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## Patterns of *Picea mariana* (Black Spruce) growth and raised bog development in Victory Basin, Vermont<sup>1</sup>

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### ABSTRACT

BUBIER, J. L. (Botany Department, Field Naturalist Program, University of Vermont, Burlington, VT 05405). Patterns of *Picea mariana* (black spruce) growth and raised bog development in Victory Basin, Vermont. Bull. Torr. Bot. Club 118: 399-411, 1991.—In Victory Basin Bog, Vermont, a distinct zonation of *Picea mariana* (black spruce) occurs from an adjacent stream to the bog center, typifying a pattern in bogs throughout the boreal region: Height and density of *P. mariana* decrease toward the bog center, but age does not. The growth rate of *P. mariana* is greatest near the stream and declines away from it. This gradient in the heights of *P. mariana* accompanies a decrease in the mineral content of bog water toward the ombrotrophic bog center and an associated gradient in plant community composition. Raised bog development and stream incision appear responsible for the bog's elevated and sloping water table. Well data indicate that the slope and seasonal fluctuations of the water table are greater below the faster growing *P. mariana* than below the stunted *P. mariana* and open bog areas. Since a minimum of 5 m of peat underlie the entire study area, tree growth rates cannot be influenced by access to nutrients from the underlying mineral substrate. Peat stratigraphy suggests lateral bog expansion and stream migration since peatland initiation in post-glacial times. The dynamic interaction between peatland and stream processes continues to influence patterns of *P. mariana* growth and stream migration.

Key words: *Picea mariana*, black spruce, growth rates, peatland development, New England, ombrotrophic bog.

Black spruce *Picea mariana* (Mill.) B.S.P., a common species of boreal regions, typically forms distinctive bands around the margins of peatlands and between peatlands and streams. This pattern has been studied in Canada (Jeglum 1974; Damman and Dowham 1981; Lieffers 1986; Lieffers and Rothwell 1987; Foster *et al.* 1988a; Glaser and Janssens 1986), Finland (Heikurainen 1980), the Soviet Union (Ivanov and Shumkova 1972), and Minnesota, USA (Heinselman 1963, 1970), but not extensively in New England.

One such example occurs at Victory Basin Bog in northeastern Vermont (Fig. 1) where distinct

zones in the height and stem density of black spruce exist between a stream and the bog center. Speckled alder (*Alnus rugosa*) grows in a narrow band along the stream. Toward the bog, the alder is abruptly replaced by a pure stand of tall black spruce that parallels the stream meanders. A sharp transition to a band of short, dense trees grades to sparsely scattered clumps in the bog center (Fig. 2).

In sites elsewhere, tree growth in peatlands has been correlated with nutrient availability (Heinselman 1963; Jeglum 1974; Payandeh 1978; Wang, Mueller and Micko 1978), soil aeration (Jeglum 1974; Lieffers and Rothwell 1987), ground water level (Heinselman 1963), rates of water movement (Ingram, 1983; Crawford 1983); community floristic composition (Heinselman 1963, 1970; Jeglum 1975; Marek 1975), and peat composition (Watt and Heinselman 1965; Ingram 1983).

This study seeks to understand the processes that shaped the landscape at Victory Basin Bog and created conditions that govern past and present size, density, and distribution patterns of black spruce. The primary questions are: what processes are responsible for the black spruce height and density zones and furthermore do these zones change over time?

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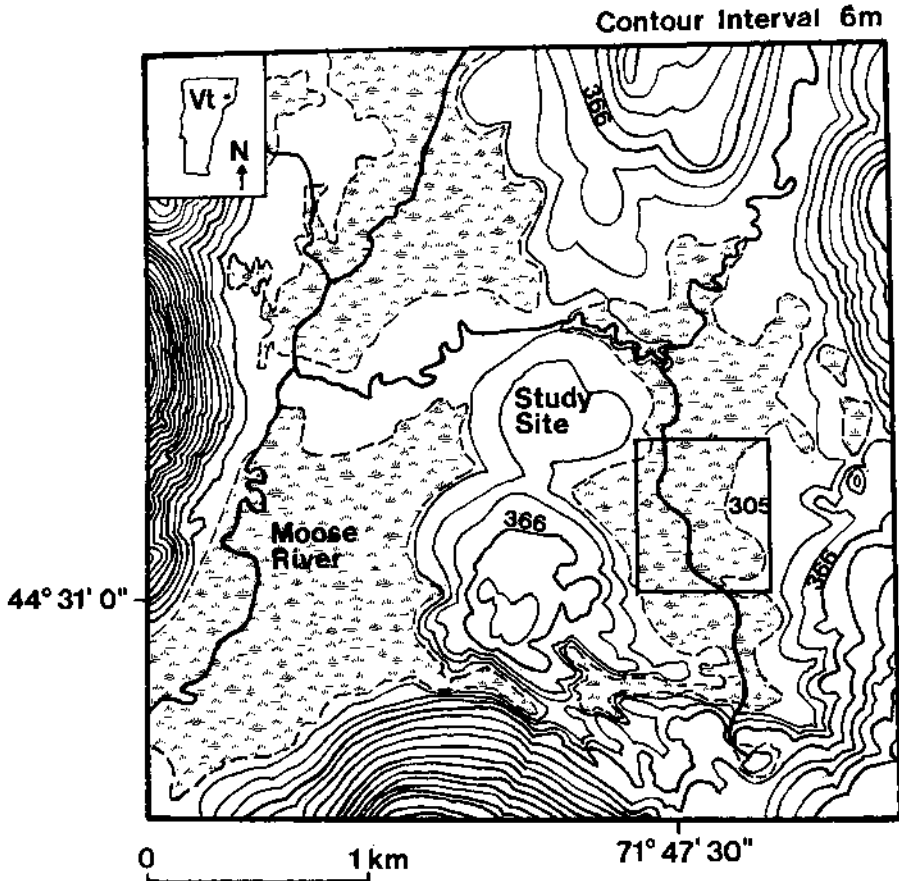


Fig. 1. Topographic map of Victory Basin, Vermont USA, with location of study site indicated.

