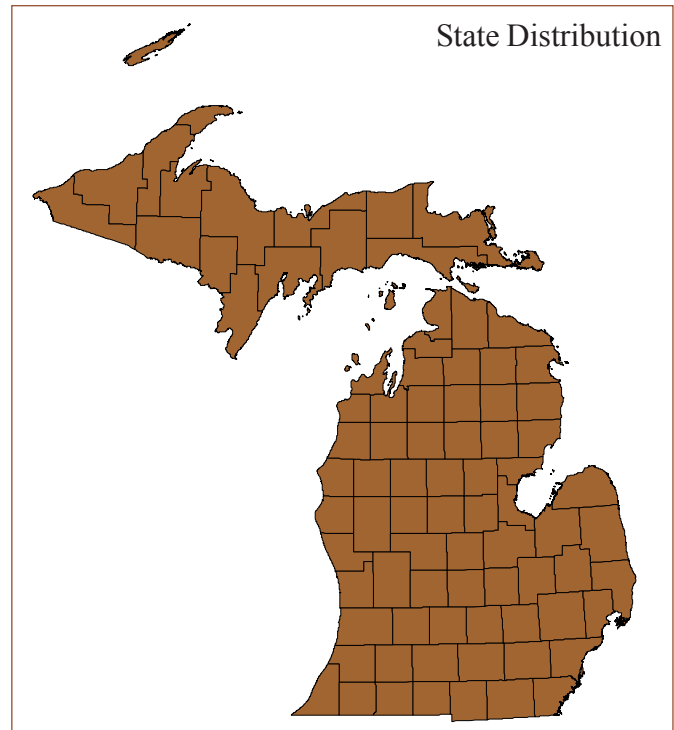




Photo by Joshua Cohen



**Overview:** Poor conifer swamp is a nutrient-poor, forested peatland characterized by acidic, saturated peat, and the prevalence of conifer trees, *Sphagnum* mosses, and ericaceous shrubs. The community is located in depressions in glacial outwash and sandy glacial lakeplains and in kettles on pitted outwash and depressions on moraines. Poor conifer swamp occasionally occurs on floating mats on the margins of lakes and ponds. Fire occurs naturally during drought periods and creates even-aged, often monospecific, stands of *Picea mariana* (black spruce). Windthrow, beaver flooding, and insect defoliation are also important disturbance factors influencing species composition and structure.

**Global and State Rank:** G4/S4

**Range:** Poor conifer swamps are a frequent forested peatland type of glaciated landscapes of the entire northern hemisphere and are characterized by similar floristic structure and composition. In North America, they are found in the northern Great Lakes Region (Michigan, Minnesota, Wisconsin, primarily north of the climatic tension zone), the northeastern United States (New York, New Hampshire, Vermont, and Maine), and throughout central Canada (Ontario, Manitoba, and Quebec) (Curtis 1959, Faber-Langendoen 2001, NatureServe 2006). Subtle variations in overall species composition and physiognomy of peatlands occur across

their range along north-south and east-west climatic gradients (Glaser 1992). In Michigan, poor conifer swamps are common throughout the northern Lower Peninsula and the Upper Peninsula and are less common south of the climatic tension zone (Amon et al. 2002). Forested peatlands are particularly abundant in the eastern Upper Peninsula. Poor conifer swamps and other peatlands occur where excess moisture is abundant (where precipitation is greater than evapotranspiration) (Halsey and Vitt 2000, Mitsch and Gosselink 2000). Conditions suitable for the development of peatlands have occurred in the northern Lake States for the past 3,000-6,000 years following climatic cooling (Boelter and Verry 1977, Heinselman 1970, Miller and Futyma 1987). *Sphagnum* dominated peatlands reached their current extent 2,000-3,000 years ago (Halsey and Vitt 2000).

Several other natural peatland communities also occur in Michigan and can be distinguished from ombrotrophic (nutrient-poor) conifer swamps, based on comparisons of nutrient levels, flora, canopy closure, and groundwater influence. Poor conifer swamps receive inputs of nutrients and water primarily from precipitation. The canopy of these peatland forests ranges from open or partially closed (25% to 60%) to closed (60% to 100%) (NatureServe 2006). Like poor conifer swamps, muskegs and bogs are nutrient-poor,



acidic wetlands. However, these ombrotrophic peatlands exhibit a lesser degree of canopy closure than poor conifer swamps (muskegs having clumped and/or scattered, stunted conifers and bogs being open wetlands). Closed canopy, minerotrophic peatlands include rich conifer swamp, a *Thuja occidentalis* (northern white cedar) dominated system found north of the tension zone, and relict conifer swamp, which is dominated by *Larix laricina* (tamarack) and occurs primarily south of the tension zone (Kost 2001). Additional open wetlands occurring on peat include northern fen and poor fen. Fens are minerotrophic (nutrient-rich) wetlands that are dominated by sedges, rushes, and grasses (Mitsch and Gosselink 2000). The hydrology of fens is influenced by groundwater, and as a result, fens have higher nutrient availability, increased alkalinity (less acidity), and greater species richness compared to bogs, with poor fens being most similar to bogs in terms of these factors and species composition.

**Rank Justification:** Poor conifer swamps are frequent features of the northern Great Lakes Region, occurring throughout the northern Lower Peninsula and the Upper Peninsula and sporadically south of the climatic tension zone. The northern lake states contain over six million hectares (15 million acres) of peatland (Boelter and Verry 1977). Analysis of General Land Office survey notes in Michigan reveals that poor conifer swamp once occupied over 1.4 million hectares (3.5 million acres) (Comer et al. 1995). Recent estimates of lowland conifer swamp in Michigan reveal a significant decrease in coniferous swamps with approximations ranging from nearly 600,000 hectares (1.5 million acres) (MIRIS 1978) to less than 280,000 hectares (690,000 acres) (Michigan DNR 2000, 2001a, and 2001b). Within the southern portion of their range, poor conifer swamps occur as isolated depressional wetlands separated by large expanses of agricultural lands. Southern peatlands were typically drained, cleared, and put into agricultural production with a drainage boom occurring in the 1920s (Curtis 1959, Vogl 1964). Turn of the century logging of tamarack, black spruce, and cedar from peatland systems favored the conversion of forested peatlands to open, ombrotrophic bogs (Gates 1942, Dansereau and Segadas-Vianna 1952, Riley 1989). Historically, widespread fires following the turn of the century logging drastically altered many peatlands, either converting poor conifer swamp to open bog systems or destroying the peat and converting peatlands to systems without organic soils (mineral soil wetlands) (Dean and

Coburn 1927, Gates 1942, Curtis 1959, Miller and Futyma 1987). Beginning in the 1920s, effective fire control by the U.S. Forest Service and state agencies reduced the acreage of fires ignited by man or lightning (Swain 1973). In landscapes where frequent fire was the prevalent disturbance factor, fire suppression has led to the conversion of open bogs to closed-canopy peatlands (Curtis 1959, Riley 1989) and the maintenance of closed-canopy poor conifer swamps. Poor conifer swamps that remained forested following the initial logging often developed uneven-aged structure because vegetative layering by black spruce initiated succession (Stanek 1961, Stanek 1968, Morin and Gagnon 1991).

The current anthropogenic disturbance factor directly impacting forested peatlands is logging. Black spruce and tamarack have become increasingly important sources for the burgeoning pulp industry (Curtis 1959, Morgenstern 1978, Taylor et al. 1988, Groot and Horton 1994, Groot 2002, Locky et al. 2005). Current silvicultural practices in poor conifer swamps are even-aged management systems. Clear-cutting of forested peatlands has resulted in the simplification of the age-class distribution and structural diversity of poor conifer swamps (Bergeron et al. 1999, Harper et al. 2003). Old-growth, naturally uneven-aged poor conifer swamps have been reduced from the landscapes where peatlands are intensively managed on short rotation periods (e.g., less than 100 years) (Bergeron et al. 1999). Full-tree harvesting, the most prevalent technique employed in these systems, typically causes reduced survival of residual trees and damage to the organic soils due to deep rutting of the peat (MacDonell and Groot 1997). As logging intensity increases within forested peatlands, residual diameter and volume growth often decrease (Groot and Horton 1994, Groot 2002). Harvesting in poor conifer swamps is often followed by poor tree regeneration and growth as the result of competition from native ericaceous shrubs (Peterson 1965, Foster 1985, Thompson and Mallik 1989, Zhu and Mallik 1994, Yamasaki et al. 1998) and the thickening of the sphagnum peat through paludification (Fenton et al. 2005). Salvage harvesting of recently burned poor conifer swamps is a common practice that severely reduces nutrient pools, decreases the water holding capacity of the underlying peat, and can ultimately cause the loss of site productivity (Brais et al. 2000).



