The mycorrhizal species of Rhizoctonia

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Rhizoctonia Species: Taxonomy, Molecular Biology, Ecology, Pathology and Disease Control

edited by
**Baruch Sneh, Suha Jabaji-Hare,
Stephen Neate and Gerda Dijkstra**

The book *Rhizoctonia Species: Taxonomy, Molecular Biology, Ecology, Pathology and Disease Control*, written by the world's most reputable experts in their respective fields of *Rhizoctonia* research, summarizes years of research in the various aspects of the ubiquitous complex group of soil-borne fungi belonging to the anamorph genus *Rhizoctonia*. Species of *Rhizoctonia* cause worldwide economically important diseases on most of the world's important plants such as cereals, potato, cotton, sugarbeet, vegetables, ornamentals, and trees. The subject reviews covered in the book include classic as well as modern approaches to *Rhizoctonia* research in: Taxonomy and Evolution, Genetics and Pathogenicity, Plant-Rhizoctonia Interactions, Ecology, Population and Disease Dynamics, Disease Occurrence and Management in Various Crops, Cultural Control, Biological Control, Germplasm for Resistance, Chemical and Integrated Control Strategies. The book is a selected collection of newly written, carefully integrated and illustrated reviews describing our knowledge of the *Rhizoctonia* species and the experimental work that is the foundation of this information. It will be an important publication for *Rhizoctonia* Investigators, Plant Pathologists, Students, Extension Specialists, Crop Producers and Companies dealing with Plant Disease Control.

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I. INTRODUCTION

The form genus *Rhizoctonia* DC. not only contains a number of species known to be troublesome pathogens, but also some that are beneficial to plants through the formation of mycorrhiza. Most plants living in symbiosis with *Rhizoctonia* are found in the family Orchidaceae; other examples are members of *Genitiana* (Gentianaceae) and bryophytes belonging to the genus *Aneura*. These types of mycorrhiza appear to be physiologically similar to orchid mycorrhiza (Stahl, 1949), which is by far the best described.

All orchids are mycorrhizal plants and usually associated with species of *Rhizoctonia* although a few, mainly chlorophyll deficient species host other fungi, such as *Armillaria mellea* (Vahl:Fr.) Kumm. (Terashita, 1985) [see also Currah and Zehner (1992)]. Numerous strains of *Rhizoctonia* species have been isolated from orchids, and a certain level of specificity between orchid and fungus is suggested.

Data mainly relating to the orchid *Rhizoctonia* interaction will be presented in this chapter. Beginning with a brief historic outline, there will be a description of the structures and functions of the mycorrhiza, followed by a section on the taxonomy of the endophytes. Patterns of specificity in the association with orchids are discussed. A short review of other mycorrhizal interactions involving *Rhizoctonia* will be given and, finally, the most important issues for future research will be evaluated.

II. HISTORY OF ORCHID MYCORRHIZA

According to Ramsbottom (1923), anatomical drawings by Link (1840) were the first recorded observations of hyphal structures in the cells of an orchid seedling. However, Link did not describe the structures as hyphae and in our opinion his illustration could represent starch grains.

Irmisch (1853) later explicitly described fungal hyphae in the rhizome system of the chlorophyll deficient orchid *Corallorhiza innata* R.Br. (= *C. trifida* Chatelain). Although the nutritional status of such orchids was extensively discussed, no linkage with the presence of intracellular hyphae was made.

A functional relationship between orchid nutrition and the presence of endophytic hyphae was first suggested by Frank (1891). Based on experience with other types of mycorrhiza, Frank assumed that the relationship was mutualistic, and suggested that the endophytes would be difficult or impossible to cultivate outside of the orchid because of specific nutritional requirements. However, isolation of orchid endophytes and the *in vitro* synthesis of mycorrhizal seedlings was achieved by Bernard (1909)

and Burgeff (1909). Bernard (1909) referred the orchid endophytes to *Rhizoctonia* in describing the three first species, i.e., *R. repens*, *R. mucoroides*, and *R. lanuginosa*. Other anamorphic species occurring as orchid endophytes were subsequently described by Costantin and Dufour (1920), Burgeff (1932; 1936) and Curtis (1939). The teleomorphs of a number of rhizoctonias associated with orchids were induced and described by Warcup and Talbot (1966; 1967; 1971; 1980), thus providing a better basis for discussion of specificity patterns between orchids and endophytes (Warcup, 1973; 1981). Recently, several new taxa of *Rhizoctonia* from a number of North American orchids have been described or validated (Currah, 1987; Currah *et al.*, 1987; 1988; 1990; Currah and Zelnert, 1992; Zelnert and Currah, 1996).

