Endophytic fungi in evergreen shrubs in western Oregon: A preliminary study

ORLANDO PETRINI
Institute for Special Botany, Swiss Federal Institute of Technology, Zürich, CH-8092, Switzerland
AND
JEFFREY STONE[1] AND FANNY E. CARROLL
Department of Biology, University of Oregon, Eugene, OR, U.S.A. 97403
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Endophytic fungi were isolated from five species of broad-leaved evergreen shrubs from 16 sites in western Oregon. Rates of infection were 76% for *Mahonia nervosa*, 44% for *Arctostaphylos uva-ursi*, 37% for *Gaultheria shallon*, 29% for *Mahonia aquifolium*, and 25% for *Umbellularia californica*. Incidence of leaf infections by more than one fungal taxon was 20–56%, 72–90% of which had only two infections. Rates of overall infection were higher in samples taken from densely wooded sites than in samples taken from more open sites. A pattern of species dominance is seen where the most common endophyte of a given host is isolated less frequently from other hosts; less commonly isolated endophytes appear to be less host specific. The most commonly isolated endophytes include *Phyllosticta pyrolae* on *A. uva-ursi* and *G. shallon*, *Leptothyrium berberidis* on *M. nervosa*, *Septogloeum* sp. on *M. nervosa* and *U. californica*, and *Phomopsis* sp., predominantly on *M. aquifolium*, but present on all hosts. Some of the fungi isolated from evergreen shrubs in this study were previously isolated from conifer needles; however, most represent new records.

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Des champignons endophytes ont été isolés de cinq espèces d'arbustes à feuilles persistantes provenant de 16 localités de l'ouest de l'Oregon. Les taux d'infection ont été de: 76% chez *Mahonia nervosa*, 44% chez *Arctostaphylos uva-ursi*, 37% chez *Gaultheria shallon*, 29% chez *Mahonia aquifolium* et 25% chez *Umbellularia californica*. L'incidence d'infection fongique multiple dans les feuilles est de 20 à 56%. Dans 72 à 90% de ces cas, deux infections seulement sont présentes. Le taux d'infection est plus élevé dans les échantillons prélevés en forêt dense que dans ceux qui proviennent de localités à végétation plus éparse. Un modèle de dominance d'une espèce est observé dans les cas où le champignon endophyte prédominant chez un hôte semble être relativement spécifique à cet hôte; les champignons isolés moins souvent ne montrent aucune spécificité. Les champignons endophytes isolés le plus souvent comprennent: *Phyllosticta pyrolae* chez *A. uva-ursi* et *G. shallon*, *Leptothyrium berberidis* chez *M. nervosa*, *Septogloeum* sp. chez *M. nervosa* et *U. californica* et *Phomopsis* sp., prédominant chez *M. aquifolium* mais présent chez tous les hôtes. Certains champignons isolés dans le présent travail ont aussi été isolés des aiguilles de conifères mais la plupart des associations espèces fongiques – hôtes n'ont pas été mentionnées précédemment.

Introduction

The presence of endophytic fungi in a number of cryptogams and phanerogams was established on the basis of histological evidence provided by several authors (Boullard 1951; reviewed by Schuster 1966 and Carroll et al. 1977). Scattered papers in the phytopathological literature reported the presence of endophytes in the leaves of a variety of evergreen plants, as reviewed by Carroll et al. (1977). Only recently, however, were cultural studies undertaken in order to document the occurrence of endophytic fungi in grasses and evergreen plants in Europe (Petrini et al. 1979; Luginbühl 1980) and in the needles of some conifers in Europe and North America (Bernstein and Carroll 1977; Carroll et al. 1977; Carroll and Carroll 1978; Petrini and Carroll 1981; Petrini and Müller 1980). Thus, it appears that widespread ocurrence of asymptomatic fungal infections in a variety of plants has only begun to be recognized.

Evergreen shrubs and trees are widespread in the Pacific Northwest and are a primary component of the flora of western Oregon. The wide distribution of broad-leaved evergreen plants as understory vegetation in a variety of different ecological regimes (Franklin and Dyrness 1973) permits testing and extension of ecological models based upon previous studies of conifer endophytes.