In addition to direct impacts to vegetation, alteration of peatland hydrology from road building, creation of drainage ditches and dams, and runoff from logging and agriculture has led to the drastic change of peatland composition and structure (Curtis 1959, Vogl 1964, Schwintzer and Williams 1974, Jeglum 1975, Riley 1989, Grigal 1990, Chapman et al. 2003, Asada et al. 2005). Peatland vegetation is extremely sensitive to minor changes in water levels and chemistry (Siegel 1988, Riley 1989). Succession to more minerotrophic wetlands can occur as the result of increased alkalinity and raised water levels, which can cause the increased decomposition of acidic peats. Flooding of poor conifer swamps can cause the death of canopy trees and the conversion of forested peatland to open wetlands (Jeglum 1974, Jeglum 1975, Liefers and MacDonald 1990, Asada et al. 2005). Roads and highways traversing through large peatlands complexes, especially in the Upper Peninsula, have caused the blockage of drainage (impoundment of water) and the alteration of poor conifer swamps to open peatlands. Conversely, lowering of water tables from drainage as a result of ditches along roads can allow for increased growth of trees in poor conifer swamps and also tree and shrub encroachment into open bogs and the eventual succession to closed canopy peatland. In addition, drainage of peatlands can result in the rapid decomposition of peat due to the creation of aerobic conditions (Curtis 1959). The dependence of poor conifer swamps on precipitation for both nutrients and water makes them especially susceptible to acid rain and air pollution (Gorham and Tilton 1978, Siegel 1988, Chapman et al. 2003). Atmospheric deposition can contribute Nitrogen, Sulphur, Calcium and heavy metals to peatlands (Damman 1990, Chapman et al. 2003). Dust-fall and atmospheric deposition from air pollution are particularly threats to peatland systems in the southern portion of their range, where poor conifer swamps are surrounded by cultivated land and close to industrial and urban centers (Damman 1978, Gorham and Tilton 1978, Damman 1988, Damman 1990).

**Physiographic Context:** Two landscape features are conducive to the development of peat; small ice-block basins and poorly-drained, level terrain (Boelter and Verry 1977). Poor conifer swamps occur in depressions on pitted outwash and moraines and on flat areas or mild depressions in glacial outwash and glacial lakeplains (Gates 1942, Curtis 1959, Crow 1969, Henry et al. 1973, Boelter and Verry 1977, Foster 1985, Bubier 1991, NatureServe

2006, Kost et al. 2007). Peatlands occurring on former glacial lake beds and drainageways tend to be more extensive than kettle peatlands, which are limited in area by the size of the glacial ice-block that formed the basin (Lindeman 1941). Peatlands range in size from a few thousand square meters to several thousand hectares (Futyma and Miller 1986). The overall topography of poor conifer swamps is flat to gently undulating with microtopography characterized by hummocks and hollows (Heinselman 1963, Vitt and Slack 1975, Wheeler et al. 1983, Glaser et al. 1990, Bubier 1991, Locky et al. 2005, NatureServe 2006). The pronounced microtopography in these systems leads to extreme and fine-scale gradients in soil moisture and pH (Bridgham et al. 1996).



Photo by Gary Reese

Poor conifer swamps occur in depressions in sandy glacial outwash (dark green signature above), glacial lakeplain, and moraines.

Poor conifer swamps within large wetland complexes typically occur adjacent to other peatland communities, often grading into bog, poor fen, muskeg, and/or rich conifer swamp. More minerotrophic systems such as northern fen, prairie fen, shrub thicket, wet meadow, rich conifer swamp, hardwood-conifer swamp, southern swamp, and relict conifer swamp can occur along the outer margins of poor conifer swamps where groundwater seepage from the adjacent uplands is prevalent. As a general rule, the center of peatland systems are most ombrotrophic, receiving primarily atmospheric inputs and exhibiting the greatest peat depths, while the borders are more minerotrophic, influenced by groundwater and characterized by shallower peat (Jeglum 1975, Damman 1986). Poor conifer swamps often occur adjacent to lakes and meandering streams (usually less than third order). Poor conifer swamp and rich conifer swamp can also occur in the first bottom of floodplain valleys in backswamps





where over the bank flooding from the river is infrequent and organic matter can accumulate. A wide array of upland community types can occur adjacent to poor conifer swamp; some of the more frequent neighboring upland systems include dry northern forest, dry-mesic northern forest, and mesic northern forest.

**Hydrology:** Climate, topography, near surface geology, soils, and vegetation influence the hydrology of poor conifer swamps (Miller and Futyma 1987). Poor conifer swamps are poorly drained ombrotrophic to weakly minerotrophic peatlands, receiving inputs of water and nutrients primarily from ion-poor precipitation (Heinselman 1970, Verry 1975, Boelter and Verry 1977, Schwintzer 1981, Schwintzer and Tomberlin 1982, Siegel 1988, Riley 1989, Glaser et al. 1990, Mitsch and Gosselink 2000, NatureServe 2006). The rooting zone of ombrotrophic peatlands is dominated by inputs of atmospheric water and nutrients (Bedford and Godwin 2003). Weakly minerotrophic conditions are more likely to occur in poor conifer swamps confined to small basins rather than large peatland complexes (NatureServe 2006). The water retaining capacity of sphagnum peat is tremendous and as a result, poor conifer swamps are saturated, anoxic systems with water tables near the surface (Burns 1906, Dansereau and Segadas-Vianna 1952, Curtis 1959, Heinselman 1970, Schwintzer 1978b, Jasieniuk and Johnson 1982, Liefers and Rothwell 1986, Siegel and Glaser 1987, Bubier 1991, Glaser 1992, McLaughlin et al. 1994, Islam et al. 2003, O'Connell et al. 2003b, Islam and MacDonald 2004, Fenton et al. 2005). The stagnant surface waters of poor conifer swamps are characterized by high acidity, low available nutrients, low specific conductivity, cool temperatures, anaerobic conditions, and high levels of dissolved organic matter that imparts a brown color (Gates 1942, Sjors 1950, Henry et al. 1973, Verry 1975, Schwintzer 1978a, Glaser et al. 1981, Jasieniuk and Johnson 1982, Wheeler et al. 1983, Liefers and Rothwell 1986, Riley 1989, Damman 1990, Bubier 1991, Glaser 1992, Islam et al. 2003, Fenton et al. 2005). The accumulation of peat within these systems alters drainage patterns and raises water tables (Brinson 1993).

Studies of ombrotrophic peatlands across the northern Great Lakes have found pH measurements of water and peat to range from 3.2 to 4.3 (Heinselman 1970, Boelter and Verry 1977, Schwintzer 1981, Schwintzer and Tomberlin 1982, Wheeler et al. 1983, Glaser et al. 1990). The high acidity of poor conifer swamps limits the availability and uptake of essential mineral plant nutrients,

which are inherently scarce in these systems because of the lack of groundwater input (Glaser 1992). Poor conifer swamps are characterized by low primary productivity, which is correlated with the very low concentrations of available Calcium, Magnesium, Nitrogen, Phosphorous, and Potassium in the surface water and peat (Heinselman 1963, Heinselman 1970, Schwintzer 1978a, Schwintzer 1981, Schwintzer and Tomberlin 1982, Wheeler et al. 1983, Glaser 1992, Bedford et al. 1999, Mitsch and Gosselin 2000, Islam et al. 2003).

**Soils:** The organic soils of poor conifer swamps are composed of peat, which forms a continuous mat that can be as little as 15 cm deep but is often at least 40 cm deep (Vogl 1964, McLaughlin et al. 1994, Locky et al. 2005). Peat depths of one to two meters are common for the interior of poor conifer swamps (Michigan Natural Features Inventory database). The rooting zone within poor conifer swamps is typically quite shallow, confined to the upper 15 cm of the surface peat (Barnes and Wagner 1981, Karlin and Bliss 1984, Levan and Riha 1986, Glaser and Janssens 1986, Liefers and Rothwell 1987, Islam et al. 2003, Hamel et al. 2004). Peat of poor conifer swamps is characterized by high carbon content (Halsey and Vitt 2000, O'Connell et al. 2003a and 2003b). Depth of peat and soil moisture vary within a site (Jeglum 1975, Taylor et al. 1988). Peat depth is typically greatest near the center of a peatland and decreases towards the peatland margin or in areas with groundwater influence (Jeglum 1975). Peat is a fibrous network of partially decomposed organic material that is formed under anaerobic conditions (Heinselman 1963, Almendinger et al. 1986). The surface peats of poor conifer swamps are dominated by saturated fibric peat, which is loosely compacted and spongy, contains partially decomposed sphagnum moss with fragments of wood and occasionally sedge, and like the surface water, is extremely acidic, cool, and characterized by low nutrient availability and oxygen levels (Burns 1906, Curtis 1959, Heinselman 1963, Heinselman 1970, Schwintzer and Williams 1974, Boelter and Verry 1977, Morgenstern 1978, Almendinger et al. 1986, Futyma and Miller 1986, Pepin et al. 2002, Islam and MacDonald 2004). Fibric peat has high water-retaining capacity and large intercellular pores that permit rapid water movement (Boelter and Verry 1977, Swanson and Grigal 1989, Jasieniuk and Johnson 1982, Pepin et al. 2002). Peat composition changes with depth and is dependent on the successional history of a given



peatland. Generally, fiber content and hydraulic conductivity decrease with depth; deeper peats are more decomposed, have smaller pores, retain more water due to their proximity to the water table, and drain slower than surface peats (Curtis 1959, Verry 1975, Boelter and Verry 1977, Jasieniuk and Johnson 1982, Futyma and Miller 1986). Deep humidified peats can effectively seal basins and create a perched water table.

