THE UNIVERSITY OF MANITOBA

SNOW MOLD DISEASE OF TURFGRASSES IN MANITOBA

THE CAUSAL ORGANISMS AND THEIR CONTROL

BY APPLICATION OF BORAX AND OTHER ORGANIC

NON - MERCURIAL COMPOUNDS

BY

LESLIE R. ALLEN

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With the completion of this study, came an end to soaken-wet feet, aching backs and thoroughly chilled bones.

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GENERAL ABSTRACT

An in vitro test was conducted to determine the effects of different rates of borax on the growth and/or hydrogen cyanide production of various pathogenic low-temperature basidiomycete (LTB) isolates. All rates of borax reduced the mycelial growth of each isolate considerably, but appeared to have no effect on the hydrogen cyanide gas production by the gas producing LTB-Type B (W5) and LTB-Saskatchewan isolates. Borax was found to be more detrimental to the growth of LTB-Manitoba and LTB-Type A (W1), which appeared to be similiar in many ways, than to LTB-Saskatchewan and LTB-Type B (W5).

A second in vitro test investigated the effects of borax concentration and pH on the growth of three pathogenic isolates of the LTB, each being incubated on different culture media. Borax was inhibitory to the growth of all the isolates, particularly at a concentration exceeding 100 ppm. Borax, at all concentrations, was extremely inhibitory to fungal growth with increasing pH on all culture media used. Borax was not a highly lethal compound in vitro, but did have good fungistatic ability against the LTB isolates. On the basis of growth inhibition, the LTB-Manitoba isolate was the most sensitive and the LTB-Saskatchewan least sensitive to the effects of this compound.

Finally a field study, conducted at various locations in southern Manitoba, during the fall and winter of 1973-74 was performed to determine the causal organisms and to find a non-mercurial, organic compound or mixture of compounds which would effectively control snow mold of turfgrasses in our area. Snow

mold damage was caused predominately by Typhula FW[1]. Sclerotinia borealis and the psychrophilic, sterile basidiomycete was also abundant. Damage caused by F. nivale was not excessive. Variation in pathogen abundance did occur and was probably due to a complex of factors which were not revealed in this study. At several of the areas studied and surveyed a complex of 3 or 4 pathogens was found causing damage to the turfgrass. Chemical application towards the end of October provided the most effective control of snow mold in Manitoba. Mercuric chloride (standard control compound) gave excellent control of the snow mold pathogens at all test locations. A combination of borax and Terraclor 75W also provided excellent broad spectrum control of snow mold in 1973-74. Phytotoxicity was a major problem but if this could be eliminated via a more uniform application and reduction in rates used, the borax: Terraclor 75W combination shows promise for snow mold control in Manitoba. All compounds were effective in controlling specific group(s) of pathogens except mercuric chloride and the borax combination treatments which gave a broad spectrum control.

1) Nomenclature of species given by Dr. J. D. Smith, C. D. A. Research Station, Saskatoon, Saskatchewan.

GENERAL INTRODUCTION

Throughout the ages man has always strived to change the environment about him. He has altered the landscape for political, economic and aesthetic achievements. Today there is an increasing demand for such aesthetic areas as parks, golf courses, country clubs, etc., to remove oneself from the tensions and aggravations of modern day life. The major component of these relaxation centres is turf which, in association with ornamental flowers, shrubs and trees, gives beauty and serenity to the area. Nothing is more displeasing than to see the vegetation of these areas obliterated by disease.

The most devastating disease of turf and turfgrasses in Western Canada is the overwintering disease commonly referred to as snow mold. It is to be expected that, with an increased interest in sports and amenity turf, there will develop a better appreciation of the part played by overwintering and other diseases in turf quality and appearance (81). This will lead to the development of simple, inexpensive control techniques that will pose no threat to our environment.

Several fungal pathogens are known to be causal agents of snow mold disease and depending on the conditions prevalent, one or more of the pathogens may predominate at a particular location in a given year. Furthermore, the host range of each of the snow mold pathogens is extremely diverse. Because of these complexities, effective snow mold control is best achieved by chemical treatment of the turf.

