**Specificity of plastic plant adaptation and the endophytes involved**

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**Abstract**

Plants are able to respond and individually adapt plastically to biotic and abiotic changes in the environment as a way to maintain function and fitness under varying conditions. However, it is not always clear what causes this plasticity and which factors are involved. It has also been reported that endophytes, which are mostly bacteria and fungi living inside a host, can influence the plants they are living in and help them to cope with stressful situations, pathogens and herbivores or increase the nutrient uptake or growth. The endophytes are very common, but also widespread, diverse and show sometimes changing but mostly beneficial effects on different plants, with varying and unclear specificity. Despite the importance and wide interest, little is known about the species and their different communities. This review summarizes the effects, functions and diversity of the plastic plant adaptation and the role of endophytes in plants, with the aim to increase the understanding about these subjects and especially about their connection and specificity. Different sides and functions of the plant plasticity and its endophytes are discussed to eventually get more understanding of the current knowledge, processes and about their specificity.

**Introduction**

Plants harbor distinct microbial communities which live inside plants and can have varying behavior, from pathogenic to mutualistic (Haruna et al, 2018). Endophytes are bacterial or fungal microorganisms that colonize various tissues of healthy host plants inter- and/or intracellularly, in a commensal or beneﬁcial manner (Kaul et al, 2016). The term “endophyte” is derived from the Greek, *endon* = within and *phyte* = plant (Hughes, 2016). The presence of non-pathogenic organisms inside the living plants was first defined by De Bary (1866), as “*any organism that grows within plant tissues are termed as endophytes*” and used broadly afterwards (Gouda et al, 2016). Different groups of organisms such as fungi, bacteria, actinomycetes and mycoplasma are reported as endophytes of plants (Arnold, 2007). Collectively, more than 100 years of research suggest that most, if not all, plants in natural ecosystems are symbiotic with mycorrhizal fungi and/or fungal or bacterial endophytes (Petrini, 1986). And 400-million-year-old fossils indicated that plants have been associated with endophytes for a very long time (Hughes, 2016). Although many kinds of endosymbionts can be very important for plants, some endosymbiotic bacteria (like *Burkholderia*) reside inside endophytic fungi themselves and produce active compounds that even influence the plants (Hoffman & Arnold, 2010). Despite their importance, this specific topic is not further discussed in this thesis.

Endophytes reside entirely within plant tissues and may grow within roots, stems and/or leaves, emerging to often occur sparsely as hypha in the intercellular fluids and wall spaces of their plant hosts (Bacon & White, 2000). Moreover, endophytes are a promising source of natural metabolites with bioactivity (Kausari et al, 2014) and also have the ability to beneﬁt the host plants with biotic and abiotic stress tolerance as well as improved nutrient acquisition and plant growth promotion (Kaul et al, 2016). They show complex interactions with their hosts which involve mutualism and antagonism (Johnson, Graham, & Smith, 1997). Plants strictly limit the growth of endophytes, and these endophytes use many mechanisms to gradually adapt to their living environments (Dudeja et al, 2012). In order to maintain stable symbiosis, endophytes produce several compounds that promote growth of plants and help them adapt better to the environment (Das & Varma, 2009). So the symbiosis between endophytes and plants is crucial, because endophytes play a key role in plant adaptation and tolerance to e.g. protect against stress (Rodriguez, Woodward, & Redman, 2010) and water availability (Gibert et al, 2012) by encoding for several secondary metabolites including volatile organic compounds (Lugtenberg et al, 2016).

A major mode of adaptation in plants is phenotypic plasticity, which is the capacity of a single genotype to produce and change in behavior, morphology and physiology induced by different environments (Price, Qvarnström, & Irwin, 2003). This is heritable, under genetic control and a way to adapt to changing environments. It is a short-term response and alternative way compared to the classic neo-Darwin model (natural selection) and adaptation occurs through individual development and physiology as well as through change in population gene frequencies (Merilä & Hendry, 2014). Thus, a single genotype may be able to maintain function and hence reproductive fitness under a variety of environmental conditions (Sultan, 1995).

Although plants respond phenotypically to changes in the abiotic environment, the influence of biotic factors such as symbionts on phenotypic expression has mostly been ignored. But it has been reported that endophytes could influence host morphology and physiology (Cheplick & Faeth, 2009). Despite growing knowledge of the ecological importance and potential uses of plant-associated microorganisms, little is known about the true structure and composition of the bacterial and fungal endophyte communities. Better characterization of the specificity of endophytes in relation to host plant species and different plant parts, and the amount of variation in endophyte diversity, could increase the understanding of the potentially important roles that endophytes play in the growth, ecology and plasticity of plants (Haruna et al, 2018). Here fore, the aim of this thesis is to understand more about the specificity of plastic plant adaptation and the endophytes that are involved in it, although still many is unknown about this subject.

**Plant phenotypic plasticity**

*Plastic acclimation to differing environments*

Many plants can adapt to environmental changes by regulating their development, morphology and growth. For instance, plants with very low light show reduced growth, morphological changes and biomass allocation to leaf tissue (increasing specific leaf area to enhance light-harvesting and photosynthetic efficiency) compared to plants grown in normal light (Sultan en Bazzaz 1993). Another specific response (plastic adjustment) that was shown after drought stress was the increase of root-to-shoot biomass ratio, which maximizes the supply of water available to those tissues and flooding of the same species caused an altered root system morphology and deployment with very fine roots (which is well known in wetland species). So some plants have a broad range of adaptive plasticity while some phenotypes were specific for the limiting resource (Sultan 1995). Plant biomass, drought tolerance and gas exchange or water efficiency can also be improved by controlling the opening/closing, density and size of stomatal pores (Mizutani en Kanaoka 2017).

