

New England Plant Conservation Program

Pterospora andromedea Nutt.
Pinedrops

Conservation and Research Plan
for New England

Prepared by:
Alice Schori
Canaan, New Hampshire

For:

New England Wild Flower Society
180 Hemenway Road
Framingham, MA 01701
508/877-7630
e-mail: conserve@newfs.org • website: www.newfs.org

Approved, Regional Advisory Council, 2002

SUMMARY

Pterospora andromedea Nuttall (pinedrops) is a nonphotosynthetic, perennial (or possibly long-term monocarpic) member of the myco-heterotrophic subfamily Monotropoideae of the Ericaceae (Heath family). The New England populations of this plant are found in coniferous or mixed woods over limestone or rich clay. The genus is monotypic and is endemic to North America. It is not uncommon in the western cordillera where it ranges from southern Canada to Mexico. A separate population encompasses an area extending from northern Michigan and Wisconsin, through Ontario, to Québec, the maritime provinces, New York and New England.

In New England, *Flora Conservanda* lists the species as Division 2, a regionally rare taxon with fewer than 20 occurrences seen since 1970. The only currently known populations in New England are one occurrence in New Hampshire and two in Vermont. Historically, it was more widespread in Vermont, and there was an unverified report of a collection from Massachusetts in the 1800's. Factors contributing to the rarity of the species include: normally very small population size; loss of habitat; reliance on a specific fungal host; and probably unknown factors affecting the distribution and abundance of the fungus on which it depends. Overcollection, acid precipitation, and fire suppression may also be factors in its decline.

The highest conservation priority is to permanently protect existing populations and, if necessary, manage their habitats. Monitoring and close observation of existing populations may contribute to an understanding of population dynamics and to pollinator identification. Development of a better understanding of specific habitat needs and identification of appropriate habitat in New England are essential to the search for as yet undiscovered populations and to any possible future reintroduction efforts. Research leading to better knowledge of the distribution and habitat requirements of the associated fungus (or fungi) should also be supported. Currently, techniques for successful propagation have not been developed, so an important conservation goal is support of propagation research being done in the West.

PREFACE

This document is an excerpt of a New England Plant Conservation Program (NEPCoP) Conservation and Research Plan. Because they contain sensitive information, full plans are made available to conservation organizations, government agencies and individuals with responsibility for rare plant conservation. This excerpt contains general information on the species biology, ecology, and distribution of rare plant species in New England.

NEPCoP is a voluntary association of private organizations and government agencies in each of the six states of New England, interested in working together to protect from extirpation, and promote the recovery of the endangered flora of the region.

In 1996, NEPCoP published "*Flora Conservanda: New England*," which listed the plants in need of conservation in the region. NEPCoP regional plant Conservation Plans recommend actions that should lead to the conservation of Flora Conservanda species. These recommendations derive from a voluntary collaboration of planning partners, and their implementation is contingent on the commitment of federal, state, local, and private conservation organizations.

NEPCoP Conservation Plans do not necessarily represent the official position or approval of all state task forces or NEPCoP member organizations; they do, however, represent a consensus of NEPCoP's Regional Advisory Council. NEPCoP Conservation Plans are subject to modification as dictated by new findings, changes in species status, and the accomplishment of conservation actions.

Completion of the NEPCoP Conservation and Research Plans was made possible by generous funding from an anonymous source, and data were provided by state Natural Heritage Programs. NEPCoP gratefully acknowledges the permission and cooperation of many private and public landowners who granted access to their land for plant monitoring and data collection. If you require additional information on the distribution of this rare plant species in your town

This document should be cited as follows:

Schori, Alice. 2002. *Pterospora andromedea* Nutt. (Pinedrops) New England Plant Conservation Program Conservation and Research Plan for New England. New England Wild Flower Society, Framingham, Massachusetts, USA. <http://www.newfs.org>.

© 2002 New England Wild Flower Society

I. BACKGROUND

INTRODUCTION

Pterospora andromedea Nuttall (pinedrops) is a perennial (or possibly long-term monocarpic) member of the myco-heterotrophic subfamily Monotropoideae of the Ericaceae (Heath family). The genus *Pterospora* is monotypic, consisting of one species, *P. andromedea*, and is endemic to North America, ranging from southern Canada to Mexico. The species is widespread in the Rocky Mountains and West (Wallace 1975a). A separate population center encompasses an area extending from northern Michigan and Wisconsin, through Ontario, to Québec, the maritime provinces, New York and New England. The only currently known populations in New England occur in New Hampshire and Vermont. Historically it was more widespread in Vermont, and there was a report of a collection from Massachusetts in the 1800's (Tuckerman and Frost 1875).

In New England, *Pterospora andromedea* is accorded the state ranks of S1 or SX. Its recent rediscovery in New Hampshire will change its rank there from SX to S1. Its global rank is G5 (demonstrably widespread, abundant, and secure globally, though it may be quite rare in parts of its range, especially at the periphery). The eastern population appears to be in decline region-wide. In *Flora Conservanda*, it is listed as Division 2, a regionally rare taxon with fewer than 20 occurrences (seen since 1970) in New England (Brumback and Mehrhoff et al. 1996). Except in Québec, which has several sites with large numbers of flowering stems, the plant seems to occur in very small, scattered populations. It is probably threatened mainly by loss of habitat and perhaps by unknown factors affecting the distribution and abundance of the species of mycorrhizae on which it depends. It is likely that overzealous collection of herbarium specimens contributed to its decline. Acid precipitation, fire suppression, and herbivory by deer have all been postulated as factors in its decline.

This conservation plan summarizes available information about the taxonomy, ecology, extant and historic occurrences, and conservation status of *Pterospora andromedea* in New England. It also presents proposed actions to secure the long-term survival of the species in New England.

DESCRIPTION

The genus *Pterospora* is monotypic. The following is a combined generic and specific description drawn from Copeland (1941), Fernald (1950), Bakshi (1959), Wallace (1975a), Gleason and Cronquist (1991), and Wallace (in Hickman 1993).

Pterospora andromedea Nuttall, also known as pinedrops, Albany beech-drops, or giant bird's nest, is a nonphotosynthetic, perennial or possibly long-term monocarpic

myco-heterotroph. The name *Pterospora* (from Greek *pteros*, a wing, and *spora*, seed) refers to the tiny (less than 0.2 mm in diameter) seeds with a broad, rounded, reticulated, membranous terminal wing less than 1 mm wide. The specific epithet *andromeda* alludes to the similarity of the nodding flowers to those of *Andromeda*.

According to various authors, the root mass of *Pterospora* may be perennial or it may be long-term monocarpic (taking several years to develop before the plant can flower). It forms a dense, globular clump rarely more than 7 cm in diameter. The root mass lies within 10-40 cm of the soil surface, usually in or at the top of the A₁ horizon. The brittle but fleshy, irregularly branched roots, 1-2 mm in diameter, seldom reach 2 mm in length before branching. Roots are entirely sheathed by their associated mycorrhizal fungus, so that there is no actual contact between roots and soil. Bakshi (1959) reported that some roots elongate, forming additional root-balls at intervals of 3-8 cm. Floral axes generally extend relatively straight up from the root mass, rather than curving around from the underside.

The above-ground part of the plant is a tall, unbranched, wand-like, racemose inflorescence, reportedly up to two meters, but usually one meter or less in height. New England specimens, dried and live, observed by this author tend to be on the small side, mostly under 50 cm and none exceeding 65 cm. Western plants are usually 70 to 100 cm tall. Stems are erect, stout (usually 0.5 to 1.5 cm in diameter below the lowermost flowers), tough, pink to reddish or purplish, eventually turning brown. A useful diagnostic feature that distinguishes it from other monotropes is the stickiness of the surface, which has been described as clammy-pubescent or glandular-pubescent. Thick, sessile, triangular to lanceolate structures along the stem have been variously described as leaves, scales, or sterile bracts. At the base of the stem, the scales are relatively large, broad-based, and overlapping, but they become smaller and scattered above. Bakshi (1959) makes a distinction between leaves with a few stomata on the undersides and bracts with no stomata.

Flowers are borne on slender, downcurved, glandular pubescent pedicels that become rigid when dry. Each is subtended by a narrow, lanceolate, glandular pubescent bract with finely ciliate margins. Fascicles of two to five pedicels may occur, but more commonly single pedicels are distributed more or less equally around the axis of the raceme. The calyx is composed of five persistent, glandular pubescent, pink to reddish, lance-ovate sepals. The glabrous, globular-urceolate (urn-shaped), yellow to cream to pinkish-white corolla has five short, rounded, recurved lobes that are free for 1/4 or less of their length. Each of the 10 stamens, 3-5 mm long, has a glabrous, flattened filament with an expanded base. Anthers are basifixed, about 1 mm in diameter, and have two awns or horns directed toward the corolla. The ovary is superior, 5-locular, with axile placentation. The discoid, 5-lobed stigma is borne on a short (<3 mm), columnar style.

Capsules are pendent, depressed-globose, 5-lobed, <13 mm in diameter, and loculicidal, opening from the morphological base to the tip. Bakshi (1959) reported 20 to 128 capsules per plant, with 2000 to 4000 seeds per capsule, and a weight of 0.0005 g per 100 seeds.

TAXONOMIC RELATIONSHIPS, HISTORY, AND SYNONYMY

Pterospora andromedea was first described by Nuttall (1818) as collected “[i]n Upper Canada, near the Falls of Niagara. Mr. C. Whitlow.” The type specimen being unknown, a neotype was designated by Wallace (1975a): USA, California, Butte Co., Jonesville, 15 July 1931, E. B. Copeland 668, RSA; duplicates at BN, CAS, DS, MO, NY, ORE, P, UC.

A description of *Monotropa procera* Torrey ex Eaton, based on material collected by Dr. James near Albany, New York, was published a few months after Nuttall’s description of *Pterospora* (Wallace 1975a). No other synonyms are known.

