© Suoseura — Finnish Peatland Society
Helsinki 2007
ISSN 0039-5471
Suo 58(2): 37–47

Interaction of mire microtopography, water supply, and peat accumulation in boreal mires

Suon pienmuotojen, veden saatavuuden ja turpeen kertymisen vuorovaikutus pohjoisilla luonnontilaisilla soilla

David K. Swanson

David K. Swanson, USDA Forest Service, PO Box 907, Baker City, OR 97814 USA, email: dkswanson@fs.fed.us

Studies of mire hydrology and carbon accumulation have shown 1) an exponential increase in the rate of horizontal water movement with increasing height of the water table, and 2) a curvilinear relationship between the water table elevation and carbon accumulation rate, with a single maximum. Equations for these relationships suggest that optimal carbon accumulation will occur where the water table is at moderate depth and the surface has little microtopography. Wet conditions tend to enhance microtopographic relief by differential peat accumulation, while dry conditions tend to reduce relief. For mires with abundant dry microsites, increasing the water supply typically increases the rate of carbon accumulation, but this effect could be transient because microtopographic relief may also increase and have a negative effect on carbon accumulation. The runoff-inhibiting nature of ridge and hollow patterns makes patterned mires especially vulnerable to loss of carbon fixation ability with increasing wetness. While dry periods often cause peat loss in the short term, over the long term their effect may be positive because they hinder the formation of strong microtopography. This helps explain why high peat accumulation rates and some of the world's most extensive peatlands occur in continental regions with a marginally adequate moisture supply.

Key Words: hydrology, microtopography, mire patterning, peat accumulation

Introduction

The relationship between water supply and carbon accumulation rates in mires is complex. While peat obviously requires saturation to accumulate and persist, several studies have shown that very wet microsites or pools are carbon sources rather than sinks (e.g. Waddington & Roulet 2000; Heikkinen et al. 2002). Microtopography and surface patterns in mires are important because they lead to large variations in water table position over short distances and consequent great local variability in the carbon balance (e.g. the aforementioned references and Alm et al. 1997).

The purpose of this paper is to explore the relationships among water supply, microtopography, and the rate of carbon accumulation in mires. It is based on the simultaneous solution of equations that describe 1) the rate of horizontal flow of water and 2) the rate of carbon accumulation in mire, both as a function of water-table position. The basic form of these two relationships is fairly well known: in the former, the rate of horizontal water movement increases exponentially as the water table rises (Ivanov 1981); in the latter, peat accumulation is most rapid at some optimal intermediate water table position and drops off to negative values at very low or high water tables (Waddington & Roulet 1996, 2000; Belyea & Clymo 2001). This study focuses on computations that describe a simplified mire system consisting of two dominant microtopographical elements. Two spatial arrangements of the microtopography are explored, one where topographic highs (ridges or strings) and lows (hollows or flarks) are oriented perpendicular to slope, and one where highs (hummocks) and lows (hollows) are scattered in a disorganized (isotropic) fashion. In either case a steady-state microtopography is defined as one that has the same rate of peat accumulation on the highs and lows, such that the relative height of the microtopography is unchanged as the mire evolves. This fact allows us to describe the topography and carbon accumulation rates for a limited set of steady-state outcomes, to which the infinite variety of non-steady state outcomes can be compared.

Methods

The rate of horizontal movement of water in a mire is assumed to follow the flow law developed by Ivanov (1981):

$$q_z = M_z dz/dx \quad (1)$$

where q_z is the horizontal flow across a vertical section of the mire of unit width, M_z is the modulus of horizontal seepage when the water table is at elevation z relative to the mire surface, and dz/dx is the slope of the water table (*i.e.*, the gradient in hydraulic head). Ivanov (1981, Appendix 1) presents numerous measured values for M_z and z from 13 profiles in various types of mires. The data show a good linear correlation between $\log(M_z)$ and z, with coefficients generally similar across a wide variety of mire types. Many of Ivanov's measurements apply to peat landscapes that include several microtopographical elements, while here we need a relationship that will serve for an individual microtopographical element (i.e. hummock or hollow). Thus I chose two of Ivanov's profiles that represent areas with little microtopography, have a strong correlation between $\text{Log}(M_z)$ and z ($r^2 = 0.89$, n = 17 and $r^2 = 0.99$, n = 16), and have identical regression coefficients when rounded to the nearest integer:

$$\text{Log}(M_z) = (z + 25)/8 \quad (2)$$

with z in cm (negative z is a water table below the surface). The two sites are described as "*Sphagnum*-shrub-*Eriophorum* sparsely forested with pine" and "unforested *Sphagnum*-sedge with even microrelief".

The composite modulus of seepage for a mire with two microtopographical elements that have different water tables (and thus two contrasting moduli) was computed as follows. For an unpatterned mire, the composite modulus is the geometric mean of the two component moduli (Renard & de Marsily 1997):

$$M = M_1^{A_1} \times M_2^{A_2} \quad (3)$$

where M is the composite modulus, M_1 and M_2 are the moduli for the two microtopographical elements (highs and lows), and A_1 and A_2 are the fraction of the mire area occupied by each. For a patterned mire the composite modulus is the harmonic mean of the two component moduli:

$$M = 1/(A_1/M_1 + A_2/M_2) \quad (4)$$

The harmonic mean provides an exact solution for cases where zones of contrasting permeability are oriented perpendicular to the flow (Renard & de Marsily, 1997).

