Conservation Assessment
For
Pterospora andromedea Nutt.
(Pine-drops)

USDA Forest Service, Eastern Region
Hiawatha National Forest
November 2004

This Conservation Assessment was prepared to compile the published and unpublished information on *Pterospora andromedea* Nutt. This report provides information to serve as a Conservation Assessment for the Eastern Region of the Forest Service. It is an administrative study only and does not represent a management decision by the U.S. Forest Service. Although the best scientific information available was used and subject experts were consulted in preparation of this document and its review, it is expected that new information will arise. In the spirit of continuous learning and adaptive management, if the reader has any information that will assist in conserving this species, please contact the Eastern Region of the Forest Service – Threatened and Endangered Species Program at 310 Wisconsin Avenue, Suite 580 Milwaukee, Wisconsin 53203.

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Executive Summary

Before Bakshi's study (1959), *Pterospora andromedea* Nutt., of the family Monotropaceae, was considered a saprophytic plant; now it has been determined a more accurate description would be a root parasite. Like other genera in this family this species has lost its green color and is dependent upon a fungus associated with the roots of conifers for its nutrition.

This species shows an east-west disjunction; in the west it ranges from British Columbia and southwestern Saskatchewan south primarily in the mountains throughout the western United States into Mexico. It also occurs in the Black Hills of South Dakota then its distribution skips to the Great Lakes Region, primarily Michigan, and sparsely eastward in Ontario and more frequently in Quebec (Marquis & Voss 1981). In the western United States, pine-drops occurs in mixed or coniferous forests at 200 to 12,000 feet elevation growing under trees or other understory vegetation (Wallace 1975). In the eastern United States, *P. andromedea* corresponds to the distribution of *Pinus strobus* (white pine) which is centered around the Great Lakes (Schori 2002). Many of the Canadian records are very old, some occurring before the 1900s (Gillett 1972); this is also true for the eastern states of New York, Vermont, and New Hampshire (MICH herbarium 2003).

Pterospora andromedea is a non-photosynthetic plant up to three feet tall; it does not send up a flowering stalk every year so its presence can remain undetected. Limiting the distribution of this species is its specialization on a single fungus group within the genus, *Rhizopogon* (Cullings *et al.* 1996). With such a limited host fungus dependence, preservation of an ecologically intact forest with soil microbe and mycorrhizal diversity is necessary for maintenance of this species (Higman & Penskar 1999).

Reasons for decline of this species are unclear. Habitat loss appears to be a major cause including conversion of mixed forests to pine plantations. Fire suppression is probably a factor as well (Schori 2002).

Introduction/Objectives

The National Forest Management Act and USDA Forest Service policy require that National Forest Service lands be managed to maintain viable populations of all native plant and animal species. A viable population is one that has established populations and a distribution of reproductive individuals sufficient to ensure the continued existence of the species throughout its range within a given planning area. In addition to those species listed as Endangered or Threatened under the Endangered Species Act, or Species of Concern by the U.S. Fish and Wildlife Service, the Forest Service lists species that are sensitive within each region – Regional Forester Sensitive Species (RFSS). A designation of "sensitive" affords some additional regulatory protection.

Pterospora andromedea Nutt. is a Regional Forester Sensitive Species (RFSS) in the Eastern Region of the Forest Service. It is listed as an R9 (Region 9) sensitive species on the Hiawatha, the Huron-Manistee, and the Ottawa National Forests all located in

Michigan. It has Threatened status in Michigan. Its Global Rank is G5 since it is widespread in the mountainous ranges of the western United States. However, it is rare in the northern and eastern sections of the United States; in the eastern region some states only have historic element occurrences.

The objectives of this document are to:

1. Provide an overview of current scientific knowledge for this species.
2. Provide a summary of the distribution and status of this species, rangewide and with particular emphasis on the Eastern United States.
3. Provide the available background information needed to prepare a subsequent Conservation Approach.

Nomenclature and Taxonomy:

Family: Monotropaceae

Scientific name: *Pterospora andromedea* Nuttall

Common names: pine-drops, giant birds nest, Albany beech-drops

Synonyn: *Monotropa procera* Torrey (Bakshi 1959).

USDA NRCS Plant Code: PTAN2

Taxonomy note: There are good indications that the eastern population of *P. andromedea* is a distinct subpopulation from the Rocky Mountains: the two populations are disjunct, the soil types are quite different, and most importantly they appear to be associated with different species of *Rhizopogon* (Bidartondo & Bruns 2002). These might represent sub-species.
Nomenclature Note: *Pterospora* refers to winged (Ptero) seeds (spora). Its flask-shaped flowers are similar to *Andromedea* (Bakshi 1959).

Monotropaceae notes:
The Monotropaceae, while usually treated as a unit, has been assigned several different positions in the past with relationship to the Ericaceae (Wallace 1975):
1. As a separate family (Nuttall 1818, Desvaux 1827, Lindley 1836, A.P. DeCandolle 1839, Bentham & Hooker 1876, Small 1914, and Cronquist 1968 cited in Wallace 1975, Gleason & Cronquist 1991)
2. As a subfamily of the Ericaceae (Henderson 1919, Copeland 1939, Thorne 1968, and Stevens 1971 cited in Wallace 1975, Hickman 1993, Takhtajan 1980 cited in Cole 1994)
3. Or as a subfamily of the Pyrolaceae (Drude 1889, Lawrence 1951 cited in Wallace 1975).

Pterospora andromedea belongs in the subfamily Monotropoideae (Indian Pipe subfamily) of the Ericaceae (Heath family). This subfamily includes only 13 species in 10 genera (Wallace 1975). They are all non-photosynthetic mycorrhizal epiparasites (myco-heterotrophs) that are associated with five distinctly related families of ectomycorrhizal fungi (Bidartondo and Bruns 2002). Photosynthesis is thought to have been lost at least twice in the herbaceous *Pyrolaceae* and *Monotropaceae* group (Kron 1996). *Pterospora*'s closest "sister taxon" is the spectacular snow plant, *Sarcodes sanguinea* which occurs only in the West from Oregon to northern Baja California (Wallace 1975).

The Monotropoidaceae are unified by their mycotrophic achlorophyllous habit and associated morphological features such as "leaves reduced to scales". Other characteristics which unite this group include pollen in monads, regular and perfect flowers, lack of poricidal anthers, and floral axes developed from adventitious buds on brittle, perennial root masses (Wallace 1975). Simple, annual floral axes which arise from adventitious buds on the perennial roots are the only above-ground portions of these plants. The perennial root system is generally of brittle, succulent, highly branched roots (Wallace 1975).

The members of the Monotropoideae were previously considered to be saprophytes. More recent studies indicate that they are better treated as achlorophyllus mycotrophic angiosperms (Furman & Trappe 1971, Bjorkman 1960 cited in Wallace 1975). Bjorkman (1960) termed this habit epiparasitic, but Wallace (1975) felt this term was misleading and suggested the term mycoparasitism. This relationship involves the indirect parasitism of a host plant since it grows with a fungal associate on the roots of its ultimate host.

Species Description

Pterospora andromedea (pine-drops) is a distinctive herbaceous plant lacking chlorophyll, growing up to three feet tall with pinkish to reddish brown flowers born in a long raceme at the end of the stem. The upright stems of *P. andromedea* are more than twice as tall as either of the more widespread species *Monotropa uniflora* (Indian pipe) and *M. hypopithys* (pinesap) which also lack chlorophyll. Both Indian pipe and pinesap have nodding stems that become erect in fruit, unlike the strongly nodding flowers and fruits of *Pterospora andromedea*. Indian pipe is distinctively white as opposed to being pinkish to reddish brown in color (Voss 1996), also Indian pipe has only one large flower on each stem while pine-drops has numerous flowers (Higman & Penskar 1999).

Species Technical Characteristics: (Material adapted from Bakshi 1959, Chadde 1999, Great Plains Flora Association 1986, Henderson 1919, and Higman & Penskar 1999, Wallace 1975)

Habit: Herbaceous upright plant lacking chlorophyll

Height: Stems from 2 - 3 feet (30-60 cm)

Roots: There are several primary roots which branch and re-branch, all intertwining to form a compact globoid mass up to 7 cm. in diameter. Due to re-branching the root mass is very much condensed, thickened, and fleshy.

Stem: Unbranched stems (2-3 feet) are pink to brownish-red in color. Stems are covered with gland tipped hairs giving the stem a clammy-sticky feel. The fleshy stems live only one season, but the distinctive dry brown stalks may persist for several years.

