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Endophytic fungi in foliage of some Cupressaceae in Oregon

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Endophytic fungi were isolated from foliage of four host species of Cupressaceae sampled from 19 sites in Oregon. *Chamaecyparis lawsoniana* and *Thuja plicata* showed high overall rates of infection (30–50%) while *Calocedrus decurrens* and *Juniperus occidentalis* showed lower rates (10–35%). For any particular host, samples from homogeneous stands with a closed canopy showed higher infection rates than those from mixed stands with an open canopy. For a given tree, infection rates tended to increase with increasing foliage age and decreasing distance from the trunk (exceptions are noted in the text below). The most commonly isolated endophytes include *Linodochium* sp. and *Geniculosporium* sp. on *C. decurrens*; *Scolecosporella* sp., *Nodulisporium* sp., *Geniculosporium* sp., and *Chloroscypha alutipes* on *C. lawsoniana*; *Retinocyclus abietis* anamorph and *Hormonema* sp. on *J. occidentalis*; and *Chloroscypha seaveri* on *T. plicata*.

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Les champignons endophytes vivant dans les écaillies apparemment saines de quatre plantes hôtes de la famille des Cupressacées et récoltées dans 19 localités de l'Oregon, ont été isolés. Chez *Chamaecyparis lawsoniana* et *Thuja plicata*, le taux d'infection est élevé (30–50%), alors qu'il est plus bas chez *Calocedrus decurrens* et *Juniperus occidentalis* (10–35%). Les échantillons qui proviennent de localités à végétation homogène et à couverture végétale supérieure dense sont plus infectés que ceux qui proviennent de localités à végétation hétérogène et à couverture supérieure plus éparse. Pour un arbre donné, le taux d'infection augmente généralement en rapport direct avec l'âge des écaillies et la distance de l'extrémité des branches. Les champignons isolés le plus souvent sont: *Linodochium* sp. et *Geniculosporium* sp. chez *C. decurrens*; *Scolecosporella* sp., *Nodulisporium* sp., *Geniculosporium* sp. et *Chloroscypha alutipes* chez *C. lawsoniana*; *Retinocyclus abietis* anamorphe et *Hormonema* sp. chez *J. occidentalis*; et *Chloroscypha seaveri* chez *T. plicata*.

Introduction

During the past 30 years, scattered papers in the phytopathological literature have reported the presence of symptomless fungal infections in leaves from a variety of evergreen plants (reviewed by Carroll *et al.* 1977) as well as from some European ferns (Boullard 1951). Little attention was paid to this phenomenon, however, until fungal endophytes were described from living needles of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Bernstein and Carroll 1977) and from the foliage of several conifers in western Europe (Carroll *et al.* 1977). Subsequent investigations have involved an extensive survey of coniferous needle endophytes in the Pacific Northwest (Carroll and Carroll 1978), a description of the endophytic flora of *Juniperus communis* L. in Switzerland (Petrini and Müller 1979) and a study of endophytes in some evergreen plants and grasses in Europe (Petrini *et al.* 1979). Taken together, these studies suggest that endophytic fungi are widespread and occur in diverse groups of vascular plants.

The present investigation was undertaken in order to document the species composition of the endophytic

flora of the Cupressaceae in the Pacific Northwest (a group of conifers not studied by Carroll and Carroll in 1978), to verify and extend some ecological models proposed in the previous papers, and to address some taxonomic problems associated with endophytic fungi.

Materials and methods

Field sites and sample selection

Calocedrus decurrens (Torr.) Florin (= *Libocedrus decurrens* Torr.), *Juniperus occidentalis* Hook., and *Thuja plicata* J. Donn ex D. Don are widespread in Oregon and were investigated in this study. In addition, *Chamaecyparis lawsoniana* (A. Murr.) Parl. was sampled as an example of a locally abundant but endemic species (southwest Oregon). Five sites were chosen for each host; within each site foliage was collected from four different trees (see Table 1 for synopsis of sites). Individual branches were cut from the lower crown of the arbitrarily chosen trees with a 13-m pole pruner. Branches were tagged for identification and kept unenclosed after collection, as recommended by Millar and Richards (1974) and Bernstein and Carroll (1977). Samples were returned to the laboratory within 24 h and were stored at 6°C no longer than 24 h prior to culturing.