The leaf morphology can also change between aerial and underwater environments and as a response to temperature change, while these temperature morphological changes are again closely related to light conditions. The leaf blades are wide and few leaves have serrations when this plant is grown aboveground, while it forms needle-like leaves when grown under water and in colder temperatures or with weaker light (low red/far-red ratio). As the shape of leaves changes in both directions when growth conditions are switched, it is highly plastic (Chitwood en Sinha 2016).

Structural defenses may also be induced specifically in response to grazing, because it caused longer and more densely distributed defensive thorns than without grazing, while it was also proven to deter these animals. Also, other plants respond plastically to density or shade by elongating the stems, which enhances fitness under crowded conditions by a phytochrome-mediated response to the change in light quality. The plasticity and germination was also temperature dependent, with lower germination and plasticity after increased summer and decreased winter temperatures (Fernández-Pascual en Jiménez-Alfaro 2014).

*Quantifying adaptive phenotypic plasticity*

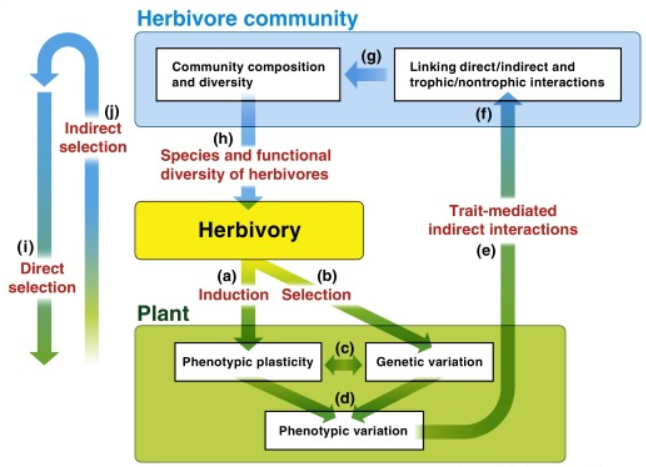
Phenotypic plasticity is a major mode of adaptation to differing environments in plants, but it might be difficult to interpret and study because it depends on the sample, environmental factors and many phenotypic traits (Bradshaw en Hardwick 1989). So plants in unfavorable conditions might show acclimation with maximum function, but they also show reduced growth. For this reason, phenotypic change associated with varying environmental conditions cannot always be assumed to represent adaptive plastic adjustment (Taylor en Aarssen 1988). The adaptation occurs through individual development and physiology as well as through change in population gene frequencies.  
So genotypes cannot be classified as more and less ‘plastic’, since the amount of phenotypic variability across environments varies per trait in one individual. The traits may show different patterns, amounts and directions of response per genotype, but also among populations and taxa (Battjes en Bachmann 1994). Finally, the timing of trait measurements may shape the results, because the same seasons and growth site but a different time can even show phenotypic differences. In addition to major abiotic factors, biotic factors may represent key environmental pressures to which plants respond phenotypically. So it is not always clear which environmental variable is most important and often there is a complex chain of causation with more factors involved. However, the environmental specificity (more factors) and genotypes used may clarify trait definitions and adaptive predictions (Pigliucci en Schlichting 1995).

*Plasticity and life history*

The capacity of phenotypic plasticity is associated with the reproductive strategies of the plant, which is in turn shaped by the environmental heterogeneity. Plants that reproduce clonally show in general high phenotypic plasticity in a wide range of habitats, although they normally produce lines that are adapted to the environment, which can lead to ecological generalization via this plasticity. However, sexual reproduction has increased genetic variation and expressed greater performance trait plasticity and functional trait plasticity than clonal plants. So they only perform well in a limited range of habitats and are specialized to the environment. Plants living in environments with potentially stressful conditions like temperature or drought stress expressed greater performance trait plasticity than good habitat plants too. Also, widespread invasive species express greater phenotypic plasticity than native species (Fazlioglu & Bonser, 2016). So in general, phenotypes are more plastic in environments that are more variable.

*Herbivore-induced plasticity*

When damage caused by herbivory varies for a plant either per environment or in time, a plastic plant defense strategy (induced resistance) may work better than one that is fixed (constitutive resistance) (Karban, 2011). Also, induced plants after herbivore attack have greater resistance than un-induced plants, which is an ability of plant plasticity. Another benefit of these plastic inducible defenses is heterogeneity, which makes the host plant unpredictable to herbivores so it may occur more over evolutionary time (Karban, 2011). The herbivore-induced phenotypic variation by phenotypic plasticity has significant effects on the structure and diversity of herbivore communities, which can in turn promote the adaptive evolution of the plant, its insect community members and the herbivore selection (Ghalambor et al, 2007). It also enhances specific trait-mediated indirect interactions among herbivore community members by affecting their preference/performance, and thus links direct and indirect interactions (Ohgushi, 2016). Plant phenotypic plasticity caused by herbivore community composition evolved the use of herbivore traits as a host response, as shown in figure 1. So this plasticity is specific, although it is very widespread in nature (Miner et al, 2005).

