Journal of Ecology 2003 **91**, 86–102

Hydrological studies on blanket peat: the significance of the acrotelm-catotelm model

J. HOLDEN and T. P. BURT*

School of Geography, University of Leeds, Leeds, LS2 9JT, and *Department of Geography, University of Durham, Science Laboratories, South Road, Durham, DH1 3LE, UK

Summary

1 Runoff production in blanket peat catchments of the northern Pennine hills, UK was measured through monitoring and experimentation at the plot, hillslope and catchment scale. Water flow from soil pipes was measured in one of the study catchments and overland flow, throughflow and water table were measured in runoff plots; rainfall simulation and tension-infiltrometry provided information on infiltration characteristics of the peat.

2 Saturation-excess overland flow was found to dominate the flashy flow regime; acrotelm stormflow, subsurface pipeflow and macropore flow were also found to be important components of the ecohydrological system.

3 Surface cover, topography and preferential flowpaths were found to be important factors in controlling infiltration and runoff production.

4 Streamflow generation processes that are consistent with the acrotelm-catotelm model are shown to occur in blanket peat with and without *Sphagnum* cover, but in one of the catchments studied an estimated 10% of the discharge bypassed this route and discharged via pipes.

5 The spatial and temporal variation in hillslope-scale runoff production was demonstrated in the study catchments. This variability in runoff production will be important for hydroecological understanding in peatlands but is often neglected because of over-simplification of processes provided by the traditional two-dimensional acrotelm-catotelm model.

Key-words: bog, diplotelmic model, ecohydrology, hillsope hydrology, macropores, mire, peat hydrology, soil pipes, wetlands

Journal of Ecology (2003) 91, 86-102

Introduction

Since the mid 20th century Russian scientists have adopted a diplotelmic system for understanding the functioning of peatlands. This comprises an upper 'active' peat layer with a high hydraulic conductivity and fluctuating water table, and a more 'inert' lower layer which corresponds to the permanently saturated main body of peat (Ivanov 1948, 1953, 1981; Lopatin 1949; Romanov 1968). This layering system for analysing mires became widely accepted from the late 1970s and is now used regularly in ecohydrological and peat development modelling and budgeting (e.g. Ingram 1982, 1983, 1991; Kirkby *et al.* 1995; Smit 1996; McKillop *et al.* 1999; Hilbert *et al.* 2000). Ingram (1978, 1983) notes that the distinction between the upper, periodically aerated, partly living soil layer (acrotelm) and the lower anaerobic layer (catotelm), which is dead except for the aerenchymatous roots of helophytic angiosperms, is an important concept and fundamental to any understanding of the hydrology, ecology and pedology of mires. According to Ingram's definition, the acrotelm is affected by a fluctuating water table (the lowest water table depth is therefore the base of the acrotelm), has a high hydraulic conductivity and a variable water content, is rich in peat-forming aerobic bacteria and other microorganisms and has a live matrix of growing plant material. The catotelm has a water content invariable with time, a small hydraulic conductivity, is not subject to air entry and is devoid of peat-forming aerobic microorganisms.

The movement of water is a controlling ecological factor in peatlands (Hammond *et al.* 1990; Ingram 1991), yet little work has been done on the spatial heterogeneity of surface and subsurface flow in wetland environments,

Correspondence: J. Holden (fax + 44 113 3433308, e-mail j.holden@geog.leeds.ac.uk).

or on the spatial structuring of hydraulic peat properties (Chappell & Ternan 1992; Baird 1995). Neither of the reviews of peat hydrology by Ingram (1983) and Gilman (1994) discussed the spatial and temporal nature of runoff production within these environments, and very little mention of the infiltration process was made. It is notable too that the study by Conway & Millar (1960), which demonstrated the flashy nature of storm runoff from blanket peat and examined the influence of surface condition on runoff response, contained no observations of soil and hillslope hydrology. Management of peatlands requires an understanding of hydrological processes. Practitioners of peatland ecology and hydrology will want to employ simulation models in helping them make their management decisions, but the success of this practice will depend on having appropriate and reliable models available (MacAlister & Parkin 1998).

The acrotelm-catotelm model implies that most runoff production and nutrient transfer will occur within the upper peat layer, close to or at the peat surface. At the same time most models of water movement in mires are based on groundwater flow through the catotelm. Thus if the catotelm is inert the flow model application may be flawed. The main applications of the diplotelmic model have been to ombrotrophic mires (and particularly raised bogs). Many model calculations rely heavily on measurements of hydraulic conductivity of the peats. However, measurements of hydraulic conductivity in peat soils are rarely within one order of magnitude error bands (e.g. Holden et al. 2001). Furthermore, there is evidence that the hydraulic conductivity of peat soils can vary over several orders of magnitude over just a few vertical or lateral metres (Rycroft et al. 1975; Holden & Burt in press). This makes groundwater flow modelling difficult because the size of computational cells is usually greater than the scale at which significant variability in hydraulic parameters occur (Bromley & Robinson 1995; Baird 1997b). The dominance of traditional water balance approaches in peatland environments and recent reliance on the acrotelm-catotelm model in ecohydrological and runoff modelling (e.g. Kirkby et al. 1995; McKillop et al. 1999) has meant that many hydrological processes occurring in peatlands remain poorly understood.

Blanket peats cover over 8% of the British Isles. They represent the largest single contribution to blanket peat worldwide (Tallis *et al.* 1998). These peats are concentrated mainly in upland headwaters supplying runoff to many major British rivers yet the utility of the acrotelm-catotelm model has never been tested. Various runoff pathways attenuate and delay water movement through and across a peatland to differing extents, providing transport of nutrients and sediment; hence a knowledge of the relevant mechanisms is important (Kirkby 1985). It is now known that the hydrological processes operating on hillslopes range from infiltration-excess overland flow to saturationexcess overland flow, through subsurface flow within

© 2003 British Ecological Society, *Journal of Ecology*, **91**, 86–102 the matrix, within macropores and through natural pipes, to flow through the underlying geology (Burt 1996). The nature of these flow processes in peat catchments is poorly understood. Their relative importance in any catchment varies with climate, topography, soil character, vegetation cover and land use, and may vary at one location (e.g. seasonally) with antecedent moisture and with precipitation intensity and duration (Burt 1996). The runoff processes are by no means independent of one another and water travelling over the surface at one point may later take the form of subsurface flow through the matrix and then flow through macropores, for example. It is important to distinguish between the different forms of overland flow and subsurface flow because the speed of water movement and the nature of nutrient and sediment fluxes is often controlled by the flow process. For example, there are important differences between infiltration-excess overland flow and saturation-excess overland flow. Infiltration-excess overland flow is produced when the rainfall intensity is greater than the infiltration rate and the overland flow therefore consists of water that has not been within the soil. This type of surface runoff is most likely on soils with low infiltration capacity (the 'partial area' concept - Betson 1964). Saturation-excess overland flow can occur at much lower rainfall intensities and is produced when the soil profile is completely saturated; the water at the surface is a mixture of water that has been within the soil mass that is returning to the surface from upslope and fresh rainwater. Saturationexcess overland flow can occur for long periods after rainfall has ceased, particularly at the foot of a hillslope where the soil continues to be supplied by water draining from upslope. There have been few studies of infiltration in peats, but Burt et al. (1990) suggested that infiltration-excess overland flow may be important within many blanket peat catchments. However, peatlands tend to have a high water table suggesting that saturation-excess mechanisms are likely to produce more runoff than infiltration-excess overland flow mechanisms. The source areas (parts of the hillslope which contribute runoff) for saturation-excess overland flow may be very different from those for infiltration-excess overland flow and will vary over time (the 'variable source area concept' - Hewlett 1961). The differences between runoff produced by these processes has often been determined hydrochemically (e.g. Ogunkoya & Jenkins 1991), with saturation-excess overland flow generally having a greater solute concentration than infiltrationexcess overland flow (since it is a mixture of old soil water and precipitation unable to infiltrate into the soil). Clearly both forms of overland flow are also capable of transporting sediment over the surface of a peatland.

