Association of *Verticicladiella procera* and *Leptographium terrebrantis* with insects in the Lake States[1]

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Received March 8, 1983[2]

Accepted August 2, 1983

WINGFIELD, M. J. 1983. Association of *Verticicladiella procera* and *Leptographium terrebrantis* with insects in the Lake States. Can. J. For. Res. **13**: 1238–1245.

Verticicladiella procera Kendrick was isolated from damage associated with *Dendroctonus valens* Lec., *Hylobius radicis* Buch., *Hylobius rhizophagus* M.B.W., *Hylobius pales* (Herbst), and *Pachylobius picivorus* (Germ.) on pines in Minnesota, Wisconsin, and Michigan. The fungus was also isolated from surface-sterilized adult *D. valens*, *H. radicis*, *H. pales*, and *P. picivorus*. *Leptographium terrebrantis* Barras and Perry was isolated from the galleries of *D. valens* on trees stressed by fire, flooding, windthrow, and tissue attacked by *H. radicis* or *H. rhizophagus*. *Verticicladiella procera* was not pathogenic on white pine seedlings whereas *L. terrebrantis* killed 70% of seedlings inoculated. *Verticicladiella procera* appears to be weakly pathogenic and is associated with primary (*H. radicis* and *H. rhizophagus*) and secondary (*P. picivorus*, *D. valens*, *H. pales*) forest insects in the north central United States. *Leptographium terrebrantis* was more virulent than *V. procera* and was associated with a secondary bark beetle which commonly attacks stressed trees.

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Verticicladiella procera Kendrick a été isolé des pins en association avec *Dendroctonus valens* Lec., *Hylobius radicis* Buch., *Hylobius rhizophagus* M.B.W., *Hylobius pales* (Herbst) et *Pachylobius picivorus* (Germ.) au Minnesota, Wisconsin et Michigan. Ce champignon a aussi été récupéré sur des spécimens adultes de *D. valens*, *H. radicis*, *H. pales* et *P. picivorus* après une stérilisation superficielle. *Leptographium terrebrantis* Barras et Perry a été isolé dans les galeries de *D. valens* sur des arbres affectés par le feu, les innondations, les chablis et dans les tissus attaqués par *H. radicis* ou *H. rhizophagus*. Innoculés sur des semis de pin blanc, *V. procera* n'était pas pathogène alors que *L. terrebrantis* a causé 70% de mortalité. *Verticicladiella procera* semble être un pathogène peu agressif associé aux insectes primaires (*H. radicis* et *H. rhizophagus*) et secondaires (*P. picivorus*, *D. valens*, *H. pales*) du centre-nord des États-Unis. *Leptographium terrebrantis* est plus virulent que *V. procera* et est associé à un insecte secondaire qui se développe dans l'écorce des arbres affaiblis.

[Traduit par le journal]

Introduction

Verticicladiella procera Kendrick was first described in 1962 based on isolates from numerous pine species from Canada, Sweden, and the United States (Kendrick 1962). The fungus has been associated with a root and root-collar disease of eastern white pine (*Pinus strobus* L.) commonly called white pine root decline (Dochinger 1966; Towers 1977; Sinclair and Hudler 1980). White pine mortality associated with *V. procera* has been reported from the eastern United States (Dochinger 1966; Houston 1969; Lackner and Alexander 1982; McCall and Merrill 1980; Sinclair and Hudler 1980; Towers 1977), Yugoslavia (Halambek 1976), and New Zealand (Shaw and Dick 1980; Wingfield and Marasas 1983). Characteristic symptoms of white pine root decline include decreased shoot growth, delayed budbreak, needle wilt, exudation of resin from the root-collar area, and resin soaking of affected wood (Houston 1969; Lackner and Alexander 1982; Swai and Hindal 1981; Sinclair and Hudler 1980). In addition to white pine root decline, *V. procera* has been associated with diseased roots of many other conifer species in the United States (Livingston and Wingfield 1982; Mielke 1979; Towers 1977). In most diseased trees with which it was associated, *V. procera* did not appear to be the primary cause of tree mortality.