**Climate:** Peatlands develop in humid climates where precipitation exceeds evapotranspiration (Boelter and Verry 1977, Gignac et al. 2000, Halsey and Vitt 2000). The northern Lake States are characterized by a humid, continental climate with long cold winters and short summers that are moist and cool to warm (Gates 1942, Boelter and Verry 1977, Damman 1990, Mitsch and Gosselink 2000). The Michigan range of poor conifer swamp falls within the area classified by Braun (1950) as the Northern Hardwood-Conifer Region (Hemlock/White Pine/Northern Hardwoods Region) and within the following regions classified by Albert et al. (1986) and Albert (1995): Region I, Southern Lower Michigan; Region II, Northern Lower Michigan; Region III, Eastern Upper Michigan; and Region IV, Western Upper Michigan. The Northern Hardwood-Conifer Region has a cool snow-forest climate with warm summers. The mean number of freeze-free days is between 90 and 220, and the average number of days per year with snow cover of 2.5 cm or more is between 10 and 140. The normal annual total precipitation ranges from 740 to 900 mm with a mean of 823 mm. Sphagnum-dominated peatlands are found in areas where annual precipitation is greater than 500 mm (Halsey and Vitt 2000). The daily maximum temperature in July ranges from 24 to 32 °C (75 to 90 °F), the daily minimum temperature in January ranges from -21 to -4 °C (-5 to 25 °F), and the mean annual temperature is 7 °C (45 °F) (Albert et al. 1986, Barnes 1991). Temperatures vary less in poor conifer swamps compared to the surrounding landscape because of the insulating effect of the saturated peat carpet during the growing season and snow cover in the winter (Curtis 1959, Heinselman 1963, Glaser 1992). Poor conifer swamps are characterized by moderating microclimates that are cooler in the summer, warmer in the winter, and more even throughout the year compared to the regional climate (Curtis 1959).

**Natural Processes:** Peatland formation is controlled by the interaction of climate, hydrology, nutrient supply, and vegetation (Miller and Futyma 1987). Peat establishment requires an abundant supply of water. As noted, ombrotrophic peatlands occur in regions where

precipitation is greater than evapotranspiration and on sites with blocked drainage (Dansereau and Segadas-Vianna 1952, Boelter and Verry 1977, Mitsch and Gosselink 2000). Saturated and inundated conditions inhibit organic matter decomposition and allow for the accumulation of peat (Almendinger and Leete 1998). Under cool, anaerobic, and acidic conditions, the rate of organic matter accumulation exceeds organic decay (Schwintzer and Williams 1974, Foster 1985, Damman 1988, Damman 1990, Bridgham et al. 1996, Mitsch and Gosselink 2000). The low levels of oxygen protect plants from microorganisms and chemical actions that cause decay (Miller 1981, Damman 1988). Likewise, high levels of acidity have an inhibitory effect on decomposers (Heinselman 1963, Damman 1988, Mitsch and Gosselink 2000). Once sphagnum mosses become established on the peat mat, they maintain and enhance saturated, acidic, and cool conditions, which in turn promote continued peat development (Janssen 1967, Zoltai and Vitt 1995, Nicholson et al. 1996, Halsey and Vitt 2000, Bisbee et al. 2001, O'Connell et al. 2003b). The ability of sphagnum to absorb and hold cations increases the acidity and decreases the nutrient availability of peatlands (Osvald 1935, Curtis 1959, Verry 1975, Vitt and Slack 1975, Boelter and Verry 1977, Halsey and Vitt 2000). In addition, bryophytes take up and sequester nutrients from precipitation, throughfall, and litter decomposition before it is available to trees (Halsey and Vitt 2000, O'Connell et al. 2003a). Sphagnum moss, which has numerous pores, partitions, and capillary space, has an enormous water-holding capacity (Osvald 1935, Dansereau and Segadas-Vianna 1952, Curtis 1959, Bisbee et al. 2001). Sphagnum peat can hold 15 to 30 times its own weight in water (Miller 1981, Mitsch and Gosselink 2000). The accumulation of peat exerts control over a site's hydrology, biogeochemistry, and plant community composition (Bridgham et al. 1996). Peatlands not only alter landscape patterns but become the landscape (Brinson 1993).

Development and expansion of peatlands occurs via two distinct processes: lake-filling and paludification. Lake-filling or terrestrialization occurs in small lakes with minimal wave action, where gradual peat accumulation results in the development of a bog mat that can fill the basin or occur as a floating mat in the lake or as a grounded mat along the water's edge (Burns 1906, Gates 1942, Bay 1967, Curtis 1959, Heinselman 1963, Futyma and Miller 1986, Klinger



1996, Mitsch and Gosselink 2000). Floating mats of fen sedges (i.e., *Carex lasiocarpa*) pioneer open water and generate interlacing masses of roots and rhizomes that are buoyed up by the water. Organic matter then accumulates in the form of peat and is eventually invaded by sphagnum and ericaceous shrubs (Osvald 1935, Gates 1942, Crow 1969, Schwintzer and Williams 1974, Swineheart and Parker 2000). Fallen logs in kettle lakes and ponds can also provide the substrate for peatland vegetation establishment and invasion of the water: *Chamaedaphne calyculata* (leatherleaf) is particularly adept at expanding along logs (Dean and Coburn 1927, Gates 1942, Dansereau and Segadas-Vianna 1952). The adventitious roots of leatherleaf, which can grow laterally above the water's surface, provide a substrate for the establishment of sphagnum mosses (Asada et al. 2005). Peatland vegetation has been recorded advancing into kettle lakes at a rate of 2.1cm/year (Schwintzer and Williams 1974). Estimates of vertical accumulation of bog peat range between 100 to 200cm/1000 years (Mitsch and Gosselink 2000). Succession in lake-filled peatlands typically proceeds from lake to marsh to fen to bog to poor conifer swamp (Heinselman 1963, Boelter and Verry 1977, Schwintzer 1981, Futyma and Miller 1986, Swineheart and Parker 2000). Succession within peatland systems is not unidirectional but stochastic, with rates and pathways of succession determined by a complex array of interacting biotic and abiotic factors (Jasieniuk and Johnson 1982, Klinger 1996).



Photo by Joshua Cohen

Poor conifer swamp often invades grounded bog mats along the margins of lake-filled peatlands.

Bogs can succeed to poor conifer swamp or remain as bogs depending on the site's hydrology (lowered water tables will allow for the establishment of trees), disturbance regime (fire and flooding will keep open systems open), and species composition (a seed source of conifer trees in the vicinity is required and some ericaceous species can limit seedling establishment and tree growth). Where poor conifer swamp is invading an open bog, the youngest trees are found closest to the bog while the oldest trees are farthest from the bog (Klinger 1996).

Paludification is the blanketing of terrestrial systems (often forests) by the overgrowth of peatland vegetation (Dansereau and Segadas-Vianna 1952, Heinselman 1963, Janssen 1968, Klinger 1996, Mitsch and Gosselink 2000). For both lake-filling and paludification, peat accumulates above the water table and the peatland becomes isolated from groundwater influence (Heinselman 1970, Boelter and Verry 1977, Glaser and Janssens 1986, Miller and Futyma 1987, Mitsch and Gosselink 2000). Paludification implicitly follows terrestrialization. Terrestrialization causes the blockage of drainage by peat accumulation. As a result, downward percolation of water into the underlying mineral substratum is impeded and lateral movement is favored, leading to the swamping of ground adjacent to lake-filled basins and the eventual expansion of the peatland vegetation (Futyma and Miller 1986). Paludified peatlands generally develop on flat areas (typically lakeplain) where peat builds vertically and spreads horizontally (Heinselman 1965, Boelter and Verry 1977). The lateral expansion of peatland into forested systems can result in the increase in the water table and acidity and a subsequent decrease in soil temperatures, nutrient availability, decomposition rates, canopy cover, growth rates, and seedling establishment, and a shift in species composition with swamp conifers, especially black spruce, becoming more prevalent (Klinger 1996, Harper et al. 2003, Ruel et al. 2004, Fenton et al. 2005, Harper et al. 2005).

Once established, poor conifer swamp can persist for hundreds of years given stable hydraulic conditions and the absence of fire. Poor conifer swamps can be even-aged or uneven-aged depending on the disturbance history and age of a site. Younger stands, regenerated following fire tend to be even-aged with tall dense canopies, while older stands tend to be uneven-aged with more open canopies and variable heights (Curtis





1959, Barnes and Wagner 1981, Taylor et al. 1988, Morin and Gagnon 1991, Groot and Horton 1994, Groot 2002, Harper et al. 2002). Within even-aged stands, stratification of species into distinct size classes is common. This structural feature occurs because one species (e.g., black spruce) obtains a disproportionate share of the finite resources at the expense of the other species (e.g., tamarack or balsam fir) (Newton and Smith 1988). Within dense, stands of even-aged black spruce, density dependent mortality or self-thinning typically occurs after several decades (Carleton and Wannamaker 1987). As poor conifer swamps age, they tend to become more complex structurally but with relatively stable tree species composition. The structural diversity of old-growth poor conifer swamps (200 to 300 years old) provides important habitat for regional biodiversity. Small-scale disturbance factors, such as windthrow events and insect herbivory (e.g., spruce budworm), generate numerous snags, coarse woody debris, and gaps within the canopy. These canopy gaps are captured primarily by black spruce layering but also by swamp conifer seedlings. Compared to trees established from seed, layers tend to be of shorter stature. As stands age, they become more open with discontinuous canopies. In addition to structural complexity, epiphytic diversity tends to increase with stand age since older trees are available for a longer period of time for epiphytic colonization, vegetative expansion, and sexual reproduction (Bergeron and Dubuc 1989, Groot and Horton 1994, Groot 2002, Harper et al. 2002, Harper et al. 2003, Ruel et al. 2004, Harper et al. 2005). Old-growth, uneven-aged poor conifer swamps are most prevalent in fire resistant landscapes and in extensive areas of peatland forest, which have reduced fire frequencies (Groot 2002).

