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Endophyte – the evolution of a term, and clarification of its use and definition

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For many terms in biology, giving an ironclad definition which is robust over biological time, is like trying to present a single, immutable, measurement for the length of the femur bone of a horse. You can say how long it is now, and how long it was at different stages in the evolutionary history of the animal, but you probably can not predict what it will be a millennium from now. Definitions of many biological terms are the same, they evolve over time. Just as our knowledge evolves, so we change the meaning of terms to better describe what we need to say. This is very apparent when one compares terms in the scientific literature, or the unabridged Oxford dictionary of the English language, from several decades ago, to the meaning we give to the same terms today.

So what about the term Endophyte? Wennström (1994) argues that it is an abused and misused term to the extent that its use is no longer meaningful. He further suggests that we should either use the term with its original definition, or redefine the term, but argues against the latter. Wennström (1994) used Ainsworth (1971) as an example of the original definition and incorrectly stated it as “an organism that lives in another organism”. Ainsworth (1971) actually defines endophyte as “a plant living inside another organism”. Endophyte owes its origin to De Barry (1866) who first coined the term. Since then it has become deeply embedded in the literature. Within the last decade, different authors have proposed a range of similar, but more complex definitions (e.g., Carroll 1986, Petrini 1991, Wilson 1993). However, endophyte does not stand alone as a term whose definition has changed over time, or as a term whose definition biologists might not agree over. What about the definition of a species? There are probably many definitions of this term. They have changed over time. Darwin's concept of a species is quite different to the biologists of today, and biologists might not all agree on the concept of a species (Moore

1990). But does this make the term meaningless? I would argue that it does not.

I will propose a useful working definition of endophyte which is meaningful at our current level of understanding about the microorganisms to which we have applied the term. In addition, I will identify areas where the term has been erroneously used as a synonym, and show why it is a valuable term whose meaning has simply evolved to keep up with our increasing understanding of the biology.

Definition

At the most basic level, endophyte could simply refer to the location of the organism: endo means within and phyte means plant. Thus, an endophyte is an organism which lives inside a plant. This is contrasted to epiphyte which refers to organisms living on the outside of the plant. The organisms commonly associated with the term endophyte are fungi and bacteria (Fahey et al. 1991) and I will restrict my use of the term to these organisms. Thus, at its simplest level, any fungus or bacterium found inside plant tissues would be considered an endophyte. However, I would sympathize with Wennström's (1994) argument that, used in this way, it is vague and not very useful. This is probably why, over time, its meaning has become restricted in important ways such that it has evolved into a very useful, meaningful term. It is now used to indicate what type of association the fungi or bacteria, which live inside the plant, have with the host. Just as the term pathogen indicates the type of interaction one organism has with its host, so the term endophyte has changed from its original suggested definition, which described the location, to describe the nature of the association. The most important way endophyte describes the

nature of the interaction, is that the fungi or bacteria found inside the plants do not elicit symptoms of disease, i.e., the infection is symptomless. Thus I strongly argue against Wennström's (1994) comment that "(1) the endophytes today have few features in common". They share the following unique features: they all live inside plant tissues and do not cause disease symptoms. Therefore, I propose the following definition (at least with our current level of understanding): endophytes are fungi or bacteria which, for all or part of their life cycle, invade the tissues of living plants and cause unapparent and asymptomatic infections entirely within plant tissues but cause no symptoms of disease. Hence, the term endophyte describes not only the location, but the type of infection strategy of a particular fungus or bacteria without regard to the taxonomy or infection cycle.

Used in this way, it would exclude mycorrhizal fungi, but include the following:

1) Fungi which have dormant or latent phases within plant tissues prior to causing disease symptoms on the plant host. Although these fungi are clearly pathogenic, they can still have an endophytic phase to their life cycle.

2) Fungi which are known pathogens of a plant host but never exhibit disease symptoms after infection. For example, *Colletotrichum magna* typically causes anthracnose in cucurbit plants. However, a single locus mutation converted this plant pathogen into a symptomless colonizer of the interior of the plant, i.e., an endophyte (Freeman and Rodriguez 1993).

