



ARTICLE

Freshwater Ecology

From genes to landscapes: Pattern formation and self-regulation in raised bogs with an example from Tierra del Fuego

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Abstract

We studied a pristine, prominently patterned raised bog in Tierra del Fuego, Argentina, to disentangle the complex interactions among plants and water and peat. The studied bog lacks complicating features often posed by other bogs. It is completely dominated by *Sphagnum magellanicum*, which covers all niches and growth forms, and is joined by only a dozen higher plant species; it is entirely ombrotrophic with very sharp borders to the surrounding fen; it has only one type of peat that shows an only limited range in degree of decomposition; and it is situated in a very even climate with minimal differences in rainfall and temperature over the year. We present detailed measurements along a 498-m-long transect crossing the bog, including water table measurements ($n = 498$), contiguous vegetation relevés ($n = 248$), hydraulic conductivity just below the water table ($n = 246$), and hydraulic conductivity in 11 depth profiles ($n = 291$); degree of humification of the corresponding peat was assessed in conjunction with the hydraulic conductivity measurements ($n = 537$). *Sphagnum magellanicum* moss samples were collected every 2 m along this transect as well and genotyped ($n = 242$). In addition, along short, 26-m-long transects crossing strings and flarks water table and hydraulic conductivity just below the water table were measured every meter. *Sphagnum* growth forms were assessed, and the vegetation of the entire bog was mapped in 10×10 -m relevés ($n = 3322$). A simulation model was applied to a generalized shape of the bog and produced surface patterns that well matched those seen in the field. The results were integrated with information from the literature and discussed in the framework of a self-regulating and self-organizing raised bog. We identified 19 hydrological feedback mechanisms. We found that the various mechanisms overlap in both space and time, which means there is redundancy in the self-regulation of the system. Raised bogs, when in a natural state, are among the most resilient ecosystems known; resilience that is provided by feedbacks and backup systems to these feedbacks.

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KEYWORDS

ecosystem diversity, genotyping, hydraulic conductivity, peatland, self-organization, *Sphagnum magellanicum*, vegetation relevés

Everything is connected. (Dirk Gently)

INTRODUCTION

Peatland ecosystems can show striking surface patterns, which have prompted research since the early days of peatland science. Regularities and variants were described not only focusing on vegetation cover but also addressing properties of water and peat. The hummocks and hollows typically occurring on raised bogs posed difficulties for the developing vegetation science, as they obviously did not represent homogeneous areas. The solution was to distinguish “vegetation complexes,” which comprise more or less regular patterns of different types of hummocks, hollows, or pools (Bogdanovskaya-Gieneff, 1928; Cajander, 1913; Osvald, 1923).

Besides describing the hummocks, hollows, and pools of the Augstumal raised bog, Weber (1902) also made a distinction on a larger spatial scale between a central plateau, a marginal slope or rand, and the fen peatland surrounding the bog. Cajander (1913) remarked that these distinct larger scale constituents are so closely linked that they can only be understood when viewed in conjunction. This led to peatlands in general being viewed and classified as hierarchical, nested systems with discernible units at different spatial scales in terms of plants, peat, and water and their interactions (Bogdanovskaya-Gieneff, 1949; Foster et al., 1988; Galkina, 1946; Masing, 1984; Sjörs, 1948).

In peatlands, there are strong interlinkages between plant cover, water, and peat. These dependencies are particularly apparent in raised bogs. To paraphrase Heinrich Dau (1821), plants grow at the top and add loose material that successively changes into ever denser peat under the influence of decomposition and weight of the peat above. The presence of water, through which oxygen diffuses more slowly than it is consumed by the microorganisms of decay, ensures that the plant material does not fully decompose after death but transforms into peat instead. The presence of peat ensures that water does not simply run off the raised dome. Altogether, the system manages to stay “high yet wet.”

The strong interdependencies between plants, water, and peat give rise to feedback mechanisms (Joosten, 1993; Joosten & Couwenberg, 2019; Van Breemen, 1995; Waddington et al., 2014). These feedbacks include direct (immediate) and indirect (mediate) reactions. An example

of the former is when *Sphagnum* capitula lose water and whiten, which increases albedo, thus reducing evaporative losses (Eggelsmann, 1963; Harris, 2008). Or, in another example, if the capitulum dries out repeatedly, apical dominance is diminished, resulting in more side branches and a denser growth form, which increases capillarity, keeping the capitulum moist (Green, 1968; Masing, 1984; Smolyanitsky, 1977). These negative feedbacks are a direct response of the individual plant.

Other, indirect feedbacks work through higher level structures or “entities” with emergent properties that result from the interaction between lower level entities. For example, a single moss stem with a dense growth form will not affect water tables in its vicinity. A hummock, which is in some way merely a collection of mosses with dense growth form, will affect water flow to some extent; a string, which is a coalesced group of hummocks arranged perpendicular to the slope, will affect water flow and water tables very effectively. The local-scale reaction of single plants to dry conditions can create higher level entities such as hummocks and strings that can effectively reduce runoff and keep the peatland wet. The sum is more than its parts: It not only needs mosses with dense growth form, but a sufficiently large number of them and a certain spatial arrangement.

From a system ecological point of view, feedbacks that go through higher order entities not only are self-regulating but are also the basis of self-organization. Local order responses and interactions create higher order entities that help stabilize the system (Couwenberg & Joosten, 1999). In an earlier paper, we showed how self-organization of raised bogs can explain diversity in these systems (Couwenberg & Joosten, 2005). We used a spatially explicit, heuristic, simulation model in which we defined responses between water and plants/peat at the level of small patches of moss. These local interactions created groups of patches representing hummocks and hollows. On a yet larger scale, hummocks and hollows combined to form three different ecotopes: a plateau, a hummock–hollow complex, and a rand. We showed how different parameter settings resulted in different combinations of these sites that actually defined different types of bogs. Our modeling thus provided an objective basis for the hierarchical classification approaches first developed by Cajander (1913) and Galkina (1946) in which classes on a higher level are defined as particular combinations of elements from the lower level. Moreover, the modeling showed that the scale levels chosen by Cajander

and Galkina are “real” and not a mere classification construct of the human mind.

The modeling also hinted at the implications of the patterning for the bog. As Dau (1823) already noted, for a raised bog to remain “high and wet,” the peat must be dense enough to retard water flow down and out of the dome. In other words, pore space must be small. However, small pore space also means small storativity and hence high water table fluctuations associated with losses and decomposition. (Storativity is the sum of specific yield, which refers to the drainable pore space of an uncompressible medium, and specific storage, which refers to changes in drainable pore space of a compressible medium. In an elastic medium like peat, changes in specific storage can be dominant (Hemond & Goldman, 1985; Price & Schlotzhauer, 1999)). Through feedbacks, a compromise is established in the bog between small enough pores to reduce runoff of water and large enough pores to guarantee or even enhance storage of water (Joosten, 1993; Joosten & Couwenberg, 2019). On all levels of organization, surface elements can be found that are focused either on the task of obstructing flow of water or on the task of storing water. We posit that if the compromise between these tasks cannot be met on a lower organizational level, it has to be realized on a higher one for the bog to persist.

To test these ideas and modeling results, we studied a pristine patterned raised bog in terms of its plant cover, its water, and its peat. We assessed observables essential to the workings of the model, namely, water tables and hydraulic conductivity. In addition, we looked at plant cover, *Sphagnum* growth forms and genotypes, and degree of decomposition of the peat to better understand the triangular relations between plants, water, and peat.

Roadmap

In presenting our results and observations, we treat the entities on the different organizational levels as ecotopes, which means we view them as homogeneous and focus on the difference to other entities/ecotopes on the same scale level. For example, we distinguish between dry hummocks and wet hollows. We look at how hummocks differ from hollows, but we do not look at differences between separate hummocks or within single hollows. We will start at the low level of hummocks and hollows and move up to the level of the raised bog dome as one member of a group of contiguous domes and fens. Once we reach this highest level, we will journey back to the lowest level of single moss plants, but this time we will focus on the differences and patterns within the ecotopes. These inner differences can show intermediate stages

that help understanding how (only) quantitative differences within ecotopes can result in qualitative differences between ecotopes. Finally, we will look on the raised bog as a whole and how its self-regulation mechanisms work on different levels of organization. And we will look at how self-regulation mechanisms and their shortcomings can drive self-organization of the raised bog on different levels.

METHODS

Study site

To be able to disentangle the complex interactions between plants and water and peat, we chose a pristine, explicitly patterned raised bog in Tierra del Fuego, because of its minimalistic simplicity: It essentially carries only one species of *Sphagnum*, which covers all niches and growth forms, and is joined by only a dozen higher plant species; it is entirely ombrotrophic with very sharp borders to the surrounding fen; it has only one type of peat that shows an only limited range in degree of decomposition; and it is situated in a very even climate with minimal differences in rainfall and temperature over the year.

The bog is located in the Valle de Andorra, 5 km north of the coastal town of Ushuaia in the Argentinean part of Tierra del Fuego (54°45' S; 68°20' W, approximately 200 m above sea level [asl]; Figure 1). Remains of the Pleistocene glacier that formed the valley are still found on the northern slopes.

The climate of central Valle de Andorra is cool and humid with a mean annual precipitation of 610 mm. Precipitation is distributed nearly equally over the year with a slight maximum in April. The mean annual air temperature is 3.0°C with a range of approximately 10°C in monthly mean air temperatures. Frost occurs in all months. The cooler and wetter conditions in the Valle de Andorra compared with nearby Ushuaia are mainly caused by the higher altitude, shading by the northern mountain range Sierra Vinciguerra and the barrier effect of the southern mountain range Sierra Martial against mild air from the sea (Iturraspe et al., 1989, 2012).

The studied mire is the largest member of a raised bog complex and is bordered to the north by the river Arroyo Grande, to the south and east by a brook and to the west by a beaver pond (Grootjans et al., 2010; Figure 2). Since deglaciation around 11,000 BP, up to 9.8 m of peat have accumulated (Figure 3; cf. Loisel & Yu, 2013). The upper peat layers consist of *Sphagnum* sect. *Cymbifolia* peat. The mire shows clear surface patterning of alternating elongated hummocks and hollows,

aligned perpendicular to, that is, across, the slope (Figure 4).

There is some tourism and horse grazing in the valley. In 2011, the site was designated a Wetland of International Importance under the Ramsar Convention (www.ramsar.org). Peat is being cut by hand in a bog about 1 km east of the study area.

Field measurements were carried out in 2004 and 2005. Moss samples were collected in March 1999.

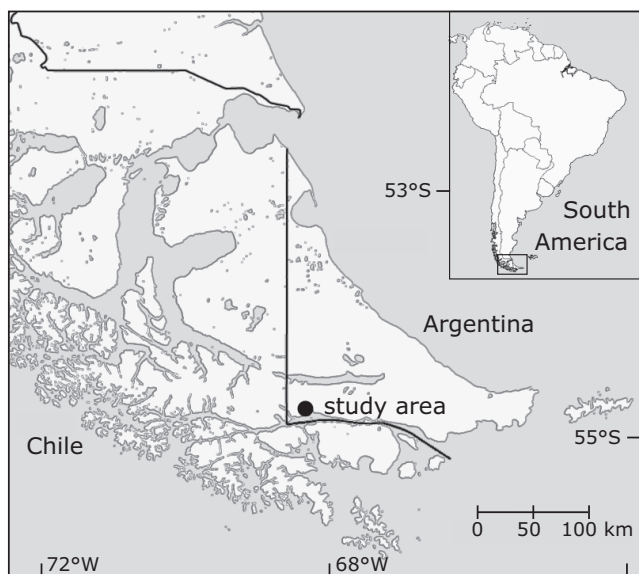


FIGURE 1 Location of the study area

Additional moss samples for DNA analysis were collected in November 2015 when also water table measurements were carried out.

Relief

Height relative to sea level of the mire surface was measured at one point using a precision GPS (Topcon Turbo SII) and further derived with the help of a transparent water filled hose as a leveling device to assess the exact horizontal. The local peatland surface was defined as the top of the *Sphagnum* capitula. Measurements were carried out every meter along Transects 1 and 2 as well as along a third transect (Transect 3) that crosses the peatland at its greatest width perpendicular to Transect 2.

