

Occurrence of mycorrhizae on ericaceous and pyrolaceous plants in northern California¹

DAVID L. LARGENT, NEIL SUGIHARA, AND CARL WISHNER

Department of Biology, Humboldt State University, Arcata, CA, U.S.A. 95521

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Four hundred and eighty plants in northern California from 27 taxa in the Ericaceae and 5 in the Pyrolaceae were surveyed for presence of ectomycorrhizae, arbutoid, or ericoid mycorrhizae between September 1977 and April 1978. Of these, 337 in the Ericaceae and 8 in the Pyrolaceae had one or more types of mycorrhizae.

At least 88% of the plants of larger shrubs or trees (*Arbutus menziesii* or *Arctostaphylos* spp.) were mycorrhizal in various locations in northern California. Of the plants in the remaining twenty-two taxa that were mycorrhizal, 67-100% had ectomycorrhizae or arbutoid mycorrhizae. Twenty-three taxa of ericaceous or pyrolaceous plants in the genera *Cassiope*, *Gaultheria*, *Kalmia*, *Ledum*, *Leucothoe*, *Phyllodoce*, *Rhododendron*, *Vaccinium*, *Pyrola*, and *Chimaphila* were also mycorrhizal. The type and abundance of mycorrhizae appear to depend on as yet undefined ecological factors.

Ectomycorrhizae (including the *Cenococcum* type) or ericoid mycorrhizae are reported for the first time in *Arbutus*, most *Arctostaphylos* spp., *Gaultheria shallon*, *Kalmia polifolia*, *Ledum glandulosum* var. *columbianum*, *Leucothoe daviesiae*, *Rhododendron macrophyllum*, *Vaccinium arbuscula*, *V. ovatum*, *V. scoparium*, *Chimaphila menziesii*, and *Pyrola picta* f. *picta*.

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Entre septembre 1977 et avril 1978, 480 plantes du nord de la Californie appartenant à 27 taxons parmi les Ericaceae et à 5 taxons parmi les Pyrolaceae ont été examinées dans le but d'y vérifier la présence d'ectomycorhizes, de mycorhizes arbutoïdes et de mycorhizes éricoïdes. Parmi ces plantes, 337 éricacées et 8 pyrolacées avaient au moins un type de mycorhize.

Au moins 88% des gros arbustes et des arbres (*Arbutus menziesii* et *Arctostaphylos* spp.) étaient mycorhizés dans diverses localités du nord de la Californie. Parmi les plantes des 22 autres taxons mycorhizés, 67-100% avaient des ectomycorhizes ou des mycorhizes arbutoïdes. Les plantes de 23 taxons appartenant aux genres *Cassiope*, *Gaultheria*, *Kalmia*, *Ledum*, *Leucothoe*, *Phyllodoce*, *Rhododendron*, *Vaccinium*, *Pyrola* et *Chimaphila* étaient aussi mycorhizées. Le type et l'abondance de mycorhizes semblent dépendre de facteurs écologiques non encore identifiés.

La présence d'ectomycorhizes (y compris le type *Cenococcum*) ou de mycorhizes éricoïdes est signalée pour la première fois chez *Arbutus*, la plupart des espèces d'*Arctostaphylos*, *Gaultheria shallon*, *Kalmia polifolia*, *Ledum glandulosum* var. *columbianum*, *Leucothoe daviesiae*, *Rhododendron macrophyllum*, *Vaccinium arbuscula*, *V. ovatum*, *V. scoparium*, *Chimaphila menziesii* et *Pyrola picta* f. *picta*.

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Introduction

Forty taxa in the Pyrolaceae and Ericaceae form an integral part of the coastal, mixed evergreen, montane, and subalpine forests in north central and northwestern California (Munz and Keck 1968; Sawyer and Thornburg 1977; Sawyer et al 1977; Barker 1976; Table 1). Except for *Arbutus menziesii* and *Arctostaphylos uva-ursi* (Trappe 1964; Zak 1973, 1974, 1976a, 1976b) the mycorrhizae of these taxa have not been studied. Accordingly, this paper represents the first reports of mycorrhizae in

most of these taxa and presents the results of a preliminary survey of the types of mycorrhizae of ericaceous and pyrolaceous plants made in northern California between September 1977 and April 1978.

