

A video simulating the growth of a raised bog

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SUMMARY

The late Hugh Ingram (HAPI) contributed many things to our knowledge of peatlands. The two best known are probably the acrotelm/catotelm terminology (Ingram 1978), and the application of Childs & Youngs (1961) hemi-elliptical groundwater mound to the cross-section of raised bogs (Ingram 1982). As a tribute to HAPI, I combine these concepts with three others to create a video showing the development of a notional raised bog during 10,000 years. After that, I consider some of the limitations of this simplistic model and why, nevertheless, it is still useful.

KEY WORDS: decay, peatland, peripheral trees, pools

INTRODUCTION

Raised bogs are dome-shaped accumulations of peat with a water table, maintained by precipitation, up to several metres above that in the surrounding mineral soils. Such bogs often have concentric long and narrow pools around a central larger one (for example Belyea & Lancaster 2002). Many also have a fringe inside the perimeter of stunted conifer trees (pine, spruce, larch).

There are many other types of bog and fen: blanket bog, restionaceous peatlands in the southern hemisphere, tropical forested peatlands, forested European peatlands, high-altitude peatlands in China, and so on. This article is not concerned with these types (though some of the same processes may apply to some of them). It is about the exemplary, though not particularly common, raised peat bogs, and particularly those formed in the mild climate of western Europe.

Some of the processes governing the growth of raised bogs have emerged during the last three decades. Clymo (1984, Figure 20) explored in line diagrams the way in which a domed peat mass might develop by growing out from a single point over a flat plain, or by starting simultaneously over the whole of a flat plain. Spectacular advances in computing speed and storage now allow these processes to be illustrated in dynamic simulations ('videos'). Such simulations allow one to experiment with process parameters. Their main value may be educational, allowing one to visualise and confirm consequences that emerge from simple analyses.

This article presents two such dynamic simulations each based on four processes: the flow of water, peat mass accumulation, pool formation, and

peripheral tree establishment.

The simplistic ideas underlying four simulated features of a raised bog may be sketched as follows.

(1) Living plants at the top of the acrotelm fix carbon by photosynthesis, and may translocate some of it into roots or rhizomes. Plant mass in the acrotelm is reduced by aerobic decay (mostly by fungi) followed by mechanical collapse, reduced space between plant fragments, and thus much increased resistance to water flow, leading to saturation and to anoxia with much reduced decay rate in the peat proper - the catotelm - as it now is. The rôle of the acrotelm is as a preprocessor returning perhaps 90 % of the fixed mass to the air as carbon dioxide or by dissolved organic matter (DOM) running out of the bog. What survives becomes the peat proper in the catotelm. The thickness of the acrotelm depends on the species growing there, and may generally range from a hollow to a hummock. Negative feedback tends to result in the rate of addition of peat being similar in space on a given bog at a given time, whatever the vegetation (Belyea & Clymo 2001).

(2) Peat is porous, and water can flow (slowly) through it. The water table in the peat is above the mineral soil and (assuming the peat is homogeneous and isotropic) is near to hemi-elliptical in cross-section (Childs & Youngs 1961, Ingram 1982). The water table on the small raised bog at Dun Moss (eastern Scotland) conformed moderately well to this expectation (Ingram 1982), and so (Ingram 1987) - in three dimensions - did that at Ellergower Moss (south-west Scotland). Early observers in Sweden had noted the steeper slope on the margins of raised bogs, usually with different vegetation (more trees)

and had adopted the Swedish word ‘rand’, meaning ‘edge’ or ‘border’, for this part of the hemi-ellipse.

In general, the water table, with more precipitation than is necessary to compensate for drainage losses to (and from) the perimeter, creates conditions that govern the acrotelm - the source of new peat mass. The simulations here ignore processes in the acrotelm summarised in the rate, p , at which mass passes from it to the catotelm. In the simplest case assumed here p is constant. In Nature it probably changes somewhat over millennia, but there are no accurate estimates of such change.

