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Pathogenicity of Leptographium procerum and L. terebrantis on Pinus strobus seedlings and established trees

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Abstract

The pathogenicity of *Leptographium terebrantis* and *Leptographium wageneri*, was compared with that of eight isolates of *L. procerum* from different parts of the world by wound inoculation of two-year-old *Pinus strobus* seedlings. Isolates of *L. procerum* caused limited discoloration around inoculation sites whereas *L. terebrantis* caused girdling cankers and *L. wageneri* systemically invaded seedlings. Only three of 160 seedlings inoculated with various isolates of *L. procerum* died; *L. terebrantis* and *L. wageneri* killed 17 and 15 of 20 seedlings inoculated respectively. Inoculation of *L. procerum* and controls caused localised discoloration around inoculation points and inoculation with *L. terebrantis* resulted in lesions up to 150 cm long on 15-year-old *P. strobus*. Lesions associated with *L. procerum* were however significantly longer than the discolored areas on control plants. In comparison with *L. terebrantis*, *L. procerum* appears to be a weak wound pathogen.

1 Introduction

Leptographium procerum (Kendrick) Wingfield, (= *Verticicladiella procera* Kendrick) (Wingfield 1985) has been associated with a disease of Eastern white pine (*Pinus strobus* L.) commonly known as white pine root decline (Dochinger 1967; Towers 1977; Sinclair and Hudler 1980). Symptoms include decreased shoot growth, delayed bud break, needle wilt, exudation of resin from the root collar, and resin soaking of affected wood (Houston, 1969; Sinclair and Hudler 1980; Lackner and Alexander 1982). Dying pines from which *L. procerum* was isolated have been reported from the United States (Dochinger 1967; Houston 1969; Towers 1977; McCall and Merrill 1980; Lackner and Alexander 1982), Yugoslavia (Halambek 1976, 1981) and New Zealand (Shaw and Dick 1980; Wingfield and Marasas 1983). The fungus has also been isolated

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from roots and root collars of many pine species other than white pine and in these cases was not associated with symptoms similar to those of white pine root decline (Towers 1977; Mielke 1979; Livingston and Wingfield 1982; Wingfield 1983).

Leptographium procerum has been suggested as the primary cause of white pine root decline (Dochinger 1967; Towers 1977; Sinclair and Hudler 1980), however, pathogenicity tests with this fungus have yielded apparently contradictory results (Halambek 1976; Lackner and Alexander 1982; Harrington 1983; Wingfield 1983). *Leptographium procerum* killed seedlings of *P. strobus* in greenhouse pathogenicity tests where roots were immersed in a spore suspension and then replanted (Halambek, 1976, 1981; Lackner and Alexander 1982). In contrast, however, *L. procerum* did not kill *P. strobus, P. ponderosa* Laws. or *Pseudotsuga menziesii* (Mirb.) Franco. seedlings when the fungus was wound inoculated into the stems (Harrington and Cobb 1983; Wingfield 1983). Possible variation in the pathogenicity of different isolates of *L. procerum* used in these studies was not considered.

Houston (1969) investigated a basal canker disease of *P. strobus* from which *L. procerum* was occasionally isolated. The fungus caused annual cankers on 8-year-old trees inoculated in plantations but was not considered to be the cause of the disease under investigation. Similarly, *L. procerum* was isolated from roots and root collars of insect attacked pine species in Minnesota and Wisconsin, but the fungus apparently was not the primary cause of tree death (Livingston and Wingfield 1982; Wingfield 1983).

Wingfield (1983) found that *L. procerum* was associated with insects (*Hylobius radicis* Buch. and *H. rhizophagus* M. B. W.) which infest the roots and root collars of healthy pine trees and *H. pales* Herbst, *Pachylobius picivorus* Germ, and *Dendroctonus valens* which infest dying trees. *Leptographium terebrantis* Barras and Perry, has been associated with *Dendroctonus terebrans* (Barras and Perry 1971; Rane and Tattar 1983 a), *D. valens* LeC. (Harrington and Cobb 1983; Wingfield 1983) and *Hylurgops porosus* LeC. (Harrington and Cobb 1983). *L. terebrantis* has been isolated in association with *L. procerum* (Wingfield 1983), possibly due to common insect associates such as *D. valens*. Unlike *L. procerum, L. terebrantis* was shown to kill seedlings of various pine species including *P. strobus* in greenhouse tests after stem wound inoculation (Harrington and Cobb 1983; Wingfield 1983). The possibility that *L. procerum* and *L. terebrantis* might function as pathogens once introduced by insects would be tested by wound inoculation.