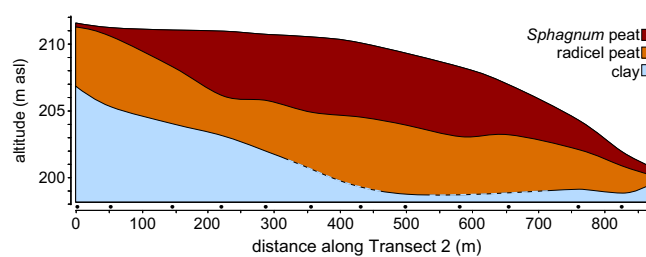


FIGURE 3 Stratigraphic cross section based on 13 corings along Transect 2. The black dots show the position of the corings. Dashed lines at the base of the radicle peat indicate where the mineral underground was not reached

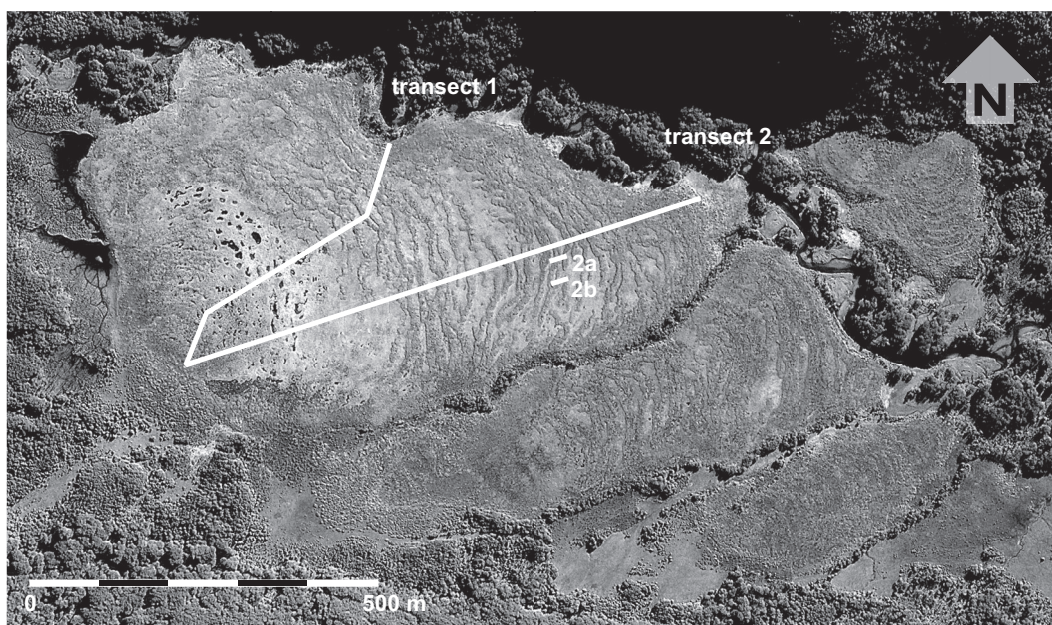


FIGURE 2 Satellite image of the study area (source: Google Earth, 2008) with approximate position of Transects 1 and 2 and the short Transects 2a and 2b. Transects start on the left and end on the right. The surrounding slopes are covered by deciduous forests dominated by southern beeches *Nothofagus pumilio* and *N. antarctica*



FIGURE 4 Oblique view from the north over the studied bog showing the rand on the lower left, the central plateau on the upper right, and the distinct hummock–hollow striping pattern in between. The forest in the background is of southern beeches *Nothofagus pumilio* and *N. antarctica*. Photo: Katja Hahne, 2004

Plant cover

In the beginning of 2005 (austral summer), vegetation was recorded along Transect 1 (Figure 2) in contiguous 2 × 2-m relevés ($n = 248$). Percentage cover of plant species, bare peat, and open water was estimated by eye. In summer 2004, the vegetation of the entire mire surface was recorded in contiguous 10 × 10-m relevés ($n = 3322$) using a modified Braun-Blanquet scale of seven units (Pfadenhauer, 1997), with the first three classes combined into one. The resulting class boundaries are at 5%, 25%, 50%, and 75%. Vascular plants are named according to Moore (1983), and moss species according to Van der Wijk et al. (1967). Note that the recent split of *S. magellanicum* into three separate species does not affect the naming of the mosses in our South American study site (Hassel et al., 2018). Two species, *Pernettya pumila* and *P. mucronata*, were difficult to distinguish in the field and were lumped as the much more common *P. pumila*. As the ecological niche of both species is very similar (Moore, 1983), this protocol will not significantly affect the results.

Plant morphology

In March 1999, using a plastic bottle (diameter 10 cm) with the bottom cut off, a volumetric sample of *S. magellanicum* mosses was collected to a depth of 15 cm at each of four sites that differed in their water table depth (50, 28, 11, and 1 cm below the *Sphagnum* capitula). The

number of branches per stem length was assessed for 100 individual stems, and dry bulk density was determined. In summer 2004, every meter along Transect 2a (26 m long), the angle of moss stems off the vertical was estimated at 15° intervals.

DNA analysis

For DNA analysis, *S. magellanicum* capitula were collected every second meter along Transect 1 in November 2015. Samples were immediately dried after collection using silica gel. For each sample, DNA was extracted from a small piece of the collected capitulum following the CTAB protocol (based on Doyle, 1991, altered by Shaw et al., 2003). Eight microsatellite markers developed for *Sphagnum* (loci M1, M9, M10, M14, M18, M20, M28, and M30; Shaw et al., 2008) were amplified in 12- μ l reaction tubes using the single-plex approach and later diluted based on expected signal strength. The same thermocycling regime was used for all eight reactions: an initial step of 95°C for 5 min, followed by 28 cycles of 95°C for 35 s, 54°C for 60 s, 72°C for 60 s, and a terminal phase of 72°C for 15 min. In addition, a five-cycle long touchdown regime ($\Delta T = -1^\circ\text{C}$) with 95°C for 35 s, 59°C for 60 s, and 72°C for 60 s was implemented to reduce unspecific binding.

Fragment analysis was performed by mixing two sets of four markers each containing 4 × 1 μ l amplicates, 5.9 μ l HiDi Formamide, and 0.1 μ l 500 LiZ size standard by using Applied Biosystems Genetic Analyzer Prism

310. GeneMapper was used for the readout and fragment length analysis. A total of 242 samples were successfully genotyped.

Similar methods have recently been used in Holarctic *Sphagnum* species and the *S. magellanicum* complex (Hassel et al., 2018; Kyrkjeide et al., 2016), demonstrating the practicability of the microsatellite loci mentioned above on the global scale and on the genus and species level. All analyses were carried out early 2016.

Water tables

Water tables relative to the surface were measured in perforated 2-m-long PVC tubes (outer diameter 4 cm, inner diameter 3.7 cm, and perforation approximately 22%). A total of 14 permanent dip wells were set up along Transect 1 (at 0, 24, 54, 134, 222, 264, 302, 307, 373, 378, 415, 450, 488, and 496 m). Water tables were measured (almost) every day here between 27 January and 13 April 2005.

Water levels relative to sea level were measured in conjunction with surface height measurements every 5 m along Transect 1, starting on 31 January 2005 and spanning 2 months ($n = 497$), using the same type of tubes as for the permanent dip wells. The tubes had a pointed tip that allowed them to be pushed into the generally loose mosses and peat, after which the water table was allowed to settle, which rarely took longer than 2 min, mostly much shorter. Water tables were measured using a well whistle. Care was taken not to move or shift weight once the tube was inserted. Water levels relative to sea level were linearly interpolated for every meter between the 5 m apart dip wells. Occasional checks revealed that error amounted to 2 cm at most, usually much less. Comparing the measurements 5 m apart with linearly interpolated values between dip wells, 10 m apart showed equally small deviations (except on the very steep final part of the transect). Water tables relative to the surface were calculated for every meter using the measured surface height relative to sea level. Using data on water table changes between measurement days from the permanent dip wells and from mobile dip wells left in the field, we made small adjustments to the measured values to arrive at a water table value for 31 January 2005 for each meter along the transect.

Water tables relative to the surface were measured every second meter along Transect 1 between 24 and 31 November 2015 ($n = 250$). Along Transects 2a and 2b, water tables were assessed every meter during single days in early 2004 (outer diameter of tubes 2 cm, inner diameter 1.7 cm, and both transects 26 m).

The 2015 measurements were made in conjunction with the collection of *S. magellanicum* capitula for genetic analysis. Hence, open water areas without *S.*

magellanicum were avoided and substitute measurements were carried out at closest proximity to the actual transect (mostly <1 m away).

Hydraulic conductivity

Hydraulic conductivity k (L/T , in this paper expressed as m/day) was determined as the average of three repeats using the modified piezometer method of Van der Schaaf (1999) and calculated by the recovery time of the initial water table in piezometers after adding water in falling head tests with an imposed head of 9 cm. Water table was measured every 10 s until 120 s, every minute until 10 min, and then every 5 min until 30 min. The water table recovered to the original level in all cases.

Along Transect 1, hydraulic conductivity was measured 10–20 cm below the water table (filter position) at 246 locations between 6 February and 30 March 2005. For piezometers, we used steel tubes (inner diameter 1.7 cm, outer diameter 1.9 cm, filter length 10 cm, and degree of perforation 22%). The measurement depth (10–20 cm below the surface) was chosen, because at lesser depth k was too high to be measured at too many sites.

In addition, at 11 locations along Transect 1, hydraulic conductivity was measured using the same equipment in depth-profiles with intervals between 5 and 20 cm starting just below the water table to a depth of approximately 2 m ($n = 291$).

Along Transects 2a and 2b, hydraulic conductivity was measured every meter at 10–30 cm below the water table (filter position) using a PVC tube (outer diameter 2 cm, inner diameter 1.7 cm, filter length 20 cm, and degree of perforation 16%). Measurements were carried out during a single day for each of the respective short transects.

Water table response

Changes in water table depth after heavy rainfall were assessed on three different days (7 March 2005: 14.2 mm rain; 23 March 2005: 13.6 mm; 5 April 2005: 21.2 mm; measured locally) at 30 sites (14 along Transect 1 and 16 along Transect 2). The change in water table is expressed relative to the amount of rainfall (cf. Heikurainen, 1963).

Degree of humification

Following the method of Von Post (1922), the degree of humification H was determined for all sample depths where hydraulic conductivity measurements were carried

out along Transect 1. Samples were taken within centimeters of the measurement tubes using a Russian type peat corer (cf. De Vleeschouwer et al., 2010) at the end of the field work period. Degree of humification is expressed on a modified von Post scale with a 0.5-step increment and was assessed using color plates for better reproducible estimations of water color.

Statistics

Statistical analysis (Welch's t tests and regression analysis) was carried out using SPSS 10.1 and Microsoft Excel 2016. We refrain from using the phrase "statistically significant" to denote certain p values associated with statistical analyses (cf. Colquhoun, 2014, 2017). Instead, effects are labeled "(un)clear," while presenting the associated p value. Regression findings refer to geometric mean analyses.

Simulation model

Surface patterning of the study site was simulated in a spatially explicit, heuristic model derived from Swanson and Grigal (1988; see Couwenberg, 2005; Couwenberg & Joosten, 2005). Simulations were carried out on a square grid of 600×1001 cells using the Matlab (MathWorks) programming environment. As the actual shape of the study site is complex and was not measured in detail in the field, the southern contour (Figure 2) was mirrored to obtain an idealized, symmetric eccentric dome shape that was transposed to the model by giving each grid cell a surface height. Heights followed an idealized smooth curve derived from measurements along Transects 2 and 3. Each cell is further characterized by values for transmissivity and water table. Transmissivity is determined as a function of the water table and has two extreme states (cf. Belyea & Clymo, 2001) that can be associated with *hummocks* with low water tables and low transmissivity, and *hollows* with high water tables and high transmissivity, respectively.

The initial water table relative to the surface (-0.02 units) and transmissivity (approximately 0.01) is equal for all cells. The draining brook, river, and pond surrounding the study site are simulated by assigning maximum transmissivity (0.10) to all cells outside the dome shape and by removing water from the system by keeping their water table at a user-defined level of -0.5 units. Water flow is assumed to be largely restricted to the acrotelm (Ivanov, 1981). Simulations are therefore restricted to the horizontal (x,y) direction, and flow is calculated by multiplying the hydraulic head difference between a central cell and each of its four neighbors by

transmissivity T (dimension L^2/T) (Darcy law of water flow). The effective transmissivity between adjoining cells is calculated as the harmonic mean of the transmissivities of both cells (Couwenberg & Joosten, 2005).

After 200 water flow iterations, which sufficed to reach quasi-steady state, the resulting water tables were modified by adding a random value (mean 0 and variance 0.01) and then used to assign a new transmissivity value to each cell according to Figure 5. Note that this transfer function differs from our previous approach (Couwenberg & Joosten, 2005), in which each cell was assigned one of two possible transmissivity values, corresponding to hollow or hummock, respectively. Here, any value of transmissivity between the two extremes is possible. Morris et al. (2013) tested the workings and assumption of our simple heuristic model and found that the principle is robust and that the simple approach produces valid results.

Each calculation with newly assigned transmissivities is called a development step. Between development steps, the water table in each cell is increased by 0.002 units to simulate rainfall.

Note that the simulation model is purely heuristic. Its parameters are not scaled to represent realistic numbers like for example in the more complex DigiBog model (Baird et al., 2012; Morris et al., 2012) or in the simulations of Eppinga et al. (Eppinga, De Ruiter, et al., 2009; Eppinga, Rietkerk, et al., 2009). The model merely serves to show how locally defined dependencies and interactions can result in large-scale patterns.