Verticicladiella and *Leptographium* species are associated with bark beetles (Coleoptera: Scolytidae) (Goheen and Cobb 1978; Wingfield and Knox-Davies 1980; Upadhyay 1981). *Leptographium terrebrantis* Barras and Perry is associated with *Dendroctonus* species (Barras and Perry 1971; Harrington and Cobb 1983) which typically colonize weakened trees (Baker 1972). Various bark beetles and weevils (Coleoptera: Curculionidae) have been found in *V. procera* infected trees (Lackner 1981; Livingston and Wingfield 1982; Shaw and Dick 1980). The possible role of these insects in spreading *V. procera* has, however, received little attention. This paper reports an association between

[1]Paper No. 13 346, Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul, MN, U.S.A. 55108.

[2]Revised manuscript received July 15, 1983.

TABLE 1. Incidence of *Verticicladiella procera* and *Leptographium terrebrantis* on trees infested with pine root-collar weevil, *Hylobius radicis* in Minnesota, Michigan, and Wisconsin

Host	Locality	No. of trees sampled	No. of trees with *V. procera*	No. of trees with *L. terrebrantis*	No. of trees with *V. procera* and *L. terrebrantis*	No. of trees with *D. valens* galleries[a]
Pinus banksiana Lamb.	Brainerd, MN	2	2	2	2	2
Pinus nigra Arnold	Durand, WI	4	4	0	0	0
	Zimmerman, MN	4	4	2	2	2
Pinus ponderosa Laws.	LaCrosse, WI	3	3	0	0	3
Pinus resinosa Ait.	Durand, WI	2	2	0	0	0
	Osseo, WI	2	2	1	1	2
	Wexford, MI	3	2	0	0	0
Pinus sylvestris L.	Boscobel, WI	4	4	0	0	0
	Brainerd, MN	3	3	1	1	1
	Isanti, MN	10	10	2	2	0
Total		37	36	8	8	10

[a]*Dendroctonus valens* infested trees stressed by pine root-collar weevil.

TABLE 2. Association of *Verticicladiella procera* and *Leptographium terrebrantis* with damage caused by *Dendroctonus valens*, *Hylobius pales*, *Hylobius rhizophagus*, *Pissodes approximatus*, and *Pachylobius picivorus* infestation on pines in Minnesota and Wisconsin

Host	Locality	Insects present[a]	No. of trees sampled	No. of trees with *V. procera*	No. of trees with *L. terrebrantis*	No. of trees with *V. procera* and *L. terrebrantis*
Pinus banksiana	Black River Falls, WI	*H. rhizophagus* (12) *D. valens* (2)	12	4	2	0
		D. valens[b]	1	0	1	0
Pinus resinosa	Black River Falls, WI	*H. rhizophagus*	3	3	0	0
		D. valens[b]	6	6	6	6
Pinus strobus L.	Belwin, MN	*D. valens*[c]	2	0	2	0
	Durand, WI	*D. valens*[d]	4	0	2	0
Pinus sylvestris	Zimmerman, MN	*H. pales* *Pissodes approximatus* *Pachylobius picivorus*	30	30	0	0
	Becker, MN	*D. valens*[e]	1	1	0	0

[a]Number of trees infested with each insect species in parentheses where all insects mentioned were not present in all trees sampled.
[b]Trees stressed by fire prior to insect attack.
[c]Trees growing in waterlogged soil.
[d]Old Christmas tree stumps.
[e]Tree partially windblown.

V. procera, *L. terrebrantis*, and various insects in the north central United States and considers the role of these associations in tree mortality.

Materials and methods

Insects and fungi on trees

Pines of a number of species with roots and root collars damaged by root-collar weevils (*Hylobius radicis* Buch.), root-tip weevils (*Hylobius rhizophagus* M.B.W.), pales weevils (*Hylobius pales* (Herbst)), pitch weevils (*Pachylobius picivorus* (Germ.)), northern pine weevils (*Pissodes approximatus* Hopk.), and red turpentine beetles (*Dendroctonus valens* Lec.) were sampled from various parts of Minnesota, Michigan, and Wisconsin (Tables 1 and 2). Roots and root collars were taken to the laboratory for detailed examination and isolation of fungi from insect galleries and diseased tissue. Most trees examined were from Christmas tree plantations and all trees ranged in age from 5 to 20 years. Jack pine and red pine attacked only by *D. valens* in Black River Falls, WI were in a plantation recently scorched by forest fire. White pine attacked only by *D. valens* in Bellwin, MN were at the edge of a shallow lake and were severely stressed by excess water (Table 2). Scots pine in Zimmerman, MN (Table 2) had been felled and still had living bottom

