The sensitivity of *Sphagnum* to surface layer conditions in a re-wetted bog: a simulation study of water stress

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SUMMARY

The behaviour of the water table in re-wetted bogs varies widely between different locations so that recolonising *Sphagnum* is vulnerable to water stress, especially when the water table is drawn down in summer. It is important to understand how physical site conditions influence the occurrence of water stress so that adequate management measures may be applied. In the work reported here, the respective roles of the hydrophysical properties of the uppermost peat layer and micro-scale site conditions are investigated using a Soil-Water-Atmosphere-Plant (SWAP) model, which simulates water table fluctuations and soil moisture conditions. The variables are: (a) cover and thickness of the *Sphagnum* layer, (b) microtopography (presence of open water), (c) hydrophysical properties of the uppermost soil layer and (d) rate of downward seepage. Data for the model are derived from field observations, from published literature, and from laboratory determinations of moisture characteristic curves and saturated and unsaturated hydraulic conductivity (k–h–Θ relationships) for peat. The simulation indicates that microtopography and the thickness of the moss layer are the dominant factors affecting groundwater behaviour and the risk of water stress. *Sphagnum* layers a few centimetres thick should be relatively well supplied with water from the underlying peat but as the *Sphagnum* carpet thickens, water movement through the unsaturated zone to the growing capitula will become increasingly difficult. *Sphagnum* layers appear to be most vulnerable to water stress when they are 5–15 cm thick. Beyond this thickness, water stored within the *Sphagnum* layer itself begins to offset the decline in the flux from below, and thus to reduce the dependence of the water supply to the stem tips on the maintenance of hydraulic continuity with the water table. The results obtained using the model underline the close interdependence between *Sphagnum* development and the accompanying changes in soil hydrophysics during the re-wetting phases of bog restoration projects.

KEY WORDS: bog restoration; Fochteloërveen; hydrophysics of peat; SWAP model; unsaturated zone.

INTRODUCTION

All of the large bog complexes in The Netherlands have been drained and used for peat mining, so that only relatively small relict areas remain. The original bog vegetation consisted of a carpet of *Sphagnum* moss with vascular plants which require wet, acid and oligotrophic conditions (e.g. *Eriophorum* spp., *Erica* spp.). To restore these bog remnants, the environmental conditions must enable *Sphagnum* to compete successfully with the vascular plants (Limpens 2003, Limpens *et al*. 2003). One factor that may impair the competitive ability of *Sphagnum* is the occurrence of water stress in the re-establishing moss layers, especially in summer when the water table is low (Spieksma 1998).

Water uptake, transport and evapotranspiration processes in *Sphagnum* differ from those in vascular plants. *Sphagnum* lacks roots and vascular channels, and is not able to regulate evaporation actively. It forms carpets in which the stems and pendant branches overlap to form spaces, or pores, which furnish the only route by which water can move from the water table through the unsaturated zone to the growing capitula at the surface. In the unsaturated zone, water is held in the pore spaces by matric forces and the pore water pressure is negative, i.e. below atmospheric pressure. Upward flow (capillary rise) occurs when the upward gradient in pore water pressure exceeds the downward gradient due to gravity (Koorevaar *et al*. 1983). During dry weather, water evaporates from the capitula, but they can remain moist for some time because evaporation reduces their water content and thus reduces pore water pressure at the surface, creating the conditions of upward pressure gradient necessary for water transport towards the surface from below.

The porosity of *Sphagnum* carpets is very high (>0.90), and they have correspondingly high water storage capacity. The leaves and stems consist of living green cells interspersed by dead hyaline cells with porous walls, which substantially enlarge the surface area and total porosity. The sizes of leaves and branches, diameters of hyaline cells and radii of pores in the hyaline cells are characteristic for each species (Clymo & Hayward 1982). Under wet conditions, all of the pore space is filled with water and forms a water reservoir. The ability of the carpet to retain water depends on pore size, and pores of a given size empty when the negative pore water pressure falls below a specific value. This relationship is described by the soil water retention curve or moisture characteristic. Under drying conditions, air will enter any active pores that are not able to retain water, interrupting the continuity of pathways for water movement between the hyaline cells and extracellular spaces. The (unsaturated) hydraulic conductivity is thus reduced so that mass flow is impeded and eventually prevented. Hydraulic conductivity declines sharply as water content decreases, so that a dry upper layer with a sharp transition to a moist lower zone may develop during periods of drought. When the hyaline cells fill with air, the moss turns white and papery; and if the evaporative demand at the surface cannot be met by transport of water from below for a prolonged period, the moss will die.

In undisturbed mires, different species of *Sphagnum* grow at different heights above the water table (Clymo & Hayward 1982), the aquatic and lawn species occurring close to the water table and the hummock-forming species in more elevated positions. During periods of low water table, the water content of hummock species is greater than that of lawn species (Rydín 1985, Wagner & Titus 1984). This is because, although evaporation from hummock species is more intense than from lawn species (Clymo 1973), the superior ability of hummock species to retain and conduct water under unsaturated conditions means that they are more efficient at delivering it to the capitula and thus at deferring the onset of water stress during drought (Overbeck & Happach 1957, Hayward & Clymo 1982, Rydín 1985).

In a natural bog, the top layer of the soil profile consists of young, undecomposed material derived mostly from *Sphagnum* moss. In a cutover mire remnant the situation is different. The top layer has been removed so that the uppermost part of the profile consists of decomposed peat which contains fewer large pores than a *Sphagnum* carpet, resulting in a lower capacity to store water and different water-retaining and water-conducting properties (Schouwenaars 1993, 1995). For bog restoration, *Sphagnum* mosses must recolonise, since they are the primary peat-forming species (Clymo 1983). The recovery process usually begins with the appearance of small patches of moss, which gradually expand to form larger mats and carpets. On cutover sites in The Netherlands, new *Sphagnum* layers have begun to develop in patches of <1 m^2, but *Sphagnum* still occupies only 1–5 % of the surface and recolonisation does not appear to be self-sustaining.

Theoretical considerations suggest that the hydrophysical properties of the *Sphagnum* and upper peat layers, along with micro-site characteristics such as local topography and proximity to open water, are likely to be central factors in determining the point of onset of water stress in *Sphagnum* (Schouwenaars 1993, Spieksma 1998), although their detailed roles are poorly understood. In order to inform and improve site management, we need a better understanding of the relative effects of these factors in the re-establishment of *Sphagnum* on cutover peatland.

Direct measurements of the physical properties of *Sphagnum* layers are rare. Moreover, the wide variation in soil properties and microtopography within a disturbed bog introduces confusing complexity and makes the collection of sufficient field data to build up a complete understanding too difficult and costly to be practical. An alternative approach is through simulation modelling, which allows us to explore clearly defined problems with controlled variables and may help to identify critical processes or to focus effort in the field.

The simplest soil water flow models act as ‘tipping buckets’, calculating losses by evaporation, transpiration and percolation as functions of the average degree of saturation of the rooting zone and thus ignoring the vertical soil moisture gradient. Van Dam & Feddes (2000) describe a more realistic hydrological model for the simulation of soil water behaviour in the unsaturated and saturated zones, which has been developed at Wageningen University since 1978. Van Dam *et al*. (2004) describe the underlying concepts and compare them to those of other models. This Soil-Water-Atmosphere-Plant (SWAP) model simulates one-dimensional water flow at variable saturation levels using Richards’ equation, which is based on Darcy’s law and the continuity equation, so that it has a strong physical basis and is generally applicable. Darcy’s equation for steady, vertical flow is:

$$v = -k(h)\left(1 + \frac{dh}{dz}\right) \qquad [1]$$

where d*h*/dz is the gradient of the water pressure head h (m) with respect to height z (m), k is hydraulic conductivity (m d^{-1}) and v is the flux density (m d^{-1}) (Gardner 1958). Richards' equation, extended to include water uptake by the roots of vascular plants, can be written as:

$$\frac{\partial \Theta}{\partial t} = C(h)\frac{\partial h}{\partial t} = \nabla[k(h)\nabla h] - \frac{\partial k_z(h)}{\partial z} - S(h) \quad [2]$$

where Θ is the volumetric water content (L^3 L^{-3}), h is the soil water pressure head (L), C is the differential moisture capacity $\partial\Theta/\partial h$ (L^{-1}), t is time (T), k_z is the hydraulic conductivity in the z direction (L T^{-1}), z is the vertical co-ordinate (positive upward) (L), and S is a sink term for root water extraction (L^3 L^{-3} T^{-1}).

The SWAP model has been tested in several studies of re-wetted peatlands, and has been shown to simulate adequately the water table fluctuations and soil moisture conditions observed in the field (Spieksma *et al*. 1996, Spieksma & Schouwenaars 1997, Spieksma *et al*. 1997, Spieksma 1998). The model outputs are the number of days from the start of the simulation when critical growth conditions arise, and the corresponding position of the water table.

In the study described here, the SWAP model was used to investigate the sensitivity of recolonising *Sphagnum* to micro-site variables by simulating water stress under drought conditions.