Four varieties of *Pterospora* were listed by Rafinesque in 1830, based on material sent to him from America. They were:

- *P. andromedea* Nuttall var. *flavicaulis* Rafinesque
- *P. andromedea* Nuttall var. *leucorhiza* Rafinesque
- *P. andromedea* Nuttall var. *elatior* Rafinesque
- *P. andromedea* Nuttall var. *pauciflora* Rafinesque

All are now considered invalid (Wallace 1975a). Wallace states emphatically that no valid subspecific entities have been described (Gary Wallace, Rancho Santa Ana Botanic Garden, personal communication).

Pterospora andromedea belongs in the subfamily Monotropoideae (Indian Pipe subfamily) of the Ericaceae (Heath family). All members of the subfamily, which includes only 13 species in 10 genera (eight of them monotypic) (Wallace 1975a and 1987), are non-photosynthetic mycorrhizal epiparasites (myco-heterotrophs) that associate with five distantly related families of ectomycorrhizal basidiomycete fungi (Bidartondo and Bruns 2002). The only other monotropoid genus that occurs in New England is *Monotropa*, which is represented here by *M. uniflora* (indian pipe) and *M. hypopithys* (pinesap). *Pterospora*’s closest “sister taxon” is the spectacular snow plant, *Sarcodes sanguinea* (Bidartondo and Bruns 2001), which occurs only in the West, from Oregon to northern Baja California (Wallace 1975a).

According to Wallace (1975a), the Monotropoideae have usually been treated as a unit, but have been placed in various families by various authors. Nuttall (1818) put them in a separate family, the Monotropaceae, and that treatment will likely be used, in spite of Wallace’s objections, in the next edition of Flora of North America (Wallace, personal communication). Drude (1889, cited in Wallace 1975a) included them as a subfamily of Pyrolaceae. Henderson (cited in Wallace 1975a), in her 1919 comparative study of Pyrolaceae and Monotropaceae, recategorized them as a subfamily of Ericaceae. The latter placement (subfamily Monotropoideae in family Ericaceae) is favored by experts currently studying the group (Gary Wallace, personal communication; Wallace 1975a, 1975b, Cullings and Bruns 1992, Bidartondo and Bruns 2001). Their closest

relatives are the Arbutioideae, another subfamily of Ericaceae (Wallace 1975b, Bidartondo and Bruns 2001).

SPECIES BIOLOGY

Myco-heterotrophy

Members of the Monotropeoideae were long believed to be saprophytes (deriving their nutrients from decaying plant matter), symbiotic saprophytes (having a mutualistic association with saprophytic fungi), or root parasites of autotrophs (deriving nutrients directly from roots of photosynthetic plants). Bakshi (1959) reviewed authors adhering to the various points of view regarding *Pterospora*. Many subscribed to the saprophyte model, which may have originated with a suggestion by Luxford, in 1842, that *Monotropa* derives nutrients from the humus around it. The symbiotic saprophyte theory was proposed by MacDougal in 1899 and MacDougal and Lloyd in 1900. Bakshi (1959) lists many other authors of floras and botany books published between 1900 and 1957 who regarded *Pterospora* as a root parasite.

As early as 1884, Kamienski (cited in Bakshi 1959) established the fact that roots of *Monotropa hypopithys* had no direct contact with soil and are not root parasites. In 1892, Frank (cited in Bakshi 1959) proposed the theory that it was parasitic on fungus, a view promoted by Bakshi (1959). A major advance in the understanding of the relationship was made by Björkman (1960) and Furman (1966, cited in Furman and Trappe 1971), whose radiotracer work in the 1960's demonstrated the movement of materials between photosynthetic and achlorophyllous plants (*Monotropa hypopithys* and *M. uniflora*) via their mycorrhizal fungal connection. In fact, Furman and Trappe (1971: 223) declared:

The approximately 400 mycotrophic achlorophyllous angiosperms are not saprophytes. Rather, they depend, for the most part, on parasitism of their mycorrhizal fungi. Since they are unable to survive without the fungal associate, they are best regarded as the highly specialized and most dependent components of an anatomically linked system of interacting plants. The designation, "most dependent," is appropriate because the fungus component can obtain nutrients and possibly carbohydrates, in some cases, directly from soil or organic matter. The green plant component, which usually appears to be part of the system, produces its own photosynthates. The achlorophyllous angiosperm, at least in the case of *Hypopitys* [sic] and *Monotropa*, is quite incapable of adequately performing either of these functions.

Luoma (1987) pointed out the possible confusion associated with the use of the term "mycotrophic." The term could be strictly applied to organisms that depend on fungi for all of their energy, but it has long been used interchangeably with "mycorrhizal." To clarify the distinction between mycorrhizal autotrophs (green plants with mycorrhizal associations) and mycorrhizal heterotrophs (generally achlorophyllous plants that depend on their associated mycorrhizal fungi as their carbon source), Leake

(1994) used the term “myco-heterotroph.” This terminology has been adopted by other researchers studying mycorrhizal associations (Smith and Read 1997, Bruns and Read 2000, Bidartondo and Bruns 2002).

Björkman’s (1960) experiments with *Monotropa hypopithys* showed that some myco-heterotrophs can strongly stimulate growth of their fungal symbionts. Studies of *Sarcodes sanguinea* (Bidartondo et al. 2000) in nature revealed that this myco-heterotroph seems to stimulate formation of clumps of its associated fungus and roots of its host tree (*Abies magnifica*). Such studies have not yet been reported for *Pterospora*. Nevertheless, it seems that some stimulation of at least the fungal partner must occur, since exploiters of mycorrhizae are actively colonized by the hyphae of their associated fungi (Robertson and Robertson 1982, Bidartondo and Bruns 2002). No clear evidence exists to show whether or not this stimulation is of benefit to the fungus. Thus, the question of whether the relationship is purely parasitic or to some, perhaps small, degree mutualistic remains unresolved, and the term “myco-heterotroph” seems preferable to “myco-parasite.”

Leake (1994) wrote an exhaustive review of the biology of myco-heterotrophs. He summarized evidence of convergent evolution among 87 genera of achlorophyllous plants. Notable features include:

- **reduction in the size** of seed and embryo and the lack of differentiation of embryo at maturity;
- **very large number of seeds** per flower and adaptation for wind dispersal;
- **adaptation to subterranean life**, with a change in function from organs of absorption to organs of storage, shown by the loss of root hairs;
- **reduction of leaves** to achlorophyllous scales on the inflorescence axis;
- **germination dependent on infection** by an appropriate symbiotic fungus;
- **asexual as well as sexual reproduction**; and
- **tendency toward small inflorescences**, often with a single terminal flower.

Except for the tendency toward small inflorescences, all of these traits are apparent in *Pterospora*.

Cummings and Welschmeyer (1998) corrected the assertion that all of these plants are entirely achlorophyllous, using high-performance liquid chromatography to demonstrate that many putatively achlorophyllous species, including *Pterospora andromedea*, do, in fact, produce at least trace amounts of chlorophyll a. Whether chlorophyll is a precursor or byproduct of other biochemical pathways or serves some non-photosynthetic function in these plants is not known. Since proportions of chlorophyll and related pigments found in this study were on the order of 1×10^{-9} to 10^{-7} , compared with 1×10^{-2} in a green leaf, it seems safe to say that *Pterospora* is non-photosynthetic.

Lutz and Sjolund (1973), Duddridge and Read (1982), and Robertson and Robertson (1982) all studied the ultrastructure of the fungal sheaths that develop around growing roots of various species of Monotropoideae and discovered that they are distinct from that of arbutoid mycorrhizae. Duddridge and Read named them “monotropoid” mycorrhizae. A concise summary of their distinctive features is given in Leake (1994).

Great strides in understanding the mycorrhizal association of *Pterospora* and other monotropes have been made possible in recent years through the use of DNA analysis. Although molecular sequencing is time-consuming and expensive, it makes it possible to characterize fungal mycelia in the absence of fruiting bodies (sporocarps). Through comparison with named sporocarp collections, mycorrhizal fungus species, or at least genera, can now be identified. Since fungi tend to fruit only when conditions are just right and hypogeous types (fruiting underground, like truffles) are especially hard to find, the ability to identify them by their mycelia is truly an exciting breakthrough.

Cullings et al. (1996) were the first to use this technology to make the unexpected discovery that *Pterospora* appeared to associate with a single species group of basidiomycetes known as *Rhizopogon subcaerulescens*. More recent and more extensive analysis by Bidartondo and Bruns (2001, 2002) indicates that it is more likely that there are two distinct lineages of *Pterospora* in the West, one of which associates exclusively with the *Rhizopogon arctostaphyli* species group, the other exclusively with the *R. salebrosus* species group (previously referred to as *R. subcaerulescens*). A single sample of *Pterospora* obtained from Québec was apparently associated with an as yet undescribed fungus from the *Rhizopogon* section *Amylopogon* lineage. The genus *Rhizopogon* is taxonomically challenging (Kretzer et al. 2000, Bidartondo and Bruns 2002), so it is likely that further refinements of our knowledge of these associations will be forthcoming. It is also possible that lineages of *Pterospora* with other associates in *Rhizopogon* or other fungal genera will be identified.

Reproduction and Phenology

Bruns and Read (2000) have shown that, at least under laboratory conditions, stimulation by *Rhizopogon* fungus is necessary to initiate germination of *Pterospora* seeds. Direct fungal contact was not necessary, suggesting that an unknown volatile or diffusible compound produced by the fungus may be the required stimulus. It is interesting that seeds respond to a broader range of *Rhizopogon* species than have been observed in association with mature plants.

Martin Bidartondo (University of California at Berkeley, personal communication) is currently experimenting with seed placed in mesh bags and buried in the ground in the Sierra Nevada. So far, he has observed extremely low germination rates (on the order of one per several thousand seeds), but apparently successful growth of the few that germinate. After one year, he found seedlings with root axes with one to three branch initials but no “shoot.” This slow growth at the earliest stage gives some credence to the notion postulated by Leake (1994) that myco-heterotrophs may take many years to progress from germination to flowering. Results from Bidartondo’s

ongoing study may help clarify this part of the plant's life cycle, which, until now, has been a matter of pure speculation. The lack of a shoot in Bidartondo's seedlings is really no surprise, since *Pterospora* probably needs to build a root mass with sufficient reserves before it can expend (or successfully tap into) the energy necessary to send up a flower stalk.