The relationship between water table position and rate of net soil carbon accumulation was obtained from measurements on the Stor-Åmyran peatland in Sweden (Waddington & Roulet 1996, 2000) (Fig. 1). This is an eccentric raised bog with a distinct microtopography of ridges 30–70 cm high, located 15 km south of Umeå (63°44'N, 20°06'E). The ridges are dominated by *Sphag-*

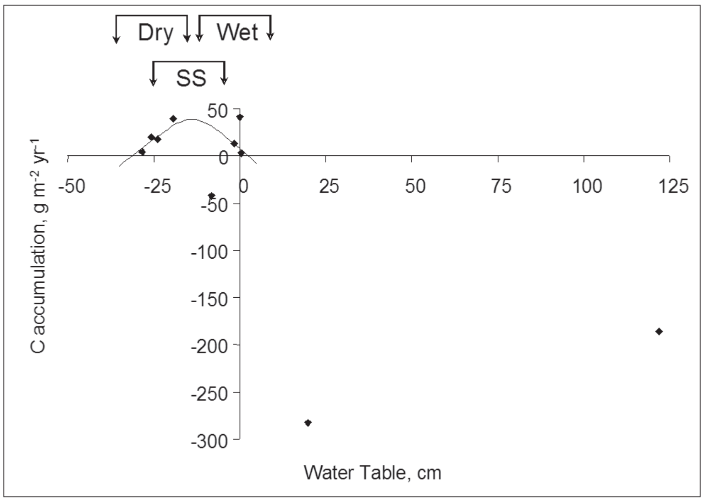

Fig. 1. Relationship between water table position and the rate of carbon accumulation in a mire. Points represent 2-year average growing-season carbon balances from gas-exchange measurements and water tables on the Stor-Åmyran peatland in Sweden (Waddington and Roulet, 1996, 2000). Negative water tables are below the ground surface. The curve consists of two lines with hyperbolic smoothing, Y = 55.03 – 0.17*X + (X+13.49)*(–3.22) *A, where A = $((X+13.49)^2+33.27)^{0.5}$/(X+13.49). Points on the curve corresponding to the ends of bracket "SS" represent steady-state microtopography: the microtopographic highs (left end) and lows (right end) have equal carbon accumulation rates. The ends of the "Dry" bracket represent microtopographical highs and lows on a mire with the same relief but drier conditions; differential peat accumulation will tend to reduce microtopographic relief. The endpoints of the "Wet" bracket represent highs and lows under wet conditions, where differential peat accumulation will increase microtopographical relief.

Kuva 1. Suon vedenpinnan ja turpeen kertymisen vuorosuhde ruotsalaisella Stor Åmyran -suolla (Waddington and Roulet, 1996, 2000). Pisteet kuvaavat kahden kasvukauden kaasunvaihto- ja vedenpintamittausten keskiarvoa, jotka on tasoitettu hyperbolisella tasoituksella. Negatiiviset luvut kuvaavat maanpinnan alapuolella olevaa vedenpintaa. SS=pienmuotojen tasapainotila, jossa mätäspinnoilla (vaihteluvälin vasen reuna) ja painannepinnoilla (oikea reuna) on sama turpeen kertymänopeus. Dry=tilanne, jossa kuivuminen aiheuttaa eroja pienmuotojen turpeen kertymisessä johtaen suon pienmuotojen vaihtelun vähenemiseen; Wet= tilanne, jossa märistä olosuhteista johtuvat turpeen kertymänopeuden erot johtavat pienmuotojen vaihtelun lisääntymiseen.

num fuscum and ericaceous shrubs. Microtopographic lows (lawns) had *S. majus* or *S. balticum* with *Eriophorum vaginatum*. The carbon balances were obtained by gas exchange measurements in plexiglass enclosures at 4 locations ranging from the peatland center to its margin. Water-table elevations are growing-season averages. The results from 2 years of measurements at each site are averaged in Fig. 1. These measurements show a steady increase in the rate of carbon accumulation as the water table rises from about 30 cm to 20 cm below the surface, and large carbon losses from the two points submerged in pools. There is considerable scatter in the carbon accumulation rates for the 0 to –10 cm water table levels, suggesting some variability in the position of optimal carbon accumulation. However, there is evidence supporting the single-humped shape of the water table-C accumulation curve shown in Fig. 1, though the peak height and position is undoubtedly variable.

Belyea & Clymo (2001) found that peat accumulation rates estimated by biomass sampling at 22 locations on an ombrotrophic mire in Scotland were at a maximum when the mean water table depth was in the range of 5 to 20 cm below the surface; zero accumulation occurred under ponded or very dry (water table greater than 40 cm down) conditions. Carbon balance measurements by gas exchange in a pine fen in Finland by Alm et al. (1997) also showed greater carbon accumulation at sites with intermediate water tables (5 cm below the surface) than either drier (23 cm) or wetter (2–3 cm) sites. Indeed, the mere fact that peat accumulation occurs where the water table is near the surface, but not where the water table is at great depth or where there is open water confirms this basic relationship. In the curve used here and depicted on Fig. 1, carbon accumulation is most rapid, nearly 40 g C m^{-2} yr^{-1}, when the mean water table is between 5 and 20 cm below the surface; net carbon loss occurs on dry sites (water table more than about 30 cm below the surface) and wet sites (water ponded over the surface). This relationship can be most confidently applied to bogs, since the data in Fig. 1 (and Belyea and Clymo's 2001 similar curve) are derived from bogs.