Leaves: Leaves are reduced to reddish-brown scales, primarily on the lower portion of the stem. Scales are small, somewhat triangular and often overlap near the base of the plant. Further up the axis they become narrower and somewhat longer. Towards the top of the stem the scales become increasingly covered with glandular hairs.

Inflorescence: Flowers are borne in a long raceme at the end of the stem. Numerous flowers are urn-shaped and nodding at the end of a short curved glandular pubescent pedicel that becomes rigid when dry. Blooms June-August.

Flower: Corolla is urn-shaped (7-8 mm long), 5-lobed, united, white to slightly pink in color; rounded lobes are short and recurved. Sepals are fused below, glandular hairy, and maroon colored. Stamens 10, anthers ovoid each with a pair of reflexed awns. Style short and columnar with a flared, shallowly 5-lobed stigma. Ovary is superior, 5-locular, with axile placentation. Nectaries represented by 10 shallow lobes projecting slightly between staminal bases.

Fruit: Rounded five-lobed pendant capsule about 1 cm in diameter with loculicidal dehiscence opening from the base of the capsule acropetally. Capsule reddish-brown turning darker at maturity. Seeds numerous 0.2-0.3 mm long, ovoid, each with a reticulate wing at one end. Up to 2000-4000 seeds per capsule with a weight of 0.0005 g per 100 seeds.

Life History

Upright stems arise from a tight ball of mycorrhizal roots which are rarely more than seven cm in diameter. The root mass usually lies at the top of the A_1 horizon. Some of the roots elongate producing 3-8 cm root-balls at intervals from which one or more adventitious buds originate (Bakshi 1959). It is not unusual to find several plants growing in an area of a few square meters. At least a few of these plants can be seen to be attached to each other. Often some of the longer roots from one plant can be found to be running in the direction of the other plants, but not quite reaching them. Bakshi (1959) postulated that after establishment of a new plant, the root connecting it with the parent plant dies.

Pterospora andromedea has a multi-layered sheath of tightly interwoven hyphae covering the surface of the roots. The root mass of *P. andromedea* is perennial, but it is unknown if it produces flowering stalks in successive years, or if it produces them once and then dies (monocarpic). The apex of the root is completely covered by the fungal sheath. Both *P. andromedea* and *Sarcodes sanguinea* possess an intracellular component consisting of a single determinate hyphae protruding into the epidermal cells. The intracellular component makes these species quite different from the arbutoid mycorrhizae of such plants as *Arbutus menziesii* and *Arctostaphylos uva-ursi* (Robertson & Robertson 1982).

The anatomy of the roots of *Pterospora andromedea* has several distinctive features. The septate hyphae of the fungus enter the epidermal cells. By the time the epidermis has disintegrated, the hypodermis (layer below the epidermis) is fully covered on the outside by the fungal hyphae. In a mature root structure there is an unbroken mycelial sheath around each root so that *P. andromedea* has no direct contact with the soil. In the laboratory Bakshi (1959), attempted to cut the fungal hyphae off from their connection with root cells; all hyphal tips ceased to grow and were found to be degenerated after 36 hours, suggesting that the fungi are true mycorrhizal taxa (Bakshi 1959).

It has been postulated that the adaptation that enabled the monotrope (member of the Monotropaceae) to absorb carbohydrates from fungi might have been an osmotic modification affecting the root. If the osmotic concentration of sugar is lower in the cells of the root than in the penetrating hyphae, the gradient could cause sugars to diffuse into the root (Harley and Smith 1983 cited in Cole 1994). *Pterospora andromedea* roots remain succulent even in dry, sandy soil. It is possible the hydrophobic phenomenon of the *P. andromedea* root surface could be an adaptation to absorb carbohydrates (Cole 1994).

Flowers are produced in about four weeks, the first typically opening in June. New shoots and inflorescenses can be produced throughout the growing season. Fruiting usually occurs in late July and August. After fertilization, the capsule requires 2 to 3 weeks to mature. Depending upon the size of the plant, from 20-128 fruiting capsules are produced, each bearing from 2000 to 4800 short-lived (3-9 weeks), wind-dispersed seeds with a white, shiny wing about five times the size of the seed (Higman & Penskar 1999).

Pollen grains are four-grooved. An interesting phenomenon in *Pterospora andromedea* is the occurrence of extensive degenerations during development of the male gametophyte. There are a few degenerative pollen grains as early as the second division of the microspore mother cells. As the flower grows the number of degenerating pollen grains gradually increases so that at the mature embryo-sac stage between 83 to 95% of the total pollen grains are sterile. However, sterile pollen does not appear to be limiting seed production; not more than 4-5% of the seeds in any ovary were found to be exembryonate (Baskshi 1959).

Anthers may dehisce even before the flowers open, and pollen grains in this case alight on the stigma of the same flower. Many insects visit the flowers. Each pollen grain may produce one or two pollen tubes, but in the latter case only one grows down the style (Baskshi 1959). 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.

Reproduction and Phenology

Germination in the greenhouse or lab has been unsuccessful, as has transplantation (Baskshi 1959). Apparently it is difficult to replicate the specific biological and ecological conditions required for germination and establishment. Bakshi (1959) tested viability of *Pterospora andromedea* seeds stored at 4^{o}C and at 21^{o}C under both dry and moist conditions. Bakshi (1959) found the seeds to be viable (determined by chemical tests) for only nine weeks or less. There has not been any other reported research on seed storage or preservation. Likewise there is no information about seed dormancy or viability in the soil. *Pterospora andromedea* grows taller than other species in the Monotropideae so it is ideally suited for wind dispersal of its tiny, winged seeds. Leake (1994) speculated that there may be little need for seed longevity since seeds are dispersed at the time when mycorrhizal fungi are particularly active.

Recent field work has shown that seeds of *Monotropa hypopithys* germinated and developed more readily in areas where mature plants occur. When germination occurred, a fungus found on mature plants was normally associated with the seeds suggesting that monotrope seeds might germinate in response to the appropriate fungus (Bruns & Read 2000). Bidartondo *et al*. (2000) found that the abundance of *Rhizopogon ellenae* on *Abies* mycorrhizae was significantly higher in areas immediately adjacent to *Sarcodes* plants. The increased abundance of both *Abies* roots and *Rhizopogon* appeared to result from stimulation by the monotrope plant (Bruns & Read 2000). Laboratory research by Bruns and Read (2000) showed that direct fungal contact was not necessary, suggesting that an unknown volatile or diffusible compound produced by the fungus may be the required stimulus.

Martin Bidartondo (pers. comm. with Schori 2002) is experimenting with seeds of *Pterospora andromedea* placed in mesh bags and buried in the ground in the Sierra Nevada. Bidartondo has observed extremely low germination rates (one per thousand seeds). However, he has observed successful growth of the few seeds that germinate. After one year, he found seedlings with root axes and one to three branches, but no shoots. Leake (1994) had postulated that myco-heterotrophs may take many years to progress from germination to flowering.

No one seems to know how long an individual *Pterospora andromedea* may live or how many years may pass between flowering. *Pterospora andromedea* has been reported as variable in its occurrence and often does not appear aboveground each year (Higman & Penskar 1999). Leake (1994) notes that the flowering of myco-heterotrophs is often highly erratic and some species can disappear for 30 years between flowering at the same site. Pine-drops variable occurrence makes it difficult to determine whether a particular population is extant, dormant, or has died out (Schori 2002).

Another possibility is 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. Bidartondo (pers. comm. with Schori 2002) believes that only genetic studies can reveal whether neighboring plants are clones. It is unclear whether a root mass with multiple inflorescences may be multiple individuals. The idea postulated by Jepson (1939), that *Pterospora andromedea* is monocarpic (blooming once after a prolonged period of root development), has not been disproved (Bidartondo & Evans 2001).

Pterospora andromedea can bloom from late June through August. In New Hampshire five stalks with developing flowers were observed on July 10, 2001. Eight more stalks emerged at the site over the remainder of the season (Schori personal observation). Bakshi (1959) observed that the first flowers did not open until the shoot was about four weeks old. Bakshi also observed that after fertilization, the capsules took two to three weeks to mature. The tough dried stalk is observable well into winter, and can persist for a year or more (Bakshi 1959).

Little is known about pollination of *Pterospora andromedea*. Wallace (1977) studied the nectaries of the Monotropoideae. Although no insects were observed visiting the species, Wallace (1977) thought that the anatomy of the flower suggests that bumblebees may be the pollinators.