Apparent contradictory results in pathogenicity tests with *L. procerum* could be related to strain differences in the fungus. In this study, the pathogenicity of isolates of *L. procerum* of diverse geographic origin was compared with that of *L. terebrantis* and *L. wageneri* (Kendrick) Wingfield by wound inoculating stems of *P. strobus* seedlings. *Leptographium wageneri*, a primary pathogen of conifers which also is associated with insects (Wagener and Mielke 1961; Cobb and Platt 1967; Smith 1967; Goheen 1976; Harrington and Cobb 1983) was included here for comparison. Because information on the pathogenicity of *L. procerum* and *L. terebrantis* under field conditions is lacking, lesion development on stems, wound inoculated with two isolates of *L. procerum* was compared with that of an isolate of *L. terebrantis* on established trees of *P. strobus*.

2 Materials and methods

2.1 Inoculation of seedlings

Eight isolates of *L. procerum* of diverse geographic and host origin, one isolate of *L. terebrantis*, and one isolate of *L. wageneri* were used in seedling inoculations (Table 1). Isolates of *L. procerum* from areas such as New Zealand, Virginia (United States) and Yugoslavia where white pine root decline has been reported were included. Sharpened wooden

toothpicks were oven-sterilized at 100°C for 3 hr and aseptically placed on the surface of 1 % Difco Malt Extract Agar (MEA) in Petri dishes. Isolates of *L. procerum, L. wageneri* and *L. terebrantis* were introduced to MEA plates containing sterilized toothpicks and incubated at 24°C for 3 wk to allow the fungi to colonize the toothpicks.

Two-year-old white pine seedlings were planted in 12-cm-diameter plastic pots and established for 9 mo in a greenhouse at approximately 25°C. The colonized toothpicks were used to inoculate twenty seedlings with each of the fungi. An equal number of seedlings was inoculated with sterile toothpicks as controls. Toothpicks were inserted into the stem at the base of each seedling, inoculation points were covered with parafilm, and seedlings were examined weekly.

After 5 mo, each seedling was recorded as living, dying (chlorotic), or dead, all seedlings were uprooted and the length of the discolored tissue resulting from inoculation was measured. Transverse and tangential sections (5 μ thick) were cut with a freezing microtome through discolored tissue of two seedlings inoculated with either *L. procerum, L. wageneri* or *L. terebrantis*. Fungi were reisolated from seedlings by removing bark from around inoculation points and placing small (2 mm^2) pieces of wood from the leading edge of discolored tissue on MEA.

2.2 Inoculation of established trees

Twenty, 15-year-old white pine trees near Brainerd, MN each received four treatments; inoculation with two isolates of *L. procerum*, on isolate of *L. terebrantis* and a control (Table 2). A 12 mm wide cork borer was used to remove four plugs of bark at 90 degrees from each other from the bole of each tree approximately 30 cm above ground level. After exposing the cambium with the cork borer, the resulting holes were filled with a 12 mm disk of MEA colonized with one of the fungi to be tested or a disk of sterile MEA for control inoculations. Bark plugs were replaced and inoculation sites were covered with waterproof tape. The sites of the four treatments applied to each tree were randomly assigned.

Trees were felled and examined 12 mo after inoculation. Bark was removed to expose discolored tissue and, where necessary, roots were exposed to reveal entire columns of discoloration. Total lesion length and width including the inoculation site were measured and bolts were cut and saved for reisolation of fungi. Isolations from discolored tissue associated with all inoculations were made by removing approximately 2 mm^2 pieces of wood and placing these on MEA. Fungi re-isolated from inoculations were identified after incubation at 24°C for one week.

