CHAPTER 4: ECOLOGY AND TAXONOMY OF WASHINGTON *SPHAGNUM* MOSS

This chapter examines the ecology and taxonomy of western Washington *Sphagnum* mosses. It includes a summary of *Sphagnum* biology, a survey of *Sphagnum* species found in western Washington, the growth habits and ecological niches of species found in the State, and responses of these species to environmental gradients and stressors.

Data on *Sphagnum* in western Washington are sparse. Data collected during a survey of bogs in King County, Washington (Cooke Scientific 1998) will be used in conjunction with information found in the literature (Schofield 1969; Moore and Belamy 1974; Larson 1982; Crum, North American Flora: Sphagnopsida 1984; Andrus 1986; Crum 1988; Klinka et al. 1989; Crosby and McGill 1995, 1997; Vitt et al. 1998; McQueen and Andrus: Flora of North America in press).

4.1 *Sphagnum* Biology

As with all mosses, the lifecycle of *Sphagnum* mosses consists of two different generations. The conspicuous, leafy *Sphagnum* plant is the gametophyte generation which is haploid (containing half of the full complement of chromosomes found in the sporophyte). It produces the egg and sperm either on different branches of the same plant (monoicous) or on different plants (dioicous). The sporophyte generation consists of a small, darkened capsule on a short, thin, leafless seta embedded in the apex of the hyaline gametophyte stalk (Figure 4.1). Inside the capsule are spores that are ejected when the capsule dries out. Each spore can germinate and produce a new haploid gametophyte. Many species do not reproduce sexually as often as others, so propagation is mostly vegetative. Spreading can occur by branching or by fragments budding into new plants. In some species, the fragments are able to remain dry for long periods of time and still grow when water becomes available, while in others, fragments will not grow after being dry for only a week (*S. capillifolium*) (McQueen 1990).

FIGURE 4.1 *Sphagnum* Sporophyte growing on gametophyte plant (Crum 1984).

Sphagnum mosses differ from other mosses in many ways. One important diagnostic feature is the organization of the branches on the plant. Branches are arranged in clumps called fascicles that consist of two or more spreading branches and one or more pendent branches (Figure 4.2). The number of pendent and spreading branches are used in species identification. *Sphagnum* grows apically (from the top). The young branches are usually packed into the top of the plant in a feature called a capitulum (Figure 4.3), the shape of which can be used for species identification (Sastad and Flatberg 1994). Most

FIGURE 4.2 *Sphagnum* branched fascicles (McQueen 1990).

Sphagnum mosses are anisophyllous, meaning they have two kinds of leaves-- those found on the branches and those found on the main stem (Figure 4.4). The two kinds of leaves are most easily differentiated under ideal growing conditions. Less-than-ideal conditions (such as insufficient moisture) can result in less differentiation between the branch and stem leaves (hemi-isophyllous). Plants that grow under conditions of fluctuating water levels can have branch and stem leaves that are undifferentiated (isophyllous). Since stem and branch leaves are most often used for species identification, the stem leaves of two different species that are in an isophyllous form can be nearly identical, so species identification can be difficult to impossible in specimens from less-than-ideal moisture and mineral regimes (Sastad and Flatberg 1994) (Figure 4.4).

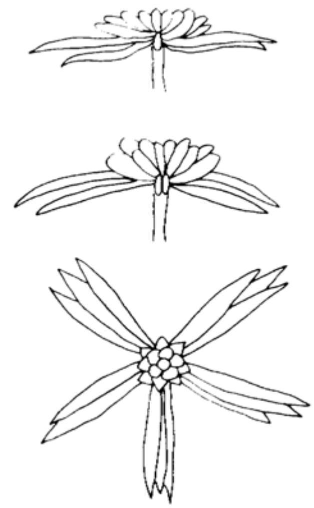

FIGURE 4.3 *Sphagnum* capitulum types (McQueen 1990).

|-L- ***S. girgensohnii***-R-| |-L- ***S.obtusum***--R-| |--L---***S.teres***----R----|

FIGURE 4.4 Branch (L) and stem leaves(R) of three species: *S. girgensohnii, S.obtusum* (not from Washington), and *S.teres*.

McQueen (1990) found that habitat characteristics could affect the timing of sporophyte production. He noted that more mineral-rich peatlands (medium and rich fens) had species that produce sporophytes in the early part of the summer in full sun near water (S. magellanicum, S. teres, S. majus, and S. fimbriatum). Species common to more mineral-poor , drier peatlands produce sporophytes in July (S. fuscum, S. capillifolium, and S. angustifolium). Species common to shady sites produce sporophytes in late August (S. russowii, S. girgensohnii, S. subtile, and S. centrale).