TABLE 3. Percentage recovery of *Verticicladiella procera* and *Leptographium terrebrantis* from insects collected in Minnesota, Wisconsin, and Michigan

Insect species	Area collected	No. of insects sampled	% of insects with: *V. procera*	*L. terrebrantis*
H. radicis	Wexford, MI	20	60	0
H. pales	Isanti, MN	16	60	0
	Zimmerman, MN	123	46	0
	Black River Falls, WI	6	50	0
P. picivorus	Isanti, MN	23	69.6	0
	Zimmerman, MN	149	28.2	0
	Black River Falls, WI	5	60	0
Pissodes approximatus	Zimmerman, MN	28	0	0
D. valens	Becker, MN	2	0	100
	Zimmerman, MN	1	100	0
	Black River Falls, WI	3	33.3	66.6
	Osseo, WI	2	0	50

branches. The stumps of these trees had been colonized by *H. pales* and *Pissodes approximatus* and the roots had been severely damaged by *Pachylobius picivorus*. Lower branches of the Scots pine remaining alive were damaged by weevil maturation feeding.

Wood adjacent to tunnels of *H. pales*, *H. radicis*, *H. rhizophagus*, *Pissodes approximatus*, and *Pachylobius picivorus* damage was surface sterilized by flaming lightly. Small (approximately 2 mm^2) pieces of xylem tissue were aseptically removed and placed on (*i*) 2% malt extract agar (MEA) (20 g Difco malt extract and 20 g Difco Bacto agar per 1000 mL of water) containing 4% lactic acid and 0.01% streptomycin, and (*ii*) a selective medium (VSM) for the isolation of *Verticicladiella* spp. and *Leptographium* spp. previously described for isolating *Verticicladiella wageneri* (Hicks *et al.* 1980). In addition to isolation, tissue with galleries of the insects mentioned was placed in glass Petri dishes containing moistened filter paper to induce sporulation of fungi. Isolations and incubated tissues were examined after 1 week for the presence of *Verticicladiella* spp. and *Leptographium* spp.

Fungi on insects

Weevils were collected for fungus isolation during a 4-month period from May through August 1981. To attract the weevils, freshly cut pine discs (2 cm thick) were placed beneath root-collar weevil-infested Scots pine in Isanti and Zimmerman (Sherburne County), MN and beneath pine-root weevil-infested jack pine and red pine in Black River Falls, WI. Discs were replaced at weekly intervals in Wisconsin and twice weekly at the two Minnesota sites. Weevils (*H. pales* and *P. picivorus*) attracted to these discs (Ciesla and Franklin 1965; Thomas and Hertel 1969) were collected when discs were replaced. Adult weevils of unknown identity were sent to Dr. I. Millers, U.S.D.A. Forest Service, Portsmouth, NH for identification.

During late June 1982, adult root-collar weevils were caught at the base of root-collar weevil-infested pines in Michigan by Dr. L. Wilson, U.S.D.A. Forest Service, East Lansing, MI, and sent to St. Paul in plastic containers for isolation. *Dendroctonus valens* adults were collected in galleries of stressed trees in four locations in Wisconsin and Minnesota (Table 2) and were also retained for isolation.

Insects (Table 3) were immersed in a 1% solution of sodium hypochlorite containing Tween 80 for 5 min, washed in sterile distilled water, and placed on VSM medium in Petri dishes. After 1 week at 25°C, Petri dishes were examined for the presence of *Leptographium* and *Verticicladiella* spp.

Pathogenicity tests

Sharpened wooden toothpicks were oven sterilized at 100°C for 3 h, then placed on the surface of MEA in Petri dishes and inoculated with isolates of *V. procera* or *L. terrebrantis* from Minnesota. Fungi were allowed to grow and colonize the toothpicks for 3 weeks. Twenty 3-year-old white pine seedlings in the greenhouse were inoculated with either of the two fungi by cutting a small slit in the root-collar area with a sharp scalpel and inserting a fungus-colonized toothpick. An equal number of trees were inoculated with sterile toothpicks as controls. As seedlings died, isolations were made on VSM medium from discolored wood in the root-collar area. After 1 year, isolations were made from all remaining seedlings.