The rate of upward growth of peat is a balance between the rate of addition of new peat at the top of the catotelm, and the cumulative rate of decay at all depths. That (anaerobic) decay does continue at all depths in the peat is strongly indicated by the downwards increase in concentration of *both* dissolved methane *and* dissolved carbon dioxide (Clymo & Pearce 1995, Clymo & Bryant 2008). This is easily explicable only if there is an underlying source of *both* gases below the base of the peat (not found in the one case it was sought), or decay continues deep in the peat - probably at all depths. The gases may escape as DOM or by ebullition, but diffusion to the air above is sufficient (Clymo & Bryant 2008).

(3) Pools form, but only where the hydrological gradient (slope) of the surface is tiny. A large central pool, surrounded by smaller pools, and a halo of concentric even smaller linear pools results (Belyea & Lancaster 2002). These pools may merge, and deepen, with time.

(4) A fringe inside the perimeter of (notionally pine/larch/spruce) trees develops where, in contrast to pools, the slope is greater than a critical value. The steeper the slope the more likely a tree is to establish. The probability that a tree will die increases with its age and with the shallowness of the slope.

As the main purpose of the article is to explain the basis for the video I cite only exemplary references, with no attempt at completeness.

METHODS

(1) Mass (height) accumulation

First, the cumulative dry mass, M , at the bog centre is found. In the following I assume unit area. For each time increment (typically 20 yr) for 10,000 yr a dry mass p ($\text{ML}^{-2}\text{T}^{-1}$) is added as a new layer at the bog surface. This new layer thus starts off containing m_0 . In the same time increment this new layer and every other one below it is allowed to decay. There are

several possible decay rules. The simplest is a constant proportional rate, α , yr^{-1} , so that

$$m_1 = \alpha m_0 \Delta t \quad [1]$$

where subscripts 0 and 1 represent the start and end of the decay period Δt . This leads to an asymptotic cumulative mass

$$M = p / \alpha \quad [2]$$

(Clymo 1984). But a constant rate of decay is unrealistic: some components of peat decay easily leaving more recalcitrant components, so α decreases. Clymo (1992) gave analytic solutions for two assumptions of how the decay rate decreases as the powers 1 and 2 of the mass remaining. However, a simulation allows any power, γ , to be used in

$$m_1 = \exp(-\gamma t) \alpha m_0 \Delta t \quad \dots [3]$$

where t is the current age of the bog. There is no limit to M with this assumption. The parameter, γ , of this approach has no clear physical meaning, and the combination of α and γ has not been estimated accurately in practice. A more interesting approach is that of Boudreau & Ruddick (1991), ‘B&R’, who start from the assumption that newly formed peat contains an unspecified number n of components, of unknown proportions, each decaying at an unknown but fixed rate - effectively a set of α_n values. This leads to a surprisingly simple relation:

$$m_t = m_0 (\beta / (\beta + t))^v \quad [4]$$

where m_t is the mass after time t , and β and v (Greek ‘nu’) are parameter values that can be interpreted in terms of the distribution of components with differing constant rates of decay. Again, we have no satisfactory estimates of the values of β and v . For the simulations I chose the constant and B&R approaches and selected plausible values for α , and for β and v . Because ‘height’ is easier to visualise than ‘mass area⁻¹’ I assume that the dry bulk density, ρ , is constant, so that height at the centre, H , is directly proportional to M .

To begin with, when the peat is shallow, the losses by decay from the peat proper in a given time interval are a small proportion of p , and the deviation from linearity of depth with time is small. But in deeper peat the sum of losses at *all* depths is larger than in shallower peat, and begins to approach p , the rate of addition at the surface. The age-depth curve bends over towards the horizontal.

(2) Water table – the peat surface

A hemi-ellipse is calculated for the now known height at the centre. The height at 10,000 yr is specified (7 m in the simulations) as is the width at

that time (half-width 500 m). This defines an ‘aspect quotient’, A_Q , of $7 / 500$. Two extreme situations are recognisable and are illustrated in the two videos. In one, the bog begins at a single point on an unbounded plain and grows outward, always with constant A_Q , so the current H determines the current width. In this approach ‘ p ’ is always constant as new growth near the edge recapitulates what happened earlier in the centre. At the other extreme the bog starts simultaneously over a large plain but does not extend as it grows. The width is fixed, so A_Q varies. The value of p is assumed constant at the centre, but elsewhere decreases as the water table controls the acrotelm behaviour. The acrotelm might increase in thickness, so aerobic decay operates for longer, and thus p (what survives to be passed on to the catotelm) actually decreases. Both extremes recognise the dominance of the hydrological constraint.