Segment selection and culture methods

Because of difficulties in separating the scale-like needles

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TABLE 1. Location of the collecting sites and description of the stands

	Sites				
	1	2	3	4	5
<i>Calocedrus decurrens</i>	Open stand of <i>C. decurrens</i> . Eugene, Lane Co.	Dense stand of <i>C. decurrens</i> and <i>Pseudotsuga menziesii</i> . Fox Hollow Research National Area, Lane Co.	Dense stand of <i>C. decurrens</i> and <i>P. menziesii</i> . Camas Swale Res. Nat. Area, Lane Co.	Mixed stand of <i>Thuja plicata</i> , <i>C. decurrens</i> , and <i>P. menziesii</i> . McKenzie River campground, Lane Co., U.S. Hwy. 126,	Mixed, open stand of <i>Pinus ponderosa</i> Douglas ex P. et C. Laws and <i>C. decurrens</i> . Suttle Lake Jct., U.S. Hwy. 126, Deschutes Co.
<i>Chamaecyparis lawsoniana</i>	Stand of <i>C. lawsoniana</i> and <i>P. menziesii</i> . Cedar Flat Rd., 4 mi. from Williams, Josephine Co.	Almost pure stand of <i>C. lawsoniana</i> . Coquille River Res. Nat. Area, Coos Co.	Almost pure stand of <i>C. lawsoniana</i> . Boundary campground NW of Coquille River Res. Nat. Area, Coos Co.	Open stand by the ocean. Oregon Institute of Marine Biology, Charleston, Coos Co.	Very dense young, mixed stand by the road. 18 mi. N from Bandon, on U.S. Hwy. 101, Coos Co.
<i>Juniperus occidentalis</i>	Open stand with <i>J. occidentalis</i> mixed with <i>P. ponderosa</i> . 2.5 mi. W from Sisters, Tollgate Road, on U.S. Hwy. 126, Deschutes Co.	Almost pure, open stand of <i>J. occidentalis</i> . 8 mi. E from Sisters, on U.S. Hwy. 126, Deschutes Co.	Old <i>Juniperus</i> stand. 6 mi. E from Bend, near Tumalo, Oregon State Park, Deschutes Co.	Almost pure <i>Juniperus</i> stand. 1.5 mi. E from Redmond, Deschutes Co.	Pure <i>Juniperus</i> stand. 10 mi. W from Hwy. 126, Deschutes Co.
<i>Thuja plicata</i>	Mixed stand with <i>P. menziesii</i> . H. J. Andrews Exp. Forest, Blue River, Lane Co.	Mixed stand with <i>Pinus contorta</i> Douglas ex Loud, <i>Picea sitchensis</i> (Bong.) Carrière and some <i>Thuja plicata</i> . Florence, Lane Co.	Almost exclusively <i>T. plicata</i> and <i>P. menziesii</i> . Mohawk Res. Nat. Area, Lane Co.	Mixed stand with <i>C. decurrens</i> . Same collecting site as for <i>C. decurrens</i> . McKenzie River Campground, U.S. Hwy. 126, Lane Co.	Mixed stand of <i>T. plicata</i> and <i>P. menziesii</i> . Olallie campground, McKenzie River, U.S. Hwy. 126, Lane Co.

NOTE: Descriptions of Research Natural Areas may be found in Franklin *et al.* 1972.

TABLE 2. Synopsis of the infection rates (in percent) with regard to the age-class and total overall infection

	Age-class 1	Age-class 2	Age-class 3	Overall infection rates
<i>Calocedrus decurrens</i>	9.2 (36/390)	18.2 (71/390)	40.5 (162/400)	22.8 (269/1180)
<i>Chamaecyparis lawsoniana</i>	27.3 (109/400)	48.5 (194/400)	57.5 (230/400)	44.4 (533/1200)
<i>Juniperus occidentalis</i>	7.5 (30/400)	21.8 (87/400)	46.5 (186/400)	25.3 (303/1200)
<i>Thuja plicata</i>	31.3 (125/400)	54.0 (216/400)	47.0 (183/399)	44.0 (524/1190)

NOTE: Numbers in parentheses refer to the numbers of infected segments divided by the total number of segments sampled.

from twigs, green twig segments bearing scale-needles were chosen as the sampling unit. Samples were chosen on the basis of both age-class and distance of the foliage from the tree trunk. In contrast with other coniferous species, terminal bud scales do not occur in any of the species studied. Absolute age-classes are thus difficult to determine. Age-classes were estimated on the basis of the dichotomous branching pattern within the foliage. The current season's growth at the tip of the branches was considered to be age-class 1; twig segments below the first dichotomy were assigned to age-class 2, and those below the second dichotomy, the last segments with green scales, to age-class 3.