The present study was undertaken to determine whether any similarity exists between the species composition of the endophytic flora of broad-leaved evergreen hosts and that already published for conifers in the Pacific Northwest. We also hoped to determine

[1]Author to whom reprint requests should be addressed.

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whether site-specific variation in endophyte infection rates could be predicted from patterns observed in coniferous hosts.

Materials and methods

Sample selection

Arctostaphylos uva-ursi (L.) K. Spreng., *Mahonia aquifolium* (Pursh) Nutt. [*Berberis aquifolium* Pursh], *Mahonia nervosa* (Pursh) Nutt. [*Berberis nervosa* Pursh], and *Gaultheria shallon* Pursh are common at moderate altitudes in western Oregon. *Umbellularia californica* (H. et A.) Nutt. is endemic to northern California and southwestern Oregon where it occurs in abundance near streams and creeks. These five hosts were chosen for the present study.

Collecting sites were chosen to reflect differences in moisture regimes within the natural range of each species in western Oregon; canopy density and associated humidity were estimated for each site (Table 1). Sites were then grouped to reflect differences in canopy density and associated moisture (Table 2).

Approximately equal amounts of foliage from different age classes were sampled from several different plants for each host from each collecting site. Branchlets were hand-pruned, tagged for identification, and kept unenclosed after collection, as recommended by Millar and Richards (1974) and Bernstein and Carroll (1977), and then returned to the laboratory within a few hours from the time of collection and stored at 6°C no longer than 24 h prior to culturing.

Culture methods

The sampling of the leaves, or the leaflets in the case of *M. aquifolium* and *M. nervosa*, followed essentially the sampling scheme proposed by Luginbühl (1980). A set of 50 healthy-looking leaves was taken for cultural study from each site; the leaves were dipped for 1 min in 96% ethanol to wet the surface, surface sterilized for 10 min in a solution of 65% commercial Chlorox (NaOCl final concentration 3.25%), and then dipped again for 30 s in 96% ethanol.

Because of their smaller size, *Arctostaphylos* leaves were cut with a sterile scalpel into four approximately equal segments. Five discs of 5-mm diameter were cut from the leaves of the other four species with a sterile No. 2 cork borer. Three of the discs were cut from the nerve region and two from the blade on each side of the nerve of each leaf. Samples from all hosts were treated identically in all other respects.

The segments and the discs were transferred in serial order to labeled positions on 100-mm Petri plates containing 2% malt extract agar. Normally the segments or discs from two leaves were incubated in 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 dishes containing 2% malt extract agar was carried out by transfer of conidia or mycelial fragments.

Scoring of infection

Leaf segments were scored daily for fungal infection during the first 2 weeks of incubation and every other day for 3 weeks thereafter. After this time, no further growth of endophytes was found. Single and multiple infections were scored on each leaf and each individual segment.

Identification and nomenclature

The evergreen hosts were identified following Hitchcock and Cronquist (1973), and author citations are based on *Hortus third* (Anonymous 1976).

The identity of fungal taxa was established on the basis of both cultural characteristics and morphology of fruiting bodies and spores. Most fungi sporulated readily on the leaf tissue but only slowly on artificial medium. Approximately 15% of the isolates did not fruit under any circumstances and thus were impossible to identify.

Statistical analysis

Overall rates of infection were computed for both discs or segments and leaves and were derived by dividing the total number of discs or leaves infected by one or more fungi by the total number of discs or leaves incubated. The multiple infection rates were obtained by dividing the number of leaves infected by two or more taxa by the total number of leaves incubated. Multiple infections of individual segments or discs by more than one taxon were less than 2% for each host and were not considered further in any other computation. Because of the difficulties in referring sterile mycelia to a given taxon, multiple infection of a leaf was scored only when at least one of the infecting fungi could be identified.