METHODS

Study site and fieldwork

The Fochteloërveen is a cutover bog located on the western slope of the Drents Plateau in the northern Netherlands (53°00'N, 6°30'E, 10 m above sea level). Its area is 1,720 ha, the remnant peat layer is 0.5–2 m thick, and it overlies a sandy aquifer (Spieksma 1998). The construction of surface bunds with control weirs began in 1965, but small-scale private peat cutting continued until the 1980s and the most recent re-wetting operations post-date 1990. Several hydrological field studies were conducted by Groningen University between 1994 and 1997 (Gosen 1996, Weber 1996, Spieksma 1998). After 30 years of re-wetting, the vegetation was still dominated by *Molinia caerulea* with some dwarf shrubs (*Calluna vulgaris* and *Erica tetralix*). *Sphagnum* occurred only in small patches on bare peat and on floating rafts in permanent pools (Vermeer & Joosten 1992).

Field measurements and peat sampling were carried out within a *ca*. 30 ha catchment in the eastern part of the Fochteloërveen. The vegetation of this area was surveyed in detail, recording cover of vascular plants and mosses. Ten of the vegetation quadrats (B1–B10) were selected at random for retention as permanent monitoring plots. Nine dipwells (perforated PVC pipes, diameter 3 cm) were installed at evenly-distributed locations across the study area labelled 201–209, and the depth of the water table in each of these was measured using a sounding ("plopping") device and tape measure at intervals of 14 days for two years, from 01 January 1995 to 31 December 1996. The altitude of the mire surface at the dipwell and permanent quadrat locations was measured to the nearest cm. During the summer of 1995, tensiometers with ceramic cups 5 cm long and 1 cm in diameter were installed at depths of 15, 30 and 50 cm at four locations and read 2–3 times per week. Rainfall was measured with an automatic tipping bucket recorder.

Hydrophysical properties of peat

Derivation of soil water retention curves

A soil water retention curve (moisture characteristic) expresses the relationship between h and Θ, where h is pore water pressure (cm) and Θ is volumetric water content (cm^3 cm^{-3}). Fifty-two undisturbed 250 cm^3 core samples of the peat layer 5–10 cm below the surface (i.e. immediately beneath the loose, cracked surface material) were collected in steel cylinders of diameter *ca*. 8 cm. Equal numbers of samples were taken from locations where the dominant vascular plant species was *Calluna vulgaris, Erica tetralix, Eriophorum vaginatum* and *Molinia caerulea*. For each vegetation type, the maximum distance between the 13 sampling locations was 500 m. The samples were returned to the laboratory in their cylinders and submerged in water for one week so that they were completely saturated. Their moisture characteristics (desorption and adsorption curves) were then determined using a sand box apparatus (Stolte *et al*. 1994) containing two 10 cm layers of uniform synthetic sand, the lower coarse-grained and the upper with (fine) grain size such that negative pore water pressures down to -100 cm could be applied. The pore water pressure in the sand could be controlled by adjusting a hanging water column with overflow attached to the sand box. The bases of the cylinders were covered with cotton cloth to prevent loss of material from the samples, they were placed on the sand box, and pore water pressures (h) of 0, -10, -20, -31, -50, -70 and -100 cm were applied in sequence (desorption) and then in reverse order (adsorption). The samples were allowed to equilibrate for one week (to constant weight) at each pore water pressure. Finally they were oven dried at 105°C and re-weighed, and the water content for each value of *h* was determined by subtraction and divided by the sample volume to obtain Θ (assuming density of water 1 g cm^{-3}) (Gosen 1996).

Determination of k–h–Θ relationships

Relationships between h, Θ and unsaturated hydraulic conductivity *k* (m d^{-1}) for peat were also determined in the laboratory, using two different methods for different ranges of pore water pressure.

Infiltro method (0 > *h* > -60 cm)

Six undisturbed peat cores 20 cm in diameter and 20 cm long were cut using steel cylinders. Five of these (INFIL5 and INFIL12–15) were taken from the peat layer 10–30 cm below the surface at a location near Dipwell 207 where the vegetation was dominated by *Eriophorum angustifolium* and the degree of humification of the uppermost peat layer was H4–5 on the von Post scale (von Post & Granlund 1926). The sixth sample (INFIL4) was from an area near Dipwell 205 with a 7 cm layer of *Sphagnum compactum* at the surface overlying slightly humified (H3–4) peat. The depth range of this sample was 0–20 cm. Immediately after collection, the samples were stood upright in trays containing a few cm of water. They were then transported to the laboratory where the depth of the water was increased gradually until, after a minimum period of one month, complete saturation was achieved.

These samples were used for the determination of hydraulic conductivity at relatively high soil water content (pore water pressure 0 to -60 cm), using the ‘drip infiltro’ or ‘improved crust’ method (Stolte *et al*. 1994). For this, tensiometers were installed at depths of 5, 10 and 15 cm to measure pore water pressure.

Each completely saturated sample was placed on wire netting, which allowed water to drain freely from its base. A Mariotte bottle was arranged to maintain a 2 cm layer of water on top of the sample, and several times a day the rate of drainage (equal to the vertical flux of water through the sample) was measured and the tensiometers were read. Constant flux conditions (indicated by steady readings from all three tensiometers) were always established within one day, and the data collected under these conditions were used to calculate saturated ($h \geq 0$) hydraulic conductivity using Equation [1].

The sample was then placed on the sand box apparatus described above, and water was applied evenly to its upper surface through an array of hypodermic needles to which the water supply, and thus the rate of infiltration to the sample, was regulated by a pump. The needles were set into a PVC plate which completely covered the upper end of the sampling cylinder so that evaporation was prevented. The gradient of pore water pressure (*dh/dz*) in the sample could be set and adjusted using the hanging water column fitted to the sand box. Initially, water was applied at such a rate that a layer of water was maintained on top of the sample, i.e. it was completely saturated. The infiltration rate was then reduced and progress towards steady-state conditions was monitored by reading the tensiometers at daily intervals. When equilibrium between the rates of infiltration and downward flux through the sample (the steady state) was attained, the water flux and the corresponding gradient of pore water pressure were recorded. From these data, the unsaturated hydraulic conductivity k(*h*) could be calculated for the layer of peat between each pair of tensiometers using Darcy’s Law (Equation [1]). The infiltration rate was then reduced in stages, repeating the equilibration and recording procedure for each new flux. For all *h* values within a class interval of 5 cm, the corresponding values of *k* were averaged and plotted against the median *h* value for the class.

Evaporation method (-60 cm > h > -800 cm)

Three undisturbed peat cores, 10 cm in diameter and 10 cm long, were collected in steel cylinders from a location near Dipwell 204 where *Erica tetralix* was the dominant plant species. One sample (EVA32) covered the depth range 10–20 cm (H4–5) and the other two (EVA33 and EVA34) were from a depth of 35–45 cm (H6–7). The samples were transported to the laboratory and completely saturated as described for the ‘infiltro method’ samples above. They were then removed from the cylinders and wrapped loosely in plastic sheeting which isolated their bases and was fastened around their sides so that only their upper surfaces were exposed. This was done to ensure that water loss by evaporation would be strictly limited to the top layer, and thus that vertically upward water flow would be maintained, even when sample diameter was reduced by the shrinkage that accompanied drying. Tensiometers were installed to measure pore water pressure at depths of 3, 5 and 7 cm in each sample.

These samples were used for the determination of unsaturated hydraulic conductivity at relatively low soil water content (pore water pressure -60 cm to -800 cm) using the ‘evaporation method’ (Wind 1972, 1979). Each wrapped sample was placed on a weighing scale, lamps and a ventilation fan were used to induce evaporation from the top of the sample, and sample weight and the corresponding pore water pressure values were recorded simultaneously several times a day. The upward flux of water due to evaporation was calculated as the weight loss per unit time.

In contrast to the infiltro method, where measurements were made under steady-state (constant flux) conditions, the conditions here were always unsteady with soil water being redistributed amongst the different layers of the sample between measurements. The *k*–*h*–Θ relationships were derived using an iterative calculation procedure based on Darcy's law and the continuity equation (Wind 1979), which was developed by Alterra Wageningen within the 'Metronia' computer program (Stolte *et al*. 1994). The changing values of Θ due to redistribution of water between readings were derived from the pore water pressure (*h*) values indicated by the tensiometers *via* an estimated water retention curve (*h*–Θ relationship). The flux through the peat layer between each pair of tensiometers could then be calculated from the changes in water content at the tensiometer locations.

Again, for all measured values of *h* within an interval of 5 cm, the corresponding values for *k* were averaged and plotted against the median *h* value for the class. An average hydraulic conductivity function for a 'representative Fochteloerveen' peat profile was derived from the k–*h*–Θ functions by classifying them according to the value of Θ (class size 0.01 cm^3 cm^{-3}) and calculating the geometric mean of *h*(Θ) and *k*(Θ) for each class.

Hydrophysical properties of *Sphagnum* carpets

Data for the hydrophysical properties of *Sphagnum* carpets were derived from the few available literature sources. Part of the k–*h*–Θ relationship was derived by combining the results of Hayward & Clymo (1982) with those of Rydín (1985), and another part using data from Clymo (1973).

