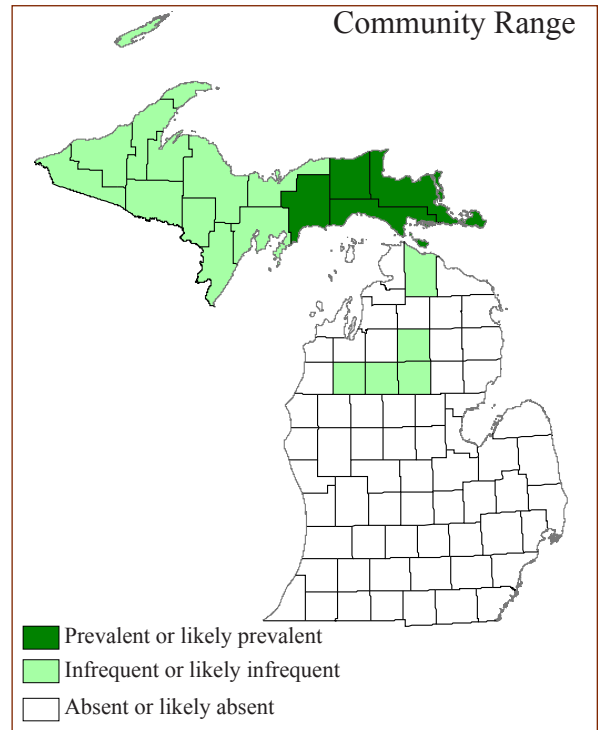




Photo by Joshua Cohen



Overview: Muskegs are a nutrient-poor, peatlands characterized by acidic, saturated peat, scattered and stunted conifer trees set in a matrix of *Sphagnum* mosses and ericaceous shrubs. Muskegs are located in large depressions in glacial outwash and sandy glacial lakeplains. Fire occurs naturally during drought periods and can alter the hydrology, mat surface, and flora of muskegs. Windthrow, beaver flooding, and insect defoliation are also important disturbance factors that influence species composition and structure.