Terminology

Many terms exist for the different ecotopes that make up a bog dome. We follow the ecotope nomenclature of

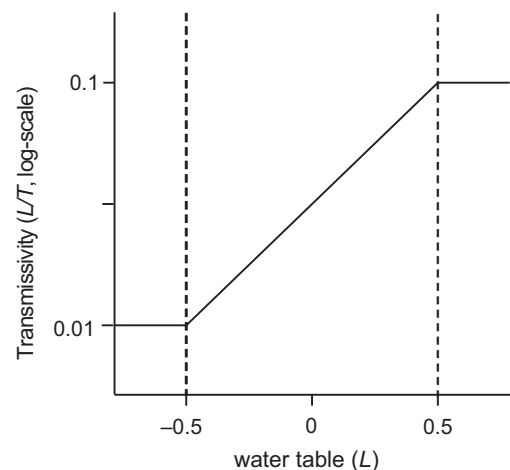


FIGURE 5 Transmissivity as a function of water table relative to the surface. Note the logarithmic scaling of the ordinate

Joosten, Couwenberg, et al. (2017), who present a review of historical sources, pointing at various approaches and inconsistencies. A distinction is made between the organizational level at which an ecotope occurs and the actual, palpable component. From smallest to largest in the hierarchy, the scale levels are referred to as *pico-*, *nano-*, *micro-*, *meso-*, and *macrotopes* (with the supertope added to refer to geographical peatland regions) (Table 1). The corresponding actual components of the peatland are referred to as *ero*, *feature*, *site*, *massif*, and *complex*. For example, on the *nanotope* scale the distinction is between *features* such as hummocks, hollows, and pools; on the *microtope* scale between *sites* such as the plateau, the “hummock–hollow complex,” and the rand.

There is no commonly accepted international term to refer to the microtope pattern of alternating elongated hummocks and hollows so prominent in our study site, at least not in raised bog settings. In Finnish, the terms *kermi* and *kulju* are used for hummock strings and hollows in raised bog settings, but the term *kulju* simply refers to a wet depression, irrespective of its orientation. The Swedish/English term *flark* is used for elongated and oriented depressions (Finnish: *rimpi*), but is restricted to fen settings. In a string–flark fen, the flarks are ground-water fed, whereas the strings can be ombrotrophic. Although we are aware of all these existing terms and their meaning (Joosten, Couwenberg, et al., 2017), we will in our study for convenience refer to the fully ombrotrophic microtope site with elongated hummock ridges and hollow troughs as “string–flark complex.”

TABLE 1 Ecotope components and organizational levels on which they occur

Organization level	Component	Example
Picotope	Mire ero	Single plant
Nanotope	Mire feature	Hummock, hollow, pool
Microtope	Mire site	Central plateau, string–flark complex, rand, lagg
Mesotope	Mire massif	Concentric raised bog, ribbed palsa mire ¹
Macrotope	Mire complex	Red Lake Peatlands ² , Great Vasyugan Mire ³
Supertope	Mire region	Atlantic bog region ⁴ , maritime forested bog region ⁵

Note: The term “ero” is from Esperanto, meaning “element.” Numbers in superscript refer to sources: 1, Joosten, Couwenberg, et al., 2017; 2, Heinselman, 1963; 3, Katz & Neustadt, 1963; 4, Moen et al., 2017; 5, Glaser & Janssens, 1986.

RESULTS AND DISCUSSION

In presenting our results, we start at the nanotope level and successively move up the organizational levels: microtope (mire sites), mesotope (mire massif), and macrotope (mire complex). Once we have reached the macrotope level, we will move down again, this time focusing on sublevels: sub-microtope, sub-nanotope, and finally picotope (mire eros) (see section “Roadmap”). In presenting our results, we include brief discussion points to place our findings in context. Finally, we present an integrative interpretation and discussion of the results.

Nanotope (mire features)

Plant cover

Only 12 species were recorded along Transect 1 (Table 2). The dominant species, *S. magellanicum*, nearly completely covers the raised bog and is absent only where there is open water or disturbance. Along Transect 1, *S. falcatulum* prominently replaces *S. magellanicum* in two open water pools. Also, *Empetrum rubrum* is present in almost every relevé, whereas the remaining species are more restricted in their occurrence (Figure 6). Using conventional plant sociology methods (cf. Wilmanns, 1998), only one association—the Pernettyo-Sphagnetum—can be distinguished (Schwaar, 1976).

Based on correlations between the percentage cover of the plant species along Transect 1 (Table 2, Figure 7), three species groups can be distinguished. The species of Group A (*Marsippospermum grandiflorum*, *Nothofagus antarctica*, *E. rubrum*, *Nanodea muscosa*, and *P. pumila*) correlate positively with each other and negatively with species of the other groups. The species of Group B (*Rostkovia magellanica*, *Carex magellanica*, and *Tetroncium magellanicum*) are negatively correlated with species of Group A and show poor correlation with species of Group C. Species of Group C (*Sphagnum falcatulum*, *Poa pratensis*, and *Carex curta*) correlate positively with each other, but do not show any clear correlation with species of the other two groups. Correlations between the cover values of the plants mapped in the 10 × 10-m relevés follow the same pattern (data not shown).

The species of Group C occur only sparingly in or near open water pools. *Sphagnum falcatulum* fills a very wet niche comparable with the northern *Sphagnum cuspidatum* (Seppelt, 2012). *S. falcatulum* is thought to disperse primarily or even exclusively through vegetative diaspores in the form of moss fragments (Karlin et al., 2013). The presence of *C. curta* and *Poa* cf. *pratensis* near the open water pools was clearly associated with disturbance by birds, which is the most likely dispersal vector for

TABLE 2 Correlations (Pearson's r) between percentage cover of single species in relevés along Transect 1 ($n = 248$)

Classification	Margra	Notant	Emprub	Nanmus	Perpum	Rosmag	Carmag	Tetmag	Sphfal	Poapra	Carcur
Margra		0.28	0.36	0.30	0.35	-0.22	-0.34	-0.40	-0.11	-0.07	-0.09
Notant	***		0.47	0.17	0.25	-0.18	-0.26	-0.26	-0.09	-0.06	-0.08
Emprub	***			0.41	0.34	-0.24	-0.52	-0.41	-0.18	-0.10	-0.13
Nanmus	***	0.006			0.63	-0.12	-0.26	-0.29	-0.06	-0.04	-0.05
Perpum	***	1×10^{-4}	***			-0.22	-0.34	-0.32	-0.11	-0.07	-0.09
Rosmag	5×10^{-4}	0.005	1×10^{-4}	0.05	7×10^{-4}		0.15	-0.13	-0.01	0.02	0.05
Carmag	***	4×10^{-5}	***	5×10^{-5}	***	0.02		0.22	0.09	0.03	0.05
Tetmag	***	4×10^{-5}	***	***	***	0.04	4×10^{-4}		-0.10	-0.07	-0.09
Sphfal	†	†	0.004	†	†	†	†	†		0.23	0.39
Poapra	†	†	†	†	†	†	†	†	3×10^{-4}		0.95
Carcur	†	†	0.04	†	†	†	†	†	***	***	

Note: The p value of each correlation is given rounded to a single digit below the diagonal; *** denotes p values below 1×10^{-5} ; † a p value of 0.1 or higher. The nine blocks in the body of the table derive from the classification in Figure 7.

Abbreviations: Carcur, *Carex curta*; Carmag, *Carex magellanica*; Emprub, *Empetrum rubrum*; Margra, *Marsippospermum grandiflorum*; Nanmus, *Nanodea muscosa*; Notant, *Nothofagus antarctica*; Perpum, *Pernettya pumila*; Poapra, *Poa pratensis*; Rosmag, *Rostkovia magellanica*; Sphfal, *Sphagnum falcatulum*; Tetmag, *Tetroncium magellanicum*.

S. falcatulum as well (cf. Lewis et al., 2014; Whinam & Copson, 2006).

The relative importance of the other two species groups is calculated as the total cover of species Group A minus the total cover of species Group B. This *plant cover index* shows a bimodal distribution (Figure 8). The two modes of the fitted curve ($r^2 = 0.94$) are $\mu_1 = 43.2\%$ ($\sigma_1 = 16.7$) and $\mu_2 = -1.5\%$ ($\sigma_2 = 9.1$). The 90% confidence intervals of the two modes do not overlap. The valley of the bimodal curve is used to draw a sharp demarcation at index value 22 (Figure 8). A trimodal curve fit was tested, but it did not create a distinct new mode.

Water tables

Water tables relative to the surface as measured along Transect 1 follow a bimodal distribution (Figure 8). The two modes of the fitted curve ($r^2 = 0.94$) are at $\mu_1 = -49.3$ cm ($\sigma_1 = 10.0$) and $\mu_2 = -15.8$ cm ($\sigma_2 = 6.5$), representing dry and wet mire features. Intermediate levels are rare. The 95% confidence intervals of the modes do not overlap. We draw a sharp demarcation in the valley of the bimodal curve fit at -31 cm between *dry* and *wet* nanotope features (Figure 8).

Water tables measured along Transect 1 in November 2015 (during spring snow melt) were generally higher than in January 2005 with a strong correlation between the two sets of measurements (linear regression slope = 0.9, $r^2 = 0.86$; Figure 9). The position of the original transect was marked by piezometer installations and

was still recognizable in the field. Small location errors cannot be excluded.

Plant cover and water table depth

There are clear relationships between the percentage cover of vascular plant species and water table (Figure 10). Yet, variation in plant cover values is high and correlation coefficients are only low (although p values are often very low; Table 3). Consequently, single species are unsuitable proxies for water table. Besides the association of species Group C with open water pools, just two species are restricted to a single water table class: *R. magellanica* occurs only at water tables above -31 cm. It is not suited as a general indicator for high water tables, however, as its distribution and constancy are only limited (Figure 6). *Nanodea muscosa* is strictly absent at water tables above -31 cm, but its low cover and constancy also make it unsuitable as a general indicator species.

With respect to the total cover of plants belonging to species Groups A and B, correlations and hence predictive value are higher than of the single constituent species (Table 4). If total cover of Group A is above 27% the water table is below -31 cm in all but seven out of 88 cases; if total cover of Group A is below 27% the water table is above -31 cm in all but eight out of 160 cases (total error 15 out of 248 cases = 6%). Similarly, if the total cover of Group B is above 0% the water table is above -31 cm in all but 18 of 175 cases; if total cover of Group B equals 0 the water table is below -31 cm in all

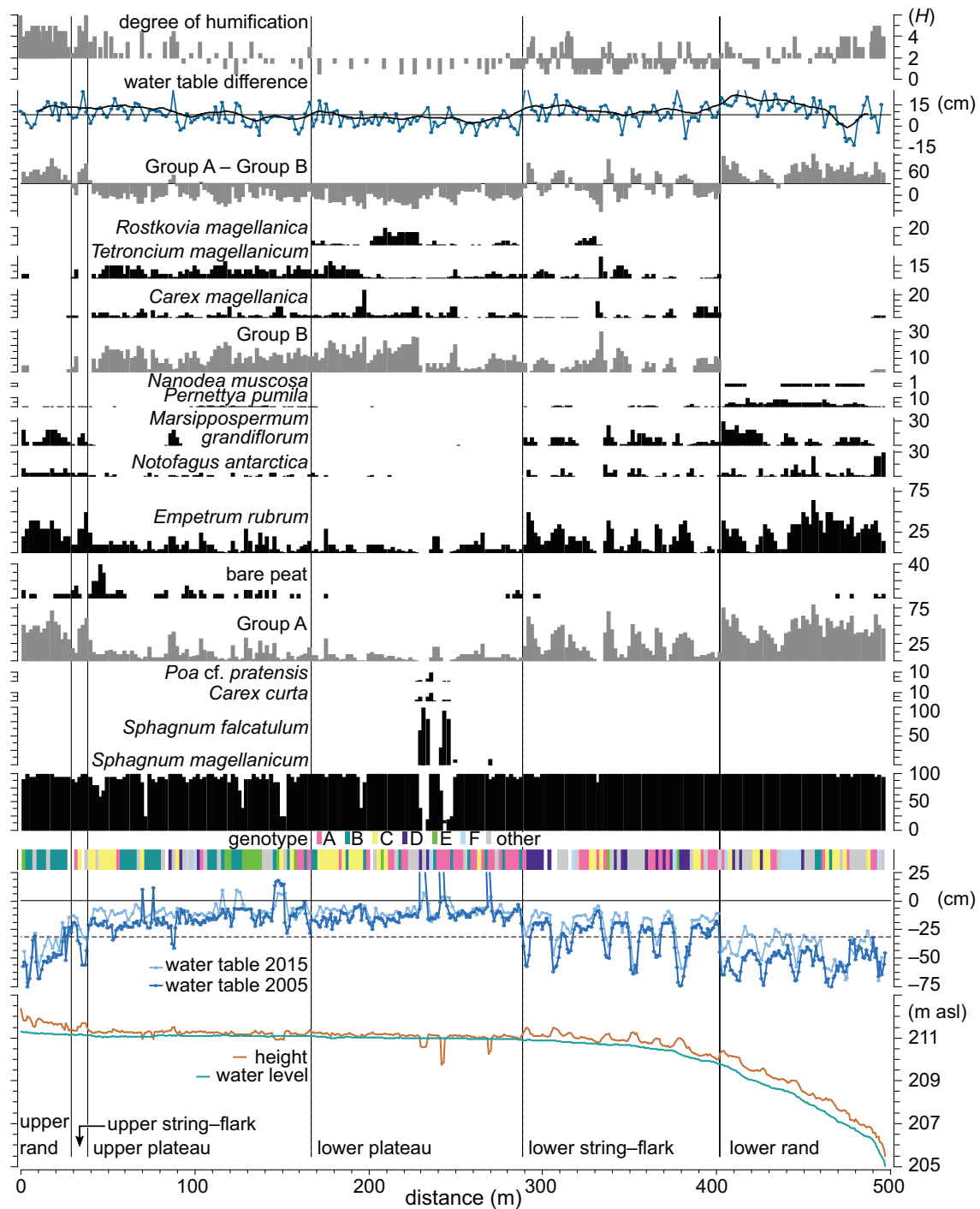


FIGURE 6 Plant cover and genotypes, water levels and surface height (in meters above sea level), water tables (relative to surface, in centimeters), and degree of humification (von Post scale, H) as measured along Transect 1. Plant cover is expressed in percentage, other units as indicated. Water table difference is the difference in water table measured in 2015 minus that measured in 2005. The 2005 water table in three deep open water pools is outside the scale. The vertical lines delineate mire sites and their subdivisions, named at the bottom of the graph

