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10 Fungal Endophytes in Submerged Roots

Felix Bärlocher

10.1

Introduction

It has long been known that plants harbour fungal endophytes, and it was suspected that systemic grass endophytes, primarily clavicipitaceous fungi, are associated with toxicity to grazing livestock (Saikkonen et al. 1998). This connection was firmly established in the 1970s (Bacon et al. 1977). The early emphasis on grasses and their endophytes have led some authors to consider the term endophyte as being synonymous with mutualist. However, many fungal pathogens may be latent in grasses without causing disease or long before the outbreak of disease symptoms (Petrini 1991; Fisher and Petrini 1993). The first systematic surveys of plants other than grasses were stimulated by the observation that many common phyllosphere fungi invade stomatal cavities of Douglas fir needles within their first year. Bernstein and Carroll (1977) demonstrated that with increasing age, all needle segments become infected with endophytes. The presence of primarily non-balansiaceous endophytes was extended to other conifers (Carroll et al. 1977) and has since been documented in every tree, shrub and herb that has been examined (Carroll 1995; Sridhar and Raviraja 1995; Saikkonen et al. 1998). Generally, a large number of species can be isolated from a given host, yet only four to five are common and likely to be host specific (Fisher and Petrini 1993). Community ordination analyses have generally shown that endophyte assemblages are specific at the host species level, and may be impoverished outside the host's natural range. While a few of these associations provide clear benefits to the plant by fungal interference with herbivores or microbial pathogens, others eventually cause damage to the plant, while some are essentially neutral. A widely accepted definition of an endophyte is as an agent of a currently asymptomatic infection, without specifying the role of the agent in the host or its development at a later stage (Petrini 1991; Fisher and Petrini 1993; Schulz et al. 1998). However, Schulz et al. (1999) showed that even in infections without visible symptoms, colonisation led to the synthesis of higher concentrations of

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potentially antimicrobial compounds. In vitro, endophytic fungi produce more herbicidally active substances than soil fungi. Schulz et al. (1999) therefore hypothesise that the host-endophyte interaction is a case of balanced antagonism: pathogens overcome the host's defences to the extent that they cause visible damage, whereas endophytic virulence is only sufficient to be able to infect and colonise without causing visible damage. If the balance shifts, the endophyte may turn pathogenic.

Much of the current interest in endophytes is based on the hope of finding unique secondary metabolites and enzymes affecting plants, herbivores and microbes, with potential applications in medicine and agriculture (Petrini et al. 1992). The continuum of endophyte interactions with plants also provides interesting case studies for the evolution of mutualism and pathology, and for understanding how environmental factors might favour one or the other (Carroll 1988). Until recently, it has commonly been believed that the first fungi were saprotrophs from which necrotrophs and biotrophs evolved, but there are convincing arguments supporting an alternative view (Parbery 1996). A recent comparison of 1,551 ribosomal sequences of the two sister groups of chitinous fungi, the Glomeromycota and the Dikaryomycota, both of which have symbiotic life-styles, suggests that the symbiosis between fungi and green plants was present before the colonisation of land by plants (Tehler et al. 2003). Finally, endophytes may not have been seriously taken into account when assessing diversity (Hawksworth 1991, 2001); Dreyfuss and Chapela (1994) concluded that over 1.3 million species of fungal endophytes remain to be discovered and described.

10.2

Aquatic Hyphomycetes

Up to 99% of the energy available to stream communities consists of terrestrial plant detritus (leaves, needles, twigs; Allan 1995). Aquatic hyphomycetes, a heterogeneous group of aquatic fungi, are an indispensable link in the food web between this detritus and stream invertebrates (Bärlocher 1992). The annual fungal production per stream bed area falls within the same order of magnitude as that of bacteria and invertebrates (Suberkropp 1997). Aquatic hyphomycetes disperse from leaf to leaf by producing conidia, whose shapes are predominantly tetra- or sigmoid. Both types have been shown to increase the conidium's likelihood of settling and germinating on new leaves; they are clearly the result of convergent evolution (Webster 1987).