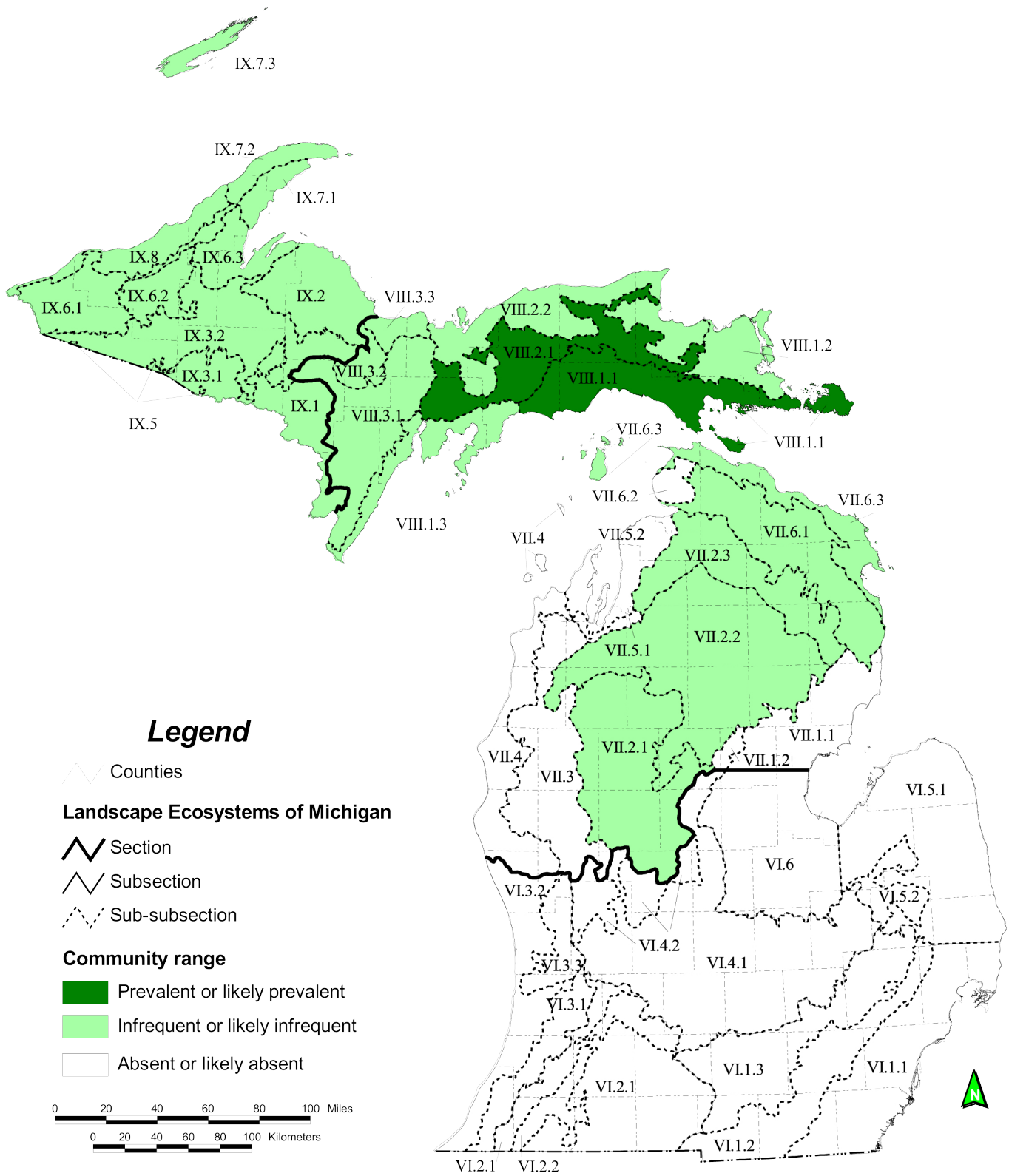
Global and State Rank: G4G5/S3

Range: Muskegs are an uncommon peatland type of glaciated landscapes of the entire northern hemisphere and are characterized by remarkably uniform floristic structure and composition across the circumboreal region (Curtis 1959). 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,

muskegs are infrequent in the Northern Lower Peninsula and occur throughout the Upper Peninsula with heavy concentrations in Schoolcraft, Luce, and Delta Counties. Circa 1800, approximately 95% of the muskeg acreage was in the Upper Peninsula with the remainder occurring as scattered patches in the Northern Lower Peninsula (Comer et al. 1995). Muskegs 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 (Heinselman 1970, Boelter and Verry 1977, 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) muskegs, based on comparisons of nutrient levels, flora, canopy closure, and groundwater influence. Muskegs, peat-covered wetlands raised above the surrounding groundwater by an accumulation of peat, receive inputs of nutrients and water primarily from precipitation (Gignac et al. 2000). The open canopy of muskegs ranges from 10% to 25% and is characterized by scattered and/





Ecoregional map of Michigan (Albert 1995) depicting distribution of muskeg (Albert et al. 2008)



or clumped conifers that are stunted. Like muskegs, poor conifer swamps and bogs are nutrient-poor, acidic wetlands. However, bogs are open wetlands lacking a canopy and poor conifer swamps exhibit a greater degree of canopy closure than muskegs. Patterned fens, which also are concentrated in Michigan in the eastern Upper Peninsula, are complex minerotrophic mosaics characterized by stunted and scattered conifers and peat ridges (strings) and graminoid-dominated hollows (flarks) oriented across the slope and perpendicular to the flow of groundwater (Comer et al. 1995, Kost et al. 2007). 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). In addition to a greater importance by graminoids, fens also are less dominated by sphagnum mosses (*Sphagnaceae*) with brown mosses (*Amblystegiaceae*) being more prevalent. 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 muskegs, with poor fens being most similar in terms of these factors and species composition.

Rank Justification: Muskegs are uncommon features of the northern Great Lakes Region, occurring throughout the Upper Peninsula and sporadically within the Northern Lower Peninsula. 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 muskeg once occupied over 57,000 hectares (141,000 acres) (Comer et al. 1995). Although there are no precise estimates of current muskeg acreage, in general, anthropogenic disturbance has decreased the extent of peatlands and dramatically altered them. Turn of the century logging of tamarack, black spruce, and cedar from peatland systems favored the conversion of forested peatlands to open, ombrotrophic bogs and muskegs (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 bogs or muskegs 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 and muskegs to closed canopy peatlands (Curtis 1959, Riley 1989) and the maintenance of closed-canopy poor conifer swamps.