III. PHYSIOLOGY OF ORCHID MYCORRHIZA

A. *Rhizoctonia* and germination of orchid seeds.

All orchids require fungal infection to complete their life cycle (Rasmussen, 1994). Orchid seedlings are heterotrophic to varying extents and obtain carbohydrates and other organic nutrients from the endophyte. In some orchid species there are mechanisms to delay germination until the presence of mycelia of a compatible endophyte induces or significantly increases germination. The primary signals have not been identified, but an array of compounds, such as ethylene and various vitamins, stimulate seed germination in orchids (Rasmussen, 1995). They are produced by strains of *Rhizoctonia* in culture (Harvais and Pekkala, 1975; Hanke and Dollwet, 1976; Barroso *et al.*, 1986b), and could be involved in the interaction.

After Bernard's and Burgeff's initial success with symbiotic seed germination *in vitro*, techniques were developed to produce many orchid species on nutrient substrates without fungi (asymbiotic), primarily by Knudson (e.g. 1922). However, in recent years the symbiotic propagation technique has regained popularity because many orchids are difficult to propagate asymbiotically, and the mycorrhizal plants develop more rapidly and are more readily established after replanting (e.g., Zettler and McInnis, 1992). This has resulted in a renewed interest in the physiology of the orchid - *Rhizoctonia* association.

B. Invasion of orchid tissues

Compatible infection by *Rhizoctonia* in orchid tissue is restricted to the roots and rhizomes that are located below ground or, in epiphytic orchids, prostrate on the substrate. Cortical tissues are the main sites of infection. Precocious infection of the orchid seed is apparently checked by production of phenolics in the suspensor region (Rasmussen, 1990). There are few other signs of defense reactions in the infected tissue and no cell mortality arises.

Infection follows simple cell wall penetration by solitary hyphae which occurs mostly through absorptive structures such as the suspensor end of the seed, rhizoids of seedlings or root hairs. In a few cases, compatible infection takes place through epidermal cells other than the root hair cells (Rasmussen, 1995). No infection cushions are formed, although the same strains may produce appressoria during pathogenic infection of other plant hosts (Williamson and Hadley, 1970).

C. Histology of infected tissue

The intracellular hyphae form dense coils (pelotons) that may occupy major parts of the plant cell lumen (Fig. 1). After a period of build-up the peloton is broken down to an aggregated clump. Infection and lysis may take place repeatedly in the same cell

and tissues, suggesting that there is a rhythmic or seasonal alternation between periods conducive to intracellular hyphal growth and stages of breakdown (digestion).

FIGURE 1. Section of a seedling of *Dactylorhiza majalis* (Rchb.) Hunt & Summer, symbiotically grown with an *Epulorhiza* sp. The large, basal cells of the seedling are heavily infected with hyphae. Some cells are newly infected (middle right) others are filled with living hyphae (bottom left), and in some cells the pelotons are in the process of collapsing (bottom right). Nuclei are enlarged in the infection zone. The apical part has small cells developing into a meristematic zone (top) that remains uninfected. Stained with PAS-ABB, x187 (ondias x56) Photo: HN Rasmussen.

Shortly before infection, the size of the host cell nucleus increases considerably due to endoreduplication and amplification of the DNA (Williamson and Hadley, 1969; Nagl, 1972) and nuclear bodies develop that may suggest an accumulation of messenger RNA (Barroso and Pais, 1990). The invading hyphae appear to establish a close contact with the nucleus of each infected cell. Plasmalemma of the infected cell invaginates in front of the advancing hyphal tip to form a vast sequestration membrane sheathing the hyphae as they traverse cytoplasm, central vacuole and nucleus of the cell. This exceedingly complicated system of membranes provides extensive, short range contact between the symbionts.

