Endophytes

An endophyte, from the Greek *endon* (within) and *phyton* (plant), is a microorganism, usually a bacterium or a fungus, that lives within a plant. Even though the host plant provides carbon to the endophyte, it is generally recognized that this symbiotic association is, on balance, either neutral or beneficial to both the endophyte and the host plant. At first, however, the beneficial role of endophytes was obscured by the observation that endophytes were responsible for toxicity disorders suffered by farm animals feeding on tall fescue[^1] and ryegrass[^2]. It was later shown that the alkaloids produced by the endophytes were part of a strategy to protect their plant host against herbivores. Further studies showed that endophytes also helped their host resist biotic and abiotic stresses. After the discovery that suppressive soils owed their natural capacity to suppress pests and diseases to microbial organisms, including endophytes, the definition of endophytes was expanded to include organisms that live outside the plant.

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Types of endophytes

**Fungal endophytes**

Fungal endophytes can be separated into three major groups. One group consists of highly specialized fungal endophytes of grasses, belonging to the family Clavicipitaceae within the Acomycota phylum. These endophytes are most often strictly obligate and vertically transmitted.

A second group comprises arbuscular mycorrhizal fungi (AMF), obligate symbionts that colonize the roots of almost all higher plants, including most cultivated plant species. AMF belong to the order of Glomales within the phylum Ascomycota and are represented by over 130 species in seven genera[^3][^4]. AMF increase nutrient uptake, growth rates, hormonal activity and tolerance to biotic and abiotic stresses.

A third group of fungal endophytes comprises hyphomyceteous fungi, such as *Fusarium oxysporum* and *Colletotrichum* sp., which have a saprophytic stage in the rhizosphere. The isolates of *Fusarium*
oxysporum that are pathogenic to bananas are called *Fusarium oxysporum* f. sp. *cubense*.

**Bacterial endophytes**

Endophytic bacteria belong to a wide variety of species and genera\[5\]. The best known are the nitrogen-fixing bacteria colonizing graminaceous plants. Another group formed by *Pseudomonas* spp. has attracted a lot of attention, but since the bacteria depend on plant exudates for growth\[6\] they are more often encountered in the rhizosphere than inside the plant.

**Benefits to host plants**

**Protection against pests and diseases**

There are many examples of different types of endophytes having antagonistic effects against all groups of plant-parasitic nematodes\[7\]\[8\]\[4\] and soil-borne fungal pathogens\[9\]\[10\]\[11\]\[12\]. Some endophytic isolates seem to act against multiple pests simultaneously\[13\]\[14\].

Antagonism against insects has been found mostly among clavicipitaceous grass endophytes. Examples of hyphomycetous endophytes against insects are less common. Plants with the *Acremonium strictum* endophyte were shown to be less suitable for larval development of certain insects\[15\]\[16\].

Examples of antagonism against bacterial and especially viral diseases are scarce\[17\]\[18\].

**Impact on plant growth**

All major endophytic groups seem to promote plant growth. Rhizosphere-colonizing bacteria that promote plant growth are called plant-growth promoting rhizobacteria (PGPR). Some endophytes, like *Colletotrichum* spp., synthesize plant hormones\[19\]. Endophytes have also been linked to drought resistance\[20\]. Various mechanisms, such as plant osmotic adjustment or greater concentrations of sugars, have been proposed\[21\]. Some endophytic bacteria have been implicated in fixing nitrogen for non-legumes\[5\].

It has been hypothesized that increased plant growth would increase tolerance of pests and diseases. In ryegrass, however, the better growing plants, as a result of being inoculated with endophytes, had more nematodes than the smaller plants that did not have endophytes\[22\].

**Modes of action**

**Parasitism**

Although it is commonly mentioned as a potential mode of action, there are not many examples of endophytes parasitizing pests or the causal agents of diseases. *Fusarium oxysporum* has been shown to parasitize the eggs of the banana weevil under lab condition\[23\].

**Competition**

Two types of competition have been documented: competition for nutrients and competition for infection sites. For example, *Pseudomonas* spp. produce siderophores that chelate iron, thus depriving pathogens of this essential nutrient\[22\] while *F. oxysporum* and *Pseudomonas* spp. have been demonstrated to compete with pathogenic *Fusarium* spp. for carbon\[24\]\[25\]. Competition for infection sites has been demonstrated between non-pathogenic and pathogenic *F. oxysporum*, resulting in a reduction of the latter, in celery\[26\] and cucumber\[11\].

**Production of secondary metabolites**

The major mode of action of endophyte is undoubtedly their production of a wide array of
secondary metabolites. Clavicipitaceous endophytes in grasses have been shown to produce secondary metabolites[^27][^28].

Less progress has been made identifying the secondary metabolites produced by hyphomycetous endophytes. For example, *F. oxysporum* endophytes isolated from tomato were shown to produce unidentified secondary metabolites that reduced nematode hatching and caused juvenile mortality. Some endophytes have also been shown to produce metabolites capable of degrading root exudates that attract nematodes[^14].

Various secondary metabolites with known antibacterial, antifungal and antiviral activity have been shown to be produced by *Colletotrichum* sp[^19].

Endophytic *Pseudomonas* spp. and actinobacteria seem to produce a wide range of antifungal compounds, including phenazine and pyrrolnitrin antibiotics[^29][^30]. There is also evidence of nematicidal compounds being produced by *Pseudomonas* spp[^13].

**Induced resistance**

Induced resistance is the activation of plant defense mechanisms after contact with biotic elicitors (pathogens, non-pathogens, insects or herbivores) or abiotic ones (such as salicylic acid and other chemicals)[^31][^32][^33]. The triggering of plant defence mechanisms prior to infection usually results in reduced pest or pathogen damage[^34].

**Use of endophytes against pests and diseases of bananas**

Micropropagated plants inoculated with AMF have been shown to be more resistant to nematodes than uninoculated ones. In bananas, the AMF *Glomus fasciculatum* has been reported as beneficial against the nematode *Radopholus similis*[^35]. Also in banana, a reduction in damage caused by the nematode *Pratylenchus goodeyi* was observed using *Glomus mosseae*. However, since AMF are produced on living plants, obtaining the necessary inoculum is expensive, cumbersome and most likely not commercially viable[^4].

*F. oxysporum* being the most common endophytic taxa in banana, it probably offers the greatest potential for commercialization, mainly because of the ease to obtain inoculums[^14].

Progress towards the commercialization of endophytes as biological control agents has been made in East Africa. In Kenya, an endophyte, originally isolated from banana tissue, *F. oxysporum* strain V5W2, is being registered as a commercial biological control agent under the leadership of Jomo Kenyatta University of Agriculture and Technology and in cooperation with the International Institute of Tropical Agriculture. Following registration, the Real IPM Company will be licensed to mass-produce the product for use in banana seed systems to control nematodes and weevils.

In Uganda, endophyte technology will be embedded directly into commercial tissue culture companies, such as Agro-Genetic Technologies when individual specific endophytes have been registered with Ugandan authorities.

Field trials testing the effectiveness of locally isolated banana endophytes to control nematodes in commercial plantations have also been carried out in Central America.

**References**

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