A Kruskal–Wallis procedure (Gibbons 1976) was used to identify differences in overall infection rates among different host species and among sites for each host. A multiple comparison procedure (Gibbons 1976) was then used to contrast overall infections rates between dry and humid sites for each host. Ranks were assigned to each disc ($n = 5$) or, in the case of *A. uva-ursi*, segment ($n = 4$), position for the 50 leaves sampled from all (k) sites for each host on the basis of frequency of infected discs or segments. Mean ranks ($\bar{R}_i$) were then computed for individual sites and site groups. Mean rank differences were determined to be statistically significant if the inequality

$$|\bar{R}_i - \bar{R}_j| \geq z\sqrt{\frac{N(N+1)}{12}\left(\frac{1}{n_i} + \frac{1}{n_j}\right)}$$

was satisfied, where $N = nk$ is the number of ranked observations for each host and z is the quantile of the standard normal curve computed for each set of p contrasts corresponding to a right-tail probability of $\alpha/2p$ at significance level α.

Results and discussion

The overall infection rates for each host species correlate well with the estimated canopy density and moisture of the collecting sites (Table 2). Infection rates tend to be lower in foliage collected from open or disturbed sites. This applies particularly for site 5 of *G. shallon* (open, wind-exposed, almost pure stand on seashore) and for site 1 of *U. californica* (open, disturbed site near highway). Carroll and Carroll (1978) and Petrini and Carroll (1981) reported similar patterns in their studies on coniferous hosts and suggested that differences in elevation, humidity, density of canopy cover, and innate host susceptibility are likely to cause

TABLE 1. Location and description of collecting sites

Host	Site				
	1	2	3	4	5
A. uva-ursi	C. Washburn Memorial State Park, Lane Co.; dense canopy, moderately humid	Sutton Campground, Florence, Lane Co.; exposed, dry	Winchester Bay, Coos Co.; moderate canopy cover, moderately humid	Tenmile Lake Rec. Area, Douglas Co.; exposed, dry	
G. shallon	Goodpasture Rd., U.S. Hwy. 126, Lane Co.; closed canopy, humid	H. J. Andrews Exp. Forest, Lane Co.; dense canopy, very humid	Marcola, Lane Co.; closed canopy, moderately humid	Sutton Campground, Florence, Lane Co.; dense canopy, humid	Cape Perpetua, Linn Co.; exposed, dry
M. aquifolium	Floral Hill Valley, Eugene, Lane Co.; dense canopy, humid	Marcola, Lane Co.; open, dry	Camas Swale Res. Natural Area, Lane Co., open, dry	Fox Hollow Res. Natural Area, Lane Co.; open, dry	
M. nervosa	Camas Swale Res. Natural Area, Lane Co.; open, dry	H. J. Andrews Exp. Forest, Lane Co.; dense canopy, very humid	H. J. Andrews Exp. Forest, Lane Co.; dense canopy, very humid	Knowles Creek Rd., Mapleton, Lane Co.; moderate canopy, dry	
U. californica	Elkton, Douglas Co.; open, dry	Scottsburg, Coos Co.; moderately open, dry	Loon Lake Rec. Area, Coos Co.; closed canopy, humid	Oregon Hwy. 55, Reedsport, Coos Co.; moderate canopy, dry	

TABLE 2. Infection rates (%) and multiple infection rates (%) in each collecting site for each host

Host[a]	Overall infection rate, %	Dry/exposed sites						Humid/closed sites				
		1	2	3	4	5	Mean, %	1	2	3	4	Mean, %
A. uva-ursi												
Infected segments (792)	44		21		32		26	58		64		61
Infected leaves (198)	80		56		73		40	94		96		95
Multiple infections	29		14		13		14	36		54		45
G. shallon												
Infected discs (1240)	37					9	9	40	39	54	45	44
Infected leaves (248)	81					40	40	90	86	96	96	92
Multiple infections	31					0	0	46	46	38	23	38
M. aquifolium												
Infected discs (980)	29		18	19	22		20	58				58
Infected leaves (196)	71		52	65	68		62	98				98
Multiple infections	29		19	21	26		16	50				50
M. nervosa												
Infected discs (1000)	76	74			64		69		86	78		82
Infected leaves (200)	99	100			96		98		100	100		100
Multiple infections	56	68			72		70		56	28		42
U. californica												
Infected discs (990)	25	8	25		18		17			47		47
Infected leaves (198)	60	34	67		48		50			90		90
Multiple infections	20	6	15		18		13			40		40

[a]Numbers in parentheses refer to the total sample size of discs or segments and leaves for each host.

the observed differences in endophyte infection among sites.