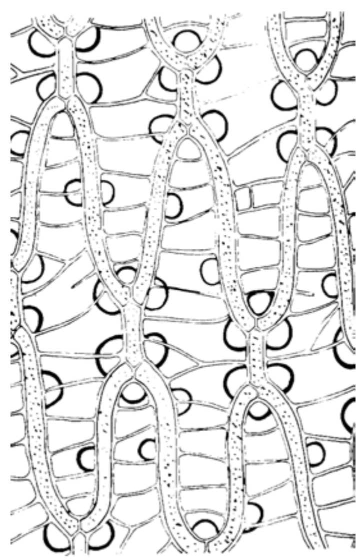

FIGURE 4.5 Typical leaf cell arrangement, hyaline and green cells.

The main stem of the *Sphagnum* plant is composed of a central region surrounded by one to five layers of hyaline cells, or may lack a differentiated cortex (Figure 4.5). The leaves are arranged with the large, dead, hollow hyaline cells interspersed with smaller live photosynthetic or green cells. The morphology of *Sphagnum* hyaline cells enables them to retain large amounts of water. They die at maturity, and in many species are thickened with annular-helical ridges (spiral fibrils) and are frequently perforated by pores with edges that may be thickened. These hollow spherical cells hold water like a vase. Some species of *Sphagnum* have been shown to hold 16 to 26 times their dry weight in water. Water will wick up both the stem and pendent branches, filling each hyaline cell and then wicking up the cell wall of the next hyaline cell and spilling into and filling it (McQueen 1990). In this way, *Sphagnum* wicks and stores water and remains moist even feet above the water table.

Species that grow in wetter habitats have weaker stems and are generally limp, with fascicles spaced widely along the stem as shown in Figure 4.3. Species of drier habitats have more rigid stems, with fascicles closer together along the stem. Species growing above the water table are often brighter pigmented (not all green). The branch arrangement and density is dependent on the water table throughout the year, and summer conditions may not be an indicator of yearly conditions. *Sphagnum* species as a group are considered “xerophytic hydrophytes” (Andrus 1986), in that they are water-loving plants with adaptations for dealing with periodic drought conditions.

Sphagnum can acidify an area by exchanging hydrogen ions for base cations (K^+, Na^+, Ca^{++}, Mg^{++}). *Sphagnum* plants use cation exchange to obtain macro and micro nutrients that are often in low concentrations in permanently inundated habitats. The low mineral nutrient and acidic environment that results is not tolerated by many vascular plants, so there is very little competition for resources.

Cation exchange is accomplished in *Sphagnum* cell walls by uronic acid (Clymo and Hayward 1982). The primary hydroxyl group on this acid is oxidized to a weak carboxyl group in which the carboxyl hydrogen is weakly held and therefore available for exchange. Hydrogen ions are released and base cations (K^+, Na^+, Ca^{++}, Mg^{++}) are adsorbed into the carboxyl site of uronic acid (Gorham 1967). Species found on top of hummocks (*S. fuscum,* [Bellamy and Riley 1967]; *S. magellanicum* and *S. fimbriatum,* [Andrus 1986]) have a higher uronic acid content than species that grow near the water level *(S. cuspidatum*). In general, the pH in drier habitats is lower (more acidic) than in wetter ones. The pH may increase (become less acidic) in a *Sphagnum* peatland during the winter when precipitation increases (see Chapter 3, Section 3.3).

An acidic, cold, constantly saturated, and mineral-poor environment impedes decomposition of the older portions of the *Sphagnum* plant below the growing apical tip. Growth and reproduction of bacteria and fungi that normally mediate decomposition are limited or prevented under these acidic, saturated, cold, and low-oxygen conditions. An additional microbial inhibitor, called sphagnol, is produced by most *Sphagnum* species (Clymo and Hayward 1982). The lack of decomposition results in the accumulation of peat. The rate of accumulation varies considerably with water chemistry, pH, *Sphagnum* species, and moisture regime (wet vs. dry). In western Washington, *Sphagnum* peat accumulates at an average rate of approximately 2.5 cm (1 inch) in 40 years (Rigg 1958). The oldest deposits in western Washington date to the last glaciation and are therefore about 10,000 years old (see Chapter 2).

Sphagnum has been used over the centuries for its antiseptic and absorptive properties. It has been used for dressing wounds, as packing material, for lamp wicks, and as an amendment for increasing the water-holding capacity and acidity of soil.

4.2 *Sphagnum* Taxonomy

Sphagnum mosses belong to one of two genera in the family *Sphagnaceae*, class *Sphagnopsida*, Division *Bryophyta*. There are approximately 100 species found in North America, with 27 species reported for western Washington (Crum, 1984). Thirteen species found (to date) in King County (Cooke 1997). Taxonomy used will follow McQueen and Andrus (in press).

The genus *Sphagnum* has been divided into ten Sections based on cortical cell anatomy, hyaline cell anatomy, number of branches per fascicle, branch color, branch leaf shape, position of green cells, the presence of fibrils, and habitat preference. The Sections and their associated North American species are listed in Table 4.1, with Washington species in bold.