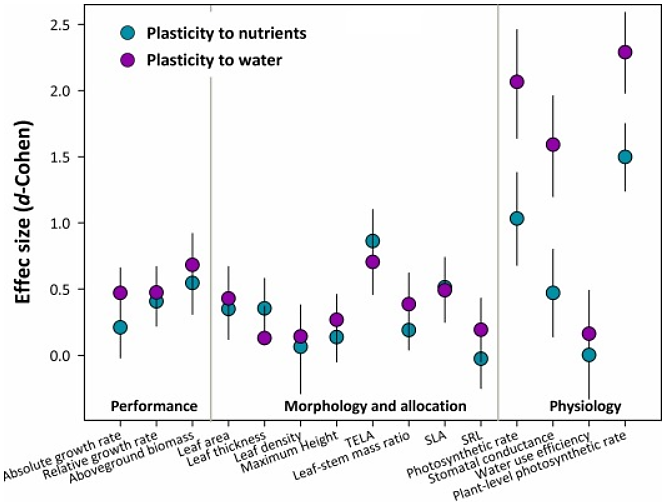
*Figure 1: Plant-herbivore community dynamics*Herbivory causes [phenotypic plasticity](https://www-sciencedirect-com.proxy-ub.rug.nl/topics/agricultural-and-biological-sciences/phenotypic-plasticity) through induction (a) and genetic variation through selection (b), they also affect each other since phenotypic plasticity has a genetic base (c). Both are important sources of phenotypic variation in plants (d). Increased phenotypic variation enhances trait-mediated indirect interactions among herbivore community members by affecting their preference and performance (e), thereby linking direct/indirect interactions in the herbivore community (f), and altering community composition and diversity of herbivores (g). As for a feedback, they can alter the herbivore species identity and functional diversity (h) via direct (i) or indirect (j) selection of insect communities on plant trait evolution (Ohgushi, 2016).

*Tissue-specific plasticity*

Secondary metabolite production (like anthocyanin and flavone) is a case of tissue-specific plasticity, because it is induced by stress stimuli (light, radiation or pathogen exposure) as a plastic response to protect the plant with photoprotective and oxidant properties (Jiang, Doseff, & Grotewold, 2016). It is mostly found and plastic in photosynthetic tissues of flowers/fruits, although the amounts are variable and the plasticity differs among plant tissues and is much lower in petals compared to calyces and stems. Also, anthocyanin is more plastic than flavone in biosynthesis. The production is dependent of environmental effects and this variable plasticity between flavonoid types may allow the plant to respond to differing (light) environments and to biotic agents (Del Valle et al, 2018).

*Effects of domestication on phenotypic plasticity*

Under low water and low nutrient availabilities, plant phenotypes can be significantly affected. They decrease specific leaf area to produce smaller and thicker leaves, and decrease stomatal conductance. The plastic response to limiting water is higher than to varying nutrient supply, although these patterns varied significantly for several key traits among crops, as shown in figure 2.

*Figure 2: Effect size of nutrient and water treatment on different key trait expression*  
Dots and error bars are the size of the effect in D-Cohen and 95% confidence intervals, averaged for several crop species and domestication statuses of plants. Plasticity to water and nutrients refers to the plastic response between the favorable control and the low water and low nutrient treatments (Matesanz & Milla, 2018).

Plants produced significantly smaller, thicker leaves and reduced their maximum height similarly as a response to nutrient limitation (5% and 8% average decrease for wild and domesticated plants) and even more as a response to water limitation (33% reduction for domesticates and 19% for wild relatives). Domesticated plants outperformed wild plants in favorable conditions, but suffered a higher loss of performance under stress or varying conditions, with a decreased growth rate and aboveground biomass. This is in contrast with studies suggesting that selection for high performance in optimum conditions might also improve it in stressful environments (Sadras & Denison, 2016).   
So with this stress, performance between domesticated and wild plants did not differ and the domestication effect disappeared because of the decrease and less optimized conditions relatively. The crop species widely differed in their growth and plasticity, but response patterns within domestication statuses were similar across crops, which indicate that domestication effects are generalized on phenotypic plasticity. The domesticated plants had larger, denser but thinner leaves and larger photosynthetic rate than wild plants, in all conditions. So during domestication, multi-crop change in plasticity occurred. Also, stress type rather than stress quantity played a more significant role in the plastic response (Matesanz & Milla, 2018).

Domestication resulted in increased phenotypic uniformity (constant phenotypes in different environments) which benefits agricultural performance. So the decreased phenotypic plasticity was a target of breeding (Makumburage & Stapleton, 2011). However, it also decreased the ability to adjust to environmental heterogeneity if the optimum phenotype varies across environments, for instance if a plastic phenotype is advantageous. Furthermore, plasticity may have evolved during domestication as a by-product of trait selection, if trait means and their plasticities are genetically correlated. And domestication could have led to better traits, without changing plasticity patterns. So domestication has not resulted in a generalized loss of plasticity, several crops retain functional plasticity despite strong directional selection during the domestication process (Sadras & Denison, 2016). For instance, a lower level of developmental plasticity in roots of wild lettuce was found compared to cultivated lettuce as a response to soil moisture heterogeneity (Gallardo, Jackson, & Thompson, 1996). However in another study, domestication had no effect on growth form plasticity to contrasting habitat conditions in domesticate and wild manioc (Ménard et al, 2013). Altogether, these results are diverse and of limited generality due to the differing biological features of each crop and each domestication process, so this plasticity might be very specific (Matesanz & Milla, 2018).