During initial infection there are indications of high hyphal secretory activity (Hadley *et al.*, 1971; Rasmussen, 1995). High polyphenol oxidase activity is noted initially in the hyphae and later in the interfacial space (Pais and Barroso, 1983; Barroso *et al.*, 1986a). The fungal cytoplasm becomes loaded with glycogen (Fig. 1), particularly in dilated portions of the peloton hyphae (Rasmussen, 1990).

The infected plant cytoplasm contains numerous mitochondria and profusely developed ER, probably involved in the production of hydrolytic enzymes (Dörr & Kollmann, 1969; Barroso *et al.*, 1986a). In the early stages of lysis the hyphal cells vacuolate and the dolipore septa begin to disintegrate (Richardson *et al.*, 1992). During subsequent hyphal degeneration, acid phosphatase activity is detected inside the hyphal wall. As the hyphal cytoplasm disorganizes and the cells collapse, the periplasmic canals in which they lie fuse so that the hyphal residue aggregates in larger clumps which remain in the plant cells.

D. Regulation

Phytoalexins such as orcinol and hircinol exhibiting strong fungicidal activity have been found in orchid tissues, and are induced following infection by *Rhizoctonia* and other fungal endophytes found in association with orchids (Nobecourt, 1923). However, 24 unspecific saprophytic and semi-parasitic soil fungi did not induce phytoalexin production in challenged orchid tissue (Gäumann *et al.*, 1960). Some *Rhizoctonia* spp., including strains of *Ceratobasidium cornigerum* (Bourdot) D.P. Rogers and *Thanatephorus cucumeris* (Frank) Donk, tolerate fairly high concentrations of phytoalexins (up to 150mg/l) (Pegg & Beardmore, according to Hadley and Pegg, 1989).

E. Metabolic exchange

The existence of orchids with highly deficient photosynthetic capacity (e.g. Leake, 1994) strongly supports a role of orchid mycorrhiza in supplementing or wholly replacing photosynthesis. Transfer of carbohydrates and phosphate through a mycelium of *Rhizoctonia* into orchid seedlings has been demonstrated *in vitro* by means of isotope labeling (Smith, 1967; Alexander *et al.*, 1984; Alexander and Hadley, 1985). The fact that many orchid seedlings require amino acids and organic compounds other than soluble carbohydrates for their growth, suggests that the fungal partner provides a variety of substances. Stimulation of orchid seedling growth may occur as early as 48 hours after infection but it is unclear whether this occurs before lysis of hyphae begins (Purves and Hadley, 1976). While necrotrophic transfer obviously takes place, there is presently no indication that it is preceded by a phase of biotrophic interchanges.

Experiments designed to demonstrate a transfer of carbohydrates from orchid to fungus were unsuccessful (Hadley and Purves, 1974; Purves and Hadley, 1976). Outgrowth of hyphae from an infected seedling onto a substrate devoid of nutrients has been advanced in favour of this kind of transfer (Smith, 1967). However, this could be explained by re-allocation within the living part of the mycelium. The present evidence does not suggest any nutritional benefits for the fungus.

IV. TAXONOMY OF RHIZOCTONIAS MYCORRHIZAL WITH ORCHIDS

The majority of fungi associated with orchids can be referred to *Rhizoctonia* sensu lato, i.e. sterile mycelia capable of entering living plant tissue and producing sclerotia (DeCandolle, 1815). In some strains sclerotia have not been observed in culture, but monilioid cells that are considered to be the precursors of sclerotia are always present. Many of the strains associated with orchids have been given anamorph names (Bernard, 1909; Costantin and Dufour, 1920; Burgeff, 1932; 1936; Curtis, 1939; Currah *et al.*, 1988; 1990; Currah and Zelmer, 1992; Zelmer and Currah, 1996). Until recently all were assigned to *Rhizoctonia* s.l., but the five anamorph genera with certain teleomorph affinity established by Moore (1987), has made it possible to refer

orchid endophytes to three of these, *Ceratophiza*, *Epulorhiza*, and *Moniliopsis*. The anamorph genus *Opadorhiza* T.F. Andersen and R.T. Moore is proposed elsewhere in this book to accommodate strains with *Sebacina* teleomorphs (see chapter I.A1). A number of strains from Australian orchids will probably be referable to this genus. No orchid endophytes have so far been referred to the genera *Acorrhizoctonia*, *Rhizoctonia* s.str. or *Chrysorhiza* T.F. Andersen and J.A. Stalpers, proposed for the anamorphs of *Waitea* (see chapter I.A3).