Fire, which is an infrequent but important disturbance factor within poor conifer swamps, controls tree population dynamics by initiating and terminating succession (Curtis 1959, Payette and Gagnon 1979, Foster 1985, Futyma and Miller 1986, Whitney 1986, Miller and Futyma 1987, Cleland et al. 2004). The primary ignition source for fires within poor conifer swamps is summer lightning strike (Rowe 1973, Foster 1985), however, historically fires started by Native Americans in surrounding uplands (Day 1953, Chapman 1984) likely spread to some swamp forests. Estimates of fire return intervals for forested peatlands range widely from over a hundred to several hundred years in fire-prone landscapes to several hundred to over a

thousand years in swamps in fire-protected landscapes (Whitney 1986, Cleland et al. 2004). Fire rotation period typically increases from south to north and with increasing organic soil moisture (Sirois and Payette 1989). The accumulation of thick organic soils often prolongs the fire cycle within these systems (Foster 1985). In addition, forest floor thickness, which increases with time since fire, is negatively correlated with fire severity (Ruel et al. 2004, Fenton et al. 2005). Fire frequency can also be reduced by fire breaks such as bodies of water and deciduous forests (Rowe 1973).

Fire severity and frequency in poor conifer swamps is closely related to climatic change and fluctuations in water level. Prolonged periods of drought and lowered water table can allow the surface peat to dry out enough to burn (Vogl 1964, Schwintzer and Williams 1974). When the surface peat burns, the fire releases organic matter from the peat, stimulates decay, slows peat accumulation, and exposes mineral soil (Vogl 1964, Rowe 1973, Damman 1990, Jean and Bouchard 1991). Fires within poor conifer swamps are typically stand-replacing crown fires that kill the majority of canopy trees (Curtis 1959, Bergeron and Dubuc 1989, Knowles 1991a, Harper et al. 2002). Depending on its severity, fire can eliminate or reduce the soil organic layer (Ruel et al. 2004, Fenton et al. 2005, Harper et al. 2005). Fires in poor conifer swamps generate a flush of growth, first in ground layer taxa and ericaceous shrubs, and then in coniferous trees. Increased growth, seed and fruit production, and flowering results from increases in light availability, soil temperature, decomposition rates, and nutrient availability (Rowe 1973, Barnes and Wagner 1981, Foster 1985, Larsen and MacDonald 1998, Ruel et al. 2004).

Exposure of the mineral soil provides a suitable medium for the establishment and germination of swamp conifers (i.e., black spruce, tamarack, jack pine, and northern white cedar) (Curtis 1959, Barnes and Wagner 1981, Brown et al. 1988). Species present in abundance before the fire are typically at an advantage for extending their distributions afterward (Rowe 1973). Cone serotiny provides black spruce and jack pine a competitive advantage in terms of seeding onto burned sites in that fire-killed trees can provide seed. Tamarack, white pine, cedar, and balsam fir must rely on wind or animal dispersal from seed trees that survived the fire or occur in neighboring, unburned stands (Knowles 1991a). The majority of seedlings



typically establish within the first couple of years following the fire (Morin and Gagnon 1991, St-Piere and Gagnon 1992, Rajora and Pluhar 2003) but recruitment at a lessened rate often continues for several decades following the disturbance and initial pulse of seedlings (Sirois and Payette 1989, Groot and Horton 1994, Larsen and MacDonald 1998). The initially established trees often serve as an internal seed source. The rate of reforestation following fire is dependent on the size and severity of the burn; centers of large burns are especially slow to restock (Foster 1985). Swamps in which the organic layer burns evenly tend to support rapid seedling establishment and become even-aged (Foster 1985); these stands can even be monospecific (typically dominated by black spruce or tamarack) if the diversity of seed source is limited (Bergeron and Dubuc 1989). Seed source availability and seedbed availability and quality determine the burned stand's tree density as well as composition (Sirois and Payette 1989). Fires of weak severity leave much of the organic layer intact, which can result in slow and irregular recruitment because of the limited availability of mineral soil seedbed (Foster 1985, Fenton et al. 2005, Harper et al. 2005) and may facilitate the conversion of poor conifer swamp to muskeg (Vogl 1964). In fire prone landscapes, periodic fire can also maintain open peatlands: conversely, fire suppression in these areas can lead to the conversion of open bogs to poor conifer swamps (Curtis 1959, Vitt and Slack 1975).

Fires typically cause change in species abundance but not in species composition. In contrast, water regime and nutrient regime changes result in drastic modification of species composition and abundance (Jasieniuk and Johnson 1982). Beaver, through their dam-building activities, can instigate substantial hydrologic change to peatland systems, either causing flooding or the lowering of the water table of poor conifer swamps depending on the location of the forest in relation to the dam (Gates 1942, Curtis 1959, Heinselman 1963, Jeglum 1975, Futyma and Miller 1986). Behind a beaver dam the water table is higher while below it, drier conditions are generated (Jeglum 1975). Short periods of flooding can cause needle chlorosis, necrotic needle tips, and decreased shoot and root growth of swamp conifers due to low oxygen concentration and nutrient availability in the rooting medium from water logging (Islam et al. 2003, Islam and MacDonald 2004). Prolonged flooding of poor conifer swamps can result in the death of canopy trees

and the conversion of forested peatlands to bogs or even open systems dominated by marsh and fen vegetation (Asada et al. 2005). Flooding can also cause grounded peat mats to become loosened from the bottom and float (Gates 1942, Asada et al. 2005). Flooding induced tree mortality is greater on grounded peat mats compared to free floating mats: free mats float up with a rising water table while grounded mats become inundated and have shallower aerobic zones (Schwintzer 1973, Schwintzer 1978a, Schwintzer 1979, Asada et al. 2005). Roots of peatland trees are physiologically active near the surface and are quickly killed when the water table rises following flooding (Glaser and Janssens 1986). Flooding typically causes tree mortality after about a decade but different tree species have different tolerances for flooding (Janssen 1967, Asada et al. 2005). Tamarack, which is often most prevalent on wet sites, exhibits greater flooding tolerance than black spruce. In response to prolonged soil flooding, tamarack produces adventitious roots which increase root hydraulic conductivity or the capacity to regulate water flow (Islam et al. 2003, Islam and MacDonald 2004). However, tamarack can also be more deleteriously affected by flooding than black spruce since it is often restricted to hollows while black spruce is elevated on hummocks (Denyer and Riley 1964).

The lowering of the water table through beaver damming or climatic changes can also dramatically effect the species composition and successional trajectory of poor conifer swamps. Lowering of a forested peatland's water table results in increased soil aeration, soil temperature, decomposition, nutrient availability, and consequently tree growth (Jasieniuk and Johnson 1982, Liefers and Rothwell 1986, Liefers and Rothwell 1987, Liefers and MacDonald 1990, MacDonald and Yin 1999, Pepin et al. 2002). Increased tree growth following lowering of the water table is especially prevalent in species such as tamarack, which often establishes in wet microsites (i.e., hollows). Species such as black spruce, which are often more prevalent on hummocks, may be detrimentally impacted by lengthy periods of drying because of water stress. Lowered water tables can dramatically reduce the micro-scale heterogeneity that characterizes peatlands by eliminating the fine-scale gradients in pH, moisture, and nutrient availability associated with hummocks and hollows (MacDonald and Yin 1999). In addition, a low water table for a prolonged period of time can cause the





decomposition of the organic layer (Curtis 1959) and the conversion of poor conifer swamp to a more minerotrophic forest type. Lowering of the water table in open peatland systems can lead to the conversion to shrub swamp or poor conifer swamp (Gignac et al. 2000).