(3) Pool formation

This process is less exact. Observation (e.g. Ingram 1983, Foster *et al.* 1988, Belyea & Lancaster 2002) is that raised bogs often have large permanent pools (‘lochans’ in Scotland) mostly near their highest point (here called ‘centre’, though not necessarily geographically central). Around these large pools one often finds smaller randomly arranged pools, grading downslope into concentric lines of smaller pools. The steeper the slope, the narrower a pool can be, because if it were wider it would drain out at the lower side. A pool on a slope with water 5 cm deeper downslope (on a slope of 0.0075) could be 7 m wide at most. Only where the slope is very small can a large permanent pool exist. This account of pools and their distribution is idealised of course, but is close to that observed by Belyea & Lancaster (2002), as it must be for a simple simulation. Real examples differ in many ways, small and large, as do hypotheses about the processes involved. The essence is that the smaller the hydraulic gradient the wider the pool and the more random the arrangement.

Pool formation in the simulations follows six ‘rules’.

(3a) A pool can form only when the hydraulic gradient (slope) of the surface is less than a specified value: 0.004 in the simulations. The steeper the slope, the narrower a pool can be before overflowing its lower side. This defines, and restricts pools to, a central area of the bog.

(3b) For every point in the pool area, pool-forming potential is then defined as inversely proportional to the slope. This gives a standardised pool-forming potential, PFP, in the range 0 (at the critical slope) to 1.0 at the centre.

(3c) For every pool, the PFP in neighbouring non-pool points is penalised by a (fixed) proportion, P . This inhibits, but does not completely prevent, the extension of existing pools.

(3d) For every non-pool point in the pool area, a uniformly distributed random number in a fixed range, R , is got. If this random number is less than PFP, then a pool is allowed to form. Thus the chance that a pool will form is controlled by R , and the severity of the pool-neighbour penalty by P . Pools formed early have the greatest influence, and they are most likely to form at the centre where the slope is least.

(3e) The base of contiguous pools becomes a mean of the constituent pools weighted by the deeper one i.e. the pool depths in a contiguous block are made the same.

(3f) If the slope at a point is increasing, an existing pool will eventually drain (in the simulation, at a slope 1.5 times the critical slope for formation). In practice, this rule operates only when the bog began growth simultaneously over the whole plain (Simulation 2).

Of these ‘rules’, 3(a) and (3f) enshrine a clear mechanism, but the others are mere plausible devices.

(4) Tree growth

Unlike pool formation, which depends on the slope being small (< 0.004), tree establishment at the margins is assumed to be possible only where the slope is relatively large (> 0.022), and thus conditions are drier. At this slope the surface (acrotelm) is likely to drain more rapidly and to be drier than near the bog centre, and thus to be more suitable for tree growth. This reflects Freléchoux *et al.* (2000) who found higher density and growth rate of trees at the margins of a peatland.

Tree formation in the simulations follows five ‘rules’.

(4a) A tree may establish only where the slope is greater than 0.022.

(4b) Whether a tree establishes in a particular time period is a random process.

(4c) Trees grow following a hyperbolic curve over time.

(4d) Once established a tree may, with luck, survive even when the surface slope falls below the critical value.

(4e) Death is also a random process. This behaviour contrasts with that of pools, which, once formed, persist.

In Nature there may be interaction between slope and precipitation (for example, the frequency of unusually dry years that allow episodic establishment of new trees), but this is not simulated in the model used here.

The simulation has three further features.

(5) *The 'ghosts' of earlier surfaces.* These are shown, linked to their original heights.

(6) *A lagg fen.* The lagg is represented cosmetically by randomly changing deciduous trees.

(7) *The surrounding forest.* The cosmetic forest on mineral soil is of randomly changing spruce with some pine. (Tree size in the surrounding forest is about five times smaller than it is in Nature, to avoid the forest distracting attention).

