

# 1 What are Endophytes?

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## 1.1

### Introduction and Definitions

Taken literally, the word endophyte means “in the plant” (endon Gr. = within, phyton = plant). The usage of this term is as broad as its literal definition and spectrum of potential hosts and inhabitants, e.g. bacteria (Kobayashi and Palumbo 2000), fungi (Stone et al. 2000), plants (Marler et al. 1999) and insects in plants (Feller 1995), but also for algae within algae (Peters 1991). Any organ of the host can be colonised. Equally variable is the usage of the term “endophyte” for variable life history strategies of the symbiosis, ranging from facultatively saprobic to parasitic to exploitive to mutualistic. The term endophyte is, for example, used for pathogenic endophytic algae (Bouarab et al. 1999), parasitic endophytic plants (Marler et al. 1999), mutualistic endophytic bacteria (Chanway 1996; Adhikari et al. 2001; Bai et al. 2002) and fungi (Carroll 1988; Jumpponen 2001; Sieber 2002; Schulz and Boyle 2005), and pathogenic bacteria and fungi in latent developmental phases (Sinclair and Cerkauskas 1996), but also for microorganisms in commensalistic symbioses (Sturz and Nowak 2000).

Some authors also designate the interactions of mycorrhizal fungi with the roots of their hosts as being endophytic (reviewed by Sieber 2002). However, we concur with Brundrett (2004; see Chap. 16 by Brundrett), who distinguishes mycorrhizal from endophytic interactions; the former having synchronised plant-fungus development and nutrient transfer at specialised interfaces. Nevertheless, as we will see in this book, distinctions between mycorrhizal and non-mycorrhizal fungi are not always clear-cut [see Chaps. 9 (Bayman and Otero), 12 (Girlanda et al.), 13 (Rice and Currah), 14 (Cairney), and 15 (Schulz)]. Not only can mycorrhizal fungi become pathogenic, but, for example, dark septate endophytes (DSE) can assume mycorrhizal functions [Jumpponen and Trappe 1998; see Chaps. 7 (Sieber

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Microbial Root Endophytes

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and Grünig), and 15 (Schulz)]. In addition, there are also cases in which fungal root endophytes seem to be saprobes, e.g. *Oidiodendron maius* (see Chap. 13 by Rice and Currah) and *Phialocephala fortinii* (Jumpponen and Trappe 1998; Jumpponen et al. 1998; see Chap. 15 by Schulz).

Although there are diverse uses for the word endophyte, “endophytes” are most commonly defined as those organisms whose “...infections are inconspicuous, the infected host tissues are at least transiently symptomless, and the microbial colonisation can be demonstrated to be internal...” (Stone et al. 2000). Although these authors used this definition to describe fungal endophytes, it is equally applicable to bacterial endophytes.

It is important to remember that the definition describes a *momentary status*. Thus it includes an assemblage of microorganisms with different life history strategies: those that grow saprophytically on dead or senescing tissues following an endophytic growth phase (Stone 1987; see Chap. 8 by Bacon and Yates), avirulent microorganisms as well as latent pathogens and virulent pathogens in the early stages of infection (Sinclair and Cerkauskas 1996; Kobayashi and Palumbo 2000). Unfortunately, taken literally, it can include all pathogens at some stage of their development. Since the plant host responds to at least some infections with mechanical defence reactions (Narisawa et al. 2004; see Chap. 15 by Schulz), there is merit to Petrini’s additional characterisation of endophytic interactions as not “causing apparent harm” (Petrini 1991), which presumably refers to an absence of macroscopically visible symptoms. Aware of the determinative discrepancies, we will nevertheless use the term “endophyte” to describe those bacteria and fungi that can be detected at a particular moment within the tissues of apparently healthy plant hosts (Schulz and Boyle 2005).

