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The Use of Bryophytes as Indicators of Hydric Soils and Wetland Hydrology during Wetland Delineations in the United States

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Abstract: Under Section 404 of the Clean Water Act, the U.S. Army Corps of Engineers is responsible for delineating wetland boundaries. Three factors are used: hydrophytic vegetation, hydric soils, and wetland hydrology. Current procedures for making hydrophytic vegetation determinations are based on vascular plants; the use of bryophytes is generally not recommended. However, the National Technical Committee on Wetland Vegetation is investigating the use of bryophytes as indicators of environmental conditions. This literature review examines relationships between bryophytes, hydric soils, and wetland hydrology for delineating wetlands. To determine whether hydric soils and wetland hydrology control the bryophyte species present in wetlands, bryophyte adaptations to these environmental variables are investigated. Response to soils and hydrology is considered at the microscale and the mesoscale. The consistency and reliability of bryophytes as indicators of wetland type are examined. Selected species and genera are identified as hydrophytes, and procedures for field sampling are proposed. Bryophyte identification resources and the necessity of voucher specimens are also discussed. To determine whether species composition differs with soil moisture levels, soil type, and hydrologic regime, bryophyte associations in wetlands and adjacent uplands are explored. Finally, situations in which bryophytes could be used in wetland delineations and areas that require further research are identified.

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Nomenclature

OBL	Obligate
USACE	United States Army Corps of Engineers
FACW	Facultative wetland
FAC	Facultative
ABLS	American Bryological and Lichenological Society
FACU	Facultative upland
IAB	International Association of Bryologists
FHS	Floristic habitat sampling
USFWS	United States Fish and Wildlife Service

Preface

Funding for this project was made possible by the Wetlands Regulatory Assistance Program (WRAP) of the U.S. Army Corps of Engineers (USACE) through Robert Lichvar at the Engineer Research and Development Center (ERDC), Cold Regions Research and Engineering Laboratory (CRREL), in support of the National Technical Committee on Wetland Vegetation.

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1 Introduction

Wetlands provide a number of valuable ecological benefits to the citizens of the United States, including, but not limited to, flood control, aquifer recharge, improved water quality, agriculture production, wildlife habitat, and recreation (Mitsch and Gosselink 2000). The U.S. Army Corps of Engineers (USACE) is responsible for minimizing wetland impacts, under Section 404 of the Clean Water Act (33 U.S.C. 1344). To avoid or minimize impacts, the extent of federal jurisdiction in wetlands is delineated using procedures described in the *Corps of Engineers Wetlands Delineation Manual* (USACE 1987).

Although the use of bryophytes has not been recommended in federal delineation procedures, two regional supplements to the *Corps of Engineers Wetlands Delineation Manual* permit the use of some nonvascular plants in specific circumstances. In both cases, soils and hydrology must first indicate wetland conditions. The *Interim Regional Supplement for the Western Mountains, Valleys, and Coast Region* proposes the use of specific bryophyte indicator species for delineations in areas dominated by *Tsuga heterophylla* (USACE 2008a). Likewise, in Alaska, certain bryophyte species may be used as vegetation indicators when vascular vegetation has been greatly disturbed or entirely removed and in landscapes dominated by *Picea mariana* (USACE 2008c). Both regional supplements require sampling the bryophyte layer using at least three 25- × 25-cm plots, placed at hummock bases. If more than 50% of the total bryophyte cover consists of bryophytes designated as “wetland specialists,” the vegetative criterion has been met.

Bryophytes are also used as secondary indicators of wetland hydrology in several USACE regions. Corticolous bryophytes that establish directly above the typical high water line in forested wetlands are commonly referred to as moss trim lines. The Atlantic and Gulf Coastal Plain and the Northcentral–Northeastern regional supplements consider moss trim lines evidence of recent inundation (USACE 2008b, d).

The National Technical Committee on Wetland Vegetation commissioned this literature review to investigate the feasibility of using bryophytes as wetland indicators, addressing the following topics:

- Are bryophytes good indicators of specific environmental conditions?
- What resources are available to compile the list of wetland bryophytes?
- Should all wetland bryophytes be included or just a select group of indicators?
- In what situations should bryophytes be used for wetland delineation?

We begin with the characteristics of useful indicator species as they apply to bryophytes in the context of wetland delineation. In Chapter 2, we examine bryophyte adaptations to hydric soils and wetland hydrology at the microscale and mesoscale and among different wetland types. Chapter 3 compares several habitat-based classification methods commonly applied to bryophytes, as well as resources available for compiling a list of wetland bryophytes. Chapter 4 discusses three groups of bryophytes that can be considered hydrophytes for the purposes of wetland delineation. Indicator genera, life forms as indicators, and sampling procedures are also discussed. In Chapter 5, correlations between the species composition of the bryophyte layer, hydric soils, and wetland hydrology are considered, using supporting evidence from the literature. Finally, recommendations are made regarding the use of bryophytes during wetland delineations. The nomenclature is according to Anderson et al. (1990) for true mosses and the Flora of North America Editorial Committee (2007) for *Sphagnum*.

2 Bryophytes as Indicators of Environmental Conditions

Introduction

Ecologists have a long history of using plant species as indicators of environmental conditions, particularly in Europe (Kent and Coker 2002). Plant species that are considered good environmental indicators have a number of common characteristics: 1) they are neither rare nor extremely common, 2) they are able to persist in a particular environment, and 3) they are easier to identify and monitor than environmental variables. In addition, response curves of useful environmental indicators steadily increase, steadily decrease, or are bell-shaped. Perhaps most importantly, the response of useful indicator species must be consistent and reliable (Diekmann 2003; Frego 2007).

We applied these characteristics to bryophytes to determine whether bryophytes might make useful indicators during wetland delineations. Bryophyte distribution is examined with regard to how frequently species occur in wetlands. Life history strategies are discussed as they relate to a species' ability to persist in a habitat. Bryophyte taxonomy and intraspecies variation are considered in relation to identification and monitoring ease. Response to important environmental variables, specifically hydric soils and wetland hydrology, is considered at two scales: the microscale and the mesoscale. Finally, we examine the consistency and reliability of bryophytes as indicators of wetland type.

Bryophyte distribution

To be useful indicators of wetland conditions, plant species should be neither rare nor extremely common. Rare species tend to be characterized by low local abundances throughout narrow geographic distributions, whereas common species are often locally abundant throughout a wide geographic range. Perhaps the best indicator species are those described as restricted. These species occupy a very broad range and may be locally abundant in parts of it. However, in most of their range, these species are locally rare because of habitat restrictions (Rabinowitz 1981). Mosses are renowned for their narrow habitat specificities (Lane and Dubois 1981;

Marino 1991; Cleavitt 2001), often specializing in habitats that occur infrequently across a landscape (Vitt and Belland 1997; Heinlen and Vitt 2003). However, bryophytes that specialize in wet microsites are not necessarily present in all or even most of the wetlands in their range. Bryophytes are limited by a number of abiotic and biotic factors, including anthropogenic disturbance, pollution, competition, dispersal, genetics, reproduction, and survival rates (Cleavitt 2005; Frego 2007). Because so much is still unknown about bryophyte biology and ecology, the absence of a bryophyte species in a given habitat indicates less than its presence (Frego 2007).

Species with broad geographic ranges and wide ecological tolerances are less likely to make useful bio-indicators. Most bryophytes have broad, disjunct ranges. Boreal species tend to exhibit a continuous, circumpolar distribution. Likewise, species that are most abundant in the temperate zone are usually characterized by disjunct, intercontinental ranges (Schofield 1985; Shaw 2001). Some species from both groups also have wide ecological tolerances, such as *Pleurozium schreberi*, *Hylocomium splendens*, *Thuidium delicatulum*, *Fissidens adianthoides*, and *Plagiomnium cuspidatum*. In the United States, *P. schreberi* and *H. splendens* are found as far south as North Carolina and Tennessee, whereas the other three species are found as far south as Florida (Crum and Anderson 1981). Ecologically, these species occur in numerous habitats, including floodplains, terraces (McFarland and Wistendahl 1976; Herring and Judd 1995; Jonsson 1997; Pollock et al. 1998), rich fens (Slack 1994), *Picea mariana* swamps (Lockey et al. 2005), bogs (Andrus et al. 1983), moist coniferous forests, and northern hardwood forests (Glime 1993). This type of species, with a wide ecological tolerance, is less likely to be useful as a wetland indicator.

In contrast, some bryophytes that are most abundant in the boreal zone exhibit narrow ecological tolerances farther south. Boreal species such as *Sphagnum palustre*, *Leptodictyum riparium*, *Bryum pseudotriquetrum*, and *Aulacomnium palustre* are likely to be excellent indicators of hydrophytic vegetation because they are restricted to cool, wet habitats in temperate and tropical zones. *B. pseudotriquetrum* is found in minerotrophic fens (Cooper and Andrus 1994; Slack 1994; Lockey et al. 2005), whereas *A. palustre* grows in many different wetland types ranging from bogs to minerotrophic fens (Andrus et al. 1983; Gignac 1992; Slack 1994). Both species are common in Canada and throughout the United States as far south as Missouri (Vitt and Horton 1990). *L. riparium* is common in hardwood swamps (Crum and Anderson 1981) and forested floodplains (Herring and Judd 1995), whereas *S. palustre* occurs in forested fens and sedge fens (Flora of North America Editorial Committee 2007). These two species are found as far south as Texas and Florida (Crum and Anderson 1981). *S. palustre* has also been collected in Hawaiian wetlands, where it is restricted to cool, wet areas at high elevations, typically between 900 and 1,900 m (Karlin and Andrus 1995).

Although most bryophytes occupy broad ranges, a number of species in the genus *Sphagnum* are restricted to particular geographic areas within North America. Distribution patterns vary with temperature and precipitation along a coastal to continental gradient (Gignac and Vitt 1990). A number of species, like *S. austinii, S. tenellum,* and *S. pacificum* are restricted to coastal areas, whereas others, like *S. squarrosum, S. teres,* and *S. warnstorfii,* have continental tendencies (Gignac and Vitt 1990; Flora of North America Editorial Committee 2007). Likewise, species such as *S. cyclophyllum* and *S. fitzgeraldii* are found only in southeastern wetlands, growing on wet sand in savannas and pine barrens (Lane and Dubois 1981; Flora of North America Editorial Committee 2007).

Bryophyte life history strategies

Good bio-indicators are also able to persist in a particular environment. Life history strategies are used to categorize bryophytes in terms of their ability to occupy, reproduce, and persist in a particular environment. Because resources are limited in most habitats, life history strategies inherently represent trade-offs in a variety of characteristics, such as avoidance or tolerance of stressful environments, dominance of sexual or asexual reproduction, short or long life span, and large or small spore size. The life history strategies employed by bryophyte species result in differential responses to disturbance along a gradient from avoidance to tolerance. These strategies greatly influence the habitat types that a species is able to occupy (During 1992). Because bryophytes employ a variety of life history strategies, those with short life spans, such as fugitives and annual shuttle species, are likely to be poor bio-indicators. The pool of species with long life history strategies, such as perennial shuttles or perennial stayers, is a better source of potential indicators.

Fugitive and annual shuttle species are typically very small acrocarps (sparsely branched plants that form reproductive structures at the apex of the main shoots, which usually grow upright). Their distribution is temporally limited, as colonies form open turfs in unpredictable or short-lived habitats. Resources are invested in producing numerous, small spores, rather than leafy shoots (During 1992). One example, *Ephemerum cohaerens* has been assigned a preliminary wetland indicator status of FACW for the United States (Reed and Bates 1994), meaning that this species usually occurs in wetlands. However, hydric vegetation determinations based on species with fugitive life history strategies, such as *E. cohaerens*, may be difficult to defend for two reasons. Small size makes these plants difficult to locate and identify in the field. Because of their limited temporal distribution, colonies present during an initial site visit may be absent on subsequent visits. Therefore, fugitive and annual shuttle species are likely to make poor indicators, even if they are restricted to wetlands.

In contrast, perennial stayers and perennial shuttle species may make useful indicators of hydrophytic vegetation because they are not deciduous and because they persist in stable habitats for relatively long periods of time (During 1992). Perennial shuttle species invest resources in both asexual and sexual reproduction. These species are often, but not always, pleurocarps (plants that tend to grow in prostrate form, are usually branched, and form lateral reproductive structures). Colonies form smooth mats, rough mats, and cushions on long-lasting substrates such as tree trunks. The obligate wetland indicator *Ulota phyllantha* (Reed and Bates 1994), which forms cushions on tree branches in coastal wetlands (Flora of North America Editorial Committee 2007), is one example. Likewise, perennial stayers occupy very stable environments such as bogs, fens, or forest floors. These species devote little energy to sexual or asexual reproduction during their long lives; instead, resources are invested in the growth of the leafy gametophyte. Common life forms include tall turfs, wefts, dendroids, and large cushions (During 1992). Many perennial stayers, such as many *Sphagnum* spp. (OBL), *Calliergon giganteum* (OBL), *Climacium dendroides* (OBL), and *Drepanocladus aduncus* (FACW), have been assigned a preliminary wetland indicator status of either obligate (OBL), meaning that they always occur in wetlands, or facultative wetland (FACW), meaning that they usually occur in wetlands. Other perennial stayers, such as *Hylocomium splendens* and *Leucobryum glaucum*, have been assigned a preliminary wetland indicator status of FAC, meaning that they are equally as likely to occur in wetlands as in nonwetlands (Reed and Bates 1994). In some regions, vegetation sampling and wetland boundary determinations can be challenging in the late fall and early spring when the herbaceous layer is absent (USACE 2008a, b). During these seasons, bryophyte species that employ either perennial stayer or perennial shuttle life history strategies may provide delineators with useful information about the nature of the plant community.

Bryophyte taxonomy/intraspecific variation

Useful bio-indicators are easier to identify and monitor than the environmental variables they represent. Therefore, taxonomically difficult groups of plants are less suitable as indicators (Diekmann 2003; Frego 2007). Small size, morphological plasticity, and species concepts based on microscopic characteristics make bryophyte taxonomy challenging (Slack 1984; List and Andrus 1989; Rydin and Jeglum 2006; Flora of North America Editorial Committee 2007). In fact, some bryologists believe field identifications are so difficult that sampling should only be conducted by trained bryologists (Slack 1984). Although McQueen (1990) contends that common *Sphagnum* species are no more difficult to identify than any other plant species, his field guide was written for amateurs whose identifications generally do not need to be definitive. Bryophyte identifications made by a professional delineator will be held to a higher standard and may be subject to legal scrutiny.

One aspect of bryophyte morphology that makes field identification challenging is their small size. Many species are so small that they do not fit the USACE definition of a macrophyte. The Corps of Engineers Wetland Delineation Manual (USACE 1987) defines macrophytes as “any plant species that can be readily observed without the aid of optical magnification, including all vascular plant species and mosses (e.g., *Sphagnum* spp.), as well as large algae (e.g., *Cara* spp., kelp).” The taxonomically important features of most bryophytes are so small and cryptic that they are not readily observed without a hand lens with a minimum 10× magnification. However, some bryophytes are large and fairly easy to identify, such as *Hylocomium splendens*, *Conocephalum conicum*, and *Leucobryum glaucum*. Unfortunately, large and easily identified species often have wide ecological tolerances and are less useful as indicators (Frego 2007).

Identification difficulties can be exacerbated by variations in basic morphology, such as leaf shape. Bryophytes are well known for their morphological plasticity in response to available moisture. For instance, Slack and Glime (1985) describe two forms of *Hygrohypnum ochraceum* in a study of riparian bryophytes. A straight-leaved form grew submerged in or just above the water level, and a form with falcate leaves was stranded well above the water level. Leaf morphology is also highly variable in the Sphagnaceae, a family whose name comes from the Greek word for unknown plant (Flora of North America Editorial Committee 2007). These mosses are well known for their morphological variation in response to fluctuating water levels (Andrus 1980; McQueen 1990; Rydin and Jeglum 2006). Under ordinary hydrological conditions, many *Sphagnum* species are identified by the unique shape of their stem leaves, which are quite different than the shape of branch leaves. However, when exposed to repeated desiccation and re-wetting, plants become difficult to identify because they produce stem leaves shaped more like branch leaves to retain water.

In some instances, positive field identifications are impossible because some species are identified by differences in cell structure (Frego 2007). For example, to identify a species from the genus *Sphagnum,* plants are stained with a concentrated aqueous or alcohol solution of crystal violet to allow examination of microscopic features, including cell shape, pores, fibrils, or cell wall texture. Identifying one unknown species may require slides of stem leaves, branch leaves, branch-leaf cross sections, stem cross sections, or the superficial surface of stem cortical cells (Flora of North America Editorial Committee 2007).