**Plant endophytes and acclimation**

*Classification of endophytes and its interactions*

At first, endophytes were categorized into two groups, the clavicipitaceous and non-clavicipitaceous. Clavicipitaceous endophytes are mostly common in grasses and have a narrow host range, while the non-clavicipitaceous have a broad host range and are mainly in non-vascular and other vascular plant species like conifers and angiosperms. Later, they were divided into four groups with clavicipitaceous as class 1 and the others in class 2-4, according to their host range, colonization, function and transmission. Class 2 endophytes colonize roots, shoots and leaves while class 3 only colonizes the aboveground tissues (shoots) and class 4 only in the roots (Rodriguez e. a., 2009). The endophytes can be bacteria, fungi, actinomycetes, or viruses and the expression depends on the plant host genotype and/or environmental conditions. Nowadays, the endophytes are classified into two general categories, the systemic and nonsystemic ones, as shown in table 1 (Wani et al, 2015).

*Table 1: Criteria for classification of endophytes into systemic and nonsystemic endophytes*

|  |  |  |
| --- | --- | --- |
| **Criteria** | **Systemic endophytes** | **Nonsystemic (transient) endophytes** |
| Taxonomy | Cocladogenetic species | Varies spatially and temporally |
| Mode of transmission | Usually vertical, in some cases horizontal as well | Horizontal only |
| Life style | Mutualistic | Changes from mutualism to parasitism with change in environment |
| Defense response | Lack host defense response | Host defense response is active |
| Ecological functions | Beneficial | Beneficial or harmful (factor dependent) |
| Evolutionary pattern | Coevolved with the host plant | Host association is transient and short lived |
| Diversity | Rare | Rich |

The systematic endophytes do not produce any visible symptoms of disease and their virulence factors are probably balanced with the plant’s defense mechanisms and tightly regulated to keep the association without symptoms (Schulz & Boyle, 2006). But when they are grown outside the host, they might lose their vitality. These endophytes are also resistant to the metabolites and/or defense mechanisms of the host. However, the transient endophytes can become pathogenic or parasitic in stressed conditions, by requiring cell death for proliferation. These endophytes might have evolved from pathogens (Hiruma, Kobae, & Toju, 2018). Their interaction exhibits phenotypic plasticity from mutualism to antagonism, depending on the environmental conditions and biocommunication (specific communication within (intraspecific) or between (interspecific) species of plants, animals, fungi, and microorganisms). These interactions are mainly based on chemical signals (Schulz & Boyle, 2006). The establishment of biotrophic lifestyles of endophytes during the colonization of host plants is an important feature of the host endophyte interactions, as it implies a strong genetic and metabolic relief to both interacting partners (Wani et al, 2015). Thus, endophytes are first detected as minor pathogens which over a period of time evolve into a symbiont with varying degrees of dependence, depending on the cost-benefit analysis of the host-endophyte association (Conn, Walker, & Franco, 2008).

Endophytes have many advantages for the plant hosts. However, the effects seem to be dependent on the endophytic strain (Qawasmeh et al, 2012). Endophytes can protect the host against stress or increase the uptake of essential chemical elements for growth and development (Nair & Padmavathy, 2014). They can also produce herbicides (3x more than soil bacteria and twice as much as phytopathogenic fungi), secondary phenolic metabolites for plant defense or other diverse chemical compounds (phytohormones, toxins, enzymes, antibiotics, volatile organic compounds, reactive oxygen species etc.) to among others stimulate the root growth, pathogen inhibition or immunity (Xin et al, 2009). The tolerance of salt and drought stress can also be increased (Gallardo-Cerda et al, 2018).

Another mechanism is the increase or induction of host metabolism gene expression (and nutrient uptake), biocontrol agents, plant growth and defense (Singh, Malik, & Singh, 2013). The endophytes and its molecules can be recognized by the plant, which triggers signal transductions and after that plant defense responses as with pathogen interactions, which changes the metabolic state (Joseph & Mini Priya, 2011). Endophytes have widespread functions and can also even play a role in soluble pigment production (Visalakchi & Muthumary, 2009) and in browning and cell death by inducing the senescence and release of tannins in the tissue (Pirttilä et al, 2008).

Fungal endophyte colonization significantly affects both primary and secondary host metabolism which shifts C to N ratios and probably has impact on herbivore and plant pathogen responses (Rasmussen et al, 2008). Different types of metabolites are produced that also play a role in specific interactions and communication with the host plant (Brader et al, 2014). Other endophytic root bacteria also contain several gene clusters involved in motility, plant polymer degradation, iron acquisition (e.g., siderophores), quorum-sensing, and detoxification of reactive oxygen species (Sessitsch et al, 2012). The endophytes can upregulate metabolism and increase the plant’s tolerance to drought, heat, metal toxicity, low pH, and high salinity, so it has a great ecological significance for the plants (Nagabhyru et al, 2013). They help plants to adapt to varied environmental conditions and bio-geographical regions and modify their normal response. Although many environmental factors influence the plant-endophyte interactions, host plant response to endophyte infection is mainly mediated by the host genotype, endophytic strain, resource availability, and environmental cues/stress with niche specialization as a result (Wani et al, 2015).