The natural disturbance regime in poor conifer swamps is also influenced by wind. The Great Lakes region is one of the most active weather zones in the northern hemisphere, with polar jet streams positioned overhead much of the year. More cyclones pass over this area than any other area in the continental U.S. (Frelich and Lorimer 1991). Trees growing in poor conifer swamp are particularly susceptible to windthrow because saturated sphagnum peat provides a poor substrate for anchoring trees (Burns 1906, Harper et al. 2002). As noted above, the living roots of woody peatland plants occur in a shallow rooting zone, generally restricted to the uppermost 15 cm where there is sufficient oxygen to maintain aerobic respiration (Barnes and Wagner 1981, Karlin and Bliss 1984, Levan and Riha 1986, Glaser and Janssens 1986, Liefers and Rothwell 1987, Islam et al. 2003, Hamel et al. 2004). The poor drainage of poor conifer swamps and the superficial rooting of swamp trees results in numerous windthrows (Dansereau and Segadas-Vianna 1952, Curtis 1959, Barnes and Wagner 1981, Harper et al. 2002, Harper et al. 2003). Most windthrow only partially disturbs a stand, creating small canopy gaps but complete canopy destruction can also occur (Groot and Horton 1994, Harper et al. 2002). Catastrophic, stand-leveling blowdowns are infrequent disturbance factors in poor conifer swamps, with return intervals likely greater than 1,000 years. As noted above, small-scale wind disturbance, along with insect herbivory, contribute to the structural diversity of poor conifer swamps by generating moderate pit and mound topography, standing snags, and woody debris. Sphagnum mosses quickly envelop the coarse woody debris.

Poor conifer swamps, which often contain dense monospecific stands, are inherently susceptible to epizootic attacks of insects and parasites. The plant parasite *Arceuthobium pusillum* (dwarf mistletoe) can increase the mortality of black spruce (Coburn et al. 1933, Gates 1942, Barnes and Wagner 1981). Three insect defoliators are most prevalent in peatlands, *Pristiphora erichsonii* (larch sawfly), *Coleophora laricella* (larch casebearer), and *Choristoneura fumiferana* (Spruce budworm) (Curtis 1959, Barnes and Wagner 1981, Newton and Jolliffe 1998).

Spruce budworm defoliates both black spruce and balsam fir but tends to be more detrimental to the later. The principal effect of spruce budworm outbreaks on black spruce stands is the increase in competitive asymmetry with smaller conspecifics suffering from greater competition-induced mortality post-defoliation (Newton and Jolliffe 1998). Tamarack growing in poor conifer swamps often suffers from repeated defoliation by larch sawfly (Beckwith and Drooz 1956, Graham 1956, Curtis 1959, Tilton 1977, Girardin et al. 2005). The life of a given tamarack is typically characterized by a series of defoliation episodes, most of which are short in duration and of moderate intensity (Graham 1956). However, prolonged larch sawfly attacks can lead to extensive mortality of tamarack. Larch sawfly outbreaks tend to be more severe on better drained sites; hydric sites have defoliation episodes of lower intensity and duration due to the severe restrictions on sawfly development and survival imposed by a high water table (Girardin et al. 2005). Although a more recent arrival in Michigan, the larch casebearer is beginning to cause heavy defoliation to tamarack, especially in the eastern and central Upper Peninsula.

In addition to insect defoliation, mammalian herbivory influences vegetative composition and structure. Small rodents such as mice, voles, shrews, and squirrels are important seed predators of the small seeds of black spruce and tamarack (Morgenstern 1978). Selective browsing by moose in the Upper Peninsula of Michigan can result in the alteration of species composition, community structure, and ultimately forest successional patterns of poor conifer swamps. On sites with black spruce and balsam fir, moose preferentially browse on balsam fir, retarding fir vertical growth, limiting fir abundance, and imparting a competitive advantage to black spruce (Risenhoover and Maass 1987, Thompson and Mallik 1989, Thompson et al. 1992). In addition, the reduction of shade provided by balsam fir can result in the increase of heath shrubs, especially *Kalmia angustifolia* (sheep-laurel) (Thompson and Mallik 1989).

Native ericaceous shrubs can profoundly limit the establishment and growth of swamp conifer trees through competitive inhibition and also through the production of allelopathic compounds. Many of the ericaceous plants that thrive in poor conifer swamps are fire-adapted and often resprout vigorously and grow densely following fire or clear-cuts (Wheeler et al. 1983). Rapid and prolific resurgence of ericads, which resprout or sucker from



underground organs, can directly limit tree seedling establishment and growth (Foster 1985, Zhu and Mallik 1994, Yamasaki et al. 1998). Sheep-laurel has been found to produce allelopathic compounds that inhibit the growth and development of black spruce. These water soluble and heat stable substances hinder the primary root development of black spruce and are also believed to negatively impact the ectomycorrhizal fungi associated with black spruce (Peterson 1965, Thompson and Mallik 1989, Zhu and Mallik 1994, Yamasaki et al. 1998). The negative effects of sheep-laurel on black spruce root growth are most pronounced under acidic conditions (Zhu and Mallik 1994).



Photo by Jodi Raab

Black spruce often forms dense, monospecific, even-aged stands following intense crown fires.

**Vegetation Description:** Poor conifer swamps are characterized by a canopy of coniferous trees, low ericaceous, evergreen shrubs, a poor herbaceous layer, and a hummocky carpet of sphagnum moss (Gates 1942, Curtis 1959, Verry 1975, Vitt and Slack 1975, Glaser et al. 1991, NatureServe 2006). The harsh growing conditions of poor conifer swamps (high acidity, low nutrient availability, and saturated peat) results in a unique but depauperate flora; relatively few species have evolved the necessary adaptations to survive ombrotrophic conditions (Siegel 1988, Glaser 1992, Mitsch and Gosselink 2000). Peatland plants have developed a diversity of adaptations to cope with low nutrient availability including carnivory, evergreen leaves with long life spans, sclerophylly (thick epidermal tissue), tight nutrient cycles, and high root biomass and root to shoot ratios (Tyrell and Boerner 1986, Bridgham et al. 1996, Mitsch and Gosselink 2000). Poor conifer swamps are characterized by an exceptionally distinct plant community with similarity throughout its range

(Curtis 1959). Very few introduced and weedy species are able to establish within peatlands because of the unique growing conditions and competition from the adapted flora (Jasieniuk and Johnson 1982, Riley 1989). Plant species diversity within peatlands is strongly correlated to the hummock-hollow microtopography; each individual hummock in a peatland is in essence a miniature ecosystem with distinct gradients in water and substrate chemistry, soil moisture, aeration, and nutrients (Karlin and Bliss 1984, Bridgham et al. 1996, Glaser et al. 1990). Within a given poor conifer swamp, floristic composition, variation, and structure are determined by gradients in pH, light, soil moisture, depth to water level, fire frequency, and cation concentrations (nutrient availability) (Sjors 1950, Heinselman 1970, Jeglum 1971, Henry et al. 1973, Jeglum 1974, Vitt and Slack 1975, Schwintzer 1978a, Glaser et al. 1981, Jasieniuk and Johnson 1982, Karlin and Bliss 1984, Vitt and Slack 1984, Jeglum and He 1995, Bridgham et al. 1996, Nicholson et al. 1996, Locky et al. 2005).

The canopy of poor conifer swamps is often dominated by black spruce which can form monospecific, even-aged stands following crown fires. Tamarack is also a frequent canopy dominant or co-dominant (Curtis 1959, Tilton 1977, Barnes and Wagner 1981, Vitt and Slack 1984, Futyma and Miller 1986, Carleton and Wannamaker 1987, Comer et al. 1995, Bergeron et al. 1999, Pepin et al. 2002, Islam and MacDonald 2004, Girardin et al. 2005). Canopy associates include *Abies balsamea* (balsam fir), *Pinus strobus* (white pine), *Pinus banksiana* (jack pine), and *Sorbus americana* (American mountain ash) (Curtis 1959, Janssen 1967, Barnes and Wagner 1981, McLaughlin et al. 1994, NatureServe 2006). Jack pine dominance in poor conifer swamps is most prevalent in fire-prone landscapes and is occasionally associated with the occurrence of scattered canopy *Pinus resinosa* (red pine) (Curtis 1959, NatureServe 2006). *Thuja occidentalis* (northern white cedar) can occur in microsites with minerotrophic influence (e.g., along meandering streams) and also along the outer margins of poor conifer swamps where groundwater seepage creates nutrient rich conditions (NatureServe 2006). Early-successional deciduous species such as *Betula papyrifera* (paper birch) and *Populus tremuloides* (trembling aspen) can occur as canopy associates, particularly when mineral soil has been exposed by fire. Canopy closure and canopy height of poor conifer swamps, which depend on climate, species composition,



site productivity (water level, nutrient availability, and moisture aeration), and time since disturbance, range widely from 25% to 100% cover and 2 to 18 meters (6 to 60 feet) in height (Curtis 1959, Jeglum 1974, Morgenstern 1978, Barnes and Wagner 1981, Bubier 1991, Hamel et al. 2004, Harper et al. 2005, Locky et al. 2005, NatureServe 2006). The number of species and percent coverage in the ground layer decreases as the amount of shade provided by the tree canopy increases. The diameter of mature canopy trees is typically between 10 and 30 cm (4 and 12 inches), with species of increasing shade tolerance (i.e., balsam fir) occupying smaller size classes (Curtis 1959, Barnes and Wagner 1981, Newton and Smith 1988). Areas of poor conifer swamp adjacent to streams typically exhibit greater tree growth because of the higher nutrient status and better drainage (Bubier 1991). Canopy cover, tree height, and basal area typically decrease with increasing sphagnum thickness and cover and ericaceous shrub cover, while the dominance of black spruce in the canopy increases (Jasieniuk and Johnson 1982, Bisbee et al. 2001, Harper et al. 2002, O'Connell et al. 2003a, Fenton et al. 2005). Stands dominated solely by black spruce are typically lake basins that have been filled in by firm peat, while tamarack-dominated poor conifer swamps are often areas where the open peat mat is still advancing over open water (Curtis 1959). Where they co-dominate, black spruce tends to be on drier microsites (i.e., hummocks) while tamarack, which is more tolerant of flooding, can establish and grow on wetter areas such as hollows (Islam et al. 2003, Islam and MacDonald 2004). Trees growing in poor conifer swamps have horizontally oriented root systems that are confined to the less saturated surface layers (the upper 10 to 20 cm) (Karlin and Bliss 1984, Liefers and Rothwell 1986, MacDonald and Yin 1999, Pepin et al. 2002).