In the past and even today mercurial compounds are being used as a general broad spectrum control measure of the snow mold or anisms on golf and bowling greens (53,66). The many disadvantages (3,8,31,53) of mercurials have made researchers realize the importance of finding non-mercurial organic compounds which are fungicidal or fungistatic to all the low-temperature turfgrass pathogens. This concern lead to the present study which investigated the causal organisms of snow mold in Manitoba and the controlling capabilities of several organic compounds and combinations of organic compounds against the pathogens present.

General Review of Literature

Introduction:

The major infectious diseases of turfgrasses are caused by fungi (5). Bacteria and viruses are not important in the total spectrum of turfgrass pathogens (5). A great many fungal diseases are known to occur in turfgrass. Helminthosporium spp., for example, are able to attack the Kentucky bluegrasses, fescues, ryegrasses, bentgrasses, and Bermudagrass and cause diseases such as melting out, zonate eyespot, helminthosporium leaf spot, brown blight and leaf blotch (17). Other turfgrass diseases include brown patch (Rhizoctonia solani), dollar spot (Sclerotinia homeocarpa), red thread, powdery mildew, septoria leaf spot, fairy ring, and last but not least snow mold, the most important disease in our area and in western Canada (17).

Snow mold has been under investigation for many years in North America, Scandinavia and Japan (53). The common psychrophilic organisms which are known to be the causal agents of the disease are: (1) Fusarium nivale (Fr.) Snyder and Hansen (21), (2) Typhula itoana Lasch ex. Fr. (73,74,88), (3) T. idahoensis Remsburg (73,74,88), (4) Sclerotinia borealis Bubak and Vleugal (51,88), (5) An unidentified low-temperature basidiomycete (LTB) (6,7), (6) T. trifolii (23), (7) T. graminum (61,74). In addition, Smith (84) has found a microsclerotium-producing LTB in association with snow mold patches on domestic lawns, golf course fairways and bowling greens in Saskatchewan. A fungus with an orange rindless sclerotium (ORS), believed to be antagonistic to the major snow mold pathogens, and a Typhula sp. which does not fit the description of T. idahoensis Remsburg or T. incarnata Lach ex. Fr. have also been isolated in Saskatchewan (81).

The majority of the literature deals primarily with the first five mentioned organisms which are known snow mold pathogens of turfgrasses (7,96) and it will be these to which attention will be directed.

Distribution of the Snow Mold Pathogens:

The distribution of these low-temperature pathogens appears to follow a geographical pattern (54). S. borealis Bub and Vleug. is found in the colder regions, the distribution of Typhula spp. is more intermediate in the temperate zone and F. nivale (Fr.) Snyder and Hansen occurs farther south in the slightly warmer regions (51,54). This distribution exists both in Scandinavia and in America (51,54). The unidentified LTB is prevalent in northern and central western Canada (7,15) but has also been isolated in Alaska (54).

However this is only a general distribution pattern and local variations in microclimate may be of more significance in determining pathogen prevalence than the climate generally. For example, Smith (84) has isolated all the causal organisms throughout southern Saskatchewan and it appears that many of these organisms are present also in Manitoba (70). In addition, Vaartnou and Elliott (96) reported severe snow mold damage to lawn caused by F. nivale in the Beaverlodge area of Alberta in 1967. Bruehl (9) reported that Typhula spp. and F. nivale often occur together in the Pacific Northwest to form a disease complex. Also Richardson & Zillinsky (76) reported F. nivale as far south as Mexico (76). Therefore, one can soon realize that the geographic separation of these psychrophils is not so distinct.

Fusarium nivale:

(A) Taxonomy and Cultural Characteristics:

Fusarium nivale (Fr.) Snyder and Hansen is the causal agent of fusarium patch or pink snow mold of winter cereals, turf and forage grasses (21,88). F. nivale is taxonomically in the class Fungi Imperfecti, order Moniliales (88). The perithecial stage of F. nivale is referred to as Calonectria graminicola (Berk and Br.) Wr. (88).

Cultural studies by Dahl (21) have disclosed that scant aerial, colourless, and sterile mycelial growth is produced on corn-meal agar. However, very abundant mycelial growth developed on oat-meal agar and spores were produced in slimy salmon-coloured masses which often covered a large part of the surface of the agar. On potato-dextrose agar there was an abundant, white fluffy, spore-bearing mycelium. On sterile grass clippings, the fungus covered each leaf with a fluffy white mycelium that in a few cases produced spores.