*Plant microbial interaction influences pathogenic plastic response*

Microbial interactions might influence the plastic potential of plant pathogens. This phenotypical acclimation caused by microbial interactions could also impact the dynamics of the pathogenic population (O’Keeffe et al, 2017). Individual pathogens change growth and multiplication as a respond to microbes in a shared plant host. For instance, a maize pathogen ([*Fusarium*](https://www-sciencedirect-com.proxy-ub.rug.nl/topics/agricultural-and-biological-sciences/fusarium) *verticillioides*) can stimulate the growth of another fungal pathogen (*Ustalago maydis*) that responds by the overexpression of toxins and siderophore biosynthetic genes (Rodriguez Estrada et al, 2012) and   
*U. maydis* also stops producing antifungal metabolites as a plastic response to this interaction. So pathogens can enhance each other in plant infection, because of the cross talk between more host defense pathways that are triggered by different pathogens. Also, *Arabidopsis thaliana* can be infected more quickly by the pathogenic fungus *Alternaria brassicola* if the plant’s defense system is already induced by the bacterium *Pseudomonas syringae* that has a different pathway (Spoel, Johnson, & Dong, 2007). The pathogenic microbes that surround a plant shape its phenotype and evolutionary potential. However, the evolution and phenotypic plasticity of virulence in pathogens both require genetic control, but are connected (Brown, Cornforth, & Mideo, 2012).

*Endophytic variation*

Endophytic population varies per species, plant and even per region and climatic condition. More endophytes were found in mature than in young leaves and in raining season in the trees *Tectona grandis* L. and*Samanea saman* Merr. (Chareprasert et al, 2006). The distribution of dominant endophytic fungi was organ-specific and differed within seasons, however, the fungus *Phyllosticta* sp. occurred in both leaves and petioles. It was first detected in August and peaked in October with none in the month of May. *Phomopsis* sp. was only detected in twigs throughout the growing season, so these endophytes are season specific in their hosts (Thongsandee, Matsuda, & Ito, 2012). The endophyte *Enterobacter cloacae,*was found to be associated with the pollen of several Mediterranean pines so it is less plant specific, although it was also only found in pines (Madmony et al, 2005). Plants growing in different geographical regions are confronted with different environmental challenges and contain also different endophytes. However, also different root conditions and plants in the same environment (next to each other) contain different endophytes, because molecular signals from the plant also differed (Lebeis, 2014). So these endophytes differ greatly and are not species or environment specific.

However, little variation within the endophytic population diversity in the grass *Festuca eskia* was found, regardless of the origins altitude and site and/or endophyte infection frequency (Philippe, 2016)*. Enterobacter* sp. contains genes (for colonization, protection and growth) that are specific for the poplar plant niche adaptation of this bacterium (Nair & Padmavathy, 2014). Some other endophytes are also known to infect specific hosts, even though a single plant part can contain different endophyte species (Bamisile et al, 2018). Examples are *Bimuria novae-zelandiae* and *Phoma chrysanthemicola*, the two most common fungal endophytes isolated from white clover roots. They are exclusively isolated and restricted to this host. Also, *Phialophora radicicola*, the predominant fungal species from ryegrass roots, was only present in ryegrass. This would suggest that although there were high levels of different fungi, they are highly host specific (Skipp & Christensen, 1989).

*Host-specific endophytic production*

A tightly controlled and very specific host-endophyte interaction is with the fungus *Fusarium solani* that lives in the bark tissues of *Camptotheca acuminata* (happy tree). Hereby, the plant produces the compound camptothecin as a chemical defense against insects and pathogens (Sirikantaramas, Yamazaki, & Saito, 2009). Precersor-camptothecin is also produced by the endophyte, but a key enzyme for the production (strictosidine synthase) was only present and thus provided by the plant. Without the endophyte, the production level was way lower, but the endophyte needs the plant to produce the compound. This production is also to protect itself from the plant-produced compound, by amino acid alterations in catalytic domains of its topoisomerase I (Kusari et al, 2011). Although, another endophyte isolated from the same tissue also had this resistance, it does not produce camptothecin itself. So both endophytes had a similar evolutionary preadaptation, regardless of their biosynthetic capability. Because all fungi invading the plant are killed by camptothecin, the endophyte already had to be resistant or preadapted, before it produced the compound itself. Because the endophytic *F. solani* is capable of producing camptothecin, it might develop additional resistance features, so these endophyte-plant interactions should be very specific and strongly selected towards steady coexistence (Kusari, Hertweck, & Spiteller, 2012). So some endophytes can produce ‘plant exclusive’ compounds, however some of them might even originally only be synthesized by their endophytes (Ji et al, 2009).

The xenohormesis hypothesis proposes that heterotrophs have evolved the ability to detect signaling and stress-induced molecules from plants, under selective pressure. Endophytic fungi might sense these chemical cues and establish a defense response which increases the survival chance. They can produce similar secondary metabolites such as pathogenesis-related genes (Howitz & Sinclair, 2008).

Because endophytes are continuously interacting with the host plant, the metabolic processes probably affect each other. The fungal plant pathogen *Nectria hematococca* expresses lethal genes that are only activated by plant signals (homoserine and asparagine) (Yang et al, 2005). Expression of a biogenesis gene cluster in the endophyte *Neotyphodium lolii* is also only induced when grown in plants or presence of plant signals (Young et al, 2006). The *Clavicipitaceae* fungi also synthesize alkaloids when they are in symbiosis with dicotyledonous plants (*Convolvulaceae*), which questions the origin of these compounds in plants. Other, otherwise silent biosynthetic pathways might also be triggered by signaling molecules (Scherlach & Hertweck, 2009)

*Signaling in plant-endophyte interactions*

Endophytic and host immune signals have cross‐regulations between pattern recognition receptor pathways and host pattern-triddered immunity (PTI) might have a role in the selection and management of these endophytes, however the similarity in the host response between commensals and pathogens is high. The majority of the endophytes probably avoid PTI to facilitate their colonization, although it prevents their overgrowth in plants (Hacquard et al, 2017). Moreover, virulence effector expression and/or delivery is substantially reduced in the non‐pathogenic mode of endophytic colonization. These findings are consistent with the idea that PTI plays a central and not really specific role in the establishment and maintenance of plant‐associated endophytes. But the environment and limitation of nutrients also influence the plant interactions (Castrillo, 2017).