Black spruce, an evergreen conifer with a transcontinental distribution and a spire-formed, tall narrow crown that tapers to a sharp point, is classified as a mid shade-tolerant species (Curtis 1959, Morgenstern 1978, Barnes and Wagner 1981, Larsen and MacDonald 1998, Rajora and Pluhar 2003). Sclerophyllous, long-lived needles allow black spruce to maximize efficient use of nutrients, while a shallow, wide-spreading root system facilitates nutrient uptake and avoids water logging (Curtis 1959, Tyrell and Boerner 1986, Bridgham et al. 1996, Islam et al. 2003, Islam and MacDonald 2004). Black spruce reproduces

both sexually, regenerating from seed, and asexually through vegetative reproduction or layering (Curtis 1959, Stanek 1961, Stanek 1968, Morgenstern 1978, Payette and Gagnon 1979, Knowles 1991b, Groot 2002). The cones of black spruce are semi-serotinous, sealed by resin that is opened by heat from fire or the sun. Black spruce have the capacity to produce large quantities of wind-dispersed seed; estimates range widely from approximately 198,000 to 810,000 per acre per year (Curtis 1959, Sirois and Payette 1989, Fleming and Mossa 1996). Seeds remain viable for as long as ten years. Trees begin producing seed as young as 10 years and stands of 30 years typically have a continuous supply of genetically diverse seeds (Foster 1985, Rajora and Pluhar 2003). The semi-serotinous cones are located at the extreme tips of the branches; thus fires that kill the canopy cohort may not damage the cones. Burned peat and exposed mineral soil provide a favorable medium for seed germination for both black spruce and tamarack (Curtis 1959). In the absence of fire, sphagnum moss (especially on hummocks), exposed mineral soil from windthrow, and rotten wood (stumps and logs) provide suitable germination sites for black spruce seed, which are restricted to seedbeds of relatively constant moisture supply (Curtis 1959, Foster 1985, Prevost 1997). Vegetative reproduction is also important in unburned stands. Layering occurs when black spruce branches are covered by sphagnum and the branches produce vertical shoots which develop into layers or new trees (Curtis 1959, Stanek 1961, Stanek 1968). Trees derived from seed are typically larger and straighter than vegetatively reproduced layers, which often have strongly curved boles (Stanek 1968, Foster 1985).



Photo by Joshua Cohen

Semi-serotinous cones of black spruce are opened by heat.





Tamarack, a deciduous conifer that is also extensively distributed across the North American continent, is classified as a highly shade-intolerant species (Graham 1956, Curtis 1959, Barnes and Wagner 1981, Brown et al. 1988, Cheliak et al. 1988, Knowles 1991a, Groot 2002, Girardin et al. 2005). Henry et al. (1973) describe it as the most shade-intolerant tree in America.

Tamarack is characterized by high nutrient conservation capacity (Tyrell and Boerner 1986). This fast-growing species has a shallow, wide-spreading root system: the spread of tamarack's roots can be greater than the tree's height (Curtis 1959, Henry et al. 1973, Barnes and Wagner 1981). Tamarack reproduces primarily sexually by regenerating from seed but is also exhibits vegetative reproduction through layering (Curtis 1959, Henry et al. 1973, Payette and Gagnon 1979). Like black spruce, tamarack is capable of adventitious root sprouting in response to deepening of the sphagnum layer (Curtis 1959, Henry et al. 1973). The small seeds of tamarack are primarily wind-dispersed, generally disseminated a distance less than two tree heights. Greater distances of seed dispersal can occur when seeds are blown over ice-covered snow. However, the majority of seeds fall within 50 meters from their parent tree, restricting gene flow within tamarack populations. Despite this dispersal limitation, tamarack populations tend to exhibit high genetic variability (Cheliak et al. 1988, Knowles 1991a). Tamarack typically generate good seed crops every four to six years, producing approximately 5,000,000 germinable seeds per acre per year (Curtis 1959). Trees begin producing viable seed as young as 12 years and stands of 50 years typically generate reliable seed crops. Seeds fall in the autumn, remain dormant through the winter, and germinate in the spring. Germination occurs on moss carpets, rotten wood, exposed peat, or mineral soil (Curtis 1959, Foster 1985, Brown et al. 1988). As noted above, fire provides a favorable seedbed for tamarack and black spruce seeds by exposing the mineral soil. Fire also reduces moss cover and thickness, which can impede seedling establishment.

A dense ground cover of bryophytes characterizes poor conifer swamps (Larsen and MacDonald 1998, Bisbee et al. 2001). Bryophytes play a critical role in determining the vegetation patterning and composition of peatlands, by affecting soil thermal regimes, hydrology, and nutrient availability (Bisbee et al. 2001). The continuous moss layer of poor conifer swamps is typically dominated by sphagnum mosses, especially

*Sphagnum angustifolium*, *S. capillifolium*, *S. fuscum*, *S. magellanicum*, and *S. recurvum* (Vitt and Slack 1975, Schwintzer 1978a, O'Connell et al. 2003a and 2003b, NatureServe 2006). Additional mosses can include *S. capillaceum*, *S. centrale*, *S. compactum*, *S. cuspidatum*, *S. papillosum*, *S. wulfianum*, and *Drepanocladus aduncus* (Gates 1942, Vitt and Slack 1975, Crum 1983, Glaser et al. 1990). Shade beneath black spruce trees is conducive to the growth of *Pleurozium schreberi* (feather moss) (Foster 1985, NatureServe 2006). Feather moss decomposes faster than sphagnum and accumulates less peat (Locky et al. 2005). Bryophytes depend on a continuous source of water because they lack roots. The primary factor determining species composition of bryophytes is soil drainage (Bisbee et al. 2001). The hummock and hollow microtopography of poor conifer swamps allows for high levels of bryophyte diversity since individual species of sphagnum occur at specific elevations, exhibiting habitat partitioning (Vitt and Slack 1975, Wheeler et al. 1983, Vitt and Slack 1984, Riley 1989). Hollows support *S. magellanicum*, *S. cuspidatum*, and *S. papillosum* (Vitt and Slack 1975, Vitt et al. 1975, Heinselman 1970, Wheeler et al. 1983, Vitt and Slack 1984, Riley 1989). The lower, moist slopes of hummocks often support *S. magellanicum* and *S. recurvum* while the drier hummock crests are dominated by *S. fuscum*, *S. capillaceum*, and *S. capillifolium* (Vitt et al. 1975, Wheeler et al. 1983, Riley 1989). The vertical zonation of species or niche diversification corresponds to gradients in pH and moisture with the hollows being wetter and more alkaline than the drier and more acidic tops of the hummocks (Vitt et al. 1975, Wheeler et al. 1983, Karlin and Bliss 1984, Vitt and Slack 1984, Bridgham et al. 2006, Nicholson et al. 1996). In addition to microtopographic variation, gradients of light or sunfleck availability, determined by canopy cover and tree spacing, also influence patterns of poor conifer swamp species composition and diversity (Vitt and Slack 1984, Bisbee et al. 2001).

The herbaceous layer of poor conifer swamps is species depauperate. Several sedges that are characteristic of poor conifer swamps include *Carex lasiocarpa* (wiregrass sedge), *C. leptalea* (bristly-stalked sedge), *C. pauciflora* (few-flower sedge), *C. oligosperma* (few-seed sedge), and *C. trisperma* (three-seeded sedge), with the last two being the most common. Fine-leaved sedges are more prevalent in



ombrotrophic peatlands while broad-leaved sedges dominate minerotrophic sites (Boelter and Verry 1977). Additional graminoids found in poor conifer swamps include *Eriophorum spissum* (sheathed cotton-grass), *E. vaginatum* (tussock cotton-grass), *E. virginicum* (tawny cotton-grass), and *Scirpus cyperinus* (wool-grass). The following are prevalent poor conifer swamp herbs: *Clintonia borealis* (blue bead lily), *Coptis trifolia* (goldthread), *Cornus canadensis* (bunchberry), *Epilobium angustifolium* (fireweed), *Iris versicolor* (wild blue flag), *Lycopus uniflorus* (water-horehound), *Maianthemum canadense* (false lily of the valley), *Smilacina trifolia* (false Solomon seal), and *Trientalis borealis* (star-flower). *Onoclea sensibilis* (sensitive fern) and *Woodwardia virginica* (chain-fern) are characteristic ferns of these systems. Insectivorous plants, such as *Drosera rotundifolia* (roundleaf sundew) and *Sarracenia purpurea* (pitcher-plant), are occasional features of poor conifer swamps. Openings within poor conifer swamp can support plants such as *Calla palustris* (wild calla), *Caltha palustris* (marsh-marigold), and *Rhynchospora alba* (white beak-rush).

