for human intervention into these processes; for example, by formulating inocula with endophytes, generating improved plant germplasm or developing small molecules that interfere with plant–microbe interactions.

The balanced plant–endophyte status

Commensalism and mutualism represent the balanced stages of plant–microbe interactions. Commensalism provides benefit to the endophyte by enabling an undisturbed existence and nutrient supply without affecting the host. Mutualism, by contrast, is defined as an interaction that is beneficial for both partners. In addition to the providing benefits for the endophyte, mutualism frequently results in the promoted growth of the host. The beneficial effects for the plant can result from an improved supply of nutrients by the endophyte, as has been shown for the arbuscular mycorrhizal symbiosis, the most intensely studied mutualistic plant–fungal interaction [5]. Arbuscular mycorrhiza fungi (AMF) are widespread in terrestrial ecosystems, and both fossils and molecular analyses date their origin at more than 460 million years ago, suggesting that these fungi assisted plants in their colonization of land [6]. In addition to providing mineral nutrients, endophytes can also improve tolerance to abiotic stress. Leaf-endophytic *Curvularia* species, for example, confer adaptation of the grass *Dichanthelium* to extreme heat [7]. In addition, mutualistic symbionts can increase resistance against pathogens, as demonstrated for AMF in roots [8] and for a highly diverse endophyte spectrum of different ascomycete endophytes in leaves [9]. Moreover, a recent report has yielded evidence of regulation of systemic defence responses by endophytes: the root-endophytic basidiomycete *Piriformospora indica* enhances the resistance of barley plants not only to necrotrophic root parasites but also to the biotrophic leaf pathogen *Blumeria graminis* [10••].

Commensalism and mutualism require a sophisticated balance between the defence responses of the plant and the nutrient demand of the endophyte. Hence, a mutualistic interaction does not mean the absence of plant defence. Defence-related gene expression has been well-studied during mycorrhization. Induction is most prominent during the early stages of infestation [11], but can also be detected during arbuscule development [12]. It is therefore a finely tuned balance of antagonisms that keeps the mycorrhizal interaction in a stable state that disadvantages neither partner.

The unbalanced plant—endophyte status

The balance between an AMF and its host can be affected by genetic factors. A number of mycorrhizal plant mutants have been isolated [13] and, compared to wildtype plants, some of these show enhanced defence reactions to colonisation by AMF [14]. Apart from genetic factors, most switches from a mutualistic to a parasitic interaction are characterized by an imbalance in nutrient exchange. Especially during early stages of the interaction, when AMF build up their extraradical mycelium without providing mineral nutrients, colonization can depress the growth of seedlings [15]. In addition, certain plant–fungus combinations give better results in terms of plant nutrition than others [16]. This is probably explained by the facts that some plants are more dependent than others on the symbiosis and that different AMF have varying needs for carbohydrates [17,18]. To what extent nutritional imbalance is correlated with the increased expression of plant defence genes is not known and is a challenge for future investigations. In contrast to imbalance in favour of the endophyte, non-assimilating plants are able to invert the actual flow of carbohydrates and to parasite the fungal partner. This is generally the case during the germination of orchids when specific fungi colonize the rhizoids of the seed coat [19]. When interacting with certain non-photosynthetic plant species, however, AMF too may switch from a mutualistic into a parasitic symbiont [20].

Switching the lifestyle

Colonization of different hosts can cause a fungus to adopt contrasting lifestyles [21]. *Colletotrichum magna*, a fungal pathogen that causes anthracnose in cucurbit plants, exerts an endophytic lifestyle when growing asymptomatically on various non-cucurbit species. Moreover, specific mutated *C. magna* isolates are able to colonize cucurbit asymptomatically, and some exhibit even mutualistic effects [22,23]. Mutualistic mutants of *C. magna* also exhibit a broader host range; for example, they can colonise the non-host plant tomato and can even infest cucurbit cultivars that are resistant to *C. magna* without eliciting disease symptoms [24]. Hence, a single gene in *C. magna* confers the switch to mutualistic interactions and the expansion of host range. However, loss of fungal pathogenicity factors does not generally result in asymptomatic development and might provoke plant defences that restrict fungal growth [25•].

More recent work demonstrates a switch from mutualism to parasitism by a mutation in a single microbial gene [26••]. In the mutualistic interaction of the clavicipitaceous fungal endophyte *Epichloë festucae* with its ryegrass host *Lolium perenne*, the benefits to the plant include improved growth and persistence through improved acquisition and enhancement of plant tolerance to a range of biotic stresses. A screen to identify symbiotic genes isolated a fungal mutant that altered the interaction from mutualism to parasitism. Molecular analysis of this mutant provided a single-copy plasmid insertion into the *NoxA* gene, which encodes an NADPH oxidase. Plants that were inoculated with the *noxA* mutant became strongly infected, lost apical dominance, became severely stunted, showed precocious senescence, and eventually died. Cytochemical analysis proved that production of reactive oxygen species (ROS) was reduced in the mutant. Tanaka *et al.* [26••] suggest a symbiosis mechanism in which ROS production by the *E. festucae* NoxA *in planta* negatively regulates fungal development and hyphal tip growth, thereby preventing excessive colonization of the plant tissue.