Geographic Distribution

The Monotropaceae are mostly restricted to the Northern Hemisphere, although a few members of this family occur as far south as Mexico (*Monotropa hypopithys*, *Monotropa uniflora,* and *Pterospora andromedea*) and *Monotropa uniflora* even approaches the equator in Columbia (Wallace 1975). The center of diversity for the Monotropaceae lies in the western United States. Species in this group are found in mixed evergreen forests from sea level to 13,000 feet (Bakshi 1959). Some species in this family are known from Asia including *Monotropa hypopithys*, *Monotropa uniflora*, and *Monotropastrum humile*. *Monotropa* is a widespread genus with a circumboreal distribution (Wallace 1975).

Pterospora andromedea has a bicentric distribution similar to that of the temperate coniferous forests of North America. In the West *P. andromedea* is largely confined to mountain ranges, but is probably not found north of the Fraser River in British Columbia (Baskshi 1959). *Pterospora andromedea* is scattered in 14 western states. It appears to be most abundant in the Cascade Range of California; another area of concentration is the Northern Coastal Range from California north through Oregon, and Washington to British Columbia. Another high area of concentration is the San Gabriel Mountains north through the Sierra Nevada Mountains. Scattered occurrences are found in the Rocky Mountains from Canada south to Arizona and New Mexico and minimally into western Texas. Its distribution continues south into Mexico with occurrences in the states of Chihuahua, Nuevo Leon, Mexico, Puebla, Tlaxcala, and Vera Cruz (Wallace 1975).

Pterospora andromedea western range extends to the Black Hills in South Dakota; it is then disjunct to the Great Lakes Region (Marquis & Voss 1981). In eastern North America it is found around Lake Huron, Lake Erie, Lake Ontario, the St. Lawrence River, and on Prince Edward Island. In the Great Lakes Region, the plant has not been collected south of the limits of Wisconsin glaciation. It is found in Michigan, Wisconsin, southern Ontario, southern Quebec, Prince Edward Island, several counties in New York and Vermont and one county in New Hampshire (USDA NRCS 2003).

Michigan / Wisconsin Distribution

Many of the recent (post-1978) occurrences for Michigan are known from forested dune communities with the greatest concentrations of occurrences found in Keeweenaw, Emmet, and Leelanau counties. Post-1979 occurrences account for 22 out of 49 reported occurrences for this species. All element occurrences harbored low numbers of individuals, from a single individual to up to 12 stems (MNFI 2003). This species occurs across the entire Upper Peninsula and in the northern Lower Peninsula along both the Lake Michigan and Lake Huron shorelines and a few scattered occurrences in the southern Lower Peninsula (MNFI 2003).

Populations have often been noted as sporadic, not appearing every year. However, Garlitz observed a colony of 10-12 stems every year for 16 years in Alpena County in the partial shade of an old white pine and red maple (MNFI EO # 38).

In Wisconsin, *P. andromedea* is known only from Ozaukee County (1927 – 1970) and Door County (1999). Habitat is listed as sandy soil, or moist sand under *Pinus resinosa* (Wisconsin State Herbarium 2003). *Pterospora andromedea* is not currently known to occur in Minnesota (USDA NRCS 2003).

New England and New York

The only known populations of *P. andromedea* in New England occur in New Hampshire and Vermont. Historically it was more widespread in Vermont. Because of vague herbarium labels it is difficult to determine the number of historic occurrences. Six towns are listed on herbarium records (Burlington, Charlotte, Colchester, Proctor, Williston, and Winooski), as well as some specimens simply listed as western Vermont. Only two extant locations are known: one in a seventh town (West Haven) was located in 1987; a second occurrence was found in 1990 in the town of Colchester on the opposite side of Malletts Bay (Schori 2002). Two historic occurrences are known for New Hampshire from Grafton County, one in the town of Hanover near Nigger Island, and another from Lebanon near Olcott's Falls. This species was recently rediscovered in Hanover, New Hampshire which changes the state rank from SX (extirpated) to S1 (extremely rare) (Schori 2002). In New York, there were 30 historic occurrences in 20 counties across the state. Currently only three occurrences persist, all three in one canyon; however, two of these occurrences have not been observed since the early 1990s (Steve Young pers. comm. with Schori 2002).

Eastern Canada

While *P. andromedea* seems somewhat secure in western Canada, Quebec is the only province with more than a dozen recent occurrences (18 extant occurrences). Sean Blaney (pers. comm. with Schori 2002) reports that it is Endangered in New Brunswick and Historic on Prince Edward Island. In Nova Scotia there are unconfirmed reports from northern Cape Breton Island (S. Blaney pers. comm. with Schori 2002). In Ontario there are 3 counties with extant occurrences and 11 counties with historic occurrences. Quebec has 18 extant occurrences 1996 –2001, and 7 historic occurrences (Schori 2002).

Ecology

Pterospora andromedea relies on a mycorrhizal fungus that is shared between the monotrope and its photosynthetic plant; materials are moved between the photosynthetic and achlorophyllous plants via a fungal bridge. It is impossible to understand the needs of *P. andromedea* without knowing the requirements of its mycorrhizal partner. According to Bidartondo (pers. comm. with Schori 2002), the *Rhizopogon* species associated with *P. andromedea* are high-nutrient-loving, fire-adapted, tolerant of disturbance, truffle-like basidiomycetes that are dispersed by rodents. They are exclusively associated with roots of conifers in the *Pinaceae* (Schori 2002, various EO data).

DNA analysis has lead to increased understanding of the mycorrhizal association of *Pterospora andromedea* and other monotropes. Molecular sequencing is time-consuming and expensive, yet it makes it possible to characterize fungal mycelia in the absence of fruiting bodies (sporocarps) by comparison with named sporocarp collections (Bidartondo and Bruns 2002). Cullings *et al*. (1996) used this technology to discover that *P. andromedea* appeared to be associated with a single species of basidiomycetes, *Rhizopogon subcaerulescens*, commonly referred to as "false-truffle" or "root balls".

More extensive analysis done by Bidartondo and Bruns (2001, 2002) indicates there are more likely two distinct lineages of *P. andromedea* in the West: one associated exclusively with *Rhizopogon arctostaphyli*, and another associated exclusively with *R. salebrosus* (previously *R. subcaerulescens*) species group. It is unclear whether there is more than one genetic lineage of *P. andromedea.* A sample of *P. andromedea* obtained from Quebec was associated with an as yet undescribed fungus from the *Rhizopogon* section *Amylopogon* lineage. As more studies are undertaken, our understanding of the genus *Rhizopogon* and its associations will lead to a clearer understanding of *Pterospora andromedea* (Schori 2002).

Members of the Monotroaceae 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 (deriving nutrients directly from the roots of photosynthetic plants). Bakshi (1959) reviewed the work of various authors. Kamienski (1884 cited in Bakshi 1959) found that roots of *Monotropa hypopithys* had no direct contact with the soil and were not root parasites. Frank (1892 cited in Bakshi

1959) proposed the theory that it was a parasite on a fungus, a view that was later promoted by Bakshi (1959). Radio-tracer work on the related species *Monotropa hypopithys* and *Monotropa uniflora* lead to an advance in understanding (Furman & Trappe 1971); this research demonstrated the movement of materials between the photosynthetic and achlorophyllous plants via their mycorrhizal fungal connection.

The ecological niche for *Pterospora andromedea* has been described as "epiparasitism" since it is parasitic on the mycorrhizal fungus rather than directly on tree roots. Cole (1994) refers to this relationship as "controlled parasitism" rather than mutualism. Cole (1994) considers members of the Monotropoideae to be evolutionarily advanced root parasites that use fungal hyphae to penetrate host roots in the absence of haustoria. Experiments with *Monotropa hypopithys* (Bjorkman cited in Schori 2002) showed that it stimulated the growth of its fungal symbionts. Similar studies of *Sarcodes sanguinea* revealed a similar response on associated fungus on the roots of *Abies magnifica* (Bidartondo *et al*. 2000). No clear evidence exists to show whether this stimulation is of any benefit to the fungus.

To clarify the distinction between mycorrhizal autotrophs (green plants with mycorrhizal associations) and mycorrhizal heterotrophs (achlorophyllous plants that depend on their associated mycorrhizal fungi as their carbon source), Leake (1994) used the term "myco-heterotroph". This terminology has since been adopted by other researchers studying mycorrhizal associations (Bruns & Read 2000, Bidartondo & Bruns 2002).