Kruskal–Wallis procedures indicate differences among sites with regard to overall infection rates significant at the 0.05 level for all hosts except *M. nervosa*, in which infection rates are uniformly high (Table 3). Mean rank differences for dry versus humid sites (Table 3) lend support to the observation that the degree of host infection correlates with canopy density and moisture of the collecting site. This trend is particulary marked when grouped dry and wet sites are contrasted (Table 4). Differences are significant at the 0.01 level for *M. aquifolium* and *U. californica* and at the 0.04 level for *A. uva-ursi* and *G. shallon*. Contrasts are also provided for *M. nervosa* although the Kruskal–Wallis test did not indicate significant variation among sites for this host.

The Kruskal–Wallis test revealed significant differences in overall infection rates among hosts significant at the 0.05 level ($H = 10.90$, $k = 5$). Infection rates were generally lower for hosts which prefer dry habitats (*M. aquifolium* and *U. californica*); infection rates for *M. nervosa*, which prefers moist habitats, were much higher than for all other hosts at all sites (Table 2). *Gaultheria shallon* and *A. uva-ursi*, which prefer moderately humid habitats, were intermediate with regard to infection rates. Although other factors of host susceptibility may be involved, the frequency of endophyte infections appears to diminish with decreasing habitat moisture. Because the size of the sampling unit (segments) of *A. uva-ursi* was slightly larger than the discs sampled from the other hosts, overall infection rates for this host may be slightly underestimated.

Rates of multiple infections ranged from 20% (*U. californica*) to 56% (*M. nervosa*) (Table 2). These were attributable to only two infections in most cases (72 to 79% for *A. uva-ursi*, *G. shallon*, *M. nervosa*, and *M. aquifolium*, 90% for *U. californica*) and rarely to three (0 to 5%). In contrast, Carroll and Carroll (1978) and Petrini and Müller (1980) reported low multiple infection values for most of the host species they studied. The relatively high rates of infection by two or more fungal taxa observed in this study could be attributed to the physical separation of the endophytes within the comparatively broad host leaves. The low rate of infection of single discs by more than one fungal taxon adds support to this assumption, and lower rates of infection for discs than for leaves indicate that endophytes are not always distributed throughout the entire leaf. However, the use of only one isolation medium might result in failure to

TABLE 3. Mean rank differences ($|\bar{R}_i - \bar{R}_j|$) for contrasts of infection rates of individual dry versus humid sites for each host (see text for computation of significance levels)

Host	H^a	Sites	$\lvert\bar{R}_i - \bar{R}_j\rvert$
A. uva-ursi	8.88**	1 versus 2	8.37*
		1 versus 4	5.13
		2 versus 3	10.87**
		3 versus 4	7.63
G. shallon	14.44***	1 versus 5	9.30
		2 versus 5	10.50
		3 versus 5	17.20***
		4 versus 5	12.00**
M. aquifolium	11.67***	1 versus 2	11.60***
		1 versus 3	10.40**
		1 versus 4	8.00
A. nervosa	4.95	1 versus 2	6.20
		1 versus 3	3.20
		2 versus 4	7.60
		3 versus 4	4.60
U. californica	15.16***	1 versus 3	14.30***
		2 versus 3	5.30
		3 versus 4	8.00

[a]Kruskal–Wallis test.
*, different at 0.10 level.
**, different at 0.05 level.
***, different at 0.01 level.