The points depicted in Fig. 1, and all carbon accumulation rates reported here, include growing season measurements only, and are not corrected for loss of carbon due to winter decomposition. Subtracting some value to account for winter loss uniformly reduces the carbon accumulation rates but otherwise does not affect the results. Carbon accumulation rates could be adjusted up or down to agree with known annual rates of accumulation in other areas. The global average boreal peat accumulation rate has been estimated at about 30 g C m^{-2} yr^{-1} (Gorham 1991).

If values are chosen for any four of the five variables including mire slope, rate of horizontal water flow, water table elevation in the microtopographic highs or lows, proportion of highs versus lows, and relief (difference in elevation between the highs and lows), a unique solution for the remaining variable can be computed from equations (1), (2), and (3) or (4). Such a solution applies to a parcel of mire that is large enough to contain the full microtopographical cycle but small enough to have approximately constant values for all of the variables. The rate of carbon accumulation can then be computed for each solution from the water tables and the equation in Fig. 1.

To simulate stable microtopography, pairs of points were chosen along horizontal lines through the curve in Fig. 1. Both points in such a pair have the same rate of carbon accumulation. The position of the water-table for the two points can be read from the x-axis, and the rate of horizontal water flow corresponding to these elevations can be computed using equations (1), (2), and (3) or (4). An important advantage of computations for steady-state conditions is that the result can be plotted on single diagram (Figs. 2 and 3). The results are sensitive in detail but not in their basic form to the specific coefficients chosen for the equations. In other words, the basic trends presented here should not be sensitive to local variations in the rate of peat accumulation, peat permeability, etc.

Results

Steady-state microtopography

A simple mire system with steady-state microtopography is modeled as two microtopographical elements with equal rates of carbon accumulation. Solutions of the equations are summarized in two diagrams that describe the stable combinations of relief, horizontal flow, and proportion of highs versus lows (Figs. 2 and 3). Figure 2 applies to unpatterned mires with an isotropic distribution of hummocks and hollows, while Fig. 3 applies to patterned mires with highs and lows are aligned in bands perpendicular to slope. The X-axis is scaled with the relief, which is the difference in height between the microtopographical highs and lows. The position of the water table relative to the surface of the highs and lows is also given below the x-axis (negative is a water table below the surface). Since the elevations of the highs and lows relative to the water table were chosen so they would have equal rates of carbon accumulation using the relationship in Fig. 1, the rate of carbon accumulation is independent of the proportion of highs to lows, and it is also scaled on the x-axis. The diagonal lines on the diagrams plot the proportion of microtopographic highs versus lows for a given horizontal flow and relief.

For example, point A0 on Fig. 2 portrays an un-patterned mire system with about 75% of the surface covered by hummocks that are 30 cm higher than the hollows. The average water table level is at –29 cm below the hummock surfaces and just above the surface (+1 cm) in the hollows, and the rate of horizontal water flow is $10^{-1.5}$ cm^2 s^{-1}. The rate of carbon accumulation is same

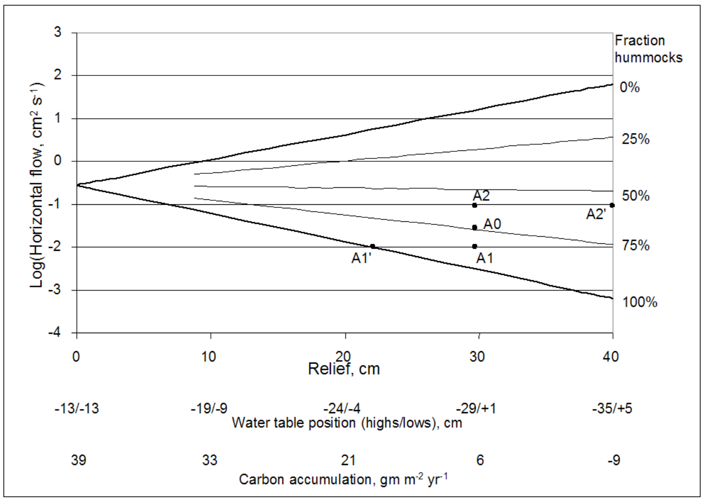

Fig. 2. Diagram of microtopographical steady-state conditions for unpatterned mires. The modeled mire systems have two microtopographic elements with equal rates of carbon accumulation. The x-axis is scaled with relief, the difference in elevation between hummocks (highs) and hollows (lows). The position of the water table relative to the hummocks (left of the slash; negative is below the surface) and hollows (right of the slash) and the rate of carbon accumulation are also provided on the x-axis. The y-axis is scaled with log of horizontal water flow for mires with a slope of 0.01. Diagonal lines on the diagram give the proportion of the mire surface occupied by hummocks for the indicated relief and horizontal flow. See the text for an explanation of the example points.

Kuva 2. Diagrammi suon pienmuotojen esiintymisestä ja ominaisuuksista ja veden virtausnopeudesta tilanteessa, jossa hiilen kertyminen turpeessa on samanlaista mätäs- ja painannepinnoilta soilla, joilla pienmuotojen vaihtelu on epäsäännöllistä. X-akseli kuvaa mätäs ja painannepinnan korkeuseroa, jonka yhteydessä esitetään myös kummankin pienmuodon mallitetut pohjavedenpinnat ja hiilien kertymänopeudet. y-akselilla kuvaa vaakasuuntaista vedenvirtausta. Diagonaalit kuvaavat mätäspinnan suhteellista osuutta suolla.

on both hummock and hollows at 6 gC m^{-2} yr^{-1}. A second example is point B0 in Fig. 3, which simulates a patterned mire system with the same rate of horizontal flow ($10^{-1.5}$ cm^2 s^{-1}) and microtopographic relief (30 cm). Here, however, this flow rate occurs with just 10% microtopographic highs, due to the damming effect of ridges oriented perpendicular to the slope.