Bryophytes as microscale indicators

Bryophytes are often recognized as indicators of small-scale environmental conditions, particularly in microhabitats several millimeters to several centimeters wide (Vitt and Belland 1997; McQueen 1990; Flora of North America Editorial Committee 2007). Most mosses are small, desiccation tolerant, and poikilohydric (i.e., their moisture content varies with that of the environment; for a review of desiccation tolerance and poikilohydry, see Proctor et al. 2007). Therefore, microscale conditions may have a stronger influence on bryophyte composition in wetlands than larger-scale environmental gradients. Little evidence is available, however, to suggest that anoxic conditions in hydric soils affect bryophytes at a microscale. Instead, the literature suggests that bryophytes are adapted morphologically, physiologically, and reproductively to wetland hydroperiods. Flood frequency and water level fluctuations exert a controlling influence on bryophyte species composition.

The literature provides no evidence that anaerobic conditions present in hydric soils control the composition of wetland bryophyte communities. Many small species grow on surfaces other than soil. Bryophytes are well known for their substrate preferences (Schofield 1985; Marino 1991; Vitt and Belland 1997; Heinlen and Vitt 2003). They inhabit the surfaces of rocks, logs, tree trunks, roots, and coarse woody debris in many wetland types, including floodplain forests (Muhle and LeBlanc 1975), cypress domes (Carr et al. 2006), red maple swamps (Hale 1965), forested headwater seeps (Hall et al. 2001), and riparian systems (Steinman and Boston 1993; Jonsson 1997; Risk 1998). The anaerobic conditions in hydric soils have little controlling influence on the bryophyte species that inhabit the oxidized surfaces of rocks, bark, and logs. Oxygen is not a limiting factor for these surface-dwelling mosses even when inundated. Instead, free carbon dioxide, which diffuses 10^4 times slower in water than in air, limits submerged bryophytes. Unlike aquatic vascular plants, mosses cannot acquire carbon dioxide from bicarbonates (Proctor 1982; Glime and Vitt 1984).

Terricolous bryophytes also appear to be unaffected by the anoxic conditions in hydric soils. Because most mosses are quite small, they inhabit the thin layer of oxygenated soil at the wetland's soil–water interface (Mitsch and Gosslink 2000). The literature provides no evidence that rhizoids, which anchor plants to the soil surface, penetrate anoxic soil horizons. Likewise, larger, humicolous bryophytes, such as *Sphagnum* spp., occupy the upper, oxygenated layer of a peatland, known as the acrotelm (Rydin and Jeglum 2006). The unique morphology of a *Sphagnum* shoot consists of an actively growing apical segment supported by a much larger portion of the plant that is dead at maturity. Some hummocks consist of tightly packed *Sphagnum* plants. Their branches, leaves, and stems create a matrix of capillary spaces filled with air and water. This matrix can extend the acrotelm from 20 to 50 cm above the water table. In microtopographic low spots, such as hollows or carpets, plants are more widely spaced, and the acrotelm generally extends from 2 cm below to just 7 cm above the water table (Belyea and Clymo 2001). As *Sphagnum* shoots decompose, they collapse into the catotelm, an anaerobic soil horizon composed of dense peat located beneath the acrotelm (Clymo 1984).

Although the anoxic conditions in hydric soils have little controlling influence on bryophyte species, wetland hydrology, specifically flood frequency and water level fluctuations, exerts a controlling influence on microscale bryophyte community composition. Unique morphologies, reproductive strategies, and physiologies of individual bryophyte species suggest that each species is adapted to microsite-specific hydrologic conditions, including seasonal flooding, drawdowns, or constant saturation (Vitt and Glime 1984; Glime and Vitt 1984). Different morphological, physiological, and reproductive adaptations among bryophyte species create small-scale vegetation gradients on a variety of substrates, in riparian systems (Gimingham and Birse 1957; Slack and Glime 1985; Kimmerer and Allen 1982), forested seeps (Hall et al. 2001), swamps (Hale 1965; Wharton et al. 1982), lacustrine wetlands (Muhle and LeBlanc 1975), and numerous peatland types (Stringer and Stringer 1973; Vitt et al. 1975; Slack et al. 1980; Lane and Dubois 1981; Cooper and Andrus 1994).

In riparian systems, for instance, the unique morphology of each bryophyte species enables it to tolerate the hydrologic conditions of a particular microsite, creating a vertical zonation of species along gradients of flood frequency and magnitude. On riparian cliffs, *Fissidens obtusifolius* occurs at frequently flooded lower elevations, whereas *Conocephalum conicum* is restricted to higher zones that are less often disturbed by flooding. Small, leafy, individually anchored plants, such as *F. obtusifolius*, offer little resistance to strong currents and are better adapted to withstand high flood frequency compared to the wide thallose mats of *C. conicum*, which are anchored at irregular intervals. When flood magnitude is great, large sections of *C. conicum* are stripped from the substrate, creating open substrate for colonization of fugitive species, such as *Gymnostomum aeruginosum*. The unique morphologies of these species enable them to occupy distinct vertical microsites on riparian cliffs. Flood frequency and magnitude exert a controlling influence on the species composition in this bryophyte community by restricting competitive dominants, *F. obtusifolius* and *C. conicum*, and enabling less competitive species to co-exist (Kimmerer and Allen 1982).

Wetland bryophytes are also reproductively adapted to wetland hydroperiods. Many species tolerate shear stress and burial associated with highly variable hydrologic regimes. Strong currents and suspended debris can tear or detach delicate leaves or thalli, which are merely one cell in thickness. As floodwaters recede, sediments and bryophyte fragments drop out of suspension. Many species reproduce vegetatively from these fragments (McFarland and Wistendahl 1976; Stream Bryophyte Group

1999). Small bryophytes that inhabit the soil surface also reproduce vegetatively when buried by sediment after flood events. *Fissidens taxifolius* and *Eurhynchium hians,* species from a forested floodplain in Ohio, generated rhizoids that tunneled up to the soil surface after burial by 10 cm of alluvium. New plants grew from secondary protonemata produced by rhizoids (McFarland and Wistendahl 1976).

Other wetland bryophytes, such as those in the family Amblystegiaceae, are adapted to reproduce sexually when water levels are low. Reproductive structures, or sporophytes, consist of long, thin setae, which elevate capsules so that spores are dispersed by laminar air flow. In contrast, a few aquatic species, such as those in the family Fontinalaceae, are adapted to disperse spores aquatically. Because these mosses are rarely stranded by fluctuating water levels, sporophytes consist of short, thick setae and capsules that are enveloped by an enlarged perichaetium. These large sheathing leaves protect the capsule from strong currents and shear stress (Vitt and Glime 1984).

Bryophytes are also physiologically adapted to the hydrologic conditions of their microsite. Although they obtain moisture from numerous sources, including surface waters, ground water, stem flow, dew, humidity, mist, fog, and precipitation, wetland bryophytes are sometimes limited by moisture availability, because they are only physiologically active when hydrated. Bryophytes that grow on rocks and tree trunks are most likely to dry out. During dry periods, they enter a state of dormancy but resume normal metabolism when water is once again available. Bryophytes experience very little water stress, transitioning fairly quickly between fully hydrated and dessicated (Clymo and Hayward 1982; Proctor et al. 2007). Therefore, a wetland microsite is "hydric" when water is plentiful and "xeric" when water is scarce (Proctor et al. 2007).

Physiological tolerance of dry periods varies among bryophyte species. Also, the environmental conditions associated with dry periods affect bryophyte tolerance of desiccation; generally, tolerance increases as temperature decreases, relative humidity increases, and the length of the dry period decreases (Proctor 1982). Bryophyte response to desiccation occurs along a continuum from absolute avoidance to extreme desiccation tolerance, with most species exhibiting a variety of intermediate responses. Bryophytes growing in wet environments are less tolerant of desiccation than are species found in intermittently inundated habitats

(Vitt and Glime 1984) or xeric habitats (Proctor et al. 2007). This differential response to desiccation is one factor responsible for the vertical zonation of bryophyte species along microtopographic gradients (Wagner and Titus 1984). In peatlands, hummock-forming *Sphagnum* species are less desiccation tolerant than mosses growing in hollows. Hummock mosses alter wetland hydrology when the water table is low and wick water up from the water table to remain hydrated (Clymo 1984; Andrus 1986; Rydin and Jeglum 2006). In contrast, bryophytes that grow in pools, or hollows, are more tolerant of desiccation, because these “xerophytic hydrophytes” often dry out completely in late summer (List and Andrus 1989). Hollow species, such as *S. fallax*, tolerate longer periods of desiccation and restore photosynthesis at higher rates after rehydration than hummock species such as *Sphagnum nemoreum* (= *S. capillifolium*) (Wagner and Titus 1984).

Wetland hydrology may also affect other environmental variables, such as substrate stability and substrate diversity, which in turn influence bryophyte composition. For example, strong currents can disturb soil, sand, and gravel and hinder moss establishment on these substrates (Stream Bryophyte Group 1999). Many riparian studies have noted the specific substrate preferences of bryophyte species and taxa (Slack and Glime 1985; Suren and Duncan 1999). Bryophytes often establish exclusively on immobile substrates such as large boulders and bedrock or small stones that are firmly implanted in the surrounding streambed (Englund 1991; Steinman and Boston 1993). Wetland hydrology also affects substrate diversity. For example, intermittent flooding in riparian systems can increase the types of substrates available for bryophyte colonization by depositing woody debris, rock, and sediments. Because many bryophytes exhibit strong preferences for a particular substrate, substrate diversity can have a controlling influence on bryophyte composition, increasing species richness and enabling terrestrial and aquatic bryophytes to coexist (Jonsson 1997; Hall et al. 2001).

At the microscale, the literature provides evidence that hydrology exerts a controlling influence on bryophyte species composition in many wetland types. Different morphologies, physiologies, and reproductive strategies among bryophyte species suggest that each species is adapted to the hydrologic conditions of the microsite that it occupies. However, to determine whether bryophytes might make useful indicators of wetland conditions at the microscale, it is also necessary to examine species response curves along hydrologic gradients.

Useful bio-indicator species respond to environmental variables with one of the following response curves: steadily increasing, steadily decreasing, or bell-shaped, provided that the variable is important to that species (Diekmann 2003). Because no environment is homogenous, bryophytes do not respond independently to a single variable. Instead, plants respond to complex gradients composed of a number of interrelated variables (Whittaker et al. 1973; Rydgren et al. 2003).

Curves of bryophyte response to microscale microtopographic/height-above-water-table gradients are mainly monotonic or unimodal, suggesting that bryophytes would make good indicators of wetland conditions. One study, conducted in a boreal swamp, compared the response curves of 63 bryophytes and 49 vascular plant species along a complex microtopographic/depth-to-water-table gradient. No significant differences were found in the shape of response curves among mosses, liverworts, *Sphagnum* spp., or vascular plants. When viewed in the context of wetland delineation, these results suggest that bryophytes and vascular plants are equally effective indicators of small-scale changes in moisture (Rydgren et al. 2003). Similarly, in Norway, bryophyte species exhibited unimodal response curves along a height-above-water-table gradient in an ombrotrophic to weakly minerotrophic peatland complex. Although the response curve of one species, *Sphagnum magellanicum*, was weakly bimodal, the author attributed this to noise in the data set (Økland 1986). The results of both studies suggest that bryophytes may be useful small-scale indicators, because bryophyte species primarily exhibit unimodal and monotonic response curves along a depth-to-water-table gradient.

Bryophytes as mesoscale indicators

For reasons discussed previously, little evidence is available to suggest that the anoxic conditions in hydric soils exert a controlling effect on bryophyte species at larger spatial scales. The literature suggests that water chemistry exerts a controlling effect on bryophyte distribution at the mesoscale or among different wetland types (List and Andrus 1989; Vitt and Chee 1990; Rydin and Jeglum 2006). Many bryophytes are associated with particular water chemistries and are classified as calcifuges, calcicoles, nitrophiles, or halophytes (Bates 2000).

Among wetlands, differences in bryophyte community composition are associated with differences in water chemistry. Vegetation patterns observed in mature bryophyte communities may reflect differences in establishment abilities among juvenile bryophytes (Slack 1997). For example, compared to calcifuge species, calcicoles are thought to be more sensitive to substrate chemistry during establishment on soil (Cleavitt 2001). Affinities of bryophytes for specific substrate chemistries have been attributed to differences in pH tolerance, sulphate tolerance (Wilkins 1977), cation exchange capacity (Bates 1982a; Clymo and Hayward 1982), and the competitive abilities of individual species (Bates 2000). However, the exact mechanisms that underlie associations between bryophyte species and water or substrate chemistries remain unclear.

Regardless of the mechanism, the literature provides evidence that water chemistry exerts a controlling effect on bryophyte composition. Calcifuge species are common in wetlands characterized by lower pH and base cation concentrations, whereas calcicoles dominate wetlands characterized by minerotrophic waters and circumneutral pH. Bryophyte composition varies with differences in water chemistry among stream types (Vitt et al. 1986) and groundwater seeps (Hall et al. 2001). Associations between bryophyte species and water chemistry are also well documented among peatlands in boreal and temperate zones. The dominant species in bryophyte communities change from *Sphagnum* spp., to brown mosses, to feather mosses along gradients of increasing pH, base cation concentrations, and shade (Vitt and Chee 1990, Rydin and Jeglum 2006).

Communities of *Sphagnum* spp. dominate ombrotrophic wetlands, such as bogs and poor fens where pH and base cation concentrations are low. Many *Sphagnum* species are considered calcifuges: they are unable to tolerate high pH and high concentrations of base cations. This genus is well known for its ability to alter wetland water chemistry by exchanging hydrogen ions for cations, creating the more favorable conditions for growth and expansion (Clymo and Hayward 1982; Andrus 1986). Several species of liverworts are commonly found intermixed with *Sphagnum*, including *Calypogeja sphagnicola*, *Cephalozia lunulifolia*, and *Mylia anomala* (List and Andrus 1989). Shade-tolerant *Sphagnum* species may carpet wetter microsites in poor to intermediate swamps. Feather mosses such as *Pleurozium schreberi*, *Hylocomium splendens*, and *Ptilium crista-castrensis*, as well as liverworts such as *Bazzania trilobata* and *Conocephalum conicum*, are more common in drier microsites like hummock tops. Because feather mosses tend to have wide ecological amplitudes, they may also occur in rich swamps, along with moderately minerotrophic, shade-tolerant species of *Sphagnum*, such as *S. wulfianum*, *S. russowii*, and *S. girgensohnii*, which may form extensive carpets (Rydin and Jeglum 2006).

Bryophyte communities in minerotrophic wetlands are dominated by brown mosses, many of which are calcicoles. Named for their distinctive yellow-brown color, these mosses include species from the family Amblystegiaceae and several others, such as rich fen indicators *Paludella squarrosa* and *Meesia triquetra*. A few *Sphagnum* species, such as *Sphagnum teres* or *S. warnstorfii*, tolerate the continuous flow of cold, minerotrophic groundwater and circumneutral pH found in rich fens (Andrus 1980). Because bryophytes occupy specific microsites along small-scale gradients (Lane and Dubois 1981; Andrus et al. 1983), calcifuge species, such as *Sphagnum rubellum*, commonly found in poor fens and bogs (Slack 1994; Flora of North America Editorial Committee 2007), may also occur in rich fens, occupying microsites that are isolated from the influence of mineral-rich groundwater, such as hummock tops (Rydin and Jeglum 2006). However, calcifuge species are unlikely to be dominant. Brown mosses are also abundant in moderately rich or transitional fens, although the water chemistry is slightly different. Unlike rich fens, concentrations of calcium and magnesium ions are generally low and peat accumulation may be negligible; however, the pH is circumneutral (Cooper and Andrus 1994; Amon et al. 2002).

When water chemistry is altered by nutrient additions, interspecific interactions and dominant bryophyte species change. In the context of wetland delineation, bryophytes that tolerate high levels of nitrogen and phosphorus will make better indicators in eutrophied wetlands. Other species that are less tolerant of anthropogenic disturbance may be less useful indicators. For instance, *Ricca fluitans* and *Ricciocarpos natans* increase in biomass in response to high levels of nitrogen (Glime 1992). In eutrophied streams, *Rhynchostegium riparioides* (= *Platyhypnidium riparioides*) is replaced by *Amblystegium riparium* (= *Leptodictyum riparium*), a species that tolerates high levels of nutrient input (Vanderpoorten and Durwael 1999). In peatlands, the growth and establishment of many bryophytes are negatively affected by nitrogen additions. One exception, *Aulacomnium palustre*, tolerates a wide range of nutrient input (Vitt and Li 1994). Likewise, in eutrophied Dutch fens, nutrient tolerant

Calliergonella cuspidata replaces *Scorpidium scorpioides* (Kooijman 1993). Ecotypic variation in response to nutrient levels has been described for riparian and peatland bryophytes at both continental and regional scales (Vitt et al. 1993; Vanderpoorten and Durwael 1999).