TABLE 4. Mean rank differences ($|\bar{R}_i - \bar{R}_j|$) for contrasts of infection rates of grouped dry versus humid sites for each host (see text for computation of significance levels)

Host	Sites	$\lvert\bar{R}_i - \bar{R}_j\rvert$
A. uva-ursi	1,3 versus 2,4	8.00**
G. shallon	5 versus 1,2,3,4	12.25**
M. aquifolium	1 versus 2,3,4	10.00***
M. nervosa	1,4 versus 2,3	5.40
U. californica	3 versus 1,2,4	9.20***

*, different at 0.10 level.
**, different at 0.05 level.
***, different at 0.01 level.

isolate some fungi (e.g., Basidiomycetes) which might occupy the same portion of the leaf as a faster-growing fungus.

The list of most common fungi isolated and their distribution frequency (Table 5) shows that several taxa are common to more than one host. Many of the isolates such as *Geniculosporium* sp., *Pezicula* sp., and *Sigmoidea* sp. are morphologically indistinguishable from the corresponding isolates from coniferous hosts (Carroll et al. 1977; Petrini and Carroll 1981; Petrini and Müller 1980), while others (e.g., *Cryptocline* spp., *Cryptosporiopsis* spp., and *Phomopsis* sp.) represent records of different species. Endophytes like *Cladosporium cladosporioides*, often considered to be a possible contaminant and only recently demonstrated to be an accidental endophyte (O'Donnell and Dickinson 1980), are not often isolated and clearly are not host specific. Some taxa (e.g., *Acremonium* sp., *Nodulisporium* sp., and some *Xylaria* anamorphs) have been often recorded as endophytes, yet they do not appear to be specific to any particular host.

The majority of isolates from a given host species comprise relatively few fungal taxa (Fig. 1). One endophyte species for each host invariably comprises the largest portion of the isolates and appears to be relatively host specific, while a constellation of incidental species common to several hosts accounts for the remainder (Table 5). The most common endophyte of the ericaceous hosts in this study, *Phyllosticta pyrolae*, as well as *Aureobasidium ribis*, *Phyllosticta vaccinii*, *Physalospora arctostaphyli*, and *Pleospora herbarum*, are also often isolated from ericaceous hosts in Switzerland (B. Widler, Eidgenössische Technische Hochscule, Zürich, personal communication, April 1980). *Septogloeum* sp. accounted for 56% of the total infected discs of *U. californica* and was also relatively abundant on *M. nervosa* and *M. aquifolium*. *Leptothyrium berberidis*, considered to be the anamorph of *Lophodermium berberidis* (Schleich.) Rehm (Nannfeldt 1932), is the most common endophyte of *M. nervosa* and is also frequently found on *M. aquifolium*. However, the close resemblance of this fungus to some anamorphs of *Coccomyces* spp. (F. DiCosmo, University of Waterloo, personal communication, April 1980) causes uncertainty as to which teleomorph this anamorph should be assigned. A similar pattern of host-specific species dominance was noted by Carroll and Carroll in their survey of coniferous hosts in the Pacific Northwest. Thus, while infection rates for each host seem to be related to ecological factors, some components of the endophytic flora reveal a degree of host specificity, at least at the family level (Carroll and Carroll 1978; Petrini and Carroll 1981). In contrast, *Phomopsis* sp., the most frequently isolated endophyte from *M. aquifolium*, was also relatively common on all hosts. Whether any significant trends exist between the species composition of the endophyte flora of related hosts is unclear and will require further study.

Host–endophyte specificity could lead to the formation of host-specific strains in fungi common to different hosts. This is a possible explanation for the variability observed in the coelomycetous fungus tentatively assigned to *Septogloeum*, which initially showed different cultural characteristics and growth form depending upon its origin (*G. shallon*, *M. aquifolium*, and *M. nervosa*,