On potato-dextrose agar F. nivale grows at temperatures from 0^{o}-32^{o} C. with an optimum of 20^{o} C. (21). Dahl (21) has also reported that no sporulation occurs when cultures are kept in total darkness, but when grown at 20^{o} C. in diffuse light, abundant mycelial growth and sporulation occurs.

(B) Hosts:

Turfgrasses which are known hosts of F. nivale are annual bluegrass, Colonial bentgrass, creeping bentgrass, Italian ryegrass, Kentucky bluegrass, perennial ryegrass, redtop, red fescue, rough bluegrass, sheep fescue, tall fescue, velvet bentgrass and many other grasses (5). Field tests by Dahl (21) and Wernham (106) have indicated that the Seaside strain of creeping bent was highly susceptible to attack by F. nivale, Washington only moderately susceptible, whereas Astoria and Metropolitan bentgrasses were resistant to attack. Lebeau (57) has isolated F. nivale from damaged areas of Penncross bentgrass. Dahl (21) found fescue to be highly susceptible to fusarium snow mold. Ricke and Vargas (77) reported F. nivale on the Merion strain of Poa pratensis. This was also shown by Lebeau in 1968 (57). The host range of F. nivale is indeed very wide (88) and in some cases is not even restricted to Gramineae (9). Bruehl (9) believed this to be presumptive evidence of a low degree of pathogenic specialization in this pathogen.

(C) Symptomatology:

When F. nivale causes disease in the absence of snow, it is referred to as fusarium patch; the damage produced under snow or at the margins of melting snowbanks is called pink snow mold. In the absence of snow, the symptoms appear on turf as irregular pale-yellow to white circular areas ranging from 2 inches to 1 foot or more in diameter (5,17,21). Mycelium is usually not apparent on the leaves under these conditions (5). Under a snow cover, or during prolonged, cool, wet weather, the irregularly circular diseased areas may be covered with a mat of aerial mycelium - at first white and then turning to a faint pink colour with longer exposure to light

(5,17,21). The areas so damaged feel slimy when wet and the surface dries to form a crust (5,17,21). In both situations, the infected areas may coalesce, thus damaging large areas of turfgrass (17).

(D) Life Cycle and Infectivity:

The pathogen survives adverse periods as dormant mycelium in the host or in debris of diseased leaves (17). Couch (17) stated that abundant conidial production occurs soon after the development of optimal environmental conditions and that the conidia are carried to the leaves by wind and/or splashing water where primary infection is accomplished by penetration through stomata. Its progress through the tissue is intercellular until the cells begin to collapse after which the pathogen moves intracellularly (21). After the mycelium becomes abundant in the tissue, sporodochia develop through the stomata in rows (21,76). Usually, only the leaves are attacked, but under severe disease conditions, the pathogen may infect the crowns (17).

(E) Factors Influencing Development:

Several factors favour the development of fusarium patch or pink snow mold. Climatic conditions that favour attacks of the disease are: cloudy weather; abundant moisture in the fall; temperatures of 0° - $5^{\circ}C$; snow falling on unfrozen ground, deep snow; and a prolonged, cold, wet spring (21,66). High nitrogen levels in turfgrass soils favour the development of _F. nivale_ (21,31,62,77). Beard (3) stated that this is because the cell walls of the turfgrass hosts are thinner and more easily penetrated by fungal hyphae. Bruehl (10) and Dahl(21) reported that a high nitrogen level allows the plants to go under the snow with a higher rate of basal metabolism than normal. This reduces carbohydrate reserves which in turn results in incomplete hardening and increased susceptibility to attack.

Smith (83) reported increased attacks of fusarium patch disease following application of ground limestone and suggested that a high pH in the upper soil regions increased disease incidence. Other reports (82) also have indicated that alkaline soil conditions favour disease development while acidic soil conditions reduce disease severity. Other management practices involving the use of straw mulches, the build-up of deep thatch layers and matting of the turf will prolong wet, cold conditions and thus favour the growth and development of *F. nivale* (21).