Five healthy looking segments for each age-class (1–3) were taken at four different positions along the axis of each branch sampled. One set was selected from the tip of each branch. Additional sets were taken from branchlets approximately 30 cm apart along the main axis of each branch and were labelled according to position (set I was the set closest to trunk, and set IV, the most distal one).

Methods for surface sterilization and a discussion of their effectiveness are given in Carroll and Carroll (1978) and Petrini and Müller (1979).

Briefly, segments were dipped in 96% ethanol for 1 min to wet the surface, surface sterilized for 10 min in a solution of 65% commercial chlorox, then dipped again for 30 s in 96% ethanol. The segments were transferred in serial order to 120-mm Petri plates containing 2% malt extract agar. Normally 10 segments of a single age-class, 5 from each of two positions on a branch, were incubated in labelled positions on a single plate. Plates were incubated at 20°C with a 12-h dark:light cycle under fluorescent lights. Isolation of fungi from plates to 60-mm Petri plates containing 2% malt extract agar was carried out by direct transfer of conidia or mycelial fragments.

Scoring of infections

Twig segments were scored for fungal infection at daily intervals for the first 3 weeks after the beginning of incubation and weekly for a period of 2 months thereafter. After this time, no further growth of endophytes was found. Single and multiple infections were scored on each individual segment.

Identification and nomenclature

The coniferous hosts were identified using Hitchcock and Cronquist (1973) and Munz and Keck (1959); author citations for host plants are based on Hortus Third (L. H. Bailey Hortorium 1976). Synonymies and identification of the fungal

taxa were established on the basis of cultural characteristics and the morphology of fruiting bodies and spores when these ultimately developed. Approximately 25% of the isolates did not fruit, making their identification impossible.

Data reduction and statistical analysis

Overall rates of infection for a given host were derived by dividing the total number of segments infected by any fungus by the total number of segments incubated. The same method was used in calculating the rates of infection with regard to age-class. Infections of individual segments by more than one fungus were rare (< 1% of total segments incubated) and were not considered in these computations. A test for the equality of percentages (Sokal and Rohlf 1969) was used to compare overall infection rates for the same host at two different sites. A Friedman test (Gibbons 1976) was used to examine any possible association between overall rates of infection and foliage age-class as well as distance of samples from the trunk. Kruskal–Wallis procedures (Gibbons 1976) were used to compare infection rates among different host species.

Results and discussion

A synopsis of the overall infection rates with regard to foliage age-class is presented in Table 2 and Fig. 1 for the four host species sampled. In *C. decurrens*, *C. lawsoniana*, and *J. occidentalis*, the rates of infection are seen to increase with the age of the segment sampled. This is a common pattern for needle endophytes and has been previously reported by Millar and Richards (1975), Bernstein and Carroll (1977), Carroll *et al.* (1977), Petrini *et al.* (1979), and Petrini and Müller (1979). In *T. plicata*, however, a decrease in overall infection rate is seen in 3-year segments. Although this trend is statistically insignificant ($0.2 < P < 0.5$), a similar pattern was reported for infection rates of Douglas-fir (*Pseudotsuga menziesii*) needles by *Schizothyrium pomi* (Sherwood and Carroll 1974). These authors suggested that infected needles were short lived and fell off before uninfected needles, with the result that infection rates were lower for the surviving older needles. A similar process may be involved here.

Endophyte infection rates also vary systematically according to position in the crown, with rates increasing

TABLE 3. Synopsis of the infection rates (in percent) in relation to the location of the sets in the tree

	Set I	Set II	Set III	Set IV
<i>Calocedrus decurrens</i>	30.3 (91/300)	25.7 (77/300)	19.6 (57/290)	15.2 (44/290)
<i>Chamaecyparis lawsoniana</i>	47.3 (142/300)	48.3 (145/300)	42.3 (127/300)	39.7 (119/300)
<i>Juniperus occidentalis</i>	24.3 (73/300)	27.7 (83/300)	22.7 (68/300)	26.3 (79/300)
<i>Thuja plicata</i>	52.2 (159/295)	47.8 (141/295)	44.7 (134/300)	31.7 (95/300)

NOTE: In parentheses are the number of infected segments divided by the total numbers of segments sampled. Set I, samples nearest trunk; sets II and III, samples from intermediate positions; set IV, edge of canopy.