The video has three parts: an explanatory introduction (5 s), the simulation (20 s), and a coda in which the final frame of the simulation is repeated (5 s). It may be 'frozen' at any point by pressing the <space> bar, or <CTRL-P> (depending on the video player) and restarted by repeating this action.

At 25 frames per second (fps) it is necessary to generate 750 separate graphics files. The simulation program is written in 'R', which has good graphical abilities (and is available for Linux, Windows, and Apple Mac). The program 'ffmpeg' (also available on the three main operating systems) was used to stitch these 750 files together into the final video occupying a few MB. The full program and the video files are provided in Supplementary Materials.

RESULTS

The two simulations are provided in three formats: '.mp4', '.FLV' and 'F4V'. Each simulation has been run on Linux, with 'Videos' and with 'VLC'; and the first two formats on Windows with 'Media Player'; and on Apple Mac with 'Quicktime' ('VLC' is available on all three operating systems).

Figure 1 is a 'still': the last frame of Simulation 1. The caption provides a key and viewing will allow one to prepare in one's own time for the dynamic videos, in which several things change simultaneously.

Simulation 1: 'Expanding' follows a raised bog that starts at a single point and expands on an unlimited plain, to the point after 10,000 yr where the bog is 1 km across and 7 m deep. Decay rate is constant. At 2000-yr intervals the surface (the 'ghost') at that time is followed as it sinks down because decay below it continues. At the left, the time course of growth is followed. It deviates increasingly from linearity (what would have happened if there were no decay), but is not yet near the asymptote it is tending towards at p/α .

Simulation 2: 'Stationary' has the same diameter and height at 10,000 yr, but growth begins simultaneously over the 1 km wide plain. Decay follows the more realistic 'B&R' model. Pools appear early because at the start the gradient is shallow all over the bog.

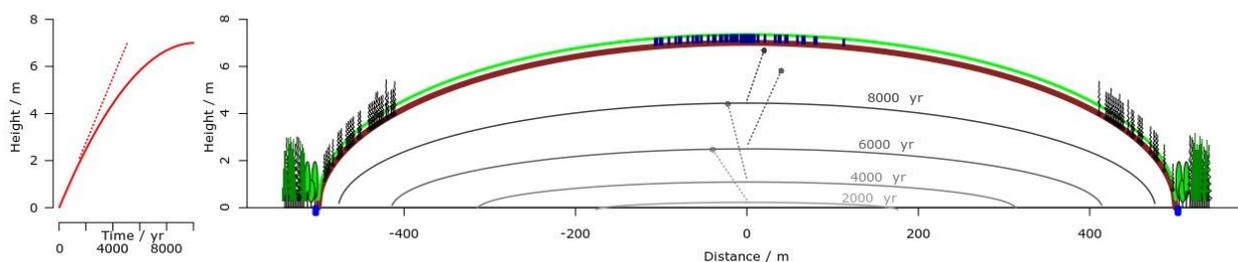
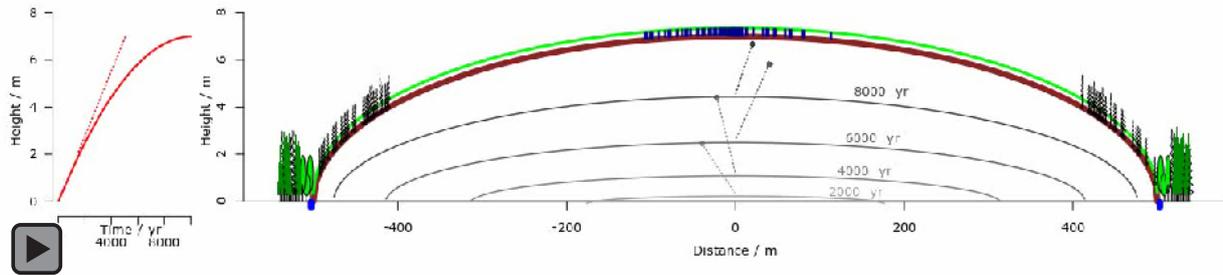
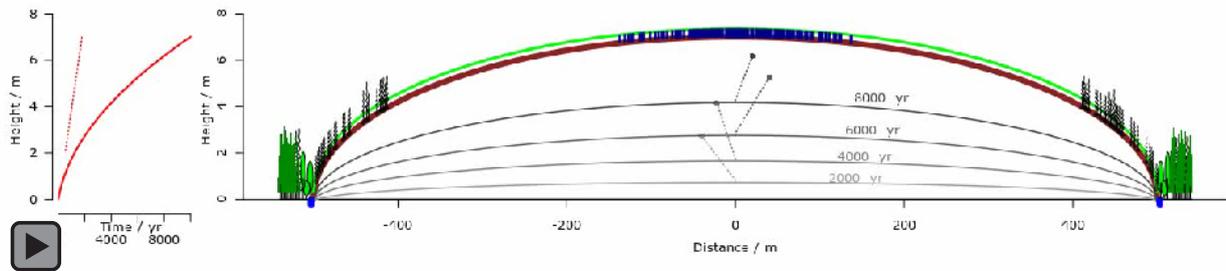