Although there are no submerged marine bryophytes, a few species are considered fairly salt tolerant. Saltwater spray is thought to exert a controlling influence on species in coastal wetlands and on islands. For instance, *Ulota phyllantha* and *Schistidium maritimum* are restricted to coastal wetlands (Flora of North America Editorial Committee 2007). In addition, a recent survey of nine salt marshes in the Gulf of St. Lawrence, Canada, found five species of mosses below the litter line in the high intertidal zone. *Campylium stellatum* and *Bryum capillare* were the most abundant. *Didymodon rigidulus, Mnium hornum*, and *Amblystegium serpens* were also present. The authors speculate that shoreline erosion is responsible for the presence of these species in salt marshes. Yet, in laboratory experiments, *C. stellatum*, a species more commonly found in minerotrophic fens, restored normal metabolism after four days submerged in seawater (Garbary et al. 2008).

To determine whether bryophytes might make useful mesoscale indicators of hydric vegetation or wetland hydrology, bryophyte response to gradients of available moisture and water chemistry must be examined. Bryophyte species that exhibit monotonic or bell-shaped response curves along a complex gradient of available moisture and water chemistry are likely to be useful mesoscale indicators.

The response curves of 48 species along a complex gradient of depth to water table/soil pH suggest that bryophytes might be useful as bioindicators. In an analysis of 138 wet/mesic, mesic, and dry forest stands in northeastern Ontario and western Quebec, most response curves of terricolous bryophytes steadily increased or steadily decreased along a gradient of increasing soil moisture, pH, and calcium ions (Carleton 1990). There were two reasons why most response curves were monotonic. First, the entire soil moisture gradient was not represented in this study; data from permanently inundated plots were not included in this analysis. Second, the mesic forest floor was occupied almost exclusively by herbaceous vascular plants; bryophytes were excluded from the mid-section of this gradient (Carleton 1990). However, the linear mesoscale response suggests that bryophytes might make useful indicators of soil moisture and chemistry.

Likewise, a boreal swamp study examined mesoscale response curves of 63 bryophyte species and 49 vascular plants along a complex gradient of mean depth to water table/soil pH. There was no significant difference among the shapes of the response curves of mosses, liverworts, *Sphagnum* spp., and vascular plants. Eighty percent of the species in all four groups exhibited unimodal or montonic response curves (Rydgren et al. 2003). Because bryophytes and vascular plant species exhibit the same types of response curves, bryophytes may be equally as effective as vascular plants at indicating mesoscale soil moisture levels.

Bryophytes as indicators of wetland type

Compared to vascular plants, bryophytes are much more sensitive to differences in surface water chemistry, specifically pH and concentrations of calcium and magnesium ions (Slack et al. 1980; Vitt and Chee 1990; Slack 1994). However, wetland bryophytes are far less likely than vascular plants to be restricted to a particular wetland type (Slack 1994; Lockey et al. 2005). Instead, associations of bryophyte species are indicative of specific types of wetlands. Because the abundance and distribution of wetland bryophytes are strongly affected by water chemistry, wetlands with similar water chemistries support similar bryophyte associations (List and Andrus 1989; Vitt and Chee 1990; Rydin and Jeglum 2006). A comparison of studies conducted in wetland interiors suggests that most bryophyte species may be considered indicators of more than one wetland type (Table 1). However, all species in Table 1 have been assigned preliminary wetland indicator status ratings of OBL or FACW, meaning that they always or usually occur in wetlands (Reed and Bates 1994).

Wetlands with similar water chemistries are characterized by similar bryophyte indicator species. Calcicoles or calcifuges—species that tolerate or avoid high concentrations of base cations—are often the primary division in a regional flora (Bates 2000). The bryophytes in Table 1 exhibit this trend. For instance, *Campylium stellatum* and *Sphagnum warnstorfii* are considered calcicoles, indicators of wetlands characterized by high base cation concentrations and circumneutral pH, such as moss-lichen-dominated rich fens, rich shrub fens, rich swamps, forested moderate fens, and some black spruce swamps (Table 1). Likewise, many *Sphagnum* spp. are calcifuges, indicative of wetlands characterized by low pH and low concentrations of calcium and magnesium ions. For instance, *S. angustifolium*, *S. magellanicum*, and *S. fuscum* are common in poor fens and bogs in northern temperate and boreal zones. Although these widespread species may also occupy coastal wetlands, distinct *Sphagnum* associations have been described for coastal wetlands in the Southeastern United States (Lane and Debois 1981) and the Pacific Northwest (Gignac and Vitt 1990).

In addition, *Sphagnum* spp. are often considered indicators in wetlands with highly variable hydrologic regimes such as northeastern and southeastern vernal pools, which dry out entirely by midsummer. Sphagnum species such as *S. fallax*, and *S. cuspidatum*, which are well known for their immense water-holding capacity and their ability to survive periods of dessication (Clymo and Hayward 1982; Wagner and Titus 1984), are described as vernal pool indicator species (Weakley and Schafale 1994; Edinger et al. 2002; Colburn 2004). Although *S. fallax* and *S. cuspidatum* may be particularly useful indicators in vernal pools, they are not restricted to this type of wetland. Instead, they occur in a wide variety 0f ombrotrophic to weakly minerotrophic wetlands along the east coast (Editorial Committee 2007).

Within the wetland boundary, wet microsites that support OBL and FACW species should be more abundant than mesic microsites that support FAC (facultative) or FACU (facultative upland) species (USACE 2008b). However, since microscale environmental conditions have a strong effect on the bryophyte species present in wetlands, terrestrial species may occupy drier microsites (Stringer and Stringer 1973). In peatlands, mesic microsites occur with much greater frequency on the margins, where the depth to the water table is greatest (Sjors 1963), and when the hydroperiod is variable (Rydin and Jeglum 2006). Although terrestrial species are not included in Table 1, *Dicranum polysetum* (FACU) is an indicator of wooded bogs (Lockey et al. 2005). Similarly, in riparian wetlands, FACU species such as *Sanionia uncinata* occupy drier areas, such as depositional bars (Pollock et al. 1998). In northeastern forested headwater seeps, the abundance of a preferred substrate is another factor that controls the presence of terrestrial bryophytes, such as *Dicranum scoparium* (FACU) or *Brotherella recurvans* (FACU) (Hall et al. 2001).

Table 1. Some bryophyte species commonly occurring in various wetland types throughout North America. All species have been assigned a preliminary wetland indicator status of OBL or FACW (Reed and Bates 1994). Species concepts not recognized by Reed and Bates are marked with an asterisk. A key to the citation information is at the end of the table.

Bryophyte Species	Minerotrophic	Moderately Minerotrophic
Drepanocladus revolvens (Sw.) Warnst. = *Limprichtia revolvens* (Sw.) Loeske	E, Lo, NG, S, SI, Sj, VS, VC	
Scorpidium scorpioides (Hedw.) Limpr.	E, Lo, NG, S, SI, Sj, VS, VC	
Sphagnum centrale C.E.O. Jensen	A, E, F, S, Sj, VS	E
Sphagnum contortum Schultz*	A, F, Sj, VS	E
Meesia triquetra (Richt.) Ågstr.	S, SI, Sj, VS	GV, Li
Tomenthypnum nitens (Hedw.) Loeske	E, S, SI, Sj, VC, VS	Lo, GV, Li
Bryum pseudotriquetrum (Hedw.) Gaertn. et al.	E, S, SI, VS	CA, Lo, VC
Sphagnum warnstorfii Russow	E, S, SI, Sj, VS	E, GV, Lo, Li VC, WS
Aulacomnium palustre (Hedw.) Schwaegr.	E, S, SI, SjVS	CA, E, GV, Lo, Li, NG, VC
Campylium stellatum (Hedw.) C. Jens.	E, Lo, NG, S, SI, Sj, VC, VS	CA, E, GV, Lo, WS
Sphagnum teres Ångström in C. J. Hartman	E, S, SI, VS	CA, GV
Sphagnum russowii Warnstorf	A, E, FNA	KA, Li
Calliergon giganteum (Schimp.) Kindb.	S, SI	E, Lo, VC
Calliergonella cuspidata (Hedw.) Loeske	S, E	CA, E, VC, WS
Helodium blandowii (Web. & Mohr) Warnst.	S, VS	Lo, VC
Drepanocladus aduncus (Hedw.) Warnst.		CA, Li, VC
Sphagnum squarrosum Crome		F, Li, VC
Calliergon stramineum (Brid.) Kindb.		CA, Li, VC
Sphagnum subsecundum Nees in J. Sturm et al.		CA, F, KA, WS
Calliergon sarmentosum (Wahlenb.) Kindb. = *Sarmenthypnum sarmentosum* (Wahlenb.) Tuom. & T. Kop.		CA, LI

Bryophyte Species	Weakly Minerotrophic to Ombrotrophic		
	Widespread across continental interior	Coastal northern	Coastal southern
Sphagnum austinii Sullivant *in* C. F. Austin*		GV, F	
Sphagnum fallax (H.Klinggräff) H. Klinggräff*		E, F, KA, VC, WS	
Sphagnum flavicomans (Cardot) Warnstorf in H. G. A. Engler		E, F, GV, KA	
Sphagnum lindbergii Schimper	F	GV, F	
Sphagnum pacificum Flatberg*		GV, F	
Sphagnum papillosum Lindberg		E, KA, F GV, Li, S	AS
Sphagnum rubellum Wilson*		E, KA, F GV, S	
Sphagnum tenellum (Bridel) Bory		GV, F	
Sphagnum cuspidatum Hoffman		E, KA, S	AS, LD, KA, Re

Table 1 (cont.). Some bryophyte species commonly occurring in various wetlands throughout North America.

Bryophyte Species	Weakly Minerotrophic to Ombrotrpohic		
	Widespread across continental interior	Coastal northern	Coastal southern
Sphagnum palustre Linnaeus		KA, GV, S,	AS, Re, Ri, WS
Sphagnum recurvum P. Beauvois		E, F	AS, KA, Re, WS
Sphagnum lescurii Sullivant in A. Gray*		F, KA	AS, Re, Ri
Sphagnum bartlettianum Warnstorf in H.G.A. Engler			AS, E, KA, LD, Re, WS
Sphagnum affine Renauld & Cardot*			AS, Re, WS
Sphagnum henryense Warnstorf			E, KA, S
Sphagnum cyclophyllum Sullivant in A. Gray*			AS, LD, Re
Sphagnum fitzgeraldii Lesquereux & James			AS, LD, Re
Sphagnum macrophyllum Bridel			AS, LD, Re
Sphagnum perichaetiale Hampe			AS, LD, Re
Sphagnum magellanicum Bridel	E, F, GV, LO, KA, NG, S, VC	E	AS, LD, Re
Aulacomnium palustre (Hedw.) Schwaegr.	S, NG, WS		
Mylia anomala (Hook.) S.Gray.	NG, Li, S		
Polytrichum strictum Brid.	Ri, F, NG, Li, VC		
Sphagnum angustifolium (Warnstorf) C.E.O. Jensen*	E, F, KA, NG, Li, Lo, S, VC, WS		
Sphagnum capillifolium (Ehrhart) Hedwig	GV, F, KA, S, WS		
Sphagnum fuscum (Schimper) H. Klinggräff	E, F, GV, KA, LI, NG, S, VC, WS		
Sphagnum jensenii H. Lindberg *	F, GV, VC		
Sphagnum majus (Russow) C.E.O. Jensen	F, GV, KA, S		

Bryophyte Species	Riparian Wetlands	Permanent Streams
Drepanocladus intermedius (Lindb.) Grout. = *Limpricheta revolvens* (Sw.) Loeske	Sj	
Dichelyma capillaceum (With.) Myr.	Gi	
Fissidens fontanus (B. Pyl.) Steud.	B	
Hypnum lindbergii Mitt.	B, Ri, Sj	
Leptodictyum humile (P. Beauv.) Ochyra	B, MW	
Leptodictyum riparium (Hedw.) Warnst.	B, Gi	
Porella pinnata L.	B, Gi, W	
Sphagnum girgensohnii Russow	F, P	
Sphagnum squarrosum Crome	F, P	
Aulacomnium palustre (Hedw.) Schwaegr.	Ri	Vi, Ri

Table 1 (cont.). Some bryophyte species commonly occurring in various wetlands throughout North America.

Bryophyte Species	Riparian Wetlands	Permanent Streams
Brachythecium rivulare Schimp. in B.S.G.	MW	E, H, G, Ri, SG, Vi
Bryum pseudotriquetrum (Hedw.) Gaertn. et al.	Ri, Sj	Vi
Campylium stellatum (Hedw.) C. Jens.	Sj	Vi
Eurhynchium hians (Hedw.) Sande Lac.	B, MW	Ri
Fontinalis neomexicana Sull. & Lesq.	P	J
Hygroamblystegium tenax (Hedw.) Jenn.	Gi	E, SG, G
Philonotis fontana (Hedw.) Brid.	Sj	Ri
Plagiomnium insigne (Mitt.) T. Kop.	P	J
Racomitrium aciculare (Hedw.) Brid.	P	J, Ri, SG
Sciaromium lescurii (Sull. *in* Gray) Broth. = *Platylomella lescurii* (Sull. *in* Gray) Andrews	Ri, Gi	G
Brachythecium frigidum (C. Müll.) Besch		Vi, J
Bryhnia novae-angliae (Sull. & Lesq. *in* Sull.) Grout		E, SG, H, G
Fontinalis antipyretica Hedw.		H, G, SG
Fontinalis dalecarlica Schimp. *in* B.S.G.		G, Ri, SG
Hygrohypnum luridum (Hedw.) Jenn.		Vi, G
Hygrohypnum ochraceum (Turn. *ex* Wils.) Loeske		E, SG, J, H, G
Platyhypnidium riparioides (Hedw.) Dix.		E, G, Ri, SG
Scapania undulata (L.) Dumort.		SG, J, H, G

Abbrevation	Citation	Location
A	Andrus 1980	New York
AS	Anderson et al. 2009	Southeastern U.S.
B	Breil 1977	Virginia, Piedmont
CA	Cooper and Andrus 1994	Wyoming
E	Edinger et al. 2002	New York
F	Flora of North America Editorial Committee 2007	North America
G	Glime 1968	Pennsylvania, Maryland, Virginia
Gi	Gilbert et al. 2007	Florida
GV	Gignac and Vitt 1990	British Columbia, Alberta
H	Hall et al. 2001	New York
J	Jonsson 1997	Oregon
KA	Karlin and Andrus 1984	New Jersey, New York
LD	Lane and Dubois 1981	North Carolina, South Carolina
Li	Lichvar et al. 2009	Alaska
Lo	Lockey et al. 2005	Manitoba

Table 1 (cont.). Some bryophyte species commonly occurring in various wetlands throughout North America.

Abbrevation	Citation	Location
MW	McFarland and Wistendahl 1976	Ohio
NG	Nicholson and Gignac 1995	Northwest Territories, Alberta, British Columbia
P	Pollock et al. 1998	Alaska
Re	Reese 1984	Southern Gulf Coast
Ri	Risk 1998	Kentucky
S	Slack 1994	New York
Sl	Slack et al. 1980	Alberta
SG	Slack and Glime 1985	New York
Sj	Sjors 1963	Northern Ontario
VC	Vitt and Chee 1990	Alberta
Vi	Vitt et al. 1986	British Columbia, Alberta
VS	Vitt and Slack 1984	Minnesota
W	Wharton et al. 1982	SE Coastal Plain (NC, SC, GA, FL)
WS	Weakley and Schafale 1994	North Carolina, Southern Blue Ridge Mts

Conclusion

Bryophytes possess most of the characteristics of useful bio-indicators. Boreal bryophytes that employ perennial stayer life history strategies will make the best wetland indicators. Because they are restricted to cool, wet habitats and are not deciduous, these species may be particularly useful for delineations in the temperate zone when herbaceous vegetation is absent. Yet most bryophytes are difficult to identify in the field, which makes them less useful as bio-indictors.

No evidence is available to suggest that anoxic conditions in hydric soils have a controlling effect on the bryophyte species present in wetlands. Instead, the literature suggests that bryophytes are morphologically, physiologically, and reproductively adapted to the hydrologic conditions of their microsite. Flood frequency and water level fluctuations exert a controlling influence on bryophyte species composition at the microscale. These small plants might make excellent indicators of soil moisture along wetland boundaries because bryophyte response curves to soil moisture and pH gradients are bell shaped or monotonically increasing or decreasing.