The shrub layer of poor conifer swamps is dominated by low, ericaceous shrubs, with *Ledum groenlandicum* (Labrador-tea) being the most prevalent. The dwarf shrub layer is typically less than three feet high. In addition to Labrador-tea, the following heath shrubs are important components of poor conifer swamps:

*Andromeda glaucophylla* (bog-rosemary), *Chamaedaphne calyculata* (leatherleaf), *Gaultheria hispidula* (creeping snowberry), *Gaultheria procumbens* (wintergreen), *Gaylussacia baccata* (huckleberry), *Kalmia angustifolia* (sheep-laurel), *K. polifolia* (bog-laurel), *Vaccinium angustifolium* (low sweet blueberry), *V. myrtilloides* (Canada blueberry), and *V. oxycoccos* (small cranberry). Ericaceous shrubs can stimulate sphagnum species through a scaffolding effect in which fast vertical sphagnum growth is facilitated by the physical support of shrub branches and adventitious roots (Fenton et al. 2005). Members of the Ericaceae generate compounds that contribute to the acidification of peatlands (Zhu and Mallik 1994). As noted above, ericads can inhibit conifer tree growth and establishment through direct competition and the production of allelopathic compounds. The tall shrub layer of poor conifer swamps is less dense than the low shrub layer and is often restricted to the periphery of the swamp or adjacent to streams that may meander through the peatland. Tall shrubs typical of poor conifer

swamps include *Aronia prunifolia* (chokeberry) and *Nemopanthus mucronatus* (mountain holly). *Alnus rugosa* (speckled alder) often occurs along peatland margins and meandering streams. The tall shrub layer is more prevalent in southern examples of poor conifer swamp where *Cephalanthus occidentalis* (buttonbush), *Ilex verticillata* (winterberry), *Toxicodendron vernix* (poison sumac), and *Vaccinium corymbosum* (highbush blueberry) are common. Stunted trees, especially black spruce, may also occur within the understory. While poor conifer swamps are dominated by plants that thrive under ombrotrophic conditions, occasionally minerotrophic indicators may be present at low cover. Plants found typically in more alkaline habitat, such as *Betula pumila* (bog birch), alder, and northern white cedar (as noted above), can occur sporadically in poor conifer swamps when their roots extend beneath the peat mat to ground-water influenced organic or mineral soil (Sjors 1950, NatureServe 2006). (Above species lists compiled from Coburn et al. 1933, Gates 1942, Dansereau and Segadas-Vianna 1952, Curtis 1959, Heinselman 1963, Vogl 1964, Janssen 1967, Heinselman 1970, Voss 1972, Schwintzer and Williams 1974, Vitt and Slack 1975, Tilton 1977, Schwintzer 1978a, Schwintzer 1981, Crum 1983, Wheeler et al. 1983, Vitt and Slack 1984, Foster 1985, Voss 1985, Futyma and Miller 1986, Miller and Futyma 1987, Riley 1989, Glaser et al. 1990, Glaser 1992, McLaughlin et al. 1994, Comer et al. 1995, Voss 1996, Larsen and MacDonald 1998, Mitsch and Gosselink 2000, Bisbee et al. 2001, Pepin et al. 2002, O'Connell et al. 2003a and 2003b, Islam and MacDonald 2004, Girardin et al. 2005, MNFI database 2006, NatureServe 2006, Kost et al. 2007).

**Michigan Indicator Species:** black spruce, *Carex oligosperma*, *C. trisperma*, Labrador-tea, leatherleaf, pitcher plant, sphagnum moss, sundew, and tamarack.

**Other Noteworthy Species:** In general, the population of animals is low in poor conifer swamps because of the low productivity of peatland plants, the unpalatability of the vegetation, and the high acidity of the peat (Mitsch and Gosselink 2000). Rare herptiles that utilize poor conifer swamps include *Emys blandingii* (Blanding's turtle, state special concern), *Glyptemys insculpta* (wood turtle, state special concern), and *Sistrurus catenatus catenatus* (eastern massasauga, state special concern). If suitable nesting trees or snags are available, *Haliaeetus leucocephalus* (bald eagle, state threatened), *Falco columbarius* (merlin, state



threatened), and *Pandion haliaetus* (osprey, state threatened) can be found nesting in these systems, and *Ardea herodias* (great blue heron, protected by the Migratory Bird Treaty Act of 1918) can establish rookeries. Other rare birds that could occur in poor conifer swamps are *Falci pennis canadensis* (spruce grouse, state special concern), and *Picoides arcticus* (black-backed woodpecker, state special concern). While spruce grouse prefer mature spruce forests, *Tympanuchus phasianellus* (sharp-tailed grouse, state special concern) can be found in recently burned poor conifer swamp in addition to muskeg and bog (Vogl 1964, Rowe 1973). *Alces alces* (moose, state threatened), *Canis lupus* (gray wolf, state threatened), and *Lynx canadensis* (lynx, state endangered) utilize peatland habitat (Mitsch and Gosselink 2000). As noted above, selective browsing by moose can result in changes to poor conifer swamp floristic composition and structure. *Castor canadensis* (beaver) can profoundly influence the hydrology of poor conifer swamp through their dam-building activities. Paleontologists believe that *Mammot americanum* (mastodon, extinct) were associated with sphagnum dominated peatlands and that spruce was a staple in their diet (Halsey and Vitt 2000).

Rare plants associated with poor conifer swamps include *Carex wiegandii* (Wiegand's sedge, state threatened), *Empetrum nigrum* (black crowberry, state threatened), *Luzula parviflora* (small-flowered wood rush, state threatened), *Rubus acaulis* (dwarf raspberry, state endangered), and *Sarracenia purpurea f. heterophylla* (yellow pitcher-plant, state threatened).

**Conservation and Biodiversity Management:** Poor conifer swamp is a widespread community type in the Great Lakes Region that contributes significantly to the overall biodiversity of northern Michigan by providing habitat for a unique suite of plants and wide variety of animal species. Numerous rare and unique species are associated with poor conifer swamp. By storing high levels of sequestered carbon and serving as carbon sinks, poor conifer swamps and related peatlands play an important role in global geochemical cycles. Peatlands also preserve paleo-environmental records; a wealth of information is stored in the remains of plants, animals, and atmospheric particles deposited and stored in peat profiles (Chapman et al. 2003). When the primary conservation objective is to maintain biodiversity in poor conifer swamps, the best management is to leave large tracts unharvested

and allow natural processes (fire, beaver flooding, and insect defoliation) to operate unhindered and stochastically generate a range of successional stages. It is crucial to allow dead and dying wood to remain within these systems to become snags, stumps, and fallen logs (Harper et al. 2005). Within areas managed solely for biodiversity, resource practitioners should refrain from salvage harvesting following fire, wind, and insect disturbance. Salvage logging, especially following fire, can severely diminish nutrient pools and site productivity in addition to reducing structural heterogeneity (Brais et al. 2000).

Where poor conifer swamps are being actively managed, maintaining poor conifer swamps in different age-classes and stages of structural development at the landscape level will contribute to the preservation of regional biodiversity (Bergeron et al. 1999, Harper et al. 2002, Harper et al. 2003, Harper et al. 2005). Maximum floristic diversity is attained when a spectrum of successional stages is maintained within the landscape (Foster 1985). Increasing old-growth and over mature poor conifer swamp and characteristics of old-growth peatlands can be accomplished by extending the rotation period of these systems (Bergeron et al. 1999). Long rotation periods (over 100 years) are favorable for numerous species, such as epiphytic lichen and trunk foraging birds that depend on old, large trees (Brais et al. 2000, Harper et al. 2003). Determining whether to manage using even-aged or uneven-aged silvicultural methods depends on the landscape context of the system. Within fire-prone landscapes, managers should consider using even-aged management while in fire-resistant systems, uneven-aged silviculture is more appropriate.

Although forested peatlands are typically managed with even-aged silviculture, uneven-aged management is both technically and biologically feasible (Groot 2002). Partial and selective cutting within poor conifer swamps has been suggested to simulate secondary disturbance such as windthrow (Harper et al. 2003). However, these uneven-aged cutting techniques do not generate pit and mound topography and fail to leave behind the same volume of coarse woody debris and snags that natural disturbances such as windthrow do. Recruitment following uneven-aged management can be from both advanced regeneration (i.e., layers) and seeding (MacDonell and Groot 1997). Black spruce layers can respond well to release from suppression, realizing significant increases in growth (Stanek 1968, Crossley 1976, Pothier et al. 1995, Prevost 1997, Groot 2002). Drawbacks to uneven-aged management include the often higher economic costs and the necessity of installing and maintaining road systems within managed peatlands, which can significantly alter successional trajectories (Groot 2002).