**Study Area. GEOGRAPHY AND GEOLOGY.** Victory Basin Bog (12–14 ha; henceforth referred to as “the bog”) is an open to partially wooded peatland within the diverse wetland complex called Victory Basin (700 ha; Alexander 1983; Bubier 1989). Victory Basin is a depression within Vermont’s northeast highlands, an elevated plateau between the White Mountains of New Hampshire to the east and the Green Mountains of Vermont to the west. At an elevation of 335 m, the basin is surrounded by 600 m mountains and is underlain by a granitic pluton (Woodland 1965) which contributes to the acidic soils of the wetland communities.

During the Wisconsin glaciation, Victory Basin was covered by some 2400 m of ice. A large recessional moraine lies southwest of Victory Basin where the Moose River flows out from the basin’s large wetland complex (Stewart and MacClintock 1969). The sub-peat substrate of the bog is lacustrine silt and clay. The gently sloping to flat terrain throughout the basin, and

the narrow outlet at the southwest corner, made the topography suitable for lake formation during the period of ice retreat. It is possible then, that part or much of the basin was a glacial lake whose outlet was blocked by ice or glacial deposits. The essentially impermeable substrate provides an ideal condition for wetland formation.

**WEATHER AND CLIMATE.** Victory Basin has one of the more severe climates in the New England/Adirondack region of the northeast USA with winter temperatures as low as  $-42^{\circ}\text{C}$  and a mean annual temperature of only  $3^{\circ}\text{C}$ . Quebec City, 160 km further north, has a similar mean annual temperature. Seasonal snowfall ranges from 250–300 cm and yearly totals are as high as 380 cm (Alexander 1983). The basin’s altitude and bowl shape facilitate cold air drainage and a colder than average climate for its latitude [ $44^{\circ}$ ]. The basin is also on the southern border of a boreal climate zone that dominates most of Can-

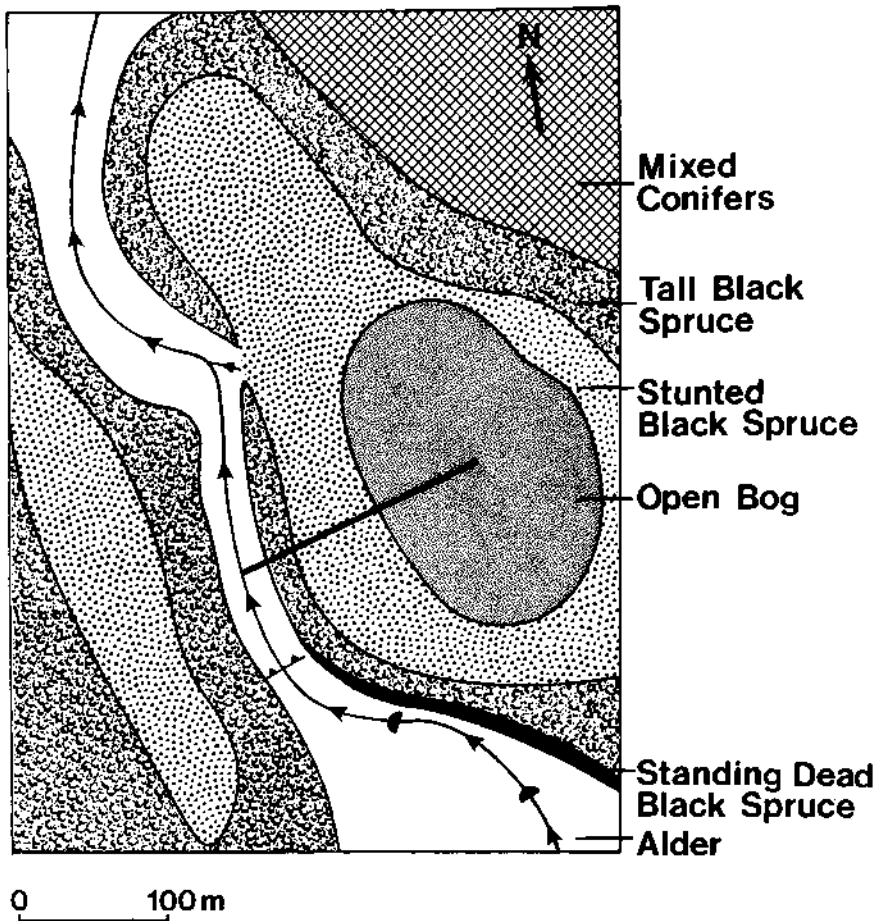


Fig. 2. Vegetation zones of Victory Basin Bog and associated peatland, 1988–1989, based on aerial photographs, ground checks, and vegetation sampling. Study site transect from stream to bog center indicated by bar, and beaver dams indicated by semi-circles.

ada, but dips south into the continental USA in only two regions: the north-central parts of Minnesota, Wisconsin and Michigan, and northern New England and New York. This southern boundary in the eastern USA roughly corresponds to the southern limit of raised bogs as well (Damman and French 1987).