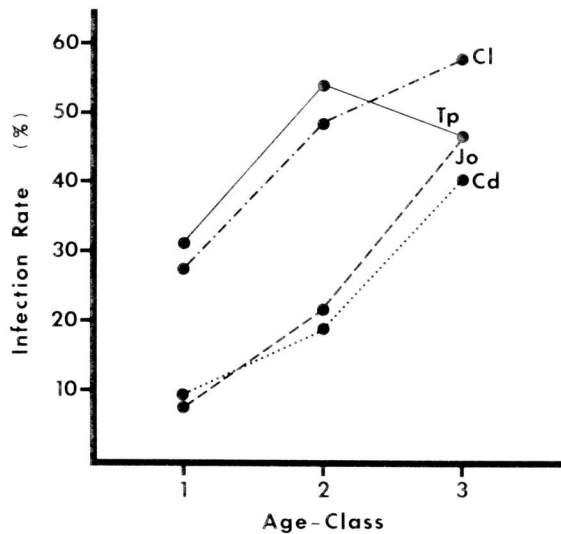


FIG. 1. Change in infection rates with increasing age of foliage segments. Cd, *Calocedrus decurrens*; Cl, *Chamaecyparis lawsoniana*; Jo, *Juniperus occidentalis*; Tp, *Thuja plicata*.

with decreasing distance from the trunk (Table 3; Fig. 2). This trend is significant at $P < 0.05$ level for *T. plicata* and *C. decurrens* and $P < 0.2$ for *C. lawsoniana*. No such trend is evident for *J. occidentalis*, an exception which may be related to the absence of green foliage (presumed to be necessary for continued infection) in the interior portions of the tree.

Rates of infection in the host species also varied among sites (Tables 4, 5). Of the collecting sites for *T. plicata*, only site 2 is significantly different from the others. Sites for *C. lawsoniana* can be separated into two groups: 1 and 4, and 2, 3, and 5. Three groups each are evident for *C. decurrens* (1 and 5, 2 and 3, 4) and *J. occidentalis* (1, 2 and 3, 4 and 5). Although we have no quantitatively objective basis for explaining such differences among sites, several trends are evident from Table 1. Infection rates appear to be high in segments taken from trees in dense stands with a closed canopy and low in open or disturbed sites. Further, infection rates are

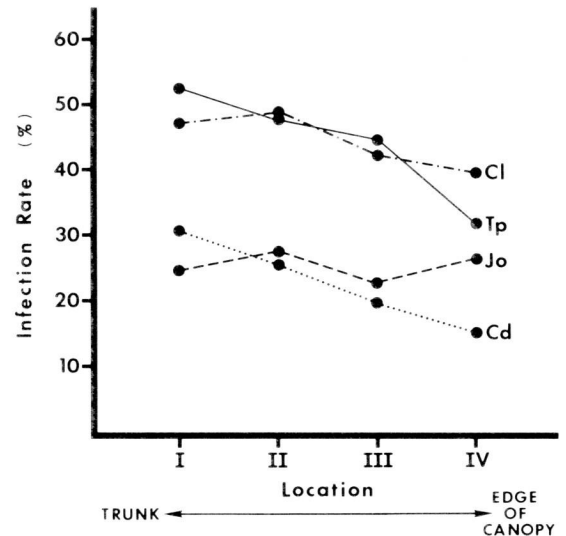


FIG. 2. Change in infection rates with increasing distance from edge of canopy. I, 90 cm from tip of main axis; II, 60 cm from tip of main axis; III, 30 cm from tip of main axis; IV, tip of main axis. Cd, *Calocedrus decurrens*; Cl, *Chamaecyparis lawsoniana*; Jo, *Juniperus occidentalis*; Tp, *Thuja plicata*.

higher in pure stands than where a mixed canopy prevails; this trend is especially evident for *J. occidentalis*, where infection rates rise sharply as one proceeds east from mixed *Juniperus-Pinus* associations to pure *Juniperus* stands.