Materials and methods

Roots of 32 taxa of ericaceous and pyrolaceous plants were collected from locations in northern California ranging from California State Highway 128 in the south, the eastern slopes of the Klamath National Forest in the east, the California-Oregon border in the north, and the Pacific Ocean in the west. The exact localities have been placed in the Depository of Unpublished Data.²

Two to three root samples from an individual plant were

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²This information is available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ont., Canada K1A 0S2.

TABLE 1. Ericaceous and pyrolaceous plants located in northern California

Taxa	Months studied
Included in this study	
Ericaceae	
<i>Arbutus menziesii</i> Pursh.	1977: October–November; 1978: January–March
<i>Arctostaphylos canescens</i> Eastw.	1977: November–December; 1978: March
<i>Arctostaphylos columbiana</i> Piper	1977: October–November; 1978: January–March
<i>Arctostaphylos glandulosa</i> Eastw.	1977: December
<i>Arctostaphylos intricata</i> Howell	1978: February
var. <i>oblongifolia</i> (Howell) Munz.	1977: November–December
<i>Arctostaphylos manzanita</i> Parry	1977: October–December
<i>Arctostaphylos nevadensis</i> Gray	1977: November
<i>Arctostaphylos nummularia</i>	1977: October–December; 1978: March
<i>Arctostaphylos patula</i> Greene	1977: October–December; 1978: March
<i>Arctostaphylos uva-ursi</i> (L.) Spring	1977: October
var. <i>coactilis</i> Fern. & Macbr.	1977: December; 1978: January
<i>Arctostaphylos viscida</i> Parry	1977: October
<i>Cassiope mertensiana</i> (Bong.) D. Don.	1977: October
<i>Gaultheria ovatifolia</i> Gray	1977: October
<i>Gaultheria shallon</i> Pursh.	1977: October–November; 1978: January–March
<i>Kalmia polifolia</i> Want.	1977: September–October
var. <i>microphylla</i> (Hook.) Rehd.	1977: September
<i>Ledum glandulosum</i> Nutt.	1977: November
var. <i>californica</i> (Kell.) C. L. Hitchc.	1977: September–October
<i>Ledum glandulosum</i> Nutt.	1977: September–October
ssp. <i>columbianum</i> (Piper) C. L. Hitchc.	1977: September–October
<i>Leucothoe davisciae</i> Torr.	1977: September–October
<i>Phyllodoce empetriformis</i> (Sm.) D. Don.	1977: September–October
<i>Rhododendron macrophyllum</i> D. Don.	1978: January–February
<i>Rhododendron occidentale</i> (T. & G.) Gray	1977: October
<i>Vaccinium arbicula</i> (Gray) Merriam	1977: September–October
<i>Vaccinium membranaceum</i> Dougl.	1977: September
<i>Vaccinium occidentale</i> Gray	1977: October
<i>Vaccinium ovatum</i> Pursh.	1977: October–November; 1978: January–March
<i>Vaccinium parvifolium</i> Sm. in Rees.	1977: October; 1978: January
<i>Vaccinium scoparium</i> Leib.	1977: September; 1978: January–February
Pyrolaceae	
<i>Chimaphila menziesii</i> (R. Br. ex D. Don.)	1977: October; 1978: March
<i>Chimaphila umbellata</i> (L.) Barton	1977: October; 1978: February–March
var. <i>occidentale</i> (Rydb.) Blake	1977: October–November; 1978: March
<i>Pyrola picta</i> Sm. f. <i>picta</i>	1977: October–December
<i>Pyrola picta</i> Sm.	1977: October–December
f. <i>aphylla</i> (Sm.) Camp.	1977: October–December
<i>Pyrola secunda</i> L.	1977: October–December
Excluded from this study	
Ericaceae	
<i>Arctostaphylos cinerea</i> Howell	
<i>A. elegans</i> Jeps.	
<i>A. parvifolia</i> Howell	
<i>A. standfordiana</i> Parry	
<i>Menziesia ferruginea</i> Sm.	
Pyrolaceae	
<i>Moneses uniflora</i> (L.) Gray var. <i>reticulata</i> (Nutt.) Blake	
<i>Pyrola asarifolia</i> Michx. var. <i>bracteata</i> (Hook.) Jeps.	
<i>P. asarifolia</i> var. <i>purpurea</i> (Bunge) Ferm.	

excavated intact, carefully wrapped in damp paper, and enclosed in watertight containers. Specimens were taken to the laboratory within 2 days after collection, and the soil was gently washed from the roots. Several rootlets from each sample were hand sectioned with a razor blade, the sections mounted in Amman's solution, and examined microscopically. Mycorrhizal

roots were preserved in a solution of Craf III and retained for reference.