**Materials and Methods. PATTERNS OF BLACK SPRUCE GROWTH.** The density, height, and diameter of all black spruce trees were determined in  $10 \times 10$  m, contiguous plots along the south side of a 170 m transect from the stream to the bog center (Fig. 2). Trees were defined as stems  $>2$  m in height. Stems  $<2$  m were considered part of the shrub layer. To test the hypothesis that differences in tree height along the transect were related to growth rate rather than age, four black spruce trees within each  $100 \text{ m}^2$  plot were

randomly selected. Height (to the nearest 50 cm), as determined by a Suunto clinometer, and diameter at 30 cm (to the nearest 0.5 cm) were recorded and trees were cored 30 cm above the ground with an increment borer. Annual rings were counted through a dissecting microscope following mounting and sanding.

**HYDROLOGY.** The effect of water table and topography on the growth rate of spruce trees was evaluated by measuring the elevation and slope of both the peat surface and the water table along the transect. Fluctuations in height of the water table were measured in perforated metal conduit pipes (2.5 cm diameter), open at both ends, and placed in the ground every 10 m along the transect from the stream to the bog center. Air was blown through a piece of tubing in the water well until water could be heard bubbling.

The length of the tubing (to the nearest 0.5 cm) from the top of the water well to the top of the water table was then recorded. Measurements were taken every 1–2 weeks from 20 April–15 August 1989.

The elevations of the soil surface and the water table were measured with a 25 m length of clear plastic tubing (0.6 cm diameter), open at both ends and filled with water. A difference in the vertical distances from water level in the tube to the ground indicated different elevations at the two ends of the outstretched tube. A surveyor's level was not used because the line of sight was obstructed by spruce trees. Elevation changes at each 10 m point were measured by this method to detect small differences in soil surface or water table slope. The top of each water well was surveyed as well as soil surface. Since soil surface elevations varied locally due to hummock and hollow microtopography (Larsen 1982), average elevations of 20 points in a 2 m radius of each water well were measured.

**WATER CHEMISTRY.** Water samples were collected and analyzed on two occasions during the 1989 growing season. On 31 May, temperature and conductivity of surface water were measured in the field at three, randomly-located spots every 10 m along the transect. Water samples were collected at these same points in acid-washed bottles, pooled, stored at 4°C for 24 hours, and analyzed for pH using a 2-point calibration digital pH meter standardized to buffers of 3.00 and 7.00. Water conductivity measured in the field was converted to specific conductance at 25°C to standardize the values (Golterman, Clymo and Ohnstad 1978).

Conductivity and pH were analyzed a second time on 6 July 1989. Because the water table had dropped significantly, surface water was not available at all sampling sites. Where surface waters were not available, the peat was depressed, but not cut or otherwise disturbed, until water was found, and three random samples every 10 m were collected in acid-washed plastic bottles and pooled. Samples were stored in a cooler immediately after removal from the field and refrigerated at 4°C for three days, then analyzed for pH, conductivity and cation concentrations. Cations were analyzed using an inductively coupled plasma (ICP) atomic emission spectrometer.

**VEGETATION ZONATION.** Vegetation was sampled using the Braun-Blanquet method of cover values (Mueller-Dombois and Ellenberg 1974)

to test the hypothesis that changes in species composition parallel changes in water chemistry. All species were recorded in three randomly placed 1 × 1 m quadrats within each 10 × 10 m plot along the transect. Visual estimates of cover for each species in each quadrat were averaged to generate a percent cover for each plot. Vascular plants were identified to species using Gleason (1968) with the assistance of E. Thompson. Only the 7 most common *Sphagnum* moss species were determined (Ireland *et al.* 1987) with the assistance of C. McQueen. Other mosses identified to genus include *Dicranum*, *Hylocomium*, and *Polytrichum*.

**BASIN TOPOGRAPHY AND PEAT STRATIGRAPHY.** Depth of peat was measured by probing with aluminum rods every 10 m along the transect. A Hiller sampler was used to remove one peat core from each of the three vegetation zones—the band of tall spruce, the stunted spruce zone, and the open bog zone. Each core was preserved in 20 cm segments and refrigerated at 4°C. A modified Troels-Smith (1955) methodology (Aaby and Berglund 1986) was used to describe the composition of the peat, degrees of decomposition (humification), and relative density of different peat types in each core.

**Results. PATTERNS OF BLACK SPRUCE GROWTH.** Height and density of black spruce decrease toward the bog center (Figs. 3, 4), but age does not. The average height of black spruce trees within plots along the transect varies from 12 m to 3 m (Fig. 3). Density of spruce trees declines 50 m to 170 m from the stream (Fig. 4). The number of trees is greatest (45/100 m<sup>2</sup> plot) at 50–60 m from the stream, corresponding approximately to the significant drop in height of spruce. The height and density data indicate that there are three zones of spruce: 1) tall (10–40 m from the stream); 2) short with declining density (40–110 m); 3) short and uniformly sparse (110–170 m). Recall that spruce are absent at the margin of the stream.

Height and age of black spruce are not significantly correlated ( $P = 0.05$ ;  $r^2 = 0.24$ ). The number of annual rings vary from 45 to 77 at 30 cm above the ground, yet heights vary from 2.0 m to 15.5 m. The oldest trees are distributed throughout the entire bog. The differences in number of rings are not based on actual total age since the rings below 30 cm were not counted. The number of rings below 30 cm is probably larger in the shorter trees making all the trees even closer in age than the data show.