As well as playing a role in the timing of a catchment flood or in providing stream baseflow the various forms of subsurface flow are also associated with different biogeochemical processes. Subsurface flow may be generated through the soil or peat matrix or by turbulent flow through macropores or pipes. Research has

indicated that macropores can be important in solute transport through soils (e.g. Thomas & Phillips 1979; Beven & Germann 1982). Macropore flow has been shown to develop in peats that have been cut and air-dried to supply Irish power stations (Holden 1998), but little work has been done on macropore flow in intact peats (e.g. Baird 1997a). Water flow through pipes is a much neglected process, yet these subsurface features are present in many peatlands (e.g. Elgee 1912; Pearsall 1950; Ingram 1983; Price 1992; Jones et al. 1997). The occurrence of pipes in many environments is strongly associated with faunal activity, but this appears unlikely in blanket peat. There have been no detailed surveys of pipe density or contribution to runoff production in peat catchments except in the shallow peaty podzols of mid-Wales (Jones 1981; Jones & Crane 1984; Jones et al. 1997), where pipes were typically found at soil horizon interfaces and could be responsible for up to 50% of the runoff generation.

Given the importance of hydrology to the understanding of peatland development and ecology, it is striking that so little is known about the nature of runoff generation within peat catchments. This paper presents results from hydrological monitoring within a blanket peat site in the northern Pennine hills, UK. Here plot, hillslope and catchment scale monitoring has been coupled with experimentation aimed to establish the roles of the various runoff production mechanisms. The objectives of this paper are:

1. To quantify the relative roles of the peat surface, the acrotelm and the catotelm in controlling runoff generation from blanket peat.

2. To monitor the spatial and temporal pattern of runoff production in blanket peats, including the extent and pattern of overland flow.

3. To make sufficient measurements of infiltration in blanket peat under a range of vegetation covers to establish the extent of infiltration and saturation excess overland flow mechanisms.

4. To gain an understanding of the importance of macropores in the infiltration process.

5. To establish the hydrological importance of piping in blanket peats.

These aims will allow a process-based assessment of the acrotelm-catotelm model. Although the acrotelmcatotelm model has broad utility it will become clear that this diplotelmic model ignores the important role of macropores and soil pipes in connecting deep and shallow parts of a peat profile, and that surface vegetation, topography and preferential flow paths are important three-dimensional components of blanket peat hydrology.

Methods

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SITE CHARACTERISTICS

Fieldwork was carried out on the Moor House National Nature Reserve (NNR), in the northern

Pennine hills, England. This UNESCO Biosphere Reserve occupies 35 km² with an altitudinal range of 290-848 m. A series of alternating beds of Carboniferous limestone, sandstone and shale provides the base for a glacial clay till onto which a blanket peat deposit of up to 3 m in depth developed during the Holocene (Johnson & Dunham 1963). Blanket peat covers around 70% of the reserve, with vegetation dominated by Calluneto-Eriophoetum-Sphagnum blanket bog. Eriophorum vaginatum, Calluna vulgaris and Sphagnum species (mainly Sphagnum rubellum, Sphagnum papillosum and Sphagnum magellanicum) dominate the site. The site is fully described in Heal & Smith (1978), Rawes & Welch (1969); Eddy et al. (1969) and Johnson & Dunham (1963). Most of the reserve can be classified as NVC M19 Calluna vulgaris – Eriophorum vaginatum blanket mire (Rodwell 1991) although above 650 m altitude NVC M20 Eriophorum vaginatum blanket mire dominates as low summer temperatures restrict Calluna growth (Rawes & Welch 1969). Although there are some areas of bare peat, most gullies have now revegetated with Sphagnum, Eriophorum and Juncus squarrosus.

The land is owned by English Nature and provides free-range grazing (mainly sheep) for villages in the Eden Valley. Grazing intensities are currently around 1.2 sheep ha⁻¹ but during the 1960s to 1990s were between 1.4 and 5.8 sheep ha⁻¹. Prior to 1952 parts of the site were periodically burned on a rotation system as part of moorland management to regenerate fresh *Calluna vulgaris* shoots for grouse. No burning has taken place since the site became a nature reserve except on small experimental plots (e.g. Rawes & Welch 1969).

A typical intact peat profile consists of an upper 5 cm of poorly humified (H2-H3 on the Von Post 1922 scale) black brown coloured peat with living roots and a crumb structure. Below this to 10 or 15 cm depth the peat tends to be brown and slightly humified (H3-H4) with occasional bands of light brown *Sphagnum* peat overlying a darker brown *Eriophorum-Calluna-Sphagnum* peat (H4). The peat then very gradually becomes more humified with depth. By 1.5 m into the profile the peat is highly humified with decomposition almost complete (H9). Frequently there are well-preserved remains of birch found at the base of the peat which overlies light coloured grey clay with sandstone boulders. The clay is often gleyed and waterlogged.

An automatic weather station at 535 m altitude has been maintained since 1991 operated by the UK Environmental Change Network (ECN) (Fig. 1); earlier climatic records exist for the same site from 1931 to 1980. Maritime air masses from the north Atlantic dominate the climate which has been classified as subarctic oceanic (Manley 1942). Mean annual temperature is 5.3 °C with 123 air frosts per year. Mean annual rainfall is 1982 mm, with 244 precipitation days per year (Burt *et al.* 1998; Holden & Adamson 2001). Rainfall intensities rarely exceed the equivalent of 12 mm h⁻¹ at the site, only six times for 15-minute logging



Fig. 1 Location of the monitoring and experimental sites on the Moor House reserve.

periods between July 1998 and December 1999, and the maximum rainfall recorded in one whole hour at the site in the period 1994–2001 was 11.6 mm.

MEASUREMENTS

1. Streamflow was recorded on the 11.4 km² Trout Beck catchment, a tributary of the Tees (Fig. 1). Discharge was gauged using a compound Crump weir operated by the Environment Agency (register number 025003) with stage height recorded every 15 min. Streamflow was also measured on Little Dodgen Pot Sike using a rated section and an Ott stage recorder. At the ECN 'target site' (at 570 m altitude) periodic sampling of soil, vegetation and faunal properties has been performed since 1991 and the water table is automatically logged by ECN (Sykes & Lane 1996).

2. Runoff from the peat during natural rainfall events between June 1998 and December 1999 was recorded on 10 open-ended hillslope plots (on six separate hill-slopes) using aluminium throughflow troughs. A trench was dug in the peat, or at suitable locations a peat face was cleaned off, and 50 cm wide aluminium troughs carefully inserted at 1 cm, 5 cm, 10 cm, 50 cm, 100 cm depth and at the base of the peat layer. A trough was

also inserted below the peat-substrate interface. Dividers were inserted flush with the edge of each trough to prevent leakage from upper layers into lower troughs and to prevent lateral flow. Discharge was measured by tipping-bucket flow recorders connected to a Campbell CR10X datalogger (Atkinson 1978; Khan & Org 1997; for details see Holden 2000).