Six of the ten sections of the genus *Sphagnum* are represented in Washington State. There are six species in the Section *Sphagnum* (*S. magellanicum, S. centrale, S. henryense, S. palustre, S.papillosum,* and *S. alaskense*). These species have many characteristics in common; their cortical cells are reinforced with fibrils, and they have broad branch leaves that are blunted and concave, and have toothed backs. There is only one species in the Section *Rigida* (*S. compactum)*. Species in this section have uniform cortical cells that have a single pore at the upper end, very small stem leaves, and broadly truncate branch leaves with toothed margins. There are two species in the Section *Subsecunda* (*S. subsecundum* and *S. contortum*). These species have branches with five or fewer fascicles and a small curved-branch capitulum. They are orange-yellow with a tinge of green, and have branch leaves arranged to one side. The branch leaves have hyaline cells that are arranged in bead-like rows along a seam down each hyaline cell for the length of the leaf. The ten species of the Section *Acutifolia* (*S. fimbriatum, S. girgensohnii, S. warnstorfii, S. russowii, S. fuscum, S. rubellum, S. bartlettianum, S. capillifolium, S. subnitens* and *S. rubiginosum)* have five or fewer fascicle branches and have triangular or trapezoidal green (photosynthetic) cells in the branch leaves. The six species in the Section *Cuspidata* (*S. lindbergii, S. riparium, S. annulatum, S. mendocinum, S. pacificum, S. angustifolium)* are green or brown, have elongate and tapered branch leaves, and have the green cells exposed on the inner (ventral) surface of the leaf. These species are usually found in wet depressions or are aquatic, and have stem

TABLE 4.1 *Sphagnum* Sections and representative species (Species found in Washington State in bold). Nomenclature mostly after; McQueen and Andrus (in press); Crum 1988 and Crosby and McGill, 1995, 1997. Nomenclature differences in parentheses.

Section	Representative species
Sphagnum	***S. magellanicum***, *S. perichaetiale*, ***S. centrale****, *S. portoricense*, ***S. henryense***, ***S. palustre***, *S. imbricatum*, *S. austinii*, ***S.papillosum*, *S. alaskense*****
Rigida	***S. compactum***, *S. strictum*
Isocladus	*S. macrophyllum*
Hemitheca,	*S. pylaesii*
Polyclada	*S. wulfianum*
Subsecunda,	*S. crispum*, *S. cyclophyllum*, ***S. subsecundum***, *S. orientale*, ***S. contortum****
Acutifolia	***S. fimbriatum*, *S. girgensohnii***, *S. molle*, *S. angermanicum*, ***S. warnstorfii***, ***S. russowii***, ***S. fuscum*, *S. rubellum* = (*S. capillifolium* var. *tenellum*)**, *S. quinquefarium*, *S. capillifolium* var. *tenerum*, *S. schofieldii*, *S. wilfii*, ***S. bartlettianum*, *S. capillifolium* = (*S. nemoreum*)**, ***S. capillaceum***, *S. junghuhnianum* var. *pseudomolle*, *S. flavicomans*, ***S. subnitens***, *S. subfulvum*, ***S. rubiginosum*****
Insulosa	*S. aongstroemii*
Cuspidata	***S. lindbergii*****, ***S. riparium****, *S. lenense*, *S. fitzgeraldii*, *S. tenellum*, *S. splendens*, *S. cuspidatum*, *S. cuspidatum* var. *serrulatum*, *S. torreyanum*, *S. majus*, *S. annulatum* var. *porosum*, ***S. annulatum****, *S. balticum*, ***S. mendocinum***, *S. obtusum*, *S. recurvum* ***S. pacificum***, *S. pulchrum*, ***S. angustifolium***
Squarrosa	***S. squarrosum***, ***S. teres***

*Species found in northeastern corner of Washington.
** Species found only on Cape Alava, Olympic National Park

leaves that are modified (resorbed hyaline cells in outer walls), occasionally to the extent that the leaf becoming split. The branch leaves are often undulate when dry. The final Section, Squarrosa, has two representative species in Washington (*S. squarrosum* and *S. teres)*. These species have branch leaves that are not undulate when dry. They are instead squarrose (leaves with the upper portion bent back at right angles to the stem). Appendix C lists all the *Sphagnum* specimens from Washington State found in the University of Washington herbarium. One of these species (*S. austinii*) is not identified by McQueen and Andrus (in press) as occurring in Washington State. No notation of verification is present on the herbarium specimens, but Crum (1984) indicates it is known from the Olympic Peninsula.

Many species of *Sphagnum* found in Washington State are similar in appearance in their macro-characteristics. These similarities are accentuated under conditions of growth that are less than ideal. A study completed in 1997 identified peatland habitats in King County dominated by *Sphagnum* and associated species (Cooke 1997). When specimens of *Sphagnum* were collected during the fall, pH was measured and observations recorded on sun/shade regime, the location the specimens in the mat (e.g. hummock top, side, or bottom, or depression), and associated species. A verified species list is given in Table 4.2.