Although it is fairly easy to refer a strain to form genus, it is extremely difficult to distinguish between species. The few mycelial characters available have been found to vary significantly between hyphae of the same mycelium, sclerotia and monilioid cells are often very variable, and substrate composition influences mycelial structures (Andersen, 1990). Furthermore, a recent survey has demonstrated that most names within *Rhizoctonia*, including most of the names of orchid endophytes, are either illegitimate or of doubtful application (Andersen and Stalpers, 1994). Type specimen or illustration is rarely preserved, and the description is inadequate for a positive identification. Only six taxa with orchid association are presently acceptable (Table I), whereas 18 names of orchid endophytes referred to *Rhizoctonia* are disregarded for various reasons and can only be re-established on the basis of validation (Table 2).

TABLE I. Accepted *Rhizoctonia* s.l. associated with orchids. Condensed from the data of Downie (1959), Currah & Zelmer (1992) and Zelmer & Currah (in press). Host species are mentioned. When more species in a genus host the fungus, only generic name is given.

Name & Author	Host
<i>Ceratophiza peracutata</i> Zelmer & Currah	<i>Platanthera praecleara</i> Sheviak & Bowles
<i>Moniliopsis anomala</i> Burgeff ex Currah	<i>Coeloglossum viride</i> (L.) Hartm.
<i>Moniliopsis solani</i> (Kühn) Moore	<i>Dactylorhiza purpurella</i> (T. & T.A. Steph.) Soó <i>Spiranthes</i> and <i>Vanilla</i> <i>Platanthera orbiculata</i> (Pursh) Lindl.
<i>Epulorhiza albertaensis</i> Currah & Zelmer	<i>Platanthera obtusata</i> (Banks ex Pursh) Lindl.
<i>E. anaticula</i> (Currah) Currah	<i>Platanthera</i> , <i>Calypto</i> and <i>Coeloglossum</i> <i>Anerorchis rotundifolia</i> (Banks) Hulten

In some investigations, reproductive structures have been induced in culture making the strains referable to species within the teleomorph genera *Ceratobasidium*, *Thanatephorus*, *Tulasnella*, and *Sebacina* (Warcup and Talbot, 1966; 1967; 1971; 1980; Currah, 1987; Warcup, 1991) (Table 3). The best results obtained in fruiting experiments is only 62% (Warcup, 1981), which demonstrates the necessity to maintain a parallel identification of anamorphs.

TABLE 2. ejected *Rhizoctonia* s.l. names associated with orchids. Condensed from data in Andersen & Stalpers (1994).

Names & Authors	Reason for rejection
<i>Ceratolhiza goodyerae-repentis</i> (Costantin & Dufour) Moore	Doubtful taxon
<i>Epulorhiza repens</i> (Bernard) Moore	Doubtful taxon
<i>Rhizoctonia aerea</i> Burgeff	Doubtful taxon
<i>R. arachnion</i> Burgeff	Doubtful taxon
<i>R. asclerotica</i> Burgeff	Invalid name
<i>R. borealis</i> J.T. Curtis	Invalid name
<i>R. floccosa</i> Burgeff	Doubtful taxon
<i>R. gracilis</i> Burgeff	Invalid name
<i>R. lanuginosa</i> Bernard	Doubtful taxon
<i>R. monilioides</i> J.T. Curtis	Invalid name
<i>R. neotiae</i> Wolff ex Burgeff	Invalid name
<i>R. psychodis</i> Thomas	Provisional name
<i>R. robusta</i> Burgeff	Invalid name
<i>R. sclerotica</i> Burgeff	Invalid name
<i>R. stahlit</i> Burgeff	Invalid name
<i>R. suavis</i> Thomas	Provisional name
<i>R. subtilis</i> Burgeff	Invalid name
<i>R. subtilis</i> v. <i>nigra</i> J.T. Curtis	Invalid name