3. On four of the hillslopes, detailed water table, pore water pressure and overland flow sampling was performed between June 1998 and December 1999 using networks of 100 dipwells, piezometers and crest-stage tubes per site (Holden 2000). Crest-stage tube entry points were placed at the surface of the peat and at 3 cm, 6 cm, and 9 cm into the peat mass. By burying the tubes to a point where the holes were level with the monitoring height, any flow or ponding to that height resulted in the tube filling with water. This system provided a means of mapping maximum water table elevation during a given period. The tubes were emptied with a large syringe keeping disturbance to a minimum. 4. A drip-type rainfall simulator as described by Bowyer-Bower & Burt (1989) was used to provide simulated rainfall on 24 different 0.5 m² plots (Fig. 1) at realistically low intensities of 3 mm h⁻¹, 6 mm h⁻¹, 9 mm h⁻¹ and 12 mm h⁻¹ during April and May 1999.

Runoff from these plots was collected from 1 cm, 5 cm and 10 cm depth, allowing infiltration and percolation rates to be established (Holden & Burt 2002a). Plots were dominated (> 90% coverage) either by *Sphagnum rubellum*, *Eriophorum vaginatum*, *Calluna vulgaris* or bare peat, and six plots for each surface cover type were used. Rainfall was simulated at one intensity until a steady runoff was produced from each layer; often this took several hours. Then the experiment was repeated at three other rainfall intensities. Two plots for each surface cover type were revisited during the dry August of 1999 to establish whether there were any seasonal differences.

5. A tension infiltrometer similar to that designed by Ankeny *et al.* (1988) was used within a 100 m \times 100 m plot at Moor House (Fig. 1). By setting up a small water tension the device only allows infiltration into the smaller pores (matrix flow) of the peat. By changing the tension this allows calculation of the amount of water that also infiltrates into macropores (Reynolds & Elrick 1991; Baird 1997a; Holden *et al.* 2001). For each of the four surface cover types used above, eight sampling locations were randomly chosen and the infiltrometer used at the peat surface, 5 cm, 10 cm and 20 cm depth. Full details of the tension infiltrometer experiments, assumptions and limitations are given in Holden *et al.* (2001) and so only a summary of the findings will be provided below.

6. Pipeflow was monitored in the Little Dodgen Pot Sike (LDPS) catchment (Fig. 1). Fifteen of the pipes

(which produced the greatest discharge) were gauged using small weirs collecting flow at the pipe outlet and a water level sensor consisting of a one-turn potentiometer turned by a float and counterbalance (Jones *et al.* 1984; see Holden and Burt (2002b) for more detail about the gauging). This produced the most comprehensive pipeflow record anywhere in the world apart from the Plynlimon study (Jones & Crane 1984; Jones 1994) and is the first in blanket peat.

Results

(A) CATCHMENT HYDROLOGY

Runoff from Trout Beck is shown in Fig. 2(a) for the 1999 water year (1st October 1998 to 30th September 1999). The flashy nature of stream response is immediately apparent. Baseflow appears to be of minimal importance, indicating little groundwater flow from the peat. Discharges below $0.5 \text{ m}^3 \text{ s}^{-1}$ occurred 75% of the time, but only 21% of the total discharge volume occurred during this period. Mean storm peak lag times are only 2.7 h (*n* = 72). Figure 2(b) displays the monthly precipitation and runoff totals for Trout Beck. There is a very close correspondence of precipitation and runoff. During August 1999, discharge from Trout Beck fell to 0.016 m³ s⁻¹.

ECN hourly water table data are given in Fig. 3(a) for the 1995–99 water years. Fluctuations in water table



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Fig. 2 Discharge from Trout Beck during the 1999 water year. (a) 15 minute readings. (b) Monthly rainfall and runoff totals.



Fig. 3 Hourly water table depth, cm, at the ECN target dipwell. (a) Time-series. (b) Water table residence curve.

are swift with recoveries occurring more rapidly than recessions. Infiltration into unsaturated peat must therefore be rapid, suggesting that infiltration-excess overland flow is unlikely to dominate. In the summer months (May to September), the water table only drops below 5 cm for short periods before a recharge event saturates the upper peat mass. The summers of 1996 and 1997 were typical in that there were three or four periods when the water table briefly dropped to around 20 cm depth. There were very warm dry periods during the summers of 1999 and 1995, but even during the extreme drought of 1995 (Marsh & Turton 1996; Burt et al. 1998; Hulme 1998) the water table level only reached a maximum depth of 42 cm. Figure 3(b) plots water table residence times for the entire period. As is typical of peatlands the water table remains close to the surface for most of the year, within 5 cm for 82.4% of

© 2003 British Ecological Society, *Journal of Ecology*, **91**, 86–102 the time. July and August 1995 were the only two months between 1991 and 2001 at the ECN sampling site in which the water table never reached the blanket peat surface; the water table was below 10 cm for 42 consecutive days and below 20 cm for 35 consecutive days.

(B) SUBCATCHMENT HYDROLOGY

Runoff troughs showed that overland flow dominated the runoff response of the catchment. Around 81% of the runoff collected was from the peat surface with another 17% from 1 cm to 5 cm depth. Most of the remaining runoff came from the peat at depths less than 50 cm deep. Hence overland flow is the most important runoff pathway. Lateral flow at depths greater than 5 cm or 10 cm is restricted such that runoff contribution from these layers is low. The results from hillslope

runoff measurement suggest that only around 2% of runoff in blanket peat catchments is generated from the peat below 5 cm depth. This adds support to the utility of the acrotelm-catotelm model.

Emphasis on the acrotelm-catotelm model may, however, neglect important spatial variations in runoff generation that occur across peatland hillslopes. Figure 4 presents hydrographs from storm events on a small blanket peat hillslope (H1 - see Fig. 1). Overland flow on the footslope is more prolonged than overland flow on the midslope or topslope. For the event on day 231, 1999, footslope overland flow continues until 01.00 hours on day 234 (although just a small amount of discharge is recorded by the trough during the recession), whereas it ceased at 13.00 hours on day 231 on the midslope and 00.00 hours on day 232 on the topslope. As the hillslope drains, return flow (water returning to the surface from within the peat) is produced on gentler slopes causing saturation-excess overland flow on the footslopes. When overland flow has ceased on the footslope, the flow record from the 5 cm trough (Fig. 4g) indicates that the near-surface layers of the peat continue to drain but with much more attenuated hydrographs. This indicates limited subsurface flow capacity within the blanket peat, and underlines the relative importance of saturation-excess overland flow.

Figure 5 shows the nature of runoff production processes on H1 at different stages of the flow recession during a 24-h period. Here overland flow (or at least surface ponding) was recorded by 100 crest stage tubes over almost the entire hillslope at the peak of the storm at 12.00 hours, day 231 (Fig. 5a). Small-scale microtopographical differences could be found on the hillslope but the measurement network allows the general hillslope runoff production to be displayed. As the hillslope drained following rainfall cessation, the more gently sloping top and footslope regions continued to produce overland flow; the steeper slopes produced flow just below the surface at 3 cm (Fig. 5b). By 00.00 hours, day 232 (Fig. 5c), surface flow only occurred on the hillslope toe regions, while steeper areas only produced subsurface flow. After 12.00 hours, day 232 (Fig. 5d) there was little change. Drainage of water from the upper soil layers of H1 was rapid; within 24 h the hillslope had reached a stable state with little water table change and negligible runoff contribution to streamflow. The only fully saturated area remaining was on the north-east flank of the hillslope where monitoring has indicated that the peat was almost permanently waterlogged. Thus, topography is important for determining dominant runoff process contributions even on gently sloping peat hillslopes. The steeper midslope sections of H1 produced overland flow less frequently than the shallower slopes. This suggests that the midslope sections produced more subsurface runoff, which collected at the bottom of the slope, and due to impeded drainage, manifested itself as return flow.