*Epichloë grass–endophyte associations*

Many grasses are very successful and can grow in a wide range. Their relation with systemic, vertically transmitted, symbiotic fungal endophytes from the genus *Epichloë* has helped a lot. The maintenance of this symbiotic relation  is dependent on regulated signaling networks and host interaction (Scott, Green, & Berry, 2018). Also branching and fusion of endophytic hyphae in leaves is crucial for symbiosis and cell-fusion genes are required, as well as membrane-associated proteins (Kayano, Tanaka, & Takemoto, 2018). The *Epichloë* are very common grass-specific endophytes that form an aerial hyphal network and can produce defensive metabolites (alkaloids) that are lethal or drive away the insects, nematodes or herbivores. These endophytes can also increase host growth, seed production, nutrient uptake and stress tolerance (Shukla et al, 2015). The toxin production by endophytes can be induced by herbivore attack and this defense can be optimized by plant adaptive plasticity in their ability to induce these defense systems (Raguso, 2015). *E. festucae* produces three main alkaloids: peramine, lolitrem B and ergovaline. The pyrrolizidine alkaloid peramine (specifically induced by chewing) deters or toxifies invertebrate herbivores, while the indole‐diterpene alkaloid lolitrem B (induced by grazing) and the ergot alkaloid ergovaline are neurotoxins for herbivores (Philippe, 2016). This induction is herbivore-specific and the symbiosis might involve a close chemical crosstalk, in which herbivore presence and type are perceived either by the grass which induces endophyte activity, or by the endophytic fungus which responds with the production of herbivore active alkaloids (Fuchs et al, 2017).

While other filamentous (pathogenic) fungi extend their hyphae by tip growth, *E*. *festucae* grows via systemically colonizing the intercellular space of expanding host leaves via a unique mechanism of intercalary hyphal extension. Strict control of the biomass, as well as the growth patterns in host plants are expected to be key requirements for avoiding a defense response by the plant (Kayano, Tanaka, & Takemoto, 2018). *Epichloë*caused faster grass growth, but reduces invertebrate species richness (because of loline alkaloids that drive them away) and alters arthropod and rhizosphere communities (Finkes et al, 2006). The endophytic effect also differs between mowed and unmowed plots, ground types, years (with other conditions) and grass species (Yurkonis et al, 2012). So the site-specific effects and other factors may be stronger than plant community and endophyte effects, causing differences in the outcome of differen studies, from highly positive to negative effects. Although the endophytes are dependent on vegetation, resources and climate, they are probably still host specific (Shukla et al, 2015).

*Direct and indirect herbivory defense*

The *Epichloë* endophyte provides, besides direct defense (alkaloid production), also increased indirect plant defense by improving the plant ‘scent’ that attracts more aphid predators. Aphids are herbivores and endophytes associated with the attacked plant can produce antagonistic and specific volatile organic compounds against them as direct defense, only in association with their specific host plant. However, these endophytes can also produce specific scents when the plants are attacked, that can be a signal to attract predatory insects that control these aphids, like the hoverfly (*Syrphidae*) (Fuchs & Krauss, 2018). Plants may also increase volatile emission when neighbor plants are infected and other plants might respond to that to prime their own defenses (Dicke, 2016).

*Grass endophyte plasticity, reproduction and specificity*

In grass, endophytic associations in plants caused a higher plasticity in seed weight (heavier seeds in favorable growth conditions) and lower plasticity in seed number for symbiotic plants. Although, a high plasticity in seed number allows plants to adjust growth to the environmental level of resources, while seed weight above a certain value ensures offspring fitness. The endopytic effect varied and was dependent of the host genotype (Gundel et al, 2012).

In plant populations, selective forces are variable and can operate simultaneously on several traits or plasticity in traits of the endophyte, host or their interaction. Some grass endophytes are specialized, although their hosts normally also contain hundreds of more generalized (horizontally transmitted) endophytic species that are found in all plant types (Christensen, Bennett, & Schmid, 2002). However, for instance the growth and vertical transmission of endophytes in woody plants (complex morphology, long maturity) is more difficult than the in grasses (small size and morphology, fast reproduction). In these tissues, the endophytes can rapidly synchronize growth with the host by reaching the meristematic tissues (Saikkonen et al, 2004).

Comparisons of fungal and plant phylogenies suggest that systemic grass endophytes are host specific, leading to host-adapted fungal races that are compatible with only certain host genotypes. Genetic specificity is particularly high in strictly asexual and vertically transmitted fungi that inhabit grasses (Clay & Schardl, 2002). However, except for the short-term benefits to the endophyte and the host, extreme specificity during selection can later be disadvantageous in adaptive habitats.

In case of grass with asexual *Neotyphodium* and its sexual form *Epichloë*, sexual reproduction (and consequently horizontal transmission) appears scattered across closely related phylogenetic fungal lineages and asexual lineages show greater genetic host specificity (Saikkonen et al, 2004).