Inspection of Figs. 1 and 2 reveals that the host species sampled fall into two groups with regard to overall infection rates: a high infection class (*T. plicata* and *C. lawsoniana*) and a low infection class (*C. decurrens* and *J. occidentalis*). While differences between these infection rates are statistically significant ($P < 0.05$) only for comparisons between *C. decurrens* and the *Thuja-Chamaecyparis* group (Kruskal-Wallis test), we suggest that a larger sample size would probably have revealed similar statistically significant trends for comparisons with *J. occidentalis*.

Carroll and Carroll (1978) demonstrated that Douglas-fir is more heavily infected in moist sites than

TABLE 4. Infection rates (in percent) at each collecting site for each host

	Site					Overall infection rate
	1	2	3	4	5	
<i>Calocedrus decurrens</i>	17.4 (40/230)	28.3 (65/230)	30.0 (72/240)	23.4 (56/240)	15.0 (36/240)	22.8 (524/1180)
<i>Chamaecyparis lawsoniana</i>	34.2 (82/240)	50.0 (120/240)	50.4 (121/240)	32.9 (79/240)	54.6 (131/240)	44.4 (533/1200)
<i>Juniperus occidentalis</i>	10.4 (25/240)	25.4 (61/240)	20.0 (48/240)	35.0 (84/240)	35.4 (85/240)	25.3 (303/1200)
<i>Thuja plicata</i>	50.8 (122/240)	22.9 (55/240)	46.2 (111/240)	49.1 (113/230)	51.2 (123/240)	44.0 (524/1190)

NOTE: Numbers in parentheses refer to the number of infected segments divided by the number of sampled segments. Locations of the sites are described in Table 1.

TABLE 5. The *t*-values for tests of equality of infection rates at each site for each host. Levels of significance were computed for a 2-tailed test with infinite degrees of freedom

	<i>Calocedrus decurrens</i>					<i>Juniperus occidentalis</i>				
	1	5	4	2	3	1	3	2	4	5
1	—	0.7	1.59	2.8**	3.23**	—	2.97**	4.38***	6.68***	6.77***
2	2.8**	3.54***	1.24	—	0.4	4.38***	1.41	—	2.3*	2.4*
3	3.23**	3.98***	1.66	0.4	—	2.97**	—	1.41	3.71***	3.8***
4	1.59	2.32*	—	1.24	1.66	6.68***	3.71***	2.3*	—	0.09
5	0.7	—	2.32*	3.54***	3.98***	6.77***	3.8***	2.4*	0.09	—

	<i>Chamaecyparis lawsoniana</i>					<i>Thuja plicata</i>				
	1	4	2	3	5	1	5	4	3	2
1	—	0.3	3.52***	3.61***	4.53***	—	0.09	0.22	1.01	6.45***
2	3.52***	3.82***	—	0.09	1.01	6.45***	6.54***	6.16***	5.44***	—
3	3.61***	3.91***	0.09	—	0.92	1.01	1.10	0.78	—	5.44***
4	0.3	—	3.82***	3.91***	4.83***	0.22	0.30	—	0.78	6.16***
5	4.53***	4.83***	1.01	0.92	—	0.09	—	0.30	1.10	6.54**

*, different at 0.05 level.
 **, different at 0.01 level.
 ***, different at 0.001 level.

in dry sites. *C. lawsoniana* and *T. plicata* typically occur in moist sites while *C. decurrens* and *J. occidentalis* are found in drier habitats (Franklin and Dyrness 1973). Unlike Douglas-fir, none of the host species we sampled occurs over a wide range of moisture regimes, and thus, we cannot decide between environmental effects and innate host susceptibility as factors in determining endophyte infection rates. Carroll and Carroll (1978) concluded that both were probably significant.

All of the above patterns may result from the interplay of just a few environmental variables, of which atmospheric humidity and inoculum potential are probably the most important. Thus, for some host species, infection rates increase from dry to wet sites. A more humid microclimate within the crown may also account for increased infection rates of a given age-class foliage with increasing distance from the edge of the crown. In similar fashion inoculum potential for a host-specific endophyte should increase as the density of the canopy

and the homogeneity of the host stands increase. Continued exposure to an inoculum could account for increasing rates of infection with age of foliage.