In temperate streams, the number of conidia in the water column declines from up to $30,000\text{ l}^{-1}$ in late fall to almost nil during summer, undoubtedly a response to the seasonal availability of terrestrial leaves

(Bärlocher 1992, 2000). Combined with the unidirectional displacement of substrates and spores in running water, this raises the question of how aquatic hyphomycetes can maintain themselves within a given reach of a stream and avoid being washed downstream. Potential solutions include (1) the fact that the fungi also colonise woody substrates, which can persist for several years in a stream, (2) the presence of teleomorphs in some species with ascospores that may be dispersed aerially, (3) dispersal of fungal-colonised leaves or conidia by animals, (4) the occurrence of the fungi in terrestrial habitats, e.g. as plant pathogens or endophytes (Bärlocher 1992). For example, Hartig (1880) first described a parasite of maple seedlings as *Cercospora acerina*. Later, its identity as *Centrospora acerina* was established, and it is now known as *Mycocentrospora acerina* (Hartig) Deighton. It is a remarkably widespread and versatile species: it is a well-known plant pathogen, has been implicated in human infections, and is a common stream fungus. Morphologically, there is no difference among various strains. Iqbal and Webster (1969) showed that strains they isolated from a stream were pathogenic to carrots and parsnips. Nemec (1969) isolated *Anguillospora longissima* (Sacc. & Syd.) Ingold and *Tetracadium marchalianum* de Wild., which had been isolated from aqueous habitats, from the roots of diseased strawberry plants. Several other species have also been isolated from terrestrial root surfaces of apparently healthy plants (Waid 1954; Taylor and Parkinson 1965; Parkinson and Thomas 1969; Watanabe 1975). These observations suggested that some aquatic hyphomycetes might be root endophytes.

10.3

Fungi in Submerged Roots

Fisher and Petrini (1989) were the first to demonstrate an endophytic phase of two aquatic hyphomycete species. They examined terrestrial roots of *Alnus glutinosa* (L.) Gaertner on the banks of Exeter Canal (Exeter, Devon, UK). Only 1.7 and 0.7% of 300 root segments were colonised by the aquatic hyphomycetes *Tricladium splendens* and *Campylospora purvula*, respectively, compared to the 19% that were colonised by the most common endophyte *Cylindrocarpon destructans*. In a later study, Fisher et al. (1991) compared aquatic and terrestrial alder roots along the banks of the River Dart (Devon, UK). They separated roots into bark and xylem (decorticated roots), and found more endophytic aquatic hyphomycetes in the former. Mean frequency of occurrence of aquatic species in submerged roots was as high as 30%, compared to 12% on terrestrial roots. In addition to typical aquatic hyphomycetes, they also found species of the genera *Fusarium* and *Cylindrocarpon*. Members of these two taxa are often found on leaves

in decaying streams. Cluster and correspondence analyses suggested that aquatic and soil root samples are colonised by two distinct endophyte populations, indicating that the external environment may have a greater influence on endophyte communities of roots than those of leaves (Fisher and Petrini 1993). Three previously unknown species (*Fontanospora fusiformis*, and two species belonging to *Filospora*) were subsequently isolated and described from submerged alder roots (Marvanová and Fisher 1991; Marvanová et al. 1992, 1997).

The host range of endophytic aquatic hyphomycetes was extended by Sridhar and Bärlocher (1992a). They found additional species in spruce (*Picea glauca* [Moench] Voss), birch (*Betula papyrifera* Marsh) and maple (*Acer spicatum* Lam.). Again, fungal endophytes were more common in the bark, suggesting that roots are colonised by fungi settling on surfaces and growing toward the interior. In addition to plating out surface-sterilised root fragments, Sridhar and Bärlocher (1992a) aerated them in distilled water and were able to observe release of typical tetra-radiate or sigmoid conidia. However, aeration had to continue for 4 days (compared to the usual 1–2 days) before spores were detected (any superficial mycelia that may have been present were killed by surface sterilisation). Spore production per unit mass was less than 1 mg^{-1} , compared to $100\text{--}150 \text{ mg}^{-1}$ from dead submerged branches, and up to $8,000 \text{ mg}^{-1}$ on dead leaves (Gessner et al. 2003). Nevertheless, the root biomass in streams is considerable and its turnover rapid (Waid 1974), suggesting that it may be an important secondary resource for aquatic hyphomycetes. Their existence as endophytes may provide them with a head start in the use of root detritus, a possible advantage of the endophytic life style that has also been suggested for leaf-decomposing saprobes (Fisher and Petrini 1993).