Peat mining and cranberry farming have degraded numerous peatlands throughout the region (Gates 1942, Curtis 1959, Eggers and Reed 1997, Chapman et al. 2003). Michigan, along with Florida and Minnesota, are leaders in peat production in the U.S. (Miller 1981). 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 drastic changes in 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 muskegs and 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). Flooding of poor conifer swamps can result in the conversion to muskeg. 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 muskegs and poor conifer swamps to open peatlands. Conversely, lowering of water tables from drainage can allow for tree and shrub encroachment into open bogs and muskegs 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 muskegs on precipitation for 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). Eutrophication from pollution and altered hydrology can detrimentally impact peatlands by generating conditions favorable for the invasion of exotic species (Riley 1989) and dominance by aggressive, common natives such as *Phalaris arundinacea* (reed canary grass) and *Typha* spp. (cat-tails) (Almendinger and Leete 1998).

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). Muskegs primarily occur on broad, flat areas or mild depressions of glacial outwash and glacial lakeplains but can also be found in large depressions on pitted outwash and moraines (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 which 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 muskegs 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 Joshua Cohen

Muskegs occur most frequently on broad, flat, expanses of paludified glacial lakeplain (above) and outwash.

Muskegs within large wetland complexes typically occur adjacent to other peatland communities, often grading into bog, patterned fen, poor fen, poor conifer swamp, and/or rich conifer swamp. More minerotrophic systems such as northern fen, northern shrub thicket, northern wet meadow, rich conifer swamp, and hardwood-conifer swamp can occur along the outer margins of muskegs 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). Muskegs frequently occur adjacent to lakes and meandering streams (usually less than third order) often weave along their margins through the adjoining minerotrophic wetlands. Upland community types that often occur adjacent to muskegs include dry northern forest, dry-mesic northern forest, and mesic northern forest. Sandy ridges dominated by white pine, red pine, and/or jack pine often occur within peatland complexes.

Hydrology: Climate, topography, near surface geology, soils, and vegetation influence the hydrology of muskegs (Miller and Futyma 1987). No apparent inlets or outlets supply or drain muskegs which are isolated from ground water influence as the result of peat accumulation (Dean and Coburn 1927, Schwintzer 1978b, Riley 1989, Swineheart and Parker 2000, Hoffman 2002, NatureServe 2006). Muskegs 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, Damman 1990, Glaser et al. 1990, Mitsch and Gosselink 2000, Bedford and Goswin 2003, 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 muskegs confined to small basins compared to large peatland complexes (NatureServe 2006).

The water retaining capacity of sphagnum peat is tremendous and as a result, muskegs are saturated, anoxic systems with water tables near the surface (Burns 1906, Dansereau and Segadas-Vianna 1952, Curtis 1959, Heinselman 1970, Schwintzer 1978b, Bubier 1991, Jasieniuk and Johnson 1982, Liefers and Rothwell 1986,



Siegel and Glaser 1987, Glaser 1992, McLaughlin et al. 1994, Eggers and Reed 1997, O'Connell et al. 2003b, Islam et al. 2003, Islam and MacDonald 2004, Fenton et al. 2005). The stagnant surface waters of muskegs 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, Bubier 1991, Glaser et al. 1981, Jasieniuk and Johnson 1982, Wheeler et al. 1983, Liefers and Rothwell 1986, Riley 1989, Damman 1990, 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 muskegs 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). Muskegs 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, Richardson and Marshall 1986, Glaser 1992, Bedford et al. 1999, Mitsch and Gosselin 2000, Islam et al. 2003).

Soils: The organic soils of muskegs are composed of peat that overlays sands and forms a continuous mat, which ranges in thickness from one to eight meters but is typically one to three meters deep (Heinselman 1965, Bay 1967, Heinselman 1970, Siegel and Glaser 1987). Depth of peat and soil moisture increases with peatland age and can 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). The rooting zone within muskegs is quite shallow, typically confined to the upper 15 cm of the surface peat (Barnes and Wagner 1981, Karlin and Bliss 1984, Glaser and Janssens 1986, Islam et al. 2003, Hamel et al. 2004). Peat of muskegs is characterized by high carbon content (Halsey and Vitt 2000, O'Connell et al. 2003a and 2003b).