The measurements of Hayward & Clymo (1982) were used to derive a water retention curve for a *Sphagnum* carpet at pore water pressures ranging from 0 to -100 cm. Rydín (1985) measured the water content of the capitula and second centimetre of the stem section together with the corresponding water table for various *Sphagnum* species including *Sphagnum capillifolium* (*rubellum*) under conditions of dim light, air temperature 20°C and humidity 35–45% with an electric fan producing a wind speed of 1 m s^{-1}. Evaporation was not measured but, given the conditions, this was estimated to be 3 mm d^{-1}. The pore water pressure gradient in the uppermost 2 cm layer was determined by combining Rydín's water content values with the water retention curve, then the assumed water flux due to evaporation was applied to yield the *k*–*h*–Θ relationship. Clymo (1973) measured the water content of *Sphagnum* layers at various depths with the water table around 30 cm below the capitula. The water retention curve was used to determine the corresponding pore water pressures at different depths and *k*–*h*–Θ relationships were thus derived for the observed range of *h* (0 to -80 cm), again assuming that the evaporation flux density was 3 mm d^{-1}.

The data from these two sources were combined and a van Genuchten fit (Gosen 1996) was used to establish a physically correct *k*–*h*–Θ relationship for the range -100cm < *h* < 0 cm to represent a young *Sphagnum* layer in the SWAP model. For values of *h* < -30 cm, the values of *k* thus obtained were similar to those obtained using the infiltro method for the single sample (INFIL4) that included a young *Sphagnum compactum* layer (see above).

Modelling

The re-establishment of *Sphagnum* on bare peat at the Fochteloërveen generally begins in small isolated patches, and the simulations explored the processes occurring in these isolated patches under drought conditions. Since the properties of the moss patches differ from those of their surroundings, a quasi-2-dimensional approach to modelling was needed. The following assumptions were made:

(1) the area of a patch was negligibly small, and the water table within a patch was the same as that in its surroundings, i.e. the water table was flat;
(2) a change in water table in the surroundings would be reproduced immediately beneath the moss patch, i.e. drainage resistance was zero.

At the start of each simulation, the water table was positioned at the top of the *Sphagnum* layer so that both the moss and the underlying peat were saturated but there was no surface inundation. This condition resembles the frequently-observed field situation where vascular plants and a *Sphagnum* moss layer compete, e.g. for water. The processes occurring in the uppermost few centimetres are important, and the model compartments here were made very thin. Moving downwards from the moss surface, the compartment thicknesses were 0.2 cm for the first centimetre, 0.5 cm for the second centimetre, 1 cm down to a depth of 1 m, and 5 cm for deeper layers. The time step was varied depending on the rate at which soil moisture conditions changed, and in some cases was less than one hour.

The model was used to simulate the fluctuations of the water table and water stress in the *Sphagnum* layer within different scenarios reflecting the real situation at the Fochteloërveen. Data were required to set the hydrological boundary conditions, for micro-site conditions, for the hydrophysical properties of the *Sphagnum* and peat layers, and to identify thresholds for the onset of critical conditions. These were derived from a combination of field data, laboratory data and literature sources as outlined below.

Hydrological boundary conditions

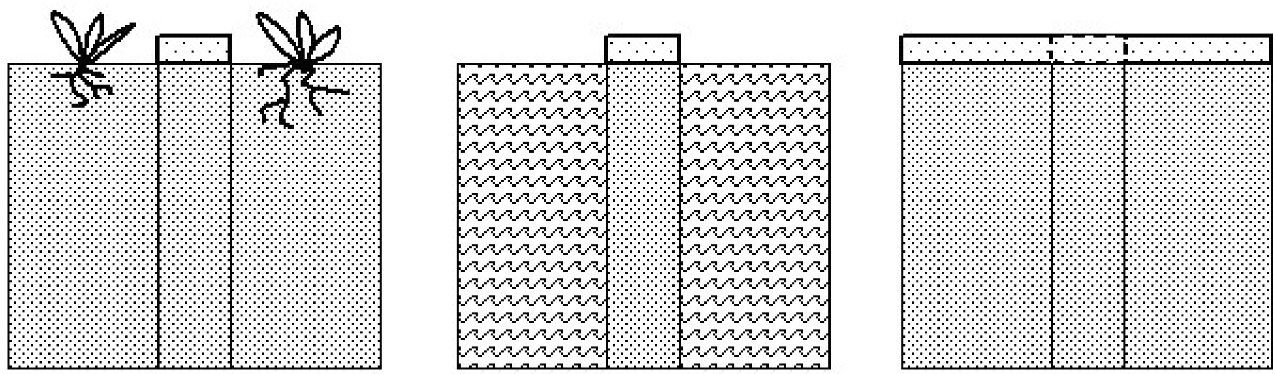
The simulated weather conditions represented a warm, rain-free period (01 June to 31 August 1998) with a daily maximum temperature of 25°C, wind speed 3 m s^{-1} and net radiation 15×10^7 J m^{-2} d^{-1}. Open water evaporation was calculated using the Penman equation, which yielded a value of 4.5 mm d^{-1}. Potential evapotranspiration (E_{ref}) for *Sphagnum* carpets under the same weather conditions was set at 4 mm d^{-1} on the basis of evaporation rates for *Sphagnum papillosum* under field conditions in the Netherlands reported by Schouwenaars (1990). For bare peat with rooted vascular plants, an E_{ref} value of 3.5 mm d^{-1} was derived from measurements of climatic variables above *Molinia* vegetation at the Dutch bog remnant Engbertsdijksvenen during the summers of 1988 and 1989 (Moors *et al*. 1995).

The lower boundary condition was set by the downward seepage flux to the underlying sand. The downward seepage calculated by Weber (1996) as the residual term of a water balance for the Fochteloërveen area showed strong seasonal variation, with a summer estimate of 0.44 mm d^{-1}. If this flux were to be sustained throughout the year, it would exceed the average annual rainfall surplus in this part of the Netherlands. This is not realistic because substantial surface runoff is observed every winter. Moreover, we may expect that downward seepage will be concentrated in locations where the peat is thinnest, such as the floors of former ditches and deeper cuttings; so that the flux of downward seepage in the 2 m thick peat layer simulated will be lower than the whole-site average. Thus, most of the simulations incorporated a downward seepage flux of 0.25 mm d^{-1} and only a few were conducted with values of 0.1 and 0.4 mm d^{-1}.

Hydrophysical micro-site conditions

The soil column of the patch was made up of two layers, with a *Sphagnum* layer overlying 2 m of more humified peat. In the scenarios simulated, the *Sphagnum* layer was 2, 10 or 20 cm thick and there were three contrasting conditions of the area immediately surrounding the *Sphagnum* patch (Figure 1), namely:

(1) bare peat with vascular plants;
(2) open water; and
(3) complete *Sphagnum* carpet.



Scenario 1: Bare peat with vascular plants (*Eriophorum angustifolium, Erica tetralix* and *Molinia caerulea*) and without open water immediately surrounding the *Sphagnum* patch.

Scenario 2: Open water. The *Sphagnum* patch forms the top of a 2 m peat column surrounded by water. The water table beneath the *Sphagnum* patch is taken to be equal to the open water level.

Scenario 3: Surface completely covered by a layer of *Sphagnum* moss, as might eventually be attained at a regenerating site.

Figure 1. Description of the three conditions of *Sphagnum* cover and micro-environment for the area surrounding the regenerating *Sphagnum* patch that were simulated in modelling, namely (1) bare peat; (2) open water; and (3) *Sphagnum* moss. Key: light stipple: mosses; darker stipple: peat; wavy lines: water.

In the SWAP model, water uptake occurs from the rooting zone. For *Sphagnum*, the layer from which evaporative water loss occurred was assumed to be equivalent to the rooting zone and its thickness was set at 5 cm. For bare peat with vascular plants the thickness of the rooting zone was set at 40 cm. The rate of water extraction S is likely to decline with depth z, so a quadratic weighting function was used with maximum value at the surface declining to zero at the base of the rooting zone (at depth D = 5 cm or 40 cm). The function used was

$$S_z = \left(\frac{D - z}{D}\right)^2 \qquad [3]$$

Water retention (k–h–Θ) relationships

The soil water retention values used in modelling were derived from the k–h–Θ relationships whose determination is described earlier in this paper. Both moisture content (Θ) and hydraulic conductivity (k) vary with pore water pressure (h) and the relationships are hysteretic. Comparing adsorption and desorption curves showed that the range of moisture content at a given pore water pressure can be 10–15% in the range $0 > h > -100$ cm. As the investigation focused on water stress arising in dry weather, most simulations were based on desorption curves only. However, in order to obtain a better understanding of the implications of the differences between drying and wetting conditions, a few simulations were conducted using both curves and the results compared. The sensitivity to variation of hydraulic conductivity was explored by carrying out model simulations with k values 0.316, 1.0 and 3.16 times the geometric means calculated for the samples tested using the evaporation method.

Selection of critical growth conditions

If the rate of upward transport of water within the soil is not limiting, evaporation will continue at the potential (E_{ref}) rate until the pore water pressure at the soil surface is lowered sufficiently to equal the partial pressure of water vapour in the air (Hillel 1980). However, the k–h relationship is such that as pore water pressure is reduced, hydraulic conductivity also declines; and in practice a critical point is reached at which the maximum possible upward flux density within the unsaturated zone can no longer supply the evaporative demand at the soil surface and rapid drying of the surface layer ensues. Critical growth conditions for the model were set in terms of the associated negative pressure heads in the uppermost layer of the profile.