On spruce roots, the number aquatic hyphomycetes in the xylem was highest in 4- to 5-year-old segments (Sridhar and Bärlocher 1992b). Total fungal biomass, estimated by ergosterol, amounted to 0.002 to 0.2% of root biomass. This compares to values exceeding 15% on decaying leaves (Gessner et al. 2003).

Iqbal et al. (1994) reported 17 species of endophytic aquatic hyphomycetes from tree roots along canal banks in Pakistan (*Mangifera indica* L., *Populus hybrida* Reichb., *Salix babylonica* L.). Two plantation crops (*Coffea arabica* Linn., *Hevea brasiliensis* M.) and four ferns (*Diplazium esculentum* (Retz) Sw., *Macrothelypteris torresiana* (Gaudich.) Ching., *Angiopteris evecta* (Forst) Hoffm., *Christela dentata* Brownsey & Jermy), all from India, were also shown to harbour aquatic endophytes in their submerged roots (Raviraja et al. 1996). Again, their incidence was higher in the bark than in the xylem of tree roots. Conidium release per root biomass upon aeration was much higher from the fern *C. dentata* ($12,900 \text{ g}^{-1}$) than from the other plants ($36\text{--}410 \text{ g}^{-1}$).

Permanently or periodically submerged roots are common in mangrove swamps. Ananda and Sridhar (2002) examined fungal epiphytes in prop roots or pneumatophores (which cycle between exposure to air and immersion in salt or brackish water) of *Avicennia officinalis* L., *Rhizophora mucronata* Lamk. and *Sonneratia caseolaris* (L.) Engl.. Aquatic hyphomycetes were represented by *Mycocentrospora acerina* in roots of *A. officinalis* L., and *Triscelophorus acuminatus* in roots of *R. mucronata* and *S. caseolaris*. In addition, various marine and terrestrial fungi were found.

Overall, 35 aquatic hyphomycete species (plus seven taxa identified to genus) have been reported from submerged roots of 13 plants, including Angiosperms, Gymnosperms and ferns in eight studies (Table 10.1). This corresponds to roughly 10% of the total number of described species (L. Marvanová, personal communication). Clearly, submerged roots can provide a stationary refuge for aquatic hyphomycetes, which may help them maintain their presence in a given stream reach despite the unidirectional flow of water.

Table 10.1. Endophytic aquatic hyphomycetes recovered from roots, submerged in saltwater (*) or freshwater (all others). Root sections: R Entire root, B bark, X xylem (decorticated root)

Fungus	Substrate	Root section	References
<i>Anguillospora filiformis</i> Greath.	<i>Acer spicatum</i>	B, X	Raviraja et al. 1996;
	<i>Betula papyrifera</i>	B, X	Sridhar and Bärlocher 1992b
	<i>Picea glauca</i>	B	Sridhar and Bärlocher 1992a
<i>A. longissima</i> (de Wild.) Ingold	<i>Mangifera indica</i>	B, X	Iqbal et al. 1995
	<i>Populus hybrida</i>	B, X	Iqbal et al. 1995
	<i>Salix babylonica</i>	B, X	Iqbal et al. 1995
<i>Articulospora antipodea</i> Roldán	<i>Picea glauca</i>	B, X	Sridhar and Bärlocher 1992a
<i>A. atra</i> Descals	<i>Alnus glutinosa</i>	B	Fisher et al. 1991
	<i>Picea glauca</i>	B, X	Sridhar and Bärlocher 1992a
<i>A. tetracladia</i> Ingold	<i>Acer spicatum</i>	B, X	Fisher et al. 1991
	<i>Alnus glutinosa</i>	B, X	Fisher et al. 1991; Sridhar and Bärlocher 1992a, 1992b
	<i>Picea glauca</i>	B, X	Sridhar and Bärlocher 1992a
<i>A. proliferata</i> Jooste, Radon & Merwe	<i>Mangifera indica</i>	B, X	Iqbal et al. 1995
	<i>Populus hybrida</i>	B, X	Iqbal et al. 1995
	<i>Salix babylonica</i>	B, X	Iqbal et al. 1995
<i>Bacillispora inflata</i> Iqbal & Bhaty	<i>Mangifera indica</i>	B	Iqbal et al. 1995
	<i>Populus hybrida</i>	B	Iqbal et al. 1995
	<i>Salix babylonica</i>	B	Iqbal et al. 1995

Table 10.1. (continued)