but two of 73 cases (total error 20 of 248 cases = 8%). Predictive performance is higher when looking at the difference between the cover of the two groups: If this *plant cover index* (total cover Group A minus total cover Group B) is above 22%, the water table is below

–31 cm in all but five of 89 cases; if it is below 22%, the water table is above –31 cm in all but three of 159 cases (total error eight of 248 cases = 3%). So, the relative dominance of species Group A over B allows for a sharp delineation of plant cover on the level of the

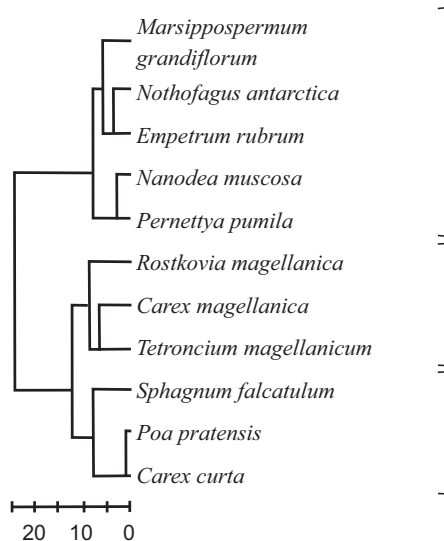


FIGURE 7 Cluster analysis of the percentage cover of species in relevés along Transect 1 ($n = 248$). Clustering used Ward linkage, squared Euclidian distance with z -standardization of percentage cover (axis at the bottom). *Sphagnum magellanicum* occurred in almost all relevés and was excluded from the analysis. Three clusters were identified, indicated by square brackets on the right

nanotope that coincides with the two water table classes (Figure 8).

We are aware that other authors have distinguished a larger number of distinct water table classes with associated vegetation cover (Lindsay, 1995; Masing, 1984; Moore et al., 2019). The distinction we make here between dry hummock and wet hollow features is based on Figure 8 alone. It will not necessarily coincide with definitions and classifications made by other authors for other mires and regions.

Peat characteristics

The average degree of humification of the peat just below the water table along Transect 1 is 1.7 (SD = 1.0, $n = 128$) for the wet and 3.0 (SD = 1.3, $n = 119$) for the dry mire features. Although the averages differ clearly ($p = 1 \times 10^{-16}$, Welch's t test), there is a considerable overlap in values. No strict demarcation can be drawn between wet and dry nanotope features on the basis of degree of humification. A very low degree of humification of 0.5 is found only in the wet features and relatively high degrees of humification (5 and 6) are restricted to dry features.

Hydraulic conductivity measured 10–20 cm below the water table along Transect 1 is higher for the wet (median $k = 8.1$ m/day, SD of \log_{10} -transformed data = 0.8, $n = 107$) than for the dry mire features (median $k = 1.2$ m/day, SD of \log_{10} -transformed

data = 1.2, $n = 119$). Although the averages differ clearly ($p = 6 \times 10^{-9}$, Welch's t test), there is considerable overlap in values. As we saw for the degree of humification, the wet and dry mire features cannot be strictly separated based on hydraulic conductivity alone. Except for three wet outliers, all values below 0.06 m/day were measured in dry sites ($n = 35$; Figure 11).

As both the degree of humification and the hydraulic conductivity along Transect 1 clearly differ between the wet and dry mire features, a correlation between the two can be expected (Romanov, 1968). The p value for the correlation between degree of decomposition and hydraulic conductivity is indeed low ($p = 6 \times 10^{-42}$), but the regression coefficient is only modest ($r^2 = 0.6$). Still, it is higher than the regression coefficients for degree of humification against depth ($r^2 = 0.3$) or hydraulic conductivity against depth ($r^2 = 0.2$) (Figure 11). We conclude that the degree of humification determines hydraulic conductivity, but that there are other factors in play.

The average hydraulic conductivity of the dry mire features is about seven times lower than for the wet ones. Yet, at the same water table, wet elements tend to show lower values than their dry counterparts. Remember that all measurements were made at 10–20 cm below the water table, which means that a deeper measurement depth is associated with a deeper water table. If the water table drops, a thicker peat layer becomes unsaturated and is no longer supported by pore water pressure (loss of buoyancy). Nevertheless, moisture content of the unsaturated peat is still (very) high and adds to its weight. This weight exerts pressure on the saturated peat below, reducing pore space and hence hydraulic conductivity (Ivanov, 1981; Price, 2003). Apparently, this deformation of the saturated peat is stronger in the wet mire features than in the dry ones (see “*Sub-microtope*”).

The denser cover of vascular plants provides more, partly even woody, roots and stems to the peat matrix of the dry mire features. These roots and stems not only provide for higher hydraulic conductivity (cf. Boelter, 1969), but also create a scaffold that ensures that the peat does not collapse as readily as the less supported moss peat of the wet mire features (Malmer et al., 1994; Waddington et al., 2010; Weber, 1902). Moreover, the *S. magellanicum* mosses of the dry mire features are sturdier than those of the wet features and not bent in the direction of water flow (see “*Picotope [mire eros]*”).

Hydraulic conductivity clearly decreases with depth in each of the 10 profiles (Figure 12). A linear regression fit between \log_{10} -transformed k values and measurement depth has a coefficient of 0.023 for wet and 0.026 for dry features ($r^2 = 0.6$ and 0.5, respectively; p values < 0.001). In other words, hydraulic conductivity in the profiles is about 2.5 orders of magnitude lower when it is measured

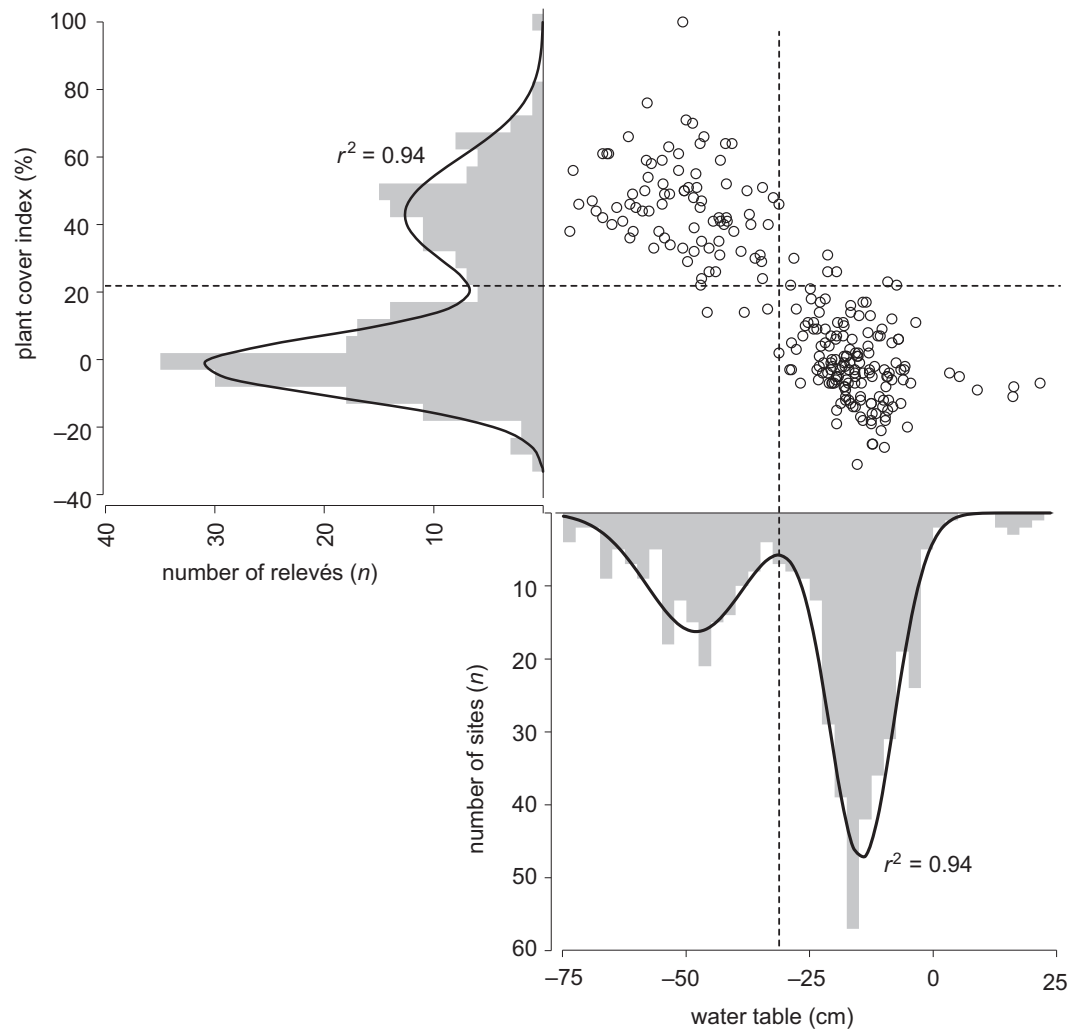


FIGURE 8 Plant cover and water table relative to the surface in three related graphs. Top left: histogram of plant cover index (cover of Group A minus cover of Group B; $n = 248$, classes span 5%; top left). Bottom right: histogram of water tables along Transect 1 for 31 January 2005 ($n = 498$, classes span 2.5 cm). Both histograms are fitted with a bimodal distribution curve of the form $f = a \times N(\mu_1, \sigma_1) + (1 - a) \times N(\mu_2, \sigma_2)$, where a denotes a scaling parameter and $N(\mu, \sigma)$ denotes a normal distribution with mean μ and standard deviation σ . Regression coefficients are high for both fits ($r^2 = 0.94$). The valley of the respective fits is used to separate the two modes, creating four quarters in the top-right plot with the actual values for plant cover index and water table in the relevés ($n = 248$). All but 10 of 248 data points fall into the upper left and lower right quarters, illustrating a strong correlation between plant cover and dry/wet mire features

1 m deeper. Whereas dry and wet features show similar hydraulic conductivity profiles when data are lumped, things are much more complex. We will address the profiles in more detail in “*Microtope [mire sites]*” and make a comparison between hydraulic conductivity measured in the profiles and along the transect in “*Sub-microtope.*”

Microtope (mire sites)

Thus far, our focus has been on generalized characteristics of water and plant cover and peat, and their interrelationships. In other words, on observations that are valid

at the level of the nanotope and that reflect characteristics and correlations without acknowledging the relationship of every measurement plot with its vicinity, nor its position on the dome. In this section, we will describe how mire features on the nanotope level combine into mire sites on the microtope level (Figure 6).