At the mesoscale, groups of bryophytes, often classified as calcifuges, calcicoles, nitrophiles, or halophytes, are associated with particular water chemistries. Studies conducted in wetland interiors suggest that bryophyte associations are not endemic to specific wetland types, particularly in continental interiors. Only *Sphagnum* associations in coastal peatlands are distinct. Most wetland bryophytes have been assigned a preliminary wetland indicator status of OBL, FACW, or FAC (Reed and Bates 1994). However, a few species with FACU indicator status are considered indicators of wetlands with seasonally fluctuating hydroperiods.

3 Resources for Compiling a List of Wetland Bryophytes

A number of resources are available for compilation of a list of wetland bryophytes. Many of these classification systems are compared in Table 2, using common bryophytes from hydric and mesic habitats. Only Reed and Bates (1994) and Walker et al. (1989) use the wetland indicator status developed by the U.S. Fish and Wildlife Service's (USFWS's) National Wetlands Inventory Center (USFWS 1996). The remaining classification systems categorize bryophyte species based on the moisture availability of their preferred habitat. Other journal articles that contain lists of wetland bryophytes or information about relationships to soils and hydrology are listed in Appendix A.

Perhaps the most useful resource (Reed and Bates 1994) is a preliminary list of bryophytes and lichens that occur in wetlands in the United States. The list was derived from a number of regional floras and includes 644 mosses, 282 liverworts, and 10 hornworts. [Note that the nomenclature was based on Crum et al. (1973) and must be updated to reflect our current understanding of relationships among genera and species.] Bryophytes were not ranked according to the wetness of their habitat. Instead, each bryophyte species was tentatively assigned to one of four indicator categories (OBL, FACW, FAC, or FACU) based on how often the species occurred in wetlands (Reed and Bates 1994). Species that occur in wetlands 99% of the time, but may, very rarely, occur in uplands, are listed as OBL. Plants that usually occur in wetlands, with a probability of 67% to 99%, are listed as FACW. Species listed as FAC have wide ecological amplitudes and are just as likely to occur in wetlands as in uplands, with a probability of 33% to 67%. Bryophytes listed as FACU may occasionally occur in wetlands, with a probability of 1% to 33%, but are more commonly found in upland habitats (USACE 1987). Walker et al. (1989) used these same categories to compile a list of bryophytes common in the Arctic foothills of Alaska. Each species was assigned a preliminary indicator status based on literature and field experience.

In addition to these species lists, a number of journal articles are also helpful in compiling a list of wetland bryophytes. Monographs describing the morphological and physiological adaptations of obligate aquatic, facultative aquatic, and semi-aquatic emergent bryophytes make useful background reading. These articles categorized genera and species as either limnophilous (found in lakes, pools or ponds) or rheophilous (occurring in streams or running water). In addition, many bryophytes are classified as obligate aquatics, which are almost always submerged; facultative aquatics, a group that tolerates water level fluctuations; or semi-aquatic emergent species, which occur in habitats with constantly saturated soils (Vitt and Glime 1984; Glime and Vitt 1984). More recently, as part of a study on hydrological permanence in forested headwater streams, Fritz et al. (2009) reviewed 26 publications from different regions of the United States and ranked a number of bryophyte species as indicators of aquatic, hygrophytic, moist, or terrestrial habitats. Species that were most often found in submerged habitats were ranked aquatic, whereas bryophytes that inhabited swampy or riparian habitats were classified as hygrophytes. Species categorized as indicators of moist conditions were most commonly found on damp soil not located near a body of water. Mosses classified as terrestrial occupied dry or xeric habitats, according to reviewed literature.

Because most boreal and temperate-zone bryophytes occupy broad, disjunct ranges (Schofield 1985; Shaw 2001), the indicator values of European bryophytes may also be a useful resource. European botanists have a long tradition of using plants as indicators of environmental conditions. The Ellenberg (1950) indicator values for soil moisture, soil pH, light, salt tolerance, and nitrogen are perhaps the most familiar. More recently, The Natural Environment Research Council's Centre for Ecology and Hydrology and Countryside Council for Wales published BRYOATT, a list of indicator values for British and Irish bryophytes (Hill et al. 2007). Bryophyte indicator values were calculated from the Ellenberg indicator values of co-occurring vascular plants, using the INDEXT computer program. The final values for each species were cross referenced with the literature, personal experience, and unpublished indicator values for Dutch bryophytes. The scale used to rank bryophytes as indicators of moisture ranges from 1, an indicator of extreme dryness, to 12, normally submerged. BRYOATT also includes more detailed information on each species' preferred habitats and substrates, i.e. "standing surface waters, floating in water" or "raised bog, on peat." Because BRYOATT includes all habitats that a species normally occupies and estimates a frequency for each one, it may be useful in compiling a list of wetland bryophytes.

A second European resource, *Distribution, Ecological Amplitude, and Phytosociological Characterization of European Bryophytes* (Dierßen 2001), describes the ecological conditions associated with the habitats of European bryophytes, including available moisture, pH, substrate, temperature, and nutrient availability. Classifications are based mainly on the author's field experience. Many bryophytes are categorized as rheophytic, limnophytic, hygrophytic, or amphiphytic. In addition, a humidity index is assigned to each species based on its ability to tolerate desiccation, ranging from e-hygrophytic (extremely wet) to h-xerophytic (extremely dry). Although the humidity classifications are difficult to decipher, they might be useful as a cross-referencing tool. The author also includes a list of vascular vegetation types in which European bryophytes are abundant. Categories describing wetlands, such as "aquatic and littoral vegetation," "vegetation of springs," and "snowfields, mires, and wet heathlands," may be of interest (Dierßen 2001).

A comparison of the indicator status of common wetland bryophytes reveals that general agreement between the classification systems is fairly high (Table 2). Bryophyte species seem to be consistent and reliable indicators. All of the species listed as OBL or FACW by Reed and Bates (1994) are considered aquatic or semi-aquatic by Vitt and Glime (1984) and are described by Fritz et al. (2009) as either aquatic or hygrophytes (Table 2). One exception, *Plagiothecium denticulatum*, is listed as FACW by Reed and Bates (1994) but considered terrestrial by Fritz et al. (2009) and Hill et al. (2007); Vitt and Glime (1984) do not mention *P. denticulatum*. Another discrepancy is that Reed and Bates (1994) list all species in the genus *Sphagnum* as OBL wetland indicators. After comparison with the other classification systems, the status of these species may need to be re-examined. *Sphagnum* species occupy a wider variety of ecological niches than commonly recognized (Andrus 1986). The other systems list a range of ecological tolerances among *Sphagnum* species. For instance, Walker et al. (1989) considers five of the 18 *Sphagnum* species in her study as FACW indicators, whereas Hill et al. (2007) classifies the *Sphagnum* spp. habitat as ranging from "found on moist or damp substrata" to "found in pools and by streams that may intermittently lack water."

Agreement is also generally high among the classifications systems with regard to FAC indicator species. None of the species listed as FAC by Reed and Bates (1994) are considered aquatic or semi-aquatic by Vitt and Glime

(Table 2). Likewise, Fritz et al. (2009) describes these same species as indicators of hygrophytic or moist terrestrial environments. However, many FAC species are considered FACW indicators by Walker et al. (1989). Other discrepancies highlight the need for regional lists of bryophyte indicators, which take ecotypic variation and climatic differences into account. The liverworts *Chiloscyphus pallescens* and *C. polyanthos* are listed as FAC by Reed and Bates but are considered to be indicators of streams, flushes, and bogs by Hill et al. (2007); Dierßen (2001) lists them as very to considerably hygrophytic.

In addition to these resources, there are also several web resources available (Appendix C). The Flora of North America Committee is assembling an on-line, three-volume collection of mosses, liverworts, and hornworts from North America; volume two, *Acrocarpous Mosses, Part 2*, and volume three, *Hepatics and Hornworts*, are still incomplete. Regional lists might also be cross referenced with the field experiences of members of the American Bryological and Lichenological Society (ABLS). The ABLS publishes the journal *The Bryologist.* A list of U.S. members is available on their website. The International Association of Bryologists (IAB) is another professional association whose American members might cross reference lists of wetland bryophytes with field experience. The IAB publishes *The Bryological Times* and manages Bryonet, an e-mail discussion forum. On Bryonet, anyone can pose a question to an international audience of bryologists by contacting the administrator, Janice Glime, at Michigan Technical University. Lists of wetland bryophytes could also be cross referenced with lists available on-line from Natural Heritage/Nature Serve programs (i.e., Carr 2003).

Table 2. Comparison of indicator systems applied to bryophyte species. A key to the abbreviations is at the end of the table.

	Vitt and Glime (1984)	Fritz et al. (2009)	Walker et al. (1989)	Hill et al. (2007)	Dierßen (2001)
Species Preliminarily Listed as OBL Wetland Indicators (Reed and Bates 1994)					
Blindia acuta (Hedw.) Bruch & Schimp. *in* B.S.G.	F, R			9	V, C, M, A, R
Calliergon giganteum (Schimp.) Kindb.	S, L		OBL	10	V, A, L
Calliergon sarmentosum (Wahlenb.) Kindb. = *Sarmenthypnum sarmentosum* (Wahlenb.) Tuom. & T. Kop.			OBL	9	
Calliergon stramineum (Brid.) Kindb.			OBL	9	V, C, M
Calliergonella cuspidata (Hedw.) Loeske	S, L			7	C, M
Cinclidium stygium Sw. *in* Schrad.	S, L			9	V
Drepanocladus revolvens (Sw.) Warnst. = *Limprichtia revolvens* (Sw.) Loeske	F, L	A	OBL	9	V, C, M
Drepanocladus sendtneri (Schimp.) Warnst.	F, L			9	V, C, M
Eurhynchium riparioides (Hedw.) P. Rich = *Platyhypnidium riparioides* (Hedw.) Dix.	F, L	A		10	V, C, M, A, R
Fissidens grandifrons Brid.	F, L				V, R
Fontinalis antipyretica Hedw.	F, L	A		12	V, L
Fontinalis dalecarlica Schimp. *in* B.S.G.	F, R	A			V, R
Hygroamblystegium fluviatile (Hedw.) Loeske		A		11	C, R
Hygrohypnum luridum (Hedw.) Jenn.	F, L	H		9	V, A, R
Hygrohypnum ochraceum (Turn. *ex* Wils.) Loeske	F, L	A		10	V, R, H
Leptodictyum riparium (Hedw.) Warnst.	F, L	A		9	V, A
Mnium medium (Bruch & Schimp. *in* B.S.G.) = *Plagiomnium medium* (Bruch & Schimp. *in* B.S.G.) T. Kop			FAC	7	V, C, M
Meesia uliginosa Hedw.			FACW	8	V, C, M
Paludella squarrosa (Hedw.) Brid.			OBL	9	V
Pohlia wahlenbergii (Web. & Mohr) Andrews	S, L			8	V, C
Polytrichum commune Hedw.			FAC	7	M
Polytrichum strictum Brid.			FACW	7	C, M
Racomitrium aciculare (Hedw.) Brid.	S, R	H		8	V, R, H
Racomitrium aquaticum (Brid. *ex* Schrad.) Brid.	S, R			6	V, C, R
Scorpidium scorpioides (Hedw.) Limpr.	O, L			10	V
Scorpidium turgescens (T. Jens.) Loeske = *Pseudocalliergon turgescens* (T. Jens.) Loeske	O, L			9	V, C, M
Sphagnum spp. Linnaeus	F, L		FACW-OBL	7–10	V, C, M
Tomenthypnum nitens (Hedw.) Loeske			FAC	9	M

Table 2 (cont.). Comparison of indicator systems applied to bryophyte species.

	Vitt and Glime (1984)	Fritz et al. (2009)	Walker et al. (1989)	Hill et al. (2007)	Dierßen (2001)
Species Preliminarily Listed as FACW Wetland Indicators (Reed and Bates 1994)					
Aulacomnium palustre (Hedw.) Schwaegr.			FACW	8	V, C
Brachythecium rivulare Schimp. *in* B.S.G.		H		8	V, A, R
Bryhnia novae-angliae (Sull. & Lesq. *in* Sull.) Grout		H			M
Bryum pseudotriquetrum (Hedw.) Gaertn. et al.	L		FAC	9	C
Campylium radicale (P. Beauv.) Grout	L			9	C
Campylium stellatum (Hedw.) C. Jens.	L		OBL	8	V, C
Cratoneuron commutatum (Brid.) G. Roth = *Palustriella commutata* (Brid.) Ochyra	L				V, C, M
Cratoneuron filicinum (Hedw.) Spruce	L	H		8	V, C
Drepanocladus aduncus (Hedw.) Warnst.	F, L			10	V, H
Fissidens obtusifolius Wils.	F, L				M, R
Drepanocladus vernicosus (Mitt.) Warnst = *Hamatocaulis vernicosus* (Mitt.) Hedenäs	F, L			9	V
Hygroamblystegium tenax (Hedw.) Jenn.	F, L	A		9	V
Hygrohypnum eugyrium (Schimp. in B.S.G.) Loeske	F, L	H		9	V, R
Hygrohypnum molle (Hedw.) Loeske	F, L			10	R, H
Hypnum lindbergii Mitt.	L	H		7	V, C
Philonotis fontana (Hedw.) Brid.	L			9	V, R
Mnium affine Bland. *ex* Funck, *sensu lato* = *Plagiomnium ellipticum* (Brid.) T. Kop.		H		6	C, M
Mylia anomala (Hook.) S. Gray			FACW	9	C
Plagiothecium denticulatum (Hedw.) Schimp. *in* B.S.G.		M		6	
Polytrichum longisetum Brid.			FACW	6	M
Racomitrium fasciculare (Hedw.) Brid.	R			2	V, C, M
Mnium punctatum Hedw. = *Rhizomnium punctatum* (Hedw.) T. Kop.		H		8	C, M
Scapania undulata (L.) Dumort.		A		10	
Grimmia maritima Turn. = *Schistidium maritimum* (Turn.) Bruch & Schimp. *in* B.S.G.	R			7	M

Table 2 (cont.). Comparison of indicator systems applied to bryophyte species.

	Vitt and Glime (1984)	Fritz et al. (2009)	Walker et al. (1989)	Hill et al. (2007)	Dierßen (2001)
Species Preliminarily Listed as FAC Wetland Indicators (Reed and Bates 1994)					
Aneura pinguis (L.) Dumort.	-		FACW	9	V, C, M
Atrichum crispum (James) Sull.	-	H		8	V, C, M
Atrichum tenellurn (Röhl.) Bruch & Schimp. *in* B.S.G.	-	H		8	M
Aulacomnium turgidum (Wahlenb.) Schwaegr.	-		FACW	4	M
Ceratodon purpureus (Hedw.) Brid.	-		FAC	4	M, X
Chiloscyphus pallescens (Ehrh. *ex* Hoffm.) Dumort.	-	H		9	V, C
Chiloscyphus polyanthos (L.) Corda	-	A		9	V, C, M
Conocephalum conicum (L.) Underw.	-	H		7	C
Dicranodontium denudatum (Brid.) Britt. *in* Williams	-	M		6	M
Eurhynchium hians (Hedw.) Sande Lac.	-	M		5	C, M
Stokesiella praelonga (Hedw.) Robins. = *Eurhynchium praelongum* (Hedw.) Schimp. *in* B.S.G.	-	M		6	
Fissidens adianthoides Hedw.	-			7	
Fissidens osmundioides Hedw.	-	H		7	V, C, M
Hylocomium splendens (Hedw.) Schimp. *in* B.S.G.	-		FACW	5	M
Leucobryum glaucum (Hedw.) Ågstr. *in* Fries	-	M		6	V, C, M
Marsupella emarginata (Ehrh.) Dumort.	-	H		8	R, H
Mnium cuspidatum Hedw. = *Plagiomnium cuspidatum* (Hedw.) T. Kop.	-	M		6	M
Mnium rostratum Schrad. = *Plagiomnium rostratum* (Schrad.) T. Kop.	-	M		7	C, M
Pleurozium schreberi (Brid.) Mitt.	-		FACW	5	M
Pohlia nutans (Hedw.) Lindb.	-		FACW	5	M
Scapania nemorosa Dumort. = *Scapania nemorea* (L.) Grolle	-	H		7	C, M
Sematophyllum demissum (Wils.) Mitt.	-	M		7	V
Thuidium delicatulum (Hedw.) Schimp. *in* B.S.G.	-	M		6	M

Table 2 (cont.). Comparison of indicator systems applied to bryophyte species.