It appears that *P. andromedea* often becomes established when its host tree is young. If root exudates from the tree stimulate germination, then there is a greater chance of establishing this connection when the tree is young and roots are near the surface. It has also been observed that *P. andromedea* often grows in profusion on slopes, this might be due to erosion exposing the tree roots making it easier for *P. andromedea* seeds to establish its relationship with the mycorrhizal fungus (Cole 1994).

Habitat

Western United States

In the western United States, *Pterospora andromedea* occurs in mixed or coniferous forests at 200 to 12,000 feet elevation, growing under trees or other understory vegetation, rarely in either open or very densely covered areas (Wallace 1975). Western plants are usually 70 to 100 cm tall and up to twice as tall as those normally occurring in the eastern United States. As one goes south *P. andromedea* is found at increasingly higher altitudes, and MacDougal (1899 cited in Henderson 1919) notes that "near its southern limits it is found at altitudes above 2000 meters".

Pterospora andromedea occurs on podzolic soils. The root clumps are confined to the A_1 horizon, and the long lateral roots run on the surface of the A_1. In the western United States, *Pterospora andromedea* is typically found in moist soil (Bakshi 1959). However, Gleason (1952) and Fernald (1950) both reported this species from dry woods or dry soil indicating that in some sections of its range, especially in the eastern United States, the soil is at least seasonally dry.

In the western United States, *P. andromedea* is most often associated with *Pinus ponderosa* (Flora of the Great Plains 1986). In the Pacific Northwest, Molina *et al*. (1999) found that *Rhizopogon* species show strong specificity to *Pinaceae*, especially to *Pinus* or *Pseudotsuga*. Other common associated species in the western United States include: *Pinus contorta, Pinus lambertiana, Abies concolor, Abies grandis, Pseudotsuga menziesii, Sequoiadendron giganteum, Calocedrus decurrens, Larix occidentalis,* and *Quercus kelloggii*. Associated herbs include *Gaultheria shallon, Arctostaphylos uva-ursi, Pyrola picta, Allotropa virgata, Chimaphila umbellata,* and *Arbutus menziesii* (Bakshi 1959).

Eastern United States

In the eastern United States, *P. andromedea* corresponds to the distribution of *Pinus strobus* (white pine) which is centered around the Great Lakes (Schori 2002). *Pinus strobus* is common in the area of the three New Hampshire occurrences (extant and historic) and occurs at both extant Vermont occurrences (Schori 2002).

Bakshi (1959) stated that the eastern population distribution of *Pterospora andromedea* does not extend south of the limits of Wisconsin glaciation. In Vermont, all extant and historic occurrences are from locations that were inundated by Lake Vermont during the retreat of the Wisconsin glacier at about 12,500 years ago. In New Hampshire, occurrences are found on sediments of Lake Hitchcock; this lake was formed by the retreating glacier when the Connecticut River was dammed by a moraine. Many Michigan occurrences are found on sandy dunes along the Great Lakes shorelines (Higman and Penskar 1999).

A similar distribution pattern is found in eastern Canada. Ontario occurrences have all been found near the Great Lakes (Haber and Keddy 1984). The Ottawa River region of Quebec contains the largest populations of *Pterospora andromedea*; this area was subjected to similar inundation and sedimentation (Antevs 1928 cited in Schori 2002).

The two extant occurrences of *P. andromedea* in Vermont are in dolomitic areas at the base of north slopes (Vermont Nongame and Natural Heritage Program). This site at the base of a steep slope has very clayey soil. New Hampshire sites (Schori 2002) along with some Quebec occurrences (Andre Sabourin, pers. comm. with Schori 2002) occur on clay soils as well. Other Quebec populations occur over limestone or marble (Andre Sabourin pers. comm. with Schori 2002). One New York occurrence was on a limestone island and many were in areas of shale (Steve Young, pers. comm. with Schori 2002).

According to Scott Bailey (Hubbard Brook Experimental Forest, pers. comm. with Schori 2002), a unifying feature of these sites may be small particle size (silt and clay), and high cation exchange capacity or base saturation, leading to increased availability of calcium, magnesium, and potassium. This is consistent with Bidartondo's assertion that *Rhizopogon* species are high-nutrient-loving (Schori 2002).

Michigan habitat

The only currently known sites for *P. andromedea* in the Eastern Region of the National Forest occur on the three Michigan National Forests; therefore, understanding the Michigan habitat becomes critical for survival of the eastern population in the United States.

In Michigan, *Pterospora andromedea* is found in dry coniferous forests containing a high percent cover of *Pinus resinosa* and *P. strobus* (red and white pine), *Abies balsamea* (balsam fir), (*Tsuga canadensis*) hemlock, and *Picea glauca* (white spruce). These sites normally have a well developed needle duff (Higman & Penskar 1999). Other overstory associates are *Juniper communis* (common juniper) and occasionally *Populus tremuloides* (aspen) or *Betula paprifera* (paper birch) (Voss 1996). In Michigan, *Pterospora andromedea* is often found in interdunal swales, and less commonly in moist conifer or maple woods (Albert & Comer 1999). The Ottawa National Forest sites, in contrast, are found on an old lake plain that is wet part of the year (S. Trull pers. comm. 2004).

Using the Floristic Quality and Wetland categories, *P. andromedea* is characterized as an upland plant (rating 5, almost never in wetlands) and given a 10 (or highest) coefficient of conservatism (only found on pristine sites).

Associated species in Michigan: Trees – *Pinus strobus* (white pine), *Pinus resinosa* (red pine), *Abies balsamea* (balsam fir), *Acer rubrum* (red maple), and *Thuja occidentalis* (white cedar). It also occurs with *Betula papyrifera* (paper birch), *Populus tremuloides* (quaking aspen), and *Populus grandidentata* (bigtooth aspen). Associated shrubs are *Juniperus communis* (common juniper) and *Vaccinium angustifolium* (lowbush blueberry) (Chadde 1999). Associated herbaceous species include *Aster macrophyllus* (large leaved aster), *Gaultheria procumbens* (wintergreen), *Pteridium aquilinum* (bracken fern), *Lycopodium obscurum* (ground-pine), and *Lycopodium clavatum* (running pine) (Higman & Penskar 1999; Chadde 1999). Other associates on the Ottawa National Forest include *Waldsteinia fragarioides* (barren strawberry), *Danthonia spicata* (poverty oats), *Achillea millefolium* (common yarrow), *Aralia nudicaulis* (wild sarsaparilla), and *Chimaphila umbellata* (pipsissewa) (Ottawa NF Element Occurrences 2002).

Rangewide Protection Status (NatureServe)

Currently, the official status for *Pterospora andromedea* Nutt. with respect to federal, state, and private agencies is:

U.S Fish and Wildlife Service: Not listed (None)
Global Heritage Status Rank: G5
U.S National Heritage Status Rank: N?

Canada Heritage Status Rank: N?

U.S. Forest Service: Regional Forester's Sensitive on the Hiawatha (MI), Huron-Manistee (MI), and the Ottawa (MI) National Forests.

The Regional Forester has identified it as a species for which viability is a concern on Hiawatha, Huron-Manistee, and Ottawa National Forests as evidenced by: **a)** significant current or predicted downward trends in population numbers or density, and or **b)** significant current or predicted downward trends in habitat capability that would reduce its existing distribution (FSM 2670.5.19).

With a global rank of 5 and a U.S. National rank of ?, The Nature Conservancy lists these rankings as:

N?: National ranking has not been adequately assessed

G5: Demonstrably secure globally, though it may be rare in portions of its range, especially at the periphery

United States Heritage Ranks

Arizona	SR	New York – Endangered	S1
California	SR	Oregon	SR
Colorado	SR	Pennsylvania – Not ranked	SU
Idaho	SR	South Dakota	SR
Massachusetts – Extripated	SX	Texas	S1
Michigan – Threatened	S2	Utah	SR
Montana	SR	Vermont – Endangered	S1
Nebraska	S2	Washington	SR
Nevada	SR	Wisconsin – Endangered	S1
New Hampshire[1] – Endangered	SX	Wyoming	S3
New Mexico	SR		

1. New Hampshire updated to S1 (Schori 2002)
2. State's legal status given for states in Eastern Region (R9) of the Federal Forest

Canada Heritage Ranks

Alberta	S3	Prince Edward Island	S3
British Columbia	S3S4	Quebec	S2
New Brunswick	S1	Saskatchewan	S1
Ontario	S2		

Definitions (NatureServe)

S1: Extremely rare; typically 5 or fewer known occurrences in the state; or only a few remaining individuals; may be especially vulnerable to extirpation.