TABLE 5. Relative frequencies of the most commonly observed fungal taxa

Host and fungal taxa[a]	% of total segments	% of total infected segments	% of total infected leaves	No. of sites at which taxon observed	Additional hosts[b]
A. uva-ursi (792)					
Aureobasidium ribis (Vassiljevski) Hermanides-Nijhof	0.5	1.2	2.0	3	
Gelatinosporium sp.	0.4	0.9	1.0	1	
Cryptosporiopsis sp.	1.8	4.0	3.5	1	
Hainesia sp.	0.5	1.2	2.0	1	
Phomopsis sp.	3.4	7.9	10.6	4	Gs, Ma, Mn, Uc
Phyllosticta pyrolae Ellis et Everh.	16.3	37.2	34.3	3	Gs, Ma
Phyllosticta vaccinii Earle	2.0	4.6	6.6	4	Gs
Physalospora arctostaphyli B. Erikss.	1.4	3.2	3.0	2	
Pleospora herbarum (Fr.) Rabenh.	2.0	4.6	6.6	3	Uc
Ramularia sp.	0.8	1.7	3.0	1	Gs, Uc
Xylaria hypoxylon (L. ex. Fr.) Grev. anamorph	0.6	1.4	2.0	2	Gs, Uc
Xylaria sp. anamorph	0.6	1.4	2.5	4	Gs, Ma, Mn, Uc
A. uva-ursi 3914 (sterile)	5.3	12.1	10.1	1	
G. shallon (1240)					
Acremonium sp.	0.6	1.7	2.4	2	Uc
Geniculosporium sp.	2.2	5.8	8.4	3	Au, Ma, Mn, Uc
Leptothyrium berberidis Cooke et Massee	1.1	3.0	3.6	1	Ma, Mn
Nodulisporium sp.	0.6	1.5	2.4	2	Au, Ma
Pezicula sp.	1.6	4.3	6.4	4	Ma, Mn
Phialophora spp.	1.9	5.2	7.2	4	Mn
Phomopsis sp.	1.6	4.3	4.8	3	Au, Ma, Mn, Uc
Phyllosticta pyrolae Ellis et Everh.	15.8	42.4	34.7	5	Au, Ma
Phyllosticta vaccinii Earle	1.4	3.7	5.6	1	Au
Ramularia sp.	1.3	3.5	4.8	4	Au, Uc
Septogloeum sp.	1.1	3.0	4.4	3	Ma, Mn, Uc
Sigmoidea sp.	0.2	0.6	1.2	2	Uc
Xylaria hypoxylon (L. ex Fr.) Grev. anamorph	0.4	1.1	2.0	2	Au, Uc
M. aquifolium (980)					
Cladosporium cladosporioides (Fresen.) De Vries	0.5	1.7	2.5	2	Au, Gs
Cryptocline sp. 1	0.9	3.1	3.5	2	Au, Gs
Cryptocline spp.	3.6	12.2	9.5	3	
Cryptosporiopsis spp.	0.6	2.1	3.0	1	
Geniculosporium sp.	1.3	4.5	6.6	4	Au, Gs, Mn, Uc
Leptothyrium berberidis Cooke et Massee	3.9	13.2	13.6	4	Gs, Mn
Pezicula sp.	0.6	2.1	3.0	2	Gs, Mn
Phomopsis sp.	11.5	39.2	31.8	4	Au, Gs, Mn, Uc
Septogloeum sp.	2.3	8.0	8.6	3	Gs, Mn, Uc
M. nervosa (1000)					
Hypoxylon serpens (Pers. ex Fr.) Kickx var. *effusum* (nits.) Miller	0.4	0.5	1.0	1	
Leptothyrium berberidis Cooke et Massee	53.4	70.6	94.0	4	Gs, Ma
Pezicula sp.	0.5	0.7	2.0	3	Gs, Ma
Phomopsis sp.	2.4	3.2	10.5	3	Au, Gs, Ma, Uc
Septogloeum sp.	13.1	17.3	41.5	4	Gs, Ma, Uc
Xylaria sp. anamorph	0.5	0.7	2.0	2	Au, Gs, Ma, Uc

TABLE 5 (*concluded*)

Host and fungal taxa[a]	% of total segments	% of total infected segments	% of total infected leaves	No. of sites at which taxon observed	Additional hosts[b]
U. californica (990)					
Cryptocline cinerescens (Bub.) von Arx	1.8	7.4	9.1	4	
Geniculosporium sp.	0.4	1.6	2.0	3	Au, Gs, Ma, Mn
Phomopsis sp.	4.2	17.3	17.7	4	Au, Gs, Ma, Mn
Septogloeum sp.	13.6	55.6	33.3	3	Gs, Ma, Mn
Xylaria hypoxylon (L. ex Fr.) Grev. anamorph	0.3	1.2	1.5	1	Au, Gs
Xylaria sp. anamorph	1.9	7.8	8.5	2	Au, Gs, Ma, Mn