At species level, very few connections have been established between anamorph and teleomorph taxa. Only three anamorph-teleomorph species relations have reached some degree of recognition, in spite of the fact that the anamorphs lack a proper nomenclatural basis (Andersen and Stalpers, 1994). *Moniliopsis (Rhizoctonia) solani* (Kuhn) Moore, the anamorph of *Thanatephorus cucumeris*, (is treated in chapter I.A1). *Ceratolhiza goodyerae-repentis* (Costantin and Dufour) Moore is tentatively considered as the anamorph of *Ceratobasidium cornigerum* (Bourdote) Rogers. All discussions of this relationship are based on application of *C. goodyerae-repentis* in the sense of Downie (1941), which mainly relies on an assumed host specificity to the orchid *Goodyera repens* (L.) R.Br. Furthermore, *C. cornigerum* may be a collective species containing more than one anamorph taxon (e.g. Burpee *et al.*, 1980). *Epulorhiza repens* (Bernard) Moore now considered to be the anamorph of *Tulasnella deliquescens* (Juel) Juel was previously thought to be *Tulasnella calospora* (Boudier) Juel due to a misidentification by Warcup and Talbot (1967) (Roberts, 1994). *T. deliquescens* is considered to be one of the most widespread orchid symbionts, as it has been found in a number of Australian orchid genera, and has been tentatively identified from several holarctic species (Warcup, 1981; Rasmussen, 1995). However, other species of *Tulasnella* have been described based on isolates from Australian orchids with limited anamorphic data. Many of the orchid endophytes from the holarctic region, supposedly referable to *Tulasnella deliquescens*, may prove to belong to some of these taxa.

TABLE 3. Teleomorphs of *Rhizoctonia* strains associated with orchids. Condensed from Warcup & Talbot (1967; 1971; 1980), Warcup (1981), and Currah (1987). For further details, see Warcup (1981). Host species are mentioned. When more species in a genus host the fungus, only generic name is given.

Names & Authors	Host
<i>Ceratobasidium</i> D.P. Rogers	
<i>C. angustisporum</i> Warcup & Talbot	<i>Pterostylis nutica</i> R.Br.
<i>C. cornigerum</i> (Bourdote) Rogers	<i>Goodyera repens</i> (L.) R.Br., <i>Pterostylis</i> and <i>Prasophyllum</i>
<i>C. globisporum</i> Warcup & Talbot	<i>Trichoglottis australiensis</i> Doctr.
<i>C. obscurum</i> D.P. Rogers	<i>Calanthe triplicata</i> (Willen.) Ames
<i>C. papillatum</i> Warcup & Talbot	<i>Acianthus reniformis</i> (R.Br.) Schlechter
	<i>Thrixspernum congestum</i> (F.M. Bail.) Doctr.,
	<i>Sarcochilus</i>
<i>C. sphaerosporum</i> Warcup & Talbot	<i>Pomatocalpa macphersonii</i> (F.Muell.) T.E. Hunt
	and various members of Sarcanthinae
<i>Thanatephorus</i> Donk	
<i>T. anomala</i> (Talbot) J.A. Stalpers & T. F. Andersen	<i>Prasophyllum macrostachyum</i> R.Br. var. <i>ringens</i> (Reichb.f.) A.S. George
<i>T. cucumeris</i> (Frank) Donk	<i>Prasophyllum odoratum</i> Rogers
	<i>Pterostylis foliata</i> Hook.f.
<i>T. gardneri</i> Warcup	<i>Rhizantella gardneri</i> Rogers
<i>T. orchidicola</i> Warcup & Talbot	<i>Orchis mascula</i> (L.) L.
	<i>Coeloglossum viride</i> (L.) Hartm.
<i>T. pennatus</i> Currah	<i>Calypso bulbosa</i> (L.) Oakes
<i>T. sterigmaticus</i> (Bourdote) Talbot	<i>Thelymitra antennifera</i> Hook.f.
<i>Tulasnella</i> J. Shroeter	
<i>T. allantospora</i> Wakefield & Pearson	<i>Corybas dilatatus</i> (Rupp & Nicholls) Rupp
<i>T. asymmetrica</i> Warcup & Talbot	<i>Thelymitra</i> and <i>Dendrobium</i>
<i>T. cruciata</i> Warcup & Talbot	<i>Acianthus caudatus</i> R.Br. and <i>Thelymitra</i>
<i>T. deliquescens</i> (Juel) Juel	<i>Dactylohliza</i> , <i>Diuris</i> , <i>Acianthus</i> , <i>Caladenia</i> , <i>Thelymitra</i> , <i>Lyperanthus</i> and <i>Dendrobium</i>
<i>T. irregularis</i> Warcup & Talbot	<i>Dendrobium dicuphnum</i> F. Muell.
<i>T. violacea</i> (Qu'let) Bourdot & Galzin	<i>Thelymitra aristata</i> Lindl.
<i>Sebacina</i> Tulasne	
<i>S. vermifera</i> Oberwinkler	<i>Glossodia major</i> R.Br. <i>Microtis</i> , <i>Acianthus</i> , <i>Caladenia</i> , <i>Elythranthra</i> , <i>Eriochilus</i> and <i>Prasophyllum</i> .