S2: Very rare; typically between 6 and 20 known occurrences; may be susceptible to becoming extirpated.

S3: Rare to uncommon; typically 21 to 50 known occurrences; S3 ranked species are not yet susceptible to becoming extirpated in the state but may be if additional populations are destroyed.

S4: Common; apparently secure under present conditions; typically 51 or more known occurrences, but may be fewer with many large populations; usually not susceptible to immediate threats.

SR: Reported but not assessed as to frequency of occurrence

SU: Not enough information available for ranking

SX: Presumed extirpated

Population Biology and Viability

Populations are often sporadic and do not send shoots above ground each year. Depending on the size of the plant, from 20 – 128 fruiting capsules are produced with up to 4800 short-lived seeds (Bakshi 1959). However germination appears to be quite low suggesting very specific conditions including one or more substances not universally available in nature are needed for germination and establishment (Bakshi 1959).   Seed viability was found to be low; initial seed viability was 18.3% and subsequently declined to zero over the 133 day testing period (Cole 1994). A short seed life of four months means that the seeds must be dispersed and establish symbiosis with a mycorrhizal fungus before the onset of winter (Cole 1994). The massive quantity of seeds produced is likely a compensating factor since the probability of an individual seed becoming established appears to be low.

Several techniques were used to attempt to induce germination. Stratification involved wrapping seeds in dry paper towels and placing them in the freezer at –10^{o}C for 1-4 weeks. Leaching was accomplished by placing in plankton netting under running tap water for 24 hours. Scarification involved abrading seeds with 400-grit sand paper until seed coats were lightly scarified or the seed coat was mostly cracked (heavy scarification). None of the seeds subjected to single treatments or a combination of treatments were observed to germinate (Cole 1994).

The small food reserve in *Pterospora andromedea* seed makes it necessary for the seed to be in close proximity to a host fungus. The propensity of *P. andromedea* to form mycorrhizae exclusively with *Rhizopogon* coupled with the failure to respond to any of the standard dormancy-breaking treatments seems to favor an exchange of chemical cues as the initiating factor. Seeds also failed to germinate even when cultured in close proximity to fungi isolated from *P. andromedea* roots, possibly indicating that the rhizosphere contains a chemical essential for germination. Therefore, the mere presence of *Rhizopogon*, the mycobiont of *Pterospora*, is not effective in inducing germination (Cole 1994). It is possible that the germination factor missing from the controlled laboratory experiments might be a root exudate from the host tree. Recent research has shown that root exudates contain soluble volatile compounds that are important in the establishment of mycorrhizal symbiosis (Koide and Schreiner 1992; Peterson and Farquhar 1994 cited in Cole 1994). *P. andromedea* seeds could use host root exudates to trigger germination and initiate symbiosis with the fungus. Another piece of evidence that root exudates play a role in establishment is the close proximity of the roots of *P. andromedea* to the roots of a fungal host tree.

On the other hand, *P. andromedea* has a wide ecological amplitude sometimes occurring under oaks as well as pines. It is quite rare in eastern North America, but it has enough flexibility to have successfully invaded several glaciated areas in the eastern United States (Bakshi 1959). The ectomycorrhizal fungus *Rhizopogon* is fairly unspecific in its association with conifers so there could be a number of potential tree hosts for *Pterospora* (Cole 1994). Element occurrences in the western United States seem to indicate more flexibility in host trees, while eastern North America element occurrences normally mention *Pinus strobus* as the host.

On average *P. andromedea* becomes established when the host tree is quite young and the tree diameter is approximately 7 cm. Intuitively this makes sense since exudates are released by the young tree rootlets to aid in the formation of mycorrhizae. Patterns of establishment for many sites would need to be examined to see if this relationship holds in other communities (Cole 1994).

In the literature, individual populations are rarely reported with more than 12 upright structures in a clump; more often just one or two upright structures are noted (MNFI EO 2003). Small patches of only a few stems at one location have been reported throughout most of its range (Bakshi 1959, Wallace 1977). Most populations in Michigan were small, just one or two upright stalks (MNFI 2003). In contrast, in Quebec there are several large populations. Andre Sabourin, an independent botanist, and Frederic Coursol, of the Flora Quebec, reported several populations of 100 or more stems along the Ottawa River Valley, and another population of approximately 500 stems on a limestone island (pers. comm. with Schori 2002).

Pterospora andromedea appears to be in serious decline throughout its eastern distribution, with the possible exception of Quebec (18 extant occurrences). Vermont had at least eight distinct historic occurrences, but only two occurrences have been observed within the past 20 years (Schori 2002). New York populations plummeted from

30 to 3 occurrences all in one canyon (Steve Young, per. comm. with Schori 2002). Half of Michigan's 43 occurrences are historic records (MNFI 2003). Ontario has also lost occurrences: 11 counties had historic records, but now there are extant populations in only four counties (Marquis & Voss 1981). Massachusetts populations are presumed extirpated and New Hampshire had two historic occurrences, but recently another site was located in Grafton County New Hampshire (Schori 2002).

There are good indications that the eastern population of *P. andromedea* is a distinct subpopulation from the Rocky Mountains: the two populations are disjunct, the soil types are quite different, and most importantly they appear to be associated with different species of *Rhizopogon* (Bidartondo & Bruns 2002). If subpopulations of plants were available for listing, Wallace (pers. comm. with Schori 2002) would have supported federal listing for the eastern subpopulation.

Potential Threats

The fact that *P. andromedea* is non-photosynthetic means it is dependent upon mycorrhizae on tree roots, mostly *Pinaceae*. The specific biological and ecological conditions for germination and establishment are unclear. Mycorrhizae associations are limited to only *Rhizopogon* sp. and their distribution further limits the distribution of *P. andromedea* (Cole 1994).

Habitat loss is probably a major factor in the loss of populations especially in New England. Rich soils that support the nutrient-loving *Rhizopogon* are desirable as farmland or as production forests. Many historic collections in Vermont were from Chittenden County; this region has been logged, used for agriculture, and heavily developed suggesting that those factors resulted in the decline. Timber harvesting and habitat lost appear to be the major causes of decline for *P. andromedea* in Quebec (Andre Sabourin, pers. comm. with Schori 2002).

Clear cutting, or even selective cutting, could have a very deleterious effect and could eliminate the autotrophic partner on which the fungus and *P. andromedea* rely. *Pterospora andromedea* populations are usually small, consisting of only a few stems at any one location. Disturbing the soil in the wrong spot could eliminate the whole population at a site (Schori 2002). In contrast, on the Ottawa National Forest in Michigan most sites of *P. andromedea* occur at forest-edge sites (I. Shackleford pers. comm. 2004).

Pedestrian traffic may degrade suitable habitat. At one New Hampshire occurrence there is an unauthorized trail that goes through the middle of a population. At another New Hampshire site an island that harbored an occurrence was heavily used by members of an outing club and by boaters. Visitors do not have established trails, but instead wander freely about the island and they have suppressed the growth of many herbaceous species (Schori 2002). One New Hampshire occurrence is on a steep slope overgrown with invasive species such as *Elaeagnus umbellata* and *Frangula alnus*. *Pterospora* *andromedea* tends to grow at sites with little herbaceous cover and a fairly open understory which are often the same sites favored by invasive plants. If these invasive plants become too dense they could have a negative effect (Schori 2002).

Global warming would not be expected to be a significant threat to this species as it grows from Canada to Mexico, across a broad range of temperatures and precipitation regimes. However, climate change could stress struggling, marginal occurrences and lead to local disappearance of populations (Schori 2002).

Predators or disease does not appear to be a problem for *P. andromedea*. 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 would likely make the plants unpalatable to herbivores. No mention of herbivory was indicated for New England occurrences (Schori 2002), and it would be logical that the sticky-clammy stems of *P. andromedea* would deter herbivores.

In the western states, fire suppression has been mentioned as another possible factor in the decline of *Pterospora andromedea* populations since some western populations of *Rhizopogon* appear to be fire adapted (Martin Bidartondo, pers. comm. with Schori 2002). After a wildfire in California, mycorrhizal fungi on pine seedlings was dominated by *Rhizopogon* species (Baar *et al.* 1999 cited in Schori 2002). Fires occur infrequently in the eastern forests, yet fire could have been a historic factor in drier conifer forests (Schori 2002). In Michigan and Wisconsin, *P. andromedea* occurs in fire-susceptible plant communities; these communities have been undergoing successional changes due to fire suppression. Albert (1994) notes that fire was important on droughty outwash plains, and bedrock ridges dominated by conifer species.