*Effect of Thermomyces endophyte on heat stress tolerance*

Although plants have evolved defense systems to protect against various stress conditions, an association with specific endophytes can also enhance the survival capacity of the plant (Khan et al, 2016). The habitat-adaptive thermophilic fungal endophyte *Thermomyces* sp. can help plant tolerance against extreme heat stress by the induction of ubiquitin degradation, histone acetylation/deacetylation and poly ADP-ribosylation pathways (Mchunu et al, 2013). This thermophile, that induces heat stress tolerance in its host, is until now only found in the extreme hot desert-adapted *Cullen plicata*. However, this isolated endophyte also helped the heat stress tolerance of other (unnaturally occurring) plants, like the highly heat sensitive cucumber plant ([*Cucumis*](https://www-sciencedirect-com.proxy-ub.rug.nl/topics/agricultural-and-biological-sciences/cucumis) [*sativus*](https://www-sciencedirect-com.proxy-ub.rug.nl/topics/agricultural-and-biological-sciences/sativum)). It enhanced the plant’s photosynthesis, water use efficiency, and root length, increased metabolite production and induced antioxidant enzyme activities. So although this thermophilic endophyte is and its interactions are usually specific for the desert living plant, it can also help the adaptation to heat stress in other plants (Alia et al, 2018).

*Factors that drive endophytic composition and specialization in orchids*

Some endophytes are common in certain areas, but present in different host plants, denoting preference and selectivity to some extent (Chen, 2013). However, endophytic community assemblage also seems to be driven by host phylogeny. In different but related *Orchis* species, similar endophytic fungi were associated (Martos et al, 2012). Also, closely related *Cyrtochilum* orchid species shared more similar endophytic fungal communities among each other compared with less related orchid species. The communities in host species can be site-adjusted because of local selection by particular environmental conditions (soil conditions, vegetation and climate). But they can also be present in the same orchid species across different sites. So the host phylogeny could be a driver of endophyte community composition (Cevallos et al, 2018).

However, this it is not the case in all studies. Some endophyte communities also overlapped among large population distributions and more distinct species at the same sites, so host phylogeny is not the determining driver. The overlapping endophytes might not be very specialized and probably have ecological plasticity and are able to play different roles in the interaction. This could be influenced by many abiotic and biotic factors, especially in habitats with harsh environmental conditions. Proximity between sites could also facilitate the endophytic dispersal and overlap (Jumpponen et al, 2017). It is likely that the overlapping endophytes between orchids at different sites have exceptional characteristics and could develop under several conditions. However, because some endophytes were not specifically associated with a single orchid species, the plants could also have ancestral ecological preferences for several widely distributed endophytes (Otero et al, 2007)

Another study indicated significant differences in the endophytic fungal communities associated with orchid species. This endophytic diversity could reflect the ecological preference of the two host species, but might also be a consequence of local factors that changed much. Therefore, the degree of endophytic specificity in these orchid species (*Cephalanthera damasonium*and*C. longifolia*) is still uncertain. The orchids may increase their fitness in a narrow range of specific habitats by selecting a highly specific endophyte. This specificity may be linked to orchid rarity when the fungal partner has a limited distribution (Swarts et al, 2010). Eventually, there was not a set of fungi uniquely associated with an orchid species (only distinct communities irrespective of the host and site of origin) and no dominant fungal taxon was present. This implies a low level of endophytic specificity and a high number of endophytes in the orchid species (Pecoraro et al, 2017).   
Another endophytic fungus (*Exophiala salmonis*) was also detected in several orchid species so it is not very host specific, but is shows a large ecological plasticity and is capable of playing different roles in host organisms (Pecoraro et al, 2017).

Due to natural selection, certain fungal endophytic lineages might have been abandoned and others favored, so the most beneficial partners were selected (Rasmussen & Rasmussen, 2009). Endophytic specificity can also be driven by differences in geographical distribution. Narrow distributions might force specificity by the orchid because of the absence of other symbionts. The most common endophyte had the widest distribution area and the rare detected ones had limited geographic distribution areas. It is also unlikely that the endophytes have evolved in response to the orchids, because they are not dependent on this host for reproduction and survival (Jacquemyn et al, 2011). However, the endophytes associated with orchids follow different strategies. Some seem to be affected by host phylogeny and sites, while this did not show any effect on other endophyte communities (Cevallos et al, 2018). So the specificity of orchid-endophyte interactions can vary considerably between species and different species associate with a different number of endophytes (Jacquemyn et al, 2011). So better understanding of the real diversity of orchid endophytes is a fundamental for any consideration on specificity.

*Endophyte communities in leaves*

Endophytic fungi communities in leaves of Manna ash (*Fraxinus ornus*) were examined on both the north and south side of of the Alps. The communities of these sites differed and the individual tree types also had a clear influence. Almost all leaves contained endophytes and more than 100 morphotypes were found. The most frequently encountered endophyte ([*Venturia*](https://www-sciencedirect-com.proxy-ub.rug.nl/topics/agricultural-and-biological-sciences/venturia-fungus)*orni*, 32%) was five times more abundant than the second most frequent endophyte ([*Colletotrichum acutatum*](https://www-sciencedirect-com.proxy-ub.rug.nl/topics/agricultural-and-biological-sciences/colletotrichum-acutatum)). The most common endophyte community structure is often one or a few species that are very abundant accompanied by multiple rare species, independent of the ecosystem (Queloz et al, 2011). These rare endophytic species occur in a wide range of plant species, so their host specificity is low. However, some most abundant endophytes only occurred in one or rarely in another region, probably due to specific biogeographic factors, which are known to have a strong influence on the composition of endophyte communities, site conditions and interactions with abiotic factors (Pautasso, Schlegel, & Holdenrieder, 2015).