Comparative plant transcriptome analysis in mutualistic and parasitic interactions

Recent analysis of plant–endophyte and compatible plant–parasite interactions enhance our understanding of common molecular re-programming principles resulting in a 'compatible' status [27–30]. A direct comparison of mutualistic and pathogenic interactions has been carried out in rice, in which whole-transcriptome responses to the AMF *Glomus intraradices* and to two root-infecting major pathogens *Magnaporthe grisea* (a hemibiotroph) [31] and *Fusarium moniliforme* (a necrotroph) were analysed [32•]. Among the approximately 50 000 rice genes that have been tested, 209 were upregulated and 15 were downregulated in the relatively late stages (more than 6 weeks after infection) of mycorrhiza development. A total of 30 genes were similarly responsive in each of the three interactions. Rice plants that were in a mutualistic interaction shared more responsive genes (73 genes) with plants that were infected by the hemibiotrophic fungus *M. grisea* than with those infected by the necrotroph *F. moniliforme* (52 genes). Importantly, a total of 12 genes (not including phosphate-responsive genes) were exclusively expressed in response to mycorrhiza, and thus represent potential marker genes for mutualism. Conspicuously, among these, genes that encode H_2O_2-producing and scavenging enzyme activities predominated, which correlates with the finding that H_2O_2 can be detected in arbuscule-containing cells [33]. This corroborates evidence that balancing of ROS might be of prime significance for maintaining compatibility in the mycorrhiza symbiosis [34].

Molecular targets for lifestyle determination

Because endophytes possess structural similarities with pathogens, they are the object of a host's non-self recognition (Figure 1). Additionally, cell wall penetration by a fungal intruder is normally accompanied by the release of plant-derived elicitor-active molecules. Hence, endophytes must avoid or overcome non-specific resistance responses to achieve successful penetration by reprogramming the invaded cell to accommodate infection structures and to maintain host cell integrity for a long-lasting interaction. Accommodation requires sophisticated recognition