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 muskegs 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 depending 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 Gosselin 2000). The Michigan range of muskeg 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 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 short, warm summers, cold winters, and a large number of cloudy days. The mean number of freeze-free days is between 90 and 160, and the average number of days per year with snow cover of 2.5 cm or more is between 80 and 140. The normal annual total precipitation



ranges from 740 to 900 mm with a mean of 823 mm. The daily maximum temperature in July ranges from 24 to 29 °C (75 to 85 °F), the daily minimum temperature in January ranges from -21 to -9 °C (-5 to 15 °F) and the mean annual temperature is 7 °C (45 °F) (Albert et al. 1986, Barnes 1991). Temperatures vary less in muskegs 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 (Burns 1906, Curtis 1959, Heinselman 1963, Glaser 1992). Muskegs 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, Heinselman 1963, Bedford and Godwin 2003).

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). Low levels of oxygen protect plants from microorganisms and chemical actions that cause decay (Miller 1981, Damman 1988). Likewise, high levels of acidity have inhibitory effects on decay organisms (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 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 can proceed from lake to marsh to fen to bog to muskeg or 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). Bogs can succeed to muskeg or remain as bogs and muskeg can succeed to poor conifer swamp or remain as muskeg 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 muskeg 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). Another potential successional pathway is the conversion of poor conifer swamp to muskeg through paludification.

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 the influence of groundwater (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 increases in the water table and acidity and a subsequent decrease in soil temperatures, nutrient availability, decomposition rates, canopy cover, growth rates, and seedling establishment: a shift in species composition also occurs 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). The accumulation of organic soils under forested peatlands can lead to the conversion to muskeg since thick sphagnum mats can limit tree establishment and growth.

Once established, muskeg can persist for hundreds of years given stable hydraulic conditions and the lack of

fires which can burn the canopy and organic soils. Fire, which is an infrequent but important disturbance factor within peatlands, controls plant 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 peatlands 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 peatlands. 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 systems in fire-protected landscapes (Whitney 1986, Cleland et al. 2004). Muskeg fire regimes most likely encompassed this wide range depending on the landscape context. 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, peat 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 muskegs 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 may expose mineral soil (Vogl 1964, Rowe 1973, Damman 1990, Jean and Bouchard 1991). Exposure of the mineral soil provides a suitable medium for swamp conifers' (i.e., black spruce, tamarack, jack pine, and northern white cedar) establishment and germination (Curtis 1959, Brown et al. 1988) and can lead to the conversion of muskegs to forested peatlands. Seed source availability and seedbed availability and quality determine the burned stands tree density as well as composition (Sirois and Payette 1989). Fires of weak severity within poor conifer swamps that kill part of the canopy but leave much of the organic layer intact 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 even precipitate the conversion of poor conifer swamp





Muskegs burn infrequently during periods of extended drought. The Sleeper Lake Fire burned through extensive areas of muskeg. Photos by Joshua G. Cohen.



to muskeg (Vogl 1964). Low severity surface fires in open peatlands can contribute to their maintenance by killing encroaching trees, promoting sprouting of ericaceous shrubs, and minimally impacting sphagnum moss cover (Curtis 1959, Vitt and Slack 1975). In fire prone landscapes, periodic fire can maintain bogs and muskegs: conversely, fire suppression in these areas can lead to the conversion of open peatlands to poor conifer swamps (Curtis 1959, Vitt and Slack 1975).

Water regime and nutrient regime changes in peatlands result in drastic modification of species composition and abundance (Jasieniuk and Johnson 1982). Beaver, through their dam-building activities, can cause substantial hydrologic change to peatland systems, either causing flooding or the lowering of the water table depending on the location of the peatland 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 the canopy trees and the conversion of forested peatlands to muskegs and 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 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 (Islam et al. 2003, Islam and MacDonald 2004).

The lowering of the water table through beaver damming or climatic changes can also dramatically effect the species composition and successional trajectory of muskegs. Lowering of a 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 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 establish 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 shift of muskeg and poor conifer swamps to more minerotrophic forest types. 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 muskegs 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 muskeg 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, Glaser and Janssens 1986, Islam et al. 2003, Hamel et al. 2004). The poor drainage of muskegs and the superficial rooting of swamp trees results in numerous windthrows (Dansereau and Segadas-Vianna 1952, Curtis 1959, Harper et al. 2002, Harper et al. 2003). However, the short stature of many of the stunted canopy trees may provide them with some protection from wind (Groot and Horton 1994). Small-scale wind disturbance,



along with insect herbivory contribute to the structural diversity of muskegs by generating moderate pit and mound topography, standing snags, and woody debris, which is quickly enveloped by the sphagnum.