Typhula spp.:

(A) Taxonomy and the confusion which exists:

The genus *Typhula* is taxonomically positioned in the class Basidiomycetes (88) because of the presence of hyphal clamp connections (18). Until Remsburg's work in 1940 (75) much confusion about the genus *Typhula* existed in the phytopathological literature. This confusion resulted from the causal organisms of the now known typhula snow molds being reported as *Sclerotium rhizodes* Averswald (74), *Sclerotium fulvum* Fries (74), *Typhula graminum* (74), and *T. itoana* (74,75,88,106). The confusion had come about partly because of the macroscopic resemblance of the sclerotia of the above-named fungi as described by early mycologists, and partly because of the inability to collect or otherwise obtain fertile sporophores, which are essential for taxonomic classification (74). These reasons in conjunction with the geographic distribution (North America, Europe, Japan and Scandinavia) of typhula snow molds (73,74), have led to the array of names given to the causal organisms. *Typhula* species which have been reported in the literature to be the causal agents of snow molds of cereals and grasses are: *T. incarnata* Lasch ex. Fr. (61,90), *T. itoana* Imai (16,79), *T. graminum* Karst (61), *T. ishikariensis* Imai (61), *T. idahoensis* Remsberg (75), *T. borealis* Ekstrand (61), *T. hyperborea* Ekstrand (61), *T. trifolii* (23), and *Typhula (FW)* spp. (81).

According to Corner, as reported by MacDonald (61), *T. incarnata* and *T. itoana* are synonyms, but *T. incarnata* has priority over *T. itoana* in usage. *T. incarnata* and *T. graminum* have been reported to be distinctly different species (61,75). According to Remsberg (75), *T. graminum* has not been demonstrated as a causal organism of snow mold. MacDonald (61) has reported that Corner believes *T. graminum* not to be uncommon but that it is a small, inconspicuous pathogen. MacDonald (61) reported that Ekstrand had divided his isolates into two species, *T. borealis* and *T. hyperborea*, on the basis of the length-width ratio of their basidiospores only. Some doubt as to the reliability of such a taxonomic character is suggested by Ekstrand's statement that; "the length of the spores is very variable in different fruit bodies and in different collections. The relationship between the length and width of the spores is very variable too, due to the variation in the length which is great even between the spores of fruit bodies from the same collection".

Ekstrand (61) has identified *T. borealis* on material collected in Sweden, Finland, Canada and Norway. Ekstrand (61) has maintained that his isolates do not fit Remsberg's description of *T. idahoensis*. Despite this, Jamalainen (41) has since acknowledged that isolates of *Typhula* occurring in Finland agree with the description of *T. idahoensis*. In addition, MacDonald (61) stated that the description given by Imai for *T. ishikariensis* agrees fairly well with those given by Remsberg (75) for *T. idahoensis* and Ekstrand (61) for *T. borealis*, considering the variability of the fungus.

Typhula FW is a common snow mold pathogen in Saskatchewan (81). It produces sclerotia which are approximately 0.25 to 0.5 mm in diameter (about half that of *T. idahoensis*), globular, tawny in colour when young and dark brown to black when mature (81).

In summary, the reported causal agents of typhula blights or snow molds are; *T. incarnata* (= *T. itoana*), *T. ishikariensis* (= *T. idahoensis* = *T. borealis* = *T. hyperborea*), *T. graminum* and *T. trifolii* and *Typhula FW* (61,81). Since *T. incarnata* and *T. ishikariensis* are the most commonly reported organisms causing typhula snow molds, the remaining discussion will be confined to them.

(B) Cultural Characteristics:

According to Remsberg (75) *T. idahoensis* grows over a range of 0° - 18° C., with an optimum temperature of 9 - 12° C. when cultured on potato-dextrose agar. Mycelial growth is abundant, fluffy and concentrically banded (75). In contrast, Sprague (88) has stated that growth is slow and its culture tedious. Dejardin (23) has shown that 5° C. was slightly better than 10° C. for growth of *T. idahoensis* and *T. trifolii* on malt yeast-glucose (MYG) agar and 20° C. was maximum.

Remsburg stated that sclerotia of *T. idahoensis* are produced in 5 - 10 days, are clustered or in concentric rings and are always produced singly never coalesced into masses (75). Recently, Cunfer (19) has shown that the cultural characteristics of monokaryotic and dikaryotic cultures of *T. idahoensis*, grown on PDA at - 1 to 20° C. for 20 days, differed primarily in sclerotia production. Generally the dikaryons produced sclerotia 1 - 2 mm in diameter that often coalesced into mounds. Most monokaryons produced fewer sclerotia than did the dikaryons and the sclerotia from the monokaryons were about one-third to two-thirds the size of dikaryotic sclerotia (19). Dejardin (23) has shown that sclerotia of *T. idahoensis* and *T. trifolii* first appeared after 4 days when incubated at 10° and 15° C. on MYG agar, but eventually were produced at all temperatures which permitted growth and most abundantly at temperatures above 10° C.