Key to Moisture Descriptions		
Reed and Bates (1994) and Walker et al. (1989)	OBL	Plants that almost always occur in wetlands, probability >99%
	FACW	Plants that usually occur in wetlands, probability 67% to 99%
	FAC	Plants equally likely to occur in wetlands and uplands, probability 33% to 67%
	FACU	Plants that sometimes occur in wetlands, probability 1% to 33%
Vitt and Glime (1984)	L	Limnophilous
	R	Rheophilous
	O	Obligate aquatic
	F	Facultative aquatic
	S	Semi-aquatic emergent
Fritz et al. (2009)	A	Aquatic
	H	Hygrophytes
	M	Moist
	T	Terrestrial
Dierßen (2001)	E	Hygrophytic - extremely wet
	V	Hygrophytic - very wet
	C	Hygrophytic - considerably wet
	M	Mesophytic - moderately wet to moderately dry
	X	Moderately xerophytic
	A	Amphiphytic
	H	Hydrophytic
	L	Limnophytic
	R	Rheophytic
Hill et al. (2007)	1	Indicator of extreme dryness, restricted to situations that often dry out for some time
	2	Between 1 and 3
	3	Dry-site indicator, more often found on dry substrata than in moist places
	4	On well-drained terrestrial substrata or on bark or rock with some shelter
	5	On moderately moist soils or on bark or rock in moderately humid places
	6	On moist soils or rock or bark in humid places
	7	On constantly moist or damp but not waterlogged substrata
	8	Between 7 and 9
	9	In waterlogged sites, either in streams and flushes or on bogs
	10	In pools and by streams that may intermittently lack water
	11	On surface of still water or regularly submerged in running water, though sometimes at or above normal water level
	12	Normally submerged

4 Select Groups of Bryophytes as Indicators

Bryophytes as hydrophytes

To address the question of whether all wetland bryophytes or select indicator species should be used in delineations, we begin with the concept of a hydrophyte, as defined for the purposes of wetland delineation. According to the USACE wetland delineation manual (USACE 1987), a hydrophyte is any macrophyte that grows in water or on a substrate that is at least periodically deficient in oxygen. Hydrophytic vegetation is present in areas where soils are permanently or intermittently inundated or are saturated long enough to exert a controlling influence on the plant species present. The dominant species in hydrophytic plant communities possess morphological, physiological, or reproductive adaptations that enable them to tolerate or avoid saturated, anoxic soils (USACE 1987). Plants that are considered to be adapted for life in anaerobic soils have been assigned a wetland indicator status of obligate wetland plant (OBL), facultative wetland plant (FACW), or facultative plant (FAC) by the U.S. Fish and Wildlife Service (1996).

Three groups of bryophytes—obligate aquatics, facultative aquatics, and semi-aquatic emergent species—can be considered hydrophytes because they grow in water or on permanently saturated soils (Vitt and Glime 1984). However, the anaerobic conditions present in hydric soils do not appear to influence bryophyte species composition. Instead, wetland hydrology exerts a controlling influence on bryophyte species composition. These three groups of bryophytes are adapted to tolerate seasonal flooding and fluctuating water levels.

Obligate aquatic bryophytes fit the definition of a hydrophyte because they avoid desiccation by inhabiting aquatic environments and are intolerant of water level fluctuations (Vitt and Glime 1984). Most obligate aquatic species are also limnophilous, growing in environments that are fairly sheltered from waves and current, such as lake bottoms, shores, pools, and flarks. Obligate aquatic bryophytes most often exhibit the streamer life form (Glime 1968). For example, many species from the genera *Fontinalis* and *Sphagnum* are characterized by long, flexuose stems and widely spaced branches with ecostate leaves that sway in slight currents (Vitt and

Glime 1984). This morphology indicates that they are adapted for life in an environment where light and free carbon dioxide are limiting factors for bryophytes (Proctor 1982; Glime and Vitt 1984). Long stems with widely spaced leaves and branches reduce self shading in a light-limited environment and create turbulence, which increases carbon dioxide uptake (Stream Bryophyte Group 1999).

Compared to obligate aquatics, facultative aquatic bryophytes are less easily recognized as hydrophytes. Although they grow in habitats that are periodically inundated or saturated, these mosses can tolerate short dry periods and can survive seasonal fluctuations in the water table. Facultative aquatic bryophytes are classified as either limnophilous, such as many in the genera *Sphagnum* and *Drepanocladus,* or rheophilous, such as some members of the genera *Fissidens* and *Fontinalis,* which grow in running water (Vitt and Glime 1984). Although the two groups exhibit different morphologies, both are adapted for life in wetlands.

Many limnophilous *Sphagnum* species are facultative aquatic bryophytes. For instance, species such as *S. fallax*, *S. cuspidatum*, and *S. recurvum* are characteristic of wetlands with highly variable hydroperiods, such as vernal pools (Weakley and Schafale 1994; Edinger et al. 2002). Their morphology is indicative of an aquatic habitat. The lax, sprawling, weak-stemmed form, and the widely spaced groups of branches known as fascicles, suggest that external water retention and transport is unnecessary (McQueen 1990). Although most often found submerged, by late summer these mosses are left stranded as their habitat dries out completely. Unlike obligate aquatic species, these facultative aquatic mosses are desiccation tolerant, routinely surviving seasonal drawdowns and dry periods (Andrus 1986).

Other facultative aquatic bryophytes, such as *Hygroamblystegium fluviatile, Fontinalis dalecarlica*, and *Hygrohypnum ochraceum*, are found mainly in streams and rivers and are considered rheophilous (Dierßen 2001). Rheophilous species exhibit morphologies that are very different from limnophilous mosses. Stiff wiry stems, short thick cells, and a strong costa (a midrib that lacks vascular tissue) provide support when strong currents create shear stress or when water levels are low. Clumps of rhizoids enable them to cling to stable substrates like very large rocks and trees during flood events (Vitt and Glime 1984). Strong currents may strip away delicate leaf tissue, which is just one cell in thickness, leaving only stems and costas. This condition occurs so commonly in some rheophilous species, such as *Hygroamblystegium noterophilum*, that it can be used to identify them in the field (Crum 1983).

Semi-aquatic emergent species are the third group of bryophytes that can be considered hydrophytes. These mosses grow in wetlands, are adapted to life in water, and do not tolerate water level fluctuations or dry conditions (Vitt and Glime 1984). Semi-aquatic emergent mosses are commonly found in wetlands with constant hydroperiods, such as fens. Although the base of the plant is submerged, the shoot tip is usually exposed. Leaf and stem ornamentations conduct water externally to hydrate exposed shoot tips. Examples include the common peatland mosses *Campylium stellatum*, *Calliergonella cuspidata, Calliergon giganteum*, *Hypnum lindbergii*, and *Bryum pseudotriquetrum* (Vitt and Glime 1984) and hummock-forming *Sphagnum* species (Clymo and Hayward 1982; Andrus 1986).

As with aquatic mosses, the morphology of semi-aquatic emergent bryophytes indicates that they are adapted for life in wet habitats. Stem ornamentations create numerous capillary spaces that conduct water to the exposed shoot apex. For instance, paraphyllia (branched or unbranched photosynthetic structures) cover the stems of *Cratoneuron commutatum*, whereas a dense tomentum of rhizoids (small, unbranched filiments) coats the stems of *B. pseudotriquetrum*. On hummock-forming *Sphagnum* species such as *S. fuscum* or *S. capillifolium*, the capillary spaces between spreading and pendant branches, leaves, and stems conduct water up from the water table, preventing the actively growing capitulum from drying out (Andrus 1980; McQueen 1990).

Obligate aquatic, facultative aquatic, and semi-aquatic emergent bryophytes can all be considered hydrophytes for the purposes of wetland delineation because they are morphologically adapted to life in water and grow in water or wetlands that are at least periodically inundated or saturated. Lists of particular wetland indicator species or genera could be created based on the characteristics of these three groups of bryophytes.

Bryophytes as indicator species: select groups vs. all bryophytes

An easier alternative than identifying all of the bryophyte species in a sample plot during wetland delineation is to identify a handful of easily recognized indicator bryophytes that are common in regional wetlands. If more than 50% of the bryophyte cover from plots located in wet microsites consists of these “wetland specialists,” then the vegetation could be considered hydrophytic (USACE 2008a, c). Because similar groups of bryophytes are found in wetlands with similar water chemistry (List and Andrus 1989; Vitt and Chee 1990; Rydin and Jeglum 2006), regional lists of easily recognized wetland specialist bryophytes could be compiled. Regional lists might be based on the obligate aquatic, semi-aquatic, and facultative aquatic bryophytes described by Vitt and Glime (1984), the field experience of local experts, and species listed as OBL and FACW on the preliminary list of bryophytes and lichens found in wetlands of the United States (Reed and Bates 1994). Another option is to develop a list of wetland indicator genera, since many bryophyte genera consist only of OBL and FACW indicator species, according to Reed and Bates (Table 3).

Although the prospect of learning to identify a small number of indicator bryophytes may be an attainable goal, there are ecological and perhaps legal drawbacks to using select groups of species as wetland indicators. First, in some wetlands, such as sedge meadows or forested bogs, wet microsites are sparsely vegetated or largely unvegetated, consisting primarily of periodically inundated or saturated muck (Peach and Zedler 2006; Stringer and Stringer 1973; Rydin and Jeglum 2006). In this situation, the bryophyte layer might possibly lack OBL wetland indicators and consist mainly of FAC and a few FACW species. Second, bryophyte vegetation gradients are often composed of numerous species, responding to very small scale environmental changes. Bryophyte communities tend to be species rich, often with large proportions of rare species (Slack et al. 1980; Vitt and Belland 1995; Jonsson 1997). In this type of community, very few individual species can be considered dominant. Therefore, indicator bryophytes on a regional list could compose less than 50% of a wetland plot. A delineator who is only familiar with wetland specialists has no way of determining whether the remaining species are terrestrial bryophytes or are uncommon or taxonomically difficult wetland species that were not included on the regional list.

If the use of bryophytes as wetland indicators is to be legally defensible, the same rigor that is applied to vascular plants must be applied to bryophytes. Bryophyte communities on both sides of a wetland boundary, from a wide range of microsites, should be examined during delineations. To demonstrate that wetland and upland plant communities differ in bryophyte composition, the prevalence index should be applied to mosses in both communities. Because correctly identifying all bryophyte species in wetland and upland plant communities can be difficult, another option is to use bryophyte life forms as indicators.

Plant ecologists, including Raunkaier, Dansereau, Küchler, and Fosberg, developed life-form classification systems that are applied to vascular and nonvascular vegetation at global scales (Kent and Coker 1992). Much of this work is reflected in wetland classification and delineation procedures currently used in the U.S. Wetland classes are defined by the life form of the dominant vegetation: aquatic bed, moss-lichen, emergent, scrub-shrub, or forested (Cowardin et al. 1979). Sampling vegetation during wetland delineations generally involves separating plants into layers or strata based on life form: tree, vine, shrub, and herb (USACE 1987).

Table 3. Genera that contain only OBL and FACW bryophyte species, according to the list of bryophytes that occur in wetlands (Reed and Bates 1994). Reed and Bates assigned indicator values to species as defined by Crum et al. (1973). Many genera and species have since been revised. In the first column, the nomenclature is according to Anderson et al. (1990) for true mosses and the Flora of North America Editorial Committee (2007) for *Sphagnum*. The third column includes examples of species that were not recognized by Crum (1973) and therefore have not been assigned wetland indicator status.

Genera According to Anderson et al. (1990) or Flora of North America Editorial Committee (2007)	Indicator Status	Species Without Indicator Status
Amblyodon Bruch & Schimp. *in* B.S.G., *nom. cons.*	FACW	
Blindia Bruch & Schimp. *in* B.S.G.	FACW	
Brachelyma Schimp. *ex* Card.	OBL	
Calliergon (Sull.) Kindb.	OBL-FACW	*C. macounii* Karcz.
Calliergonella Loeske	OBL	
Catoscopium Brid.	FACW	
Climacium Web. & Mohr	OBL-FACW	*C. kindbergii* (Ren. & Card.) Grout
Cyclodictyon Mitt.	FACW	
Cratoneuron (Sull.) Spruce	OBL-FACW	*C. arcticum* Steere
Dichodontium Schimp.	FACW	
Donrichardsia Crum & Anderson	OBL	
Drepanocladus (C. Müll.) G. Roth	OBL-FACW	*D. crassicostatus* Janssens, *D. simplicissimus* Warnst.
Ephemerum Hampe, *nom. cons.*	OBL-FACW	
Fontinalis Hedw.	OBL-OBL?	*F. welchiana* Allen
Helodium Warnst., *nom. cons.*	OBL-FACW	
Hamatocaulis Hedenäs	FACW	*H. lapponicus* (Norrl.) Hedenäs
Henicodium (C. Müll.) Kindb.	OBL	
Hookeria Sm., *nom. cons.*	FACW	
Hygroamblystegium Loeske, *nom. cons.*	OBL-FACW	
Leucolepis Lindb.	FACW	
Limbella (C. Müll.) Broth.	FACW	
Limprichtia Loeske	OBL	*L.cossonii* (Schimp.), *comb. nov.*
Meesia Hedw., *nom. cons.*	OBL	
Palustriella Ochyra	OBL-FACW	
Paludella Brid.	OBL	
Platyhypnidium Fleisch.	OBL	
Platylomella Andrews	OBL	
Pseudocalliergon (Limpr.) Loeske	OBL	
Pseudobryum (Kindb.) T. Kop.	OBL	
Sarmenthypnum Tuom. & T. Kop.	FACW	
Scorpidium (Schimp.) Limpr.	OBL	
Scouleria Hook. *in* Drumm.	OBL	
Sphagnum spp. Linnaeus	OBL	39 additional species
Tomentypnum Loeske	OBL	
Vesicularia (C. Müll.) C. Müll.	OBL-FACW	
Warnstorfia Loeske	OBL	*W. procera* (Ren. & Arnell *in* Husn.) Tuom. & T. Kop. *W. pseudosarmentosa* (Card. & Thér.) Tuom. & T. Kop.

Some vascular hydrophytes are considered to be wetland indicators because their life form changes in response to anoxic soils (USACE 1987, 2008c; Tiner 1999). The life forms of bryophytes also change in response to available moisture; compared to vascular hydrophytes, the bryophyte response is much more plastic. As used by bryologists, life form is an ecological term describing the way a bryophyte colony is shaped as the growth forms of individual plants respond to environmental conditions (Mägdefrau 1982). McGee and Kimmerer (2002) suggest that the presence of various bryophyte life forms along environmental gradients is more ecologically meaningful than the presence of particular species.

Bryophyte life forms may be useful indicators of hydric vegetation during wetland delineations because patterns of the relative abundance of life forms are correlated with moisture, light, and substrate gradients (Gimingham and Birse 1957; Mägdefrau 1982). Tall turfs are most common in wetlands with constant hydroperiods (Birse 1958). Bryophyte colonies assume looser life forms, such as wefts and dendroid forms, to gather light in shady, mesic environments (Gimingham and Birse 1957). In contrast, moss colonies on hard substrates in xeric microhabitats, such as large boulders in streams, usually exhibit uniform growth in tightly packed cushions or short turfs (Suren and Duncan 1999) to conserve moisture and prolong photosynthesis (Proctor 1982). Bates (1998) modeled relationships between life forms of terrestrial bryophytes, water, light, and substrate (Figure 1).

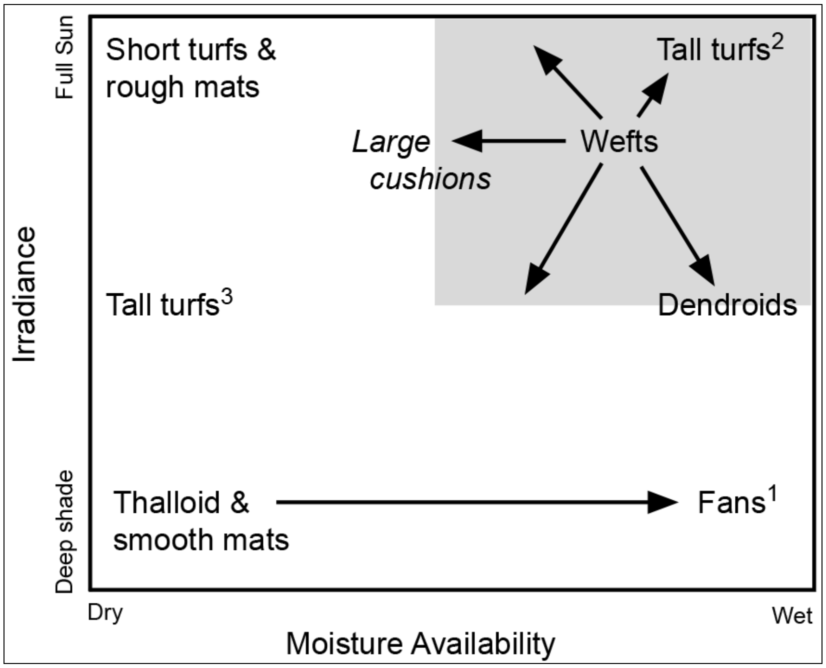

Figure 1. Approximate relationship between terricolous bryophyte life forms and the availability of moisture and sunlight in their respective habitats. The term "Wet" refers to habitats where desiccation stress is rarely encountered, not the frequency with which the life form occurs in wetlands. The shaded area represents habitats from which bryophytes are usually excluded because of interactions with vascular plants. The arrows denote ranges of tolerance that extend up to (and sometimes into) the next category. Large cushions are in italics because they occur infrequently. The superscripts denote: 1) life form on sloped, well-drained soils, 2) highly branched forms, e.g. *Sphagnum* spp., 3) sparsely branched forms, e.g. *Polytrichum* spp. Redrawn from Bates (1998).