Tree survival in muskegs is also limited by insects and parasites. The plant parasite *Arceuthobium pusillum* (dwarf mistletoe) can increase the mortality of black spruce (Coburn et al. 1933, Gates 1942). Three insect defoliators are most prevalent in peatlands, *Pristiphora erichsonii* (larch sawfly), *Coleophora laricella* (larch casebearer), and *Choristoneura fumiferana* (spruce budworm) (Curtis 1959, Newton and Jolliffe 1998). Spruce budworm defoliates both black spruce and balsam fir but tends to be more detrimental to the latter. 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 peatlands 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.

Native ericaceous shrubs can profoundly limit the establishment and growth of conifer trees within peatlands through competitive inhibition and also through the production of allelopathic compounds. Many of the ericaceous plants that thrive in muskegs are fire-adapted and often resprout vigorously and grow densely following fire (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). *Kalmia angustifolia* (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 condition (Zhu and Mallik 1994).



Photo by Joshua Cohen

Ericaceous shrubs such as leatherleaf can limit the establishment and growth of conifers within muskegs through competition.

Vegetation Description: Muskegs are characterized by low ericaceous, evergreen shrubs, a poor herbaceous layer dominated by sedges and a hummocky carpet of sphagnum moss, and widely scattered or clumped, stunted conifers (Gates 1942, Curtis 1959, Verry 1975, Vitt and Slack 1975, Glaser et al. 1991, NatureServe 2006). Floristically muskegs are homogenous and of limited plant diversity, exhibiting remarkably uniform structure and composition across their wide range (Curtis 1959, Riley 1989). The harsh growing conditions of muskegs (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 evergreen leaves, sclerophylly (thick epidermal tissue), carnivory, tight nutrient cycles, and high root biomass and root to shoot ratios (Bridgham et al. 1996, Mitsch and Gosselink 2000). Very few introduced, weedy species are able to establish within open peatlands because of the unique growing conditions and competition from the adapted flora (Riley 1989). In a study of open ombrotrophic peatlands





Muskeg is a nutrient-poor peatland characterized by acidic, saturated peat, and scattered or clumped, stunted conifer trees set in a matrix of sphagnum mosses, graminoids, and ericaceous shrubs. Photos by Joshua G. Cohen.



across eastern North America, Glaser (1992) found the native vascular flora to be limited to only 81 species and the mean number of species per peatland to be below 26. Total number of species in Michigan muskegs is typically low, often less than twenty-five (Kost et al. 2007). 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 muskeg, floristic composition and variation is 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, Bridgham et al. 1996, Nicholson et al. 1996, Locky et al. 2005).

Muskegs are dominated by mosses from the *Sphagnaceae* and shrubs from the *Ericaceae*; other well-represented families include the *Cyperaceae*, *Orchidaceae*, and *Ranunculaceae* (Gates 1942, Curtis 1959, Heinselman 1970). The most important primary producers within muskegs are ericaceous shrubs and sedges (Mitsch and Gosselink 2000). Muskeg flora is predominantly spring flowering and heliophitic (sun-loving) (Curtis 1959, Dansereau and Segadas-Vianna 1952). While muskegs are dominated by plants that thrive under ombrotrophic conditions, occasionally minerotrophic indicators may be present in muskegs at low cover. Plants found typically in more alkaline habitat such as *Betula pumila* (bog birch), *Carex aquatilis* (water sedge), and *Carex stricta* (tussock sedge), can occur sporadically in muskegs when their roots extend beneath the peat mat to organic or mineral soil influenced by ground water (NatureServe 2006).

A dense ground cover of bryophytes characterizes muskegs (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 muskegs is typically dominated by sphagnum mosses, especially *Sphagnum angustifolium*, *S. centrale*, *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. capillifolium*, *S. compactum*, *S. cuspidatum*, *S. papillosum*, *S. recurvum*, *S. rusowii*, and *Drepanocladus aduncus* (Gates 1942, Vitt and Slack 1975, Crum 1983, Glaser et al. 1990). Shade beneath the scattered conifer trees is conducive to the growth of *Pleurozium schreberi* (feathermoss) (Foster 1985, NatureServe 2006). 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 muskeg 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 tree cover and spacing, also influence patterns of species composition and diversity (Vitt and Slack 1984, Bisbee et al. 2001).