TABLE 4.2 Verified *Sphagnum* species, some Northwest localities*

Wetland	**Species present**
BBC 45/King County, WA	S. mendocinum S. palustre
Devil's Lake Bog/Jefferson County, WA	S. angustifolium S. palustre S. capillifollium S. fuscum S. mendocinium S. squarrosum
JC66 Shadow Lake Bog/King County, WA	S. capillifolium
LCR 14/King County, WA	S. pacificum
Little Lake/Snohomish County, WA	S. warnstorfii S. papillosum
Sleeper Bog/Whidbey Island, WA	S. pacificum

* Verified by Dr. Dale Vitt, University of Southern Illinois, June 2000

4.3 *Sphagnum* Ecology

Sphagnum moss occurs in a variety of habitats, nearly all moist, from the tropics to the arctic. In North America, it is found circumboreally from temperate areas of the American Midwest to the subarctic taiga in Alaska and Canada (McQueen 1990). Most *Sphagnum* species sequester mineral nutrients very efficiently and are therefore able to tolerate constantly inundated, mineral-poor situation. This is why they often dominate peatlands, although they can also tolerate circumneutral to alkaline environments (Crum 1988; McQueen 1990). There are generalist species that can live in many different types of peatlands under many different climatic regimes, but many species of *Sphagnum* have distinct requirements for tolerance to drought (degree of wetness), mineral nutrient availability, and sun or shade tolerance. Fast-growing species that are able to utilize mineral nutrients and grow quickly include *S. fimbriatum* and *S. fallax (which grows outside of Washington)*, which can grow a foot a year under ideal conditions (McQueen 1990).

Three different types of *Sphagnum*-dominated peatlands are found in Washington State: raised, flat and blanket bogs or peatlands. Raised bogs are characterized by a raised central area that is higher than the wetland margins. Species typical of these habitats in Washington are *S. fuscum, S. capillifolium, S. magellanicum,* and *S. rubellum*. Flat peatlands are those where the *Sphagnum* fills in a depression without creating a raised surface. A third type, blanket bogs, form under very humid conditions. They follow the local topography, and the *Sphagnum* creeps over the surface. These are typical of the Olympic Peninsula, but are rare elsewhere in the US (Crum, 1998). Species common in blanket bogs are S*. compactum, S. angustifolium*, *S. pacificum, S. palustre, S. squarrosum* and *S. teres*.

Peatlands which are in part groundwater-fed are more common in the western Washington landscape than strictly rainwater-fed peatlands. These groundwater-fed peatlands, called fens in some classification schemes[1], can vary from acidic to basic. The more acidic of these peatlands can have a flora and pH (4 to 5) similar to peatlands that are strictly rainwater fed, but generally tend to be wetter. Species such as *S. angustifolium, S. papillosum* and *S. magellanicum* are common. Less acidic peatlands (pH 5 to 6.5) have *Sphagnum* species that are more mineral-tolerant, including, *S. teres, S. squarrosum, S. finbriatum, S. warnstorfii,* and *S. subsecundum*. Non-acidic peatlands are not dominated by *Sphagnum*, but will often have some *Sphagnum* species which tolerate high mineral levels and higher pH (6 to 8). *Sphagnum* species found in circumneutral peatlands include: *S. centrale, S. subsecundum, S. teres, S. squarrosum, S. fimbriatum*, and in eastern Washington, *S. contortum*. In addition to these three peatland forms, some forested wetlands will also have *Sphagnum* species present. Among these in Washington are *S. mendocinum, S. rubginosum, S. russowii,* and *S. squarrosum*.

Sphagnum-dominated peatlands in King County are "flat bogs," where the mat is of uniform elevation across the peatland, or "hummock bogs," where distinct mounds of *Sphagnum* are scattered across the *Sphagnum* mat (Cooke, 1997). Some coastal peatlands contain species that are not found in any other location in the state. Andrus (Personal Communication, 2000) has found *S. lindbergii, S. alaskense,* and *S. rubiginosum* at Cape Alava in the Olympic Peninsula. The northeastern corner of the state has three species that are found nowhere else in the Washington (*S. centrale, S. annulatum*, and *S. contortum*). A few *Sphagnum* species do not grow in wetlands but are found in forested woodlands. These include *S. rubiginosum, S. compactum,* and *S. girgensohnii.*

Sphagnum takes up mineral nutrients (e.g. Ca, Mg, Na, etc.) from water and uses them to lay down new tissue and grow. The tissue may hold these minerals even when it dies, so *Sphagnum* peat systems are often sinks for minerals as long as the plant tissue remains wet and does not decompose. Locking up minerals imposes a drain on throughout the entire peat system, a condition that limits other plant growth. The update of minerals and the rate of peat formation varies by species of *Sphagnum* (Moore and Bellamy, 1974).

Primary production in *Sphagnum* peatlands is low compared to most other wetland ecosystems because of the constant inundation and associated mineral-deficient conditions (Mitsch and Gosselink 1998). Typical *Sphagnum* production varies between 50 g/m^2/year to 500 g/m^2/year (data from England, Vitt 1994, Clymo 1970*)*. *Sphagnum* peat accumulation occurs as the plant grows at the tip. A conservative

[1] Editior's note: Many investigators have argued that the source of water to peatlands is not a robust basis to distinguish peatland types and prefer a classification system that looks at multiple characters to differentiate peatlands along the bog to fen gradient. See Chapter 1 for a discussion of peatland classification and the bog to fen gradient.

linear growth rate that takes into account the fastest and slowest species in Minnesota is in the range of 3.9 to 13.1 cm / year (Grigal 1985).