Other aspects of *Pterospora*'s underground behavior are also mysterious. It has been reported that the species is variable in its occurrence and may not appear aboveground each year (Higman and Penskar 1999). Leake (1994) notes that flowering of myco-heterotrophs is often highly erratic and mentions one (the ghost orchid, *Epipogium aphyllum*) that can disappear for 30 years between successive flowering episodes at the same site! No one seems to know how long an individual *Pterospora* plant may live or how many years may pass between flowerings. This can make it very difficult to determine whether a particular population is extant and "dormant" or whether it has died out.

It is unclear how long a particular root mass of *Pterospora* may live. Wallace (1975a) called the root mass perennial. Bidartondo (personal communication) agrees that it is usual to see at least two consecutive blooming years from one root mass. Bakshi (1959) reported finding some to be perennial, others annual. (The latter term may have been used mistakenly in reference to long-term monocarpic individuals). He also reported finding multiple root balls connected by horizontal roots, suggesting that vegetative reproduction takes place. If this observation is accurate, it raises the possibility that a series of interconnected root balls, each taking years to develop, could account for the sporadic disappearance and reappearance of a plant at approximately the same location.

On the other hand, Bidartondo (personal communication) finds that the roots form such a tangled mass, with "wildly abundant" fungus and "an unbelievable amount of tree mycorrhizal roots," that it is impossible to see connections. He believes that only genetic studies can reveal whether neighboring plants are clones. He states that a single root mass in the Sierra Nevada can have more than 10 fully developed inflorescences plus several immature buds, but speculates that such a root mass may contain multiple individuals. He suggests that the idea postulated by Jepson (1939), that *Pterospora* is monocarpic, blooming only once after a prolonged period of root development, has not been disproved.

When *Pterospora* flowers, it can be quite impressive, with the red stalk and many cream-colored flowers. It can bloom from late June through August. In New Hampshire, five stalks with developing flowers and three others just emerging from leaf litter were observed on 10 July 2001. Eight more stalks emerged at the site over the remainder of the season (personal observation). Bakshi (1959) states that the first flowers do not open until the shoot is about four weeks old. He also observed that after fertilization, the capsules take two to three weeks to mature. The tough, dried stalk is observable well into the winter here, and, if not knocked over, can persist for a year or more.

Little is known about pollination of *Pterospora* flowers. Wallace (1977) studied the nectaries of the Monotropoideae. Although no insects were observed visiting the species, he thought the anatomy of the flower suggests that bumblebees may be the pollinators. Bakshi (1959) noted that pollen dispersal does not take place until the stigma of the same flower is receptive, so self-pollination is a distinct possibility.

Bakshi (1959) tested viability of *Pterospora* seed stored at 4° C and at 21° C under both dry and moist conditions. He found the seed to be viable (as determined by chemical tests) for only nine weeks or less. Perhaps because of the difficulty of getting *Pterospora* seeds to germinate, it seems that no one else has tested other methods of seed storage or preservation. Likewise, there is no information about seed dormancy or viability in the soil. Leake (1994) speculated that there may be little need for seed longevity, since seeds are dispersed at the very time when mycorrhizal fungi are particularly active.

Leake (1994) stated that *Pterospora*'s tall, lignified stalk is unusual among myco-heterotrophs. Wallace qualifies Leake's assertion by stating that all species in Monotropoideae have persistent, lignified stalks (personal communication). Nevertheless, *Pterospora* can attain much greater heights than other species in the subfamily, and is, as Leake noted, ideally suited for dispersal of the tiny, wind-borne seeds. Leake also remarked that *Pterospora*, with some of the most advanced adaptations for wind dispersal of its tiny, winged seeds, has the widest distribution of any endemic North American species of Monotropoideae.

Size of Occurrences

It has generally been believed that *Pterospora* occurs in scattered, small patches of only a few stems at any one location throughout its range (Bakshi 1959, Wallace 1977), but Voss alluded to reports of "great quantities" in the Great Lakes region (1996, cited in Higman and Penskar 1999). It is likely that this is a reference to some amazing populations in Québec. André Sabourin (independent botanist) and Frédéric Coursol (of Flora Québécoise) (personal communications) report several populations of 100 or more stems along the Ottawa River Valley, including a limestone island with a population of 500 stems.

Predation and Disease

Almost nothing has been written about predation or diseases affecting *Pterospora*. Bakshi (1959) mentioned that deer may occasionally nip the tip of a flowering stalk, but Leake (1994) postulated that pigments and tannins in myco-heterotrophs probably serve to render the plants unpalatable to herbivores. There is no mention of herbivory in records of New England occurrences. A reference to "two

aborted flowering stalks” at the West Haven, VT, site on August 16, 1990, gives no indication of possible cause.

HABITAT/ECOLOGY

It is impossible to understand the needs of *Pterospora* without knowing something about the requirements of its mycorrhizal partner(s). According to Bidartondo (personal communication), the *Rhizopogon* species associated with *Pterospora* are high-nutrient-loving, fire-adapted, disturbance-tolerant, truffle-like basidiomycetes that are dispersed by rodents. They are exclusively associated with roots of conifers in Pinaceae. Based on the paucity of herbarium specimens, he also believes that they may be very rare in the East. Smith and Zeller (1966) also believed that most *Rhizopogon* species are rare, difficult to find, and highly restricted in their distribution. They speculated that each may be associated with a single conifer species or genus. They also reported that *Rhizopogon* species appear to prefer well-drained soil and are not found in boggy areas. Molina et al. (2001) bemoaned the difficulty of surveying rare fungi because of the lack of understanding of even well-known fungal groups and the scarcity of fungal taxonomists.

Habitat types for eastern populations of *Pterospora* vary, but must be related in some as yet unknown ways that make them hospitable to *Rhizopogon* species. Clearly, one essential requirement is the presence of some member of the Pinaceae. The ranges of both *Pinus strobus* (white pine) and *Tsuga canadensis* (eastern hemlock), as shown in Harlow et al. (1991), encompass the eastern distribution of *Pterospora*, which is centered around the Great Lakes and includes an area extending from northern Michigan and Wisconsin, through Ontario, to Québec, the maritime provinces, New York and New England. In New Brunswick, *Pterospora* reportedly occurs in mature white pine forests (Hinds 2000). In Québec, *Pterospora* is apparently associated with *Pinus strobus* (white pine) (André Sabourin, personal communication). In Michigan, *Pterospora* typically occurs in dry to dry-mesic conifer forests with well-developed needle duff, although two occurrences have been reported from maple forests (Higman and Penskar 1999). In reference to these reports, Penskar noted that, “even in mesic northern forest, there are conifer associates, usually something like white pine” (personal communication via Bidartondo). White pine is common in the area of the three New Hampshire occurrences (extant and historic) and occurs at both extant Vermont occurrences. Records from two historic occurrences in Vermont mention “pines” or *Pinus strobus*, but other known herbarium records from that state contain no mention of associated species. It is unclear whether or not there could be more than one genetic lineage in the East, associated with other species of *Rhizopogon* and other members of Pinaceae.

Possible Glacial Influence

Comparison of maps reveals that all of the Vermont occurrences of *Pterospora*, extant and historic, have been in areas shown by Johnson (1998) to have been inundated by Lake Vermont during the retreat of the Wisconsin glacier about 12,500 years ago.

Known extant and historic occurrences in New Hampshire have been in the Lebanon-Hanover area on sediments deposited in the slightly more recent Lake Hitchcock, which was formed by the retreating glacier when the Connecticut River was dammed by a moraine in what is now the state of Connecticut.

Studies of clay deposits left in the Northeast by the retreating glacier show that the Ottawa River region of Québec, where the largest populations of *Pterospora* are found, was subject to similar inundation and sedimentation (Antevs 1928). Antevs' maps do not provide much detail about more easterly regions, but parts of the maritime provinces probably share a similar history. Michigan occurrences of *Pterospora* are mostly on sand dunes along the Great Lakes shorelines (Higman and Penskar 1999), and Ontario occurrences have all been near or between the Great Lakes (Haber and Keddy 1984).

Bakshi (1959) stated that the eastern population distribution of *Pterospora* does not extend south of the limits of Wisconsin glaciation. Further analysis could help clarify in more detail whether all or most extant and historic occurrences within the eastern population have been in areas influenced by inundation and sedimentation, and whether sediments with small particle size favor *Pterospora* and its mycorrhizal associate(s).

Bedrock and Soils

The two known extant occurrences of *Pterospora* in Vermont are in dolomitic areas on or at the base of north slopes (according to Vermont Nongame and Natural Heritage Program records). The site at the base of a steep slope has very clayey soil (personal observation). New Hampshire (personal observation) and some Québec occurrences (André Sabourin, personal communication) also occur on clay soils. Other Québec populations occur over limestone or marble (André Sabourin, personal communication). One New York occurrence was on a limestone island and many were in areas of shale (Steve Young, New York Natural Heritage Program, personal communication). Although some are undoubtedly nutrient-rich or calcareous areas, not enough information is available to generalize about others. There are also unconfirmed reports of *Pterospora* for northern Cape Breton Island in Nova Scotia in a somewhat calcareous area (Sean Blaney, Atlantic Canada Conservation Data Centre, personal communication).

It is notable that many or most eastern occurrences are reportedly from clay or other glacial lake deposits or from limestone, marble, or shale bedrock areas. According to Scott Bailey (Hubbard Brook Experimental Forest, personal communication), a unifying feature of these areas may be small particle size (silt and clay) and high cation exchange capacity or base saturation, leading to availability of calcium, magnesium, and potassium. This is consistent with Bidartondo's assertion that *Rhizopogon* species are high-nutrient-loving (personal communication). However, it seems to contradict commonly-held opinions about the Monotropoideae. Bakshi (1959) surmised that the

species would be generally expected to occur on podzolic soils, which are very different from these.