Natural succession often leads to replacement of white pine by hardwoods. Curtis (1971) notes that "barring catastrophe, white pines gradually die out and would probably be entirely gone within 600 years under natural conditions, leaving a climax mesic forest which would gradually increase in sugar maple dominance". The two major disasters which are most likely to affect the forest are fire and wind throw. Fire is more frequent in early stage pine forests because of low moisture and high light at these sights frequently leads to conditions of high combustibility. Following the establishment of hardwoods, chances for fire decrease due to a more even supply of moisture on the forest floor. Previous to fire suppression, fire related regression due to a ground fire, would occasionally slow or reverse the succession to hardwoods (Curtis 1971).

In the Great Lakes area, *P. andromedea* appears to be dependent on white pine (*Pinus strobus*). There are two main enemies of this pine, the white pine blister rust (*Cronartium ribicola*) and the white pine weevil (*Pissoides strobi*) (Barnes & Wagner 1981). The blister rust is a fungus that slowly girdles the branches and main stem. The fungus requires the presence of gooseberry or currant bushes to complete its life cycle. Spores are blown from the bushes to the tree needles (Smith 1952). Because this relationship is well known, efforts to eliminate host bushes have now resulted in a reasonable level of control. The other pest is the white pine weevil that attacks and kills the terminal shoots of trees causing them to become deformed and crooked making them unsuitable as timber (Smith 1952).

In the Lake Superior Highlands area, forests dominated by *Pinus strobus* (eastern white pine) have declined from 90,650 ha in 1936 to 25,000 ha in 1996 (MN DNR 1996 cited from Anderson *et al.* 2002). In this same region, eastern white pine historically constituted 30% of the trees, but currently constitutes only 5% of the overstory trees (Spingarn *et al.* 1986 cited from Anderson *et al*. 2002). The interplay of multiple factors has resulted in this decline. Factors causing this decline consist of intensive harvest, infestation by blister rust, fire suppression, and browsing by herbivores (Anderson *et al.* 2002). Fire suppression (Anderson *et al.* 2002) and high intensity fires among logging slash (Ahlgren 1973 cited from Anderson *et al.* 2002) have also altered forest composition. Anderson *et al.* (2002) studied the effects of browsing by herbivores, particularly white-tailed deer (*Odocoileus virginianus* Zimm.).

Enclosures excluding deer for 7 to 10 years did reduce browsing and substantially increased eastern white pine recruitment. These enclosures needed to be in place for five years or longer before white pine seedlings began their recovery (Anderson *et al.* 2002). While constructing enclosure structures are not feasible across the entire forest, Anderson *et al.* (2002) did find that spruce-fir (*Picea glanca*/*Abies balsamea*) patches did decrease susceptibility of eastern white pine seedlings and saplings to browsing. There was some concern, however, that spruce-fir patches might attract snowshoe hare (*Lepus americana*) another white pine herbivore seeking food, thermal cover, and protection from predators (Krefting 1975 cited from Anderson 2002).

New England

Acid precipitation is a well-documented phenomenon in the Northeast; Wallace (pers. comm. with Schori 2002) suggested that it could be a factor in the decline of eastern populations of *P. andromedea*. Eastern populations are restricted to soils with high base saturation. Clay and silt soils or fine-grained mudstone or shale, because of their small particle size, could have high nutrient availability even if somewhat acidic. Before the days of acid precipitation, the New York shales could have provided enough nutrients to satisfy the fungi. However many shales are not particularly rich in calcium. Acid precipitation could both leach essential minerals and change the soil cation exchange capacity, making nutrients less available to the fungi (Danielson & Visser 1989). Areas where soil is not strongly influenced by calcareous rock might be expected to lose their ability to sustain *P. andromedea* and *Rhizopogon* spp. if acid precipitation continues unabated (Schori 2002).

In New England, it appears that over-collecting of specimens could have been a factor in the decline of *P. andromedea.* Schori (2002) reports that Oakes and Pringle provided specimens from Vermont and New York to many herbaria all over the country in the 1800s. P*terospora andromedea* occurs mostly in very small, widely scattered populations, with only a few flowering stems at any one site. Collecting at these sites, especially before seed release, could have adversely affected this species.

Michigan
On the Ottawa National Forest two element occurrences are found near old forest roads or ATV (all-terrain vehicles) trails. Forest edge sites appear to be an advantage to *P. andromedea*; whether it is related to minor root disturbance, sunlight reaching the tree roots, or ease of locating specimens near trail edges is not clear. However, it does mean that these sites could be subjected to additional detrimental recreational hazards such as ATVs (Ottawa NF Element Occurrences 2002). On the Hiawatha National Forest, one site in close proximity to a horse trail may have been eliminated when trail maintenance was done (D. LeBlanc pers. comm. 2003).

Logging and the possible widening of logging roads or soil disturbance caused by dragging logs is a concern for this species. Since this species is often associated with conifers, it is likely to occur in areas that are used primarily for timber production. In particular, the amount of soil disturbance associated with pine regeneration needs to be assessed (USDA FS Viability 2003), and it is unclear how much soil compaction *P. andromedea* can tolerate.

Summary of Existing Habitat Protection

The nature of this plant as a root parasite makes it less likely that specific efforts are made to preserve this species compared to more showy plant species. Because of sporadic flowering of *Pterospora andromedea* it unclear whether one will find flowering stalks in the same area year after year. Its sporadic habit makes it more difficult to harness preservation interest with the general public compared to showy plants like the dwarf lake-crested iris (*Iris lacustris*) that grows in large colonies in the same location each year. *Pterospora andromedea* is a rare plant that only a few botanists understand and appreciate.

The table below lists current known occurrences for *P. andromedea* on public lands within Michigan.

Michigan Sites under Public Management

Managed Area	*County*	*Last Observed*	*Documentation of EO*
Sleeping Bear Dunes	Leelanau	1990-06	Thompson, P.W. 1948
Wilderness State Park	Emmet	1979-08	Crispin, S.R. 1979
Wilderness State Park	Emmet	1991	McVaugh, R. 1948
Wilderness State Park	Emmet	1994-02	Hagenah, D.S. 1951
Hiawatha National Forest	Delta	1999	Marr, J. 1999
Hiawatha National Forest	Schoolcraft	2001	LeBlanc, D. 2001
Hiawatha National Forest	Mackinac	1994	Jauzems, M. 1994
Mackinac Island	Mackinac	2002-08	Ridge, P. 2002
Lake Huron Sand Dunes Plant Preserve	Chippewa	1978-07	Ballard, H.E. 1981

Fort Wilkins State Park	Keweenaw	1979-08	Crispin, S.R. 1979
Ottawa National Forest	Ontonagon	1998	Matula, C. 1998
Ottawa National Forest	Ontonagon	1993	Hoefferle, A. 1993
Sleeping Bear Dunes	Leelanau	1982-08	Chapman, K.A. 1982
Mackinaw State Forest	Alpena	1989	Garlitz, D. 1989
Huron National Forest	Iosco	1990-07	Goff, F.G. 1990
Escanaba State Forest	Marquette	1992-07	Comer, P. & D. Albert
Sleeping Bear Dunes	Leelanau	1992-08	Case, F. 1993

In addition, *P. andromedea* has been known historically from Port Huron State Game Area in St. Clair County, the Huron-Manistee National Forest in Alcona and Iosco (2 historical occurrences and two current occurrences) and the Huron Mountains in northern Marquette County. The Marquette County site in the Huron Mountains would have remained undisturbed since this area is not open to the public and timber is not harvested from this acreage, but the site could have been lost to community succession. As the element occurrence is from 1959, a reassessment of this area would be necessary to know if *P. andromedea* is still present.

Management and Conservation Issues

The most clearly understood aspect of this species ecological requirements is its dependence on its indirect mycorrhizal association. Therefore, management strategies should focus on preservation of ecosystem function, with particular attention to the maintenance of soil microbe and mycorrhizal diversity (Higman & Penskar 1999) and avoidance of soil disturbance (USDA FS Viability 2003).

Several occurrences for *P. andromedea* in Michigan are found in wooded dune swales (MNFI 2002). Therefore, protecting the hydrology and avoiding soil compaction in these dune and swale complexes are important in maintaining the vegetative structure in this community type (Albert & Comer 1999). Another concern is that road development, even with the use of culverts, typically alters the hydrology.