The maximum rate of carbon accumulation occurs on the left side of both diagrams, where microtopography is negligible and the water table is near the optimum level of –10 to –15 cm. Carbon accumulation declines to below zero on the right-hand side of the diagrams, where relief is great and the mire consists of unproductive pools and dry hummocks or ridges.

The y-axis of both Figs. 2 and 3 is scaled with log of horizontal water flow for a mire with slope of 0.01. The only effect of changing the slope is a proportional change in the rate of horizontal water flow. For example, a diagram for a mire with a slope of 0.001 (ten times flatter) is identical to Fig. 2 or 3, except that all of the y-axis labels (log of flow) are reduced by 1 unit (i.e., a ten times lower flow rate).

Results for the un-patterned and patterned mires differ in several important ways. First, rates of horizontal water flow are substantially higher for the unpatterned case at any given proportion of microtopograhic highs, thanks to the less efficient damming effect of disorganized hummocks. For example, a steady-state patterned mire with 50% ridges 20–30 cm high has average rates of water flow of about 10^{-2} cm^2 s^{-1} (Fig. 3), while 50% unorganized hummocks of similar height results in flow rates more than an order of magnitude higher (Fig. 2). Second, the effect of increasing microtopographic relief differs between the patterned and un-patterned cases. On the unpatterned mire, increasing relief increases wa-

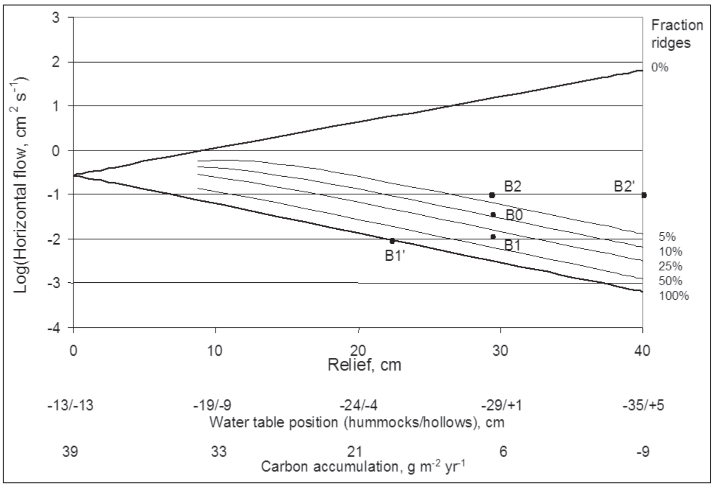

Fig. 3. Diagram of microtopographical steady-state conditions for patterned mires. The modeled mire system has two microtopographic elements with equal rates of carbon accumulation. The x-axis is scaled with relief, the difference in elevation between ridges (oriented perpendicular to slope) and hollows. The position of the water table relative to the ridges (left of the slash; negative is below the surface) and hollows (right of the slash) and the rate of carbon accumulation are also provided on the x-axis. The y-axis is scaled with log of horizontal water flow for mires with a slope of 0.01. Diagonal lines on the diagram give the proportion of the mire surface occupied by ridges for the indicated relief and horizontal flow. See the text for an explanation of the example points.

Kuva 3. Diagrammi suon pienmuotojen esiintymisestä ja ominaisuuksista ja veden virtausnopeudesta tilanteessa, jossa hiilen kertyminen turpeessa on samanlaista kermi/jänne- ja painannepinnoilta soilla, joilla pienmuotojen vaihtelu on säännöllistä. X-akseli kuvaa kermi-/jänne-(järjestyneet kohtisuoraan veden virtaussuunnan mukaan) ja painannepinnan korkeuseroa, jonka yhteydessä esitetään myös kummankin pienmuodon mallitetut pohjavedenpinnat ja hiilien kertymänopeudet. y-akselilla kuvaa vaakasuuntaista vedenvirtausta. Diagonaalit kuvaavat kermi-/jännepinnan suhteellista osuutta suolla.

ter flow on mires with less than 50% hummocks, thanks to faster flow through wetter hollows. For the patterned case, increasing relief results in reduced water flow regardless of the proportion of the mire occupied by highs.

Ridge and hollow microtopography with stable relief (i.e. relief is not increasing due to growth of pools) is limited to a specific range of conditions (Fig. 3). The triangular blank area between the 0% and 5% lines in the upper right-hand portion of Fig. 3 represents situations where patterning is not likely because the proportion of ridges would be so low that water movement by piping or through breaches in the ridges would probably occur. Increasing relief is associated with decreased flow over most of the patterned mire diagram, as increasingly high ridges are effective dams to water movement. Note that for flows in the vicinity of 10^{-1} cm^{-2} s^{-1} it is possible to have a nearly smooth, highly productive lawn (left side of the diagram) or a patterned mire with a much lower rate of peat accumulation (middle of the diagram).

Non-steady state conditions

Consider first an important implication of the relationship between carbon accumulation and water-table position (Fig. 1). For all conditions drier than the steady-state condition, such as the "dry" example in Fig. 1, peat accumulation in the microtopographic lows (represented by the right side of the bracket) will be greater than the highs (represented by the left side of the bracket), causing relief to decrease over time. In contrast, for all conditions wetter than the steady-state, such as the "wet" example in Fig. 1, peat accumulation will be greater on the highs than lows, and thus relief will grow over time.