Figure 1. Final frame of the Simulation 1 video representing the state after 10,000 yr of growth of a raised bog starting from the centre of a plain, with constant decay (see text). *Green* represents the living surface (roughly the acrotelm). *Brown* is the top of the peat proper (roughly the top of the catotelm, the rest of which below is white). *Grey* are the ghosts of former surfaces at 2000 (lowest), 4000, 6000, and 8000 (highest) yr after the start; each ghost is linked to its original position (small circle) by a dashed line. *Blue* are pools. The peripheral fringe inside the perimeter of trees on the bog surface may be considered to be pine or larch. Surrounding the peat mass are a lagg fen with deciduous trees, and a spruce/pine forest (forest trees schematic, and only 1/5 the height they would be if to scale). The graph at the left shows the growth in height with time (thicker line) and what it would have been without decay (thinner straight dashed line).



Simulation 1: ‘Expanding’. The raised bog begins at a single point in a notionally unbounded plain, and expands out to 1 km wide and 7 m deep at 10,000 yr. The decay model is constant rate (Clymo 1984). The first 5 s are explanations. Then 20 s of simulation, followed by 5 s of coda in which the final frame of growth is frozen. If you are viewing in a recent version of Adobe Acrobat running in Windows, click on the arrow to start; or hover on the graphic for a control bar to start, freeze (pause) or stop. The animation may not work with other pdf viewers and operating systems; in that case, please refer to the video files in Supplementary Material.



Simulation 2: ‘Stationary’. The raised bog begins simultaneously over the whole 1 km-wide plain, and grows to 7 m deep at 10,000 yr. The decay model is ‘B&R’ (see text). The first 5 s are explanations. Then 20 s of simulation, followed by 5 s of coda in which the final frame of growth is frozen. If you are viewing in a recent version of Adobe Acrobat running in Windows, click on the arrow to start; or hover on the graphic for a control bar to start, freeze (pause) or stop. The animation may not work with other pdf viewers and operating systems; in that case, please refer to the video files in Supplementary Material.

DISCUSSION

The state of the two simulations (above) is fairly similar after 10,000 years.

It is superficially a paradox that the bog as a whole grows steadily upward, while the grey ghosts of former surfaces show every constituent part of the bog sinking down because all below it continues to decay. All this means is that the rate of addition is more than the total losses by decay at all depths.

Pool development does simulate reality: a large central pool, surrounding smaller ones, and even smaller ones peripheral to those. The outermost may be inferred to be narrow concentric pools with length a lot greater than width because, were it otherwise,

natural selection would remove pools that had too large a drop in water depth across their width. The history of pools in the two simulations is different because in Simulation 1 (‘Expanding’) it is at least two millennia before slopes are small enough to allow pools over a significant area, while in Simulation 2 (‘Stationary’) most of the surface is flat enough for pools to form from the start. Those near the perimeter disappear as the bog develops steeper slopes towards the centre. Most of the detail of when and where pools develop in areas with suitable slope results from the stochastic mechanisms incorporated in the ‘rules’ (3b) to (3d). As evidence accumulates to support hypotheses about processes, the mechanisms revealed can be substituted for these generalised ‘rules’.