Wallace (1975a) claimed that species in this group always occur in acidic soils and reported a soil pH of 5.2 at a population in Oregon. Leake (1994) repeated the assertion that the monotropes always grow in soils that are acidic, typically of pH 5.0. It is possible for acidic soil to form above calcareous bedrock (Scott Bailey, personal communication), so it is risky to generalize about eastern sites that have not been tested, but Bailey found remarkably high pH levels in samples of clay soils collected by Schori near two *Pterospora* occurrences (Hanover, NH, pH 6.76; West Haven, VT, pH 6.95). It would be very interesting to test other eastern sites to learn whether they are generally less acidic than those in the West and to assess availability of nutrients.

Topography

Local topography at eastern occurrences of *Pterospora* seems to fall into at least three types:

- **steep slopes** or ravines at some sites in New Hampshire and Vermont (personal observation), New York (Steve Young, personal communication), Québec (André Sabourin, personal communication), and New Brunswick (Maureen Toner, personal communication);
- **dunes** in Michigan (Higman and Penskar 1999); and
- relatively **flat or gently undulating** areas in Québec (André Sabourin, personal communication).

Slope and aspect information for most sites is unavailable. (For many historic occurrences, the only information available is the name of the town or region where a specimen was collected.) Extant Vermont occurrences are on north slopes, but the New Hampshire occurrence is on a southwest-facing slope. Three Québec occurrences with records that mention aspect are on south or southeast-facing slopes (records from the Centre de données sur le patrimoine naturel du Québec).

Associated Species

Associated species of *Pterospora* necessarily include *Rhizopogon* fungi, although it is doubtful that these have been documented anywhere in the East other than for the one Québec sample included in Bidartondo and Bruns' (2002) analysis of fungal specificity.

Species of Pinaceae are the other crucial element of the myco-heterotrophic partnership. New Brunswick occurrences are in mature white pine forests (Hinds 2000). *Pinus strobus* (white pine) is reported as an associated species at all extant Québec occurrences (records from the Centre de données sur le patrimoine naturel du Québec). It

is present at New Hampshire and extant Vermont sites as well (personal observation and Vermont Nongame and Natural Heritage Program records). *Tsuga canadensis* (eastern hemlock) is present at the New Hampshire site and at least one of the Vermont sites but is not mentioned for most of the Québec sites. Another conifer present at both extant Vermont occurrences is *Thuja occidentalis* (northern white cedar), which, since it is not in Pinaceae, is not thought to be a possible host of *Rhizopogon*. Molina et al. (1999) assert that *Rhizopogon* species show strong specificity to Pinaceae, especially to *Pinus* or *Pseudotsuga*. (They found that some *Rhizopogon* species will form mycorrhizae with *Arbutus* and *Arctostaphylos*, but only when grown in dual culture with *Pinus ponderosa*.) Western populations of *Pterospora* are associated with other species of Pinaceae, including: *Pinus ponderosa* (ponderosa pine), *P. contorta* (lodgepole pine), *P. lambertiana* (sugar pine), *P. jeffreyi* (Jeffrey pine), *Pseudotsuga menziesii* (Douglas-fir), *Abies concolor* (white fir), and *A. grandis* (grand fir) (Wallace 1975a).

There are no other species consistently mentioned in the few reports of herbaceous associates to which I have had access. In fact, *Pterospora* reportedly favors areas with a very sparse herbaceous layer (Gary Wallace, personal communication). A close monotropoid relative of *Pterospora*, *Monotropa hypopithys* (pinesap), was noted at one of the Vermont sites and the New Hampshire site. It is also known that various monotropoid species, each specialized to a different genus or species group of ectomycorrhizal basidiomycetes, are likely to occur in close proximity at western sites (Bidartondo and Bruns 2001). If it can be determined to occur at other *Pterospora* sites in the East, *M. hypopithys* might be a useful indicator of habitats worth searching for *Pterospora*.

THREATS TO PTEROSPORA ANDROMEDEA

Pterospora andromedeae appears to be in serious decline throughout its eastern distribution, with the possible exception of Québec. In some areas, it has always been very rare, and in every eastern state or province with reliable records of occurrences, except Québec, either it is endangered or there has been a substantial loss of populations, or both. Prince Edward Island, which had only one documented historic occurrence, has no known extant occurrences. New Brunswick has lost at least one of six known occurrences and lists the species as endangered (Sean Blaney, personal communication). New Hampshire had at least two historic occurrences, but now has only one known occurrence. The extent of loss in Vermont is unclear, because information recorded for most of the known collections is so vague that it is usually impossible to tell whether multiple collections from one town represent a single or more than one occurrence. Some specimens were identified only as “western Vermont.” What can be said for certain is that there have been at least eight distinct occurrences in at least seven towns, and only two occurrences have been observed within the past 20 years. New York’s population has plummeted from 30 historic occurrences to three, all of which grow in one canyon (Steve Young, personal communication). The historic distribution in Québec is not known, but it is thought that about five populations were lost (extirpated) during the 20th century and that the species may be in regression there (André Sabourin, personal

communication). Ontario appears to have lost the species in 11 counties that had historic occurrences and has extant populations in only four counties (Ontario Ministry of Natural Resources 1999 and Daniel Brunton, independent ecologist, personal communication). Forty-three occurrences have been reported in Michigan, of which 22 are post-1978 records (Higman and Penskar 1999). No detailed information was available from Wisconsin, but the species is listed as endangered there.

In fact, the decline of *Pterospora*'s population segment has been sufficiently alarming that Wallace (personal communication) would have supported federal listing if such an option were available for plants and applicable to this species. There are good reasons to think of the eastern populations of *Pterospora* as a distinct subpopulation: they are disjunct from populations in the Rocky Mountains; they appear to associate with different species of *Rhizopogon* (Bidartondo and Bruns 2002); and they seem to occur on soil types quite different from those in western *Pterospora* habitats. Unfortunately, population segments of plants are not considered listable as population segments of animals are.

Loss of *Pterospora* populations may be inextricably linked with decline of *Rhizopogon* populations, although, of course, no one knows for sure. Several possible explanations for the decline of *Pterospora* and/or *Rhizopogon* have been suggested and are reviewed below.

Habitat Loss or Degradation

Habitat loss is probably a major factor in the loss of populations, especially in areas where *Pterospora* grew on relatively flat or gently rolling terrain. Rich soils that would support the nutrient-loving *Rhizopogon* are desirable as farmland or as productive forest. Clear cutting, whether for agriculture or for timber harvest, would eliminate the autotrophic partner on which the fungus and *Pterospora* rely. Even selective cutting could have a very deleterious effect. As previously stated, *Pterospora* populations are usually very small, consisting of only a few stems at any one location. Cutting the wrong tree or disturbing the soil in the wrong spot could easily eliminate a whole population. Timber harvesting and habitat loss appear to be the major causes of the decline of *Pterospora* in Québec (Andre Sabourin, personal communication).

In New Hampshire, two historic occurrences were at sites which may have been permanently inundated when the Connecticut River was dammed for hydroelectric power production. One (NH .001 [Lebanon]) was at a location that has disappeared from maps since Wilder Dam was constructed. The other (NH .003 [Hanover]) was on an island that shrank as the water rose, but, since the exact location of the historic occurrence is unknown, it cannot be said for sure that it is under water.

Many historic collections in Vermont were from Chittenden County. The region in the greater Burlington area has been logged, used for agriculture, and heavily developed. It is quite possible that some of the historic occurrences have been

irretrievably lost, but information about most specimens is too vague to permit investigation.

On the other hand, there are some areas of *Pterospora* decline where habitat loss is not a likely explanation. Most New York populations of *Pterospora* were in steep ravines, gorges, or “glens” in shaly regions that have not been heavily timbered or developed, some of which are actually protected as parks (Steve Young, personal communication). In those areas, overcollection and/or acid precipitation may be factors in the disappearance of the species.

Pedestrian traffic may degrade habitat, making it less suitable for *Pterospora*. The island that was home to the New Hampshire occurrence NH .003 (Hanover) is heavily used by members and guests of an outing club and by boaters who stop to picnic or explore. There are no real trails, so visitors wander freely all over the island and seem to be suppressing growth of herbaceous species on many parts of the island. Whether this had anything to do with the disappearance of *Pterospora* is unknown, but heavy foot traffic might be expected to have a negative impact. At another occurrence (NH .002 [Hanover]), there is an unauthorized trail right through the middle of the population. It has not eliminated the population, but any widening of the trail could be harmful.

This same occurrence of *Pterospora* in Hanover, New Hampshire (NH .002) is on a steep slope riddled with invasive species. Much of the area was previously farmed, though probably not at the immediate location of the occurrence. Now the area is close to residential areas full of introduced species. Whether these species are a threat to *Rhizopogon* and *Pterospora* is unknown. No literature discussing the possible effect of invasives on myco-heterotrophs was found. *Pterospora* tends to grow in places with little herbaceous cover and a fairly open understory. If invasive species become too dense, they might have a negative effect. On the other hand, this site is extremely steep, and any attempt to remove the invasive *Elaeagnus umbellata* and *Frangula alnus* might do more harm than good. It is possible that the sharp-thorned *Elaeagnus* is more of a threat to botanists and other intruders than to *Pterospora*.

Overcollection

Because *Pterospora* occurs mostly in very small, widely scattered populations, with only a few flowering stems at any one site (except for the large populations in Québec), overcollection of specimens, at least those taken before seed release, appears to have been a significant factor in the decline of the species in the East. Some botanists (notably Oakes and Pringle) provided specimens from Vermont and New York to many herbaria all over this country and even England during the 1800's. Data on original population sizes are not available, but small occurrences may have been seriously depleted or extirpated by such collection.