*F. ornus* is phenotypically a very plastic tree species and is able to vary its leaf traits (thickness, mass, photosynthesis, osmotic potential, etc.) according to its environmental conditions (Kalapos & Csontos, 2003). This plasticity enables the tree to adapt to a wide range of site conditions. Accordingly, differences in abiotic conditions (sun and consequently, leaf characteristics) may also influence the community of leaf endophytes (Unterseher et al, 2007). As *F. ornus* is not native to the northside of the Alps (trees of this species are planted) no tree-specific fungi are present these sites. Other studies have shown that trees in their native range are colonized by more host-specific fungi than trees outside their range. Surprisingly, no other endophytes colonized the plant, but *F. ornus*-specific endophytes were most frequently isolated irrespective of the side of the Alps on which the tree was growing. So they must have arrived either in the form of spores carried by southerly winds over the Alps or together with *F. ornus* seedlings and/or saplings. As a conclusion, *F. ornus* hosts a highly diverse endophytic community and its composition was dependent on factors such as geographic region, the individual tree and host tissue (Ibrahim, Sieber, & Schlegel, 2017).

*Tropical Rainforest Bacterial Endophytes*

In stems, leaves and roots, in replicate specimens and in different species of rainforest plants, a large overlap in bacterial endophyte variation is found, without consistent clustering by compartment or host species. The community assembly seems to be determined by random processes and that bacterial endophyte operational taxonomic units were randomly distributed among plant species and organs and that the plant endophyte community may be much more diverse, but less predictable, than would be expected from culturing efforts alone(Haruna et al, 2018). The results show that a diverse set of endophytes was associated with three common species of rainforest plants. These were woody trees from taxonomically scattered angiosperm families (Burseraceae, Pandaceae and Rubiaceae). Endophytic bacteria that were mostly associated with rainforest soil (Lin et al, 2010) were (almost) absent in plant tissue samples, so these bacterial assemblages are strongly ecologically selected by the environment and soil of the plant host(Haruna et al, 2018). There was also no similarity of bacterial species when all plants were compared within their habitat, between plant compartments, per whole plant and between plants, suggesting that stochastic processes dictate the distribution of endophytic bacteria, as was also shown in other studies (Zhang et al, 2016).

Random, spatially limited dispersal could be occurring because different plant parts offer similar essential environments or due to the hyper-diverse forest trees, which leads to less endophytic (plant-specific) selective advantage for evolutionary host tree specialization, compared to more generalized adaptation to live in a broad range of trees (Kembel & Mueller, 2014). So it also seems that the endophytic community is very diverse and host-unspecific. However, other studies with less diverse plants do show colonization by host-specific endophytes. The endophytes can have important biochemical functions, but in the diverse community there might be functional overlap (Haruna et al, 2018). However, the most often found bacterium that was also present in all three plant species and in other variable tropical plants (Bhore, Komathi, & Kandasamy, 2013) was *Bacillus anthracis*, so it might have an important role in rainforest trees. Other *Bacillus* strains were also identified, these might play a role in plant protection against phytopathogens (Duan, He, & Li, 2013).

**Conclusion and discussion**

In this thesis, the specificity of plastic plant adaptation and the interactions between a plant host and its corresponding endophytes that are involved are studied. Because both topics are quite different but also related, they have mainly been discussed separately. Although one thing they have in common is that very much is still unknown about their mechanisms, interactions and specificity.

Plants can respond plastically to changing environmental conditions, to adapt to the biotic and abiotic conditions and to be able to grow in the most favorable way. However, it is not always clear which (environmental) variable is most important, if it is really plastic adaptation or what is causing the effect. Some of the most studied and best known plant responds are phenotypically, as a result of heat, drought, salt or starvation stress, among others. The plants can respond plasticly to these environmental conditions by adaptation of their leaves, length, roots, stomata and many other things. But they can also use the help of other microorganisms, like endophytes, to benefit the growth (biomass production), nutrient uptake or stress resistance. The endophytes are very common among plants. They are widespread, enormous diverse (in functions, hosts, location and specificity) and in most cases very beneficial for their host plants. Some endophytes can also even help against herbivore or pathogen attack by helping fast plant regrowth, to drive herbivores away (directly) or by attracting herbivore eaters (indirectly). Generally discussed in this thesis, the fungi are involved in nutrient cycling, primary and secondary metabolism, in orchids and mainly as grass endophytes. The bacterial community of endophytes was mostly present in roots, nitrogen fixation and nutrient production or increase. Considering all these, endophytes definitely have many functions and mostly beneficial effects on plants, although there are significant variations/differences in endophytic community between different differing species and environments and even between frequencies, rate of beneficial effects and specificity.

However, much is still unknown about these subjects and their specificity. Although plant plasticity seems really beneficial for the plant and despite widespread interest and growing knowledge of the ecological importance and potential uses of plant-associated endophytes and their influences, very little is known about the true structure and composition of the bacterial and fungal communities. Altogether, even less is known about the plant plasticity and its interaction with the endophytes together, and the specificity of both. But more research, interaction studies and the use of genomics and transcriptomics could help to solve some of the many unanswered questions.

Even better understanding of the plant plasticity, better characterization of endophytes and their specificity in relation to host plant species, different plant parts and the amount of variation in endophyte diversity, could increase the understanding of the potentially important roles that plastic plant adaptation and the endophytes play in the growth, improvement, ecology and plasticity of plants and the specificity of both.

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