There is a significant linear regression between

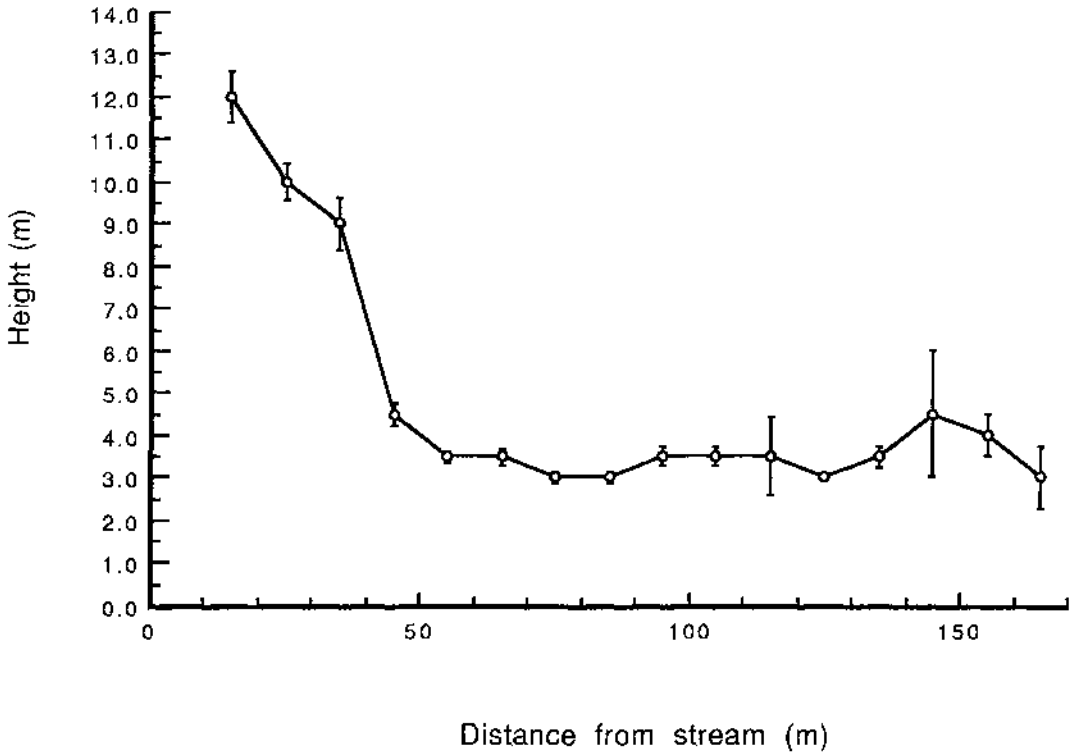


Fig. 3. Height of black spruce trees vs. distance from stream at Victory Basin Bog, Vermont. Values are means, based on trees >2 m in height surveyed in 10 x 10 m plots along a belt transect from the stream to the bog center, May 1989. Vertical bars represent the standard error of the mean.

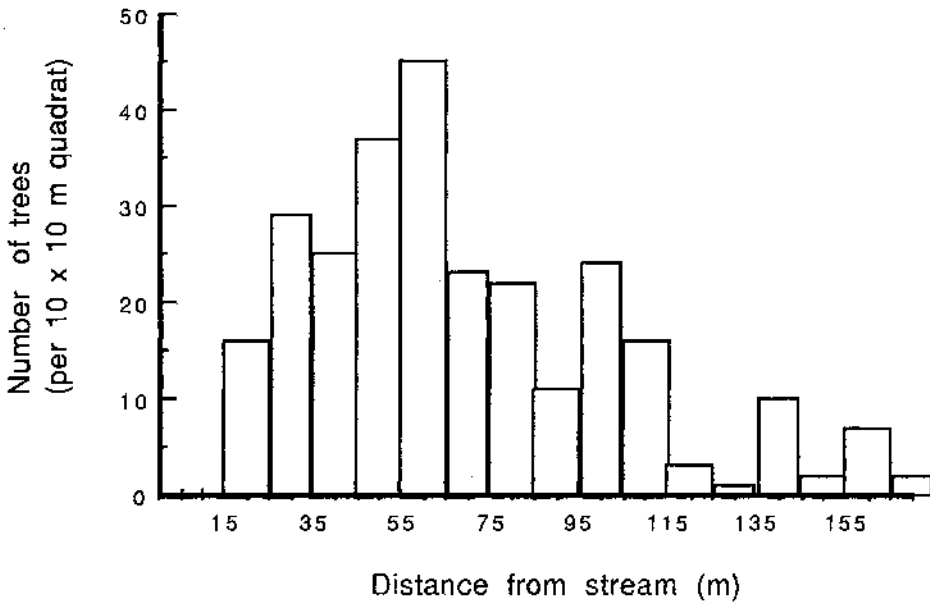


Fig. 4. Density of black spruce trees vs. distance from stream at Victory Basin Bog, Vermont. Values are numbers of all trees >2 m in height surveyed in 10 x 10 m plots along a belt transect from the stream to the bog center, May 1989.