Foster and Duke's *Field Guide to Medicinal Plants: Eastern and Central North America* (1990) lists *Pterospora* as a medicinal plant, used as a hemostatic by the

American Indians. They make no mention of its rarity, which is ironic, since they list the much more common *Monotropa uniflora* (indian pipe) as “Too scarce for harvest.” The species is also included in various lists of presumably medicinal herbs on the internet. Although it seems very unlikely that collectors are actively searching for *Pterospora* in the East, the listing in such widely available media creates the very real possibility that amateur herbalists totally unaware of the plant’s threatened or endangered status could eliminate small populations if they were lucky enough to find some accidentally.

Acid Precipitation and Climate Change

Acid precipitation is a well-documented phenomenon in the Northeast (Driscoll et al. 2001), so it was suggested by Wallace as a possible factor in the decline of eastern populations of *Pterospora* (personal communication). Bailey clarified how this could be taking place (personal communication). As stated above, eastern populations of *Rhizopogon* may be restricted to soils with high base saturation. Because of their small particle size, clay and silt soils or fine-grained mudstone or shale can have high nutrient availability even if they are somewhat acidic. Thus, the shaly ravines of New York State were good *Pterospora* habitat. Before the days of acid precipitation (whether from local or distant sources), these shales could have provided enough nutrients to satisfy the demanding fungi. Many shales, though, are not particularly rich in calcium. Acid precipitation could both leach essential minerals and change the soil’s cation exchange capacity, making nutrients less available to plants or fungi. It may not be soil pH *per se* that is the problem, since at least some species of mycorrhizal fungi are very acid tolerant (Danielson and Visser 1989).

If this theory is correct, surviving *Pterospora* populations should be those on soils with more buffering capacity or on clays that leach mobile cations less rapidly (Elizabeth Farnsworth, New England Wild Flower Society, personal communication). It may even be that eastern *Rhizopogon* species’ needs are not substantially different from their western cousins’, but that only richer sites have retained sufficient base saturation since acid precipitation became a serious problem. Areas where soil is not strongly influenced by calcareous rock may be expected to lose their ability to sustain *Pterospora* and *Rhizopogon* if acid precipitation continues unabated. If air pollution along the West Coast continues to increase and cause acid precipitation in the mountains, *Pterospora* populations there may soon start to demonstrate a similar decline.

Global warming has been suggested as another potential threat to the taxon (Anne Turner, Vermont Nongame and Natural Heritage Program, personal communication). Because *Pterospora* grows from Canada to Mexico, across a broad range of temperature and precipitation regimes, it may be expected to be more resilient in the face of climate change than many other rare species. However, climate change could help push struggling, marginal occurrences over the edge into disappearance.

Fire Suppression

Fire suppression has been mentioned as another possible factor in the decline of *Pterospora* populations since some western populations of *Rhizopogon* seem to be fire adapted (Martin Bidartondo, personal communication). Baar et al. (1999) found that the species composition of mycorrhizal fungi on pine seedlings after a stand-replacing wildfire in California was dominated by *Rhizopogon* species and ascomycetous fungi. The initial reaction of most Easterners to this idea is quite negative. Parts of the Northeast have been called jokingly “the asbestos forest” because widespread forest fire is so rare here. Nevertheless, fires do occur, albeit infrequently. It is not inconceivable that periodic fires could have been a factor in the ecology of *Pterospora* in certain parts of the eastern range, especially such places as Chittenden County, Vermont (Johnson 1998) and the dry conifer forests of Michigan described by Higman and Penskar (1999). Of course, in Chittenden County, habitat loss is probably a much greater factor than fire suppression.

Herbivory

Herbivory, particularly by deer, has been suggested as another possible factor in the decline of *Pterospora* (Steve Young, personal communication). Reduction of the deer population after the arrival of European settlers may have permitted naturally rare plants to increase their populations, resulting in many rare plant records from the late 1800's and early 1900's. Then, as deer herds increased throughout the 20th century, populations of those plants dwindled again.

This is an interesting idea, and may actually be applicable to some species known to be favored by deer, such as some orchids. However, the hypothesis that deer have large effects on survival of herbaceous species is difficult to evaluate because of lack of studies that have repeatedly censused individual plants, according to Russell et al. (2001).

There is little evidence that deer eat *Pterospora*. Bakshi (1959), who studied the species mostly in Washington and Idaho, mentioned that the only evidence of predation was occasional nipping of tips of flower stalks by deer. Sabourin has not noticed significant herbivory at large Québec occurrences in spite of the presence of many deer in the area (personal communication). There is no mention of evidence of herbivory in records of New England occurrences. Leake (1994) postulated that the presence of tannins and pigments in myco-heterotrophs serves to deter herbivory.

DISTRIBUTION AND STATUS

General Status

Pterospora andromedea is endemic to North America, ranging from southern Canada to the mountains of Mexico. The species is widespread in mountain ranges of the

West (Bakshi 1959). A separate population centered around the Great Lakes encompasses an area extending from northern Michigan and Wisconsin, through Ontario, to Québec, the maritime provinces, New York and New England. The North American and New England distributions of *Pterospora andromedea* are represented in Figures 1 and 2, respectively.

Pterospora andromedea's global rank is G5 (demonstrably widespread, abundant, and secure globally, though it may be quite rare in parts of its range, especially at the periphery). In the United States and Canada it is ranked N?, indicating uncertainty about its status. Distribution and current state or province ranks of *Pterospora* are as follows:

- **New England** - New Hampshire (S1), Vermont (S1), Massachusetts (SR)
- **Other eastern populations** - Michigan (S2), New Brunswick (S1) New York (S1), Nova Scotia (SR), Ontario (S2), Pennsylvania (SU), Prince Edward Island (SH), Québec (S2), Wisconsin (S1)
- **Western populations** - Alaska (SRF), Alberta (S2), Arizona (SR), British Columbia (SR), California (SR), Colorado (SR), Idaho (SR), Montana (SR), Nebraska (S2), Nevada (SR), New Mexico (SR), Oregon (SR), Saskatchewan (S1), Sonora (S?), South Dakota (SR), Texas (S1), Utah (SR), Washington (SR), Wyoming (S3).

It should be noted that, although Gleason and Cronquist (1991) mention Pennsylvania as part of *Pterospora*'s range, the species is not known to exist in the state, and there are no known herbarium specimens (Chris Firestone, Pennsylvania Bureau of Forestry, Wild Plant Management Program, personal communication). The state rank should therefore probably be SRF (State Reported - False) rather than SU (State Unrankable). No herbarium specimen is known for Massachusetts, so it should probably also have a rank of SRF.

The eastern population center appears to be in decline region-wide. Except in Québec, which has several sites with large numbers of flowering stems, the plant seems to occur in very small, scattered populations vulnerable to extirpation. Within the whole eastern distribution, from Wisconsin to the maritime provinces, in all states and provinces with documented occurrences, *Pterospora andromedea* is or should be ranked S1, S2, or SH. The NatureServe website lists it as SR for New Brunswick and Prince Edward Island (NatureServe 2001), but Sean Blaney reports that it is listed as Endangered in New Brunswick and historic in Prince Edward Island, where there was a documented occurrence at the extreme east end of the island (personal communication). In New York, where there were 30 historic occurrences in 20 counties across the state, occurrences have been reduced to three, all in one canyon, and two of those have not been observed since the early 1990's (Steve Young, personal communication). In *Flora Conservanda*, *Pterospora andromedea* is listed as Division 2, Regionally Rare (Brumback and Mehrhoff et al. 1996). All states and provinces with reported occurrences are listed in Table 1.

Status of all New England occurrences -- current and historical

The only currently known populations of *Pterospora andromedea* in New England occur in New Hampshire and Vermont. Historically, it was more widespread in Vermont, and there was an unconfirmed report of a sighting from Massachusetts in the 1800's. In New England, *Pterospora andromedea* was accorded the state ranks of S1 or SX. Its recent rediscovery in Hanover, New Hampshire will change its rank there from SX to S1. New Hampshire's two historic occurrences, in Hanover and Lebanon, were within two miles of the extant occurrence. Vermont had historic occurrences in six towns (Burlington, Charlotte, Colchester, Proctor, Williston, and Winooski), as well as some specimens identified only as "western Vermont," with many duplicate specimens sent to herbaria far and wide. Information recorded for most of the specimens is so vague that it is usually impossible to tell whether multiple collections from one town represent a single or more than one occurrence. One previously undiscovered occurrence was found in a seventh town (West Haven) in 1987. The other extant occurrence, discovered in 1990, is definitely a second occurrence from a town (Colchester) with a historic occurrence at a known site on the opposite side of Malletts Bay. Locations of other historic occurrences in that town are ambiguous. It is quite possible, maybe even likely, that the total of known occurrences for Vermont, extant and historic, is as small as eight. A list of known herbarium records for historic New England occurrences appears in Appendix 3.

Information about New England occurrences is from State Natural Heritage Program records and personal observation of some sites (NH .002, NH .003, and VT .002).