Decomposition rates in *Sphagnum* peatlands are low because of constant waterlogging and low pH. The top aerobic layers of *Sphagnum* mats (acrotelm) have higher associated rates of decomposition because they are aerated. Low pH and constant waterlogging cause a change in the peat microflora. This is seen as a decrease in the total number of bacteria, an absence of nitrogen-fixing and nitrifying bacteria, and a higher percentage of fungi than bacteria (Latter, Cragg and Heal, 1967; Crum 1988). (Data presented in Chapter 3, however, also show a decline in yeast fungi in *Sphagnum*-dominated peatlands.) There is also a difference in decomposition rates between *Sphagnum* species. Clymo (1965) found that *Sphagnum papillosum* decomposes at approximately half the rate of *S. cuspidatum*.

4.4 Ecological Preferences of *Sphagnum* Species

Although there are a few generalist species (species that tolerate a range of environmental conditions), most *Sphagnum* species show distinct preferences according to the following environmental attributes: light regime (open sun, partial shade, full shade), wet-to-dry gradients that are manifested by their location in the mat (in depressions, on hummocks, or in level areas of equal saturation, along moat margins), and mineral gradients (low, medium, high). Every combination of these environmental attributes is found in the *Sphagnum* peatlands of Washington State. Table 4.3 lists the range of preferences for light, moisture, mineral s, and pH, based on our preliminary work in King County and from information in the literature (Crum 1984; Andrus 1986; Crum 1988; Vitt, Marsh, and Bovey 1988; Klinka et al. 1989; McQueen 1990). It is obvious that species overlap in their ecological tolerances to these attributes. Additional local data and a study of the overlapping environmental tolerance, as was done for Minnesota peatlands by Vitt and Slack (1994), will be needed before a final preference table can be generated for Washington species.

TABLE 4.3 Washington state *Sphagnum* species and their literature-reported ecological preferences*

Species	Light	Mineral	pH[1,2]	Water	Color[3]
S. alaskense **(C.A.)**	Full sun	Poor to Medium	3.6-6.1	Hummocks	Peach
S. angustifolium	Full sun, part shade	Poor to Medium	3.6-6.1	Dense lawn to small hummocks, dry	Pale green to yellow-brown w/red or pink in the stem
S. annulatum **(EW)**	Full sun	Medium	3.8-6.2	Wet to aquatic	Brownish
S. barlettianum	Full sun, part shade	Medium	4.0-6.0	Moist sand, as mat	Red
S. capillifolium	Partial shade	Poor	3.5-4.5	Low to mid-hummock, wet	Deep red
S. centrale **(EW)**	Shade	Medium to High	3.9-7.8	Level carpets, wet	Lt. To bright green

Species	Light	Mineral	pH[1,2]	Water	Color[3]
S. compactum	Full sun	Poor to Medium	3.5-4.5	Wet sand, as compact cushion	Lt. yellow to yellow/green, occ. pink
***S. contortum* (EW)**	Full sun	High	5.9-7.8	Level, dry, loose carpets	Pale green to brownish-white
S. fimbriatum	Full sun, part shade	Medium to High	3.4-7.0	Level to loose mounds, wet	Pale green gray-green, pale yellow
S. fuscum	Full sun	Poor	3.7-5.1	Level or dry compact hummock top	Brown to reddish rusty brown
S. girgensohnii	Shade	Generalist	3.9-6.0	Level loose carpets, wet	Bright green
S. henryense	Full sun, part shade	Medium	3.8-5.9	Moist cushions to loose carpets	Green to brownish - tinged
***S. lindbergii* (C.A.)**	Full sun	Low to Medium	4.0-6.0	Thick carpets, wet	Pale green to orange
S. magellanicum	Full sun	Poor to Medium	3.5-6.2	level -moist, or hummock side	Deep red to purple, sun green w/ pink-shade
S. mendocinum	Full sun	Medium to High	4.5-7.0	Wet depressions, aquatic	Yellow-green to brown
S. pacificum	Generalist	Medium	3.5-6.1	Loose dense carpets, wet	Pale Green w/ tint of light brown
S. palustre	Generalist	Poor to Medium	3.4-6.8	Moist to dry	Green to yellow/green
S. papillosum	Full sun	Poor to Medium	4.0-6.0	Lawn former. Moist to Very wet	Green or golden-brown to lt. orange-brown
S. riparium	Full sun	Medium	3.8-6.8	Moist, loose carpets	Pale to dark green
S. rubellum	Full sun	Poor	3.5-5.5	Dense lawn, depressoins	Red to green w/ red speckles
***S. rubiginosum* (C.A.)**	Shade	Medium	No data	Carpet, dry	Reddish brown to green
S. russowii	Sun to shade	Generalist	3.8-6.1	Small hummock to lose carpets	Green to red
S. squarrosum	Sun to shade	Medium to High	4.6-7.3	Level, moist to dry, loose carpets	Pale to bright green
S. subnitens	Full sun, part shade	Poor to Medium	4.5-7.0	Carpets, moist	Red to purplish
***S. subsecundum* (sensu stricto)**	Full sun	Medium to High	4.8-6.1	Loose carpet, wet	Green, yellow, orange, dk brown
S. teres	Full sun, part shade	Medium to High	4.6-7.5	Small cushions, to loose carpets, wet	Yellow to pale green
S. warnstorfii	Sun to shade	Medium to High	4.5-7.5	Hummock side or top; loose carpet, wet	Dark reddish-purple – sun, dk. green shade