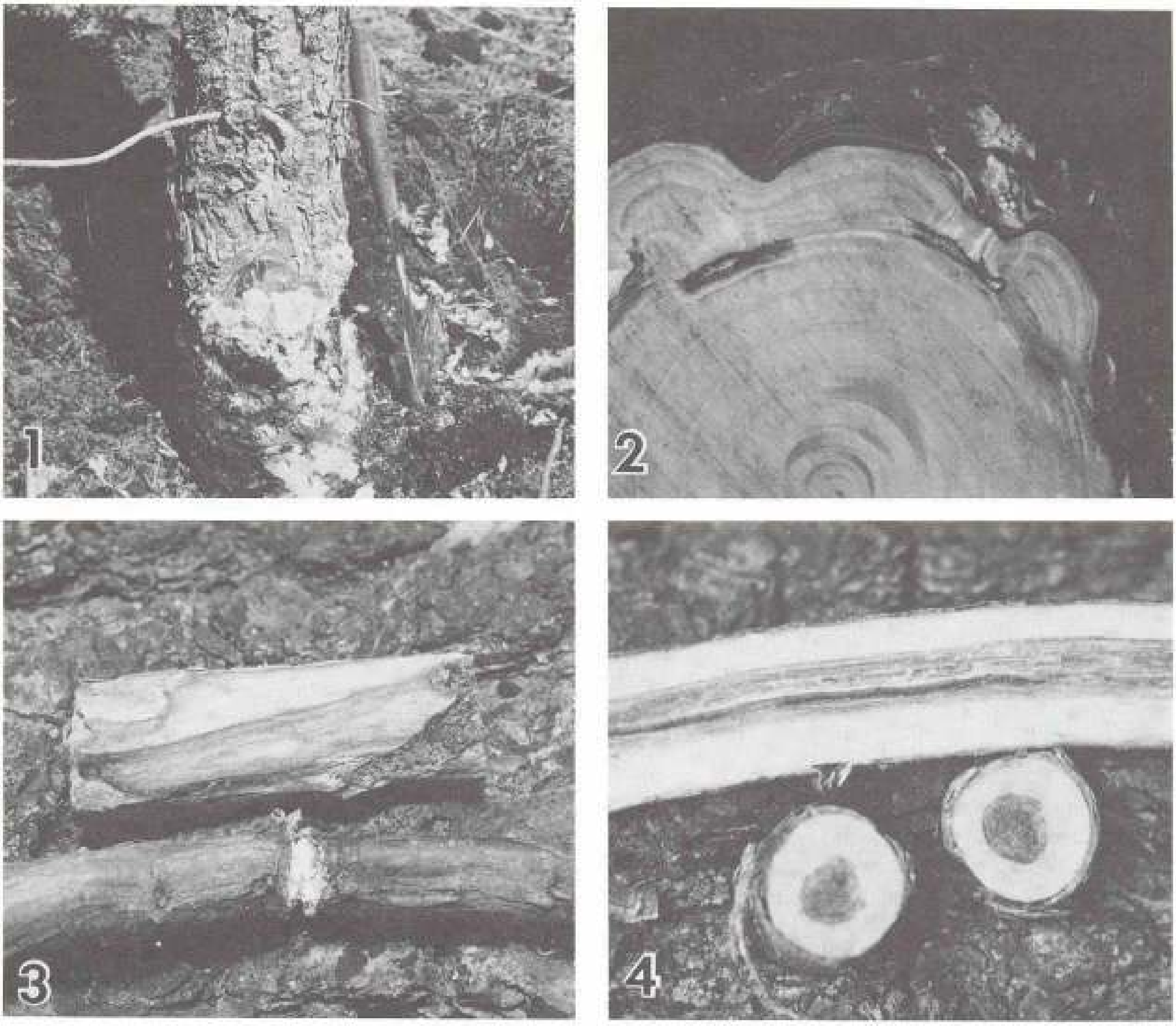
Soil isolations

Soil samples (20) from the upper 10 cm were collected between rows (10 samples) and at the base of *V. procera* infected Scots pine (10 samples) in Zimmerman, MN. After thorough mixing, 10-g subsamples of soil from each original sample were removed and cleaned of all root and plant debris. The samples were diluted in sterile water to reach a final dilution of 1:121. One millilitre of the final suspension from each soil sample was spread on the surface of VSM medium in each of two Petri dishes, incubated at 25°C, and examined after 2 weeks.