Although fungal endophytes are widespread, many of them either fruit infrequently on their natural substrates or form extremely inconspicuous fruiting bodies. As a result, many commonly isolated endophytes belong to taxa which are seldom collected in the field. Often they prove to be undescribed taxa. Table 6 presents information on the relative abundances of the most common fungi for the four host plants and their distribution frequency. Only those fungi which accounted for 1% or more of the total infections on a given host have been included. The fungal taxa which are common to two or more hosts or which are of particular taxonomic interest are listed in Table 7. Most of the fungi isolated during this study have been identified at least to genus. A number of these genera have been reported previously as endophytes in needles or evergreen leaves; these in-

TABLE 6. Relative frequencies of the most common observed fungal taxa

Host and fungal taxa	Absolute infection rate	Proportion of total observed infections (%)	No. of sites at which taxon was observed
<i>Calocedrus decurrens</i> (1180) ^a			
<i>Geniculosporium</i> sp.	4.6	20.2	4
<i>Linodochium</i> sp.	6.8	29.8	5
<i>Seiridium juniperi</i> (All.) Sutton	0.7	3.1	4
<i>Chamaecyparis lawsoniana</i> (1200)			
<i>Chloroscypha alutipes</i> (Phill.) Dennis	3.1	7.0	3
<i>Pezicula</i> sp.	1.6	3.6	5
<i>Gelatinosporium</i> sp. 2	0.7	1.5	4
<i>Geniculosporium</i> sp.	5.1	11.5	5
<i>Kabatina juniperi</i> Schneid. et von Arx	1.1	2.5	3
<i>Nodulisporium</i> sp.	6.4	14.4	5
<i>Scolecosporella</i> sp.	9	20.3	5
<i>Sigmoidea</i> sp.	1	2.2	4
<i>Xylaria</i> sp. 2 st. imp.	2.25	45.1	4
<i>Juniperus occidentalis</i> (1200)			
<i>Retinocyclus abietis</i> (Croun) Groves et Wells anamorph	10.6	41.7	5
<i>Hormonema</i> sp. ^b	3.0	11.8	5
<i>Kabatina juniperi</i> Schneid. et von Arx	0.9	3.6	5
J 5343 (sterile)	3.2	12.6	5
J 6231 (sterile)	4.1	16.2	5
<i>Thuja plicata</i>			
<i>Chloroscypha seaveri</i> (Rehm) Seaver	22.9	52.0	5
<i>Cylindrosporella</i> sp. 1	1.2	2.7	1
<i>Geniculosporium</i> sp.	2.2	5.0	4
<i>Microperella</i> sp.	1.35	3.0	3
<i>Seiridium juniperi</i> (All.) Sutton	0.9	2.0	3
<i>Luellia</i> sp.	0.85	1.9	5

^aNumbers in parentheses refer to total numbers of segments sampled.

^b Suspected to be the anamorph of *Pringsheimia chamaecyparidis* Froidevaux.

clude *Anthostomella*, *Chloroscypha*, *Gelatinosporium* (formerly reported as *Micropera* or *Heteropatella*), *Geniculosporium*, *Kabatina*, *Leptostroma*, *Nodulisporium*, *Pezicula* (and its anamorph *Cryptosporiopsis*), *Phyllosticta*, and some *Xylaria*-anamorphs (Carroll and Carroll 1978; Petrini and Müller 1979; M. Luginbühl, personal communication; O. Petrini and M. Dreyfuss, unpublished data).

Many of the fungi isolated are anamorphs known conifer-inhabiting ascomycetes. Thus, the fungus assigned to the genus *Cylindrosporella* shows some resemblance to the anamorph of *Coccomyces* spp. (F. DiCosmo, personal communication); *Sirodothis* is known to be the conidial state of *Tympanis* spp.; and *Leptostroma* is the anamorph of *Lophodermium* spp. An unknown member of the Corticiaceae has been isolated occasionally from *T. plicata*. This is the first published report of a basidiomycete as a component of an endophytic flora, although an undescribed species of *Marasmius* (Agaricales) has recently been isolated from *Trifolium* spp. and *Arctostaphylos uva-ursi* (L.) Spreng (E. Horak, B. Widler, and T. Riesen, personal communication). The paucity of Basidiomycetes in the endo-

phytic flora may be more apparent than real, an artifact of the isolation and scoring methods used. Basidiomycetes in culture fruit infrequently, and many of the isolates scored as "sterile" here and in previous papers may belong to this group.