*Nomenclature after McQueen abnd Andrus (in press). **EW** = Northeastern Washington Species **CA=** Cape Alava, Olympic area species
1 Data from Cooke, 1997
2 Data from Andrus, 1986, Vitt 1994, Vitt 1995, Crum 1984, Crum 1988
3 Colors vary in the literature by author and region. These colors are the range that is reported across North America and not necessarily indicative of western Washington.

Based on the species found and knowledge of their preferences, it is possible to estimate the mineral and pH status of an individual bog without directly measuring these characteristics. Conversely, it is possible to guess the species present in a particular habitat when light, moisture, mineral, and pH conditions are known (McQueen 1990). Vitt et al. (1995) found a correlation between species richness and mineral availability. They found that *Sphagnum*-dominated peatlands will have increased species richness as the pH increases (becomes less acidic) and the number of microhabitats increases.

Sphagnum species are distributed along environmental gradients of pH, cation (mineral) concentration, hummock and hollow (microhabitat) topography, wet versus dry, and shade versus sun regime (Glaser and Wheeler 1980, Andrus 1986). A species shift will occur when conditions in the peat mat become more or less acid than a particular moss species can tolerate.

Generalist species

Many species of *Sphagnum* are found across a range of conditions of light, moisture, and minerals (Andrus 1986, Crum 1988). In Washington these include *S. angustifolium, S. capillifolium, S. fimbriatum, S. henryense, S. pacificum, S. palustre,* and *S. squarrosum, S. subnitens and S. teres* (Andrus 1986). Some species are flexible in their tolerances for some habitat characteristics (mineral concentration, moisture, pH, or light) but may be restricted in their tolerance to other habitat characteristics (Vitt and Slack 1984).

Light regime preferences

Both shade- and sun-tolerant species are found in Washington State. Shade-tolerant species include *S. girgensohnii, S. russowii, S. teres,* and *S. warnstorfii*. Partial shade (open woodland) species include *S. fuscum, S. magellanicum, S. fimbriatum, S. angustifolium, S. centrale, and S. capillifolium*. Shade intolerant (full sun) species include *S. papillosum, S. centrale, S. contortum, S. fuscum,* and *S. rubellum* (Klinka et al. 1989, Vitt and Slack 1984, Vitt et al. 1989).

4.5 Growth Habits of *Sphagnum* Species

Growth habits (forms) vary in *Sphagnum* species along topographic and wet-to-dry gradients. *Sphagnum* can be found growing as carpets (surrounding the margins of pools or emergent mats) with emergent bryophyte cover, lawns (growing on mud) with firmer, more exposed vegetation, and hummocks rising to 1 m above the water level (Vitt et al. 1989).

Species found on more level terrain include carpets (habitats near pond edges and moats around bogs) and lawns (level areas on mineral soil): at water level-- *S. contortum;* 10 to 20 cm above water level-- *S. papillosum, S. rubellum, S. angustifolium, S. teres, and S. warnstorfii*; *S. compactum, S. barlettianum, S. centrale, S. girgensohnii, S. henryense, S. pacificum, S. squarrosum S. subnitens, S. subsecundum (sensu stricto),* and on the coast, *S. lindbergii, S. alaskense, and S.rubiginosum* (Andrus 1986, Glaser 1987, Crum 1988, Vitt et al. 1989, and Andrus, personal communication).
The hummock-hollow pattern commonly found in bogs results from the growth of individual species located at particular elevations above the water level. Certain species are able to recover from drying out

better than others. These species are usually found on the tops of hummocks, apparently farther from the water source. Proximity to the water source, however, does not necessarily correspond with actual water availability. Hollows (the depressions in a bog mat) can actually be more drought-prone than hummocks. Although they are probably the wettest portions of bogs for most of the year, rainfall deficits during the summer can cause species growing in the hollows to dry out (Andrus 1986). The structure of the underlying peat allows species on hummock tops to be wetter during times of drought than species in the hollows. This is because the stems of the hummock species often stretch 20 to 30 cm below the hummock surface, allowing for hydraulic conductivity from the water source below. In contrast, the environment in the hollows is more oxygenated and there is more decomposition. The stems of the hollow species therefore decay below the surface and do not maintain a connection with the living tissue of the plant. When the water level drops below the hollow elevation, the live stems dry out completely (Wagner and Titus, 1984).