Results

Insects and fungi on trees

Verticicladiella procera was isolated from all but one tree infested with root-collar weevils (Table 1). In 8 of the 37 trees sampled with root-collar weevil



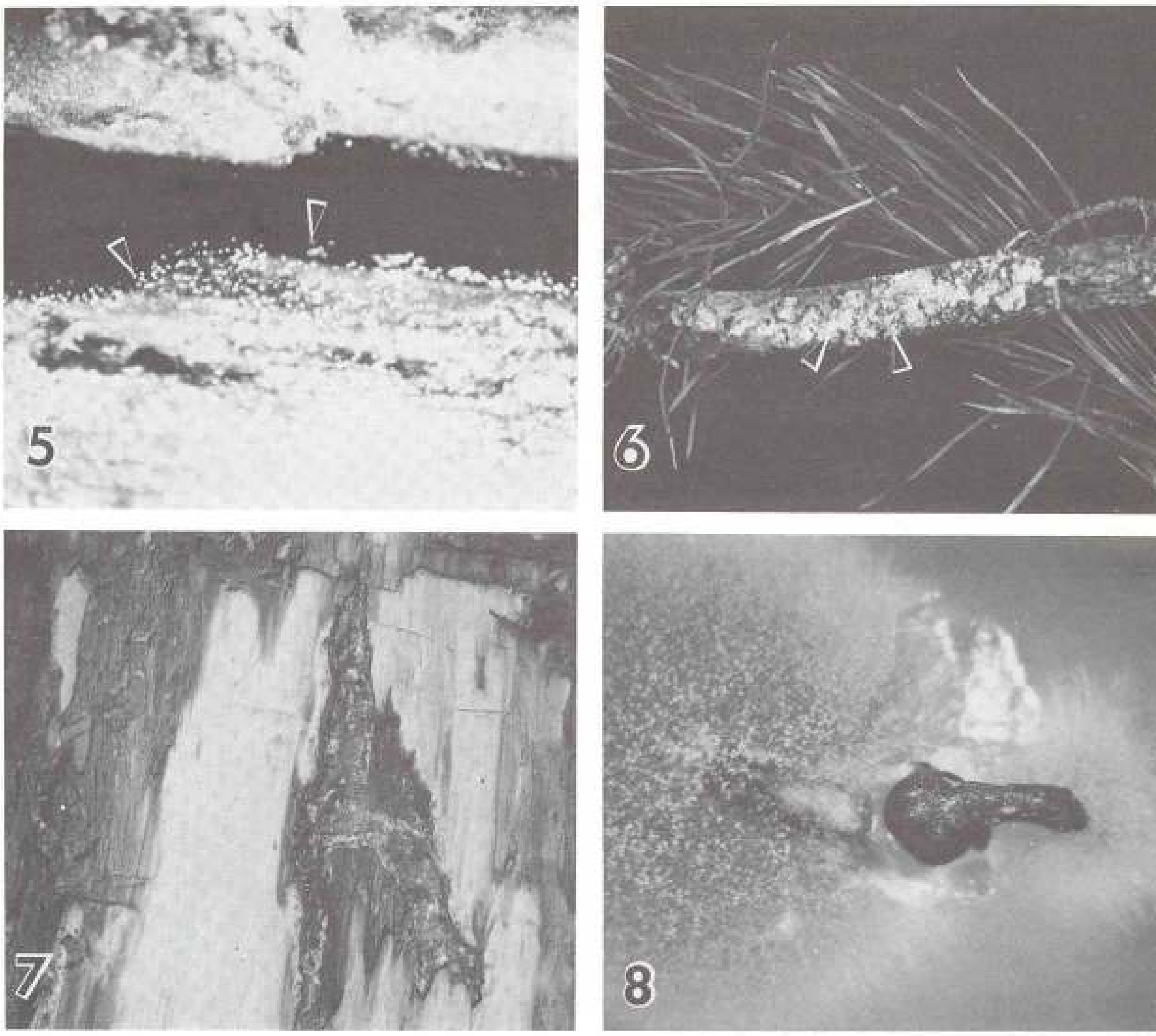
FIGS. 1–4. Tree and tree parts showing damage associated with *H. radicis* and *H. rhizophagus* infestation. Fig. 1. Bole of Scots pine with resin exudation typical of *H. radicis* infestation. Fig. 2. Cross section of ponderosa pine bole damaged by *H. radicis*. Fig. 3. Roots of jack pine damaged by *H. rhizophagus*. Fig. 4. Discoloration and decay in jack pine roots associated with *H. rhizophagus* infestation.

damage (Figs. 1 and 2), *L. terrebrantis* was isolated together with *V. procera*. In all trees, galleries of *D. valens* were found associated with root-collar weevil damage. In the absence of *V. procera*, *L. terrebrantis* was not isolated from any of the root-collar weevil-infested trees (Table 1).