Plant cover and water table depth

As we showed in the previous section, the plant cover index and water table depth allow for sharp delineation of dry and wet mire features. Along Transect 1 (from southwest to northeast in Figure 2), distinct mire sites

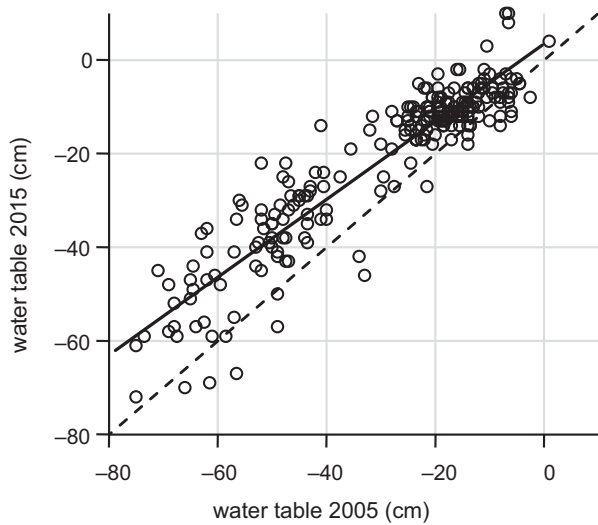


FIGURE 9 Water table relative to the surface measured along Transect 1 in November 2015 in relation to the same measured on 31 January 2005 ($n = 241$). The solid line shows a linear regression (slope = 0.9, $r^2 = 0.86$), and the dashed line denotes equality in water tables

comprised of particular sequences of mire features can be discerned (Figure 6). For the first 26 m, there is a *rand* composed solely of dry mire features. From 27 to 32 m, first wet and then dry features are found between 32 and 38 m. This alternation of wet and dry features is a *hummock-hollow complex* that—at least along the transect—consists of only one hummock and one hollow. From 39 to 288 m, there is a *central plateau*, composed solely of wet mire features. The water level is 211.13 m asl at the beginning and 210.91 m asl at the end of the plateau. From 289 to 401 m, dry and wet features alternate. This is the *string-flark complex* consisting of elongated dry ridges or strings and elongated wet flarks. From 402 m onward, there is a *rand* consisting of dry mire features only. The water level is 209.8 m asl at the beginning and 205.03 m asl at the end of the rand.

There are some small deviations from this overall pattern. On the central plateau, an isolated hummock occurs at 87–88 m. At the beginning of the plateau, the plant cover index of the relevé between 38 and 40 m is 30, indicating a dry feature, but the average water table is

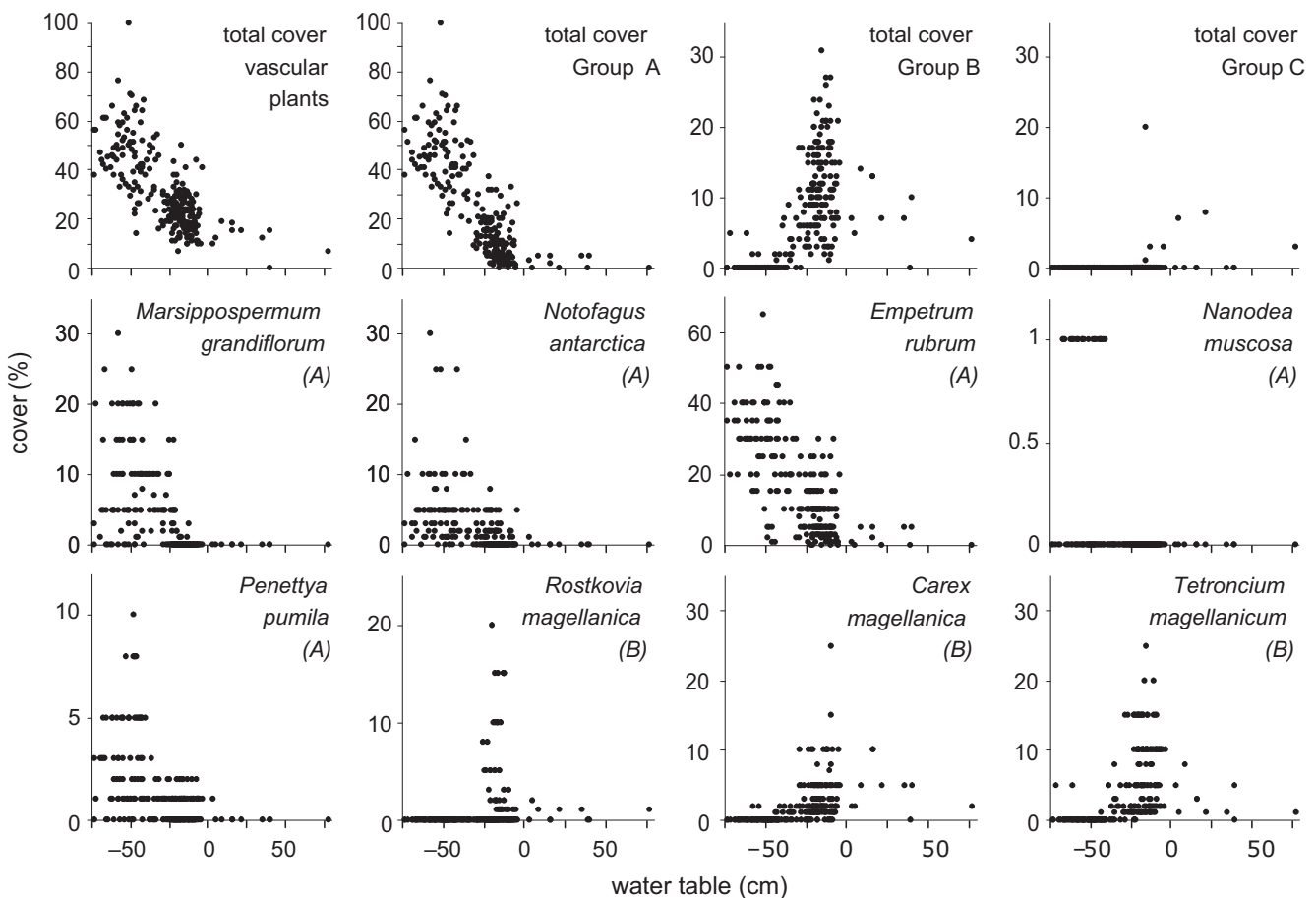


FIGURE 10 Vascular plant species cover in relation to mean water table relative to the surface on 31 January 2005 in grid relevés ($n = 248$); note differences in the range of cover (%) on the ordinate axes. The group each respective species belongs to is indicated between brackets. For an explanation on Groups A, B, and C, see Table 4

TABLE 3 Correlation (Pearson's r) between the water table on 31 January 2005 and plant percentage cover for 11 species in the 2×2 -m relevés ($n = 248$)

Species	r	p
<i>Marsippospermum grandiflorum</i>	-0.57	
<i>Nothofagus antarctica</i>	-0.45	
<i>Empetrum rubrum</i>	-0.69	
<i>Nanodea muscosa</i>	-0.43	
<i>Pernettya pumila</i>	-0.52	
Group A	-0.79	
<i>Rostkovia magellanica</i>	0.19	
<i>Carex magellanica</i>	0.47	
<i>Tetroncium magellanicum</i>	0.42	
Group B	0.59	
<i>Sphagnum falcatulum</i>	0.41	
<i>Poa pratensis</i>	0.13	0.04
<i>Carex curta</i>	0.19	0.003
Group C	0.16	0.009
Total vascular plant cover	-0.73	
Group A – Group B	-0.78	

Note: The p value of all correlations is below 1×10^{-10} , except as indicated.

TABLE 4 Indicative value for water table relative to the surface of the species Groups A and B and the plant cover index (cover Group A minus Group B)

Cover value	n	Dry	Wet	Error (%)
Group A > 27%	88	81	7	6
Group A < 27%	160	8	152	
Group B > 0%	175	18	157	8
Group B = 0%	73	71	2	
Group A – B > 22%	89	89	5	3
Group A – B < 22%	159	3	156	

Note: Group A is more associated with dry features with water table below -31 cm and Group B more with wet features with water table above -31 cm. In bold, the part of n that complies with the respective wetness category. For an explanation on Groups A and B, see Table 3.

-28 cm, indicating a wet feature. This mismatch arises from simple methodological issues: The contiguous vegetation relevés are 2×2 m large, and a transition between a wet and a dry mire feature may well occur within one relevé. Water table measurements were made every meter, using the average of three measurements to characterize the relevé, which is not necessarily perfectly representative for the 2×2 -m area. Similar mismatches are found at the transition between dry and wet features in the string–flark complex. Of the total of 57, there are five relevés in the string–flark complex with a mismatch.

On the plateau, another interruption in the contiguous series of all wet water tables occurs at 53–54 m where the water table is slightly below the -31 cm threshold for two consecutive measurements (-34 and -31.5 cm, respectively). Yet, the average water table for the relevé is above -31 cm and also the plant cover indicates a wet mire feature. At 103–105 m, plant cover just barely indicates a hummock, but water tables do not. Also, these two mismatches occur because water table measurements and associated relevés represent different mire features. In both cases, there are small isolated hummocks.

On the nanotope level, only two plant species are narrowly restricted to either dry (*N. muscosa*) or wet (*R. magellanica*) mire features. On the higher microtope level of mire sites, additional restrictions or close associations become apparent. With the exception of very minor occurrences at the very beginning or end of the transect, *T. magellanicum* and *C. magellanica* occur only on the central plateau and in the string–flark complex: All three species of Group B are absent in the rand. Where they appear to be associated with strings, it involves the five mismatched relevés in the string–flark complex mentioned above. This means that along Transect 1, plants of species Group B actually *are* restricted to wet mire features.

With respect to plant species of Group A—which are associated with dry conditions—the only narrowly restricted species on the nanotope level, *N. muscosa*, is on the microtope level restricted to the rand only; it does not occur on the equally dry strings of the string–flark complex. Of the other species of Group A, only *Marsippospermum grandiflorum* is restricted to dry features and thus to the rand and the string–flark complex. The other species of the group occur on wet features as well, although higher than 5% cover of *P. pumila* is restricted to the rand.

The difference in water table along Transect 1 between November 2015 and January 2005 tends to be larger for the wet features of the flarks than for those of the plateau (but see “Sub-microtope”). A likely explanation is that the water table response in the flarks is coupled with that in the neighboring strings. The strings have more strongly decomposed peat with less pore space and elasticity, as exemplified by lower hydraulic conductivity (Figure 11). As a result, their storativity will be lower meaning that water table fluctuations will be larger. If there is much precipitation, or in times of snow melt, a rising water table in a string will cause the water table to rise to a similar extent in the upstream flark as well.

Changes in water table in response to heavy rainfall are complex, but ultimately related to pore space and storativity (Heliotis & DeWitt, 1987; Price & Schlotzauer, 1999). Correspondingly, the response in the dry features was larger (Figure 13). In the wet features, the response was mixed:

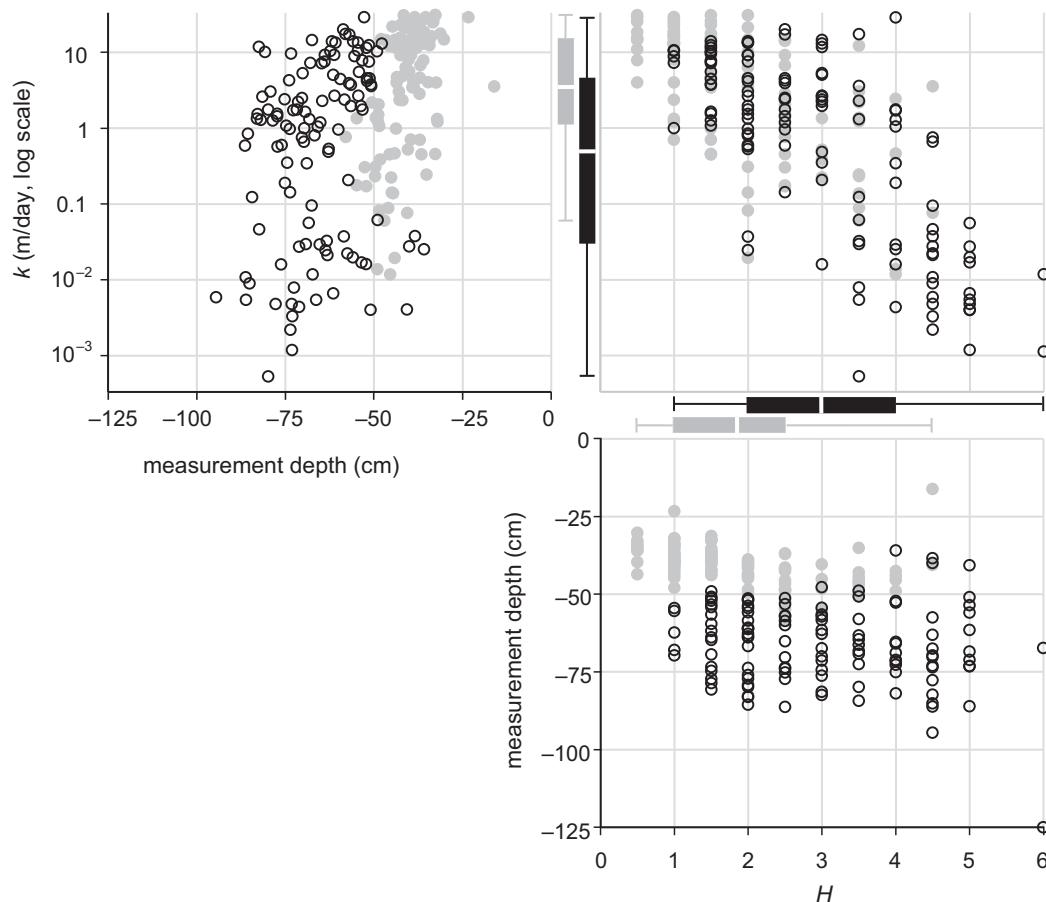


FIGURE 11 Hydraulic conductivity k and degree of humification H (von Post) in three related graphs, namely, in relation to each other (top right) and to measurement depth (top left and bottom right, respectively). Black circles denote dry sites with water table depth below -31 cm on 31 January 2005; gray dots wet sites with water table above -31 cm. Measurements were made at 10–20 cm below the water table (filter depth); dots are placed 15 cm below the water table at the time of measurement. Note that measurements were carried out over a period of several weeks and that considerable differences in water table depth can exist compared with 31 January 2005. Boxplots drawn between the graphs show the mean and quartiles with whiskers denoting the range of values (without outliers). Note the logarithmic scale of the hydraulic conductivity axis

It was limited in the plateau, but large in the flarks. This large response does not match with the large pore space of the flarks as attested by their high hydraulic conductivity as shown in the next section.