Fig. 4 Runoff production on H1 on days 220–235, 1999. (a) Precipitation. (b) Trout Beck. (c) Topslope overland flow. (d) Midslope overland flow. (e) Footlslope overland flow. (f) Midslope 5 cm flow. (g) Footlslope 5 cm flow.





Fig. 5 Minimum depth of flow relative to the peat surface on H1, day 231–232, 1999 as monitored by crest-stage tubes. (a) 12.00 hours, day 231. (b) 18.00 hours, day 231. (c) 00.00 hours, day 232. (d) 12.00 hours, day 232. Contour heights relative to local datum, m.

Runoff response from the foot of a slope with a length of 230 m and altitudinal range of 26 m (H2) is shown in Fig. 6 for a five-day period during summer 1998. Small amounts of rainfall (at low intensity) produce longlasting overland flow; this confirms that infiltrationexcess overland flow is not likely to be the main surface runoff mechanism. H2 drains rapidly such that runoff production from the base of the hillslope almost ceased within 45 h of the rain stopping. The throughflow response from 5 cm depth is more attenuated, with longer recessions than overland flow. Very little flow was measured emerging from the 10 cm layers at each site. Crest stage tube mapping demonstrates how hillslope saturation changes over time during a rainfall event for the bottom part of the slope (Fig. 7). As with H1, much of the slope produces overland flow during the main part of the rainfall event. As the hillslope drains, certain areas of the slope appear more likely to stay saturated; consequently these areas become zones where overland flow is more likely. Given that surface flow is dominant, then some areas are more likely to act as contributing areas than others. For example, the north-west side of H2 appears to produce overland flow for a more prolonged period than other parts of the hillslope. Salt dilution gauging (Burt 1988) in a ditch at the bottom of the slope confirmed that runoff contributions from H2 were greatest downslope of

© 2003 British Ecological Society, *Journal of Ecology*, **91**, 86–102 this persistently saturated zone as this was where the injected solution of sodium chloride was diluted the most.

(C) RAINFALL SIMULATION EXPERIMENTS

Rainfall simulation experiments confirmed the dominance of overland flow on both vegetated and bare peat surfaces. For most experiments overland flow was produced even under low-intensity rainfall. Figure 8 shows runoff rates from all layers and plots. Some layers did not produce runoff during the experiments and therefore not every graph in Fig. 8 shows six datasets. Runoff production decreases with depth; however, the variability in runoff with depth between plots indicates that water movement within the peat is highly variable. Only one of the 24 plots produced no surface runoff during 12 mm h⁻¹ rainfall simulation. This suggests that on bare peat and below a vegetation cover, surface flow is likely to be a widespread phenomenon if rainfall is prolonged.

There was no significant difference in mean steadystate infiltration rates between *Eriophorum vaginatum* or *Calluna vulgaris* covered surfaces and bare surfaces. Mean infiltration rates into *Sphagnum rubellum* were significantly lower than for the other surfaces. ANOVA showed that depth and rainfall intensity were overwhelmingly significant controls on runoff rates



Fig. 6 Runoff production from Trout Beck and the footslope of H2, day 277–282, 1998. (a) Precipitation. (b) Trout Beck. (c) H2 overland flow. (d) H2 5 cm depth. (e) H2 10 cm depth.

(P < 0.00005). Surface vegetation cover also seemed to have some influence (P = 0.06). It is not necessarily surface cover that is the control; rather, the surface cover may be indicative of the properties of the type of peat below. It is well known that particular vegetation types prefer different water table conditions (Ingram 1983); furthermore, the vegetation may directly affect peat structure via root structure, litter deposition and building up of the peat deposit.

© 2003 British Ecological Society, *Journal of Ecology*, **91**, 86–102 For *Eriophorum*-covered peat, the mean runoff between 1 cm and 5 cm is just as great as that at the surface, but only 1.2% of input rainfall is collected as throughflow between 5 cm and 10 cm depth. So peat below *Eriophorum vaginatum* allows rapid flow within the top 5 cm but

below this layer very little lateral flow occurs at all. For all vegetated surfaces runoff decreases with depth, but for bare peat the mean proportion of runoff between 5 cm and 10 cm is 8.0% greater than that between 1 cm and 5 cm and only 2.4% less than surface runoff.

Rainfall simulation tests during August 1999 were compared to those from April and May 1999. Paired *t*tests demonstrate that there was a significant difference in runoff production for all surfaces except *Sphagnum* (n = 96, t = 2.03, P < 0.03). For the other plots, steady-state infiltration rates are greatly increased for all intensities such that surface runoff is reduced in summer. Significantly, more runoff is produced from the 5–10 cm layer during the summer.



Fig. 7 Minimum depth of runoff from the peat surface on H2, Julian days 277–281. (a) 09.00 hours, day 277. (b) 12.00 hours, day 278. (c) 12.00 hours, day 279. (d) 18.00 hours, day 279. (e) 12.00 hours, day 281. Contour heights relative to local datum, m.

(D) MACROPORE FLOW

Tension infiltrometer tests (Holden et al. 2001) showed that macropores were important pathways for runoff within blanket peat. Macropore contribution (pores greater than 1 mm in diameter) to infiltration was found to be around 35%. Sphagnum-covered peat had a significantly greater macroporosity and hydraulic conductivity down to 20 cm depth than other surface cover types, but this is probably of little overall consequence to runoff production at Moor House where Eriophorum and Calluna dominate the vegetation cover, however it could be significant elsewhere. Macroporosity was greatest at 5 cm depth, being slightly lower at the surface, but declining rapidly below 5 cm depth. This is to be expected given that the most dense root networks and least densely spaced Sphagnum branches would be in the upper part of the peat profile (Ingram 1983).

Figure 9 provides discharge data from Trout Beck and for two macropore outlets at depths of 45 cm and 60 cm on an exposed peat face for a four-week period during 1999. Peak discharge from the macropore outlets was 0.6 L min⁻¹. Some of the response during the study period was diurnal and related to snow melt. However, hydrograph response is rapid and mirrors the Trout Beck regime, with mean peak flow lag times of just 1.6 h since peak rain. The macropore networks clearly allow water from the surface to reach deeper layers rapidly, bypassing the peat matrix.

Flow at the base of the peat was monitored at all eight throughflow trough sites; only one site produced runoff. Discharge was low, with a maximum recorded rate of only 0.0145 L min⁻¹ per metre of contour width, ephemeral and strongly linked to rainfall events. Discharge at the peat–clay interface was not therefore a result of continuous slow seepage from the peat mass.

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Fig. 8 Steady-state runoff rates by vegetation type with rainfall intensity for each field plot. (a) Surface runoff. (b) Runoff at 5 cm depth. (c) Runoff at 10 cm depth.

No flow was recorded from 10 cm depth to the base of the peat (100 cm) at this plot (H5) and it seems likely that macropores connect the surface to the peat base, bypassing the matrix.