V. SPECIFICITY BETWEEN RHIZOCTONIAS AND ORCHIDS

It was originally assumed that a highly specific relationship existed between the orchids and their endophytes, and fungi were often named after the host of the initial isolate, e.g. M.R. (*Mycelium Radiciis*) (*Habenaria psychodis* (Burgeff, 1909). Later it was recognized that plant-fungal relation was not highly specific in general, although fungal type preference seems to occur in many orchids (Burgeff, 1936; Curtis, 1939; Warcup, 1971; 1981). However, beside the difficulties in identifying imperfect strains there are three major issues that confound the evaluation of specificity.

- Isolation procedures have varied considerably, some placing fairly large pieces of orchid root tissue on an agar plate (Curtis, 1939) while others used meticulous preparation of single pelotons from root tissue, enabling a critical distinction between epiphytes and inter-, and intracellular endophytes (Warcup and Talbot, 1967, 1971, 1980; Rasmussen *et al.*, 1990a). Only the latter can be considered mycorrhizal.
- Isolates have mainly been derived from roots of adult orchids. However, at the photoautotrophic stage the plants are no longer totally dependent on the endophyte, and they have been shown to accommodate a variety of fungal strains (Warcup, 1981; Alexander and Hadley, 1983). Adult plant material is thus less useful for an evaluation of specificity patterns. Seeds may be responsive to a range of fungi during and immediately after germination, but this gives no clue to the subsequent success in seedling development (Warcup, 1973). It is known that fungi stimulating the highest germination rate *in vitro* are often different from those that support the best protocorm growth [Figs. 5.2 and 5.3 in Rasmussen (1995)]. The most critical phase concerning symbiont compatibility is during seedling development and the transition from seedling to a leaf-bearing adult (Muir, 1989), also characterized by a shift from holomycotrophy to partial mycotrophy and photoautotrophy.

- Laboratory experiments involving *in vitro* formation of mycorrhizal associations do not correspond closely to natural conditions and, as a result, atypical mycorrhizal associations that would not occur in nature may be established (Rasmussen, 1995). In cases when fungal strains have been isolated from orchid seedlings found underground the identification of the host is more or less uncertain (Rasmussen *et al.*, 1990a). A new 'seed packet' method has been developed (Rasmussen and Whigham, 1993) which allows both a controlled study of germination under natural conditions, and of a fungal association with seeds of known origin under natural conditions that are relevant for the species in question (Rasmussen and Whigham, 1993; Masuhara and Katsuya, 1994).

In studies of Australian orchids (Warcup 1971; 1973; 1981), careful isolation; teleomorph identification of strains (Warcup and Talbot, 1967; 1971; 1980), and germination tests *in vitro*, revealed some degree of specificity between certain fungi and genera or species of orchids, particularly in species belonging to *Pterostylis*, *Caladenia* and *Thelymitra*. The species grew adjacent to each other in the same habitat, but hosted three different endophytes, belonging to *Ceratobasidium*, *Sebacina* and *Tulasnella*, respectively (Warcup, 1973). Both species - species, species - genus, and genus - genus specificity levels were demonstrated (Warcup, 1981).