3 Results

3.1 Inoculation of seedlings

After 5 mo, all but three of 160 seedlings inoculated with various *L. procerum* isolates were healthy (Table 1). Two of the three seedlings that died had been inoculated with an isolate of *L. procerum* from Minnesota (CMW 34) and the third seedling with an isolate from New York (CMW 46). The extent of the discoloration associated with the three *L. procerum* seedlings that died did not appear to be sufficient to cause death. Seventeen of 20 seedlings inoculated with *L. terebrantis* and 15 seedlings inoculated with *L. wageneri* were either dead or dying after the 5 mo period (Table 1). One control seedling died.

Seedlings inoculated with *L. procerum* had produced callus tissue which enclosed inoculation wounds (Fig. 1). Wood tissue around *L. procerum* inoculations was resin soaked and discolored; the average length of discolored tissue did not exceed 2.3 cm. Inoculations with *L. terebrantis* resulted in more darkly stained wood than that associated with *L. procerum* and the fungus appeared to colonize both bark and wood, and caused cankers

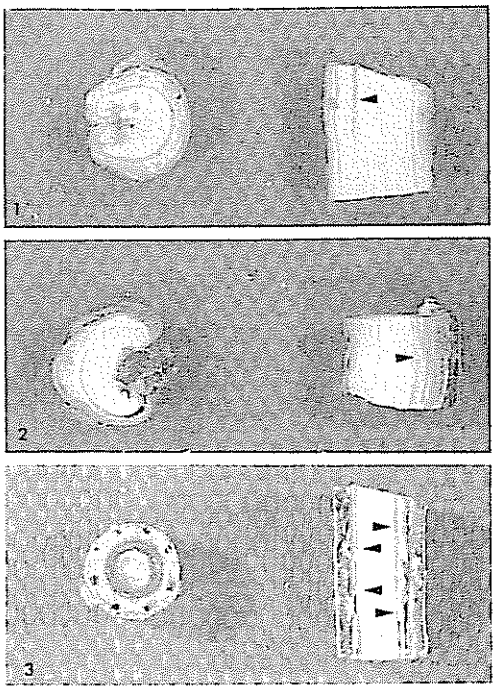


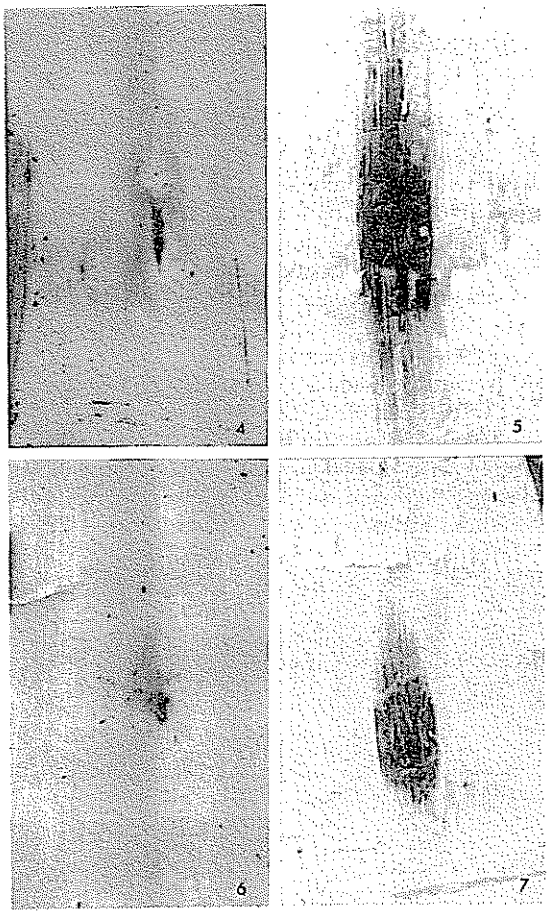
Fig. 1–3. Transverse and longitudinal sections through inoculation points on 2-year-old *P. strobus* seedlings showing wound response and wood discoloration (Arrows) 5 mo after inoculation with *L. procerum*, *L. wageneri* and *L. terebrantis*. Fig. 1. Seedling inoculated with *L. procerum* showing slight discoloration and wound closure. Fig. 2. Dark discoloration, inhibition of wound closure and canker development associated with *L. terebrantis* inoculation. Fig. 3. Systemic infection of seedling inoculated with *L. wageneri* with discoloration of wood, bark tissues unaffected and restriction of the fungus to the xylem