The literature suggests that wetland hydrology exerts a controlling influence on the life forms of bryophyte colonies. For instance, along a 520-m transect that stretched from lakeshore to upland forest, Muhle and LeBlanc (1975) categorized the life forms of xylicolous bryophytes into three extremely broad classes: cushions, turfs, and mats. Bryophytes formed turfs and mats on logs that were permanently or intermittently flooded, whereas cushions and mats occurred on logs in upland forests. Associations between bryophyte life form and hydrologic regime were also described in a recent study of forested headwater streams. Wefts and mats were associated with hydric, permanent streams; turfs and cushions occurred more often in xeric, ephemeral streams (Fritz et al. 2009). Region 10 of the Environmental Protection Agency and the Portland District of USACE are exploring the possibility of using bryophyte life forms to classify hydrological permanence in Oregon headwater streams and to distinguish among permanent, intermittent, and ephemeral stream types (Fritz 2008).

Two concerns are associated with using life forms as indicators during wetland delineations. First, much confusion has resulted among bryologists from using the terms “life form” and “growth form” interchangeably (LaFarge-England 1996). In addition, some bryologists have described life forms meticulously (Gimingham and Birse 1957), whereas others have applied them as broad categories (Muhle and LeBlanc 1975). Hill et al. (2007) presents a standardized classification system as part of the BRYOATT project (Table 4). A standardized system would have to be adopted if bryophyte life forms were to be used as indicators during wetland delineations in the United States. Another concern is that few studies have applied statistical analyses to observed relationships between bryophyte life forms, wetland hydrology, and hydric soils. However, if regional studies documenting relationships between bryophyte species composition, soil type, and wetland hydrology are undertaken, it would not be difficult to examine correlations with life forms as well. Fritz et al. (2009) provide an example of research that explores the use of bryophyte species, families, life forms, and growth forms as indicators of hydrological permanence.

Table 4. Standardized list of the common life forms of British and Irish bryophytes, reproduced from Hill et al. (2007).

	Bryophyte Life Form
Ac	Aquatic colonial (formless loose colonies)
At	Aquatic trailing (attached to substrate)
Cu	Cushion (dome-shaped colonies)
De	Dendroid (with stolons and erect shoots)
Fa	Fan (branches in plane on vertical substrate)
Le	Lemnoid (floating on the water)
Mr	Mat, rough (creeping, lateral branches erect)
Ms	Mat, smooth (creeping, branches lying flat)
Mt	Mat, thalloid (creeping, thalli forming a layer)
Sc	Solitary creeping (creeping solitary shoots)
St	Solitary thalloid (rosette forming, patch not mat)
Tf	Turf (vertical stems with little or no branching)
Thread	Thread (solitary thread-like creeping stems)
Tp	Turf, protonemal (persistent protonema)
Ts	Turf, scattered (scattered vertical shoots)
Tuft	Tuft (loose cushions, not dome shaped)
We	Weft (intertwining branched layers)

Bryophyte sampling

Sampling wetland specialist bryophytes

To determine the best method for sampling bryophytes during wetland delineations, we begin with methods developed by USACE for sampling wetland specialist bryophytes. Although the use of bryophytes as indicators of hydrophytic vegetation has not been generally recommended (USACE 1987) in the past, sampling methods have recently been developed for the bryophyte layer in Alaska's *Picea mariana*-dominated wetlands and in wetlands dominated by *Tsuga heterophylla* in the Pacific Northwest. Hydric soils and indicators of wetland hydrology must be confirmed before the bryophyte layer is examined. Since bryophyte species composition varies over microtopographic gradients, wet microsites should harbor wetland indicator species. Thus, three 25- × 25-cm plots placed at hummock bases are used to measure the percent cover of specific wetland indicator bryophytes that are associated with each wetland type (USACE 2008a, c).

Several drawbacks are present in sampling select microsites for wetland specialist bryophytes. First, the procedure of surveying wet microsites for wetland indicators species will be difficult to apply in some wetland types across the United States. As mentioned previously, some wet microsites are largely unvegetated, consisting primarily of periodically inundated or saturated muck (Stringer and Stringer 1973; Peach and Zedler 2006; Rydin and Jeglum 2006). In wetlands characterized by highly variable hydroperiods, wet microsites may be difficult to locate in dry seasons. Of the three factors used to delineate wetlands, hydrology is often the least exact and most difficult to document in the field (USACE 1987).

Second, the homogenous samples obtained from hollows do not represent the entire bryophyte community. Regional supplements acknowledge that bryophyte species composition changes over microtopographic gradients, describing it as a "sorting of different species on the tops of hummocks versus the swales" (USACE 2008a, c). Although small homogenous samples obtained from swales may be easier to identify, they do not meet the standards required by the *Corps of Engineers Wetlands Delineation Manual* (1987) because they contain a small subset of the bryophyte community. The manual requires representative observation points, whose apparent characteristics best represent the characteristics of the entire plant community (USACE 1987). If some wetland microsites, such as hummock tops and sides, are excluded from sampling, boundary determinations will be difficult to defend, since the samples are clearly biased.

The small plots used to sample the bryophyte layer are another reason for concern. Our ability to detect patterns is influenced by a study's grain (the size of the sampling units) and extent (the overall area of the study). Just as it is impossible to explain or predict below a study's grain, we cannot generalize beyond a study's extent (Wiens 1989). Even with confirmed indicators of hydric soils and wetland hydrology, it would be difficult to defend hydrophytic vegetation determinations based on a total sample area of three 25- × 25-cm plots, particularly when USACE recommends sampling the tree layer in plots with a 9.1-m (30-ft) radius and the herb and shrub layers in plots with a 1.5-m (5-ft) radius (USACE 1987).

If entire plant communities are to be classified as hydrophytic based on the bryophyte layer, samples must be larger and more representative so that bryophytes are examined with the same scientific rigor that is applied to trees, shrubs, and herbs. To obtain larger, representative samples of the bryophyte community, a number of substrates and a variety of microhabitats will have to be examined. Although this goal could be achieved using intensive and random small-plot sampling, this procedure is neither efficient nor practical for wetland delineations. However, bryophyte cover is also quite difficult and time consuming to measure in large plots (Slack 1984).

Sampling recommendations

Given the need to sample a larger percentage of the bryophyte community, we suggest sampling bryophytes and vascular plants in the same plots. When selecting representative observation points for the plant community, delineators should consider the bryophyte layer. To sample heterogonous bryophyte communities characterized by small-scale variation, we suggest using floristic habitat sampling (FHS) and point sampling methods. For a detailed description of FHS, which is a sampling method designed to describe species richness over large spatial scales, see Newmaster (2000). To sample bryophyte communities with clumped distributions, such as those found in forested wetlands, FHS is recommended (Newmaster et al. 2005). Wetlands with even, continuous bryophyte cover should be surveyed using point intercept methods. If plots are within the wetland boundary, there should be a larger percentage of wet microsites, which support OBL and FACW species, than mesic or xeric microsites, which support FAC or FACU species (USACE 2008a-d).

Clumped bryophyte distributions

To produce defensible vegetation determinations based on the bryophyte layer, the FHS method of vegetation sampling should be used in wetlands where bryophytes are clustered in microsites. Bryophyte vegetation should be sampled in plots with a radius of 9.1 m, along with trees (Figure 2). Floristic habitat sampling is commonly used in mesic upland forests (Newmaster et al. 2005) and a wide variety of wetland types (Vitt et al. 1995; Lockey et al. 2005). The following procedure is modified from Newmaster (2000) and USACE (2008a-d).

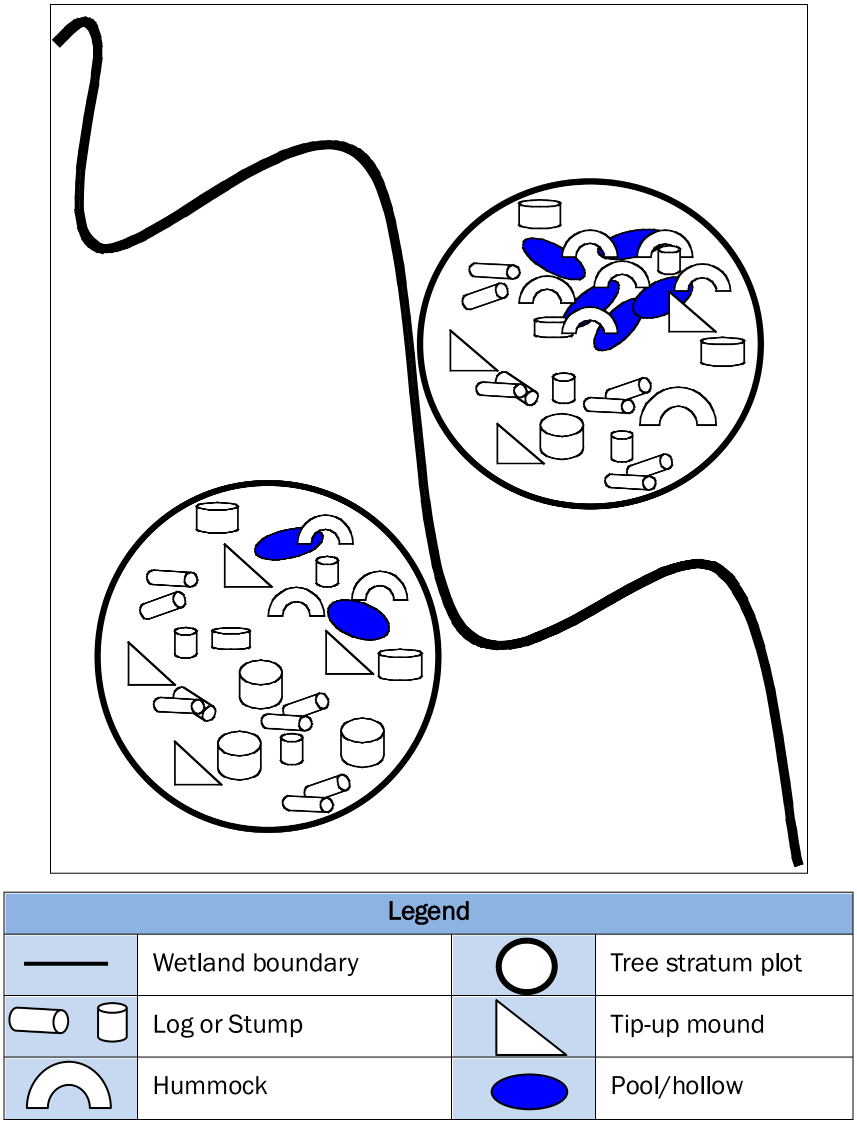

Figure 2. Hypothetical example of floristic habitat sampling in a forested fen, where the bryophyte distribution is clumped. All bryophyte microsites within the tree stratum plot (9.1-m radius) that might come into contact with wetland hydrology are systematically searched for bryophyte species.

1. Within the 9.1-m-radius plot used to sample the tree stratum, search for bryophytes in each microsite type that could potentially come in contact with surface waters, ground water, or its capillary fringe.
2. In each microsite type, identify all bryophytes and record these species as present.
3. When all microhabitats have been searched, sum each species' frequency across all microhabitat types. At least 80% of the species in the plot must be identified correctly.
4. Group all species by their wetland indicator status (Reed and Bates 1994).

5. Use the prevalence index to make hydrophytic vegetation determinations (Table 5).

$$PI = \frac{F_{obl} + 2\ F_{facw} + 3\ F_{fac} + 4\ F_{facu} + 5\ F_{upl}}{F_{obl} + F_{facw} + F_{fac} + F_{facu} + F_{upl}}$$

where:

PI = Prevalence Index
F_{obl} = Frequency of obligate (OBL) plant species
F_{facw} = Frequency of facultative wetland (FACW) plant species
F_{fac} = Frequency of facultative (FAC) plant species
F_{facu} = Frequency of facultative upland (FACU) plant species
F_{upl} = Frequency of upland (UPL) plant species.

The community is hydrophytic if the prevalence index is 3.0 or less.

Using this method to classify the bryophyte layer would simplify wetland delineations in several ways. Only presence/absence data are collected, which is less time consuming and more accurate than estimating percent cover in large plots (Bates 1982b; Slack 1984). Vegetation determinations would be based on the familiar Prevalence Index. Bryophyte index values based on presence/absence data distinguish hydric soils from nonhydric soils better than weighted averages based on percent cover (Walker et al. 1989).

Another advantage is that delineators would not have to decide where to place small plots in order to obtain a representative, homogenous sample. Instead, all bryophytes in the tree stratum plot that could come into contact with wetland hydrology are sampled. Because the bryophyte and tree layers are sampled at the same spatial scale, hydric vegetation determinations based on the bryophyte layer would be easier to defend. Although bryophytes inhabiting mesic and dry microsites would be included, these microsites should be less prevalent than hydric microsites within the wetland boundary (USACE 2008a-d). The data presented in Table 5 suggest that index values of wetland bryophyte communities may be less than 3.0, even though FACU species are likely to be present in mesic microsites inside the wetland boundary. However, regional studies that correlate changes in bryophyte index values with hydric and nonhydric soils in a variety of wetland types are needed.

Table 5. Prevalence Index applied to data from the wetland boundary of a forested fen in central New York. The community is hydrophytic because the Prevalence Index is less than 3.0.

	Microsite Type						Reed and Bates (1994)		
	Log	Tip-up	Stump	Hummock	Hollow	Total	Status	Weight	=
Hypnum imponens						1	UPL	5	5
Amblystegium varium						1	FACU	4	4
Tetraphis pellucida						1	FACU	4	4
Bazzania trilobata						1	FAC	3	3
Campylium chrysophyllum						1	FAC	3	3
Eurhynchium hians						1	FAC	3	3
Leucobryum glaucum						1	FAC	3	3
Plagiomnium cuspidatum						1	FAC	3	3
Thuidium delicatulum						5	FAC	3	15
Brachythecium oedipodium						1	FACW	2	2
Brachythecium rutabulum						1	FACW	2	2
Bryhnia novae-angliae						2	FACW	2	4
Ctenidium molluscum						1	FACW	2	2
Plagiomnium ellipticum						1	FACW	2	2
Hypnum lindbergii						2	FACW?	2	4
Rhizomnium punctatum						1	FACW	2	2
Sphagnum teres						1	OBL	1	1
Climacium dendroides						1	OBL	1	1
				sum(a)=		24	sum(b)=		63
				PI =		b/a			
				PI =		63/24			
				PI =		2.63			

A few drawbacks are associated with FHS. First, this method can be labor intensive. Sampling only terricolous bryophytes might seem more efficient and practical. However, by limiting sampling to terricolous mosses, many wetland indicator species would be excluded, biasing the sample. Facultative aquatic bryophytes, most of which are OBL and FACW indicators (Reed and Bates 1994), may be most abundant on rocks (Vitt and Glime 1984), tree trunks (Gilbert et al. 2007), or logs (Muhle and LeBlanc 1975), depending on the wetland type. A second concern is that this method requires field identification of both terrestrial and aquatic bryophytes. Some experts believe that only trained bryologists should conduct field sampling in which bryophytes are identified to species (Slack 1984). As noted earlier, alternative methods include identifying bryophytes by life form or genus.