## 1.2 Colonisation

In spite of the fact that bacteria are prokaryotes and fungi are eukaryotes, they share many attributes of their associations with plant hosts, e.g. both colonise root tissues inter- and intra-cellularly, and often systemically (Table 1.1). They do, however, differ somewhat in their modes of colonisation. Bacteria primarily colonise intercellularly (Hinton and Bacon 1995; Hallmann et al. 1997), though they have also been found intracellularly, e.g. *Azoarcus* spp. (Hurek et al. 1994). They are frequently found in the vascular tissues of host plants (Kobayashi and Palumbo 2000), which is advantageous for distribution, whereas asymptomatic colonisation by fungi may be inter- and intra-cellular throughout the root. Although DSE sometimes colonise the vascular cylinder in asymptomatic interactions (Barrow 2003), such colonisation is frequently associated with pathogenicity (Bacon and Hinton 1996; Schulz and Boyle 2005).

**Table 1.1.** Characteristics of the interactions of bacterial vs. fungal endophytes with plant roots (see also all other book chapters)

Criteria	Bacteria	Fungi
Host spectrum	Broad, depends on habitat, host, season	Broad, depends on habitat, host, season
Mode and site of infection	Passive through wounds and other tissue openings or active with enzymes or vectors, e.g. insects	Active: through stomata, cell wall or wounds
Nutritional source during first stage infection	Host exudates, dead cortex cells, plant debris	Storage material in the spores, dead cortex cells, plant debris, host exudates
Nutritional source during colonisation, i.e. during a “steady state” status	Components of the symplast and apoplast	Components of the symplast and apoplast
Growth in root	Inter- and/or intra-cellular, slow, low colonisation densities	Inter- and/or intracellular, often extensive
Growth from roots into the shoot	Yes	Sometimes
Systemic growth in roots	Possible	Possible
Tissue colonised	Primarily intercellular, also vascular tissue	Usually not within vascular tissue
Specialised structures for nutrient access	Nodules, glands	Sometimes
Physiological status	Only little data available	Balanced antagonisms, active interaction
Outcome of the interaction	Commensalism, mutualism or latent pathogenicity	Commensalism, mutualism or latent pathogenicity
Benefits for the microbial symbiont	A reliable supply of nutrients and protection from environmental stresses, passive transfer and spread between hosts via vectors, e.g. insects	A reliable supply of nutrients and protection from environmental stresses, advantages for reproduction and colonisation at host senescence
Potential benefits for the plant symbiont	Induced resistance, improved growth (N-fixation, phytohormones), synthesis of metabolites antagonistic to plant pathogens and parasites	Induced resistance, improved growth (phytohormones, improved access to minerals and nutrients), synthesis of metabolites antagonistic to predators and antagonists
Reproduction	Usually passive transfer and spread between hosts via vectors, e.g. insects, but also active, e.g. Pseudomonads	Active and passive following host senescence, sometimes with vectors

The assemblages of fungi that colonise plant roots are diverse (Vandenkoornhuysen et al. 2002). In contrast to endophytic growth in the above-ground plant organs, endophytic growth of fungi within the roots has frequently been found to be extensive (Stone et al. 2000; Schulz and Boyle 2005; see Chap. 11 by Lopez-Llorca et al.). Root colonisation can be both inter- and intra-cellular, the hyphae often forming intracellular coils, e.g. DSE (Jumpponen and Trappe 1998; Stone et al. 2000; Sieber 2002), the basidiomycete *Piriformospora indica* (Varma et al. 2000), or *Oidiodendron maius* (see Chap. 13 by Rice and Currah) and *Heteroconium chaetospora* (Usuki and Narisawa 2005), which can even form characteristic ericoid mycorrhizal infection units (see Chap. 14 by Cairney). DSE may also form ectendomycorrhiza (Lubuglio and Wilcox 1988) and ectomycorrhizal-like structures (Wilcox and Wang 1987; Fernando and Currah 1996; Kaldorf et al. 2004; see Chap. 15 by Schulz).