Overall, *P. andromedea* numbers appear to be decreasing from pre-European settlement times in the eastern United States. Although the dynamics are not understood, second-growth forests do not seem to favor the reestablishment of this species as many historical occurrences have been lost in eastern states. In Michigan, there is evidence for habitat loss in the southern tier of counties where woodlots have been lost to agriculture or urban spawl; it is less clear what its status is further north within the state.

Soil disturbance is often cited as a reason for its disappearance, but some element occurrences (EOs) are found on hillsides subjected to soil erosion or at woods edge near trails (Ottawa EOs 2002). Population establishment dynamics are unclear and further research is needed.

In the Great Lakes Region, browsing by deer interferes with the establishment and recruitment of eastern white pine seedlings (Anderson *et al.* 2002), which is the most frequent host tree for *P. andromedea* in the eastern United States. Many foresters in this region now protect their eastern white pine seedlings by placing thick paper envelopes or bud caps over the terminal leaders each fall and removing them each spring (Anderson *et al.* 2002).

Research and Monitoring

Pterospora andromedea is a myco-parasitic plant dependent upon the mycorrhizal fungus growing on tree roots. It is unclear how fungus dependence limits its distribution, and what environmental factors influence the frequency with which it sends up its fruiting structure. Discussion continues as to whether these myco-parasitic plants are harmful or helpful to the trees with which they are associated.

Further investigation of the mycorrhizal system of *Pterospora andromedea* is of critical importance for facilitating protection planning for this species. Also critical is an understanding of what triggers pine-drops to send up a reproductive structure, and what are the exact requirements for germination and establishment. What pollinates the flowers, is there cross-breeding? Are isolated small populations genetically sustainable? Research is needed on how to induce germination and growth. Other research questions include how to assess the age of *Pterospora andromedea* root masses, and how long after disturbance does an individual send up fruiting structures. Does species diversity play a part or can monoculture pine plantations support this species?

Monitoring is somewhat problematic since populations do not send up fruiting structures each year; an individual plant can occupy a site for years and not be seen. Yet long-term monitoring of marked sites could help to answer some of the research needs posed in the previous paragraph. Long term monitoring should give some indication as to the continued health of populations. Currently in Michigan it is unknown whether this species is in decline and what factors could cause decline.

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Appendix for Pterospora andromedea

Hiawatha National Forest (Upper Peninsula of Michigan) (USDA Threatened and Endangered Plant Species Atlas 2003)

Location	Date Last Observed	Remarks
Trenary SE Quad Delta County	1999	Forest Service Atlas
Schoolcraft County	July 26, 2001	Near Swan Lake; upland forest of *Populus grandidentata* with *Pinus strobus* understory. Note: New horse trail may have negatively impacted this site.
Pt. Aux Chenes Mackinac County	Sept. 01, 1994	1 plant at edge of *Juniperus communis* thicket on old dune ridge. Also listed by MNFI
Round Island Mackinac County	Not indicated	Ref. in old atlas – 2 occurrences
Evergreen Shores Mackinac County	Not indicated	Ref. in old atlas – 2 occurrences

Michigan – Ottawa National Forest (Plant survey forms)

Location/ County	Date Last Obs.	Remarks
Ontonagon County, N. Military Hill (adjacent private land)	June 2001	Dry northern forest of *Pinus strobus* and *Abies balsamea* on top of a ridge. Likely part of a metapopulation with the two occurrences below.
Ontonagon County, Hwy 45 north of Bruce Crossing	July 27, 1998	Several clumps were close to a forest road and the North Country Trail where pine canopy of *Pinus resinosa* and *Pinus strobus* was more open.
Ontonagon County, O Kun De Kun Falls	August 10, 1993	3 flowering plants at base of aspen surrounded by white pine, balsam fir, and white spruce. Near old road/ATV trail.

Huron-Manistee National Forest (Michigan Lower Peninsula)

Location/ County	Date Last Observed	Remarks
Alcona County	June 07, 1953	Hemlock-hardwood hillside
Iosco County	June 07, 1953	Hemlock-hardwood hillside
Iosco County	July 30, 1990	
Iosco County	2000	Specimen not gathered, seen by A. Cleveland (pers. comm. 2003)

Michigan – Other Upper Peninsula Locations (MNFI electronic database 2003)
Counties (Keweenaw, Dickinson, Schoolcraft, Chippewa, and Mackinac)

Location/ County	Date Last Observed	Remarks
Keweenaw County, Mount Bohemia	July 18, 1953	Northern forest
Keweenaw County, Mount Bohemia	July 18, 1953	Northern forest
Keweenaw County, Cliff Mine – 5 occurrences	August 09, 1979	Shallow soil at summit of range; found under *Pinus banksiana* and *Pinus resinosa*.
Keweenaw County, Silver Isle	August 26, 1928	Edge of spruce/aspen forest
Keweenaw County, Copper Harbor	August 08, 1979	Spruce, fir, and white pine forest
Keweenaw County, Eagle Harbor	August 01, 1981	Edge of elevated roadbed near border of Pinus strobus and P. resinosa.
Keweenaw County, Silver Creek	August 02, 1981	Two plants in *Thuja, Pinus strobus, Abies* forest in pine needles litter.
Keweenaw County, Grand Marais – 2 occurrences	July 31, 1985	1 plant beneath large *Pinus strobus* in open forest.
Keweenaw County, Lake Bailey	Sept. 18, 1999	4 plants seen on steep south facing slope (MICH herbarium, J.K. Marr)
Dickinson County, Fumee Creek Roadside Park	July 08, 1981	11 stalks seen in a 3 x 3 m area on the upper SW face of a limestone ridge dominated by *Pinus resinosa* and *Thuja occidentalis*.
Schoolcraft County, Gulliver Lake Dunes	August 23, 1929	Between the 1st and 2nd dune ridge.
Marquette County, Huron Mountains – 2 occurrences	July 19, 1959	A rocky bluff; under *Tsuga canadensis, Pinus banksiana*, and *Pinus resinosa*.
Marquette County, Little Presque Isle Point – 2 occurrences	July 29, 1992	5 plants occurring on a ridge of a dune swale complex under a canopy of *Quercus rubra, Pinus strobus*, and *Abies balsamea*.
Mackinac County, Mackinac Island	August 23, 2002	8 stems growing under *Abies balsamea* & *Thuja occidentalis*
Mackinac County, Rabbit Back Peak	August 23, 1951	A dry coniferous forest
Chippewa County, M-134 dunes	July 23, 1978	Sand blowouts created disturbance at site
Chippewa County, Hannah Creek	August 12, 1979	A rocky hill of Niagara formation with *Pinus strobus* and *P. resinosa*
Chippewa County, Marble Head NE shore of Drummond Island	Sept. 01, 1994	2 fruit stalks from last year; on limestone outcrop growing in thin

		soil in Pinus strobus litter.
Chippewa County, Drummond Island	August 06, 1960	A damp coniferous forest.

Michigan – Lower Peninsula Locations (MNFI 2003) (**Historical** entries only)
Counties (St. Clair, Antrim, Grand Traverse, Ottawa)

Location/ County	Date Last Observed	Remarks
Grand Haven, Ottawa County	July 20, 1871	No data on specimen label
St. Clair County – 6 occurrences	August 06, 1893	Pine covered bluffs on high banks
Elk Rapids, Antrim County	July 18, 1902	2 occurrences
Elk Rapids, Grand Traverse	July 18, 1902	1 occurrence
St. Clair County	August 07, 1892	Among pines on a bluff

Michigan – Lower Peninsula Locations (not including Huron-Manistee) (MNFI 2003)

Location/ County	Date Last Observed	Remarks
Trails End, Emmet County	July 19, 1952	Found under *Pinus resinosa*
Leelanau County – 2 occurrences	July 23, 1954	Pine barrens
Big Stone Bay, Emmet County	August 14, 1979	Conifer forest dominated by *Pinus strobus*; also under *Pinus resinosa*
North Point Shores, Alpena Co.	July 24, 1986	White/red pine forest on sandy soil
Good Harbor Bay, Leelanau Co. – 3 occurrences	June 1990	5 stems in moist sand under conifers
Trails End, Emmet County	August 11, 1982	3 clumps of 2-4 stems with *Juniperus communis* on the back side of an old dune ridge
Good Harbor Bay, Leelanau County	August 19, 1982	Jack pine barren with narrow strip of white pine
Hoeft State Park, Presque Isle	July 18, 1954	Dry-mesic northern forest
Evergreen Beach, Presque Isle	August 03, 1969	Under *Pinus strobus*
Mackinaw City, Emmet Co.	Summer 1982	Dry northern forest
Spruce Road, Alpena Co.	Summer 1989	Small colony of 10-12 stems in partial shade of old *Pinus strobus*
Sturgeon Bay, Emmet Co.	July 20, 1994	A pine-hardwood forest on an old dune (*Pinus strobus*, *Populus balsamea*, and *Abies balsamea*)

Wisconsin (University of Wisconsin at Madison, 2003)

County	Date Last Observed	Remarks
Door	May 25, 1999	Sandy soil under Pinus resinosa
Door	Not indicated	

Ozaukee	August 5, 1967	Shaded soil along swale
Ozaukee	July 24, 1970	Moist sand under conifers
Ozaukee	August 15, 1928	
Ozaukee	June 26, 1967	Pine-hardwood forest

Wisconsin: State Endangered
Minnesota: Not known from state (USDA NRCS 2003)

Eastern States

Vermont: State Endangered. Two current records in two counties (Rutland and Chittenden in western Vermont) (USDA NRCS 2003); sandy bluffs under *Pinus strobus* (1879) (MICH herbarium). Historically between 6 to 12 collections from Chittenden and Rutland Counties; some might have been duplicates.