Peat characteristics

For the peat samples taken just below the water table, there is no strong correlation between the degree of humification and depth and thus no clear distinction between wet and dry mire features on the nanotope level (see “*Nanotope [mire features]*”). Inevitably, clear patterns in the degree of humification are largely absent on the microtope level as well. The degree of decomposition is generally high in the rand, although slightly decomposed peat was found there as well (Figure 6). Similarly, the degree of decomposition is generally low in the

central plateau, but also here higher degrees of decomposition are found, and not only in the isolated hummock at 87–88 m. In the string–flark complex, the degree of decomposition changes from relatively high to low and back again, but a low degree of decomposition is not exclusive to flarks, nor is a high degree exclusive to strings.

Degree of humification was assessed in conjunction with the measurements of hydraulic conductivity just below the water table, which were carried out over a period of almost 8 weeks. Water tables changed considerably during this period, which means measurements were made at different depths relative to the water tables on 31 January 2005 shown in Figure 6. At the time, degree of humification and hydraulic conductivity were determined, and water tables in the upper rand (first 27 m along the transect) were on average 4 cm lower than on 31 January 2005. In the hummock–hollow complex (28–38 m), they were 12 cm lower, on the plateau

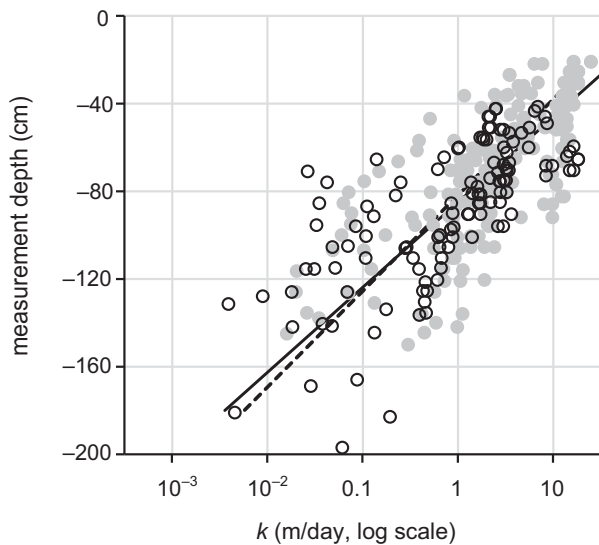


FIGURE 12 Hydraulic conductivity k against depth below the surface as measured in the depth profiles. Black circles denote dry sites with water tables below -31 cm on 31 January 2005; gray dots wet sites with water table above -31 cm. Filter length was 10 cm, and dots are placed at its center. Note the logarithmic scale of the hydraulic conductivity axis

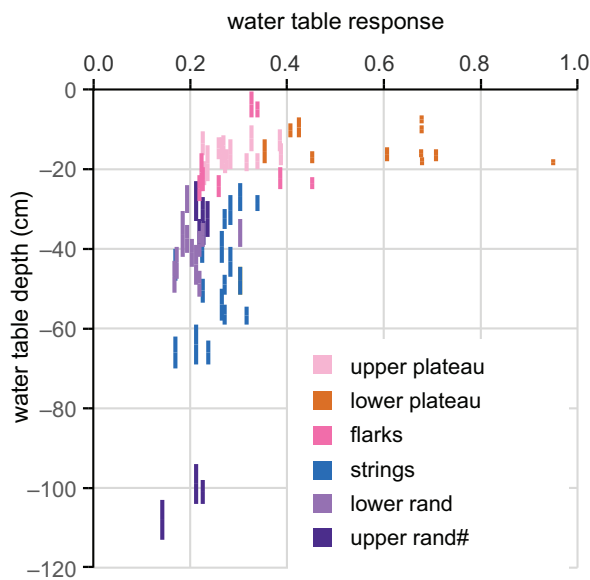


FIGURE 13 Water table response after heavy rainfall. The response is expressed as the amount of rain divided by the increase in water table relative to the surface. The vertical lines span the water table before and after the rainfall events

(39–288 m) 10 cm lower, in the string–flark complex (289–401 m) 2 cm lower, and in the lower rand (402–498 m) 5 cm lower. This sampling procedure can certainly explain some of the deviations. Sampling different depths means sampling peat of different age: the deeper,

the older, and in tendency more decomposed. Note, however, that in the depth profiles changes in the degree of humification with depth are not regular nor unidirectional (Figure 14).

Although the trend is clear, also in the profiles the correlation between degree of humification and hydraulic conductivity is only weak (cf. Figure 14). Yet, hydraulic conductivity is in most cases strongly correlated with depth ($r^2 > 0.7$ for eight out of 11 profiles). If degree of humification can only in part explain why hydraulic conductivity decreases with depth, compaction offers the most obvious additional explanation. It leads to a loss of pore space, with lower hydraulic conductivity as a result. The deeper the peat, the older it is and the more often it has been exposed to water table drops and associated weight from unsaturated peat above. Part of the resulting compaction is irreversible (“creep”; Clymo, 1978), and a distinct gradient results in porosity and therewith in hydraulic conductivity.

The decrease in hydraulic conductivity with depth differs between the different mire sites (Figure 14). The central plateau and the rand show a steep decrease of about three orders of magnitude over a 1-m depth range. The strings and flarks of the string–flark complex show a decrease of only two orders of magnitude over the same 1-m depth range. In other words, wet and dry mire features show different hydraulic conductivity profiles depending on which mire site they belong to. But how to explain the gentler decrease in hydraulic conductivity both in the flarks compared with the plateau and in the strings compared with the rand?

In a previous paper, we presented a simulation model of surface pattern development and we postulated that strings and flarks would move down the slope and that this movement should be identifiable in the peat (Couwenberg & Joosten, 2005). Using ground-penetrating radar, Kettridge et al. (2012) indeed found downslope movement of dry and wet mire features over time. The results are alternating thin layers of relatively strong hummock and weaker hollow peat (Figure 15). Therefore, the peat underneath the dry and wet mire features of the string–flark complex is not hummock- or hollow-type peat, but a string–flark peat. This peat is a product of the mire site; it originates on the higher microtopo scale level.

The “hybrid” peat of the string–flark complex combines the characteristics of the wet and dry features found on the plateau and rand. Just like the plateau, the wet flarks have high water tables and loose near-surface peat with high storativity. The dry strings have low hydraulic conductivity at typical low water tables, but a sturdy peat structure, just like the rand. As mentioned, after heavy rainfall, the water table in the flarks increases

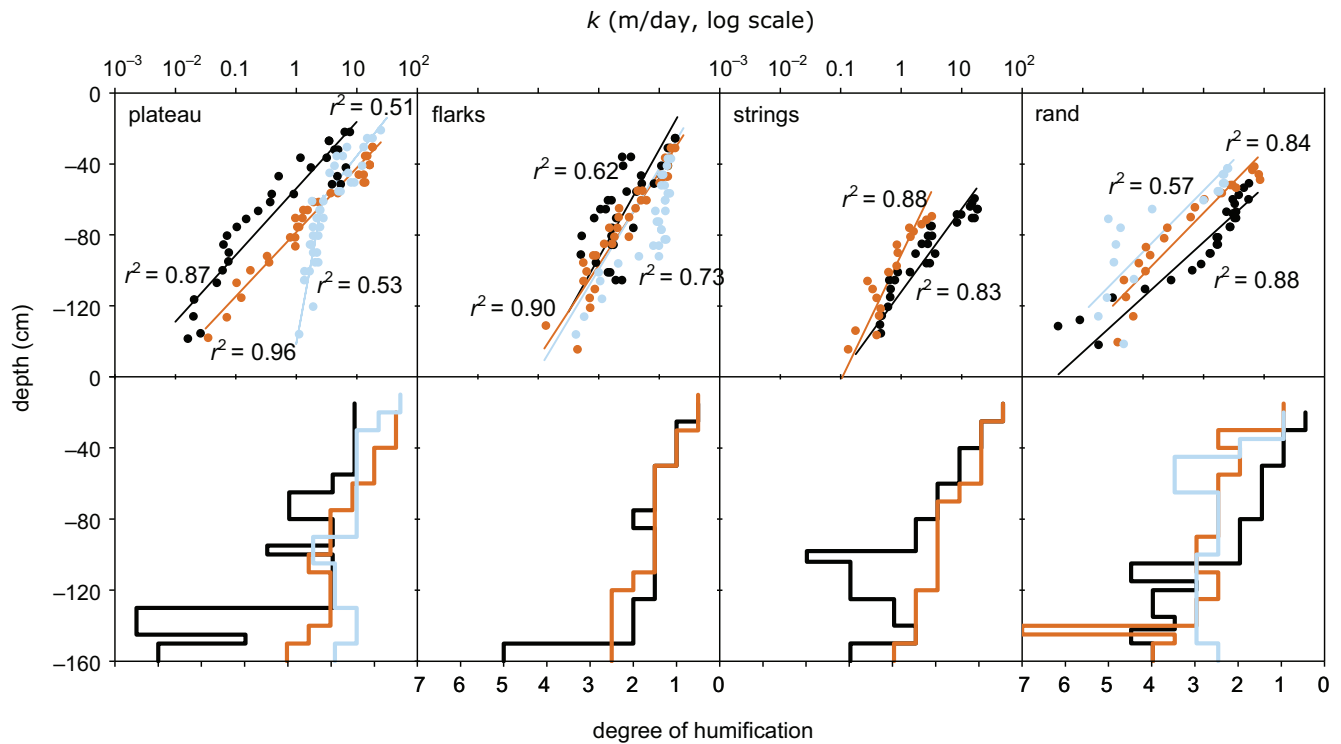


FIGURE 14 Hydraulic conductivity (top) and degree of humification (von Post, bottom) as measured in the depth profiles in four ecotopes (plateau, flarks, strings, and rand). In each ecotope, three profiles were measured, each indicated by its own color. Only two profiles were measured in strings and degree of humification was recorded in two flark profiles only



FIGURE 15 Hybrid “zebra” peat formed in the string–flark complex. The photograph was taken in the cutover bog east of the study site (Photo: Hans Joosten, December 2006)

in tandem with the water table in the strings. Similarly, the high storativity of the flarks will limit water table drops in dry times (cf. Sjörs, 1948). Being coupled to and

“fed” by the flarks, the strings will show limited drops in water table as well. Overall, the string–flark complex is well buffered against water table draw downs, but also

has sturdy peat that will not collapse as readily as the peat of the plateau. Less deep water tables combined with more sturdy peat make for a less steep decrease in hydraulic conductivity with depth.

In the plateau, the decrease in hydraulic conductivity with depth is steeper because the peat is less sturdy and although limited in number and extent, water table draw-downs lead to relatively strong irreversible compaction. In the rand, the peat is sturdy, but water table draw-downs are frequent and deep and decomposition and compaction are the result.

Mesotope (mire massif)

For all the attention to differences in hydraulic conductivity gradients, the overall decrease in hydraulic conductivity with depth is logarithmic and large. The decrease is related to loss of pore space with depth, which not only affects hydraulic conductivity, but also storativity. Their high storativity limits water table fluctuations to the upper peat layers. The peat below this “aktivnyy gorizont” (sensu Ivanov, 1981) is always water saturated. Water is still flowing out of this saturated peat layer following Darcy’s law, but only slowly. The result is a mound of water and peat, the shape of which can be approximated by the Dupuit equation (cf. Glaser et al., 2004; Ivanov, 1981). The shape of the Valle de Andorra bog indeed roughly follows this elliptic equation (Figure 2).