Fungus	Substrate	Root section	References
<i>Campylospora chaetocladia</i> Ranzoni	<i>Salix babylonica</i>	B	Iqbal et al. 1995
<i>Clavariopsis aquatica</i> de Wild.	<i>Alnus glutinosa</i>	B, X	Fisher et al. 1991
	<i>Picea glauca</i>	X	Sridhar and Bärlocher 1992a
	<i>Populus hybrida</i>	B	Iqbal et al. 1995
	<i>Salix babylonica</i>	B	Iqbal et al. 1995
<i>C. azlanii</i> Nawawi	<i>Mangifera indica</i>	B	Iqbal et al. 1995
<i>Cylindrocarpon aquaticum</i> (Nils.) Marvanová & Descals	<i>Acer spicatum</i>	B, X	Sridhar and Bärlocher 1992a
	<i>Mangifera indica</i>	B, X	Iqbal et al. 1995
	<i>Picea glauca</i>	B	Sridhar and Bärlocher 1992a
	<i>Populus hybrida</i>	B, X	Iqbal et al. 1995
	<i>Salix babylonica</i>	B, X	Iqbal et al. 1995
<i>Filosporella</i> sp.	<i>Alnus glutinosa</i>	B	Fisher et al. 1991
<i>F. fistucella</i> Marvanová & Fisher	<i>Alnus glutinosa</i>	B	Marvanová and Fisher 1991
<i>F. versimorpha</i> Marvanová et al.	<i>Alnus glutinosa</i>	B	Marvanová et al. 1992
<i>Flagellospora curvula</i> Ingold	<i>Mangifera indica</i>	B	Iqbal et al. 1995
	<i>Populus hybrida</i>	B	Iqbal et al. 1995
	<i>Salix babylonica</i>	B, X	Iqbal et al. 1995
<i>F. fusarioides</i> Iqbal	<i>Mangifera indica</i>	B, X	Iqbal et al. 1995
	<i>Populus hybrida</i>	B, X	Iqbal et al. 1995
	<i>Salix babylonica</i>	B, X	Iqbal et al. 1995
<i>F. penicillioides</i> Ingold	<i>Mangifera indica</i>	B, X	Iqbal et al. 1995
	<i>Populus hybrida</i>	B, X	Iqbal et al. 1995
	<i>Salix babylonica</i>	B, X	Iqbal et al. 1995
<i>Fontanospora fusiramosa</i> Marvanová et al.	<i>Alnus glutinosa</i>	R	Marvanová et al. 1997
<i>Geniculospora</i> sp.	<i>Picea glauca</i>	B, X	Sridhar and Bärlocher 1992b
<i>Heliscus lugdunensis</i> Sacc. & Therry	<i>Acer spicatum</i>	B, X	Sridhar and Bärlocher 1992a
	<i>Alnus glutinosa</i>	B, X	Iqbal et al. 1995
	<i>Betula papyrifera</i>	B, X	Sridhar and Bärlocher 1992a
	<i>Picea glauca</i>	B, X	Sridhar and Bärlocher 1992a, 1992b
	<i>Salix babylonica</i>	B, X	Iqbal et al. 1995
<i>Lunulospora curvula</i> Ingold	<i>Alnus glutinosa</i>	B	Fisher et al. 1991
	<i>Angiopteris evecta</i>	R	Raviraja et al. 1996
	<i>Christela dentata</i>	R	Raviraja et al. 1996
	<i>Coffee arabica</i>	B, X	Raviraja et al. 1996

Table 10.1. (continued)