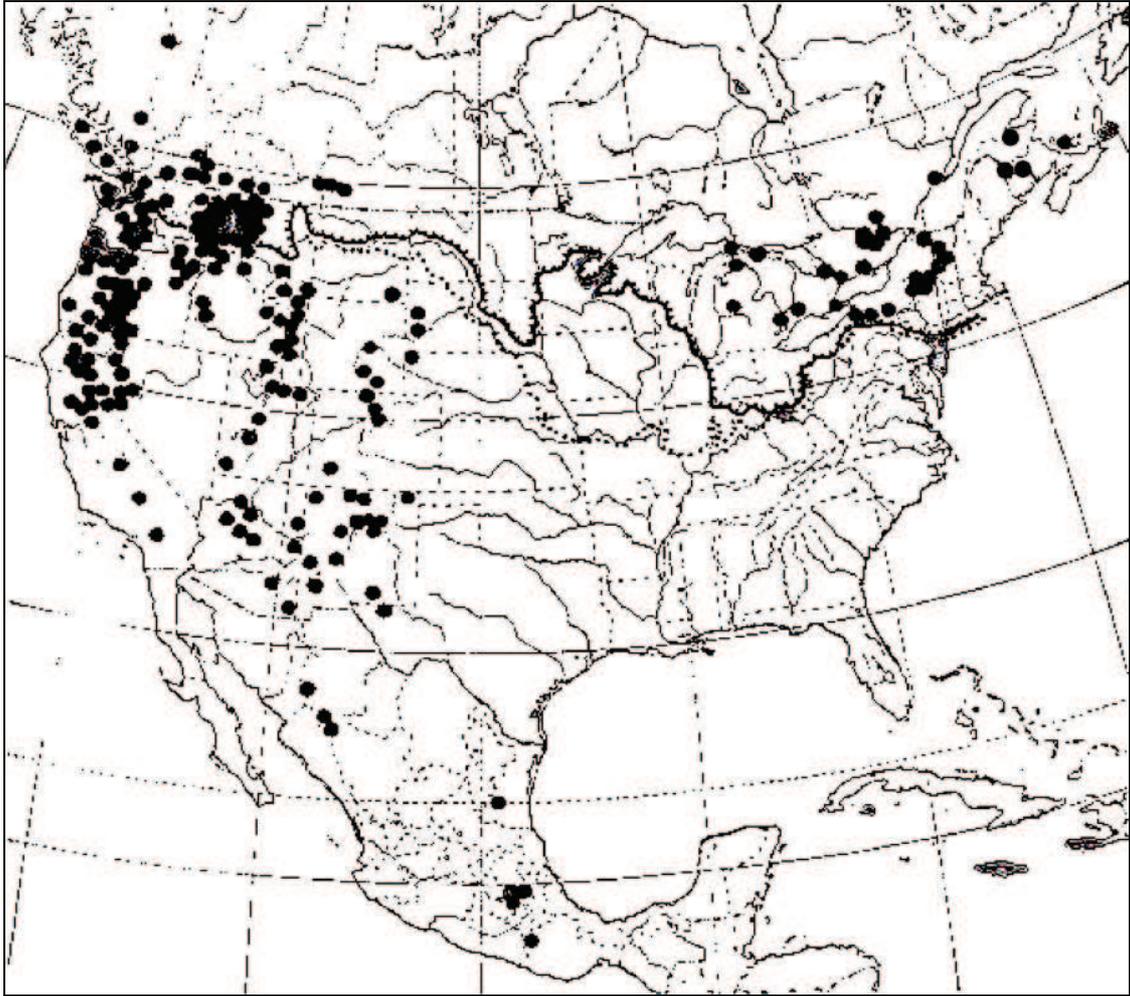


Figure 1. Occurrences of *Pterospora andromedea* in North America. Adapted from Bakshi (1959) with additional data on occurrences from Hinds (2000) and Wallace (1975a). Dots indicate presence of the taxon. Dotted line illustrates the southward extent of continental glaciers during the Pleistocene epoch; bold line indicates southward extent during the Wisconsinian.

Table 1. Occurrence and status of <i>Pterospora andromedea</i> in North America based on information from Natural Heritage Programs and Gary Wallace.			
OCCURS & LISTED (AS S1, S2, OR T & E)	OCCURS & NOT LISTED (AS S1, S2, OR T & E)	OCCURRENCE UNVERIFIED	HISTORIC (LIKELY EXTIRPATED)
Alberta (S2)	Sonora (S?)	Alaska (SRF)	Prince Edward Island (SH): 1 historic occurrence
Michigan (S2, T): 22 extant and 21 historic occurrences	Wyoming (S3)	Massachusetts (SR): 1 unconfirmed historic occurrence	
Nebraska (S2)	Arizona (SR)	Nova Scotia (SR): unconfirmed reports from northern Cape Breton Island (Blaney, personal communication)	
New Brunswick (S1, E): 6 occurrences, at least one probably historic (Blaney, personal communication)	British Columbia (SR)	Pennsylvania (SU): no known specimen or occurrence, unrankable	
New Hampshire (S1): 1 extant and 2 historic occurrences	California (SR): occurs in 7 subdivisions of the California Floristic Province and 1 subdivision of the Great Basin Province (Wallace 1993)	South Dakota (SR): verified historic occurrences; current status unknown	
New York (S1, E): 3 extant and 30 historic occurrences	Colorado (SR)		
Ontario (S2): 3 counties with extant occurrences and 11 counties with historic occurrences	Idaho (SR)		
Québec (S2): 18 extant and 7 historic occurrences	Montana (SR)		
Saskatchewan (S1)	Nevada (SR)		
Texas (S1)	New Mexico (SR)		
Vermont (S1, E): 2 extant occurrences and unknown number of historic occurrences in 6 towns	Oregon (SR)		
Wisconsin (S1, E): 3 counties with extant occurrences	Utah (SR)		
	Washington (SR)		

N.B. "Extant" generally refers to populations observed within the past 20 years, but precise definitions used by the various Natural Heritage programs are not known.

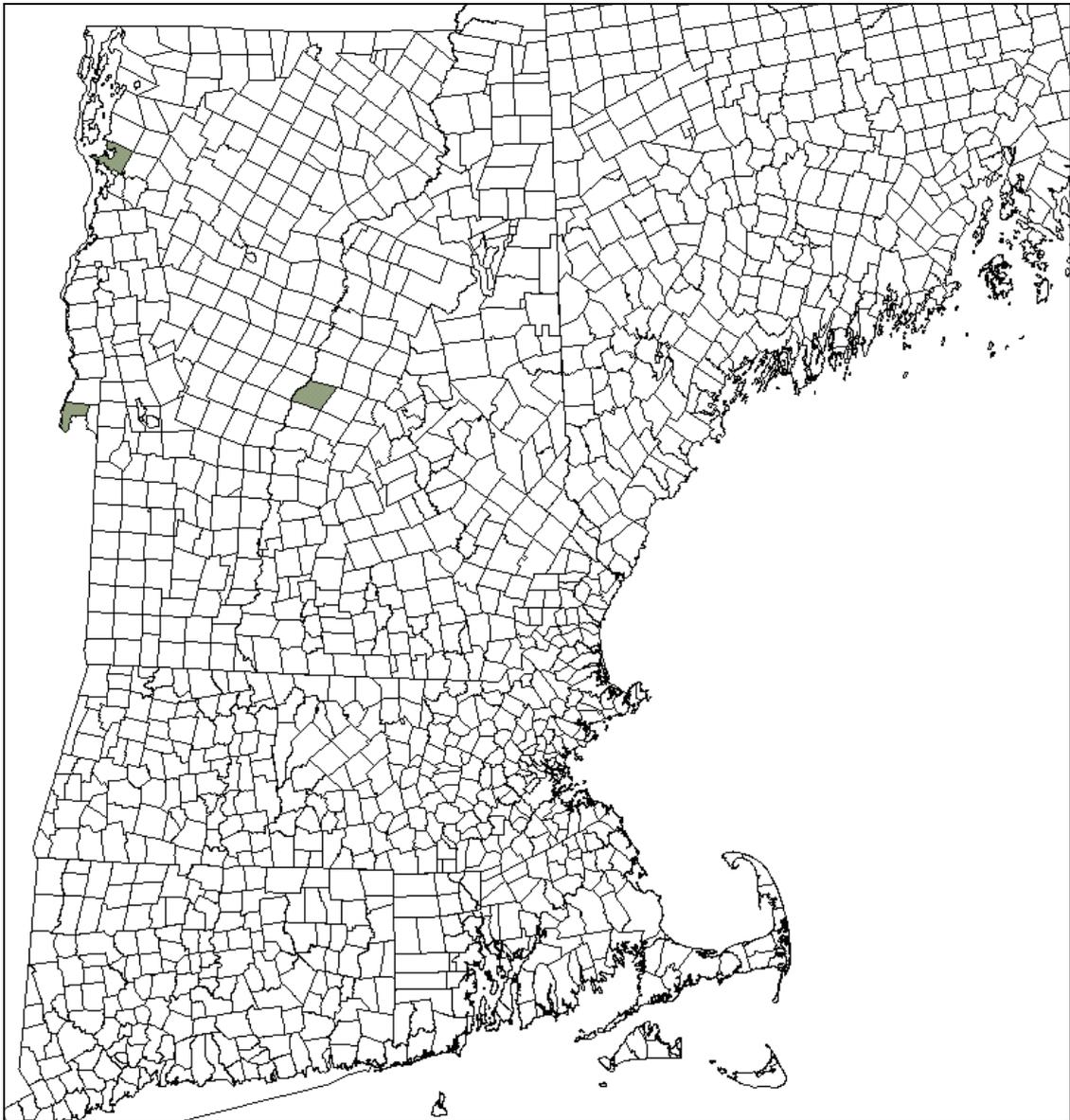


Figure 2. Extant occurrences of *Pterospora andromeda* in New England. Town boundaries for New England states are shown. Towns shaded in gray have one to five confirmed, extant occurrences of the taxon.