A generalized shape of the mire massif was fed into our simulation model, which produced patterns on two distinct scale levels (Figure 16). On the lower nanotope level, the characteristic strings and flarks are found; on the higher microtope level, this string–flark complex occurs alongside the rand and plateau. The extent and location of these mire sites correspond well with the pattern in the studied peatland as indicated by the plant cover (Figure 17). Remember that the initial state of the simulated surface is an even lawn of “mosses” at intermediate water table. Once the simulation starts, the rand will drain and the now dry cells will be given low transmissivity. Depending on slope and water input a rand of a certain width will develop (see Couwenberg & Joosten, 2005). Upslope of this rand, water will pond and cells will become wet and be given high transmissivity. These will in turn drain upslope cells that become dry and be given low transmissivity, etc. This ponding and draining of respective upslope areas is only effective if the slope is steep enough. Going from the rand inward, once the slope becomes too gentle, runoff will be small, water will remain and a wet plateau develops (Couwenberg & Joosten, 2005).

Although the model allows for it, cells with intermediate water tables are rare and largely restricted to the plateau. As is the case in the field, also the simulation model shows strong divergence into dry and wet elements in the string–flark complex. Once a cell located on a slope becomes wetter, its transmissivity will be higher and so water will more easily flow into it, keeping it wet; once a cell becomes drier, the opposite occurs. The simulated intermediate water tables did not occur in reality on the plateau.

So, the shape and slope of the massif (mesotope level) drive the development of lower level patterns. The slope of the water level asl differs between the five microtopes delineated along Transect 1: Over the initial 38 m of Transect 1, covering the upper rand and upper hummock–hollow complex, the height of the water level drops by 19 cm, with an average slope around 0.5%. The water level remains nearly flat across the central plateau with a slope <2.5‰ (calculated as a running linear spline over 49 m). The slope then becomes steeper in the string–flark complex, increasing to 2.9% at 401 m (average approximately 1%, range: 0.25%–2.9%). In the final 95-m rand of Transect 1, the height of the water level drops by 4.76 m (average slope 5%). The height measurements along Transect 2 show a similar change in slope (Figure 3). After an initial rather steep section over approximately 50 m, the height drops by only 0.5 m over the next approximately 200-m-wide central plateau (slope approximately 2.5‰), by 2.25 m over the following approximately 230-m string–flark complex (slope approximately 1%), and by approximately 7.5 m over the final 290-m rand (slope approximately 2.5%).

In an overview of mires in continental Russia, Ivanov (1981, p. 93) presents slopes well below 0.5% for string–flark sites and more gentle slopes of up to 2% for

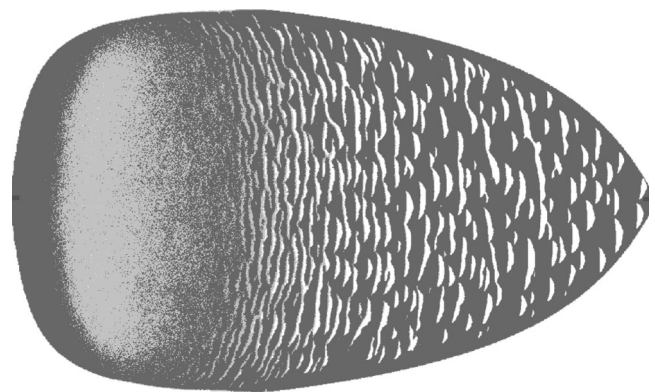


FIGURE 16 Surface pattern produced by the simulation model after 200 development steps. Dark tones indicated dry features, and bright tones wet features. Note that any state between dry and wet is possible in the model. Pixels with an intermediate tone can be seen on the plateau and on the upper part of flarks

the rand as well. The slopes that initiate development of the different sites are not universal. Rather, pattern formation depends on flowing water acting as the organizing force. This force can express itself only if there is enough water on a slope that is steep enough and with differences in transmissivity between wet and dry ecotopes that are large enough (Couwenberg, 2005). So, in addition to the slope, climate and landscape setting play a role in determining the availability of water (affecting both input and output). Transmissivity of hummocks is strongly diminished if ice is present, which of course depends on the climate setting as well. In this light, the lower slopes reported by Ivanov (1981) for mires in continental Russia are no surprise. The absence of clear striping patterns on tropical domes may be related to their gentler slopes and to smaller difference in transmissivity between hummocks and depressions (Dommain et al., 2010).

Despite the range in slope and despite the variety in wet and dry features and sites, practically the entire massif is covered by *S. magellanicum*.

Macrotope (mire complex)

Although we did not take an in-depth look at the next higher level of organization, the macrotope, we can share some observations. The studied massif is one of five that form a mire complex together with surrounding lagg zones and separating brooks. The two Eastern massifs still have fen characteristics and can be considered “transitional.” As the peat stratigraphy (Figure 3) indicates, originally a percolation fen (*sensu* Joosten, Moen, et al., 2017) with slightly decomposed sedge peat developed between the mountains in the South and the river in the North. The fen was fed by groundwater seeping from the foothills. Groundwater is still seeping into the lagg zone of the mire complex here, as indicated by the presence of *Primula magellanica* (Pérez-Haase et al., 2019) and of “schwimmeisen” (mixed-valent Fe films) on the surface of ephemeral pools (*cf.* Grathoff et al., 2007).

At one point in time, *S. magellanicum* established, indicating that rainwater started to suppress the influence of alkaline groundwater at the surface in the mire (*cf.* Wassen & Joosten, 1996), leading to the development of the raised bogs. In a peat core taken on the plateau approximately 54 m along Transect 1, *Sphagnum* established slightly over 2300 years ago and accumulated about 2.5 m of peat (Loisel & Yu, 2013). There is up to 5.5 m of *Sphagnum* peat along Transect 2 (Figure 3), suggesting that the transition from fen to bog started much earlier. Below the thickest *Sphagnum* peat layers along Transect 2, we found two tephras about 2.5 and 1.3 m below the transition from fen to bog peat. These

tephras are likely associated with the Hudson I and Burney II events, suggesting that the bog started to establish well after 4200 years ago (Loisel & Bunsen, 2020).

It is highly unlikely that the brooks already existed in the percolation fen. The fine sedge peat (*cf.* Schulz et al., 2019) deposited by this fen is only slightly decomposed. Yet, when coring, it was hardly possible to penetrate the sedge peat and upon opening the Russian type corer, the peat expanded to double its size. Apparently, the original peat was very loose and fibrous and thus highly permeable (Verry et al., 2011), enabling the groundwater to flow to the river in a diffuse way through the peat. It was highly compacted by the raised bog on top of it. Indeed, the peat stratigraphy shows a conspicuous depression in what must originally have been a gradual and smooth sedge peat surface (*cf.* Schipper et al., 2007; Wassen & Joosten, 1996) under the area with the thick bog deposits (Figure 3). Assuming that the fen used to have a flat surface with a constant slope, the fen peat has been compressed by up to 2 m and is now only 60%–70% of its original thickness. Hydraulic conductivities measured in piezometer tubes with their filter in the fen peat showed values below 10^{-4} m/day (data not shown).

Brooks are a common feature of raised bogs (Weber, 1902). When a rainwater fed raised bog becomes older and larger, its rain receiving surface will increase quadratically (πr^2), but its circumference only linearly with its radius ($2\pi r$). More runoff water will have to leave a relatively shorter border, and at one point, this border will break and a brook will develop (Masing, 1984). Yet, such a brook would originate in the bog and not dissect it fully. So, the layout of the brooks tells us that raised bog development started in at least three areas in the former percolation fen and increasingly forced the diffuse groundwater flow to concentrate in the developing brooks, which also received the runoff water from the bog domes.

The landscape setting with its relief and seepage enabled the percolation fen that in turn provided a template for the three raised bog massifs. Fen areas are still present upslope of the bog massifs and fed by seepage water from the hills stagnating in front of the heavily compressed fen peat and the raised bog rand. In this sense, the bog massifs act like giant hummocks that also divert part of the seepage water to the sides. The mire complex is easily recognizable as a single unit on remote sensing imagery such as Figure 2. Its components are easily recognizable as units as well, but it is also easily recognized that each of the massifs looks very different, as do other units belonging to the same macrotope component.

We started this section at the nanotope and have now arrived at the macrotope scale. On our “way up,” we have focused on differences *between* the various components on each scale level. In the following, we will move back

down the scale levels and focus on differences that exist *within* recognizable components on every scale level.

Sub-microtope

On the level of the microtope, different expressions can be distinguished within each of the three types of mire sites: an upper and a lower rand, an upper and a lower hummock–hollow complex, and an upper and a lower plateau (Figure 6). Coming from upslope, the upper rand of the bog starts with steep *S. magellanicum* hummocks that rise up to a meter above the fen lagg. In the upper rand, the absolute height of the water and the surface appear to slope downwards toward the plateau, which is not uncommon for eccentric raised bogs (Eurola, 1962). The lower rand slopes away from the plateau and is steeper than the upper rand. Despite these differences in slope and its direction, water tables cover the same range in the two rand sites. The upper and lower rand also share the same species that display similar plant cover values. Although along Transect 1, *Nanodea muscosa* occurs solely on the lower rand and is absent from the top, this rare species occurs only intermittently along the rand and was found along the southern slope as well (data not shown).

In the upper rand, the peat just below the water table consistently shows a relatively high degree of humification, whereas the peat of the lower rand is generally less decomposed. Probably the peat of the upper rand still receives some groundwater, which stimulates decomposition. Stronger decomposition would normally be associated with reduced pore space. Indeed, the hydraulic conductivity just below the water table is much lower in the upper than in the lower rand (Figure 18).

The upper hummock–hollow complex consists of a series of hummocks arranged in an open ring shape that follows the contour of the massif, but the hummocks have not all coalesced to form one elongated string. Our earlier simulations showed that such strings of individual hummocks occur early during the development of the string or when the slope is only gentle (Couwenberg, 2005; Couwenberg & Joosten, 2005). The *Sphagnum* peat layer is thinnest here and the pattern is younger accordingly. The slope is similar to that at the start of the lower hummock–hollow complex (= the string–flark complex), where the first strings coming from the plateau are not fully closed either—which might be because of the gentle slope or because they are only young, or both. In terms of water table and vegetation cover, the upper and lower hummock–hollow complex do not differ.

The degree of humification is clearly higher in the upper hummock–hollow complex. Accordingly, the few

hydraulic conductivities measured here are consistently lower than at similar depth in the lower string–flark complex (Figure 18). There is one measurement from a lower string and one from a lower flark that show similarly low—or even lower—values. We will address these measurements in the next section.

Also, the plateau can be subdivided into an upper (39–167 m) and a lower part (168–288 m). On the satellite image (Figure 2), the upper plateau shows as a darker gray shade than the lower. The large pools with *S. falcatulum* are all located on the lower plateau (Figure 19). *Marsippospermum grandiflorum* is mostly absent from the entire plateau. The occurrence of *N.*

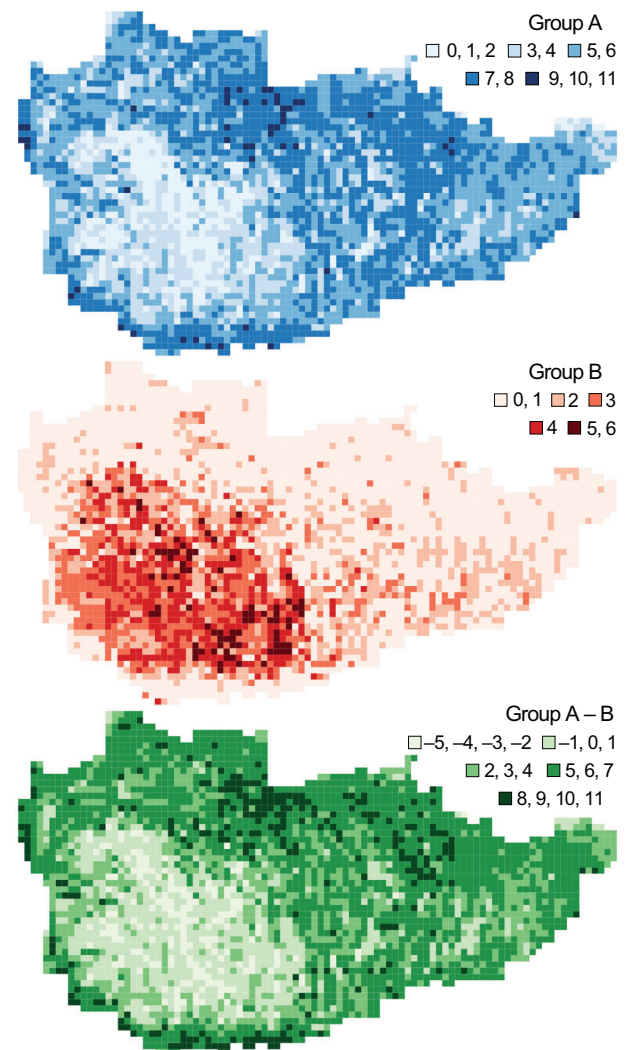


FIGURE 17 Maps of the bog depicting the cumulative cover of species Group A, species Group B, and for the vegetation index (cover of Group A minus cover of Group B). The underlying relevés were 10×10 m large. Cumulative cover is the sum of the cover of each species belonging to the group. Plant cover of single plant species was assessed in a modified scale of five units (plus zero). For an explanation on Groups A and B, see Table 3