We will examine specific examples that illustrate the effect of changing the water supply to a theoretical unpatterned mire dominated by hummocks (the point A0 in Fig. 2). As mentioned previously, point A0 in Fig. 2 represents a steady-state microtopography of disorganized hummocks with relief of 30 cm, surface dominated by hummocks (73%), horizontal water flow of $10^{-1.5}$ cm^2 s^{-1} at 0.01 slope, and carbon accumulation rate of 6 g m^{-2} yr^{-1} resulting from a water table at –29 cm below the hummocks and +1 cm (barely above the surface) on the hollows. If the flow is reduced approximately threefold to 10^{-2} cm^2 s^{-1}, computations with equations (1), (2), and (3) show that the water table drops to –33 cm under the hummocks and –3 cm under the hollows. After a period of adjustment for the plant communities involved, the resulting carbon accumulation rates would be about –5 g m^{-2} yr^{-1} under the hummocks and 18 g m^{-2} yr^{-1} under the hollows, which averages to 1 g m^{-2} yr^{-1} overall. Drying results in a decrease in carbon accumulation due to the dominance of hummocks now too dry to accumulate peat. Carbon accumulation in the hollows combined with carbon loss on the hummocks will cause the microtopography to become less pronounced over time. A new steady-state at the reduced flow of 10^{-2} cm^2 s^{-1} would therefore lie to the left of point A1, between A1 and A1', and have more area occupied by hummocks than the original point A0. Carbon accumulation rates at a new steady-state situation could range from 6 g m^{-2} yr^{-1} at point A1 to as high as 18 g m^{-2} yr^{-1} at point A1'; in other words, due to the decrease in microrelief, the rate of carbon accumulation would recover from the immediate drop that occurred after the decrease in water supply, and ultimately the new steady-state condition would have a carbon accumulation rate equal to or greater than the original rate at A0.

Next consider if the water flow is increased approximately threefold to 10^{-1} cm^2 s^{-1} on the unpatterned mire represented by point A0 (Fig. 2). Computations with equations (1), (2), and (3) show that the water table rises to –25 cm under the hummocks and +5 cm under the hollows. After a period of adjustment for the plant communities involved, the resulting carbon accumulation rates would be about 17 g m^{-2} yr^{-1} under the hummocks, –7 g m^{-2} yr^{-1} under the hollows, and 10 g m^{-2} yr^{-1} overall. Note that this represents an increase in rate of carbon accumulation relative to the starting point A0 (which was 6 g m^{-2} yr^{-1}). In this case the microtopography should *increase* due to peat accumulation under hummock and loss in the hollows. The resulting new steady-state, if achieved, would lie between points A2 and A2', with hummocks over 30 cm high, just over half of the mire occupied by hummocks, and a peat accumulation rate equal to or lower than the original of point A0. Thus the increase in rate of peat accumulation that occurred immediately after the increase in water supply would be transient.

Moving now to the patterned mire case, point B0 in Fig. 3 represents a patterned mire with steady-state microtopography and horizontal water flow of $10^{-1.5}$ cm^2 s^{-1}. Ridges (10% of the area) have a water table at –29 cm (below the surface), hollows (90% of the area) have a water table at +1 cm (above the surface), and the carbon accumulation rate of hollows and ridges is the same at about 6 g m^{-2} yr^{-1}. If the flow is reduced approximately threefold to 10^{-2} cm^2 s^{-1}, computations with equations (1), (2), and (4) show that the water table drops to –33 cm under the ridges and –3 cm under the hollows. After a period of adjustment for the plant communities involved the resulting carbon accumulation rates would be about –5 g m^{-2} yr^{-1} under the ridges, 17 g m^{-2} yr^{-1} under the hollows, and 15 g m^{-2} yr^{-1} overall, thanks to the areal dominance by the hollows. Note that the post-drying carbon accumulation rate would be higher than the original rate, because the mire was dominated by wet hollows that were brought into better peat-accumulation position by drying. Peat loss from the ridges and gain in the hollows would cause the microrelief to decrease over time. This means that the new possible steady-state position would lie on the 10^{-2} cm^2 s^{-1} flow line between B1 and B1'as a result of decreasing relief. Note that the entire range from B1 to B1' has a greater proportion of ridges than did B0. The reason is that for a steady state to re-establish would require wider ridges to retain water and compensate for less water flow (point B1) or less water flow and lower ridges (all points to the left of B1). Ridge expansion could occur by rapid peat accumulation on ridge margin microsites with intermediate water tables near the optimum for peat accumulation. All of the possible new steady-state scenarios along the line B1–B1' have a higher rate of carbon accumulation than the original rate of 6 g m^{-2} yr^{-1} at B0, ranging up to of 18 g m^{-2} yr^{-1} at point B1'. The initial "dry" transient state described above also has a higher rate of carbon accumulation (15 g m^{-2} yr^{-1}) than the original B0. Thus drying of the patterned mire parcel represented by B0 would lead to an increase in carbon accumulation rates in both the short and long term.

It is possible to roughly estimate the rate at which relief would change as a result of differential carbon accumulation under microtopographic highs and lows. If we assume a peat density of approximately 0.1 g cm^{-2} and a carbon content of approximately 50% of the dry peat weight, for each 10 gC m^{-2} yr^{-1} difference in carbon accumulation between highs and lows there would be a 2 mm change in microrelief per decade. Thus with hollows initially accumulating about 24 g C m^{-2} yr^{-1} more than the ridges, as in our drying scenario above, the 30-cm relief in example B0 would be reduced initially by about 4.4 mm per decade.