Each mycorrhiza was classified into one of three general categories. Ectomycorrhizae were defined as having a fungal mantle and Hartig net but no intracellular penetration by the fungal symbiont; arbutoid, if fungal mantle, Hartig net, and

intracellular penetration by the fungal symbiont were all present; ericoid, if septate hyphae were scattered to rare on the surface of the rootlet, a Hartig net was absent, and intracellular penetration by the fungus was present. If a fungal mantle was obvious on the rootlet but a Hartig net was difficult to discern, or if the rootlet examined was heavily tanninized so that intracellular hyphae were difficult to observe, the mycorrhiza was categorized as ectotrophic-arbutoid. Ectotrophic mycorrhizae were further divided into two subtypes, those formed by *Cenococcum geophilum* Fr. (= *C. graniforme* (Sow.) Ferd. & Winge) whose black hyphae form a distinct, easily recognized mycorrhiza (Trappe 1964) and those formed by other fungi. Because vesicular-arbuscular mycorrhizae have not been reported for ericaceous plants (Table 2) and require time-consuming staining techniques, their determination was excluded in the present study.

Root samples of 451 plants from 27 taxa in the Ericaceae and 29 from 5 taxa in the Pyrolaceae were studied for the presence of the three types of mycorrhizae. Eight taxa in these families present in northern California were not included because of their rare occurrence, limited distribution, or difficulty in identification (Table 1).

Results

Of the 451 plants examined in the Ericaceae, 337 possessed mycorrhizae, whereas only 8 of the 29 plants in the Pyrolaceae were mycorrhizal. All taxa, except *Pyrola secunda*, possessed one or more of the three types of mycorrhizae (Table 3).

Ericaceae

The majority of the plants of *Arbutus menziesii* and of the 10 species of *Arctostaphylos* possessed ectomycorrhizae (including *Cenococcum*) or arbutoid mycorrhizae.

Cenococcum-type ectomycorrhizae were observed in *Arbutus menziesii* and in all species of *Arctostaphylos* studied except *A. glandulosa* (with one individual studied) and *A. uva-ursi* (six individuals). These species commonly possessed more than one mycorrhizal type. *Arctostaphylos uva-ursi* has been recorded as a host to *Cenococcum* by Trappe (1964) and Zak (1973). Ericoid mycorrhizae were observed in two species of *Arctostaphylos*, *A. nevadensis*, and *A. patula*.

Half or more of the plants were mycorrhizal in 10 of the other taxa studied. Only one type of mycorrhiza was observed on the two individuals studied of *Cassiope mertensiana* (ericoid), *Gaultheria ovatifolia* (ericoid), and *Rhododendron occidentale* (arbutoid-ectomycorrhiza). In *Vaccinium occidentale* two of the three plants were found to possess mycorrhiza, both ericoid. Three of the plants had ericoid mycorrhizae in *Ledum glanulosum* var. *californicum*. Five of the plants formed mycorrhizae in *Rhododendron macrophyllum* (three ectomycorrhizal and two arbutoid-ectomycorrhizal), six in *Kalmia polifolia* (two ectomycorrhizal and four ericoid), and seven in *Ledum glanulosum* var. *columbianum* (six *Cenococcum*-type

TABLE 2. Previously reported mycorrhizae of ericaceous and pyrolaceous plants (excluding *Cenococcum*-type)