Even-aged management of poor conifer swamps should be restricted to fire-prone landscapes and timber rotations should reflect site specific fire return intervals. A common misconception about even-aged management of forested peatlands is that clear-cuts or final harvests are surrogates for crown fires (Harper et al. 2003, Fenton et al. 2005). As noted earlier, stand-replacing crown fires within poor conifer swamps kill the majority of the canopy trees (Curtis 1959, Bergeron and Dubuc 1989, Knowles 1991a, Harper et al. 2002). These fires create numerous snags and generate patches of residual live trees. Even-aged management within conifer swamps should strive to maintain patches of residual trees and numerous snags. Scattered seed trees and cone-bearing logging slash can provide an important source for natural regeneration (Fleming and Mossa 1996). Black spruce stocking often decreases linearly with distance from seed-tree groups (Prevost 1997). In areas where managers are planting or seeding in swamp conifers, a local seed source should be collected from a large number of diverse seed trees to help maintain genetic diversity and locally adapted gene pools (Rajora and Pluhar 2003). For black spruce, larger seeds typically produce larger seedlings with higher growth and survival rates since seed size can buffer young seedlings from climatic and edaphic influences (Wang et al. 1994).

With both even-aged and uneven-aged management of forested peatlands, protecting the residual regeneration and seed trees and generating or preserving suitable sites for seedling establishment are critical. "Careful logging" is stressed by numerous researchers as a means of preserving advanced regeneration (Morin and Gagnon 1991, MacDonnell and Groot 1997, Prevost 1997, Ruel et al. 2004). Harvesters can avoid damage to residual trees by planning ahead of time where to travel, where to drop felled trees (directional felling), and where to process and pile the bucked logs (Pothier et al. 1995, MacDonnell and Groot 1997). Selection of less intensive silvicultural systems can also minimize damage to the residual stand. In a comparison of cut-to-length versus full-length harvesting, MacDonnell and Groot (1997) found that cut-to-length harvesting produced less damage to residual trees, advanced regeneration, and the organic soils. Full-length harvesting caused greater damage to residual trees and advanced growth and damage to peat soils with deep ruts in the organic soil (MacDonnell and Groot 1997). Impacts to organic peats can be minimized by using high-flotation tires or restricting operation in forested peatlands to winter time when snow cover and frozen soils provide protection from rutting (Pothier et al. 1995).

Integral to the maintenance of forested peatlands is the preservation of hydrologic regimes. As noted, peatland systems are sensitive to changes in water chemistry and water levels. Roads passing through peatlands can cause dramatic changes including conversion to more minerotrophic open wetlands in flooded areas and increased forest productivity where drying results from blocked drainage. The installation and maintenance of culverts under roads passing through peatlands can avert flooding and drying (Jeglum 1975). Managers may also use flooding and drainage to control forest productivity and species composition. More open wetland systems can be created through flooding. Flooding, which drowns cocooning larch sawfly larvae, can also be utilized to reduce the severity and duration of larch sawfly defoliation events (Graham 1956). Drainage, which can cause increases in the depth to the water table, the substrate temperature and aeration, and nutrient availability, improves growth of both black spruce and tamarack (Liefers and Rothwell 1986, Liefers and MacDonald 1990, MacDonald and Yin 1999). Tamarack, which is often restricted to hollows while black spruce thrives on hummocks, typically realizes greater growth following lowering of the water table (MacDonald and Yin 1999). Despite the dramatic gains in tree productivity following peatland drainage, managers should employ this technique cautiously. As noted above, protracted lowering of the water table can result in water stress to vegetation growing on the hummocks, the reduction of micro-scale heterogeneity, and the decomposition of the organic soils (MacDonald and Yin 1999).

**Research Needs:** Poor conifer swamp has a broad distribution and exhibits subtle regional, physiographic, hydrologic, and edaphic variants. The lack of a universally accepted classification system of forested peatlands and the diversity of variations throughout their range demands the continual refinement of regional classifications that focus on the inter-relationships between vegetation, physiography, hydrology, and disturbance (Heinselman 1963, Fitzgerald and Bailey 1975, Barnes et al. 1982, Bisbee et al. 2001, Locky et al. 2005). Systematic surveys for poor conifer swamps and related peatlands are needed to help prioritize conservation and management efforts. Little is known about the fire regimes of poor conifer swamps and the interaction of disturbance factors within these systems. Of particular importance is the study of how fire intensity and periodicity change depending on landscape context. Site specific fire frequencies can be estimated by investigating fossil pollen and charcoal records stored in peat (Larsen and MacDonald 1998).



Understanding the complex interaction of fire, insect defoliation, and changes in hydrologic regimes is a critical research need. Scientists should continue investigating what primary factors are driving the severity, frequency, and longevity of insect defoliation episodes (Graham 1956). As noted by Hammerson (1994), beaver significantly alter the ecosystems they occupy. An important research question to examine is how the wetland ecosystems of the Great Lakes have been and continue to be affected by fluctuations in populations of beaver. Numerous studies have examined how flooding and drainage effect tree dynamics of peatlands but have failed to determine how these hydrologic changes impact the organic soils and the shrub and herbaceous layers (Asada et al. 2005).



Photo by Joshua Cohen

How beaver flooding and other forms of hydrologic alteration impact poor conifer swamps merits continued study

A better understanding is needed of the influence of direct and indirect anthropogenic disturbance on peatlands (Amon et al. 2002). Little is known about how the resilience and biodiversity of poor conifer swamps is affected by clear-cutting, which has been erroneously assumed to be a surrogate for crown-fires (Bergeron et al. 1999). Effects of management within poor conifer swamps should be monitored to allow for assessment and refinement. Experimentation with uneven-aged management of poor conifer swamps in fire resistant landscapes will provide insights about alternatives to even-aged silviculture (Groot 2002). Sustainable management of forested peatlands requires assessment of methods for establishing conifer regeneration and whether or not layers grow as well as seed-generated

seedlings (Prevost 1997, Fenton et al. 2005). More research is needed to elucidate the relationship of chemical factors and nutrient levels to floristic community structure of peatlands (Amon et al. 2002). Given the sensitivity of peatlands to slight changes in hydrology and nutrient availability, it is important for scientists to predict how peatlands will be affected by global warming and atmospheric deposition of nutrients and acidifying agents (Heinselman 1970, Riley 1989, Bedford et al. 1999, Gignac et al. 2000, Mitsch and Gosselink 2000, O'Connell et al. 2003a and 2003b). Peat deposits are of great scientific interest because they contain historical and ecological records in the form of fossils of plants and animals and organic matter that contributed to the deposit. Stratigraphical analysis of peat cores provides insights into past climatic change and associated vegetation change, floristic distribution, the development of wetland ecosystems, and the successional pathways of peatlands (Heinselman 1963, Glaser et al. 1981, Miller 1981, Glaser and Janssens 1986, Riley 1989, Gignac et al. 2000).

**Similar Communities:** bog, muskeg, northern fen, patterned fen, poor fen, rich conifer swamp, rich tamarack swamp.

**Other Classifications:**

**Michigan Natural Features Inventory Circa 1800 Vegetation (MNFI):**

Mixed Conifer Swamp (4200), Black Spruce/Mixed Conifer Swamp (4232), and Tamarack/Mixed Conifer Swamp (4233)

**Michigan Department of Natural Resources (MDNR):** Q-mixed conifer swamp, S-black spruce swamp, T-tamarack swamp

**Other Classifications:**

**Michigan Resource Information Systems (MIRIS):** 42 (wetland conifer), 423 (lowland conifer), black spruce (42326), and tamarack (42335)

**The Nature Conservancy National Classification:**  
CODE; ALLIANCE; ASSOCIATION; COMMON NAME

I.A.8.N.g; *Picea mariana* Saturated Forest Alliance; *Picea mariana* – (*Larix laricina*) / *Ledum groenlandicum* / *Sphagnum* spp. Forest; Black Spruce – (Tamarack) / Labrador-tea / Peatmoss Species Forest; Black Spruce – (Tamarack) / Labrador-tea Poor Swamp



**The Nature Conservancy National Classification:**

CODE; ALLIANCE; ASSOCIATION; COMMON NAME

I.A.8.N.g; *Picea mariana* Saturated Forest Alliance; *Picea mariana* / *Ledum groenlandicum* / *Carex trisperma* / *Sphagnum* spp. Forest; Black Spruce / Labrador-tea / Three-seed Sedge / Peatmoss Species Forest; Black Spruce Bog

I.A.8.N.g; *Picea mariana* Saturated Forest Alliance; *Pinus banksiana* – (*Picea mariana*) – Mixed Hardwoods / *Sphagnum* spp. Forest; Jack Pine – (Black Spruce) – Mixed Hardwoods / Peatmoss Species Forest; Jack Pine Swamp

IV.A.1.N.g; *Chamaedaphne calyculata* Saturated Dwarf-Shrubland Alliance; *Picea mariana* / *Chamaedaphne calyculata* / *Sphagnum* spp. Dwarf-shrubland; Black Spruce / Leatherleaf / Peatmoss Species Dwarf-Shrubland; Black Spruce / Leatherleaf Semi-treed Bog

**NatureServe Ecological Systems Classification:**

CES103.724: Boreal-Laurentian Conifer Acid Swamp

**Related Abstracts:** black-backed woodpecker, Blanding’s turtle, eastern massasauga, great blue heron rookery, merlin, muskeg, rich conifer swamp, rich tamarack swamp, and yellow pitcher plant.

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