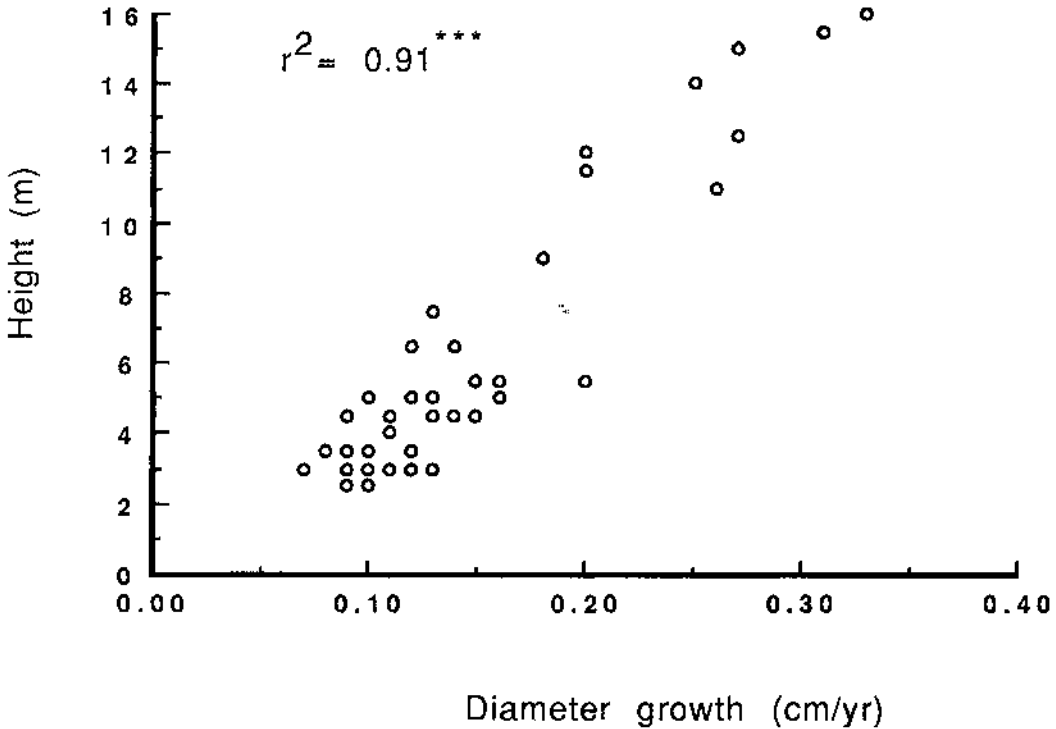


Fig. 5. Relationship between height and diameter growth of black spruce at Victory Basin Bog, Vermont. Circles represent individual trees > 2 m in height sampled along a belt transect from the stream to the bog center, 22 May 1989.

height of spruce and growth rate ( $P = 0.001$ ;  $r^2 = 0.91$ ) as defined by diameter per number of annual rings (Fig. 5). This indicates that spruce grow better near the stream and more poorly away from it. Since the trees in the bog center are shorter due to slower growth rates rather than age, the transect does not represent a classic hydrarch succession model with trees gradually colonizing the center as organic matter fills in from the edges of the bog. At least with this generation of trees, another model of peatland development has shaped the black spruce pattern.

**HYDROLOGY.** The elevations of both soil surface and water table are higher at the bog center than at the stream (Fig. 6). The soil surface in the center of the bog is 66.5 cm higher than the stream-side edge of the tall spruce band. The water table at the bog center is higher than the stream by a comparable amount, approximately 65.0 cm on average from April to August.

The entire bog was not surveyed, but several factors suggest that the center of the bog is higher than the edges. First, elevations of the bog surface were measured past the 170 m mark. For 50 m past the bog's center, the surface decreases in

elevation. Second, water flow in the lagg bordering the bog on the east side shows water moving away from the bog center. These elevation gradients from the center to the edges may strongly influence chemical and consequently floristic patterns in the peatland. Water drains from the bog to the edges so that the center receives input of nutrients only from precipitation.

The slope of the water table varies along the transect (Fig. 6). Around mid-May, a levelling-off occurred roughly in the stunted spruce zone. The slope was greatest beneath the zone of tall trees, especially toward the end of July. Seasonal fluctuations of the water table vary significantly along the transect as well (Fig. 6). The difference between the spring high water table on 4 April and the summer low on 1 August showed significant variation among the three spruce zones: 42.5 cm in the tall spruce zone (0–40 m), 31.5 cm in the stunted spruce zone (40–110 m), and 24.5 cm in the open bog zone (110–170 m). However, the mean depth to water table from 4 April to 1 August did not vary significantly among the three spruce zones: 23 cm in the tall spruce zone, 26 cm in the stunted spruce zone, and 25 cm in the open bog zone.

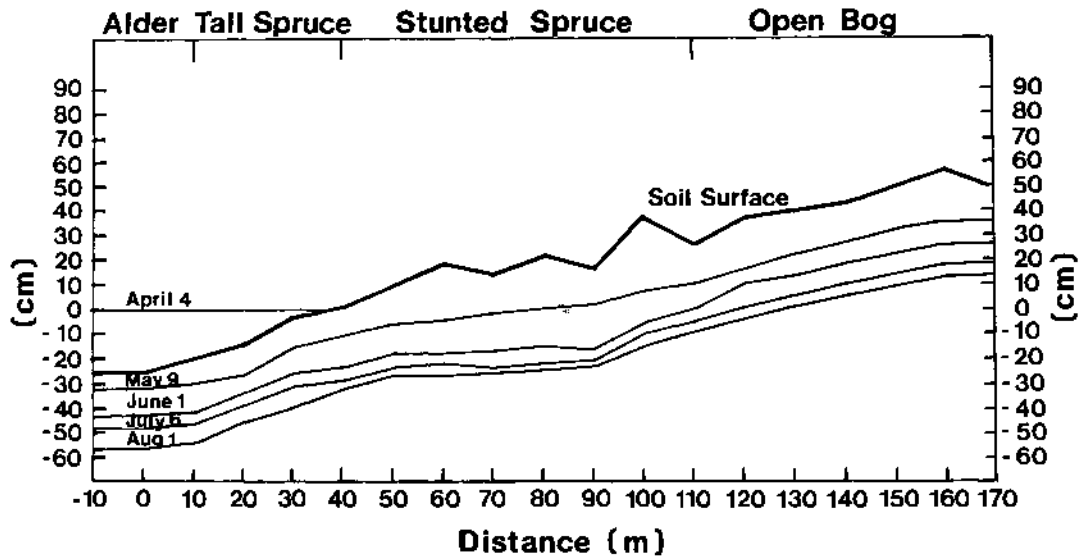


Fig. 6. Soil surface (thick line) and water table elevations (cm) relative to April 4 water line (0 on vertical axis), April–August 1989, from stream (0 m) to bog center (170 m). Dates refer to water table elevations. Vegetation zones along transect indicated.