Consider finally the effect of a threefold increase in flow to 10^{-1} cm^2 s^{-1} on the patterned mire represented by point B0 (Fig. 3). From equations (1), (2), and (4) we determine that the water table would rise to –25 and +5 under ridges and hollows, respectively, resulting in carbon accumulation (after an adjustment period for the vegetation) of 18 g m^{-2} yr^{-1} under ridges, –8 g m^{-2} yr^{-1} under hollows, and –6 g m^{-2} yr^{-1} overall. Peat accumulation on the ridges and loss from the hollows would cause the microrelief to increase, and thus any new steady-state condition would fall along line B2–B2'. In reality a steady-state with such a tiny fraction of the mire occupied by ridges is probably unlikely because water would move by piping or through breaches in the ridges (i.e. water movement would no longer follow the flow law assumed in our computations). Furthermore, continuing peat accumulation on the ridges would help to maintain them, at least until pools with wave erosion and ice action develop. Thus the most likely result would probably be the prolonged disequilibrium persistence of ridges on about 10% of the mire, with hollows that become increasingly deep over time.

Discussion

These computations suggest that the response of peat accumulation to changes in water supply is complex. On a mire dominated by dry microtopographic elements, the immediate effect of decreased water supply is, not surprisingly, a decrease in the rate of carbon accumulation. A decrease in the rate of carbon accumulation on mires under unusually dry conditions has been documented with field measurements by Shurpali et al. (1995), Alm et al. (1999), Griffis et al. (2000), and Lafleur et al. (2003). All of these studies were on mires without well-organized surface microtopography, and the first three studies at least were on mires dominated by dry microsites. Thus they resemble the "drying" scenario of point A0, A1, and A1' in Fig. 2 discussed above. Furthermore, a prolonged decrease in water supply should cause a reduction in microtopographic relief, because microtopographical lows are more favorable than highs for peat accumulation. Such a decline in microrelief due to lowering of the water table has been confirmed experimentally in large monoliths by Weltzin et al. (2001). Alm et al.'s (1999) carbon balance measurements in an unusually dry season showed rapid loss of carbon from hummocks (–157 g C m^{-2} yr^{-1}) but near zero balance (–4 g C m^{-2} yr^{-1}) in wet lawns. Model computations presented here suggest that strong microtopography inhibits peat accumulation because it places much of the mire surface into positions that are either too wet or too dry for optimum peat accumulation. Thus after an initial decline in rate of peat accumulation due to a decline in water supply, peat accumulation could recover over the long term thanks to the reduction in microrelief. Measurements of the carbon balance on drained mires by Laine et al. (1996) led them to conclude that drying of mires due to climate change in many cases will not lead to carbon loss.

For mires dominated by dry microsites, the immediate effect of increasing water supply is, not surprisingly, increased peat accumulation. However, as suggested by the "wet" example of points A0, A2, and A2' in Fig. 2, this effect should be transient as increased wetness leads to growth in microrelief and consequent decline in peat accumulation rates. It is possible, of course, that under transient conditions of drought or excess water the rate of carbon accumulation will not have a one-humped curvilinear relationship with water table position, because sudden change places plants into environments where their productivity is impaired. However, at least one study (Bubier et al. 2003) suggests that adjustment of plant communities to changing moisture supply could be quite rapid.

Results presented here suggest that mires with strong ridge and hollow patterns should be especially vulnerable to loss of carbon fixation ability. The runoff-inhibiting nature of the pattern restricts steady-state microtopographic conditions to a rather narrow range of conditions (the region below the line of 5% microtopographic highs in Fig. 3). A water supply in excess of these limits on a patterned mire can produce a situation where only the highs accumulate peat and lows become unvegetated pools, a situation that is commonly observed (e.g. Foster & Fritz 1987; Foster et al., 1988; Belyea & Lancaster 2002). This helps explain why long-term peat accumulation rates are distinctly lower on strongly patterned mires (e.g. Korhola et al. 1995; Tolonen & Turunen 1996; Mäkilä et al. 2001; Turunen et al 2001). Note that a rise in the water table that causes degradation of mire hollows could also be caused by decreasing mire surface slope under an unchanging water supply as the mire evolves.

The results also suggest an explanation for some global patterns in the rate of peat accumulation. If peat accumulation is ideal under moderately wet conditions (those adequate to maintain saturation but dry enough to prevent widespread formation of strong microtopography), then one might expect peat accumulation rates to be highest in moderately humid environments. Several lines of evidence suggest that this is indeed the case. Some of the world's most extensive mires occur in regions with marginally adequate moisture for ombrotrophic peat accumulation: the continental grassland border regions of southwestern Siberia (Walter, 1977; Sheng et al. 2004) and northwestern Minnesota (Heinselman 1963). Both of these regions have unique ombrotrophic peatlands that lack strong surface microtopography or pools. The world's largest peatland complex, the Vasyugan mire in the Ob-Irtysh interfluve region of southwestern Siberia, is an ombrotrophic system that exists under just 0 to 200 mm annual excess of precipitation over evapotranpiration (Kremenetski et al. 2003). An intensively studied peat core from a ryam bog (dry, un-patterned, ombrotrophic mire) in the southern (i.e. driest) part of Vasyugan mire complex showed a high long-term average rate of peat accumulation (40 g C m^{-2} yr^{-1}) for nearly 10,000 years (Borren et al. 2004). Average peat thicknesses in the West Siberian lowlands appear to increase in the oligotrophic bog zone to a maximum near its southern (dry) limit (Kremenetski et al. 2003). Gorham et al. (2003) studied a transect in peat accumulation rates across North America and found that rates were highest near the dry limit of widespread peat accumulation in Minnesota, where, according to Baker et al. (1979), the annual excess of precipitation is virtually the same as in southwestern Siberia (0 to 200 mm). Hilbert et al. (2000) also found, by different modeling methods, that optimal peat accumulation should be associated with some intermediate water supply.