The herbaceous layer of muskegs is species depauperate and dominated by cyperaceous plants. Several sedges that are characteristic of muskegs include *Carex exilis* (coastal sedge), *C. limosa* (mud sedge), *C. lasiocarpa* (wiregrass sedge), *C. pauciflora* (few-flower sedge), *C. oligosperma* (few-seed sedge), and *C. trisperma* (three-seeded sedge). Fine-leaved sedges are more prevalent in ombrotrophic peatlands while broad-leaved sedges dominate minerotrophic sites (Boelter and Verry 1977). Additional graminoids found in muskegs include *Cladium mariscoides* (twig-rush), *Dulichium arundinaceum* (three-way sedge), *Eriophorum angustifolium* (tall cotton-grass), *E. spissum* (sheathed cotton-grass), *E. vaginatum* (tussock cotton-grass), *E.*



virginicum (tawny cotton-grass), *Glyceria canadensis* (rattlesnake mannagrass), and *Rhynchospora alba* (white beak-sedge). The following are prevalent muskeg herbs: *Aster nemoralis* (bog aster), *Coptis trifolia* (goldthread), *Epilobium angustifolium* (fireweed), *E. ciliatum* (fringed willow-herb), *Iris versicolor* (wild blue flag), *Menyanthes trifoliata* (bog bean), *Smilacina stellata* (starry false Solomon seal), *S. trifolia* (false Mayflower), *Trientalis borealis* (star-flower), and *Triglochin maritima* (arrow-grass). Insectivorous plants, *Drosera rotundifolia* (roundleaf sundew), *Drosera intermedia* (spoon-leaf sundew), *Sarracenia purpurea* (pitcher-plant), and *Utricularia intermedia* (flat-leaved bladderwort), are common features of muskegs.



Photo by Joshua Cohen

Insectivorous plants such as sundews and bladderworts have developed carnivorous adaptations to cope with the low nutrient availability of ombrotrophic peatlands

The shrub layer of muskegs is dominated by low, ericaceous shrubs, with *Chamaedaphne calyculata* (leatherleaf) being the most prevalent. The dwarf shrub layer is typically less than three feet high and usually covers at least 40% of the muskeg area (Michigan Natural Feature Inventory 2003). In addition to leatherleaf, the following heath shrubs are important components of muskegs: *Andromeda glaucophylla* (bog-rosemary), *Gaultheria hispidula* (creeping snowberry), *G. procumbens* (wintergreen), *Kalmia*

angustifolia (sheep-laurel), *K. polifolia* (bog-laurel), *Ledum groenlandicum* (Labrador-tea), *Vaccinium angustifolium* (low sweet blueberry), *V. macrocarpon* (large cranberry), *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 which 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 muskegs is less dense than the low shrub layer and is often restricted to the periphery of the community. Tall shrubs typical of muskegs include *Aronia prunifolia* (chokeberry), *Nemopanthus mucronatus* (mountain holly), *Salix discolor* (pussy willow), *S. pedicellaris* (bog willow), *Spiraea alba* (white meadowsweet), *S. tomentosa* (steplebush), and *Viburnum cassinoides* (wild-raisin). As noted, bog birch can occur at low cover when its roots extend beneath the peat mat to ground-water influenced soils. *Alnus rugosa* (speckled alder) often occurs along peatland margins and meandering streams.

Trees within muskegs are widely scattered or clumped and stunted (Krumholz form), usually no taller than two to three meters. Clumping of trees is concentrated on higher hummocks with intervening hollows often devoid of trees. Tree cover is typically between 10 to 25% (NatureServe 2006). Diameters of the dwarf trees of muskegs typically range between 5 to 15 cm (2 to 6 inches). Trees growing in peatlands have horizontally oriented root systems that are confined to the less saturated surface layers (the upper 10-20 cm) (Barnes and Wagner 1981, Karlin and Bliss 1984, Liefers and Rothwell 1986, MacDonald and Yin 1999, Pepin et al. 2002). The most common canopy dominants are *Picea mariana* (black spruce) and *Larix laricina* (tamarack). Additional associates include *Pinus banksiana* (jack pine) and *Pinus strobus* (white pine). (Above species lists were compiled from the following sources: Coburn et al. 1933, Gates 1942, Dansereau and Segadas-Vianna 1952, Curtis 1959, Heinselman 1963, Vogl 1964, Heinselman 1965, Bay 1967, Janssen 1967, Heinselman 1970, Schwintzer and Williams 1974, Vitt and Slack 1975, Vitt et al. 1975, Tilton 1977, Schwintzer 1978a, Glaser et al. 1981, Schwintzer 1981, Crum 1983, Wheeler et al. 1983, Vitt and Slack 1984, Foster 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, Eggers and Reed 1997, 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, Michigan Natural Features Inventory database 2006, NatureServe 2006, Kost et al. 2007).