Fungus	Substrate	Root section	References
	<i>Hevea brasiliensis</i>	X	Raviraja et al. 1996
	<i>Mangifera indica</i>	B	Iqbal et al. 1995
	<i>Populus hybrida</i>	B	Iqbal et al. 1995
	<i>Salix babylonica</i>	B	Iqbal et al. 1995
<i>Mycocentrospora</i> sp. 1	<i>Alnus glutinosa</i>	B	Fisher et al. 1991
<i>Mycocentrospora</i> sp. 2	<i>Acer spicatum</i>	B, X	Sridhar and Bärlocher 1992a
	<i>Picea glauca</i>	B, X	Sridhar and Bärlocher 1992a
<i>Mycocentrospora</i> sp. 3	<i>Coffea arabica</i>	B	Raviraja et al. 1996
	<i>Diplazium esculentum</i>	R	Raviraja et al. 1996
	<i>Hevea brasiliensis</i>	X	Raviraja et al. 1996
	<i>Macrothelypteris torresiana</i>	R	Raviraja et al. 1996
<i>M. acerina</i> (Hartig) Deighton	* <i>Avicennia officinalis</i>	R	Ananda and Sridhar 2002
<i>M. clavata</i> Iqbal	<i>Betula papyrifera</i>	B, X	Sridhar and Bärlocher 1992a
	<i>Picea glauca</i>	B, X	Sridhar and Bärlocher 1992a
<i>M. iqbalii</i> sp. ind. F. Bareen	<i>Mangifera indica</i>	B, X	Iqbal et al. 1995
	<i>Salix babylonica</i>	B, X	Iqbal et al. 1995
<i>Phalangispora constricta</i> Nawawi & Webster	<i>Picea glauca</i>	B, X	Sridhar and Bärlocher 1992b
<i>Pseudoanguillospora</i> sp.	<i>Alnus glutinosa</i>	B	Fisher et al. 1991
<i>Tetrabrachium elegans</i>	<i>Acer spicatum</i>	B, x	Sridhar and Bärlocher 1992a
Nawawi & Kuthubutheen	<i>Betula papyrifera</i>	B, X	Sridhar and Bärlocher 1992a
	<i>Picea glauca</i>	B	Sridhar and Bärlocher 1992a
<i>Tetracladium</i> sp	<i>Angiopteris evecta</i>	R	Raviraja et al. 1996
<i>T. furcatum</i> Descals	<i>Angiopteris evecta</i>	R	Raviraja et al. 1996
<i>T. marchalianum</i> de Wild.	<i>Mangifera indica</i>	B	Iqbal et al. 1995
	<i>Populus hybrida</i>	B	Iqbal et al. 1995
	<i>Salix babylonica</i>	B	Iqbal et al. 1995
<i>T. setigerum</i> (Grove) Ingold	<i>Picea glauca</i>	B	Sridhar and Bärlocher 1992b
<i>Tricladium chaetocladium</i> Ingold	<i>Alnus glutinosa</i>	B	Fisher et al. 1991
	<i>Alnus glutinosa</i>	B	Fisher et al. 1991
<i>Tricellula aquatica</i> Webster	<i>Mangifera indica</i>	B	Iqbal et al. 1995
<i>Triscelophorus acuminatus</i> Nawawi	<i>Angiopteris evecta</i>	R	Raviraja et al. 1996
	<i>Christela dentata</i>	R	Raviraja et al. 1996
	<i>Coffea arabica</i>	B	Raviraja et al. 1996
	<i>Diplazium esculatum</i>	R	Raviraja et al. 1996
	<i>Hevea brasiliensis</i>	B, X	Raviraja et al. 1996

Table 10.1. (continued)

Fungus	Substrate	Root section	References
<i>T. konajensis</i> Sridhar & Kaveriappa	<i>Macrothelypteris torresiana</i>	R	Raviraja et al. 1996
	* <i>Rhizophora mucronata</i>	R	Ananda and Sridhar 2002
	* <i>Sonneratia caseolaris</i>	R	Ananda and Sridhar 2002
	<i>Antipteris evecta</i>	R	Raviraja et al. 1996
	<i>Christela dentata</i>	R	Raviraja et al. 1996
	<i>Coffea arabica</i>	B	Raviraja et al. 1996
	<i>Macrothelypteris torresiana</i>	R	Raviraja et al. 1996
<i>T. monosporus</i> Ingold	<i>Angiopteris evecta</i>	R	Raviraja et al. 1996
	<i>Christela dentata</i>	R	Raviraja et al. 1996
	<i>Coffea arabica</i>	B, X	Raviraja et al. 1996
	<i>Diplazium esculatum</i>	R	Raviraja et al. 1996
	<i>Macrothelypteris torresiana</i>	R	Raviraja et al. 1996
	<i>Mangifera indica</i>	B	Iqbal et al. 1995
	<i>Populus hybrida</i>	B	Iqbal et al. 1995
<i>Tumularia aquatica</i> (Ingold) Marvanová & Descals	<i>Salix babylonica</i>	B	Iqbal et al. 1995
	<i>Alnus glutinosa</i>	B	Fisher et al. 1991
<i>Varicosporium elodeae</i> Kegel	<i>Alnus glutinosa</i>	B	Fisher et al. 1991
	<i>Picea glauca</i>	B, X	Sridhar and Bärlocher 1992a, 1992b
<i>V. giganteum</i> Crane	<i>Picea glauca</i>	B, X	Sridhar and Bärlocher 1992a, 1992b