The concept of an optimal zone of peat accumulation at intermediate climatic wetness parallels the global relationship between peat accumulation and temperature: peat accumulation is optimal where mean annual soil temperatures are near 0°C and declines in both warmer and colder environments (Swanson et al., 2000). This zone of optimal peat accumulation should shift in response to changes in global temperature and precipitation.

Conclusions

Since peat requires saturation with water to accumulate and persist, one might expect mires to be tenuously dependent on constant moisture conditions under a stable humid climate. However, the computations made in this study suggest that the relationship of peat accumulation rate to water supply is complex, that peat accumulation can occur over a wide range of water supplies, and that peat accumulation is not uniformly improved by increasing wetness. All else being equal, a mire with strong microtopography should fix less carbon than a smooth mire, and strong patterning makes a mire vulnerable to peat loss if water levels rise. While occasional dry periods may cause peat loss in the short term, their long-term effect may be positive because they hinder the formation of strong microtopography. These model results are confirmed by the existence of extensive unpatterned ombrotrophic mires with high peat accumulation rates in continental regions with a moisture supply marginally adequate for ombrotrophic peat accumulation.

Acknowledgments

Thanks to J.M. Waddington for data on carbon accumulation rates and helpful comments. Thanks also to D.F. Grigal, M. Mäkilä, and an anonymous reviewer for helpful comments.

References

Alm, J., Talanov, A., Saarnio, S., Silvola, J., Ikkonen, E., Aaltonen, H., Nykänen, H. & Martikainen, P. 1997. Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen, Finland. Oecologia 110: 423–431.

Alm, J, Schulman, L., Walden, J., Nykänen, Martikainen P.J. & Silvola, J. 1999. Carbon balance of a boreal bog during a year with an exceptionally dry summer. Ecology 80(1): 161–174.

Baker, D.G., Nelson, W.W. & Kuehnast, E.L. 1979. Climate of Minnesota, Part XII – The hydrologic cycle and soil water. Technical Bulletin 322, University of Minnesota Agricultural Experiment Station, St. Paul, Minnesota.

Belyea, L.R. & Clymo, R.S. 2001. Feedback control of the rate of peat formation. Proc. Royal Society of London B268: 1315–1321.

Belyea, L.R. & Lancaster, J. 2002. Inferring landscape dynamics of bog pools from scaling relationships and spatial patterns. Journal of Ecology 90: 223–234.

Borren, W., Bleuten, W. & Lapshina, E.D. 2004. Holocene peat and carbon accumulation rates in the southern taiga of western Siberia. Quaternary Research 61: 42–51.

Bubier, J., Cril,l P., Mosedale, A., Frolking, S. & Linder, E. 2003. Peatland responses to varying interannual moisture conditions as measured by automatic CO_2 chambers. Global Biogeochemical Cycles 17(2): 1066, doi:10.1029/2002GB001946.

Foster, D.R. & Fritz, S.C. 1987. Mire development, pool formation and landscape processes on patterned fens in Dalarna, central Sweden. Journal of Ecology 75: 409–437.

Foster, D.R., Wright, H.E. Jr., Thelaus, M. & King, G.A. 1988. Bog development and landform dynamics in central Sweden and south-eastern Labrador, Canada. Journal of Ecology 76: 1164–1185.

Gorham, E. 1991. Northern peatlands: role in the carbon cycle and probable response to climatic warming. Ecological Applications 1(2): 182–195.

Gorham, D., Janssens, J.A. & Glaser, P.A. 2003. Rates of peat accumulation during the post-glacial period in 32 sites from Alaska to Newfoundland, with special emphasis on northern Minnesota. Canadian Journal of Botany 81: 429–438.

Griffis, T.J., Rouse, W.R. & Waddington, J.M. 2000. Interannual variability of net ecosystem CO_2 exchange at a subarctic fen. Global Biogeochemical Cycles 14(4): 1109–1122.

Hienselman, M.L. 1963. Forest sites, bog processes, and peatland types in the glacial Lake Agassiz region, Minnesota. Ecological Monographs 33: 327–374.

Heikkinen, J.E.P., Maljanen, M., Aurela, M., Hargreaves, K.J. & Martikainen, P.J. 2002. Carbon dioxide and methane dynamics in a sub-Arctic peatland in northern Finland. Polar Research 21(1): 49–62.

Hilbert, D.W., Roulet, N. & Moore, T. 2000. Modelling and analysis of peatlands as dynamical systems. Journal of Ecology 88: 230–242.

Ivanov, K.E. 1981. Water movement in mirelands (translators A. Thompson and H.A.P. Ingram). Academic Press, London.

Korhola, A., Tolonen, K., Turunen, J. & Junger, H. 1995. Estimating long-term carbon accumulation rates in boreal peatlands by radiocarbon dating. Radiocarbon 37(2): 575–584.

Kremenetski, K.V., Velichko, A.A., Borisova, O.K., MacDonald, G.M., Smith, L.C., Frey, K.E. & Orlova, L.A. 2003. Peatlands of the western Siberian lowlands: current knowledge on zonation, carbon content and Late Quaternary history. Quaternary Science Reviews 22: 703–723.