Continuous bryophyte distribution

In wetlands where the moss cover is even and continuous, hydric vegetation determinations based on the bryophyte layer could be made using point sampling methods. Bryophyte vegetation could be sampled, along with herbaceous vegetation, in plots with a radius of 1.5 m (Figure 3). Point sampling methods are modified from standard USACE procedures (USACE 2008a-d):

1. Establish a 3.0-m baseline tangent to the plot used to sample the herbaceous layer. If the plot is located near the wetland boundary, the baseline should be perpendicular to the wetland boundary.
2. Establish three transects, 3.0 m in length, at even intervals, perpendicular to the baseline. Transects are oriented parallel to the wetland boundary and bisect the herbaceous plot. Transects should be level and elevated above hummock tops. Transects should never extend across the wetland boundary or into adjacent plant communities.
3. Take point samples at 0.25-m intervals along each transect. At each point, extend a long pin or an imaginary vertical line through the vascular vegetation until it hits a bryophyte. Identify the species intercepted by each point.
4. Sum each species' frequency and look up its indicator status.
5. Apply the Prevalence Index.

There are several advantages to classifying the bryophyte layer using the familiar procedures of point-intercept sampling and the Prevalence Index. Wetland bryophyte communities are often heterogeneous and characterized by high species diversity (Jonsson 1997; Slack 1994). Point sampling is particularly useful in communities with these characteristics as it reduces bias and provides more accurate estimates of abundance when compared to visual estimates of cover (USACE 2008b). Again, delineators will not have to decide where to locate plots to obtain representative samples. Because the bryophyte and herbaceous strata are sampled at the same spatial scale, hydrophytic vegetation determinations based on the bryophyte layer would be easier to defend. The point-intercept method would provide a large (n = 36), representative sample of the bryophyte community, including species from a range of microsites. Yet, within the wetland boundary, hydric microsites should be more prevalent than drier ones (USACE 2008b).

Drawbacks are also associated with point-intercept sampling. First, this method is generally more labor intensive than visually estimating cover (USACE 2008b). However, in large plots, visual estimates of bryophyte cover are difficult, especially for delineators who may be unfamiliar with the flora (Slack 1984; McCune and Grace 2002). Identifying points should be more accurate and less time consuming than estimating cover (Bates 1982b). However, as previously discussed, point sampling potentially requires delineators to identify numerous bryophyte species from hydric, mesic, and xeric microsites.

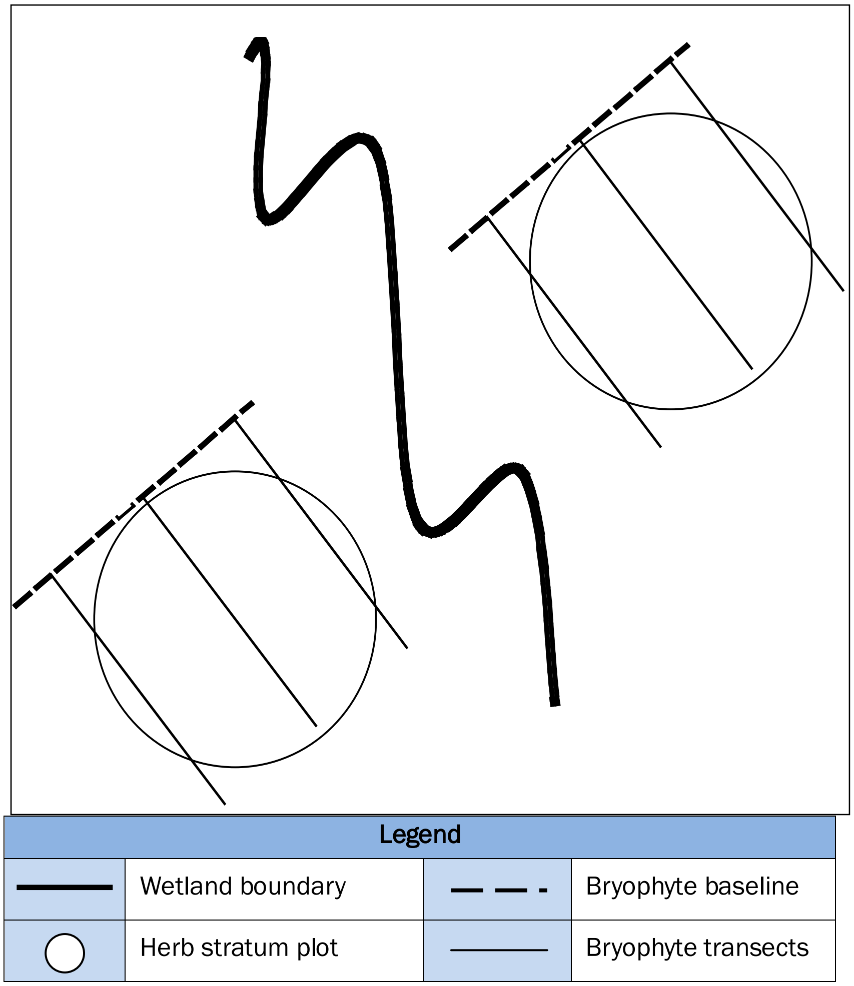

Figure 3. Hypothetical example using point sampling when the bryophyte distribution is even and continuous. The orientation of the baseline and transects for point sampling the bryophyte layer are illustrated in relation to the 1.5-m-radius plot used to sample the herbaceous layer.

The practice of basing vegetation determinations on three, subjectively located 25- × 25-cm plots needs to be re-evaluated. Samples from small plots may be easier to identify because they are homogenous, but they are not representative. To produce hydrophytic vegetation determinations based on the bryophyte layer that are scientifically sound and defensible, bryophyte plots must be larger and represent the entire community. No significant difference exists between the response curves of bryophytes and vascular plants along microtopographic gradients (Rygdren et al. 2003). If vegetation sampling methods capture small-scale variation along hummock-to-hollow gradients in the vascular plant strata, then small-scale variation in bryophyte community composition must also be represented. If FHS and point sampling methods were applied within the large plots currently used to classify vascular vegetation, samples would be more representative and hydrophytic vegetation determinations based on the bryophyte layer would be more defensible.

Identification resources and voucher specimens

Though bryology has a strong history in North America, it has never attained the popularity of bryology in Europe or the popularity of mycology and ornithology in amateur circles. As such, few field guides for mosses, liverworts, and hornworts have been published with the layperson in mind; however, Appendix B lists several available and out-of-print field guides. Much of the available literature is technical. Local and regional floras are available for many areas of the United States, though they are not always readily available, and most are out of print. These floras have been published in journals and many as books (Appendix C). Local university libraries and herbaria are the best places to locate copies. Efforts have been made to develop floras for all of North America. Currently, an effort is underway through the Flora of North America project to develop three volumes that describe the bryophyte flora of North America; a single volume has been published to date (Flora of North America Editorial Committee 2007).

The use of bryophytes as indicators of hydrophytic vegetation requires proper identification and preparation of voucher specimens. A variety of resources are available that can aid in bryophyte identification. One should begin with guides that have been written with the layperson in mind. These field guides can help in the recognition of the most obvious taxa. Recently, Bill and Nancy Malcom's excellent reference guide, *Mosses and Other Bryophytes*, became available in the United States through the California Native Plant Society. Although it is published in New Zealand, this illustrated glossary of bryological terms may be particularly helpful to beginners. Several guides are available for the western United States and the Canadian provinces. However, few guides are available for the rest of the United States. One recently published exception is the guide (Munch 2006) to outstanding taxa of mosses and liverworts in Pennsylvania; this guide is valuable for much of eastern North America. Most field guides can be helpful in identifying the most readily recognized taxa, but not necessarily for those taxa most useful for wetland delineation. Field guides hold a limited value for someone seeking to identify bryophytes to the species level. The limited demand for bryological field guides equates to limited printing of most guides and a general scarcity. As with older biological literature, the species names are often no longer correct and therefore require some cross referencing with the most recent checklists. The field guides can help in identifying bryophytes to a particular genus or possibly a group of species, but positive identification takes time and requires microscopes and specialized texts.

Regional bryophyte herbaria can also be invaluable resources when trying to identify bryophyte taxa. The herbaria often house extensive collections of bryophyte literature and identified bryophyte specimens that can be used for comparison to unknown specimens or for learning the taxa that are important for wetland delineation. (See Appendix E for a list of regional herbaria arranged by USACE regions; eight of the 10 are represented.)

Voucher specimens serve a variety of roles. For bryophytes, the difficulty of positively identifying species in the field makes vouchers important for verifying identifications. These collections can allow the delineator to make detailed observations under the microscope and relate these observations to their field observations. Voucher specimens can also be sent to an expert for identification or verification. A photograph will not suffice for the purposes of bryophyte identification. Finally, and some would argue most importantly, the voucher specimen serves as a record of the flora of the region and should be submitted to a herbarium and made available to anyone working on the flora.

Samples collected for voucher specimens should be representative of the colony; if possible they should have sporophytes and other reproductive structures that may aid in identification. The specimens should fit into a voucher envelope, approximately 10 × 15 cm. They should be cleaned of excess soil and other debris and then allowed to air dry. The label information should include the name of the species; detailed habitat and substrate information; the location in which it was collected; the collector's name and the collection date; the determiner's name and the date determined; and any other information that might be important. Schofield (1985) describes in greater detail the steps for specimen collection and voucher preparation.

Conclusion

Three groups of bryophytes can be considered hydrophytes: obligate aquatics, facultative aquatic, and semi-aquatic emergent species (Vitt and Glime 1984). These plants can be considered hydrophytes because they are morphologically adapted for life in water and grow in wetlands or deep water habitats. Regional lists of indicator species or genera could be created based on the characteristics of these three groups, or bryophyte indicator status could be based on life form. To produce defensible wetland delineations, we recommend applying the same scientific standards to bryophytes that are currently applied to vascular plants. All bryophytes in both wetland and upland plant communities should be identified to species. Another option is identification of life form, since the literature suggests that life forms are an equivalent scientific standard with regard to patterns of abundance along environmental gradients.

To use the bryophyte layer to produce boundary determinations that are scientifically sound and defensible, small-scale variations in bryophyte species composition must be included when sampling bryophytes during wetland delineations. Because wetland hydrology exerts a controlling influence on bryophyte species composition, we advocate sampling all bryophyte habitats and substrates that may come in contact with surface waters, groundwater, or its capillary fringe. Including all substrates is particularly important because aquatic bryophytes frequently grow on surfaces of rocks, trees, and logs. The microsite-specific FHS method of habitat sampling and the Prevalence Index are recommended for assessing the bryophyte layer. When bryophyte cover is even and continuous, point sampling techniques and the Prevalence Index are recommended. The use of bryophytes as indicators of hydrophytic vegetation requires proper identification and preparation of voucher specimens. Local herbaria are useful resources for learning to recognize wetland taxa or confirming field identifications.

5 Using Bryophytes in Wetland Delineations

Evidence from the literature suggests that 1) bryophytes are morphologically, physiologically, and reproductively adapted to microsite-specific hydrologic conditions, and 2) flood frequency and water level fluctuations exert a controlling influence on bryophyte species composition. To determine whether patterns of bryophyte species composition vary with patterns of inundation frequency, we apply preliminary wetland indicator status to data collected along inundation gradients.

Because there is no evidence in the literature suggesting that the anaerobic conditions in hydric soils exert a controlling effect on bryophyte composition, the reliability of bryophytes as indicators of hydric soils is still unclear. However, the presence of hydric soils or changes in soil moisture levels could be correlated with changes in the species composition of the bryophyte layer, even though the former does not appear to cause the latter. Here we examine data from field studies of bryophytes along soil moisture gradients to determine whether patterns of bryophyte species composition are correlated with patterns of soil moisture and soil type. Recommendations for the use of bryophytes as indicators of wetland hydrology and hydric soils are made based on evidence provided by the literature.

Bryophytes as indicators of wetland hydrology

Wetlands are defined primarily in terms of hydrology: the frequency and magnitude of inundation or saturation by surface or ground waters (USACE 1987). The literature suggests that bryophytes may make excellent small-scale indicators of the extent of wetland hydrology. Data from field studies provide evidence that patterns of wetland indicator status associated with bryophyte composition change along a gradient of inundation frequency. Other research suggests that epiphytic species are reliable indicators of typical water levels.

A clear pattern emerges when preliminary wetland indicator status (Reed and Bates 1994) is applied to bryophyte associations in riparian and lacustrine wetlands (Table 6). Bryophytes with FACW or OBL indicator status dominate permanently or semi-permanently flooded plots in stream channels and on lake shores, although drier microsites may support a few

UPL species such as pendant epiphytes (Pollock et al. 1998). Obligate wetland indicators are generally absent in intermittently flooded areas such as floodplains or mud flats. Terrestrial species with FACU or UPL indicator status are most abundant in upland areas. Facultative species are present along the entire gradient.

The literature also suggests that terrestrial bryophytes growing on tree trunks in wetlands are excellent indicators of the high water level. A recent study in cypress domes in the southeastern United States compared long-term records of hydrology with biological indicators of wetland hydrology along an inundation/elevation gradient. Mosses were found primarily in cypress dome interiors, covering *Taxodium ascendens* trunks down to the high-water line. Estimates provided by long-term hydrologic data suggest that bryophytes were inundated just 2% to 3% of the time. These epiphytes were not identified to species (Carr et al. 2006).

Corticolous bryophytes growing on tree bases may be excellent indicators of high water levels. In Florida, the Department of Environmental Protection considers aquatic bryophytes growing on tree bases to be primary indicators of wetland hydrology. Theses aquatic “moss collars” are considered evidence of existing hydropatterns, because they occur in areas that are normally submerged. Moss collars are common in forested floodplains that experience prolonged inundation and large seasonal drawdowns: rivers, streams, bayous, sloughs, and strands (Gilbert et al. 2007). For example, the extent of the liverwort *Porella pinnata* on tree bases in bottomland hardwood swamps is an indication that water levels have been consistent for at least 58 days, or 16% of the year (Wharton et al. 1982). However, basal epiphytes must be identified to species because terrestrial mosses frequently cover tree bases in upland forests (Studlar 1982; McGee and Kimmerer 2002) and grow directly above aquatic liverworts in southeastern bottomland hardwood swamps (Wharton et al. 1982).

Table 6. Comparison of preliminary wetland indicator status and bryophyte composition in riverine and lacustrine wetlands and adjacent uplands. The preliminary wetland indicator status is according to Reed and Bates (1994).

Hydric Stands	Mesic Stands	Xeric Stands
Pollock et al. (1998) – Terricolous bryophytes, Alaska		
Channel shelf, depositional bar	Floodplain	Terrace
Fontinalis neomexicana (OBL) *Racomitrium aciculare* (OBL) *Plagiomnium insigne* (FACW) *Isothecium myosuroides* (FACW) *Rhizomnium glabrescens* (FAC) *Rhytidiadelphus loreus* (FAC) *Eurhynchium praelongum* (FAC) *Sanionia uncinata* (FACU) *Antitrichia curtipendula* (UPL)	*Pleuroziopsis ruthenica* (FAC) *Rhizomnium glabrescens* (FAC) *Rhytidiadelphus loreus* (FAC) *Rhytidiadelphus squarrosus* (FAC) *Pogonatum contortum* (UPL)	*Sphagnum girgensohnii* (OBL) *Plagiomnium insigne* (FACW) *Hylocomium splendens* (FAC) *Rhytidiadelphus loreus* (FAC) *Rhizomnium glabrescens* (FAC) *Dicranum fuscescens* (FACU)
Jonsson (1997) – All substrates, Oregon		
Stream channel	Floodplain	Terrace
Hygrohypnum ochraceum (OBL) *Fontinalis neomexicana* (OBL) *Racomitrium aciculare* (OBL) *Scleropodium obtusifolium* (OBL) *Dichodontium pellucidum* (FACW) *Scapania undulata* (FACW) *Fissidens ventricosus* (FACW) *Chiloscyphus polyanthos* (FAC) *Eurhynchium praelongum* var. *stokesii* (FAC)	*Brachythecium frigidum* (FACW) *Leucolepis acanthoneuron* (FACW) *Racomitrium varium* (FAC) *Eurhynchium praelongum* var. *stokesii* (FAC) *Conocephalum conicum* (FAC) *Hypnum subimponens* (FAC) *Cephalozia lunulifolia* (FACU)	*Plagiomnium insigne* (FACW) *Hylocomium splendens* (FAC) *Rhytidiadelphus loreus* (FAC) *Rhizomnium glabrescens* (FAC) *Rhytidiadelphus triquetrus* (FACU) *Scapania bolanderi* (UPL) *Dicranum howellii* (UPL) *Pseudotaxiphyllum elegans* (UPL) *Rhytidiopsis robusta* (UPL) *Porella navicularis* (UPL)
Muhle and LeBlanc (1975) – Lignicolous bryophytes, Ontario		
Lacustrine shore	Mudflats	Upland forest
Leptodictyum riparium (OBL) *Fontinalis novae-angliae* (OBL) *Climacium dendroides* (OBL) *Bryum pseudotriquetrum* (FACW) *Campylium polygamum* (FACW) *Hypnum lindbergii* (FACW?) *Chiloscyphus pallescens* (FAC)	*Bryhnia novae-angliae* (FACW) *Plagiothecium denticulatum* (FACW) *Plagiomnium cuspidatum* (FAC) *Tetraphis pellucida* (FACU)	*Plagiomnium ciliare* (FACW) *Campylium hispidulum* (FACU) *Cephalozia media* (FACU) *Brachythecium salebrosum* (FACU) *Dicranum scoparium* (FACU) *Lophocolea heterophylla* (FACU) *Oncophorus wahlenbergii* (FACU) *Hypnum pallescens* (UPL) *Callicladium haldanianum* (UPL)

Because wetland hydrology exerts a direct controlling effect on bryophyte species composition along wetland to upland gradients, using bryophytes as indicators of wetland hydrology will be defensible. Aquatic and semi-aquatic bryophytes that exhibit perennial stayer life history strategies and are most abundant in the boreal zone will make the best indicators. This type of species is restricted to cool, moist habitats in temperate and tropical zones. Changing patterns of species composition on soils, logs, rocks, and tree trunks could be used to document the extent of the influence of wetland hydrology. Because aquatic and semi-aquatic bryophytes are restricted to habitats that are permanently saturated or seasonally flooded, they will be useful as hydrology indicators in peatlands, forested lacustrine floodplains, forested riparian wetlands, and vernal pools located in the Northcentral/Northeast Region, the Atlantic and Gulf Coastal Plain Region, and the Western Mountains, Valleys, and Coast Regions, as well as in sub-regions of Alaska that are not underlain by permafrost.