(E) PIPEFLOW

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The pipeflow response from two to three metre deep blanket peat was found to be different from that reported in the shallow peaty podzols of the Welsh uplands. Peak runoff rates were significantly higher and initial response to rainfall significantly quicker (by up to 6 h). Mean pipe morphology and hydrograph response for the LDPS catchment are given in Table 1. There was no significant difference between total runoff or timing of response between deep (> 1 m) or shallow pipes. Response times from all the pipes were short, even from pipes deep within the peat, and peak



Fig. 9 Discharge from two macropore outlets during day 97-125, 1999. (a) Precipitation. (b) Trout Beck. (c) Outlet at 45 cm depth. (d) Outlet at 60 cm depth.

Table 1 Mean morphology and discharge of the 30 pipe outlets sampled in the LDPS catchment, July-December 1999

Factor	Mean	SD
Peat depth in catchment	1.54 m	0.58 m
Pipe roof depth	0.90 m	0.57 m
Pipe diameter	0.19 m	0.16 m
Pipe length	61.50 m	34.51 m
Storm discharge*	79.1 m ³	
Peak discharge*	0.0053 m ³ s ⁻¹	
Start lag time*†	2.4 h	1.5 h
Peak lag time*‡	4.0 h	2.2 h

*15 of the 30 pipes sampled were continuously gauged. †Time from first recorded rainfall to hydrograph rise.

[‡]Time from peak rainfall to peak discharge.

flow was as great as 4.6 L min⁻¹. Overall, pipeflow contributed around 10% of the streamflow volume at LDPS. On the rising and falling limbs of the stream Ecological Society, hydrograph, however, pipes could contribute up to 30% Journal of Ecology, of streamflow.

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Discussion

OVERLAND FLOW AND MATRIX THROUGHFLOW

Rainfall simulation and hillslope runoff measurement have demonstrated that overland flow dominates the runoff response at Moor House. Catchment rainfall: runoff ratios were very high and result from efficient transfer of water to the channel across the hillslopes. Thus, in contradiction to an often expressed view, the Moor House blanket peats do not behave like a 'sponge' (Ingram 1983); rather water is released rapidly following rainfall or snowmelt. Baseflows were poorly maintained and many small tributaries dry up completely after only a week without rain. Trout Beck itself probably only continues to flow during droughts because of groundwater discharge from limestone beds below the peat. Water tables were rapidly recharged following rainfall (indicating that infiltration-excess overland flow was unlikely) and were maintained above 5 cm

depth for 82% of the time. The spatial pattern of overland flow development on hillslopes clearly showed that saturation-excess overland flow was occurring and that infiltration-excess overland flow was not. The spatial pattern of peat saturation has a dominant influence on runoff production in blanket peat. This does not invalidate the diplotelmic model, but reminds us that spatial variation in hillslope runoff generation is not unimportant in blanket peat. Concentrated lines of flow were observed by hillslope crest-stage tube mapping. These flow lines have sometimes been attributed to headstreams which were originally developed in mineral ground, but have become overgrown by peat rather than collapsing later (Tomlinson 1979). Ingram (1967) also identified 'water tracks' in peats where preferential flow seemed to occur.

Overland flow has been found to occur across peats with and without *Sphagnum* at Moor House. Ingram & Bragg (1984) and Ingram (1991) suggest that the acrotelm itself possesses the essential characteristics of a layer which suppresses overland flow, and is thus self-sustaining. This is particularly important because *Sphagnum*, for example, has no roots and could in theory be washed away by overland flow (Bragg & Tallis 2001). Crest-stage tube mapping and rainfall simulator plots however, have shown that widespread overland flow does occur on vegetated peat hillslopes. Indeed, overland flow can frequently be seen over both longestablished and regenerating *Sphagnum* without resulting in erosion and field observations suggest *Sphagnum* carpets can survive rapid and deep overland flow.

Rainfall simulation, runoff troughs and water table results suggest that the 'acrotelm' at Moor House is thin. Once the water table at the ECN site was lower than 5 cm depth, Evans et al. (1999) suggested that its level was controlled solely by evapotranspiration as the water table was stable during night hours. This supports the acrotelm-catotelm model since it suggests that most lateral water movement through the peat takes place in the upper peat layers. The evidence also shows that the hydrologically active part of the acrotelm appears to be very thin and does not include the entire acrotelm defined as the entire depth of peat down to the lowest water table level. The peat matrix below 5 cm depth only produced around 2% of runoff from the hillslopes monitored. Hence the low hydraulic conductivities found at relatively shallow depths within the blanket peat (Rycroft et al. 1975; Holden et al. 2001) result in minimal flow contributions from most of the peat mass. This is strong evidence against the idea of Baird et al. (1998), who argued that because of the thickness of the catotelm it may contribute significantly to flow even if it has a low hydraulic conductivity.

It is likely that 'acrotelms' of different natures and hence different surface properties exist. Ingram & Bragg (1984), for example, view the acrotelm of a raised mire as comprising poorly decomposed, high hydraulic conductivity *Sphagnum* peat often 50 cm thick. Such an acrotelm is uncommon in the blanket peat of the northern Pennines except in localized flushes or hollows. Hence the nature of the peat surface and upper peat layers are likely to be very important factors in determining runoff production processes within different types of peatland. Boelter (1964) makes an important but often ignored point, that the hydrologic role of any bog depends on the type of peat found in the bog. The term 'acrotelm' might be thought somewhat less useful therefore, given this wide variability in thickness, but its salient characteristic of high hydraulic conductivity seems to be present irrespective of its depth; it would only be the propensity to encourage overland flow that would vary.

Rainfall simulator results at Moor House indicate that bare peat has equivalent infiltration rates to that of a vegetated peat. This may be related to surface desiccation as bare peat surfaces degrade allowing increased infiltration to take place, such that the nearsurface peat that was once the catotelm in effect becomes a thin acrotelm. Comparison of seasonal rainfall simulations showed that infiltration was greater under bare, Eriophorum and Calluna dominated peats during the dry summer of 1999 than in the spring and significantly more runoff is produced from between 5 cm and 10 cm depth. Structural cracking could be observed on the peat surface during the summer under these vegetation communities and thus more water was probably moving through macropore networks. Sphagnum rubellum may have protected the surface from desiccation during the 1999 summer. As well as shading the surface Sphagnum rubellum tends to grow in wetter areas which have higher water tables, such as in topographical hollows which are very poorly drained and so these areas may be less likely to dry out, unless the drought is very severe.

Drought summers like that in 1995 at Moor House mean that the water table drops to much lower layers than would normally be the case. Thus, the depth of the acrotelm deepens temporarily and aeration of lower peat layers takes place. Verry (1984) suggested that Ingram's (1983) definition of the acrotelm-catotelm boundary needed changing to account for drought events. However, the definition itself may not need changing; the peat properties themselves may change with aeration and drying (Holden & Burt 2002c). Thus, the assumption that blanket peat will remain largely saturated with little temporal variability in water table level may not hold in future with a more volatile climate. There are implications for future peatland hydrology, ecology and erosion given that water tables and their fluctuations are important for vegetational distribution (Ingram 1983; Hammond et al. 1990), and that continued intrusions of the water table into the usually anaerobic catotelm may change its physical and hydrological properties allowing colloidal constituents to undergo irreversible physical alteration (Ingram 1991; Egglesman et al. 1993; Holden & Burt 2002c), encouraging the leaching of dissolved organic carbon in subsequent periods of high runoff.