New Hampshire: State Endangered. One county (Grafton); dry, pine woods. Relocated in 2001 on private land and a change in status to Endangered was recommended (Bill Nichols pers. comm. with Schori 2002). Historically two element occurrences in Graton County at Hanover and Lebanon.

New York: State Endangered; Specimens from Buffalo and Niagara Falls, New York (1898) (MICH herbarium). Currently 3 element occurrences all from one canyon (Mt. Morris Canyon in Letchworth State Park in Livingston County (SteveYoung pers. comm. with Schori 2002). Twenty historic occurrences from 1835 to 1929, and one historic occurrence from 1952 are at the Cornell Herbarium (Schori 2002).

New York – Natural Heritage Program at Cornell (Extant records)

County	**Location**	**Last Obs.**	**Description**
Livingston	Mt. Morris Canyon	July 7, 1991	Small white pine stand
Livingston	Mt. Morris Canyon	Nov. 4, 1992	Near edge of gorge under *Pinus strobus* + *Tsuga canadensis*
Livingston	Mt. Morris Canyon	Aug. 22, 2001	Appalachian oak-pine forest under white pine with *Pinus strobus, P. resinosa, Acer rubrum*

Associated species at Mt. Morris Canyon: *Cornus florida*, *Vaccinium pallidum. Lathyrus ochroleucus, Carex pensylvanica,* and *Lilium philadelphicum.*

Massachusetts reportedly one specimen at GH, but it was not seen in collection there in 2001 (Schori 2002). It is listed as presumed extirpated.

Western States

Primarily a species of the western United States. It is known from South Dakota, Nebraska, Texas, New Mexico, Colorado, Wyoming, Montana, Idaho, Utah, Arizona, Nevada, California, Oregon, and Washington (USDA NRCS 2003).

Note: Individual state entries give a sense of associates and elevation in the western states, but they are far from a complete distribution record as only specimens at the University of Michigan were examined.

- South Dakota (Black Hills): dry soil (Flora of the Great Plains 1986). Six counties in western portion of state (USDA NRCS 2003). Open *Pinus ponderosa* forest (MICH herbarium).
- Utah: Northeastern section in mountains (Elevation range 2420 to 3250 meters) (Utah State University, Department of Geography 2003). Dixie National Forest elevation 8,800 feet (MICH herbarium).
- Wyoming: Rocky Mts. At 8200 ft. and Teton National Park (MICH herbarium)
- California: Base of sugar pine (*P. lambertiana*) at 4000 ft. (MICH herbarium)
- Oregon: Deschultes National Forest, *Pinus ponderosa* woods in thin brown soil over lava (MICH herbarium).

Canada

- British Columbia: Deep humus in coniferous forests north to approximately 55^{o}N

- Alberta and Saskatchewan: To southern Alberta and Saskatchewan: Waterton Lakes, Pincher Creek, Cypress Hills, and Breitung (Scoggan 1979).

- Manitoba: Known from Manitoba (Scoggan 1979).

- Ontario: (reported by Gillett 1972 unless indicated otherwise).
  Type from Niagara Falls, Welland County (Scoggan 1979).
  Marmora, Ontario under pines at dry site (Gillett 1972).

  Wasaga Beach, Simcoe County, Ontario (July 1948), woods on ancient dune shore

  Middlesax County, Komoka, Ontario (Aug. 1 1888).
  Hamilton, Ontario (several collections 1861-1880).

  Grand Bend at Lake Huron in oak woods (July 17, 1940).

  Calabogie, Ontario (Aug. 10, 1952).

  Bruce Peninsula (Thomson 1970) Keppel Township of Grey County
  Long Point, Haldimand-Norfolk, Ontario (about 80 km southwest of Hamilton)

Most notable find was *Pterospora andromedea* by Scott (1898) supported by Boughner's 1898 report.
Located again by Sutherland 1987 *cf* Reznicek & Catling 1989 and listed from Long Point, but otherwise not known from the region.
Not observed by Reznicek & Catling (1989)

- Manitoulin Island (Morton & Venn 1984):
  Bell (1870) reported it from Gore Bay and Cockburn Island
  Grassel (1932) collected at Gore Bay and Meldrum Point (specimens at MICH)
  Soper and Warren (1963) at Kagawong along the river
  Stills occurs at Elizabeth Bay (Morton & Venn 1984).

- Prince Edward Isle:
  May be extinct (Scoggan 1979), collected from Prospect Creek by J. Macoun in 1888

- New Brunswick: Very rare; found on Curry Mountain and Keswick Ridge in York County and along the Restigouche River in Restigouche County (Hinds 1986).

- Quebec: (primarily western portion) (reported by Gillett 1972).
  Paugan Falls, Quebec, Ottawa Field Naturalists' Club Outing, (July 3, 1971)
  Gatineau County, Gatineau River (July 31, 1903)
  Spencer Wood, Quebec (1820)
  Gatineau County, Gatineau River (between Ironsides and Chelsea) (1889)

Quebec – Centre de donnees sur le patrimoine naturel du Quebec

Town	**Last Obs.**	Rank	Description
Duhamel-Ouest	18 July 1997	A	West slope on clay near lake; 3 ha of over 270 stems
L'Isle-aux-Allumettes	19 July 1997	A	Flat to gently rolling terrain around non-riparian alvar; cedar woods on limestone; 300 scattered individuals
Saint-Bruno-de-Guigues	16 July 1999	A	Riparian calcareous clay slope; 500 individuals, flowering and fruiting
Northfield	10 July 2001	B	Young white pine woods with white birch; at base of slope on dolomite; 100 stems in full flower
Duhamel-Ouest	18 July 1997	B	Clay slope at edge of lake; 180 stems
Duhamel-Ouest	19 July 1997	B	Mid-slope young *Pinus strobus* woods; 130 stems
Aylmer	9 Oct 2001	C	White pine forest (90 yrs) with sugar maple; 24 individuals
Les Eboulements	5 Sept 1999	C	Mature cedar grove with white pine and white spruce, near St. Lawrence River; 71 stems

Saint-Justin	29 Sept 2001	C	Steep clay slope; white pine woods; 38 stems; and 15 from previous year
Portage-du-Fort	12 Aug 1996	C	Rolling to hilly terrain on marble; 30 stems
Portage-du-Fort	12 Aug 1996	C	Mature riparian forest with clearing; old cedar grove with balsam; 12 stems
Clarendon	19 Sept 2000	D	Mature (70 yr) white pine woods on high steep bank; 20 individuals
Northfield	27 July 2001	D	White pine woods at base of slope on dolomitic and calcitic marble outcrop
Matapedia	9 Aug 1996	D	Mid-slope on SW escarpment near dam; mixed woods
Bryson	17 Oct 1997	D	South slope of marble hill; old pine forest; 8 stems
Campbell’s Bay	17 Oct 1997	D	South-facing clay slope near Ottawa River; 9 stems
Bristol	27 June 1998	D	Semi-open white pine/cedar woods; 14 stems
Chelsea	4 Sept 1997	D	Steep clay bank; closed *Pinus strobus* forest; 3 stems

In addition, there are 7 historic occurrences (Centre de donnees sur le patrimoine natural du Quebec).

Ranks for populations health range from A (excellent, with expected long term viability) to D (poor, with poor prospects for survivorship of population).