Figure 1
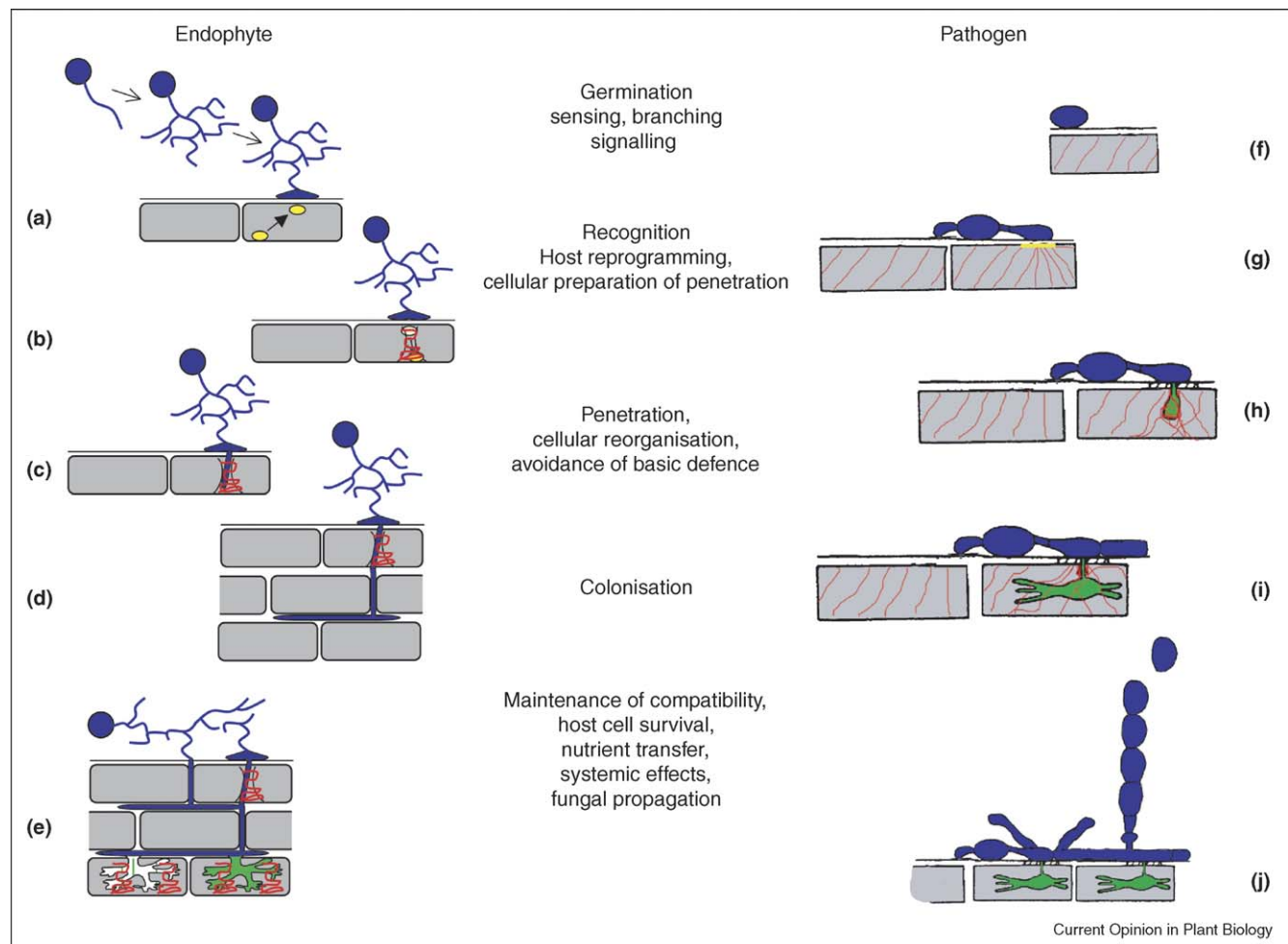
Symbiotic development of biotrophic endophytes and pathogens. **(a)** Once AM spores germinate and the germ tube approaches a root, apical dominance is abandoned and the branching of hyphae is triggered by 5-deoxy-strigol [37••]. Upon physical contact, the fungus forms an appressorium, which appears to induce the movement of the plant nucleus towards the contact site. **(b)** Cytoskeletal elements and the endoplasmic reticulum form the pre-penetration apparatus along the axis of nuclear movement [48••]. **(c)** The structure is entered by an infection hypha, from which **(d)** colonization of root cortex begins. Initial infestation is accompanied by a balanced induction of plant defence genes. **(e)** When the fungus finally reaches the inner cortex, it penetrates the cell wall and builds up a tree-like hyphal structure, the arbuscule. Arbuscule-containing cells have specific cytoskeletal structures and accumulate ROS. While arbuscules develop and decease, the fungus spreads further in the root and also colonises the surrounding soil. There it takes up mineral nutrients, which are transported into the root and exchanged for carbohydrates. **(f)** Once a powdery mildew fungus germinates, it forms an appressorium for host cell wall penetration. **(g)** Appressoria seem to release signals for the formation of membrane domains (yellow) into which host susceptibility factors and defence factors are recruited [42••]. In a compatible interaction, the host nucleus transiently migrates to the site of attempted penetration (not shown) and some actin filaments (red) polarise toward this site. **(h)** During penetration, host cell membrane is formed around the fungal feeding structure (green), which is closely enveloped by actin filaments and led by a ring of actin around the growing tip [46•]. **(i)** When the haustorium matures, a meshwork of cortical actin is maintained around the haustorial neck, whereas actin polarisation resolves. **(j)** Eventually, the parasite establishes secondary haustoria and fulfils its lifecycle by producing a new generation of conidia.

of the endophyte as a friendly intruder; for mycorrhiza, this recognition is realized by host receptor-kinase-mediated transmembrane signalling [35]. Receptor-kinase-mediated recognition is also involved in non-specific recognition of pathogens [36•]. Thus, the similarity of recognition of endophytes and parasites by plants indicates that a potential common basis might have been specified during the evolution of symbioses. Interestingly, a small plant-derived molecule that induces branching in a mycorrhizal fungus was identified as a strigolactone [37••]. As related molecules are also detected by the parasitic weeds *Striga* and *Orobanche*, similar molecules seem to play important roles during both friendly and unfriendly interactions.

For friendly interactions, it is not yet clear to what extents friendly recognition overbalances unfriendly recognition, the avoidance and modification of elicitors circumvents recognition, or antagonistic pathways are engaged to

switch off plant defence. Failure of defence is, however, not sufficient to enable a successful interaction if reorganisation of the host cell is required for the accommodation of fungal structures. The establishment of arbuscules calls for host activity in membrane dynamics, cytoskeleton reorganisation, host nucleus and organelle positioning and for further changes to the cellular architecture [38–41]. The underlying mechanisms are not understood, but some clues might come from plant interactions with obligate biotrophic pathogens in which the establishment and maintenance of fungal accommodation have been partially elucidated.