High evaporation rates have been observed in *Molinia caerulea* fields in the Netherlands even under dry conditions (Spieksma *et al*. 1997). On this basis, for bare peat with rooted vascular plants,

Table 1. Summary of information available from literature on critical moisture thresholds, expressed in terms of water content or pore water pressure.

Moisture condition	Effect on *Sphagnum*	Literature source
8 g water g^{-1} dry weight / 0.14 cm^3 cm^{-3} (average for a 5 cm *Sphagnum* layer)	photosynthesis reduced	Williams & Flanagan (1996); Rydín & McDonald (1985a,b)
4.5 g water g^{-1} dry weight	100% survival after 1 day, 90% after 5 days, 82% after 10 days	Wagner & Titus (1984)
3 g water g^{-1} dry weight (average for a 5 cm *Sphagnum* layer)	50% reduction in photosynthesis	Williams & Flanagan (1996); Rydín & McDonald (1985a,b)
1.2 g water g^{-1} dry weight	*Sphagnum nemoreum* recovered 70% of original photosynthesis rate after 1 day, did not recover after 5 days	Clymo (1973)
1.2 g water g^{-1} dry weight	86% survival after 1 day, 5% after 5 days, 3% after 10 days	Wagner & Titus (1984)
0.06 cm^3 cm^{-3}	weakened competitive ability expected	Wagner & Titus (1984)
0.01 cm^3 cm^{-3}	minimum value for survival of *S. capillifolium*	Wagner & Titus (1984)
pF 3.4	survival 100% (*S. capillifolium*)	Clymo (1973)
pF 4.1	survival 48% (*S. capillifolium*)	Clymo (1973)
pressure head < -12,600 cm (pF < 4.1)	*Sphagnum* capitula wilt and die	Wagner & Titus (1984)
pF 4.4	survival 27% (*S. capillifolium*)	Clymo (1973)

the threshold at which evaporation would fall below the maximum rate due to limitation of upward mass movement through the unsaturated zone was set at a pressure head of -1,000 cm (pF 3; pF = log -*h*) and that at which evaporation would cease altogether was set at -16,000 cm (pF 4.2). Between these two pressure head values, a linear reduction in evaporation from the potential rate to zero was assumed.

Critical thresholds for *Sphagnum* layers were derived on the basis of information from the literature, which offers a range of possible values because experimental procedures and scenarios have varied between workers (Table 1). The following critical physical growth conditions were selected for *Sphagnum capillifolium* patches, and were used to assess the simulation results:

1: moisture content in the upper 0.2 cm less than 0.06 cm^3 cm^{-3} (pF 2.7);
2: moisture content in the upper 0.2 cm less than 0.01 cm^3 cm^{-3} (pF 4.1);
3: moisture content in the upper 1.0 cm less than 0.01 cm^3 cm^{-3} (pF 4.1); and
4: moisture content in the upper 2.0 cm less than 0.01 cm^3 cm^{-3} (pF 4.1).

It is noteworthy that, for Criterion 4, the model may predict death of the uppermost 2 cm of the moss layer during a period of drought, which would cancel out the average annual growth of *Sphagnum*, and in the early stages of *Sphagnum* re-establishment may even mean death of the entire moss layer (Schouwenaars, personal observations). In view of the potential for such a fundamental change in the predicted direction of development, the sensitivity of the model to variation in the critical moisture conditions assumed for the *Sphagnum* top layer was also explored by comparing the outcomes obtained using these four criteria.

RESULTS

Field measurements

Sample results of the field measurements, for five of the dipwells and five permanent quadrats, are summarised in Table 2. The mire surface within the study catchment was almost flat, with maximum variation in altitude of *ca*. 30 cm. During 1995 and 1996, most of it was relatively wet with shallow (0–19 cm) inundation in winter and the water table falling no more than 15–20 cm below the surface in summer. The annual range of water table fluctuation in the dipwells varied from 14 cm at the wettest site to 48 cm at drier sites.

At the tensiometer sites, the water table did not fall more than 70 cm below the mire surface during the period of measurements. The measurements proved to be difficult under these conditions and the data were not good enough to use for further analysis. No differences in pressure head could be measured. This might be due to the difficult field measurement procedure. Another explanation might be that under the prevailing field conditions the upward gradients in pore water pressure were almost equal to, and only slightly steeper than, the opposing gradient induced by gravity. Most probably there was an upward water flux under near-equilibrium conditions which would mean, under the observed conditions (almost dry weather, no indication of limited evaporation), that the unsaturated hydraulic conductivity was relatively high at pressure heads between 0 and -100 cm.

Hydrophysical properties of soil layers (*k*–*h*–Θ relationships)

The *h*–Θ relationships (adsorption and desorption curves) are presented in Figure 2. There were no significant differences between corresponding points on the curves for the four different vegetation types.

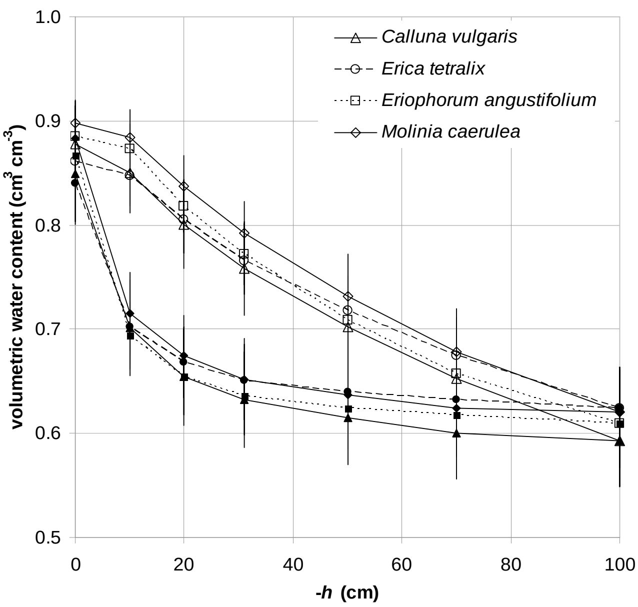


Figure 2. Water retention curves (mean values and standard deviation, n = 13) for peat samples taken from depth 5–10 cm beneath four different vegetation types, distinguished on the basis of dominant species. For each vegetation type, both the desorption (upper, hollow symbols) curve and the adsorption (lower, filled symbols) curve is shown.

Table 2. Summary of surface altitude, vegetation and water table fluctuations during the period 01 January 1995 to 31 December 1996 at some locations in the Fochteloerveen. The water table data are derived from dipwell measurements at intervals of 2 weeks; for the permanent quadrat locations they have been calculated by linear interpolation between dipwells.

	location	surface altitude (m a.s.l.)	water table (cm above mire surface)			vegetation	
			highest	lowest	range	vascular plants	*Sphagnum* species
DIPWELLS	202	10.85	-1	-43	42	*Erica tetralix* *Molinia caerulea*	not present
DIPWELLS	204	10.85	-1	-47	46	as 202	not present
DIPWELLS	205	10.81	1	-18	19	*Calluna vulgaris* *Erica tetralix* *Molinia caerulea*	present, not determined
DIPWELLS	206	10.63	19	5	14	*Eriophorum vaginatum* *Molinia caerulea*	*S. cuspidatum*
DIPWELLS	207	10.77	7	-9	16	as 205	present, not determined
PERMANENT QUADRATS	B4 (20m from 206)	10.67	18	-6	24	*Molinia caerulea* *Eriophorum vaginatum* *E. angustifolium* *Erica tetralix*	*S. cuspidatum* *S. fimbriatum* *S. papillosum* *S. recurvum*
PERMANENT QUADRATS	B5 (30m from 206)	10.68	17	-5	22	as B4 with *Calluna vulgaris*	*S. cuspidatum* *S. fimbriatum* *S. molle* *S. papillosum* *S. recurvum*
PERMANENT QUADRATS	B6 (20m from 205)	10.72	11	-11	22	as B5	*S. compactum* *S. molle* *S. papillosum* *S. recurvum* *S. rubellum* *S. subnitens*
PERMANENT QUADRATS	B8 (40m from 205)	10.76	7	-15	22	as B5	*S. fimbriatum* *S. molle*
PERMANENT QUADRATS	B10 (50m from 202)	10.74	10	-38	48	as B4 with *Pinus sylvestris*	*S. compactum* *S. fimbriatum* *S. molle*

Figure 3 shows sample *k–h* relationships determined by the infiltro method. For the five peat samples (INFIL5 and INFIL12–15), hydraulic conductivity was of the order of 1 cm d^{-1} when pore water pressure was close to atmospheric pressure ($h \approx 0$), and declined to *ca*. 0.1 cm d^{-1} as h approached -50 cm. For the sample taken from a living *Sphagnum compactum* layer (INFIL4), hydraulic conductivity was *ca*. 100 times that of the peat samples at $h \approx 0$ and declined to less than 1 cm d^{-1} only when h fell below -15 cm.