Table 1

Pinus strobus seedling health and lesion lengths associated with inoculations of L. wageneri, L. terebrantis and different isolates of L. procerum after 5 mo[a]

Inoculum	Isolate number	Source		% Seedlings			Mean discoloration length (cm)
		Host	Area	Healthy	Dying	Dead	
L. procerum	(CMW 56)	*P. resinosa* Ait.	Illinois, USA	100	0	0	1.54 a
L. procerum	(CMW 12)	*P. strobus*	Iowa, USA	100	0	0	1.61 a
L. procerum	(CMW 23)	*P. clausa* (Engelm.) Sarg.	Florida, USA	100	0	0	1.58 a
L. procerum	(CMW 34)	*P. sylvestris* L.	Minnesota, USA	90	0	10	1.68 a
L. procerum	(CMW 46)	*P. strobus*	New York, USA	95	0	5	1.80 a
L. procerum	(CMW 3)	*P. strobus*	Virginia, USA	100	0	0	1.62 a
L. procerum	(CMW 17)	*P. strobus*	New Zealand	100	0	0	2.26 a
L. procerum	(CMW 25)	*P. strobus*	Yugoslavia	100	0	0	1.71 a
L. wageneri	(CMW 55)	*P. ponderosa*	California, USA	25	10	65	8.65 b
L. terebrantis	(CMW 9)	*P. sylvestris*	Minnesota, USA	15	5	80	2.26 c
Control		–	–	95	0	5	0.72 d

a Twenty 2 year-old seedlings inoculated in each treatment.
b Means in a column followed by the same letter did not differ significantly (P = 0.05) by Tukey's method of multiple comparison (HSD = 0.28 cm).



Figs. 4–7. Response of 15-year-old *P. strobus* to inoculation with *L. procerum*, and control. Wound closure (Fig. 4) and wood discoloration (Fig. 5) associated with *V. procera* inoculations. Wound closure (Fig. 6) and wood discoloration (Fig. 7) associated with control inoculations

(Fig. 2) which girdled the seedlings. The average length of discoloration in *L. terebrantis* inoculations was significantly greater (P = 0.05) than that associated with inoculation of *L. procerum* isolates (Table 1).

Inoculation of seedlings with *L. wageneri* resulted in dark black staining of the xylem tissue only. This fungus did not infect bark tissue and resulted in extensive colonization of the xylem tissues (Fig. 3). The discolored tissue extended into the roots and in many cases reached the apex of the main stem. The average length of the discolored column associated with *L. wageneri* infection was 8.65 cm. This was significantly (P = 0.05) longer than discoloration associated with any other isolate.

Control seedlings produced callus tissue which enclosed inoculation wounds. Wood discoloration associated with control wounds was similar to that associated with *L. procerum* inoculations although the extent of discoloration was significantly less (P = 0.05) than that associated with any other treatment (Table 1).