In the interaction of barley with the biotrophic fungal pathogen *Blumeria graminis* f. sp. *hordei*, host membrane subdomains enrich susceptibility factors, such as the receptor-like MLO protein, and seem to form gates for pathogen entry [42••]. *B. graminis* might contribute to the formation of such membrane domains by releasing signals from its penetration hyphae. MLO, a negative regulator of plant defence, interacts in these membrane domains with calmodulin, which is also involved in successful entry [43]. MLO also interacts with ROR2 (REQUIRED FOR MLO-SPECIFIED RESISTANCE2), a plasma membrane syntaxin that is required for basic resistance to powdery mildew fungi and accumulates in similar membrane domains [42••,44]. Hence, the same membrane domain might be involved in susceptibility (virulence) and defence. The involvement of membrane domains in the establishment of endophytic interactions was recently supported by the identification of a receptor-kinase that is upregulated by *P. indica* in roots of *Arabidopsis* and that accumulates in a lipid-raft-like membrane fraction [45]. Furthermore, MLO interferes with strong polarisation of the actin cytoskeleton during defence [46•]. Interestingly, fewer arbuscules were found in a *mlo* barley mutant than in wildtype plants [47]. This might indicate the involvement of MLO in establishing both parasitic haustoria in leaves and arbuscules in roots. It was therefore not surprising to find that actin reorganisation plays a role in both parasitic and mutualistic interactions, forming networks of microfilaments around fungal feeding structures [39,41,46•]. Moreover, cytoskeleton structures play an important role during early steps of symbiotic development. Recently, an AMF-induced pre-penetration apparatus consisting of cytoskeleton and endoplasmic reticulum was discovered in *Medicago truncatula*. This apparatus appears to build a cytoplasm bridge for plasma membrane invagination and subsequent fungal invasion [48••]. By contrast, a symbiosis-defective mutant of *Lotus japonicus* shows incompatible cytoskeleton reorganization and cell death when confronted with the AMF *Gigaspora margarita* [41]. Similarly, host actin structures seem to lead haustoria of *B. graminis* into host cells [46•]. Taking this evidence together, one can draw the fascinating picture that a plant intruder drums host susceptibility factors into crucial cellular subdomains, and

that the host accumulates defence compounds in the same domains, providing a molecular platform for balancing defence.

Another player in interactions between plants and endophytes or parasites could be calcium. Ca^{2+} spiking and Ca^{2+}- and calmodulin-dependent protein kinases (CDPKs) are involved in establishing AMF and in plant–pathogen interactions [13,49,50••,51–53]. RNA-interference-mediated knockdown of CDPK1 in *Medicago* induces defects in root development and failure of mycorrhization, together with actin disruption and defence gene expression [50••]. Interestingly, ROS production is also enhanced in CDPK1 knockdown lines. ROS generation is similarly linked to MLO, and MLO itself might balance defence reactions, as supported by its role in background resistance to cell-death-provoking pathogens such as *Fusarium graminearum* [25•].

Once an endophyte has entered a plant cell, cellular integrity has to be maintained for the period of interaction. In many plant–fungus interactions, the plant reacts to invasion by ROS production and a subsequent hypersensitive cell death reaction. As mentioned above, ROS can be also detected in plant–endophyte interactions. Whether fungal activity contributes to ROS production in the mycorrhiza symbiosis is not well understood. A recently detected fungal H_2O_2 generation that is mediated by superoxide dismutase in arbuscules could be involved either in removing the superoxide anion or in provoking an antioxidative plant response to H_2O_2 [54]. In any case, the plant oxidative burst seems to be balanced because cell death is rarely observed in response to AMF. The mechanism that achieves this balance is yet not known, but plant and fungal antioxidants might contribute to the protection of invaded cells against defence-associated ROS production. Like AMF, *P. indica* enhances the antioxidative capacities of barley [10••]. It remains to be shown, however, if the induction of the antioxidative apparatus in endophyte-infested plants reflects a defence reaction of the host and/or if it is part of creating a friendly environment for the fungus.

Conclusions

Mutualistic interactions between fungal invaders and a host plant are deciphered as a balance, under environmental, physiological and genetic control, that results in fitness benefits for both partners. Under this view, parasitism is an unbalanced symbiosis. As biotic and abiotic stresses commonly result in the production of ROS, rapid and strong activation and scavenging of ROS is potentially a prime mechanism in maintaining this balance. The host cytoskeleton and cell survival are potential targets for fungal virulence factors during mutualistic symbioses. We are just beginning to understand the molecular mechanism that balances defence against virulence. However, the development of tools for non-

invasive observation of fungal and plant subcellular activities during the establishment of mutualistic interactions will provide a deeper understanding of the highly localized reorganisation of the cell for defence and hospitality.

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