Limitations in the simulations

Limitations of these simulations are legion. Here are a few of them.

(A) The simple groundwater mound hypothesis assumes that the peat is a homogeneous isotropic mass. That this is not so has been shown (e.g. Beckwith *et al.* 2003).

(B) For Simulation 1, values of p and α may be inferred from the gentle curve relating depth to age (Clymo 1984). The general slope determines p fairly well but α less well because it depends on the curvature of the depth / age plot, which is small. For Simulation 2, the value of p is again to be had from the general trend of the depth-age curve, but the gentle curve allows numerous equally poor estimates of the pair of parameters β and v for which a change in one can compensate for a change in the other. The choice of a pair is arbitrary and, until we get a direct measure of these very slow decay rates, will remain so.

(C) The assumption of constant p is implausible (Belyea & Baird 2006). In the stratigraphic record we see major changes of plant remains. For example, Svensson (1988) found three major phases at Storemosse (Sweden), with more humified boundaries between them. These changes were plausibly correlated with climate changes. Yet dramatic changes are often short term (a few hundred years) compared with the millennia of bog growth. The age-depth graph often (not always) shows a fairly steady march through the millennia, with short disruptions (Aaby & Tauber 1975). Constant p may not be as absurd as it seems. But some age-depth curves are convex rather than concave e.g. Ikonen (1993). These may indicate decreases in p with time (or peat depth). Again, we lack direct measurements.

(D) Neither this nor other peat growth models attempt to include special features such as under- or in-peat ‘pipes’.

(E) The age structure of pines on a bog varies. For example, Freléchoux *et al.* (2000) found that the stunted well-separated pines at the higher fringes of a bog were of differing age and generally older than those at the margin, which were taller and even-aged. This may be because of an unusual year favouring germination and establishment. The simulations model only the random establishment of trees (though it would be easy enough to model synchronous establishment).

(F) Last, but most important, there are several more realistic and, therefore, more complex process-based models of peatland development. Examples are Winston (1994); Frolking *et al.* (2001,

2010): model HPM, the Holocene Peat Model; Belyea & Baird (2006) which led to Baird *et al.* (2012) and Morris *et al.* 2012): DigiBog. This is not the place to compare and contrast these complicated process-based models, but a common feature is that they need numerous parameter values, and often driving variables (for example rainfall, temperature). It is the underlying processes and the parameter values that make the models more accurate. Using these models to estimate parameter values is difficult if not impossible, and some of the parameters can not easily be measured directly. They also have difficulties with parameter interactions (Quillet *et al.* 2013).

So, have the outdated models presented here lost all value? Not entirely. Their results approximate Nature’s reality. They force attention on hydrology, on the structure (acrotelm, catotelm) of the peat, HAPI’s areas of interest; on the low rates of decay in the catotelm, and on the generally reducing difference between annual input of peat and increasing cumulative losses. They are based on only two or three parameters, each with an easily understood meaning, and they can therefore be understood by non-specialists. In short they have an educational quality that justifies their continued existence and dynamic presentation. Simple and complex models both have their places.

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REFERENCES

- Aaby, B. & Tauber, H. (1975) Rates of peat formation in relation to humification and local environment, as shown by studies of a raised bog in Denmark. *Boreas*, 4, 1–17.
- Baird, A.J., Morris, P.J. & Belyea, L.R. (2012) The DigiBog peatland development model 1: rationale, conceptual model, and hydrological basis. *Ecohydrology* 5, 242–255.
- Beckwith, C.W., Baird A.J. & Heathwaite, A.L. (2003) Anisotropy and depth-related heterogeneity of hydraulic conductivity in a bog peat. I: laboratory measurements. *Hydrological Processes*, 17, 89–101.
- Belyea, L.R. & Baird, A.J. (2006) Beyond the “limits to peat bog growth”: cross-scale feedback in peatland development. *Ecological Monographs*, 76, 299–322.