**WATER CHEMISTRY.** Cation concentrations, pH, and conductivity are all extremely low, indicating the low nutrient status typical of oligotrophic peatlands (Clausen and Brooks 1980; Damman 1986). Variation exists, however, from the stream to the bog center. The pH data from 31 May 1989 show a significant linear regression ( $P = 0.05$ ;  $r^2 = 0.38$ ) with readings of 4.2 near the stream and 3.4 in the bog center. The data on specific conductance of bog water, not adjusted for pH, on that same date show a highly significant linear regression from 30 to 170 m ( $P = 0.01$ ;  $r^2 = 0.77$ ) ranging from 55 to 30  $\mu\text{mhos}$ . The 6 July data generally show a higher nutrient status near the stream; calcium (Ca), potassium (K), and magnesium (Mg) are notably elevated with readings of 3.1, 0.7, and 0.7 ppm respectively. Average values of these same cations are 1.0 (Ca), 0.7 (K), and 0.2 (Mg) ppm in the stunted zone and 0.9 (Ca), 0.3 (K), and 0.2 (Mg) ppm in the bog center. The pH data for 6 July confirm the highest reading in the stream (6.3) but fairly uniform from 4.4 to 4.2 elsewhere. The pH values were considerably higher in July than in May.

**VEGETATION ZONATION.** The phytosociological data (Table 1) show distinct changes in species assemblages along the transect from a minerotrophic community near the stream to an extremely nutrient-poor community in the bog center. From 0 to 10 m, the community consists primarily of *Alnus rugosa*, and includes stream-

side species such as *Iris versicolor* and *Impatiens biflora*. At 10 m, the *Alnus* ends abruptly and *Picea mariana* appears for the first time, replacing *Alnus* as the dominant woody species.

By 50 m from the stream, several species are no longer present, including *Abies balsamea*, *Acer rubrum*, *Sorbus americana*, *Gaultheria procumbens*, *Maianthemum canadense*, *Carex disperma*, *Cornus canadensis*, *Sphagnum wulfianum*, *S. girgensohnii*, and *Hylocomium* sp. These species are typical of the fastest growing, black spruce forests in Minnesota (Heinselman 1963, 1970; Glaser 1987) and Canada (Jeglum 1975; Foster 1984) that are better drained and have higher nutrient inputs. At the same transition point (50 m), several species appear for the first time: *Carex trisperma*, *Chamaedaphne calyculata*, *Vaccinium oxycoccus*, *Kalmia polifolia*, *Smilacina trifolia*, *Ledum groenlandicum*, *Carex pauciflora*, and *Sphagnum fuscum*. These species are typical of more oligotrophic, nutrient-poor peatlands (Foster 1984; Glaser 1987), and occur frequently in areas of poorer growth of black spruce in Minnesota peatlands (Heinselman 1963, 1970; Jeglum 1975). The *Sphagnum fuscum* cover class is 50–75% at this point. This species is associated with highly acidic, nutrient-poor conditions and rapid peat accumulation (Clymo 1963, 1983; Foster 1984; Crum 1988).

This transition in community composition corresponds roughly with the abrupt decrease at 40 m distance in black spruce height (Fig. 3) and



Table 1. Continued.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Distance from stream (m × 10)*																	
Mosses																	
<i>Sphagnum</i> sp.	4																
<i>Hylacomium</i> sp.		+	1	1													
<i>Dicranum</i> sp.		1	1	1	+												
<i>Sphagnum wulfianum</i>		1	+	1	1												
<i>S. girgensohnii</i>		3	3	2	2												
<i>S. centrale</i>		1	+	2	1	1	1										
<i>S. fallax</i>		3	2	3	2	2	2	2	1	2							
<i>S. fuscum</i>					1	4	4	4	4	4	5	5	5	5	5	5	5
<i>S. magellanicum</i>										1	+	1	+	1	+	1	1
<i>S. rubellum</i>										+	+	1	2	1	1	1	1

\* 1 = 0-10 m from stream; 2 = 10-20 m; 3 = 20-30 m; etc.

density (Fig. 4). The vegetation changes also correspond approximately with the break in water table slope (Fig. 6) from a sloping profile beneath the tall spruce to a more level regime below the stunted spruce zone.

The transition from the stunted spruce zone to the open bog zones does not match quite as well with changes in community composition. Transitions do occur, but over a wider distance than in the 40 to 50 m area. In the stunted spruce zone, *Andromeda glaucophylla*, *Eriophorum spissum*, and *Sarracenia purpurea* appear for the first time. These species generally become more abundant in the open bog zone; they are also indicators of more oligotrophic conditions (Damman and French 1987). Several other species that are present in the tall spruce zone first decline in cover values and then drop out altogether in the stunted spruce zone. These include *Gaultheria hispidula*, *Coptis groenlandica*, *Sphagnum centrale*, and *S. fallax*.

At 100 m from the stream, the transition from the dense, stunted spruce zone to the open bog zone, *Sphagnum magellanicum* and *S. rubellum* (*S. capillifolium* var. *tenellum*, C. McQueen, personal communication) appear for the first time. Both are characteristic of ombrotrophic hollows (Foster 1984). *Sphagnum fuscum* becomes more dominant with 76-100% cover. *Rhododendron canadense*, *Smilacina trifolia*, *Carex pauciflora*, *Viburnum cassinoides*, and *Andromeda glaucophylla* become less dominant and drop out altogether in the last 10-20 m before the bog center, indicating that this is the most nutrient-poor, ombrotrophic portion of the peatland (Damman and French 1987). This conforms exactly with its elevated topography and central location.