MACROPORE AND PIPE THROUGHFLOW

Tension-infiltrometer tests showed macropores to be significant pathways for runoff generation in the blanket peat at Moor House. Baird & Gaffney (2000) found clear evidence of plot-scale bypassing flow using potassium bromide tracers in the Somerset Levels. Their hydraulic conductivity data suggested low transmission rates, yet the tracer appeared much more quickly than predicted. Bypass flow to the peat base was recorded at one of the hillslope runoff troughs at Moor House. This flow may be important for the stability of blanket peat slopes within which frequent peat slides and bog bursts have been reported (e.g. Crisp et al. 1964; Tallis 2001). Holden & Burt (2002c) performed laboratory rainfall simulation on peat blocks. In the initial runs there were no significant differences from the field-based study discussed above. A four-week drought was then applied to the blocks. Even after 21 days of rewetting the number of macropores remaining was significantly greater in peat blocks subjected to drought compared to those which were kept wet. Structural changes took place within the upper peat layers following drought beneath both bare and vegetated surfaces and many of these changes were found to be long-lasting.

Jones (1981, 1994) showed that in the shallow peaty podzols of mid-Wales pipes were found typically at soil horizon interfaces. However, pipes were found in the deep peat at Moor House throughout the profile, ranging from within the underlying substrate at around 3 m depth to pipes that were within a few centimetres of the surface. Pipes were up to 1 m in diameter and several hundred metres in length. Holden & Burt (2002b) outline the pipe morphologies within the Little Dodgen Pot Sike (LDPS) catchment at Moor House and Holden et al. (2002) show how these subsurface pipes can be identified and mapped using ground-penetrating radar (GPR). The pipe networks are more extensive than indicated by surface observation or mapping of pipe outlets alone. Pipe depth and diameter can be completely different just a few metres upslope from the outlet (Terajima et al. 2000).

Pipes in LDPS were found to supply up to 30% of streamflow with a mean of 10% yet most of the drainage path was well below the acrotelm. Pipes can directly couple source areas for water, sediment and nutrients several hundred metres distant to the river channel. Most pipes in LDPS respond to low rainfall intensities and totals even after a dry period. In contrast to the mainly ephemeral systems examined by Gilman & Newson (1980) and McCaig (1983) there is no evidence to suggest a minimum rainfall threshold for pipeflow at Moor House. It seems that pipes in deep blanket peat are well-connected to the surface, receiving drainage far more quickly and in greater volumes than would be expected simply from diffuse seepage through the overburden. Holden & Burt (2002b) suggest that most of the pipes receive their water from saturation-excess overland flow and near-surface flow; the water enters

© 2003 British Ecological Society, *Journal of Ecology*, **91**, 86–102 pipe networks near the surface or where the pipes are open to the surface. Macropores may provide bypass routes for water into pipe networks, and pipe formation itself has been linked to crack formation in the peat following dry weather (e.g. Gilman & Newson 1980; Jones 1981; Jones et al. 1997). Collapse features are common, allowing surface water to readily enter the pipe network. However, little is known about the initiation of pipes or their enlargement by erosion. Often sediment is deposited on the peat and vegetation surface where a pipe has overflowed during a storm event. This sediment can contain a large proportion of mineral material from the underlying substrate. The existence of pipes and macropores therefore opens the way for the fluxes of water, sediment and nutrient contributions from deep within the peat rather than simply by rapid transfer through the acrotelm.

There are also links between other wetland landscape features and pipes which require further research. In LDPS there are four areas where bog pools are common and all of these are associated with piping (Holden et al. 2002). Many of the pipes seem to originate in pool-hummock complexes and some pipes drain directly into gully heads. Jones (1981) and Price (1992) have both suggested that soil piping is confined to the steeper parts of blanket bogs but research in the north Pennines does not corroborate these views. There is evidence from GPR that the areas of blanket peat with the greatest density of pipes tend to be on the gentlest slopes (Holden et al. 2002). On steeper slopes the pipe network tends to be less dense with single-thread pipe systems more common. This is reminiscent of Bower's (1960) Type I and Type II gully erosion systems in blanket peat: she argued that gullies are more branched on flatter slopes, feeding into straighter, unbranching gullies on steeper slopes. Further work is required to test whether the pipe networks are of a similar form, and to search for any links between piping, hummock-pool terrain and gully erosion.

Conclusions

Rapid and efficient transfer of water from the hillslopes to the channel results in flashy hydrographs and large storm peaks in blanket peat catchments. Thus, unlike some lowland wetlands, blanket peat catchments tend to be sources of flooding rather than attenuators of flow. Saturation-excess overland flow, together with near-surface throughflow in the acrotelm, dominate storm runoff production in the northern Pennines, and very little water is produced from the peat matrix below 5 cm depth. Nevertheless, there is still a significant contribution to runoff from the macropore and pipe flow pathways from deeper within the peat. At Moor House the evidence suggests that around 35% runoff moves through the macropore network, 10% through soil pipes and 80% as saturation-excess overland flow. Only 20% seems to be produced as shallow throughflow. While these estimates add up to greater than 100% this reflects the fact that the same water may pass through several pathways on the way to the stream. The dominance of overland flow also reflects the importance of footslopes and hillslope hollows as contributing areas for runoff production where saturation-excess overland dominates.

There are clear links between runoff production and vegetation, topography and preferential flowpaths at a range of scales. Surface cover type played a significant role in infiltration and runoff generation during rainfall simulation and tension infiltrometer tests. Macropores and soil pipes, as well as being important flowpaths, may also provide coupling between deep and shallow sources of solutes and sediments. Bypassing flow can occur at the macropore-scale, or on a hillslope plot where there is plot-scale heterogeneity, or at a hillslope-scale where there may be preferential water tracks or soil pipes. However, there is much work to be done to unravel the complex linkages that exist between these subsurface and surface preferential pathways and the surrounding wetland landscapes. The importance of macropores to the hydrology of blanket peats implies that they may also be important to ecological and biogeochemical processes in blanket peat catchments. This may be a crucial area for future research given the potential effects of changes in peat hydrology on in-stream water chemistry and leaching of dissolved organic carbon.

This paper has highlighted both the utility and inadequacy of using the acrotelm-catotelm model in ecohydrological research in blanket peat catchments. Often wetland scientists envisage blanket peatlands in a one or two-dimensional space, and the use of the acrotelm-catotelm model seems to have further encouraged this. We have highlighted the three-dimensional and highly variable nature of runoff flowpaths within blanket peat catchments. While we would agree with Ingram (1983) that an understanding of the acrotelmcatotelm model is fundamental to any clear understanding of the hydrology and ecology of mires, we would also argue that the model has been overused to the extent that the spatial and temporal nature of ecohydrological functioning in wetlands has been largely ignored. The acrotelm-catotelm model provides a useful starting point for understanding runoff generation and peatland development, but is misleading in its simplicity. The model works well for raised mires, which are much simpler systems than blanket mires but it will be important to establish in much more detail the ecohydrological, solutional and sedimentological relationships that exist between water flow processes and pathways and ecological processes in peatland environments.

Acknowledgements

© 2003 British Ecological Society, *Journal of Ecology*, **91**, 86–102 Thanks are given to the Environment Agency for river flow data, to English Nature for access to Moor House NNR, and to UK Environmental Change Network for water table data. The continuing support of John Adamson (ECN, CEH Merlewood) is gratefully acknowledged.