[a]Numbers in parentheses refer to total numbers of discs (segments) sampled. Only those fungi which accounted for 1% or more of the total infection for a given host, were common to two or more hosts, or which are of taxonomic interest have been included.
[b]Au, *A. uva-ursi*; Gs, *G. shallon*; Ma, *M. aquifolium*; Mn, *M. nervosa*; Uc, *U. californica*.

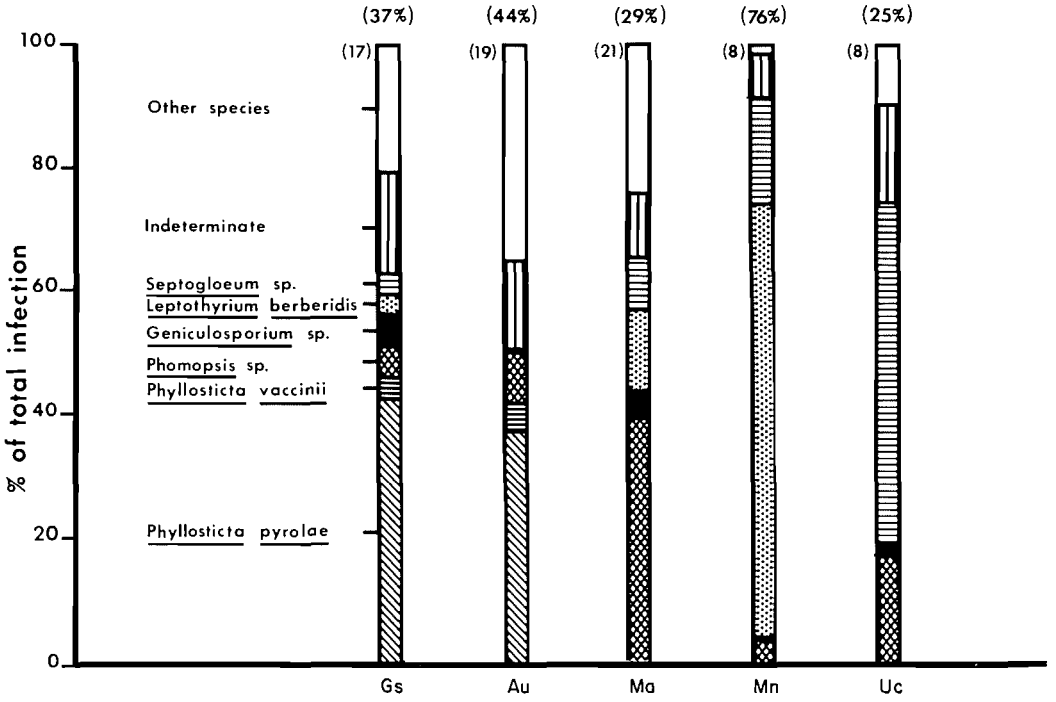

FIG. 1. Relative contribution to total infection by six frequently isolated fungal taxa. Numbers in parentheses above each bar refer to the overall infection rate for each host. Numbers in parentheses at the upper left of each bar refer to the number of additional species for each host. Au, *A. uva-ursi*; Gs, *G. shallon*; Ma, *M. aquifolium*; Mn, *M. nervosa*; Uc, *U. californica*.

or *U. californica*). Since no significant morphological differences could be found in mature sporulating cultures, it is impossible to assign these three groups to three different species. Strains of the same fungus isolated from different parts of the same host differ in their ability to digest different substrates (G. C. Carroll and O. Petrini, submitted for publication). Genetic variability within the same species could account for these observations; however, many features of the biology of endophytic fungi are unresolved. Further investigation of the physiology of such strains could provide information on the nutritional relationship between endophytes and host leaves and on the hierarchy of substrate utilization by endophytes inhabiting the same leaf.

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