Bryophytes as indicators of hydric soils

Throughout North America, bryologists have reported associations between soil moisture levels and changes in patterns of bryophyte composition. Strong correlations between hydric soils and the weighted averages of vascular vegetation are also well documented. However, few studies have examined correlations between the presence of hydric and nonhydric soils and the weighted average of the bryophyte layer. Although the literature provided no evidence of a causative relationship between these two variables, research suggests that they may be correlated.

Observational field studies suggest that bryophyte composition varies with soil moisture levels (Table 7). A clear pattern emerges when preliminary wetland indicator status is applied to bryophyte associations in hydric, mesic, and xeric stands (Reed and Bates 1994). Bryophytes with OBL and FACW indicator status dominate stands with shallow water tables and deep organic layers (Stringer and Stringer 1974). In mesic stands, the bryophyte indicator status ranged from FACW to FACU. In well-drained upland stands with deep water tables, FACU and UPL bryophytes are most abundant. Facultative species are present in all stand types.

Along a soil moisture gradient, the compositional changes within each vegetation layer occur at different rates. No association exists between the changing patterns of species composition among the tree, shrub, herb, epiphyte, or terricolous bryophyte layers (McCune and Antos 1981). The herb layer generally reflects the current hydrologic regime, whereas dominant tree species often reflect past hydrological conditions (Segelquist et al. 1990). Because compositional changes in the terricolous bryophyte layer are independent of other layers, and because bryophytes are excellent microsite indicators (Vitt and Belland 1997), these small plants may make excellent indicators of hydric soils along wetland ecotones that are dominated by vascular vegetation with FAC indicator status.

When bryophytes are included in research documenting hydric soil–vegetation correlations, they appear to make good indicators. In a Rhode Island study that examined five vegetative strata, the herb layer, which included *Sphagnum* spp., best distinguished hydric from nonhydric soils and wetland from upland areas (Allen et al. 1989). Likewise, a Dutch study found that strong correlations between average water table height and the weighted averages of vascular plants were unaffected when bryophytes were included in the calculations (Schaffers and Sýkora 2000).

Soil–vegetation correlation studies that treat bryophytes as a separate layer suggest that mosses are most effective as indicators in regions where distinctions between hydric and nonhydric soils are unambiguous. In the arctic foothills of Alaska, where soils are underlain by a layer of permafrost, the weighted averages of the bryophyte layer were not effective for distinguishing between hydric and nonhydric soil types, even though bryophyte index values and soil moisture levels were strongly correlated (Walker et al. 1989). In contrast, weighted averages and index values of the moss and tree layers were most effective in distinguishing between hydric and nonhydric soils in south-central Alaska. Neither layer, however, could distinguish seasonally flooded wetland soils from upland soils (Boland-Schuman 1994). On the other hand, bryophytes might make excellent indicators in peatland delineations, since species composition varies with the depth of the organic layer (Stringer and Stringer 1974), and OBL and FACW species are present along peatland margins (Cooper and Andrus 1994). Overall, the evidence provided by the literature is insufficient to definitively state whether patterns of bryophyte species composition are consistently and reliably correlated with the presence of hydric and nonhydric soils throughout the continental United States.

Before bryophytes can be used as wetland indicators, regional studies must be conducted in different wetland types to determine whether correlations exist among hydric and nonhydric soils, bryophyte-weighted averages, and index values. Similar vascular plant studies conducted throughout the United States provide precedent (Segelquist et al. 1990).

Table 7. Comparison of species composition and preliminary wetland indicator status of bryophytes present in hydric, mesic, and xeric vegetation stands. The preliminary wetland indicator status is according to Reed and Bates (1994).

Hydric Stands	Mesic Stands	Xeric Stands
Cooper and Andrus (1994), Wyoming		
Fen expanse	Fen margin	
Calliergon trifarium (OBL) *Calliergon stramineum* (OBL) *Calliergonella cuspidata* (OBL) *Sphagnum teres* (OBL) *Sphagnum subsecundum* (OBL) *Drepanocladus aduncus* (FACW) *Calliergon sarmentosum* (= *Sarmenthypnum sarmentosum*) (FACW) *Pogonatum alpinum* (FACU)	*Polytrichum strictum* (OBL) *Tomenthypnum nitens* (OBL) *Aulacomnium palustre* (FACW) *Campylium stellatum* (FACW) *Philonotis fontana* (FACW) *Pohlia nutans* (FAC) *Bryum pallescens* (FACU) *Brachythecium starkei* (FACU) *Brachythecium erythrorrhizon* (UPL)	
Carleton (1990), Ontario		
Conifer bog/swamp	Mesic *Populus* spp. stands	Xeric *Pinus* spp. stands
Sphagnum capillifolium (OBL) *Sphagnum* spp. (OBL)	*Brachythecium curtum* (= *B. oedipodium*) (FACW) *Drepanocladus aduncus* (FACW) *Brachythecium salebrosum* (FACU)	*Pleurozium schreberi* (FAC) *Dicranum fuscens* (FACU) *Dicranum polysetum* (FACU) *Ptilidium pulcherrimum* (UPL)
Lee and La Roi (1979), Alberta		
Fens	Mesic forest	Xeric forest
Sphagnum warnstorfii (OBL) *Tomenthypnum nitens* (OBL) *Aulacomnium palustre* (FACW)	*Hylocomium splendens* (FAC) *Pleurozium schreberi* (FAC) *Ptilium crista-castrensis* (FACU) *Sanionia uncinatus* (FACU)	*Thuidium abietinum*(FACU) *Tortula ruralis* (UPL) *Hypnum vaucheri* (UPL) *Grimmia anodon* (UPL)
Stringer and Stringer (1974), Winnipeg		
Wet conifer stands	Mesic conifer stands	Xeric conifer stands
Tomenthypnum nitens (OBL) *Sphagnum capillaceum* (= *S. capillifolium*) (OBL) *Campylium stellatum* (FACW) *Aulacomnium palustre* (FACW) *Mnium rugicum* (= *Plagiomnium ellipticum*)(FACW) *Thuidium recognitum* (FAC)	*Brachythecium rutabulum* (FACW) *Mnium rugicum* (= *Plagiomnium ellipticum*) (FACW) *Mnium cuspidatum* (= *Plagiomnium cuspidatum*) (FAC) *Thuidium recognitum* (FAC) *Amblystegium juratzkanum* (= *Amblystegium serpens* var. *juratzkanum*) (FACU) *Brachythecium salebrosum* (FACU)	*Brachythecium rutabulum* (FACW) *Mnium cuspidatum* (= *Plagiomnium cuspidatum*)(FAC) *Ceratodon purpureus* (FAC) *Amblystegium* juratzkanum (= *Amblystegium serpens* var. *juratzkanum*)) (FACU) *Brachythecium salebrosum* (FACU)

Walker et al. (1989) provide an example of methods. If these studies are undertaken, we recommend that bryophyte life forms (such as cushion, turf, mat), growth form (acrocarps vs. pleurocarps), genera, and families should also be examined as possible indicators. Compared to recording species composition in the field, the extra time required to document bryophyte life forms and growth forms is insignificant. Fritz et al. (2009) demonstrated that these characteristics can make excellent indicators of hydrological permanence. This type of classification can be more rapidly integrated into current delineation procedures than species-based identification.

Conclusions

The literature suggests that bryophytes possess most of the characteristics of useful bio-indicators. Many bryophytes occupy large, disjunct ranges, exhibit narrow ecological tolerances, and persist in stable habitats. Because they are not deciduous, these species may be particularly useful in boreal and temperate zones when herbaceous vegetation is absent. In addition, microscale and mesoscale studies of bryophyte response to moisture and pH gradients suggest that they would make excellent indicators. However, many bryophytes are small and difficult to identify in the field, which makes them less useful as bio-indicators. Their small size also raises the question of whether they can be considered macrophytic vegetation for the purposes of wetland delineation, since many species concepts are based, in large part, on differences in cell morphology.

Using bryophytes as indicators of hydrology could be sound and defensible because wetland hydrology exerts a direct controlling effect on the bryophyte species present in wetlands. The unique morphologies, physiologies, and reproductive strategies of individual bryophyte species suggest that each species is adapted to microsite-specific hydrologic conditions. Inundation frequency and water level fluctuations create microscale vegetation gradients within wetlands, whereas water chemistry controls bryophyte composition at the mesoscale. Because bryophyte species composition changes with inundation frequency, these changes may be useful in delineating the extent of wetland hydrology. Moss trim lines make unambiguous indicators of the high water line. However, moss collars should be identified to species because both aquatic and terrestrial mosses grow on tree bases.

The reliability of bryophytes as indicators of hydric soils is still unclear. No evidence is available to indicate that hydric soils affect patterns of bryophyte composition. Although many studies have shown that bryophytes are strongly correlated with soil moisture and average water table levels, wet soils are not necessarily hydric. The literature provides insufficient evidence to determine whether patterns of bryophyte species composition are consistently and reliably correlated with the presence of hydric and nonhydric soils. Before bryophytes are used as indicators of hydric soils, regional studies (such as Walker et al. 1989) that document correlations between hydric and nonhydric soils, bryophyte-weighted averages, and index values must be conducted in different wetland types.

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Appendix B. Bryophyte Field Guides

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Appendix C. Major Floristic Works on North American Bryophytes

Peat mosses

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Appendix D. Web Resources

Peat mosses

Bryophyte flora of North America:
http://www.efloras.org/florataxon.aspx?flora_id=50&taxon_id=130947

True mosses

American Bryological and Lichenological Society:
https://mywebspace.wisc.edu/jpbennet/web/abls/

Bryophyte flora of North America:
http://www.efloras.org/flora_page.aspx?flora_id=50

Checklist of the mosses of the interior highlands of North America:
http://biology.missouristate.edu/Herbarium/Plants%20of%20the%20Interior%20Highlands/CHECKLIST%20OF%20MOSSES%20OF%20THE%20INTERIOR%20HIGHLANDS.htm

Checklist of the mosses of North Carolina:
http://www.biology.duke.edu/bryology/NC-Checklist.html

International Association of Bryologists:
http://www.bryology.org/

Checklist of New Jersey mosses:
http://phobos.ramapo.edu/~ekarlin/research/mosses.html

Liverworts and hornworts

Checklist of the liverworts and hornworts of the interior highlands of North America in Arkansas, Illinois, Missouri and Oklahoma:
http://biology.missouristate.edu/herbarium/liverw_t.htm

Additional bryophyte resources

Bryophyte glossary:
http://www.mobot.org/MOBOT/tropicos/most/Glossary/glosefr.html

Bryophyte nomenclature:
http://www.mobot.org/MOBOT/tropicos/most/bryolist.shtml

Bryophyte ecology:
http://www.bryoecol.mtu.edu/

Appendix E. Bryophyte Herbaria of the U.S., Organized by USACE Regions

Herbarium Symbol	Herbarium Name	Herbarium Symbol	Herbarium Name
Northcentral and Northeast Region		**Midwest Region**	
BH	Cornell University	ILLS	Illinois Natural History Survey
BING	State University of NY, Binghamton	IND	Indiana University
BKL	Brooklyn Botanic Garden	ISC	Iowa State University
BUF	Buffalo Museum of Science	KSP	Theodore M. Sperry Herbarium
CHRB	Rutgers University	MO	Missouri Botanical Garden
CONN	University of Connecticut	MU	Miami University
F	Field Museum of Natural History	NEB	University of Nebraska
FH	Harvard University	OS	Ohio State University
KE	Kent State University	SIU	Southern Illinois University
KIRI	University of Rhode Island	**Great Plains Region**	
MAINE	University of Maine	BRIT	Botanical Research Institute of Texas
MCTC	Michigan Technological University	GFND	University of North Dakota
MICH	University of Michigan	KSC	Kansas State University
MIL	Milwaukee Public Museum	NDA	North Dakota State University
MIN	University of Minnesota	OKL	University of Oklahoma
MSC	Michigan State College	RM	University of Wyoming
NY	New York Botanical Garden	TAMU	Texas A & M University
NYS	New York State Museum	TEX	University of Texas
UWEC	University of Wisconsin, Eau Claire	TTC	Texas Tech University
UWSP	University of Wisconsin, Stevens Point	**Arid West Region**	
VT	University of Vermont	ARIZ	University of Arizona
WIS	University of Wisconsin	ASU	Arizona State University
YU	Yale University	BRY	Brigham Young University
Atlantic Coast and Gulf Coastal Plain Region		CAS	California Academy of Science
FLAS	University of Florida	NMC	New Mexico State University
NO	Tulane University	OSC	Oregon State University
ODU	Old Dominion University	RENO	University of Nevada
US	Smithsonian Institution	SFSU	San Francisco State University
USCH	University of South Carolina	SRSC	Sul Ross State University
USF	University of South Florida	UC	University of California, Berkeley
Eastern Mountains and Piedmont Region		UCSC	University of California, Santa Cruz
BHO	Ohio University	UT	University of Utah
BOON	Appalachian State University	WS	Washington State University
CINC	University of Cincinnati	**Western Mountains, Valleys and Coastal Region**	
CLEMS	Clemson University	COLO	University of Colorado
DUKE	Duke University	CS	Colorado State University
GA	University of Georgia	FLD	Fort Lewis College
KY	University of Kentucky	GFC	Great Falls College
MARY	University of Maryland	MNA	Museum of Northern Arizona
NCU	University of North Carolina, Chapel Hill	MONT	Montana State University
PH	Philadelphia Academy of Natural Sciences	WTU	University of Washington
TENN	University of Tennessee	**Alaska Region**	
UNAF	University of North Alabama	ALA	University of Alaska Museum
VPI	Virginia Polytechnic Institute		

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14. ABSTRACT

Under Section 404 of the Clean Water Act, the U.S. Army Corps of Engineers is responsible for delineating wetland boundaries, using hydrophytic vegetation, hydric soils, and wetland hydrology. Current procedures for making hydrophytic vegetation determinations are based on vascular plants; the use of bryophytes is generally not recommended. However, the National Technical Committee on Wetland Vegetation is investigating the use of bryophytes as indicators of environmental conditions. This literature review examines relationships between bryophytes, hydric soils, and wetland hydrology for delineating wetlands. To determine whether hydric soils and wetland hydrology control the bryophyte species present in wetlands, bryophyte adaptations to these environmental variables are investigated. Response to soils and hydrology is considered at the microscale and the mesoscale. The consistency and reliability of bryophytes as indicators of wetland type are examined. Selected species and genera are identified as hydrophytes, and procedures for field sampling are proposed. Bryophyte identification resources and the necessity of voucher specimens are also discussed. To determine whether species composition differs with soil moisture levels, soil type, and hydrologic regime, bryophyte associations in wetlands and adjacent uplands are explored. Finally, situations in which bryophytes could be used in wetland delineations and areas that require further research are identified.

15. SUBJECT TERMS Bryophytes Clean Water Act	Hydric soils Hydrophytic vegetation Mosses	Wetland delineation Wetland hydrology

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