References

- Ankeny, M.D., Kaspar, T.C. & Horton, R. (1988) Design for an automated tension infiltrometer. *Journal of the Soil Science Society of America*, 52, 893–896.
- Atkinson, T.C. (1978) Techniques for measuring subsurface flow on hillslopes. *Hillslope Hydrology* (ed. M.J. Kikby), pp. 73–120. John Wiley, Chichester.
- Baird, A.J. (1995) Hydrological investigations of soil water and groundwater processes in wetlands. *Hydrology and Hydrochemistry of British Wetlands* (eds J.M.R. Hughes & A.L. Heathwaite), pp. 111–129. John Wiley, Chichester.
- Baird, A.J. (1997a) Field estimation of macropore functioning and surface hydraulic conductivity in a fen peat. *Hydrological Processes*, 11, 287–295.
- Baird, A.J. (1997b) Continuity in hydrological systems. Contemporary Hydrology: Towards Holistic Environmental Science (ed. R. Wilby), pp. 25–58. Wiley, Chichester.
- Baird, A.J., Beckwith, C. & Heathwaite, A.L. (1998) Water movement in undamaged blanket peats. *Blanket Mire Degradation, Proceedings* (eds J.H. Tallis, R. Meade & P.D. Hulme), pp. 128–139. Mires Research Group, British Ecological Society, Manchester.
- Baird, A.J. & Gaffney, S.W. (2000) Solute movement in a drained fen peat: a tracer study in a Somerset (UK) wetland. *Hydrological Processes*, 14, 2489–2503.
- Betson, R.P. (1964) What is watershed runoff? Journal of Geophysical Research, 69, 1541–1552.
- Beven, K.J. & Germann, P. (1982) Macropores and water flow in soils. *Water Resources Research*, 18, 1311–1325.
- Boelter, D.H. (1964) Water storage characteristics of several peats in situ. Soil Science Society of America Proceedings, 28, 433–435.
- Bower, M.M. (1960) Peat erosion in the Pennines. Advancement of Science, 64, 323–331.
- Bowyer-Bower, T.A.S. & Burt, T.P. (1989) Rainfall simulators for investigating soil response to rainfall. *Soil Technology*, 2, 1–16.
- Bragg, O.M. & Tallis, J.H. (2001) The sensitivity of peatcovered upland landscapes. *Catena*, 42, 345–360.
- Bromley, J. & Robinson, M. (1995) Groundwater in raised mire systems: models, mounds and myths. *Hydrology and Hydrochemistry of British Wetlands* (eds J.M.R. Hughes & A.L. Heathwaite), pp. 95–109. Wiley, Chichester.
- Burt, T.P. (1988) A practical exercise to demonstrate the variable source area model. *Journal for Geography in Higher Education*, **12**, 177–186.
- Burt, T.P. (1996) The hydrology of headwater catchments. *River Flows and Channel Forms* (eds G.E. Petts & P. Calow), pp. 6–31. Blackwell Science, Oxford.
- Burt, T.P., Adamson, J.K. & Lane, A.M.J. (1998) Long-term rainfall and streamflow records for north central England; putting the Environmental Change Network site at Moor House National Nature Reserve in context. *Hydrological Science Journal*, 43, 775–787.
- Burt, T.P., Heathwaite, A.L. & Labadz, J.C. (1990) Runoff production in peat covered-catchments. *Process Studies in Hillslope Hydrology* (eds M.G. Anderson & T.P. Burt), pp. 463–500. John Wiley, Chichester.
- Chappell, N. & Ternan, L. (1992) Flow path dimensionality and hydrological modeling. *Hydrological Processes*, 6, 327–345.
- Conway, V.M. & Millar, A. (1960) The hydrology of some small peat-covered catchments in the northern Pennines. *Journal of the Institute of Water Engineers*, 14, 415–424.
- Crisp, D.T., Rawes, M. & Welch, D. (1964) A Pennine peat slide. *Geographical Journal*, **130**, 519–524.
- Eddy, A., Welch, D. & Rawes, M. (1969) The vegetation of Moor House National Nature Reserve in the North Pennines, England. *Vegetatio*, 16, 239–284.
- Egglesmann, R., Heathwaite, A.L., Gross-Braukmann, G., Kuster, E., Naucke, W., Schich, M. & Schweikle, V. (1993)

Physical processes and properties of mires. *Mires, Process, Exploration and Conservation* (eds A.L. Heathwaite & K.H. Gottlich), pp. 171–262. Wiley, Chichester.

- Elgee, F. (1912) *The moorlands of north-eastern Yorkshire*. A Brown, London.
- Evans, M.G., Burt, T.P., Holden, J. & Adamson, J. (1999) Runoff generation and water table fluctuations in blanket peat: evidence from UK data spanning the dry summer of 1995. *Journal of Hydrology*, **221**, 141–160.
- Gilman, K. (1994) Hydrology and wetland conservation. John Wiley, Chichester.
- Gilman, K. & Newson, M.D. (1980) Soil pipes and pipeflow; a hydrological study in upland Wales. British Geomorphological Research Group Research Monograph no. 1. Geo Books, Norwich.
- Hammond, R.F., Van der Krogt, G. & Osinga, T. (1990) Vegetation and water-tables on two raised bog remnants in County Kildare. *Ecology and Conservation of Irish Peatlands* (ed. G.J. Doyle), pp. 121–134. Royal Irish Academy, Dublin.
- Heal, O.W. & Smith, R. (1978) The Moor House Program: introduction and site description. *Production Ecology of British Moors and Montane Grasslands* (eds O.W. Heal & D.F. Perkins), pp. 3–16. Springer, Berlin.
- Hewlett, J.D. (1961) Watershed management. *Report for 1961 Southeastern Forest Experiment Station*, pp. 62–66. US Forest Service, Ashville, North Carolina.
- Hilbert, D.W., Roulet, N. & Moore, T. (2000) Modelling and analysis of peatlands as dynamical systems. *Journal of Ecology*, 88, 230–242.
- Holden, N.M. (1998) By-pass of water through laboratory columns of milled peat. *International Peat Journal*, **8**, 13–22.
- Holden, J. (2000) *Runoff production in blanket peat covered catchments.* Unpublished PhD Thesis, University of Durham, Durham.
- Holden, J. & Adamson, J. (2001) Gordon Manley and the north Pennines. *Journal of Meteorology*, 26, 329–333.
- Holden, J. & Burt, T.P. (2002a) Infiltration, runoff and sediment production in blanket peat catchments: implications of field rainfall simulation experiments. *Hydrological Processes*, 16, 2537–2557.
- Holden, J. & Burt, T.P. (2002b) Piping and pipeflow in a deep peat catchment. *Catena*, 48, 163–199.
- Holden, J. & Burt, T.P. (2002c) Laboratory experiments on drought and runoff in blanket peat. *European Journal of Soil Science*, **53**, 675–689.
- Holden, J. & Burt, T.P. (in press) Hydraulic conductivity in upland blanket peat: measurement and variability. *Hydrological Processes*.
- Holden, J., Burt, T.P. & Cox, N.J. (2001) Macroporosity and infiltration in blanket peat: the implications of tension disc infiltrometer measurements. *Hydrological Processes*, 15, 289–303.
- Holden, J., Burt, T.P. & Vilas, M. (2002) Application of ground penetrating radar to the identification of subsurface piping in blanket peat. *Earth Surface Processes and Landforms*, 27, 235–249.
- Hulme, M. (1998) The climate in the UK from November 1994 to October 1995. *Weather*, **53**, 242–257.
- Ingram (1983) Hydrology. Ecosystems of the World 4A, Mires: swamp, bog, fen and moor (ed. A.J.P. Gore), pp. 67– 158. Elsevier, Oxford.
- Ingram, H.A.P. (1967) Problems of hydrology and plant distribution in mires. *Journal of Ecology*, **55**, 711–724.
- Ingram, H.A.P. (1978) Soil layers in mires: function and terminology. *Journal of Soil Science*, **29**, 224–227.