Several of the fungal taxa found in the Cupressaceae we investigated were previously reported from other hosts in this family. High infection rates of *Chloroscypha seaveri* (Rehm) Seaver on *T. plicata* are mirrored by the frequent occurrence of *C. chloromela* Seaver on needles on *Sequoia sempervirens* (D. Don) Endl. (Carroll and Carroll 1978). Petrini and Müller (1979) report a number of genera and species for *J. communis* from Switzerland which were also found in the present study (e.g., *Geniculosporium*, *Kabatina juniperi*, *Pezicula* sp.). These results suggest that fungal endophytes exhibit a fair degree of host specificity, at least for families of host plants, and that such specificity may be more important than the geographical location of the host plant *per se* in determining endophyte distribution patterns. Carroll and Carroll (1978) reported similar findings for members of the Pinaceae in the Pacific Northwest and were even able to show that the degree of

TABLE 7. Fungi found on a minimum of two hosts or noteworthy isolates. The proportion of total observed infections for each host is given

	<i>C. decurrens</i>	<i>C. lawsoniana</i>	<i>J. occidentalis</i>	<i>T. plicata</i>
Basidiomycetes				
<i>Luellia</i> sp.		0.25		0.85
Ascomycetes				
<i>Anthostomella</i> cf. <i>tomicum</i> (Lév.) Sacc.		0.15		
<i>Diaporthe</i> sp.	0.35	0.25		0.15
<i>Pezicula</i> sp. (<i>Cryptosporiopsis</i> -anamorph)	0.15	1.6		0.2
<i>Xylaria hypoxylon</i> (L. ex Fr.) Grev.		0.15		0.35
Deuteromycetes				
Hyphomycetes				
<i>Alternaria alternata</i> (Fr.) Keissler	0.5		0.1	
<i>Aureobasidium</i> sp. 1	0.25			
<i>Retinocyclas abietis</i> (Croun) Groves et Wells anamorph		0.15	10.6	
<i>Geniculosporium</i> sp.	4.6	5.1		2.2
<i>Nodulisporium</i> sp.	0.6	6.41		0.1
<i>Periconia hispidula</i> (Pers. ex Pers.) Mason & M. B. Ellis	0.1			0.15
<i>Phialophora decumbens</i> (Beyma) Schol-Schwarz	0.6		0.1	0.1
<i>Phialophora hoffmanni</i> -group (Beyma) Schol-Schwarz			0.1	0.1
<i>Sigmoidea</i> sp.		1		0.1
<i>Xylaria</i> sp. 2 st.imp.	0.15	2.25		
Coelomycetes				
<i>Coniothyrium</i> sp.	0.35	0.1		
<i>Cylindrosporella</i> sp. 2			0.1	
<i>Gelatinosporium</i> sp. 1	0.5			0.1
<i>Gelatinosporium</i> sp. 2	0.25	0.65		0.15
<i>Hemidothis</i> sp.		0.1		
<i>Kabatina juniperi</i> Schneid. et von Arx	0.20	1.1		0.90
<i>Leptostroma</i> sp.		0.15		0.1
<i>Myxormia</i> sp.			0.16	
<i>Pestalotia funerea</i> Desm.		0.1		0.1
<i>Phyllosticta</i> sp.		0.75		
<i>Seiridium juniperi</i> (All.) Sutton	0.7			0.90
<i>Sirodothis</i> sp. 1	0.15			
<i>Sirodothis</i> sp. 2		0.1		
<i>Stigmina thujina</i> (Dearn.) Sutton				0.1

taxonomic affinity of the host conifers was reflected in the degree of similarity of the endophyte floras. Such host-dependant distribution patterns are widely seen among biotrophic parasites and mutualistic symbionts. Although a possible symbiotic association between fungal endophytes and the leaves of higher plants has been often suggested (Carroll *et al.* 1977; Carroll and Carroll 1978; Petrini and Müller 1979), such a relationship has yet to be demonstrated. If model systems for such investigations are sought, we suggest that endophytes showing the highest degree of host-specificity are the appropriate organisms to choose.

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