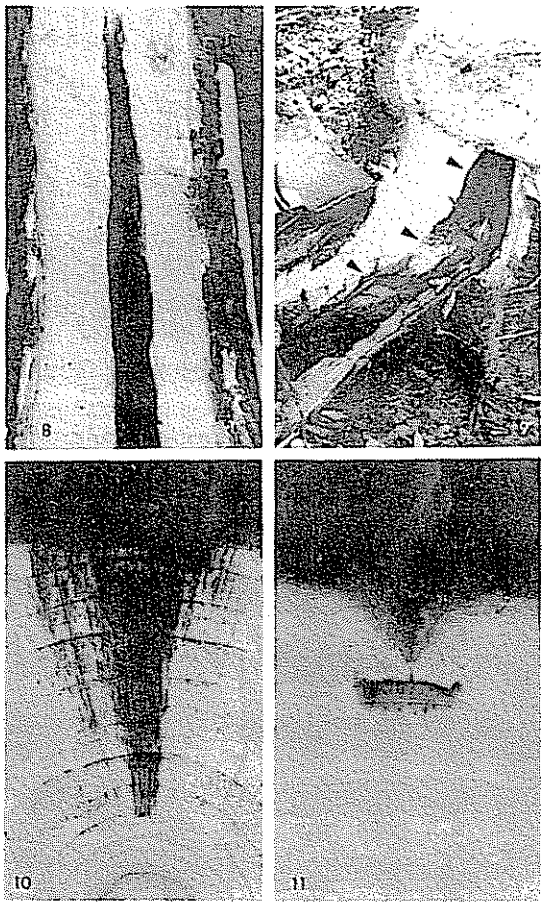
Sections through discolored wood associated with inoculations revealed that *L. procerum* and *L. terebrantis* had colonized ray parenchyma tissue and tracheids. *Leptographium wageneri*, however, colonized only the tracheids and was not observed in rays or ray parenchyma tissue. Medullary rays alongside tracheids colonized by *L. wageneri* were plugged with dark resinous material.

All seedlings from which reisolations were attempted yielded the inoculated fungus. None of the test fungi were isolated from discolored tissue associated with control wounds.

3.2 Inoculation of established trees

Inoculation of 15-year-old *P. strobus* did not result in tree death or visible symptoms in the crowns after 12 mo. Wounds inoculated with both isolates of *L. procerum* and controls were covered with new wood (Figs. 4 and 6). After the new wood had been removed, small resin soaked lesions associated with the original wounds and controls were noted (Figs. 5 and 7). Inoculations with *L. terebrantis* prevented the formation of new wood in the area around inoculation sites and resulted in dark brown to black lesions in the xylem up to 150 cm long (Fig. 8) which often extended into the roots (Fig. 9).

Resin soaked lesions associated with the two *L. procerum* isolates (CMW 34 and CMW 58) averaged 8.49 and 8.33 cm in length and 1.33 and 1.57 cm in width, respectively (Table 2). These lesions were localized at the inoculation sites (Figs. 4 and 5). Control wounds resulted in lesions which averaged 1.2 cm in width and 4.46 cm in length; they were covered with new wood and localized around the inoculation points (Figs. 6 and 7). Average length and width of *L. terebrantis* lesions were 46.66 and 3.89 cm respectively; the lesions had extended into the roots (Figs. 8 and 9). Cross sections of boles in the area



Figs. 8–11. Response of 15-year-old *P. strobus* to inoculation with *L. terebrantis* and *L. procerum*. Trunk (Fig. 8) and root (Fig. 9) discoloration associated with *L. terebrantis* inoculations. Fig. 10. Transverse section showing wedge shaped dark discoloration of wood extending through nine growth rings associated with *L. terebrantis* inoculation. Fig. 11. Transverse section showing wound closure after inoculation with *L. procerum* and discoloration of wood localized around inoculation point

Table 2

Lesion length and widths on 15-year-old P. strobus trees associated with inoculations with L. terebrantis and two isolates of L. procerum[a]

Inoculum		Source		Mean lesion	
		Host	Area	Length (cm)	Width (cm)
L. procerum	(CMW 34)	*P. sylvestris*	Minnesota, USA	8.49 a	1.33 a
L. procerum	(CMW 58)	*P. strobus*	Minnesota, USA	8.33 a	1.57 a
L. terebrantis	(CMW 9)	*P. sylvestris*	Minnesota, USA	46.66 b	3.89 b
Control		–	–	4.46 c	1.20 a

a Twenty trees inoculated (each received all four treatments).
b Means in a column followed by the same letter did not differ significantly (P = 0.05) by Tukey's method of multiple comparison (Lesion lengths HSD = 0.39 cm, Lesion widths HSD = 0.14 cm).

of inoculations revealed that *L. terebrantis* had resulted in wedge shaped lesions extending through nine growth rings towards the center of the inoculated trees (Fig. 10). Lesions associated with *L. procerum* inoculations were not significantly (P = 0.05) wider than control lesions but were significantly (P = 0.05) longer. Lesions resulting after *L. terebrantis* inoculations were significantly (P = 0.05) wider and longer than *L. procerum* (Fig. 11) and control inoculations. Lesions resulting from inoculation of the two *L. procerum* isolates were not significantly different from each other (Table 2).