Fungi in the above two categories probably comprise a very large group of organisms which exist on every plant species. The important issue here is not whether the organism is pathogenic or endophytic, or whether one labels the organism a pathogen or an endophyte, but why infection by endophytes has not triggered a defense response by the plant to eject the fungus? Furthermore, unless there is a benefit of infection to the plant, most endophytes are parasites (or commensal) on the plant host since they derive most or all nutrients from the host they infect.

To further qualify...

Endophyte can be further qualified with other terms. For example, stating if it is seed borne, horizontally transmitted, intracellular, or mutualistic, etc., will all add ecological meaning. However, endophyte is often used synonymously with mutualist. Although certain endophytes clearly form mutualistic associations with the plant host, the term endophyte should bear no more or no less affinity to the term mutualist than it does the term pathogen. It is possible to have an endophyte within a plant which, at different times, can have mutualistic and pathogenic associations with its host, e.g., *Epichloë typhina* which infects *Festuca rubra*, and *Atkinsonella hypoxylon* which infects *Danthonia spicata*. As mutualists,

both fungi can increase the plant's resistance to certain herbivores (Cheplick and Clay 1988) and as pathogens or parasites, both can castrate the host plants and produce fungal stromata or hypothalli in place of seeds (Clay and Jones 1984, Leuchtman 1992).

More an endophyte or pathogen?

I disagree with Wennström (1994), that by including the systemic rusts and smuts which live asymptotically in the plant from one to several years, often sporulating for only short periods, "(1) it will further complicate things, (2) there is nothing to gain from including them, and (3) the definition is already too vague". By including such fungi as endophytes, or including them as fungi which have endophytic stages, nothing will be complicated, instead we can describe a lengthy part of the life cycle with just a few well defined terms. These asymptomatic systemic rusts and smuts fit both the roles of endophyte and pathogen, thus "endophyte" and "pathogen" do not oppose each other but describe different infection strategies. However, maybe one could argue that these rusts and smuts have a longer endophytic than pathogenic phase since most of their life cycle is spent as a symptomless fungal infection within the plant?

I suggest caution however, when we try to label a particular species as an endophyte, or a pathogen. There is a continuum of infection patterns: some microbe-plant interactions are completely symptomless. In this case one can justifiably label the microbes as endophytes. Some interactions have lengthy symptomless phases but short phases with obvious symptoms of disease, and some have short or no symptomless phase but cause disease as soon as they infect the plant. In the latter case, clearly the microbe is a pathogen. However, how should we label the species which show brief periods of disease symptoms? For these "uncooperative" organisms (and if it is really so important per se, to place continuously variable entities into discretely labeled groups) they clearly fit the definitions of both, but at different times in the life cycle. Therefore, the term which best fits the context of the situation should be used. As long as an adequate mention is made of the rest of the life cycle of the organism, there should not be any confusion. For example, when discussing the asymptomatic stage of the life cycle, the term endophyte can be used; when discussing the disease causing stage, the term pathogen can be used; and when discussing the transition period, the phrase transition from endophyte to pathogen can be used.

Latitude in the grey areas

Endophyte has become more restrictive than the above definition in ways not easily described. For example, if a

fungus grows out from a piece of healthy-looking surface-sterilized plant material, it is usually considered an endophyte. However, fungi such as *Cladosporium* sp. and *Alternaria* sp. form asymptomatic infections and occur very frequently on temperate plants. Strictly speaking, these fungi are endophytes but they are often ignored or not considered “true” endophytes. This might be a grey area as their classification is at the whim of the investigator. I feel latitude of this type is perfectly acceptable and we should not be slaves to rules and definitions, rather we should place the priority on the biological context of the situation.

Endophyte: a very useful term, now let's get on with the biology

With the above definition, exclusions and inclusions, fungal endophytes will comprise a vast number of fungi. This should not lessen the usefulness of the term nor cause confusion provided it is further qualified and not erroneously used as a synonym for other terms. However, let's not use too much of our time deciding whether an organism is an endophyte, a pathogen or saprophyte, etc. Some of the important issues are: why they are there? What are they doing? And how do they affect the host plant?

This paper was written largely in response to Wennström (1994). I would like to conclude with some comments made by the reviewer of this manuscript. He was adamantly opposed to my suggestion of including the systemic rusts and smuts as endophytes, but he concluded his review by saying that technically they are endophytes, as are all other fungi that live inside their host!

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