Many orchid roots are systemically and mycoheterotrophically colonised by fungi of the genus *Rhizoctonia* (Ma et al. 2003; see Chap. 16 by Brundrett) and *Leptodontidium* (Bidartondo et al. 2004). In some cases, e.g. *Fusarium verticillioides* (= *F. moniliforme*), colonisation by an avirulent strain was found to be systemic and intercellular, whereas pathogenic strains also colonised intracellularly (Bacon and Hinton 1996). Latent pathogens, e.g. *Cryptosporiopsis* sp. (Kehr 1992; Verkley 1999) may occasionally penetrate the vascular bundles (Schulz and Boyle 2005).

Bacteria usually invade the roots passively, e.g. at open sites on roots such as lateral root emergence or wounds (Kobayashi and Palumbo 2000), even achieving systemic colonisation from a single site of entry (Hallmann et al. 1997). Although colonisation densities of nonpathogenic endophytic bacteria are rarely as high as those of pathogenic bacteria, they are highest in the root tissue; perhaps because this is the primary site of infection (Kobayashi and Palumbo 2000; Hallmann et al. 1997; see Chap. 2 by Hallmann and Berg).

## 1.3

### Assemblages and Adaptation

Both fungal and bacterial endophytes have been isolated from the roots of almost all hosts studied to date [Petrini 1991; Stone et al. 2000; Kobayashi and Palumbo 2000; Sieber 2002; see Chaps. 2 (Hallmann and Berg), 3 (Kloepper and Ryu), and 7 (Sieber and Grünig)]. The assemblages of endophytes that colonise a particular host vary both with habitat and host, some even being adapted to very specialised habitats, e.g. the aquatic fungi that colonise submerged roots (see Chap. 10 by Bärlocher). Recent molecular methods enable better analyses of the geographical distribution of given

groups of microorganisms, for example that of the DSE [Jumpponen 1999, see Chaps. 7 (Sieber and Grünig), 12 (Girlanda et al.), and 15 (Cairney)].

Both diversity and colonisation density frequently increase during the course of the vegetation period (Smalla et al. 2001), since horizontal transmission predominates (Carroll 1988, 1995; Petrini 1991; Guske et al. 1996; Hallmann et al. 1997; Arnold and Herre 2003, see Chap. 2 by Hallmann and Berg). Particularly asexual sporulation increases in autumn at the end of the vegetation period.

Communities of endophytes inhabiting a particular host may be ubiquitous, or have what is frequently referred to as host specificity (e.g. Carroll 1988; Petrini 1996; Stone et al. 2000; Berg et al. 2002; Cohen 2004). We concur with Carroll (1999) and Zhou and Hyde (2001) that the term “specificity” should be reserved for organisms that will only grow in one host (Schulz and Boyle 2005). If this is not the case, this phenomenon could be termed host preference (Carroll 1999) or host-exclusivity (Zhou and Hyde 2001). Whether the interaction represents specificity, preference or exclusivity, an adaptation of host and endophyte to one another has occurred. The adaptation may not only be to a particular host, but to endophytic growth in one plant organ, e.g. in the roots in contrast to the shoots [Petrini 1991; Hallmann et al. 1997; Sieber 2002; Schulz and Boyle 2005; see Chaps. 2 (Hallmann and Berg), and 7 (Sieber and Grünig)].

It is often extremely difficult to know whether or not a particular fungus or bacterium that has been detected in healthy plant tissue has actually been growing within the host tissue or has been incidentally isolated, i. e. is normally found on other substrates. As reviewed by Schulz and Boyle (2005) and in Chap. 17 by Hallmann et al., there are four methods presently in use for detecting and identifying fungi and bacteria in plant tissue: (1) histological observation (see Chap. 6 by Anand et al.), most recently in combination with molecular methods (see Chap. 18 by Bloemberg and Carvajal), (2) surface sterilisation of the host tissue and isolation of the emerging fungi on appropriate growth media, (3) detection by specific chemistry, e.g. immunological methods (see Chap. 18 by Bloemberg and Carvajal), or (4) by direct amplification of fungal DNA from colonised plant tissues [Vandenkoornhuyse et al. 2002; see Chaps. 17 (Hallmann et al.), and 19 (van Overbeek et al.)], having first ascertained that there are no fungal residues on the plant surface (Arnold et al. 2006). Methods for quantification are reviewed by Sieber (2002), Schulz and Boyle (2005) and in Chap. 17 (Hallmann et al.).