Corresponding studies on orchids from the northern hemisphere have proven to be largely inconclusive (Downie, 1941; Hadley 1970; Currah *et al.*, 1988; 1990; Muir, 1989). There are indications that some of the orchids are not highly selective with respect to the endophyte, e.g. *Dactylorhiza purpurella* (T. and T.A. Steph.) Soó (Downie, 1959), and furthermore, a number of orchid species and genera host members of *Tulasnella* (*Epulorhiza*) (Currah *et al.*, 1990; Rasmussen *et al.*, 1990a; 1990b; Currah and Zelnner, 1992; Rasmussen, 1995; Zelnner and Currah, 1996). Another notable observation is the apparent lack in the northern hemisphere of orchid endophytes belonging to *Sebacina*. The Canadian strain tentatively identified as *Sebacina* sp. from *Platanthera orbiculata* (Pursh) Lindl. (Currah *et al.*, 1990) can now be referred to *Tulasnella* (Andersen, 1996).

VI. RHIZOCTONIA MYCORRHIZAL WITH OTHER PLANTS

There are few records of *Rhizoctonia* in mycorrhizal relationships with non-orchid plant groups. The fungi such as *R. pinii-insignis* (nom. inval.), isolated from roots of *Pinus radiata* Don (= *Pinus insignis* Dougl.), may be involved in a mycorrhizal relationship as it improved growth of the test plants, lupin and pea (Castellani, 1935). However, the best documented case is the bryophyte genus *Aneura* (Rayner, 1927; Stahl, 1949), where both achlorophyllous and green species form mycorrhiza with *Rhizoctonia*. The mycorrhiza was found to be strikingly similar to the orchid mycorrhiza with respect to penetration, formation of hyphal coils in cortical cells, and subsequent hyphal digestion (Rayner, 1927). Stahl (1949) isolated a number of *Rhizoctonia* strains from the moss, and referred them tentatively to taxa described by Burgeff (1932; 1936). Unidentified septate fungi with a similar infection pattern have been found in gametophytes of *Psilotum nudum* (L.) Beauv. (Bierhorst, 1953). It is possible that they belong to *Rhizoctonia* (Harley, 1969).

In the Gentianaceae most species host mycorrhizal fungi, and many species show similarities to the orchids with respect to seed size (Harley, 1969). Mycorrhiza of some *Gentiana* species investigated by Neumann (1934) were of the orchid type, and one of the mycelia did belong to *Rhizoctonia*. *Gentiana* seeds are difficult to germinate *in vitro* and no successful synthesis of mycorrhiza was reported.

Species belonging to the Burmanniaceae and Triuridaceae have been claimed to form mycorrhiza with *Rhizoctonia* (Harley 1969), but no certain identification has been possible, and this association remains unclear.

VII. CONCLUSION

There is a great need for more taxonomic work on the mycorrhizal species of *Rhizoctonia*. The six accepted species associated with orchids are hardly enough to accommodate the diversity of endophytes derived from this large plant family. An important step would be to carefully describe new taxa or continue to validate previously introduced taxa (Currah *et al.*, 1990; Currah and Zelnner, 1992; Zelnner and Currah, 1996). Anamorph-teleomorph species relations are still poorly known and, whenever possible, descriptions of new anamorph taxa should be based on material with known teleomorph origin. When a larger number of clearly defined, recognizable taxa are available, a better understanding of patterns of specificity can be achieved.

Among Northern temperate species, the identity of the endophytes, particularly in the rhizomatous genera such as *Cypripedium*, *Epipactis* and *Cephalanthera*, is still

largely unknown. Studies of the endophytes of some of the basal groups within the orchidaceae would be particularly interesting from an evolutionary point of view.

The chemical background for recognition and response, i.e. the communication between the two organisms, is an issue which has so far received very little attention with respect to the orchid-*Rhizoctonia* interaction. There are also interesting questions to be raised with respect to the associations of *Rhizoctonia* to non-orchid plant groups.

In conclusion, it seems that much remains to be learned and that we are only beginning to explore the diversity of mycorrhizal relationships between *Rhizoctonia* and plants.

VIII. REFERENCES

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V.15 PHOTOGRAPHS OF SYMPTOMS INCITED BY *RHIZOCTONIA* SPP. ON VARIOUS CROPS

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