10.4

Conclusions and Outlook

Work on submerged roots, primarily in fresh water, has been dominated by a very specific objective: to evaluate their role as habitat for aquatic hyphomycetes. Other aspects of the plant-endophyte relationship include the potential production of unique secondary metabolites allowing the fungi to live within the plant without overt symptoms, and which might be toxic to potential pathogens or herbivores. Several observations suggest that aquatic fungi can produce diffusible antibiotics. For example, *Massarina aquatica*, the teleomorph of *Tumularia aquatica*, releases antifungal substances (Fisher and Anson 1983). Similar observations on other

species have been reported by Asthana and Shearer (1990) and Poch et al. (1992). Chamier et al. (1984) demonstrated inhibition of bacteria by aquatic hyphomycetes in field experiments. Isolation and characterisation of antimicrobial compounds from *Anguillospora longissima* and *A. crassa* resulted in the discovery of novel metabolites (Harrigan et al. 1995). Two surveys of aquatic hyphomycetes and ascomycetes demonstrated that antibacterial and antifungal substances are produced by about one-half of the species tested (Gulis and Stephanovich 1999; Shearer and Zare-Maivan 1988). Lignicolous aquatic ascomycetes and hyphomycetes were generally more antagonistic than foliicolous species, possibly because long-lasting substrata, such as wood, favour colonisation by species capable of defending captured resources (Shearer 1992). It is currently unknown how such compounds affect the root's susceptibility toward pathogens or herbivores.

Sexual and asexual reproduction of the endophyte are often initiated upon the death of the host tissue (Fisher et al. 1986). Sridhar and Bärlocher (1992a) reported that *Heliscus lugdunensis* produced a teleomorph upon subculturing; aquatic hyphomycetes endophytic in roots may therefore be useful in establishing additional anamorph-teleomorph connections (Webster 1992; Sivichai and Jones 2003).

It is generally accepted that aquatic hyphomycetes and ascomycetes had terrestrial ancestors, and several have indeed close terrestrial relatives (Kong et al. 2000; Liew et al. 2002). Shearer (1993) suggested that when terrestrial plants invaded freshwater habitats, they brought with them fungal pathogens, endophytes and saprobes. Alternatively, plant detritus, pre-colonised by fungal biotrophs or saprotrophs may have fallen into streams. Some of these fungi may subsequently have adapted to dispersal and reproduction in water. The most comprehensive analysis of fungal gene sequences suggests that the biotrophic lifestyle was a synapomorphic trait (i.e. present in a common ancestor; Tehler et al. 2003). The first fungi that colonised the terrestrial habitat most likely did so while closely associated with plants. The question remains whether such fungi first evolved into terrestrial saprobes, and then into aquatic hyphomycetes, or whether there was a direct transition from terrestrial biotrophs to aquatic saprobes. Were the presumed ancestors restricted to specific plant organs, e.g. aerial twigs and leaves, or roots? Upon their death, roots submerged in streams may have released propagules of fungal endophytes, some of which settled on other types of imported terrestrial detritus, such as leaves. Over time, this may have favoured adaptation to life in running water. Or, terrestrial leaves infected with endophytes were shed and landed in streams. Even water-films on soil or between layers of terrestrial leaf layer may have selected for tetrahedral spore shapes (Bandoni 1975) and predisposed some fungi for their eventual evolution into aquatic hyphomycetes. There are several reports of aquatic hyphomycete conidia in rainwater dripping from trees

(Ando and Tubaki 1984; Bärlocher 1992; Czezug and Orłowska 1999), and Widler and Müller (1984) isolated two undescribed species of *Gyoerffyyella* and *Varicosporium* from green twigs. Iqbal et al. (1995) reported 14 species from submerged green leaves.

It will be of considerable interest to investigate the common route of invasion by aquatic hyphomycetes: do they first colonise the roots, and then spread through the rest of the plant, or do some invade aerial parts? A thorough study of endophytes in aerial and subterranean plant parts at various ages, and molecular data of such strains may eventually allow us to reconstruct the origins of aquatic hyphomycetes.

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