## 1.4 Life History Strategies

Organisms detected at any one moment in asymptomatic plant tissue and arbitrarily named “endophytes” include microorganisms with different life history strategies. Endophytes represent, both as individuals and collectively, a continuum of mostly variable associations: mutualism, commensalism, latent pathogenicity, and exploitation. The phenotypes of the interactions are often plastic, depending on the genetic dispositions of the two partners, their developmental stage and nutritional status, but also on environmental factors (see Chap. 12 by Girlanda et al.). The role of genetic disposition was demonstrated by Freeman and Rodriguez (1993): a single mutation resulted in loss of a virulence factor, transforming a pathogenic fungus, *Colletotrichum magna*, into an endophyte. Similarly, avirulence genes and the machinery of pathogenicity may be lacking or suppressed in bacterial endophytes (Kobayashi and Palumbo 2000).

Just as fungi have been found to develop ectomycorrhiza in one host and what appear to be ericoid mycorrhiza in another host (Villarreal-Ruiz et al. 2004), a mycorrhizal fungus can grow endophytically in the roots of a non-host (see Chap. 12 by Girlanda et al.). The importance of a particular combination of host and microorganism as well as their reciprocal influences also becomes apparent when a fungal or bacterial pathogen is inoculated into a non-host and is no longer virulent, colonising as an asymptomatic endophyte (Carroll 1999; Kobayashi and Palumbo 2000; Schulz and Boyle 2005) The influence of the host plant in determining the mycorrhizal, endophytic or even pathogenic character of a DSE association is likely to be a prime factor. In plant communities, the multiple mutualistic potential of these fungi, establishing hyphal links or inoculum reservoirs, may favour inter-plant interactions (see Chap. 12 by Girlanda et al.).

Interactions are frequently complex, involving more than two partners. Endophytic bacteria and fungi may interact not only with the plant host, but also with other organisms, including mycorrhizal fungi (see Chap. 9 by Bayman and Otero) and metazoa. For example, nematophagous fungi, which are ubiquitous organisms in soils, not only can switch from a saprophytic to a parasitic stage to kill and digest living nematodes, but can also grow endophytically in plant roots (see Chap. 11 by Lopez-Llorca et al.).

Mutualistic interactions involving fungi and bacteria that endophytically colonise plant roots benefit the microbial partner with a reliable supply of nutrients as well as protection from environmental stresses. As reported in this book, benefits for the host plant may include improved growth [see Chaps. 6 (Anand et al.), 13 (Rice and Currah), 15 (Schulz), and 19 (van Overbeek et al.)], induced resistance [see Chaps. 3 (Kloepper and Ryu), 4 (Berg and Hallmann), 6 (Anand et al.), and 15 (Schulz)], biocontrol of

plant parasitic nematodes (see Chap. 11 by Lopez-Llorca et al.) and of fungi in agriculture [see Chaps. 3 (Kloepper and Ryu), 4 (Berg and Hallmann), 15 (Schulz)] and forestry (see Chap. 6 by Anand et al.), as well as microbial synthesis of metabolites antagonistic to predators [Schulz et al. 2002; Schulz and Boyle 2005; see Chaps. 6 (Anand et al.), 8 (Bacon and Yates), 15 (Schulz), and 19 (van Overbeek et al.)] When synthesized in agricultural crops in situ, mycotoxins synthesised by endophytes, e.g. *Fusarium verticillioides* in maize, are potentially problematic for human consumption of these crops (see Chap. 8 by Bacon and Yates).