**BASIN TOPOGRAPHY AND PEAT STRATIGRAPHY.** Probing revealed that peat underlies the entire transect, including the stream. Five meters of peat lie beneath the stream and tall spruce zone, gradually increasing to approximately 5.5 m in the bog center. Since the underlying clays are essentially level (as revealed by the leveling measurements) the difference can be explained by a thicker accumulation of peat corresponding to the higher surface elevation in the center (Fig. 6).

Peat coring at three sites suggested differences in hydrology along the transect. The characteristics of the acrotelm (zone of surface peat above low water table level) and catotelm (permanently anaerobic zone below low water table level) vary

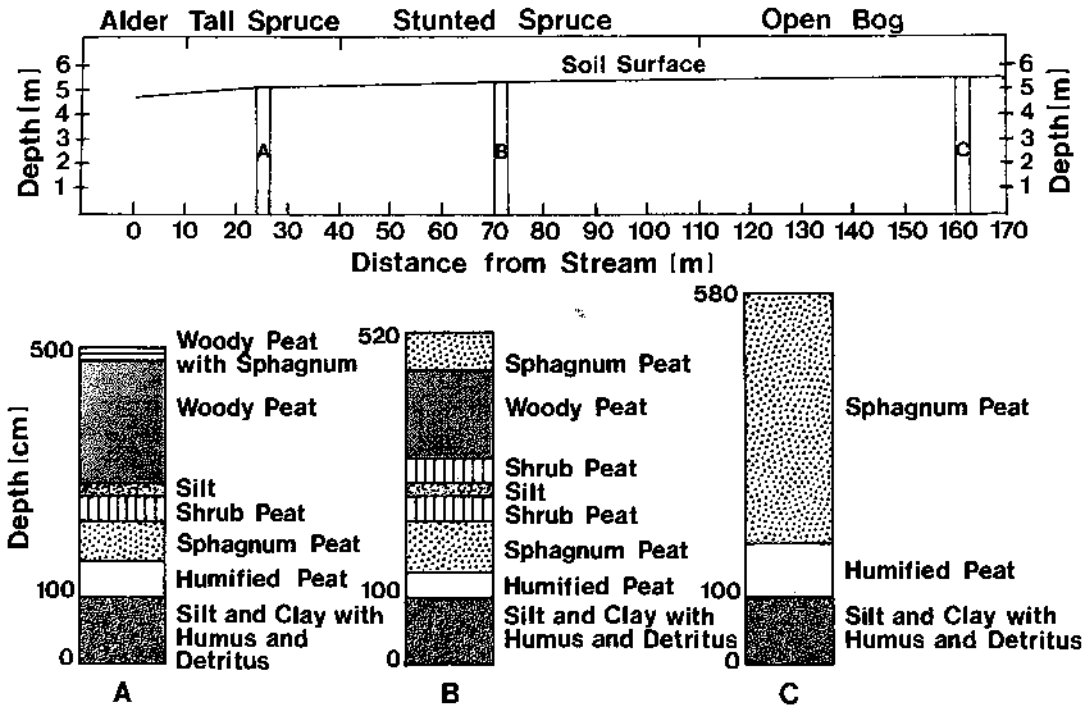


Fig. 7. Profile of transect from stream to bog center showing depth of peat and description of cores taken 18 June 1989 at Victory Basin Bog, Vermont. Vegetation zones indicated.

from the tall spruce zone to the bog center. For example, the upper 40 cm of peat in the open bog zone is composed of non-humified *Sphagnum* peat, while the upper 20 cm of peat in the tall spruce zone consists of moderately humified *Sphagnum* and woody peat (Fig. 7). This suggests that the water table is consistently higher in the bog center.

In addition to differences in the upper layers of peat in the three peat cores, there are changes at depth as well. The bog center has a relatively uniform deposit of *Sphagnum* peat with ericaceous shrub fragments approximately 4 m thick. Very little tree wood is present in this core, indicating lack of forest cover at any time during peatland development. Near the bottom of the core, a layer of humified moss peat with *Nuphar* and *Potamogeton* seeds lies on top of silt and clay suggesting that a shallow lake or marsh once filled the basin.

The cores in the tall and stunted spruce zones show a different sequence of events. Similar layers of silt and clay overlie by humified moss with aquatic plant macrofossils are present at the base of all three cores. A thin layer of *Sphagnum* peat occurs in the tall and stunted spruce zone cores. At that point (approx. 200 cm from the

bottom), the peatland vegetation was relatively uniform throughout. Few or no trees grew along the transect. A silt layer occurs in both spruce zone cores and lies between thin deposits of moss and herbaceous peat with *Alnus* seeds and fragments. The silt layer indicates the presence of a stream since silt appears nowhere else in the cores and *Alnus* grows only within 10 m of the stream at present. The silt deposit does not appear at all in the open bog zone, which is evidence against a theory of a single, large, flooding event.

A 200 cm thick deposit of woody peat overlies the silt layer in both spruce zone cores indicating that trees once grew in the area. As the stream migrated away, along its margins were numerous trees, just as is the case today. Finally, the top 60 cm of the core in the stunted spruce zone is composed primarily of *Sphagnum* peat. This change from woody peat to *Sphagnum* peat is evidence that bog spreading occurred as water tables rose.