According to Remsburg (75) sterile brown sporophores develop abundantly from the chestnut-brown sclerotia of *T. idahoensis* in culture. Remsburg (75) however, and many others since, have shown that short rays of light plays an important role in the fructification of these fungi. Through a series of tests Remsburg (75) has shown that fertile sporophores can be produced in culture when exposed to light waves in the region of 2700 to 3250 Angstroms.

In contrast to the growth of *T. idahoensis*, oxygen uptake was optimal and the respiratory quotients higher at 20° C. than at

5^{o} C. (23). This suggests that growth becomes completely uncoupled from respiration at 20^{o} C. and above (23). Therefore it is possible that the mechanisms responsible for coupling growth to respiration may be abnormally heat-sensitive and thus determine the maximum temperature for growth (23). However the exact coupling mechanisms are not known.

Dejardin (23) has also shown that the optimum pH for growth of T. idahoensis, T. trifolii and T. incarnata lies between 6 and 7.

Dejardin (23) has observed the growth range of T. incarnata, T. idahoensis and T. trifolii to be from temperatures of approximately -5^{o} C. to a maximum of 20^{o} C. Unlike T. idahoensis and T. trifolii, growth of T. incarnata was optimal at 10^{o} C. When grown on potato dextrose agar, T. incarnata has been shown to exhibit growth over a range of 0^{o} - 18^{o} C. with an optimum of 9^{o} - 12^{o} C. (75). Furthermore mycelial growth is abundant, white, webby, radiating, concentrically banded and fan shaped (75). On MYG agar, at 20^{o} C. T. incarnata grew slowly, the resulting colonies being brown instead of white and irregular in appearance (23).

Remsburg (75) has stated that sclerotia of T. incarnata appear in 5 - 10 days, are pinkish orange when young and tawny to hazel brown when mature, single or coalesced with a tendency to develop in concentric rings (75). Sterile sporophores frequently develop from the sclerotia, but unlike T. idahoensis they are white in colour (75). Miss Remsberg (75) has observed that a reddish-brown stromatic crust often develops in culture with small sclerotia arising on it.

(C) Hosts Attacked:

Throughout North America, Northern Europe and Japan, certain fungal species of the genus Typhula are important psychrophilic pathogens of cereals and grasses (8,9,10,40,75). Others have been reported to cause severe damage to legumes such as alfalfa (16) and to strawberries (60). Cormack and Lebeau (16) have reported T. idahoensis to be highly virulent on creeping red fescue, red top and winter wheat, while moderately virulent to Kentucky bluegrass. T. incarnata is known to attack such hosts as quackgrass, annual bluegrass, Kentucky bluegrass, rough bluegrass, and Holcus mollis, colonial bentgrass, creeping bentgrass, Italian ryegrass, perennial ryegrass, red fescue, tall fescue and velvet bentgrass (5,33). Roberts (63) has found differences in Typhula susceptibility among the many bentgrass varieties. From the less to the more susceptible he listed Astoria, Congressional, Penncross, Old Orchard, Washington, Arlington and Seaside bentgrasses. In 1941 Wernham (106) reported the reactions of several varieties of Agrostis palustris and A. tenuis to T. itoana attack. He found the varieties Metropolitan, Astoria and Washington were very susceptible, susceptible and moderately susceptible, respectively, to attack by the pathogen. Beard, as reported by Britton (5), stated that varieties of creeping bentgrass vary widely in susceptibility to T. itoana, Seaside and Cohansey being very susceptible; Penncross, Washington and Toronto moderately susceptible and Congressional and Astoria being quite resistant. Vargas et al. (100) found that the Kentucky bluegrass cultivars of Delta, Merion, Park, Newport, and Prato were quite susceptible to T. itoana attack.