Species found on low hummocks (10-20 cm above water level) in Washington State include *S. centrale, S. fimbriatum,* and occasionally *S. angustifolium* (Cooke 1997, Andrus 1986). Higher hummocks (50 or greater cm in height) include *S. fuscum, S. capillifolium, S. magellanicum*, *S. papillosum, S. rubellum,* and some *S. angustifolium* (Vitt and Slack 1984). Table 4.4 summarizes information from the literature on the habitat preferences for Sphagnum species for many parts of the U.S.

Table 4.4 *Sphagnum* species commonly associated in particular habitats (information after Vitt 1995, Crum 1988, 1990; Slack et al. 1980, Andrus 1986, McQueen 1984,).

Habitat Preference	Species
Closed canopy forests	*S. compactum, S. girgensohnii, S. rubiginosum*
High hummock, dry	*S. fuscum, S. capillifolium*, *S. warnstorfii, S. papillosum, S. austinii*
Mid to low hummock, open habitats	*S. magellanicum , S. warnstorfii, S. russowii*
Hollows of hummocky terrain, slightly submerged not more than 5cm above water	*S. pacificum*
Mineral-rich fens, full sun	*S. fuscum, S. warnstorfii, S. contortum, S. teres, S. centrale, S. riparium, S. mendocimium, S. subsecuundum,*
Lawn	*S. angustifolium, S. rubellum, S papillosum, S. teres*
Loose carpets, shaded woodland	*S. girgensohnii, S. russowii, S. centrale, capillifolium, S. rubiginosum* *S. squarrosum, S. warnstorfii, S. pacificum*

4.6 Responses to Environmental Stresses

Sphagnum moss plants have no roots and therefore depend on the water they are growing in for moisture and minerals. This dependence on the immediate environment makes for a plant that is susceptible to changes in the immediate area. Most *Sphagnum* species have specific requirements for light, mineral nutrients, pH, and water regime. Fluctuations in water levels, water chemistry (cation concentrations, pH), light regime, or physical disturbance can, therefore, have a profound influence on a *Sphagnum* plant. Human disturbances such as ditching, draining, flooding, grading, and logging, which are common in *Sphagnum*-dominated peatlands, may have big effects on their ecology.

Acid rain has been implicated as causing the loss of *Sphagnum* species in Great Britain, but this has not been found to apply in the United States. Austin and Wieder (1987) found that unless the acid rain lowered pH levels in wetlands to 3 or less, no inhibition of growth was observed in *S. fallax, S. henryense,* and *S. pulchrum*. No change was observed in *Sphagnum* growth as a result of elevated levels of OH^-, $SO_4^=$, NO_3^-, and NH_4^-. Rochefort et al. (1990) found the opposite trend in peatlands in Ontario. He found that additions of N resulted in immediate uptake and growth response until too much N uptake resulted in slowed growth and eventual death.

Some species are very sensitive to changes in pH and cation concentrations. These species are adapted to mineral -poor conditions (bogs and poor fens) that experience mineral-rich water inputs (through re-channeling surface drainage). They include, *S. angustifolium, S. capillaceum, S. compactum, S. palustre, S. papillosum, S.rubellum*, and *S. subnitens*. These species will often display rapid dieback when exposed to mineral -rich waters. In situations where the mineral concentrations rise slowly, one can observe a shift from species adapted to low mineral levels to species (usually fast-growing) that tolerate mineral-rich environments (Clymo and Hayward 1982, Crum 1988, McQueen 1990).

Physical disturbance, including trampling and grading, has an immediate effect on all *Sphagnum* mosses. Some *Sphagnum* species (e.g. *S. fallax* found elsewhere in the United States) are able to regenerate easily from fragments (Crum 1988). No work has been done on the regenerative characteristics of local *Sphagnum* species. Observations of disturbed *Sphagnum*-dominated peatlands (Cooke 1997) show that most *Sphagnum* in King County do not tolerate physical disturbance and in most cases, disturbed portions of peatlands no longer contain *Sphagnum*.

Changes in water elevations produces perhaps the strongest shifts in *Sphagnum* species. When inundated, hummock species may be replaced by loose wet carpet species. Species that are carpet formers will be replaced by lawn species if the peatland becomes drier.

4.7 Chapter Four References

Anderson, L.E. 1990. A checklist of *Sphagnum* in North America north of Mexico. The Bryologist 93: 500-501.

Anderson, L.E., Crum, H.E., and Buckem W.R. 1990. List of mosses of North America north of Mexico. The Bryologist 93: 448-399.

Andrus, R.E. 1986. Some aspects of *Sphagnum* Ecology. Can. J. Bot. 64: 416-426

Andrus, R.E. 2000. Personal conversation, November 2000.

Austin, K.A., and Wieder, R.K. 1987. Effects of elevated H+, SO_4 2-, NO3-, and NH4+ in simulated acid precipitation on the growth and chlorophyll content of 3 north American *Sphagnum* species. The Bryologist, 90(3) 221-229.