Verticicladiella procera was isolated from discolored root xylem of four jack pine damaged by root-tip weevils (*H. rhizophagus*) (Figs. 3 and 4) and from roots of all three red pine infested by this insect (Table 2). In jack pine, two trees had been attacked in the lower bole by *D. valens* and *L. terrebrantis* was isolated from their galleries (Table 2). *Verticicladiella procera* was isolated from roots recently infested by weevils but not from decayed roots damaged during previous years.

All Scots pine sampled in Zimmerman, MN (Table 2) yielded *V. procera* from the roots damaged by *P. picivorus* (Fig. 5) and from the galleries of weevils (*Pissodes approximatus* and *H. pales*) in the tree stumps. Puncture holes in green (living) roots caused by *P. picivorus* were surrounded by necrotic bark and cambium and *V. procera* was consistently isolated from these lesions. *Verticicladiella procera* was, however, not isolated from maturation feeding damage (Fig. 6) on the lower green branches.

Verticicladiella procera was isolated from dead cambium associated with *D. valens* galleries on one fire-damaged jack pine (Table 2). Red pine at the same



FIGS. 5–8. Symptoms associated with infestation of *D. valens*, *H. pales*, and *P. picivorus* on pine and isolation of *V. procera* from *H. pales*. Fig. 5. *Verticicladiella procera* conidiophores (arrows) on roots of Scots pine damaged by *P. picivorus*. Fig. 6. Maturation feeding damage (arrows) by *H. pales* on Scots pine branches. Fig. 7. Cambial discoloration on red pine bole associated with *D. valens* infestation. Fig. 8. *Verticicladiella procera* sporulating in association with *H. pales* on agar.

location had *V. procera* and *L. terrebrantis* consistently associated with *D. valens* infestation (Fig. 7). *Leptographium terrebrantis* was isolated from the stressed white pine in Bellwin, MN and *V. procera* was isolated from the partially windblown Scots pine sampled in Becker, MN (Table 2).

Fungi on insects

Verticicladiella procera was commonly isolated from *H. radicis*, *H. pales*, and *P. picivorus* (Fig. 8, Table 3). Both *V. procera* and *L. terrebrantis* were isolated from *D. valens*, though the percentage recovery was low with *V. procera*. Neither of these fungi were isolated from *Pissodes approximatus* (Table 3).

Pathogenicity tests

No seedling inoculated with *V. procera* died after 1 year. Small local lesions were, however, present around the points of inoculation and *V. procera* was reisolated from these areas. Seventy percent (14 of 20) of seedlings inoculated with *L. terrebrantis* died. The majority of these seedlings died within the first 3 months and were girdled by the fungus. *Leptographium terrebrantis* was reisolated from all seedlings that died and from lesions associated with the inoculation on seedlings that did not die. No control seedlings died.

Soil isolations

Verticicladiella procera was isolated from 3 of the 20 soil samples. These three samples were all from the bases of *V. procera* infected trees.

Discussion

In this study, *V. procera* was not associated with symptoms characteristic of a primary fungal disease such as white pine root decline described from the eastern United States (Dochinger 1967; Sinclair and Hudler 1980; Towers 1977). Rather, the fungus was associated with damage caused by various insects on several pine species. *Verticicladiella* spp. are commonly carried by insects (Davidson and Robinson-Jeffrey 1965; Goheen and Cobb 1978; Kendrick 1962; Robinson-Jeffrey and Grinchenko 1964; Wingfield and Knox-Davies 1980). *Verticicladiella procera* has been isolated from bark beetles (Scolytidae) and found sporulating in the galleries of *Hylobius* spp. (Lackner and Alexander 1982; Swai 1980). In this study, *V. procera* was associated with two weevil species (*H. radicis* and *H. rhizophagus*) which are insect pests of pine and able to infest healthy trees (Kennedy and Wilson 1971; Mosher and Wilson 1977; Millers *et al.* 1963; Wilson 1968). *Verticicladiella procera* appeared to be secondary to the activities of these insects. *Verticicladiella procera* was also associated with other insects (*H. pales*, *P. picivorus*, and *D. valens*) which attack dying and stressed trees (Baker 1972).