Lafleur, P.M., Roulet, N.T., Bubier, J.L., Frolking, S. & Moore, T.R. 2003. Interannual variability in the peatland-atmosphere carbon dioxide exchange at an ombrotrophic bog. Global Biogeochemcial Cycles 17(2): 1036, doi:10.1029/2002GB001983.

Laine, J., Silvola, J., Tolonen, K., Alm, J., Nykänen, H., Vasander, H., Sallantaus, T., Savolainen, I., Sinisalo, J. & Martikainen, P.J. 1996. Effect of water-level drawdown on global climatic warming: northern peatlands. Ambio 25(3): 179–184.

Mäkilä, M., Saarnisto, M. & Kankainen, T. 2001. Aapa mires as a carbon sink and source during the Holocene. Journal of Ecology 89: 589–599.

Renard, Ph. & de Marsily, G. 1997. Calculating equivalent permeability: a review. Advances in Water Resources 20(5): 253–278.
Sheng, Y., Smith, L.C., MacDonald, G.M., Kremenetski, K.V., Frey, K.E., Velichko, A.A., Lee, M., Beilman, D.W. & Dubinin P. 2004. A high-resolution GIS-based inventory of the west Siberian peat carbon pool. Global Biogeochemical Cycles 18: GB3004, doi:10.1029/2003GB002190, 14 pp.
Shurpali, N.J., Verma, S.B., Kim, J. & Arkenbauer, T.J. 1995. Carbon dioxide exchange in a peatland ecosystem. Journal of Geophyscial Resarch 100(D7): 14319–14326.
Swanson, D.K., Lacelle, B. & Tarnocai, C. 2000. Temperature and the boreal-subarctic maximum in soil organic carbon. Geographie physique et Quaternaire 54(2): 153–163.
Tolonen, K. & Turunen, J. 1996. Accumulation rates of carbon in mires in Finland and implications for climatic change. The Holocene 6(2): 171–178.
Turunen, J., Tahvanainen, T. & Tolonen, K. 2001. Carbon accumulation in West Siberian mires, Russia. Global Biogeochemical Cycles 15: 285–296.
Waddington, J.M. & Roulet, N.T. 1996. Atmosphere-wetland carbon exchanges: scale dependency of CO_2 and CH_4 exchange on the developmental topography of a peatland. Global Biogeochemical Cycles 10(2): 233–245.
Waddington, J.M. & Roulet, N.T. 2000. Carbon balance of a boreal patterned peatland. Global Change Biology 6: 87–97.
Walter, H. 1977. The oligotrophic peatlands of Western Siberia — The largest peinohelobiome in the world. Vegetatio 34: 167–178.
Weltzin, J.F., Harth, C., Bridgham, S.D., Pastor, J. & Vonderharr, M. 2001. Production and microtopography of bog bryophytes: response to warming and water-table manipulations. Oecologia 128: 557–565.

Tiivistelmä: Suon pienmuotojen, veden saatavuuden ja turpeen kertymisen vuorovaikutus pohjoisilla luonnontilaisilla soilla

Tutkimuksessa selvitettiin suon pinnan pienmuotojen, hydrologian ja hiilen kertymisen vuorovaikutusta pohjoisilta soilta teoreettisen tarkastelun ja kirjallisuuden avulla. Aiemmat tutkimukset pohjoisten soiden hydrologiasta ja hiilen kertymisestä ovat osoittaneet, että veden vaakasuuntainen virtaus suossa kasvaa eksponentiaalisesti kun vedenpinnan korkeus turpeessa kasvaa. Aiemmin on myös todettu, että vedenpinnan korkeuden ja hiilen kertymisen välillä on käyräviivainen riippuvuus, jolla on tietty maksimikohtansa. Tutkimuksessa laaditut yhtälöt osoittavat, että eniten hiiltä sitoutuu suoekosysteemiin tilanteissa, joissa vedenpinnan taso ei ole kovin korkealla ja suon mikrotopografisten pinnanmuotojen (mätäs- ja painannepintojen) vaihtelu on pieni. Märissä olosuhteissa suon pienmuotojen korkeuserojen ennustetaan lisääntyvän ja hiilen kertymänopeuden ero mätäs- ja painannepintojen välillä kasvaa kun taas kuivissa olosuhteissa ilmiö on päinvastainen. Soilla, joilla esiintyy runsaasti kuivempaa mätäspintaa, turpeen kosteuden lisääntyminen näyttää nopeuttavan hiilen kertymistä, mutta tämä voi olla vain tilapäistä, koska pienmuotojen korkeuserot saattavat myös kasvaa, joka johtaa aikaa myöten hiilen kertymänopeuden hidastumiseen. Suot, joilla esiintyy säännöllisiä vedenvirtausta heikentäviä kermejä/ jänteitä ja painannepintoja ovat erityisen herkkiä hiilen sitoutumisen pienenemiselle suon märkyyden lisääntyessä. Koska kuivat jaksot rajoittavat usein turpeen kertymistä vain lyhytaikaisesti, niillä voi olla pitkällä tähtäimellä hiilen kertymistä ajatellen edullisia vaikutuksia, koska ne estävät suuren pienmuotojen vaihtelun syntymistä suolle. Nämä löydökset saattavat osaltaan selittää miksi tietyt pinta-alaltaan maailman suurimmat suoalueet ja suurimmat turpeen kertymisnopeudet tavataan ilmastoltaan verraten kuivilla mantereisilla alueilla pohjoisella havumetsävyöhykkeellä.

Received 26.6.2006, Accepted 14.5.2007