The *k–h–*Θ relationships determined using the evaporation method are presented in Figure 4 (Θ*–h* relationship) and Figure 5 (*k–h* relationship). For the pore water pressure range -50 cm to -100 cm the water contents of the samples varied from 0.75 to 0.60 cm^3 cm^{-3} and their unsaturated conductivities from $4x10^{-2}$ to $4x10^{-3}$ cm d^{-1}. At lower pore water pressures (-300 cm to -400 cm) the water contents of the samples were between 0.55 and 0.30 cm^3 cm^{-3} and the values for unsaturated conductivity were $<5x10^{-3}$ cm d^{-1}.

The combined *k–h–*Θ relationships for both a young *Sphagnum* layer and a 'representative Fochteloërveen' peat layer are presented in Figures 6 and 7. Water can be extracted more readily from a *Sphagnum* layer than from peat at small negative pore water pressures (Figure 6). In consequence, whilst the hydraulic conductivity of a *Sphagnum* layer is two orders of magnitude greater than that of

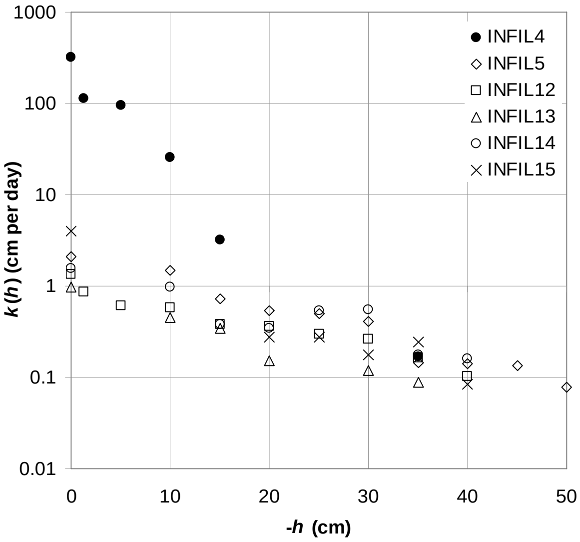


Figure 3. Relationships between hydraulic conductivity $k(h)$ (logarithmic scale) and $-h$ (absolute value of negative pore water pressure) determined using the 'infiltro' method for samples from a site dominated by *Eriophorum angustifolium.* Samples INFIL5 and 12–15 consisted of peat (H4–5 on the von Post scale) taken from depth 10–30 cm. Sample INFIL4 was taken from depth 0–20 cm in a living *Sphagnum compactum* cushion. The first (left-hand) value of $k(h)$ in each series (h = 0) indicates the saturated hydraulic conductivity. Values for h = -1.5 cm indicate the mean $k(h)$ value for $0 > h > -2.5$ cm. For values of $h < -2.5$ cm, each point represents the mean of all measured $k(h)$ values corresponding to values of h within a 5 cm class.

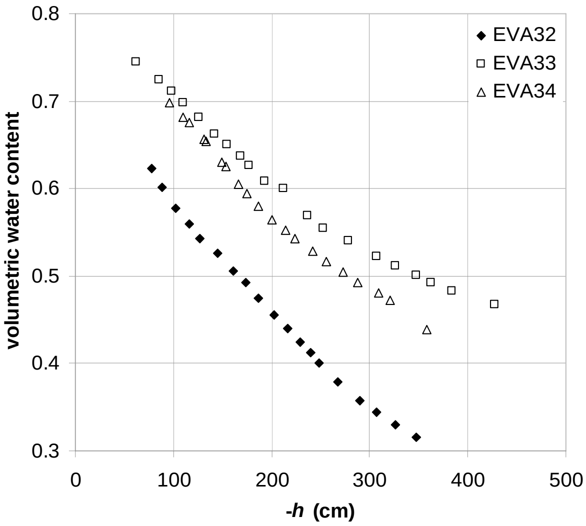


Figure 4. Water retention characteristics at low pore water pressure for three samples from a wet site with *Sphagnum.* Sample EVA32 was taken from depth 10–20 cm in slightly humified (H4–5) *Sphagnum* peat. Samples EVA33 and EVA34 were from a more humified (H6–7) layer (depth 35–45 cm) at the same location.

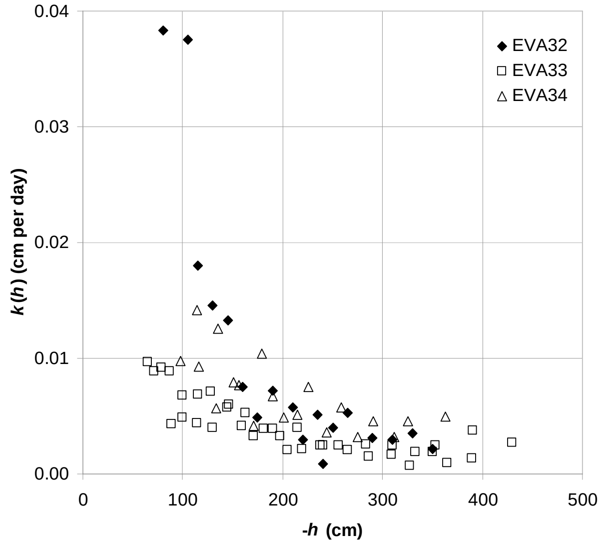


Figure 5. Relationships between unsaturated hydraulic conductivity $k(h)$ and pore water pressure ($-h$) at low pore water pressure for three samples (EVA32–34 as for Figure 4) from a wet site with *Sphagnum.* Each point represents the average $k(h)$ value for a 5 cm class of h.

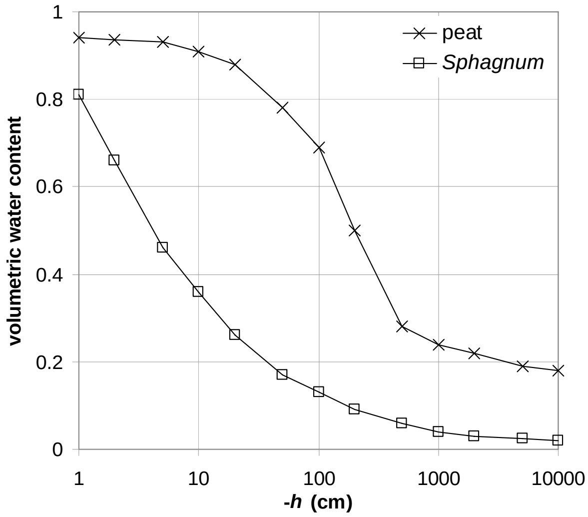


Figure 6. Water retention curves (Θ–h relationship) for a *Sphagnum* moss layer (derived from literature and measurements) and for the underlying peat (measured) as used in the sensitivity analysis.

peat under near-saturated conditions, its permeability declines rapidly as water is withdrawn, and falls below that of peat when the pore water pressure is only -10 cm (Figure 7). Thus the upward movement of water in *Sphagnum* layers may often be limiting under field conditions because values of h below -10 cm often occur. These data illustrate clearly the hydrophysical differences between the two layers and will be used to further elaborate and explain the predicted differences in onset of water stress between the modelled scenarios.