The pine root-collar weevil (*H. radicis*) is an important pest of forest trees in the northeastern United States. The insect is particularly damaging on Scots pine but jack pine and red pine can also be severely damaged (Wilson 1968; Mosher and Wilson 1977). The symptoms associated with root-collar weevil-infestation (resin exudation at the root collar and progressive decline of trees over a number of years, Wilson 1968) are similar to white pine root decline symptoms. The common association of *V. procera* with these symptoms could lead to confusion between root-collar weevil-infestation and white pine root decline. Root-collar weevils, however, seldom attack five-needle pines (Shaffner and McIntyre 1944; Schmiege 1958) and were not associated with white pine here.

The pine root-tip weevil (*H. rhizophagus*) has been associated with root degradation of jack pine and red pine in Wisconsin (Millers *et al.* 1963; Mosher and Wilson 1977). These weevils are primarily active on the small roots and seldom reach the root-collar area (Millers *et al.* 1963; Mosher and Wilson 1977). In a study of fungi associated with the damage caused by this insect, Krebill (1962) commonly recovered a *Leptographium* species. The description of the *Leptographium* sp. provided by Krebill (1962) matches the description of *V. procera* and it seems likely that these fungi are the same. In this study and that of Krebill (1962), *V. procera* appeared to be an early colonist of damaged roots which later became infected with decay fungi. This would be similar to the observed patterns of succession associated with damage in conifers (Lachance 1975; Smerlis 1957; Whitney 1961).

Both *H. pales* and *P. picivorus* breed in the stumps and roots of stressed trees (Baker 1972). These insects are most damaging to seedlings planted on former pine sites where they breed and multiply in old stumps. In this study, *H. pales* and *P. picivorus* were trapped near cut Scots pine and were thus not associated with tree death.

Verticicladiella procera has also been isolated from the soil in pine plantations by other investigators (Lackner 1982; Swai and Hindal 1981). It is possible that roots and root collars wounded by insects discussed in this study could have been colonized by *V. procera* present in the soil. However the isolation of *V. procera* from many of the insects and the low recovery of the fungus from the soil suggests that *V. procera* is probably introduced into the trees by the insects.

Both *V. procera* and *L. terrebrantis* were isolated from *D. valens* and damage on trees associated with this insect. *Leptographium terrebrantis* was first isolated from *Dendroctonus terrebrans* (Barras and Perry 1971). The fungus has also been isolated from *D. valens* and *Hylurgops porosus* (Le Conte) in California (Harrington and Cobb 1983). *Dendroctonus valens* usually attacks stressed trees (Baker 1972) explaining its association with fire damaged, felled, and waterlogged trees in this study. In most cases where *L. terrebrantis* was isolated from root-collar or root-tip weevil-damaged trees, signs of *D. valens* activity were also present. Apparently, *D. valens* colonized trees stressed by root-collar and root-tip weevils and introduced *L. terrebrantis*.

Verticicladiella procera was not able to kill white pine seedlings in pathogenicity tests conducted here. This observation is similar to that of Harrington and Cobb (1983) who inoculated ponderosa pine seedlings. Houston (1969), however, was able to induce annual cankers with *V. procera* in New York and more recently Lackner and Alexander (1982) reported killing *Pinus strobus* seedlings in greenhouse pathogenicity tests with *V. procera*. It is possible that isolates of *V. procera* associated with white pine root decline in the eastern United States are more virulent than those from Minnesota. In addition, greenhouse pathogenicity tests may not represent the field situation accurately. Results of this study, however, suggest that *V. procera* was a weak pathogen associated with the forest insects mentioned.

Leptographium terrebrantis was pathogenic on white pine seedlings. However, this fungus is carried by a bark beetle (*D. valens*) that usually infests stressed trees. If *L. terrebrantis* were carried by an insect such as the root-collar weevil, trees attacked would possibly die more rapidly.

Acknowledgements

I am most grateful to Dr. Louis Wilson for advice and for supplying adult root-collar weevils for isolation; Dr. Imants Millers for identifying pitch and pales weevils; Frank Morse, Jane Hess, and Kathy Zuzek for technical assistance; and Drs. Robert A. Blanchette, Thomas A. Harrington, and Thomas H. Nicholls for help with the manuscript. This research was supported in part by funds provided by the U.S.D.A. Forest Service, North Central Forest Experiment Station, grant No. RWU-NC-2205.

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