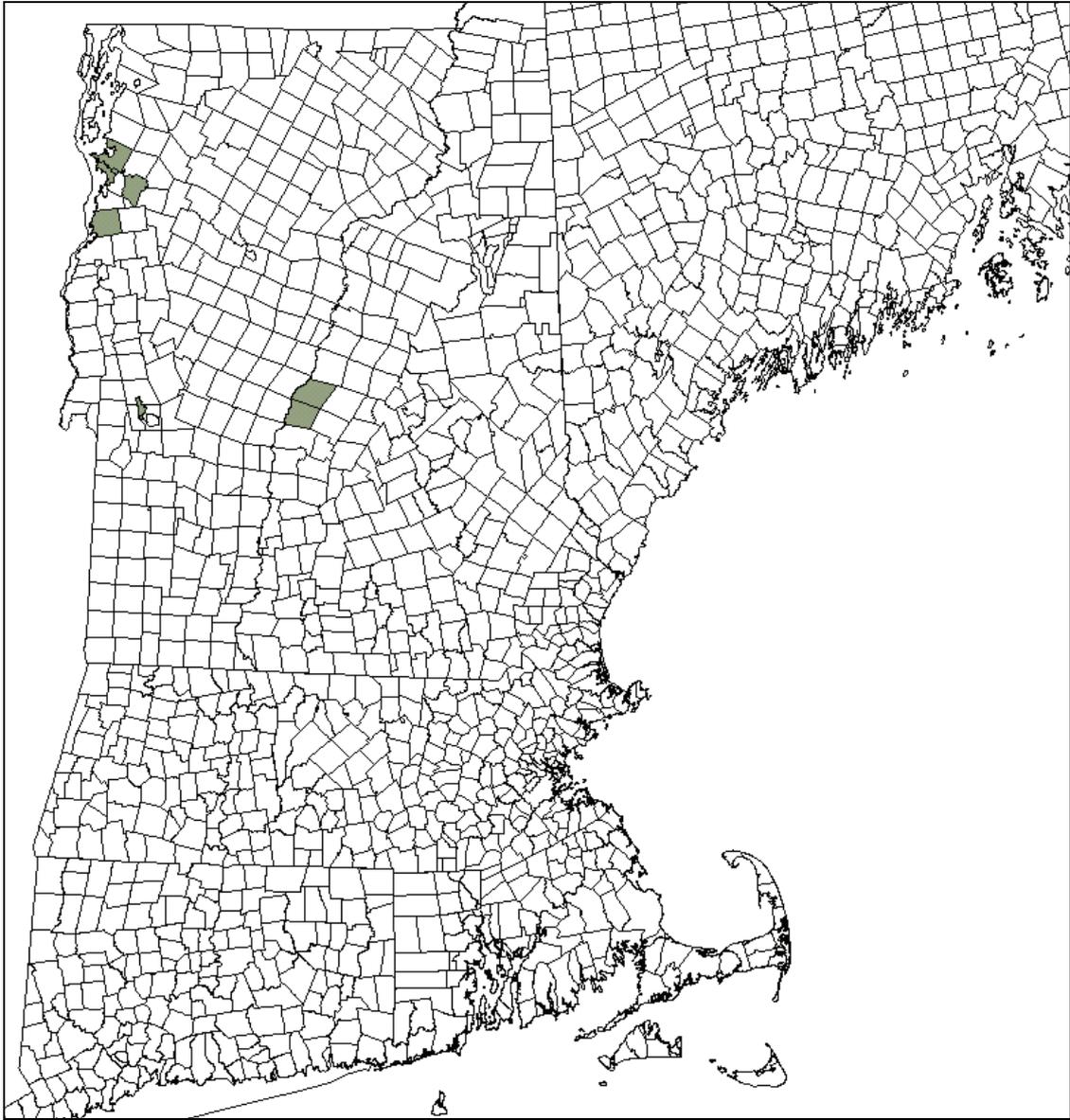


Figure 3. Historical occurrences of *Pterospora andromedea* in New England. Towns shaded in gray have one to five historic records of the taxon.

Table 2. New England Occurrence Records for <i>Pterospora andromedea</i>. Shaded occurrences are considered extant.			
State	EO #	County	Town
NH	.001	Grafton	Lebanon
NH	.002	Grafton	Hanover
NH	.003	Grafton	Hanover
VT	.001	Chittenden	Colchester
VT	.002	Rutland	West Haven
VT	.003	Chittenden	Colchester
MA	no #	Hampshire	Easthampton

CURRENT CONSERVATION MEASURES IN NEW ENGLAND

Pterospora andromedea is listed as Endangered in Vermont and is thereby afforded a small measure of protection at the two privately-owned sites where it is known to occur in that state. A state-Endangered species cannot be disturbed without a permit from the Agency of Natural Resources. An unfortunate side-effect of this regulation is that a landowner may feel that his development rights have been “taken” by the State because of the presence of rare plants. However, under the Endangered and Threatened Species Law, Title 10, Chapter 123, Section 5408 (d), it is stated that “[n]o rule adopted under this chapter shall cause undue interference with normal agricultural or silvicultural practices” (Steve Parren, Vermont Nongame and Natural Heritage Program, personal communication). Since either logging or agricultural activity could easily eliminate a population of *Pterospora*, in effect, there is very little real protection. Owners of one Vermont site (VT .002 [West Haven]) seem to be pleased to have interesting plants on their property and participated in an unsuccessful search during the 2001 season. Their site is being monitored occasionally by the Vermont Nongame and Natural Heritage Program. Other sites in Vermont are either not known with sufficient precision to determine ownership (VT .001 [Colchester]) or are privately owned and probably not protected (VT .003 [Colchester]).

In New Hampshire, *Pterospora andromedea* will be listed as Endangered at the end of May 2002 (Bill Nichols, New Hampshire Natural Heritage Inventory, personal communication) but is not legally protected. Populations on private lands are protected only against taking without permission by persons other than the landowner. Local conservation organizations have been hoping to secure a conservation easement on part of the property that harbors the one extant population but have not succeeded to date. The current status of their efforts is unclear.

II. CONSERVATION

CONSERVATION OBJECTIVES FOR THE TAXON IN NEW ENGLAND

The primary conservation objectives for *Pterospora andromedea* in New England are to permanently protect, monitor, and, if necessary manage, the three extant populations and their associated natural communities. Cooperation with researchers engaged in species biology studies and the establishment of permanent monitoring plots for the collection of life history data are recommended. Analysis of historic records and current land use in areas where *Pterospora* formerly occurred may shed light on causes for its disappearance and, in turn, strategies for halting the decline. Equally important will be studies of mycorrhizal and plant associates aimed at making it possible to identify appropriate habitat for *de novo* searches and sites for possible introduction. Propagation research should be supported in the hope that it may eventually be feasible to undertake introduction or reintroduction at appropriate sites.

It appears that *Pterospora andromedea* has been rare in New England, at least as long as botanists have been taking note of it. Herbarium records and reliable recent reports indicate that, although *Pterospora andromedea* historically has been found in at least seven towns in western Vermont, the number of separate occurrences may be as low as eight. Most of the old records are so vague that it is not known whether different specimens from a town are all from one site or from several sites within the town. Two historic records and one recent (2000) discovery in New Hampshire are all from an area near the Connecticut River in the towns of Lebanon and Hanover. The single report from Massachusetts is unconfirmed (no herbarium specimen has been found). *Pterospora* has never been reported in Maine, Connecticut, or Rhode Island.

Within the past twenty years, only three populations of *Pterospora andromedea* have been observed in New England. Two of those populations apparently consist of only two or three plants, so their long-term viability seems questionable. The third population, in Hanover, New Hampshire (NH .002), with 16 flowering stems from the 2001 growing season, seems somewhat more secure, but is likely to be completely genetically isolated from other populations. The other nearest known occurrence, in West Haven, Vermont (VT .002), is about 75 km away. Nevertheless, small, isolated populations seem to be the rule for this species (Bakshi 1959, Higman and Penskar 1999), so these factors are not necessarily unusual or problematic. Even so, although the species is regionally widespread and secure in the western United States, it appears to be declining throughout most of its eastern range and hanging on by a thread in New England.

As Higman and Penskar (1999) have stated in their special plant abstract for *Pterospora andromedea* in Michigan: "Little is known regarding specific management strategies for this species with the exception of the need to maintain its mycorrhizal

association. Any strategy that lacks an understanding of this relationship is doomed to failure. Until additional knowledge regarding the biology and ecology of this species is available, management strategies should focus on preservation of ecosystem function, with particular attention paid to the maintenance of soil microbe and mycorrhizal diversity.” Of course, that is easier said than done. Conservation of forests in areas where *Pterospora andromedea* occurs or occurred historically may be the only currently practical strategy. Within these areas, particular attention should be paid to protection of pine trees and other species of Pinaceae.

III. LITERATURE CITED

- Antevs, E. 1928. *The Last Glaciation with Special Reference to the Ice Retreat in Northeastern North America*. American Geographical Society, New York, New York, USA.
- Baar, J., T. R. Horton, A. M. Kretzer, and T. D. Bruns. 1999. Mycorrhizal colonization of *Pinus muricata* from resistant propagules after a stand-replacing wildfire. *New Phytologist* 143: 409-418.
- Bakshi, T. S. 1959. Ecology and morphology of *Pterospora andromedea*. *Botanical Gazette* 120: 203-217.
- Bidartondo, M. I., A. M. Kretzer, and E. M. Pine. 2000. High root concentration and uneven ectomycorrhizal diversity near *Sarcodes sanguinea* (Ericaceae): A cheater that stimulates its victims? *American Journal of Botany* 87: 1783-1788.
- Bidartondo, M. I. and T. D. Bruns. 2001. Extreme specificity in epiparasitic Monotropoideae (Ericaceae): widespread phylogenetic and geographical structure. *Molecular Ecology* 10: 2285-2295.
- Bidartondo, M. I. and T. D. Bruns. 2002. Fine-level mycorrhizal specificity in the Monotropoideae (Ericaceae): specificity for fungal species groups. *Molecular Ecology* 11: 557-569.
- Björkman, E. 1960. *Monotropa hypopitys* L. - an epiparasite on tree roots. *Physiologia Plantarum* 13: 308-327.
- Brumback W. E., L. J. Mehrhoff, R. W. Enser, S. C. Gawler, R. G. Popp, P. Somers, D. D. Sperduto, W. D. Countryman, and C. B. Hellquist. 1996. *Flora Conservanda*: New England. The New England Plant Conservation Program (NEPCoP) list of plants in need of conservation. *Rhodora* 98: 233-361.
- Bruns, T. D. and D. J. Read. 2000. *In vitro* germination of nonphotosynthetic, myco-heterotrophic plants stimulated by fungi isolated from adult plants. *New Phytologist* 148: 335-342.
- Copeland, H. F. 1941. Further studies on Monotropoideae. *Madroño* 6: 97-144.
- Cullings, K. W. and T. D. Bruns. 1992. Phylogenetic origin of the Monotropoideae inferred from partial 28S ribosomal RNA gene sequences. *Canadian Journal of Botany* 70: 1703-1708.