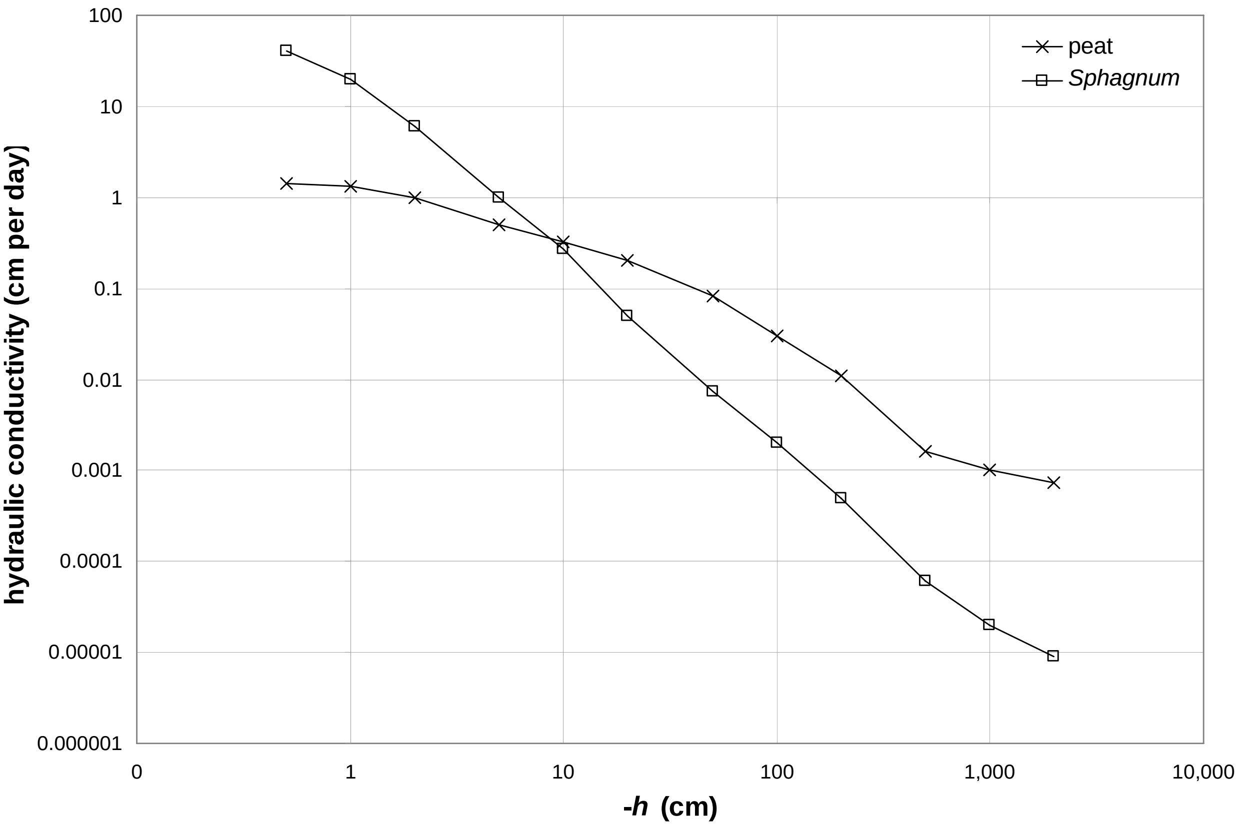


Figure 7. Relationship between unsaturated hydraulic conductivity $k(h)$ and pore water pressure h for a *Sphagnum* moss layer (derived from literature and measurements) and of the underlying peat (measured) as used in the sensitivity analysis.

Modelling

Figure 8 shows the results of the SWAP simulations for different moss layer thicknesses and for the three physical site conditions illustrated in Figure 1.

The water table beneath an isolated *Sphagnum* cushion surrounded by bare peat (Scenario 1) was drawn down to below -80 cm (relative to the surface) after 40 days, whereas beneath a moss cushion surrounded by open water (Scenario 2) it was still above -40 cm after 80 days. Water table drawdown for these scenarios was insensitive to the thickness of the moss layer on the regenerating patch. However, for Scenario 3 (complete *Sphagnum* cover), the water table appeared to become increasingly resistant to drawdown as the moss carpet thickened (Figures 8a–c).

The upward water flux 1 cm below the moss capitula remained relatively high (1–2 mm d^{-1}) for > 30 days when the moss layer was thin (2 cm); regardless of whether the patch was surrounded by bare peat or by a *Sphagnum* carpet, the water supply to the capitula appeared to depend only upon the moisture conditions in the underlying peat (Figure 8d). When the moss layer thickened to 10 cm or more, the upward water flux in Scenario 1 (isolated cushion) was reduced sharply to almost zero within 5–10 days. On the other hand, in Scenario 3 (complete *Sphagnum* cover), the upward water flux did not drop sharply until 20 days (10 cm *Sphagnum* layer) or 30 days (20 cm *Sphagnum* layer) had elapsed (Figures 8e–f). Thus, whilst increasing the thickness of a complete *Sphagnum* carpet from 10 cm to 20 cm seemed to improve the water supply to the capitula, similar thickening of an isolated cushion surrounded by bare peat resulted in a reduction of the upward water flow that seriously impaired the supply to the growing surface layer.

Figure 9 shows the results of simulations that explored the effect of varying the hydraulic conductivity of the peat underlying a 2 cm *Sphagnum* layer. The results for Scenarios 1 (isolated cushion) and 3 (complete *Sphagnum* cover) are similar, indicating that the period for which the upward capillary flux is sustained increases as the hydraulic conductivity of the underlying peat increases. For the highest hydraulic conductivity simulated (3.16 times the ‘real’ value), the upward flux could apparently be sustained indefinitely in Scenario 2 (*Sphagnum* patch surrounded by open water). The results of similar simulations for *Sphagnum* layers 10 cm and 20 cm thick showed no variation in upward flux when the permeability of the underlying peat was altered, suggesting that the hydraulic conductivity of the peat is likely to influence water stress conditions at the surface of a *Sphagnum* patch only in the initial phase of (re)growth.

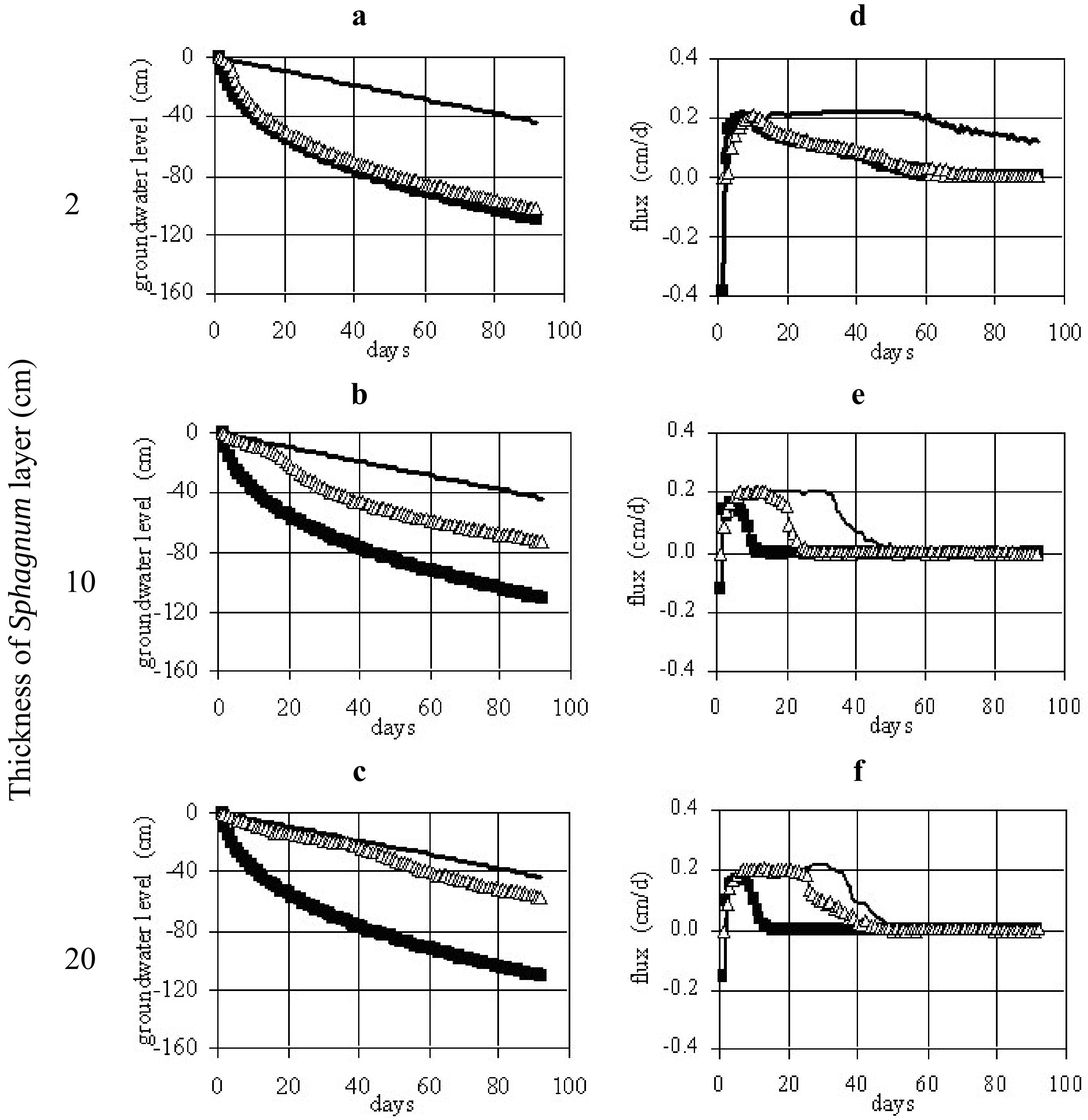


Figure 8. Variations of water table relative to the mire surface (a, b, c) and water fluxes 1 cm below the top of the *Sphagnum* layer (d, e, f) during the simulation period 01 June – 31 August 1998, for three moss layer thicknesses and the three site condition scenarios 1: bare peat (solid squares), 2: open water (no symbol) and 3: *Sphagnum* moss (hollow triangles) described in Figure 1. The entire profile was saturated at the start of each simulation and abscissae indicate the number of days from the start.