Photo by Joshua Cohen
Scattered and stunted conifers establish on hummocks

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

Other Noteworthy Species: Muskegs provide habitat for numerous rare insect species including *Boloria freija* (freija fritillary, state special concern butterfly), *Boloria frigga* (frigga fritillary, state special concern butterfly), *Erebia discoidalis* (red-disked alpine, state special concern butterfly), *Oecanthus laricis* (tamarack tree cricket, state special concern), *Somatochlora incurvata* (incurvate emerald, state special concern dragonfly), and *Williamsoni fletcheri* (ebony boghaunter, state special concern dragonfly). Numerous butterflies and moths are restricted to bogs, muskegs, and fens because their food plants occur within these peatland systems (Riley 1989). Rare herptiles that utilize muskegs include *Clemmys guttata* (spotted turtle, state threatened) and *Emydoidea blandingii* (Blanding's turtle, state special concern). If suitable nesting trees or snags are available, *Haliaeetus leucocephalus* (bald eagle, state special

concern), *Falco columbarius* (merlin, state threatened), and *Pandion haliaetus* (osprey, state special concern) 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 muskegs are *Botaurus lentiginosus* (American bittern, state special concern), *Circus cyaneus* (northern harrier, state special concern), *Coturnicops noveboracensis* (yellow rail, state threatened), *Falciptennis canadensis* (spruce grouse, state special concern), *Picoides arcticus* (black-backed woodpecker, state special concern), and *Tympanuchus phasianellus* (sharp-tailed grouse, state special concern). While spruce grouse prefer mature spruce forests, sharp-tailed grouse can be found in recently burned poor conifer swamp in addition to muskeg and bog (Vogl 1964, Rowe 1973). Small mammals associated with open peatland habitat include *Sorex fumeus* (smoky shrew, state threatened) and *Cryptotis parva* (least shrew, state threatened). *Alces americanus* (moose, state special concern), *Canis lupus* (gray wolf, state threatened), and *Lynx canadensis* (lynx, state endangered) utilize muskegs (Mitsch and Gosselink 2000).

In general, the population of animals is low in muskegs because of the low productivity of peatland plants, the unpalatability of the vegetation, and the high acidity of the peat (Mitsch and Gosselink 2000). Bogs and muskegs provide important habitat for small mammals such as *Blarina brevicauda* (short-tailed shrew), *Castor canadensis* (beaver), *Microtus pennsylvanicus* (meadow vole), *Mustela vison* (mink), *Ondatra zibethicus* (muskrat), and *Sorex cinereus* (masked shrew) (Curtis 1959, Mitsch and Gosselink 2000). Both muskrats and beaver can profoundly influence the hydrology of open peatlands. Muskrats create open water channels through the peat and beavers can cause substantial flooding through their dam-building activities (Gates 1942, Heinselman 1963).

Rare plants potentially associated with muskeg include *Amerorchis rotundifolia* (round-leaved orchis, state endangered), *Carex heleonastes* (Hudson Bay sedge, state endangered), *C. wiegandii* (Wiegand's sedge, state special concern), *Empetrum nigrum* (black crowberry, state threatened), and *Rubus acaulis* (dwarf raspberry, state endangered).

Conservation and Biodiversity Management: Muskeg is an uncommon community type in the northern 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 muskegs. By storing high levels of sequestered carbon and serving as carbon sinks, bogs and related peatlands, such as muskegs, play an important role in global geochemical cycles. Muskegs also preserve paleoenvironmental 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). The primary mechanism for preserving muskegs is to maintain their hydrology. As noted, peatland systems are sensitive to slight changes in water chemistry. A serious threat to muskeg hydrology is posed by off-road-vehicle traffic, which can drastically alter the hydrology through rutting. Reducing access to peatland systems will mitigate detrimental impacts. Avoiding the construction of new roads that traverse peatlands will help prevent unintended hydrologic alteration. Roads passing through or near 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). Resource managers operating in uplands and forested peatlands adjacent to muskegs should take care to minimize the impacts of management to hydrologic regimes, especially increased surface flow. This can be accomplished by establishing a no-cut buffer around muskegs and avoiding road construction and complete canopy removal in stands immediately adjacent to muskegs. Elevation of an open peatland's water table and clear-cutting within muskegs can result in the expansion of leatherleaf and sphagnum and a subsequent decrease in floristic diversity (Schwintzer 1979, Zhu and Mallik 1994, Yamasaki et al. 1998, Ruel et al. 2004).