- Cullings, K. W., T. M. Szaro, and T. D. Bruns. 1996. Evolution of extreme specialization within a lineage of ectomycorrhizal epiparasites. *Nature* 379: 63-66.
- Cummings, M. P. and N. A. Welschmeyer. 1998. Pigment composition of putatively achlorophyllous angiosperms. *Plant Systematics and Evolution* 210: 105-111.
- Danielson, R. M. and S. Visser. 1989. Effects of forest soil acidification on ectomycorrhizal and vesicular-arbuscular mycorrhizal development. *New Phytologist* 112: 41-47.
- Duddridge, J. A. and D. J. Read. 1982. An ultrastructural analysis of the development of mycorrhizas in *Monotropa hypopitys* L. *New Phytologist* 92: 203-214.
- Fernald, M. L. 1950. *Gray's Manual of Botany*, Volume 2. Eighth Edition. Dioscorides Press, Portland, Oregon, USA.
- Flynn, N. F. 1916. One afternoon's botanizing. *Vermont Botanical and Bird Club Joint Bulletin* 2:19.
- Foster, S. and J. A. Duke. 1990. *A Field Guide to Medicinal Plants: Eastern and Central North America*. Peterson Field Guide Series. Houghton Mifflin Company, New York, New York, USA.
- Furman, T. E. and J. M. Trappe. 1971. Phylogeny and ecology of mycotrophic achlorophyllous angiosperms. *Quarterly Review of Biology* 46: 219-225.
- Gleason, H. A. and A. Cronquist. 1991. *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*, Second Edition. The New York Botanical Garden, Bronx, New York, USA.
- Haber, E. and C. J. Keddy. 1984. In: Argus, G. W. and C. J. Keddy (Editors). *Atlas of the Rare Vascular Plants of Ontario*. Botany Division, National Museum of Natural Science, Ottawa, Ontario, Canada.
- Harlow, W. M., E. S. Harrar, J. W. Hardin, and F. M. White. 1991. *Textbook of Dendrology: Covering the Important Forest Trees of the United States and Canada*, Seventh Edition. McGraw-Hill, Inc., New York, New York, USA.
- Hickman, J. C. (Editor). *The Jepson Manual: Higher Plants of California*. (Third printing with corrections, 1996) University of California Press, Berkeley and Los Angeles, California, USA.
- Higman, P. J. and M. R. Penskar. 1999. Special plant abstract for *Pterospora andromedea* (pine-drops). Michigan Natural Features Inventory, Lansing, Michigan, USA. Available at: http://www.dnr.state.mi.us/wildlife/heritage/mnfi/abstracts/botany/pterospora_andromedea.pdf

- Hinds, H. R. 2000. *Flora of New Brunswick*, Second Edition. University of New Brunswick, Fredericton, New Brunswick, Canada.
- Jepson, W. L. *A Flora of California*, Volume 3, Part 1. University of California, Berkeley, California, USA.
- Johnson, C. W. 1998. *The Nature of Vermont*. University Press of New England, Hanover, New Hampshire, USA.
- Kretzer, A. M., M. I. Bidartondo, L. C. Grubisha, J. W. Spatafora, T. M. Szaro, and T. D. Bruns. 2000. Regional specialization of *Sarcodes sanguinea* (Ericaceae) on a single fungal symbiont from the *Rhizopogon ellенаe* (Rhizopogonaceae) species complex. *American Journal of Botany* 87: 1778-1782.
- Leake, J. R. 1994. Tansley Review No. 69. The biology of myco-heterotrophic ('saprophytic') plants. *New Phytologist* 127: 171-216.
- Luoma, D. L. 1987 *Synecology of Monotropoideae within Limpy Rock Research Natural Area, Umpqua National Forest, Oregon*. Master of Science thesis, Department of Geography, Oregon State University, Corvallis, Oregon.
- Lutz, R. W. and R. D. Sjolund. 1973. *Monotropa uniflora*: ultrastructural details of its mycorrhizal habit. *American Journal of Botany* 60: 339-345.
- MacDougal, D. T. 1899. Symbiotic saprophytism. *Annals of Botany* 13: 1-47.
- MacDougal, D. T. and F. E. Lloyd. 1900. The roots and mycorrhizas of some of the Monotropaceae. *Bulletin of the New York Botanical Garden* 1: 419-429.
- Molina, R. J., J. M. Trappe, L. C. Grubisha, and J. W. Spatafora. 1999. *Rhizopogon*. Pages 129-161 in Cairney, J. W. G. and S. M. Chambers (Editors). *Ectomycorrhizal Fungi Key: Genera in Profile*. Springer Verlag, Berlin and Heidelberg, Germany.
- Molina, R., D. Pilz, J. Smith, S. Dunham, T. Dreisbach, T. O'Dell, and M. Castellano. 2001. Conservation and management of forest fungi in the Pacific Northwestern United States: an integrated ecosystem approach. Pages 19-63 in Moore, D., M. M. Nauta, S. E. Evans, and M. Rotheroe (Editors). *Fungal Conservation: Issues and Solutions*. Cambridge University Press, Cambridge, UK.
- NatureServe: An online encyclopedia of life [web application]. 2001. Version 1.5. Arlington, Virginia, USA. Association for Biodiversity Information. Available at: <http://www.natureserve.org/>

Nuttall, T. 1818. *The Genera of North American Plants, and Catalogue of the Species, to the year 1817*, Volume 1. Printed for the author by D. Heartt, Philadelphia, Pennsylvania, USA.

Ontario Ministry of Natural Resources. 1999. Rare vascular plant list. Available at: <http://www.mnr.gov.on.ca/MNR/nhic/newslett/lists/rarevascular.pdf>

Robertson, D. C. and J. A. Robertson. 1982. Ultrastructure of *Pterospora andromedea* Nuttall and *Sarcodes sanguinea* Torrey mycorrhizas. *New Phytologist* 92: 539-551.

Russell, F. L., D. B. Zippin, and N. L. Fowler. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. *American Midland Naturalist* 146:1-26.

Smith, S. E. and D. J. Read. 1997. *Mycorrhizal Symbiosis*, Second Edition. Academic Press, Harcourt Brace & Co., Publishers. San Diego, California, USA.

Smith, A. H. and S. M. Zeller. 1966. A preliminary account of the North American species of *Rhizopogon*. *Memoirs of the New York Botanical Garden* 14(2): 1-178.

Stone, G. E. 1913. *A List of Plants Growing Without Cultivation in Franklin, Hampshire, and Hampden Counties*. Carpenter and Morehouse Press, Amherst, Massachusetts, USA.

Tuckerman, E. and C. C. Frost. 1875. *A Catalogue of Plants Growing Without Cultivation Within Thirty Miles of Amherst College*. Edwin Nelson (publisher), Amherst, Massachusetts, USA.

Wallace, G. D. 1975a. Studies of the Monotropeoideae (Ericaceae): taxonomy and distribution. *Wassmann Journal of Biology* 33: 1-88.

Wallace, G. D. 1975b. Interrelationships of the subfamilies of the Ericaceae and derivation of the Monotropeoideae. *Botaniska Notiser* 128: 286-298.

Wallace, G. D. 1977. Studies of the Monotropeoideae (Ericaceae). Floral nectaries: anatomy and function in pollination ecology. *American Journal of Botany* 64(2): 199-206.

Wallace, G. D. 1987. Transfer of *Eremotropa sciaphila* to *Monotropastrum* (Ericaceae: Monotropeoideae). *Taxon* 36: 128-130.

Wallace, G. D. 1993. Ericaceae. Pages 544-567, and 569 in Hickman, J. C. (Editor). *The Jepson Manual: Higher Plants of California*. (Third printing with corrections, 1996) University of California Press, Berkeley and Los Angeles, California, USA.

IV. APPENDICES

- 1. Other Useful References Not Specifically Cited and Indirect Citations**
- 2. Known Historic Occurrences of *Pterospora* in New England**
- 3. Occurrences of *Pterospora andromedea* in New York State**
- 4. Occurrences of *Pterospora andromedea* in Québec Province**
- 5. An Explanation of Conservation Ranks Used by The Nature Conservancy and NatureServe**

1. Other Useful References Not Specifically Cited

Bidartondo, M. I., A. M. Kretzer, E. M. Pine, and T. D. Bruns. 2000. High root concentration and uneven ectomycorrhizal diversity near *Sarcodes sanguinea* (Ericaceae): a cheater that stimulates its victims? *American Journal of Botany* 87: 1783-1788.

Kartesz, J. T. 1994. *A Synonymized Checklist of the Vascular Flora of the U.S., Canada, and Greenland*, Second Edition. 2 volumes. Timber Press, Portland, Oregon, USA.

Schneck, M., W. E. Sharpe, and J. R. Drohan. 1999. *Acid rain: the Pennsylvania connection*. The Pennsylvania State University, University Park, Pennsylvania, USA. Available at: <http://pubs.cas.psu.edu/FreePubs/pdfs/UH127.pdf>

Takahashi, H. 1987. Pollen morphology and its taxonomic significance of the Monotropoideae (Ericaceae). *Botanical Magazine Tokyo* 100: 385-405.

Indirect Citations

Drude, O. 1889. Pirolaceae. Pages 3-11 in Engler, A. and K. Prantl. *Die Natürlichen Pflanzenfamilien*, Volume 4, Part 1. W. Engelmann, Berlin, Germany.

Frank, A. B. 1892. *Lehrbuch der Botanik*. Leipzig, Germany.

Furman, T. E. 1966. Symbiotic relationships of *Monotropa*. *American Journal of Botany* 53: 627.

Henderson, M. 1919. A comparative study of the structure and saprophytism of the Pyrolaceae and Monotropaceae with reference to their derivation from the Ericaceae. *Contributions from the Botanical Laboratory and the Morris Arboretum of the University of Pennsylvania* 5: 42-109.

Kamienski, F. 1884. Les organes végétatifs du *Monotropa hypopitys*. *Mémoires de la Société des Sciences Naturelles et Mathématiques de Cherbourg* 24: 5-40. (The same citation appears in several articles with varying combinations of year and volume #, but this appears to be the correct form of the citation.)

Luxford, G. 1842. Botanical notes. *The Phytologist* 1: 42-44.