1. BARE PEAT

2. OPEN WATER

3. *SPHAGNUM* MOSS

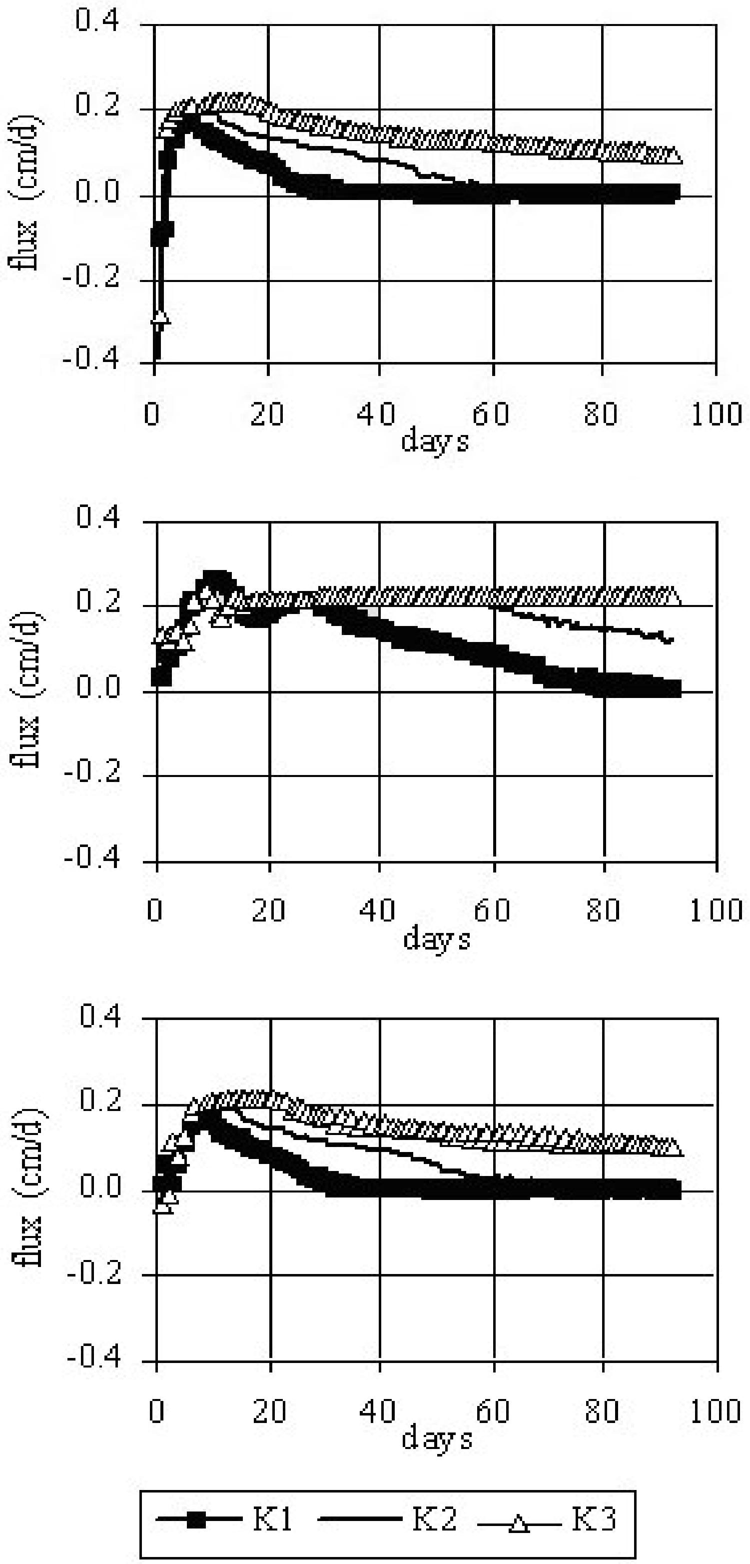


Figure 9. Variations in water flux 1 cm below the upper surface of a 2 cm thick *Sphagnum* moss layer during the simulation period 01 June – 31 August 1998 for the three site condition scenarios described in Figure 1. All simulations began with the moss layer saturated. Three different hydraulic conductivity (k) values are used for the peat underlying the *Sphagnum* layer: K1: k = 0.316 × geometric mean value for Samples EVA32–34; K2: k = geometric mean value; and K3: k = 3.16 × geometric mean value. Abscissae indicate the number of days from the start of each simulation.

Table 3 and Figure 10 explore the sensitivity of the results for occurrence of water stress to differences in the critical growth conditions selected, for the scenarios represented in Figures 1, 8 and 9. For some simulations the effect of using soil water retention data from the adsorption as well as the desorption limb of the Θ–*h* relationship is also explored. As before, the influence of the physical characteristics of the peat declines as the cover and thickness of the moss layer increases. This is clearly demonstrated for a complete 20 cm thick *Sphagnum* layer (Scenario 3), where differences in soil conditions caused by hysteresis (adsorption *versus* desorption) are negligible. Irrespective of the criterion applied, critical conditions took longest to develop in the micro-environment with open water (Scenario 2), and conditions were more favourable for regeneration at sites that were surrounded by moss carpets (Scenario 3) than at those surrounded by bare peat with vascular plants (Scenario 1).

Variation of the lower boundary condition (rate of downward seepage) also affected the results. In general, downward seepage of 0.4 mm d^{-1} caused critical conditions to develop up to four days earlier than seepage of 0.1 mm d^{-1}. In Scenario 2 (open water), the higher seepage had drawn down the water table by a negligible 3 cm at the end of the simulation period. For Scenario 1 and Scenario 3 simulations with a thin moss layer (2 cm) surrounded by bare peat or a *Sphagnum* carpet, the difference in water table due to the higher seepage was 10 cm or more; but with 10 cm and 20 cm moss layers, critical conditions generally developed long before the end of the simulation period so that differences in water table arising from differences in seepage over the relatively short time intervals involved were also small.

Table 3. Summary of the results of SWAP simulations conducted to explore the sensitivity of the model for the three regrowth scenarios to hysteresis in soil physical properties and the criterion for critical growth conditions adopted. For each of Criteria 1–4 and Scenarios 1–3 (Figure 1), the number of days (DAY) after the start of the simulation and the position of the water table (GWL) at which critical growth conditions arise in *Sphagnum* cushions 2, 10 and 20 cm thick is shown. All simulations began with the water table at the upper surface of the *Sphagnum* moss layer.

	SELECTED CRITERION FOR CRITICAL GROWTH CONDITIONS							
	1. moisture content in top 0.2 cm < 0.06 $cm^3\ cm^{-3}$		2. moisture content in top 0.2 cm < 0.01 $cm^3\ cm^{-3}$		3. moisture content in top 1.0 cm < 0.01 $cm^3\ cm^{-3}$		4. moisture content in top 2.0 cm < 0.01 $cm^3\ cm^{-3}$	
	DAY	GWL (cm)	DAY	GWL (cm)	DAY	GWL (cm)	DAY	GWL (cm)
Scenario 1. Isolated patch of *Sphagnum* moss surrounded by bare peat								
moss 2 cm thick	8	-38	10	-42	47	-84	> 92	
(in *italic:* adsorption)	*6*	*-33*	*7*	*-36*	*30*	*-70*	*63*	*-96*
moss 10 cm thick	8	-38	8	-38	9	-40	13	-48
moss 20 cm thick	8	-43	9	-40	11	-44	16	-53
Scenario 2. *Sphagnum* moss patch surrounded by open water								
moss 2 cm thick	51	-25	57	-28	> 92		> 92	
moss 10 cm thick	31	-15	32	-16	41	-20	65	-32
(in *italic:* adsorption)	*30*	*-15*	*30*	*-15*	*35*	*-18*	*47*	*-24*
moss 20 cm thick	35	-18	36	-18	44	-23	59	-29
Scenario 3. 100% *Sphagnum* moss cover								
moss 2 cm thick	11	-37	12	-39	50	-80	> 92	
moss 10 cm thick	19	-23	20	-25	22	-29	29	-38
moss 20 cm thick	23	-17	25	-18	35	-21	49	-33
(in *italic:* adsorption)	*23*	*-17*	*25*	*-18*	*35*	*-21*	*49*	*-33*