Resource managers can employ several techniques to actively manage for muskeg. Within poor conifer swamps with deep organic soils, forest operations that eliminate the tree layer or substantially remove the overstory tend to result in poor tree growth and regeneration and ultimately fragmented canopies (Ruel et al. 2004). Silvicultural management of peatlands to create or preserve open canopy should be employed during the winter to minimize damage to the peat and impacts to the hydrologic regime. Where shrub/tree encroachment threatens to convert open wetlands to shrub-dominated systems or forested swamps, prescribed fire or selective cutting can be employed to maintain open conditions. Prescribed fire can also be utilized to convert poor conifer swamp to bog or muskeg (Vogl 1964). Repeat burnings within bogs and muskegs can result in the development of minerotrophic

conditions and the succession to graminoid-dominated mineral soil wetlands such as wet meadow and emergent marsh. Managers may also use flooding and drainage to control forest productivity, mortality, and species composition. Muskeg can be created through temporary flooding of poor conifer swamps. Conversely, drainage, by increasing the depth to the water table, the substrate temperature and aeration, and nutrient availability can improve growth of both black spruce and tamarack (Liefers and Rothwell 1986, Liefers and MacDonald 1990, MacDonald and Yin 1999). Tamarack, which is often prevalent in 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. Protracted lowering of the water table can result in drought stress to vegetation growing on the hummocks, the reduction of micro-scale heterogeneity, the decomposition of organic soils, and ultimately the loss of uncommon peatland types such as muskeg (MacDonald and Yin 1999).



Photo by Joshua G. Cohen

Muskeg is uncommon in Michigan and provides habitat for a unique suite of flora and a wide variety of fauna.

Research Needs: Muskeg has a broad distribution and exhibits subtle regional, physiographic, hydrologic, and edaphic variants. The lack of a universally accepted classification system of 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). Muskegs and related community types (i.e., bog, patterned fen, and poor conifer swamp) can be difficult to differentiate (Heinselman 1963, NatureServe 2006). Research on abiotic and biotic indicators that help distinguish similar peatlands would be useful for field identification. Systematic surveys for muskegs and related peatlands are needed to help prioritize conservation and management efforts. Little is known about the fire regimes of muskegs and the interaction of disturbance factors within these systems. Of particular importance is the study of how fire intensity and periodicity are influenced by 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 and climate 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). Experimentation is needed to determine how best to prevent shrub and tree encroachment of muskegs that are threatened by conversion to shrub thicket or conifer swamp. A better understanding is needed of the influence of direct and indirect anthropogenic disturbance on peatlands (Amon et al. 2002). Effects of management within muskegs should be monitored to allow for assessment and refinement. 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, northern fen, patterned fen, poor fen, poor conifer swamp, rich tamarack swamp, rich conifer swamp.

Other Classifications:

Michigan Natural Features Inventory Circa 1800 Vegetation (MNFI):

Muskeg/Bog (6124), Muskeg (6125)

Michigan Department of Natural Resources (MDNR): D-treed bog, V-bog

Michigan Resource Information Systems

(MIRIS): 612 (shrub/scrub wetland), 62 (non-forested wetland)

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

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

III.B.2.N.g *Betula pumila* – (*Salix* spp.) Saturated Shrubland Alliance; *Larix laricina* / *Chamaedaphne calyculata* / *Carex lasiocarpa* Shrubland; Tamarack / Leatherleaf / Wiregrass Sedge Shrubland; Tamarack Scrub Poor Fen

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:

CES103.581: Boreal-Laurentian Bog
 CES103.724: Boreal-Laurentian Conifer Acid Swamp

Related Abstracts: black-backed woodpecker, Blanding's turtle, eastern great blue heron rookery, merlin, poor conifer swamp, rich conifer swamp, rich tamarack swamp.



Photo by Joshua Cohen

Muskeg, Luce County, Michigan.

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Muskeg, Marquette County, Michigan.

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