Genus	No. of species examined	Type of mycorrhiza	Reference
<i>Arbutus</i>	2	Arbutoid	Dufrenroy (1964) Rivett (1924) Zak (1974)
<i>Arctostaphylos</i>	1	Arbutoid Ericoid in peat	Menz (1909) Christoph (1921) Friesleban (1933, 1934) Peyronel (1930) Madej (1968) Mejstrik and Hadac (1975) Rayner (1915) Friesleban (1936) Nieuwdrop (1969) Read and Sibley (1973)
<i>Calluna</i>	1	Ericoid	Pearson and Read (1973a, 1973b)
<i>Cassiope</i>	1	Ericoid	Khan (1972)
<i>Epigaea</i>	1	Ericoid	Councilman (1923)
<i>Erica</i>	16	Ericoid	Friesleban (1936) Stalder and Schulz (1957) Nieuwdrop (1969) Robinson (1973) Pearson and Read (1973a, 1973b)
<i>Gaultheria</i>	3	Ericoid	McNabb (1961) Khan (1972)
<i>Kalmia</i>	2	Ericoid	Friesleban (1936)
<i>Ledum</i>	2	Ericoid	Friesleban (1936) Bain (1937)
<i>Leiophyllum</i>	1	Ericoid	Friesleban (1936)
<i>Menziesia</i>	2	Ericoid	Friesleban (1936)
<i>Pernettya</i>	2	Ericoid	Friesleban (1936) Brook (1952) Morrison (1957) McNabb (1961)
<i>Pyrola</i>	?	Arbutoid	Christoph (1921) Luck (1940, 1941) Khan (1972)
<i>Rhododendron</i>	2	Ericoid	Lihnell (1942) Gordon (1937) Khan (1972)
<i>Vaccinium</i>	10	Ericoid Arbutoid in one	Rayner (1915, 1929) Doak (1928) Hasselbaum (1931) Friesleban (1934) Bain (1937) Nieuwdrop (1969) Pearson and Read (1973a) Sibley and Read (1974a, 1974b, 1975, 1976)

TABLE 3. Types of mycorrhizae in ericaceous shrubs and pyrolaceous plants of northern California

	No. of plants examined	No. of plants with one or more than one mycorrhiza	Total no. observed	ECT				ER	None
				Other	Cen	AR	AR/ECT		
<i>Arbutus menziesii</i>	55	6	55	7	16	24	8	0	6
<i>Arctostaphylos canescens</i>	13	1	13	2	5	2	4	0	1
<i>Arctostaphylos columbiana</i>	47	4	51	5	5	34	7	0	0
<i>Arctostaphylos glandulosa</i>	1	0	1	0	0	0	1	0	0
<i>Arctostaphylos intricata</i>	21	3	24	6	6	11	1	0	0
<i>Arctostaphylos manzanita</i>	18	2	21	4	4	6	7	0	0
<i>Arctostaphylos nevadensis</i>	44	2	45	5	7	16	16	1	1
<i>Arctostaphylos nummularia</i>	1	0	1	1	0	0	0	0	0
<i>Arctostaphylos patula</i>	52	13	66	12	8	30	13	3	2
<i>Arctostaphylos uva-ursi</i>	6	0	6	1	0	4	1	0	0
<i>Arctostaphylos viscida</i>	10	2	11	1	3	4	3	0	1
<i>Cassiope mertensiana</i>	2	0	1	0	0	0	0	1	0
<i>Gaultheria ovatifolia</i>	2	0	1	0	0	0	0	1	1
<i>Gaultheria shallon</i>	29	0	11	2	1	1	2	5	18
<i>Kalmia polifolia</i>	9	0	6	2	0	0	0	4	3
<i>Ledum glandulosum</i> var. <i>californica</i>	5	0	3	0	0	0	0	3	0
<i>Ledum glandulosum</i> ssp. <i>glandulosum</i>	8	1	7	0	6	0	0	1	2
<i>Leucothoe davisiae</i>	21	0	15	0	6	3	0	6	6
<i>Phyllodoce empetriformis</i>	14	0	4	0	0	0	0	4	10
<i>Rhododendron macrophyllum</i>	6	0	5	2	1	0	2	0	1
<i>Rhododendron occidentale</i>	2	0	1	0	0	0	1	0	0
<i>Vaccinium arbustula</i>	17	0	8	2	0	0	0	6	9
<i>Vaccinium membranaceum</i>	4	0	2	0	0	0	0	2	2
<i>Vaccinium occidentale</i>	3	0	2	0	0	0	0	2	1
<i>Vaccinium ovatum</i>	37	0	16	0	8	1	3	4	21
<i>Vaccinium parvifolium</i>	8	0	2	1	0	0	0	1	6
<i>Vaccinium scoparium</i>	17	0	3	0	2	0	1	0	14
<i>Chimaphila menziesii</i>	2	0	2	0	0	1	1	0	0
<i>Chimaphila umbellata</i>	15	0	3	2	0	0	0	1	12
<i>Pyrola picta</i> f. <i>picta</i>	8	0	2	0	0	1	0	1	6
<i>Pyrola picta</i> f. <i>aphylla</i>	1	0	1	0	0	0	0	1	0
<i>Pyrola secunda</i>	3	0	0	0	0	0	0	0	3

NOTE: ECT, ectomycorrhizae; AR, arbutoid; AR/ECT, arbutoid or ectomycorrhizae; ER, ericoid; Cen, *Cenococcum geophilum*.

and one ericoid). In *Leucothoe davisiae*, 15 of 21 plants had mycorrhizae of all three types.