© 2003 British Ecological Society, *Journal of Ecology*, **91**, 86–102

- Ingram, H.A.P. (1982) Size and shape in raised mire ecosystems: a geophysical model. *Nature*, 297, 300–303.
- Ingram, H.A.P. (1991) Introduction to the ecohydrology of mires in the context of cultural perturbation. *Peatland*

ecosystems and man: an impact assessment (eds O.M. Bragg, P.D. Hulme, H.A.P Ingram & R.A. Robertson), pp. 67–93. Department of Biological Sciences, Dundee University/ International Peat Society, Helsinki.

- Ingram, H.A.P. & Bragg, O.M. (1984) The diptotelmic mire: some hydrological consequences reviewed. *Proceedings of* the Seventh International Peat Congress, Dublin, pp. 220– 234. International Peat Society, Dublin.
- Ivanov, K.E. (1948) Filtration in the top layer of convex mire massifs. *Meteorologiya*. I. Gidrologiya, 2, 46–59. (In Russian).
- Ivanov, K.E. (1953) Gidrologiya bolot. [Hydrology of mires]. Gidrometeoizdat, Leningrad.
- Ivanov, K.E. (1981) Water movement in mirelands. Academic Press, London.
- Johnson, G.A.L. & Dunham, K.C. (1963) The Geology of Moor House. Monographs of nature conservancy, 2. HMSO, London.
- Jones, J.A.A. (1981) The nature of soil piping: a review of research. British Geomorphological Research Group Monograph Series 3. Geo Books, Norwich.
- Jones, J.A.A. (1994) Subsurface flow and subsurface erosion. Process and form in geomorphology (ed. D.R. Stoddart), pp. 74–120. Routledge, London.
- Jones, J.A.A. & Crane, F.G. (1984) Pipeflow and pipe erosion in the Maesnant experimental catchment. *Catchment Experiments in Fluvial Geomorphology* (eds T.P. Burt & D.E. Walling), pp. 55–72. Geobooks, Norwich.
- Jones, J.A.A., Lawton, M., Wareing, D.P. & Crane, F.G. (1984) An economical data logging system for field experiments. British Geomorphological Research Group, Technical Bulletin, 31.
- Jones, J.A.A., Richardson, J.M. & Jacob, H.J. (1997) Factors controlling the distribution of piping in Britain: a reconnaissance. *Geomorphology*, 20, 289–306.
- Khan, A.A.H. & Org, C.K. (1997) Design and calibration of tipping bucket system for field runoff and sediment quantification. *Journal of Soil and Water Conservation*, 52, 437–443.
- Kirkby, M.J. (1985) Hillslope Hydrology. Hydrological Forecasting (eds M.G. Anderson & T.P. Burt), pp. 37–75. Wiley, Chichester.
- Kirkby, M.J., Kneale, P.E., Lewis, S.L. & Smith, R.T. (1995) Modelling the form and distribution of peat mires. *Hydrology and Hydrochemistry of British Wetlands* (eds J.M.R. Hughes & A.L. Heathwaite), pp. 83–93. John Wiley, Chichester.
- Lopatin, A.V. (1949) The hydrological significance of raised mires. *Vest. Leningrad. Gos. University*, 2, 37–49. (In Russian).
- MacAlister, C. & Parkin, G. (1998) Towards a whole-system model for the hydrology of peat mires. Patterned Mires and Mire Pools: Origin and Development; Flora and Fauna. *Proceedings: University of Durham*, 6–7 April, 1998 (eds V. Standen, J.H. Tallis & R. Meade), pp. 116–126. British Ecological Society, Durham.
- Manley, G. (1942) Meteorological observations on Dun Fell, a mountain station in northern England. *Quarterly Journal* of the Royal Meteorological Society, **68**, 151–165.
- Marsh, T.J. & Turton, P.S. (1996) The 1995 drought a water resources perspective. *Weather*, **51**, 46–53.
- McCaig, M. (1983) Contributions to storm quickflow in a small headwater catchment – the role of natural pipes and soil macropores. *Earth Surface Processes and Landforms*, 8, 239–252.
- McKillop, R., Kouwen, N. & Soulis, E.D. (1999) Modeling the rainfall-runoff response of a headwater wetland. *Water Resources Research*, 35, 1165–1177.
- Ogunkoya, O.O. & Jenkins, A. (1991) Analysis of runoff pathways and flow contributions using deuterium and stream chemistry. *Hydrological Processes*, **5**, 271–282.

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- Pearsall, W.H. (1950) Mountains and moorlands. Collins, London. Price, J.S. (1992) Blanket bog in Newfoundland: Part 2. Hydrological processes. Journal of Hydrology, 135, 103–119.
- Rawes, M. & Welch, D. (1969) Further studies on sheep grazing in the northern Pennines. *Journal of the British Grassland Society*, **19**, 56–61.
- Reynolds, E.D. & Elrick, D.E. (1991) Determination of hydraulic conductivity using a tension infiltrometer. *Journal* of the Soil Science Society of America, 55, 633–639.
- Rodwell, J.S. (1991) *British plant communities volume 2: mires and heaths*. University of Cambridge, Cambridge.
- Romanov, V.V. (1968) *Hydrophysics of bogs*. (Translated by N. Kaner). Israel Program of Scientific Translations, Jerusalem.
- Rycroft, D.W., Williams, D.J.A. & Ingram, H.A.P. (1975) The transmission of water through peat. II. Field Experiments. *Journal of Ecology*, 63, 557–568.
- Smit, H. (1996) The runoff generation of a Scottish raised mire: an ecohydrological study. Unpublished PhD Thesis, University of Dundee, Dundee.
- Sykes, J.M. & Lane, A.M.J. (1996) The United Kingdom Environmental Change Network: Protocols for standard measurements of terrestial sites. Natural Environmental Research Council, London.
- Tallis, J.H. (2001) Bog bursts. Biologist, 48, 218-223.

- Tallis, J.H., Meade, R. & Hulme, P.D. (1998) Introduction. Blanket Mire Degradation, Proceedings (eds J.H. Tallis, R. Meade & P.D. Hulme), pp. 1–2. Mires Research Group, British Ecological Society, Manchester.
- Terajima, T., Sakamoto, T. & Shirai, T. (2000) Morphology, structure and flow phases in soil pipes developing in forested hillslopes underlain by a Quaternary sand-gravel formation, Hokkaido, northern main island in Japan. *Hydrological Processes*, 14, 713–726.
- Thomas, G.W. & Phillips, R.E. (1979) Consequences of water movement in macropores. *Journal of Environmental Quality*, 8, 149–152.
- Tomlinson, R.W. (1979) Water levels in peatlands and some implications for runoff and erosional processes. *Geographical Approaches to Fluvial Processes* (ed. A.F. Pitty), pp. 149–162. Geo Books, Norwich.
- Verry, E.S. (1984) Microtopography and water table fluctuation in a sphagnum mire. *Proceedings of the 7th International Peat Congress, Dublin 1984*, Volume 2, pp. 11–31.
- Von Post, L. (1922) SGU peat inventory and some preliminary results. Svenska Mosskulturforeningens Tidskrift, Jonkoping, Sweden, 36, 1–37.

Received 9 May 2002 revision accepted 28 October 2002