Bellamy D.J. and and Riley, J. 1967. Some ecological statistics of a “miniature” bog. Oikos 18: 33-40.

Cooke Scientific Services, Inc. 1997. King County Bog Inventory, Water & Land Resources Division, 1997. Updated 1999.

Clymo, R.S., 1965. Experiments on the breakdown of *Sphagnum* in two bogs. J Ecol. 53, 747.

Clymo, R.S., 1970. The growth of *Sphagnum*, methods of measurement. J Ecol. 58, 13.

Clymo, R.S. and Hayward, P.M. 1982. The ecology of sphagnum. Pages 229-289 in A.J.E. Smith (ed Bryophyte Ecology. Chapman and Hall, London.

Crum, Howard. 1984 North American Flora: Sphagnopsida, Sphagnaceae. New York Botnaical Gardens, Bronx, NY.

Crum, Howard., 1988. A Focus on Peatlands and Peat Mosses. The University of Michigan Press, Ann Arbor, Michigan.

Crosby, M. R. and Magill, R. E. 1995. Monographs in Systematic Botany from the Missouri Botanical garden, Volume 62: Index of Mosses 90 to 93. Missouri Botanical Garden, St. Louis.

Crosby, M. R. and Magill, R. E. 1997. Monographs in Systematic Botany from the Missouri Botanical garden, Volume 62: Index of Mosses 93 to 95. Missouri Botanical Garden, St. Louis.

Glaser, P.., and Weeler, G.A. 1980. The development of surface patterns in Med lake peatland, northern Minnesota. Proceedings of the Sixth International Peat Congress, Duluth, MN. Aug 17-23. Pp 31-45.

Glaser, P.H. 1987. The ecology of patterned boreal peatlands of northern Minnesota, a community profile. USDI isw and Wildlife Service, Washington D.C.. Biological Report 85

Glaser, P.H., Janssend, J.A., and Siegel, D.I. 1990. The response of vegetation to chemical and hydrological gradients in the lost river peatland, Northern Minnesota. Journal of Ecol. 78: 1021-1048.

Gorham, Eville, 1967. Some chemical aspects of wetland ecology. Annual Muskeg research Conference Proceedings 12: 20-38.

Grigal, D.F. 1985. *Sphagnum* production in forested bogs of northern Minnesota. Can. J. Bot. 63: 1204-1207.

Klinka,, K., Krajina, V.J., Ceska, A., and A.M. Scagel. 1989. Indicator Plants of Coastal British Columbia. University of British Columbia Press, Vancouver, B.C.

Larsen, J.A., 1982 Ecology of the Northern Lowland Bogs and Conifer Forests. Academic Press.

Latter, P.M., Cragg, J.B., and Heal, O.W. 1967. Comparative studies on the microbiology of four moorland soils in the North Pennies. J. Ecol: 55, 445.

McQueen, Cyrus. 1990. Field Guide to the peat Mosses of Boreal North America. University Press of New England. Hanover NH.

Mitsch, W.J. and Gosselink, J.G. 1998. Wetlands, 3rd edition. Van Nostrand Reinhoold, New York.

Rigg, 1958. Peat Resources of Washington. Washington State Division of Mines and Geology. Bulletin No. 44. Olympia, WA.

Rochefort, L, Vitt, D.H., ad Bayley, S.E. 1990. Growth, productoin and desomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. Ecology, 71, 1986-2000.

Sastad, S. M. and Flatberg, K.I. 1994. Leaf size and shape in the *Sphagnum recurvum* complex: taxonomic significance and habiat variation. Journal of Bryology 18:261-275.

Schofield, W. B. 1969. Some Common Mosses of British Columbia. British Columbia Provincial Museum Department of Recreation and Conservation. Vancouver, B.C.

Slack, N.G., Vitt,D.H., and Hroton, D.G. 1980 veetation gradients of minrotrophically rich fens in western Alberta. (Can. J. Bot.58:330-350.

Vitt, D.H., Achuff, P., and Andrus, R.E. 1975. The vertical zonation of *Sphagnum* species in hummock-hollow complexes in northern Michigan. Mich. Bot. 14:190-200.

Vitt, D.H. an Slack, N.G. 1984. Niche diversificaiton of *Sphagnum* relative to environmental factors in northern Minesota peatlands. Can. J. Bot. 62:1409-1430.

Vitt, D.H., Horton, D.G., Slack, N.G., and Malmer,N. 1989. *Sphagnum*-dominated peatlands of the hyperoceanic British Columbia coast: patterns in surface chemistry and vegetation.

Vitt, D.H. 1994. An overview of factors that influence the development of Canadian peatlands. Memoirs of the Entomological Society of Canada. 169: 7-20.

Vitt, D.H., Yuhung, L, and Belland, R.J. 1995. Patterns of bryophyte diversity in peatlands of continental western Canada. The bryologist 98(2) 218-227.

Wagner, D.J. and Titus, J.E.. 1984. Comparative desiccation tolerance of two *Sphagnum* mosses. Oecologia, 62: 182-187.