Factors responsible for improving plant growth are the microbial synthesis of phytohormones [Tudzynski 1997; Tudzynski and Sharon 2002; Kobayashi and Palumbo 2000; see Chaps. 6 (Anand et al.) and 15 (Schulz)], access to minerals and/or other nutrients from the soil (Caldwell et al. 2000; Barrow 2003; see Chap. 13 by Rice and Currah), bacterial fixation of atmospheric nitrogen, which has been demonstrated not only for the nodule-forming members of the Rhizobiaceae, but also for non-nodule-forming bacteria, e.g. *Acetobactor* and *Azoarcus* (Reinhold-Hurek and Hurek 1998; see Chap. 5 by Saad et al.). In the associations of nitrogen-fixing rhizobia with legumes, some of the same signalling molecules are involved as in the interactions of mycorrhizal fungi with their hosts, e.g. flavonoids and nod-factors (Lapopin and Franken 2000; Martin et al. 2001; Mirabella et al. 2002; Imaizumi-Anraku et al. 2005; see Chap. 5 by Saad et al.). And as has recently been shown, plastid membrane proteins involved in the first signalling interactions are crucial for the entry of both symbionts into the host roots (Imaizumi-Anraku et al. 2005).

## 1.5

### Balanced Antagonism

According to Heath (1997), only a few fungi are actually capable of causing disease in any one plant, since they must first cross several barriers and overcome other plant defences. This must also be true for bacteria. Thus, one question has motivated many investigations: how does the endophyte manage to exist, and often to grow, within its host without causing visible disease symptoms? We have proposed a working hypothesis based on observations from the interactions studied thus far (Schulz et al. 1999; Schulz and Boyle 2005). Asymptomatic colonisation is a balance of antagonisms between host and endophyte (Fig. 1.1). Endophytes and pathogens both possess many of the same virulence factors: the endophytes studied thus far produced the exoenzymes necessary to infect and colonise the host (Sieber et al. 1991; Petrini et al. 1992; Ahlich-Schlegel 1997; Boyle et al. 2001; Lumyong et al. 2002), even though only some of these endophytes are presumably

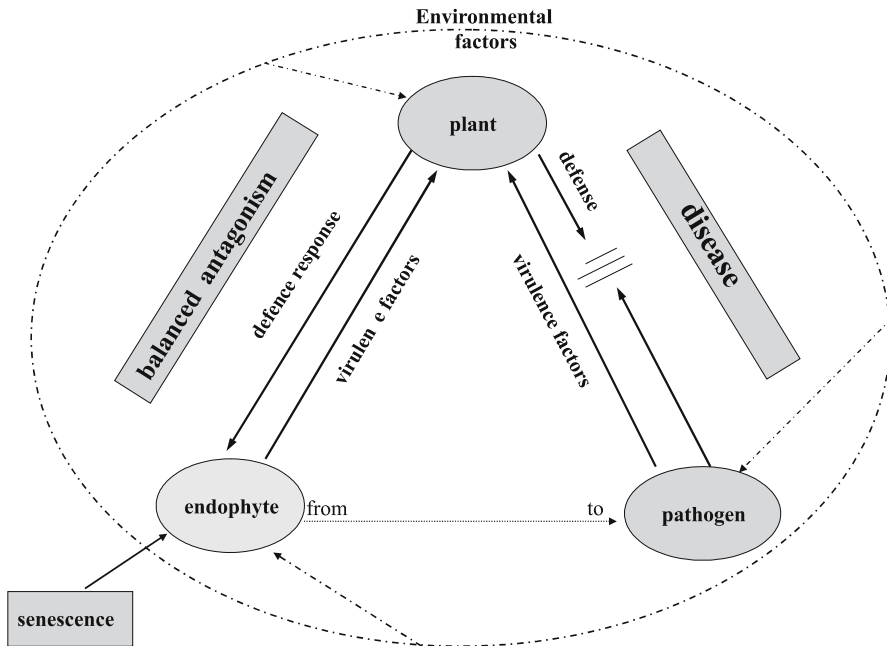


Fig. 1.1. Hypothesis: a balance of antagonisms between endophytic virulence and plant defence response results in asymptomatic colonisation (reproduced with permission from Schulz and Boyle 2005)