**Discussion.** PROCESSES INFLUENCING GROWTH RATES OF BLACK SPRUCE. The results from the hydrology, water chemistry, vegetation zonation, and peat stratigraphy of Victory Basin Bog all provide evidence to explain the zonation pattern

of black spruce. As with most peatlands, these factors are highly interdependent. The surface topography indicates that the bog is raised, isolating the center from nutrient sources other than precipitation. The water table is also raised in the bog center further indicating that the stream has little influence on vegetation away from the bog's edges.

Small variations in depths of water table have large consequences for tree growth in peatlands throughout the boreal region; presumably due to greater amounts of oxygen available to the roots (Crawford 1983; Lieffers and Rothwell 1987). In the Soviet Union, a mean annual drop in water table depth of only 2 cm corresponded to a 1 m height increase in *Pinus sylvestris* (Scots pine) (Kulczinski 1949). However, in many boreal peatlands, seasonal variations and extremes are at least as important as water table depth (Heinselman, 1963; Ivanov 1981; Sjors 1983). The results at Victory Basin suggest that seasonal fluctuations are more important than mean depth to water table, although the data are limited to a 5 month period.

Greater water movement has been correlated with improved tree growth due to better drainage and ion transport for uptake by roots (Ingram 1967; Crawford 1983). Rates of water movement in Victory Basin were not measured, but the changes in slope of the water table suggest that movement is greatest beneath the tall spruce (Fig. 6). The steeper slope from 0 to 40 m is probably related to stream incision, while the slope from 100 to 170 m may be related to greater peat accumulation in the more ombrotrophic part of the bog.

The results of depth probing and peat stratigraphy provide other clues for the spruce zonation pattern. The 5 m of peat below the tall spruce eliminates the mineral substrate as a possible nutrient source. The more decomposed layer of the peat below the tall spruce is probably related to improved drainage. Heinselman (1963, 1970) found a negative correlation between site quality for black spruce and thickness of the upper horizon of undecomposed *Sphagnum*. Good sites were underlain by well-decomposed woody or mixed peats.

The interactions between water supply and decomposition rates influence not only oscillations in water table level, but other factors such as pH and supply of plant nutrients. They in turn affect floristic variation (Malmr 1986). The water chemistry and phytosociological data strongly support the notion of decreasing nutrient avail-

ability from the stream to the bog center; the center is ombrotrophic or nearly so. In addition to stream incision, steepened groundwater slope, stream flooding, and a raised peat dome, the nutrient characteristics are probably enhanced by the ability of *Sphagnum* to lower pH, which decreases decomposition and encourages peat accumulation at a greater rate in the bog center. Thus, insofar as spruce is affected by nutrient availability, the patterns of spruce density, height, and growth rates are consistent with the vegetation data. Areas for further research include measuring rooting depth of black spruce, rates of water movement, phosphorus (P) and nitrogen (N) concentrations in the soil, and foliar evidence for P or N deficiencies.

The results of this study suggest several explanations for differences in spruce growth rates. First, the short spruce trees are stunted because (a) the water table is persistently high, thereby diminishing the oxygenated zone for roots; (b) nutrient availability is decreased by low pH values, an ombrotrophic nutrient source due to raised surface and water table elevations, and minimal ion transport due to slow water movement. Second, the growth of the tall spruce is enhanced by (a) nutrients from spring stream flooding; (b) greater ion transport due to relatively steep water table slopes, and (c) a greater concentration of ions due to greater decomposition in the more oxygenated peat in the zone of stream incision.

**PROPOSED MODEL OF PEATLAND DEVELOPMENT AND ECOSYSTEM DYNAMICS.** At Victory Basin Bog, deglaciation set the stage for peatland development. The flat topography and impermeable substrate impeded the flow of water and facilitated the development of a shallow lake or marsh. A cold climate immediately following deglaciation, a shallow water basin with little or no outflow, and perhaps an excess of precipitation over evaporation may have encouraged the growth of *Sphagnum*. As *Sphagnum* accumulated, it further acidified the environment, raised water levels, and discouraged the colonization of minerotrophic species.

At some point in time, a stream began flowing through the basin, perhaps due to beaver activity upstream. The stream probably improved drainage in the peat by cutting a channel and increasing water table slope and water movement facilitating the growth of black spruce. *Sphagnum* continued to dominate the bog center, however, raising water tables, slowing decomposition, increasing the rate of peat accumulation and dis-

couraging tree growth. The accumulation of peat may have actually forced the stream to migrate westward from the bog center. Since the tall trees may have been present only because of conditions created by the stream, they too may have migrated in association with the stream. The peat stratigraphy supports this proposed evolution with woody peat overlying the silt and alder layer in the stunted spruce zone (Fig. 7).

The natural self-perpetuating cycle of *Sphagnum* growth, peat accumulation, and water table rise may have accelerated around the turn of the 20th century with logging and fire. The entire Victory Basin was logged at that time. Several large fires also occurred in the basin, including one around 1910 (R. Stanley, Victory Fire Warden, personal communication). The fact that the trees along the transect are approximately the same age (within 20–30 years) supports the possibility that a single event caused near-synchronous recruitment of a cohort of spruce trees.

The stream channel today is probably still migrating as *Sphagnum* peat accumulates faster in the bog center than at the edges, causing further lateral expansion of the bog. Beavers are also shaping the fate of the tall spruce and the overall hydrology of the basin. Several abandoned dams exist along the stream adjacent to the bog and an actively-maintained one further upstream (Fig. 2). A band of tall, dead or dying black spruce occurs just above the active dam. Beavers are likely flooding the trees by eliminating the changes in water table slope and seasonal fluctuations near the stream channel. If the bog continues to grow and the beavers continue to flood the stream zone, the water depth, slope and seasonal oscillations could be so small as to inhibit tree growth altogether; this could result in a transition from alders to open bog dominated by *Sphagnum* and ericaceous shrubs.

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