(D) Differences between *T. itoana* and *T. idahoensis*:

Remsburg (74) has stated that *T. idahoensis* causes a disease of the same type as that caused by *T. itoana.* However, in addition to the differences previously referred to *T. itoana* and *T. idahoensis* do differ in other respects. *T. itoana* has been reported to be a facultative parasite and under certain conditions can become well established saprophytically before injuring living tissue (40). Cunfer and Bruehl (18) observed that *T. idahoensis* grew as a saprophyte only when competition from other micro-organisms was minimal and rarely found it as a saprophyte on straw in the field. The development and virulence of *T. idahoensis* has been reported to be much greater than that of *T. itoana* on winter wheats (8,10). Bruehl and Cunfer (10) have shown that *T. idahoensis* was pathogenic on wheat at temperatures of -1.5° C. whereas *T. itoana* was not. *T. idahoensis* is believed to attack leaves primarily with most of its sclerotia being formed on the expanded leaves (22). On the other hand, *T. itoana* is less restricted to aerial tissues and its sclerotia are formed most frequently below the soil surface between basal leaf sheaths and on roots (22). Holton (38) found *T. idahoensis* prevalent in areas of heavy snow cover of long duration while *T. itoana* predominated in areas with light snow cover of relatively short duration.

(E) Disease Symptomatology:

A variety of descriptive terms have been coined for the snow mold disease caused by *T. itoana* and *T. idahoensis*, but typhula blight, snow scald, or grey snow mold have had the widest acceptance (40). Jackson and Fenstermacker (40) have noticed that under cool wet conditions in the late fall and spring, mild disease symptoms appear on turf as small, roughly circular 3 to 6 inch diameter water-soaked patches that are light yellow to fawn in colour. However, the snow mold Typhulas are particularly active under a snow cover, after which the symptoms are intensified and invaded plants are covered with a dense, aerial mycelial growth (17,40). The mycelium is white, but often appears as shades of grey due to atmospheric pollutants in the snow that are deposited on the hyphae as the snow melts (hence the name "grey snow mold"). Affected areas range up to 2 ft. in diameter and frequently coalesce to involve larger areas of turfgrass (17,40). During the spring thaw the presence of numerous ovoid to spherical sclerotia embedded in the leaves and crowns of infected plants is the chief diagnostic feature of typhula blight (17,40).

(F) Life Cycle of the Pathogen:

The pathogen survives the warm summer months in the form of sclerotia (58,75). In late October, November, and early December under the stimulus of cool temperatures (10-17° C.), humidity above 70% and exposure to light rays of short wavelength (2700-3200 Å), the sclerotia germinate to form sporohpores or mycelia (40,75,89). Even though basidiospores are not considered to be important sources of inoculum (18,22,89), they could allow sexual recombination to occur providing added potential for variation in this pathogen (19). In the absence of light, under a snow cover and over an unfrozen ground, mycelial growth progresses and initiates the primary infection centers (17). With rising air temperatures in the spring, the pathogenic capabilities of the fungus are decreased and sclerotia are produced thus serving to carry the fungus in a dormant condition over the summer months (40). A period of desiccation is necessary before the sclerotia will produce new growth (40). Davidson and Bruehl (22) reported that Lehmann believes this to be the reason new sclerotia do not germinate in the spring.

(G) Factors Influencing Development of the Pathogen:

The environmental conditions which favour typhula blights can be divided into two classes: 1) the cool weather of late October, November, and December, high humidity, and exposure to light rays of short wavelength which stimulate sclerotial germination and 2) early snow falling on wet, unfrozen ground which greatly enhances infection (17,40,89). Davidson and Bruehl (22) found that tillage or burying the sclerotia of T. idahoensis to depths of greater than 2 cm. rendered them ineffective. Lehmann, as reported by Davidson and Bruehl (22), found that sandy soil favoured the development of typhula blights which he attributed to reduced antagonism. Studies by Davidson and Bruehl (22) support Lehmann's hypothesis. This disease is also reported to be favoured by excessive late nitrogen applications and grass left long in the fall (82).

The Unidentified Low Temperature Basidiomycete (LTB):

(A) Interesting Characteristics of the Pathogen:

A basidiomycetous fungus causing snow mold of turfgrass in Alberta was first described by Broadfoot (6). The same fungus was later found to cause a severe winter crown rot of legumes (7) and its pathogenicity on a variety of species of grasses and legumes has been demonstrated under natural (14,15) and artificial (16) conditions. The apparent lack of fruiting bodies or spores, the ability to grow at low temperatures and the presence of hyphal clamp connections has