latent pathogens. The majority can produce phytotoxic metabolites (Schulz et al. 2002; Schulz and Boyle 2005). The host can respond with the same defence reactions as to a pathogen, i. e. with preformed and induced defence metabolites [Yates et al. 1997; Schulz et al. 1999; Mucciarelli et al. 2003; see Chaps. 3 (Kloepper and Ryu), and 11 (Lopez-Llorca et al.)], and general defence responses (Narisawa et al. 2004; Schulz and Boyle 2005). As long as fungal virulence and plant defence are balanced, the interaction remains asymptomatic. In all of these interactions we are referring to a *momentary status*, an often fragile balance of antagonisms.

If the host-pathogen interaction becomes imbalanced, either disease results or the fungus is killed. In some cases, the virulence of weak pathogens such as *Pezizula* spp. (Kehr 1992) is sufficient for disease development only when the host is stressed or senescent. Whether the interaction is balanced or imbalanced depends on the general status of the partners, the virulence of the fungus, and the defences of the host – both virulence and defence being variable and influenced by environmental factors, nutritional status and developmental stages of the partners. Although this hypothesis has been developed to explain the interactions of fungal endophytes with their



hosts, further studies may well provide evidence that it is also applicable to endophytic bacteria.

Balanced antagonistic interactions are plastic in expression, depending on the *momentary status* of host and endophyte, but also on biotic and abiotic environmental factors and on the tolerance of each of the partners to these factors. In particular, many endophytes seem to be masters of phenotypic plasticity: infecting as a pathogen, colonising cryptically, and finally sporulating as a pathogen or saprophyte. This necessitates a balance with the potential for variability, which means that these endophytic interactions are creative, having the potential for evolutionary development – the symbioses can evolve both in the direction of more highly specialised mutualisms and in the direction of more highly specialised parasitisms and exploitation. Indeed, there is evidence that mycorrhizal fungi may have evolved from the endophytic activity of saprophytic fungi (see Chap. 16 by Brundrett), but also that plastids that have evolved from endosymbiotic bacteria facilitate further symbioses with other bacterial and fungal symbionts (Imaizumi-Anraku et al. 2005).

## 1.6 Conclusions

The usage of the term “endophyte” is as broad as its literal definition and spectrum of potential hosts and inhabitants. The most common usage of the term “endophyte” for organisms whose infections are internal and inconspicuous, and in which the infected host tissues are at least transiently symptomless, is equally applicable to bacterial prokaryotes and fungal eukaryotes.

Endophytes include an assemblage of microorganisms with different life history strategies: those that, following an endophytic growth phase, grow saprophytically on dead or senescing tissue, avirulent microorganisms, incidentals, but also latent pathogens and virulent pathogens at early stages of infection. These parasitic interactions may vary from mutualistic to commensalistic to latently pathogenic and exploitive. Phenotypes of the interactions are often plastic, depending on the genetic dispositions of the two partners, their developmental stage and nutritional status, but also on environmental factors.

We have proposed a working hypothesis based on observations from the interactions studied thus far to explain asymptomatic microbial colonisation as a balance of antagonisms between host and endophyte (Fig. 1.1; Schulz and Boyle 2005). This often fragile balance of antagonism is a *momentary status* and depends on the general status of the partners, the virulence of the fungus and defences of the host, environmental fac-

tors, nutritional status, as well as the developmental stages of the partners.

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