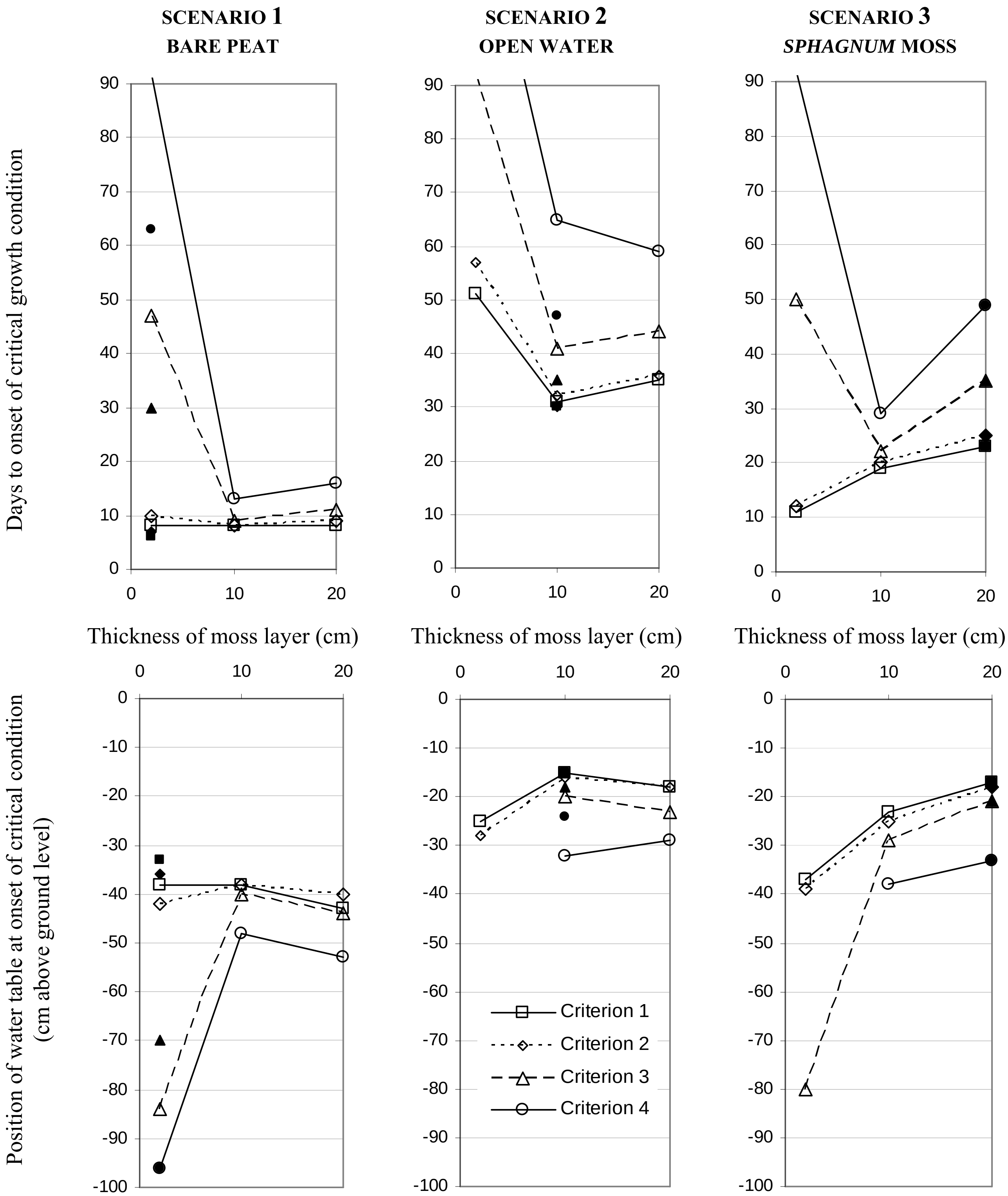


Figure 10. Graphical representation of the sensitivity analysis presented in Table 3. Each vertical pair of graphs shows the model outputs at the onset of critical growth conditions (upper: days from start of simulation run and lower: position of water table relative to the mire surface) for *Sphagnum* carpets 2, 10 and 20 cm thick in one of the scenarios (1–3) presented in Figure 1. The effects of employing four different definitions for the critical growth condition (Criteria 1–4), as detailed in Table 3, are compared in each graph. Filled symbols indicate the effect of using data from the adsorption rather than the desorption limb of the moisture characterstic.

DISCUSSION

The SWAP model is based on realistic representations of physical processes and although it was developed for, and has been used mostly in, agrohydrological studies, it appears to provide an adequate description of water flow in peat. There are, however, some limitations to its realism as it has been applied here. For example, we used a single k–h–Θ relationship to describe the hydrophysical properties of the *Sphagnum* layer and a second relationship for the underlying peat layer. In reality, hydrophysical properties vary with depth within both layers. Also, we set the thickness of the *Sphagnum* layer from which evaporative water loss occurred at 5 cm. In reality, the depth of the zone in a moss layer from which evaporation occurs varies with wind speed. The effect was demonstrated by Ishihara *et al*. (1992), who measured a high rate of wind-induced turbulent transfer of water vapour in large pores below the surface of a bed of glass beads; and its operation in *Sphagnum* layers appears to be confirmed by the work of Williams & Flanagan (1996) and Clymo (1973), who give evaporation values for different species which are strongly influenced by both wind speed and temperature.

The model simulations were conducted for *Sphagnum capillifolium*, which grows in locations with an average water table 20 cm below the surface under natural conditions (Gerdol *et al*. 1998). The structure of *Sphagnum* carpets varies with species. In general, those that grow in locations that are elevated relative to the water table (hummock species) form more compact carpets than those that grow close to the water table (lawn and hollow species). Structure can affect the hydraulic conductivity of the moss layer, and hydraulic conductivity in turn strongly influences growth conditions, so that we may expect the development of critical water stress conditions to vary between species. Since more compact structure will result in relatively high hydraulic conductivity at low moisture content, critical conditions can be expected to develop earlier than predicted here in mosses with looser and more open structure than *Sphagnum capillifolium*, and later if the structure is more compact.

The improvement in conditions for *Sphagnum* regeneration when the patch is (already) surrounded by *Sphagnum* is a result of the high storage capacity of the moss layer. The effect is clearly visible in Figures 8b–c and 8e–f; as the water storage capacity of the surface layer increases, the fall in water table declines and the upward flux of water persists for longer. From all the simulations it can be concluded that the (hydro-)physical condition (micro-environment) of the peatland surface is the dominant variable affecting water table fluctuations and the onset of water stress conditions. When small patches of moss are surrounded by vascular plants growing on bare peat, the water table falls rapidly during dry periods, and under these conditions *Sphagnum* experiences water stress much earlier than when it is growing in pools or at sites with complete moss cover.

Table 3 and Figures 8–10 show clearly that the depth of the water table is not the most important variable for water stress in *Sphagnum* vegetation. For instance, the water table can be *ca*. 80 cm below a 2 cm thick moss layer before the upward water flux is reduced so severely that the moisture content of its uppermost 1.0 cm falls below 0.01 $cm^3\ cm^{-3}$ (Criterion 3), whereas for moss layers 10 cm and 20 cm thick a water table depth of 20 cm (Scenario 3) or 40 cm (Scenario 1) may already be too deep for a sufficient water supply to the surface to be maintained (Table 3, Figure 10).

For all site conditions, the risk of water stress is relatively low in the initial stages of *Sphagnum* re-establishment and maximal when the *Sphagnum* layer is around 10 cm thick. This is due to the fact that the hydraulic conductivity of the *Sphagnum* carpet exceeds that of peat when $h > -10$ cm, and falls below that of peat at lower pore water pressures (Figure 7). Thus, under the frequent condition of water table position between -10 and -20 cm relative to the moss surface (model results in the simulation period, e.g. Figures 8b and 8c), the hydraulic conductivity of the lower half of a 20 cm moss layer will be higher than that of the peat underlying a moss layer 10 cm thick. On the other hand, when the water table is in the lower part of its range (so that water content and pore water pressure in the unsaturated zone are low), a 10 cm moss layer will transmit water less readily than will the peat underlying a 2 cm moss layer. Thus, hydraulic continuity between the surface and the water table may be sustained for longer during drought when the moss layer is only a few centimetres thick than when *Sphagnum* regeneration is farther advanced, the relatively vulnerable stage when the *Sphagnum* carpet is 5–15 cm thick arising only after several years' growth. This is consistent with field observations that *Sphagnum* lawns can expand relatively rapidly over bare peat but often remain thin. Hummock-forming species, on the other hand, may achieve drought tolerance through an alternative mechanism; by bunching into cushions to form thick moss layers they locally increase the water storage capacity of the unsaturated zone, albeit at the expense of sustained hydraulic contact with a falling water table.

Unless the evaporation demand is met by an upward flux of water, the moss layer dries out and wilts quickly. Hence the development of critical conditions should be delayed where the hydraulic conductivity of the peat underlying the moss layer is relatively high. Figure 9 indicates that peat hydraulic conductivity has considerable influence on growth conditions and upward flux for the simulations with a moss thickness of 2 cm (Figure 9). As for the sensitivity for hysteresis (illustrated in Table 3 and Figure 10; adsorption versus desorption data) the influence of peat properties declines as the moss layer becomes thicker. In general, although hydraulic conductivity can affect the upward flux and growth conditions (Figure 9), other variables such as thickness of the *Sphagnum* layer and site conditions appear to dominate.

CONCLUSIONS

1. The applicability of the SWAP model means that this study gives a reasonable indication of the importance of differences in soil layer properties for *Sphagnum* growth. This is probably true also for the relative impact of micro-environmental conditions (presence or absence of open water), although the various assumptions made with respect to water transport and evaporation in the uppermost layer of a *Sphagnum* carpet make this part of the work less reliable. The lack of good field data for model validation is problematic.
2. The results of modelling suggest that small isolated *Sphagnum* patches surrounded by bare peat with vascular plants are extremely vulnerable to water stress, and that the risk of drying out is much reduced when the moss patches grow in the immediate vicinity of open water (e.g. pools). Indeed, under some climatic conditions, the presence of open water (small pools) seems to be vital for the re-establishment of *Sphagnum* on bare peat.
3. The model indicates that the establishment of *Sphagnum* on bare peat is easier than its growth thereafter because there is a relatively vulnerable stage when carpet thickness reaches 5–15 cm, probably after several years' regeneration. This is consistent with practical experience at permanently wet sites, where after the initial development of lawn species the succession to hummock-forming species is often long delayed (Smolders *et al*. 2003). The model simulations give a possible physical explanation for these observations.
4. The model simulation indicates that maximum vulnerability to water stress will develop as the *Sphagnum* carpet thickens, some time after it is first re-established. It is recommended that other (preferably physically based) models incorporating additional assumptions and different field and soil data should be applied to determine whether the same patterns of risk can be reproduced using alternative models and data. This would strengthen our understanding of the role of water-related ecological conditions in the re-establishment of *Sphagnum*-dominated plant communities.

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