- Belyea, L.R. & Clymo, R.S. (2001) Feedback control of the rate of peat formation. *Proceedings of the Royal Society of London B*, 268, 1315–1321.
- Belyea, L.R. & Lancaster, J. (2002) Inferring landscape dynamics of bog pools from scaling relationships and spatial patterns. *Journal of Ecology*, 90, 223–234.
- Boudreau, B.P. & Ruddick, B.R. (1991) On a reactive continuum representation of organic matter diagenesis. *American Journal of Science*, 291, 507–538.
- Childs, E.C. & Youngs, E.G. (1961) A study of some three-dimensional field-drainage problems. *Soil Science*, 92, 15–24.
- Clymo, R.S. (1984) The limits to peat bog growth. *Philosophical Transactions of the Royal Society of London B*, 303, 605–654.
- Clymo, R.S. (1992) Models of peat growth. *Suo*, 43, 127–136.
- Clymo, R.S. & Bryant, C.L. (2008) Diffusion and mass flow of dissolved carbon dioxide, methane, and dissolved organic carbon in a 7-m deep raised bog. *Geochimica et Cosmochimica Acta*, 72, 2048–2066.
- Clymo, R.S. & Pearce, D.M.E. (1995) Methane and carbon dioxide production in, transport through, and efflux from a peatland. *Philosophical Transactions of the Royal Society of London A*, 350, 249–259.
- Foster, D.R., Wright, H.E., Thelaus, M. & King, G.A. (1988). Bog development and landform dynamics in central Sweden and southeastern Labrador, Canada. *Journal of Ecology*, 76, 1164–1185.
- Freléchoux, F., Buttler, A., Schweingruber, F.H., & Gobat, J-M. (2000) Stand structure, invasion, and growth dynamics of bog pine (*Pinus uncinata* var. *rotundata*) in relation to peat cutting and drainage in the Jura Mountains, Switzerland. *Canadian Journal of Forest Research*, 30, 1114–1126.
- Frolking, S., Roulet, N.T., Moore, T.R., Richard, P.J.H., Lavoie, M. & Muller, S.D. (2001) Modelling northern peatland decomposition and peat accumulation. *Ecosystems*, 4, 479–498.
- Frolking, S., Roulet, N.T., Tuittila, E., Bubier, J.L., Quillet, A., Talbot, J. & Richard, P.J.H. (2010) A new model of Holocene peatland net primary production, decomposition, water balance, and peat accumulation. *Earth System Dynamics Discussions*, 1, 1–21.
- Ikonen, L. (1993) *Holocene Development and Peat Growth of the Raised Bog Pesansuo in Southwestern Finland*. Bulletin 370, Geological Survey of Finland, Espoo, 79 pp.
- Ingram, H.A.P. (1978) Soil layers in mires: function and terminology. *Journal of Soil Science*, 29, 224–227.
- Ingram, H.A.P. (1982) Size and shape in raised mire ecosystems: a geophysical model. *Nature, London*, 297, 300–303.
- Ingram, H.A.P. (1983) Hydrology. In: Gore, A.J.P. (ed.) *Ecosystems of the World. 4A. Mires, Swamp, Bog, Fen, and Moor*, Elsevier Scientific, Oxford, 67–158.
- Ingram, H.A.P. (1987) Ecohydrology of Scottish peatlands. *Transactions of the Royal Society of Edinburgh: Earth Sciences*, 78(04), 287–296.
- Morris, P.J., Baird, A.J. & Belyea, L.R. (2012) The DigiBog peatland development model 2: ecohydrological simulations in 2D. *Ecohydrology*, 5, 256–268, doi: 10.1002/eco.229.
- Quillet, A., Frolking, S., Garneau, M., Talbot, J. & Peng, C. (2013) Assessing the role of parameter interactions in the sensitivity analysis of a model of peatland dynamics. *Ecological Modelling*, 248, 30–40.
- Svensson, G. (1988) Bog development and environmental conditions as shown by the stratigraphy of Store Mosse mire in southern Sweden. *Boreas*, 17, 89–111.
- Winston, R.E. (1994) Models of the geomorphology, hydrology, and development of domed peat bodies. *Geological Society of America Bulletin*, 106, 1594–1604.

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