4 Discussion

These results suggest that *L. procerum* is a weak wound pathogen which is unable to kill seedlings. The results are similar to those obtained previously for wound inoculations of *P. strobus* seedlings (WINGFIELD 1983) and *P. ponderosa* seedlings (HARRINGTON and COBB 1983), but are different to results obtained by LAGKNER and ALEXANDER (1982) and HALAMBEK (1976, 1981) who reported killing *P. strobus* seedlings after inoculation of roots by dipping them in conidial suspensions. The different results may have been due to difference in inoculation techniques.

Root dip inoculations are appropriate for investigation of white pine root decline, where *Leptographium procerum* is alleged to be the primary pathogen. *L. procerum* has been isolated from soils in the eastern United States (LACKNER and ALEXANDER 1982; SWAI and HINDAL 1981) where white pine root decline is most commonly found. LACKNER and ALEXANDER (1984) also have reported that *L. procerum* was able to infect seedlings planted in naturally infested soil. The way in which the fungus colonizes the roots in these cases has not been determined. The pathogenicity of *L. procerum* resulting from root dip inoculations is apparently enhanced by moist soil conditions (M. HALAMBEK, pers. comm.). This could explain the association of white pine root decline with moist, poorly drained sites (HALAMBEK 1976; TOWERS 1977; SHAW and DICK 1980).

In addition to occurring in the soil and apparently acting as a root pathogen, *L. procerum* is commonly found in the roots and root collars of pines infested with root collar weevils (*Hylobius radicis*) and pine root tip weevils (*H. rhizophagous*) which infest living trees (MILLERS et al. 1963; WILSON 1968; KENNEDY and WILSON 1971; MOSHER and WILSON 1977). *L. procerum* was considered a weak wound pathogen associated with these insects (WINGFIELD 1983). *Hylobius radicis* causes symptoms on pines similar to those associated with white pine root decline although it seldom infests *P. strobus*. The association of *L. procerum* with root weevils and their damage justifies using a wound inoculation as opposed to a soil or root inoculation in this study. The results of this study suggest that

L. procerum is a weak wound pathogen of *P. strobus* stems. They, however, do not necessarily imply that *L. procerum* is not an important root pathogen which causes white pine root decline.

Inoculation of both established trees and seedlings with *L. procerum* in this study gave comparable results. In both cases the fungus appeared to be a weak wound pathogen although discoloration associated with the inoculations was significantly greater than that associated with controls. There also was very little difference in the ability to cause wound associated lesions between the many different isolates tested on seedlings or the two different isolates tested on larger trees. This may imply that results obtained in pathogenicity tests with *L. procerum* (HALAMBEK 1976; HARRINGTON and COBB 1983; LACKNER and ALEXANDER 1984; WINGFIELD 1983) are not due to variation in pathogenicity of isolates tested. More likely, these differences are due to different inoculation methods.

Leptographium terebrantis was considerably more virulent than *L. procerum* in seedlings and caused considerably larger wound cankers on established trees. Similar results were obtained with wound inoculations of *L. terebrantis* on *P. ponderosa, P. strobus* and *P. thunbergii* Parl. seedlings (HARRINGTON and COBB 1983; RANE and TATTAR 1983 a; WINGFIELD 1983). Although brief reports have appeared (HIGHLEY et al. 1982; RANE and TATTAR 1983 b) this study provides the first details of mature tree inoculations with *L. terebrantis*. *Leptographium terebrantis* is an associate of bark beetles (*Dendroctonus valens, D. terebrans* and *Hylurgops porosus*) which usually infest stressed trees (BAKER 1972; FURNISS and CAROLIN 1977). It is therefore best considered as a pine pathogen which contributes to the death of infested trees.