In four of the other taxa studied, 26–41% of the plants were mycorrhizal. In *Vaccinium arbustula*, 8 of 17 plants had mycorrhizae (6 ericoid and 2 ectomycorrhizal). In *Gaultheria shallon*, 11 of 29 plants were found to have mycorrhizae, whereas in *Vaccinium ovatum*, 16 of 37 plants possessed mycorrhizae. In each of these species, all three types of mycorrhizae were observed. In *Phyllodoce empetriformis*, 4 of the 14 plants possessed ericoid mycorrhizae.

Only 2 of 8 plants in *Vaccinium parvifolium* and 3 of 17 plants in *V. scoparium* possessed the types of mycorrhizae studied. In the former species, one mycorrhiza was ericoid and one ectotrophic, whereas in the latter species two mycorrhizae were

of the *Cenococcum*-type and one was ectomycorrhiza-arbutoid.

Pyrolaceae

Five taxa in the Pyrolaceae were examined; four possessed at least one of the three types of mycorrhizae. In *Chimaphila menziesii* and *Pyrola picta* f. *aphylla*, all plants studied were mycorrhizal. In *Pyrola picta* and *Chimaphila umbellata*, very few of the plants possessed mycorrhizae.

Discussion and conclusion

Excluding *Gaultheria* and *Rhododendron* species, it appears that all of the larger ericaceous shrubs or trees in northern California, i.e., *Arbutus menziesii* and *Arctostaphylos* spp., possess either ectomycorrhizae or arbutoid mycorrhizae. Except

for *Arctostaphylos glandulosa*, all species of *Arctostaphylos* and *Arbutus* were found to form more than one type of mycorrhiza in certain as yet undefined ecological situations.

The ericaceous and pyrolaceous plants in the genera *Cassiope*, *Kalmia*, *Ledum*, *Leucothoe*, *Phyllodoce*, *Vaccinium*, *Chimaphila*, and *Pyrola*, as well as the genera containing shrubby plants, *Gaultheria* and *Rhododendron* appear to be mycorrhizal. The type of mycorrhiza and its abundance appears to depend on unknown ecological factors. Even though many of these taxa possessed neither ectomycorrhizae, arbutoid, nor ericoid mycorrhizae, they may form vesicular–arbuscular mycorrhizae. Consequently, these species need further study before any conclusion can be made about their type of mycorrhizal association.

Previous reports indicate that ericaceous shrubs or subshrubs in *Arbutus*, *Arctostaphylos*, and *Pyrola* possess arbutoid mycorrhizae, and those in *Gaultheria*, *Kalmia*, *Ledum*, *Rhododendron*, and *Vaccinium* are ericoid (Table 2). Two exceptions to this generality exist, a report of an arbutoid mycorrhiza in *Vaccinium* and an ericoid mycorrhiza in *Arctostaphylos*. Our study reveals that ericoid mycorrhizae do occur in some species of *Arctostaphylos* but that they are rare.

Previously unreported arbutoid mycorrhizae occur in *Gaultheria shallon* as well as in *Vaccinium ovatum* and may occur in *Rhododendron macrophyllum*, *R. occidentale*, and *Vaccinium scoparium*.

Ectomycorrhizae (excluding the *Cenococcum*-type) have rarely been reported from ericaceous shrubs or subshrubs, but in northern California they were found in *Arbutus menziesii*, all 10 species of *Arctostaphylos*, and in *Gaultheria shallon*, *Kalmia polifolia*, *Rhododendron macrophyllum*, *Vaccinium arbuscula*, and *V. parvifolium*. *Cenococcum*-type ectomycorrhizae have been reported from *Arbutus menziesii* (Trappe 1964) and *Arctostaphylos uva-ursi* (Zak 1976). In northern California they form on all species of *Arctostaphylos* (except *A. glandulosa* in which only one plant was studied), as well as on *Gaultheria shallon*, *Ledum glandulosum* ssp. *columbianum*, *Leucothoe davisiae*, *Rhododendron macrophyllum*, *Vaccinium ovatifolia*, and *V. scoparium*.

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