Leptographium wageneri was considerably more virulent than *L. procerum*. Similar results were reported by HARRINGTON and COBB (1983). *Leptographium wageneri* causes a serious root disease of conifers (black stain) restricted to the Western United States (WAGENER and MIELKE 1961; COBB and PLATT 1967; SMITH 1967; GOHEEN 1976; HARRINGTON and COBB 1983). In the present study, there were fewer dead or dying seedlings after inoculation with *L. wageneri* than when *L. terebrantis* was used as inoculum. *Leptographium terebrantis* girdled seedlings at the point of inoculation, whereas *L. wageneri* became systemic and colonized only the xylem. These results support the view (SMITH 1967; HARRINGTON and COBB 1983) that *L. wageneri* is a unique pathogen within the *Leptographium* complex which is restricted to the xylem of its host.

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Summary

The pathogenicity of *Leptographium wageneri, L. terebrantis* and eight isolates of *L. procerum* from different geographic areas was compared on *Pinus strobus* seedlings. *Leptographium terebrantis* and *L. wageneri* were most pathogenic and killed seedlings whereas *L. procerum* inoculations resulted in only limited discoloration of tissues around inoculation sites. *Leptographium terebrantis* and *L. procerum* colonized the phloem and xylem whereas *L. wageneri* was restricted to the xylem tissues. No significant difference in pathogenicity was found between different *L. procerum* isolates. The pathogenicity of *L. terebrantis* and *L. procerum* was also compared on established *P. strobus* trees. *Leptographium procerum* caused only localized discoloration around inoculation points whereas *L. terebrantis* resulted in extensive columns of xylem discoloration and death of the associated phloem. Results suggest that, in comparison to *L. terebrantis, L. procerum* is a weak wound pathogen.

Résumé

Pouvoir pathogène de Leptographium procerum et L. terebrantis sur Pinus strobus (semis et arbres de 15 ans)

Le pouvoir pathogène de *L. wageneri, L. terebrantis* et 8 isolats de *L. procerum* de différentes origines géographiques a été étudié sur des semis de *Pinus strobus*. *Leptographium terebrantis* et *L. wageneri* étaient les plus pathogènes et tuaient les semis alors que les inoculations par *L. procerum* n'aboutissaient qu'à une coloration limitée des tissues autour des sites inoculés. *Leptographium terebrantis* et *L. procerum* colonisaient le phloème et le xylème, *L. wageneri* était limité aux tissus du xylème. Aucune différence significative de pouvoir pathogène n'a été trouvée entre les isolates de *L. procerum*. *Leptographium terebrantis* et *L. procerum* ont aussi été étudiés sur des *P. strobus* âgés de 15 ans. *Leptographium procerum* ne provoquait qu'une coloration localisée autour des points d'inoculation alors que *L. terebrantis* provoquait d'importantes traînées colorées dans le xylème et la mort du phloème associé. Les résultats suggèrent qu'en comparaison de *L. terebrantis, L. procerum* est un parasite de blessure faible.

Zusammenfassung

Pathogenität von Leptographium procerum und L. terebrantis gegenüber Pinus strobus-Sämlingen und 15 Jahre alten Bäumen

Die Pathogenität von *Leptographium wageneri, L. terebrantis* und acht Isolaten von *L. procerum* verschiedener geographischer Herkunft wurde an *Pinus strobus*-Sämlingen verglichen. *Leptographium terebrantis* und *L. wageneri* waren am virulentesten und brachten Sämlinge zum Absterben während *L. procerum* nur zu begrenzter Verfärbung des Gewebes um die Inokulationsstellen herum führte. *Leptographium terebrantis* und *L. procerum* besiedelten Phloem und Xylem während *L. wageneri* auf das Xylem beschränkt blieb. Zwischen den Isolaten von *L. procerum* traten keine Virulenzunterschiede auf. Die Pathogenität von *L. terebrantis* und *L. procerum* wurde auch an älteren Stroben untersucht. *Leptographium procerum* verursachte nur begrenzte Verfärbungen um die Inokulationsstellen. *Leptographium terebrantis* bewirkte dagegen in Längsrichtung des Stammes ausgedehnte Verfärbungen des Xylems und das Absterben des Phloems. Die Ergebnisse zeigen, daß *L. procerum* im Vergleich zu *L. terebrantis* ein schwacher Wundparasit ist.

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