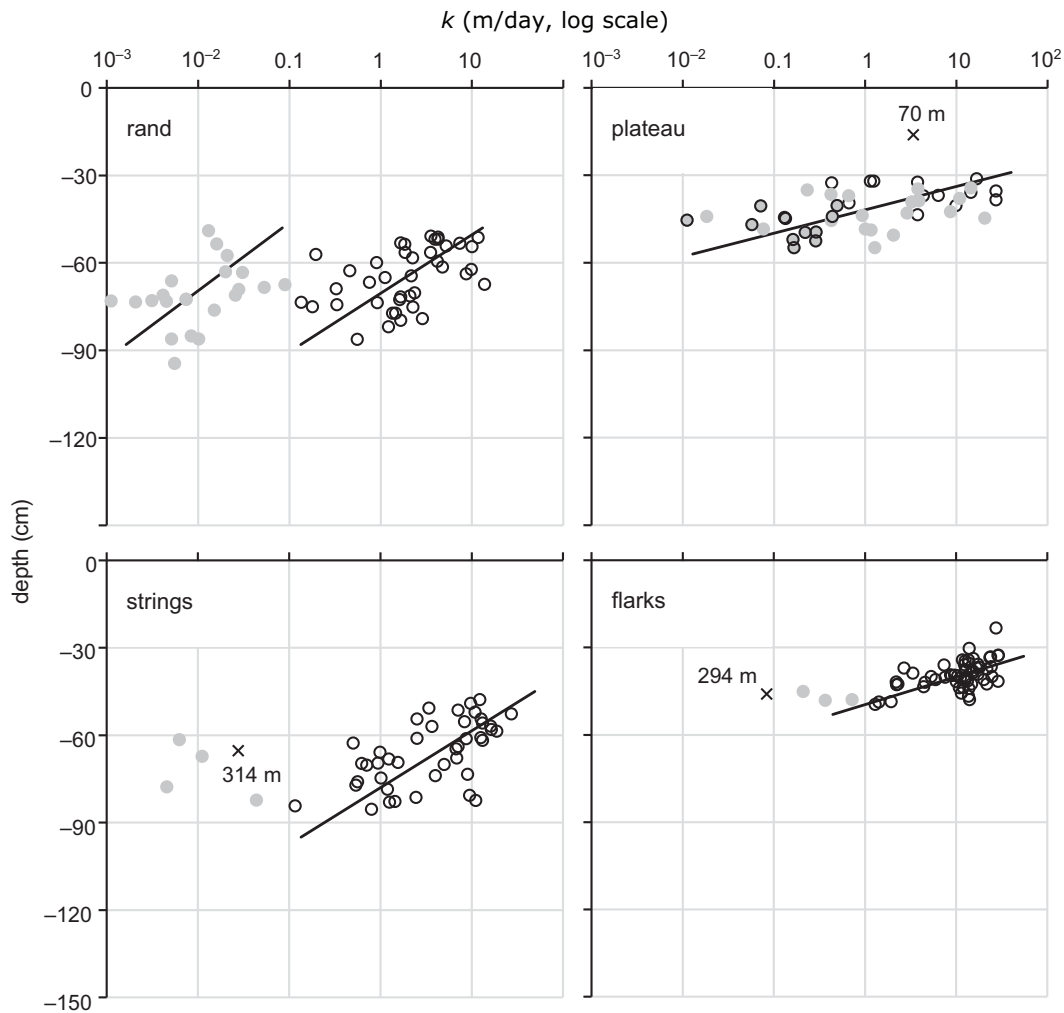


FIGURE 18 Hydraulic conductivity measured 10–20 cm below the water table in different ecotopes along Transect 1. Gray dots denote measurements made in the upper rand, upper plateau, or upper string–flark complex, open dots in their lower counterparts. For the plateau, the gray dots with black border denote measurements made over the first 46 m of the upper plateau. Crosses denote outliers marked with their distance along Transect 1 (see text). Note the logarithmic scaling of the x -axis

antarctica and *P. pumila*, two additional species of Group A, is (largely) restricted to the upper plateau; these species are (largely) absent from the lower plateau. In contrast, *R. magellanica* almost exclusively grows on the lower plateau. The 10×10 -m relevés (Figure 19) together with the satellite image show that it also occurs in a plateau area that is devoid of open water to the southeast of Transect 1. As Transect 1 did not pass through this area, it cannot be characterized any further.

Water tables are similar between the upper and lower plateau and measurements made in 2015 hardly differ from those made in 2005, except for the first 46 m where water tables were about 10 cm higher in 2015. Here, the degree of humification is higher, which suggests lower storativity and hydraulic conductivity. The hydraulic conductivity measured just below the water table is indeed always below 0.5 m/day in this part of the upper plateau (cf. Figure 18). None of the depth profiles of hydraulic

conductivity were measured in the upper plateau, and a comparison with the lower plateau is not possible here.

The hydraulic conductivity measurement made on the plateau at 70 m along the transect produced an outlier value (Figure 18). On 31 January 2005, the water table was 10.5 cm above the moss capitula here. In other words, it was an open water pool. Yet, when hydraulic conductivity was measured on 15 February, the water table was 1.1 cm below the capitula. The very loose pool must have collapsed when the water table dropped below the surface. The result is a relatively low hydraulic conductivity.

One of the depth profiles of hydraulic conductivity from the plateau shows a gradient similar to that of the string–flark complex. This profile was taken at 264 m along Transect 1, which is only 24 m away from the first string of the string–flark complex. In this sense, the string–flark complex can be thought to start with a flark

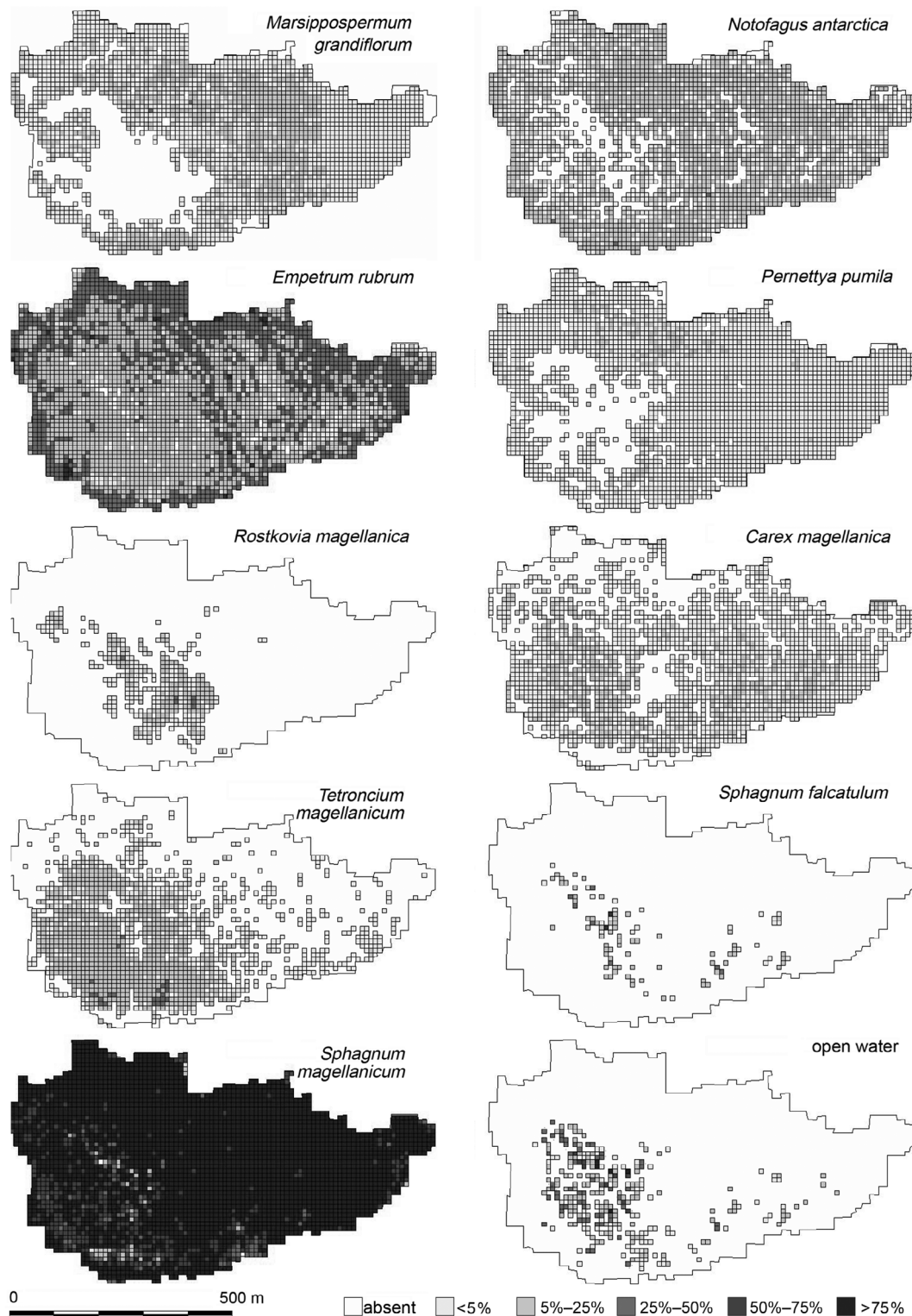


FIGURE 19 Maps of the bog depicting the cover of different plant species in contiguous relevés of 10×10 m. Plant cover was assessed in a modified scale of five units (and absent)

that is on the surface, however, indiscernible from the surrounding plateau.

The depth profiles of hydraulic conductivity showed that the decrease in conductivity with depth was steeper in the plateau and the rand than it was in the flarks and

strings (Figure 14). Going 20 cm further down the profile, hydraulic conductivity is about three times lower in the plateau and rand and only two times lower in the strings and flarks. In case of the transect measurements, the distinction is rather between the wet and dry features (Figure 18). The

wet features (plateau and flarks) show a very steep decrease in conductivity. If the water table is 20 cm lower, hydraulic conductivity decreases by a factor of about 180. In the dry features, the decrease is only by a factor 10.

As mentioned in section “*Nanotope (mire features)*,” the decrease in hydraulic conductivity in the profiles is related to stronger humification and irreversible compaction with depth. The decrease in the transect measurements points to increased weight from unsaturated peat when water tables are lower as an additional cause of decreased conductivity (Ivanov, 1981; Price, 2003). In case of the plateau, if the water table is 20 cm lower, the depth profiles tell us that the hydraulic conductivity of the peat would be three times lower, whereas the transect measurements show that the weight of unsaturated peat above additionally decreases conductivity by a factor 60. In case of the flarks, the profiles show a decrease by a factor 2 over 20 cm and weight adds a factor 90; in case of the strings, profiles show a factor 2 and weight adds a factor 5; in case of the rand, profiles show a factor 3 and weight adds a factor 3 (compare Figures 14 and 18).

As mentioned above, the hybrid peat of the string–flark complex is less prone to loss of pore space with depth, because it combines the sturdiness of the strings with the storativity of the flarks. Yet, the near-surface peat of the flarks readily collapses under the weight of unsaturated peat above. It follows that this collapse pertains to the upper layer of peat and moss only, a layer that is entirely the product of the current wet conditions.

Compression in reaction to added weight could have affected the profile measurements if water table were not constant, while measurements were made. This problem did not play a role, however. In the wet features, the measurement series for the hydraulic conductivity profiles could all be carried out during single days. Consequently, the water table in the wet features changed by 2.5 cm at most between the first and the final measurement. The lower hydraulic conductivity of the dry features took longer to measure and profile measurements were in many cases carried out over multiple days. Water table differences amounted up to 15 cm in the profiles of the rand. We visually scrutinized the (noisy) dataplots to see whether these changes in water table between measurements caused conspicuous jumps in the trend of hydraulic conductivity vs. depth, but they did not. The effect of surplus weight is anyhow smallest in the sturdy rand peat.

Sub-nanotope

Differences between mire features (nanotope) of the same type can be found in the string–flark complex and

the strings in particular. The low hydraulic conductivity of the strings results in stagnation of the water flow. As a result, the absolute water level asl is higher on the upslope than on the downslope side of a string; it shows a clear drop inside the string. This drop expresses itself as a steep (more negative) slope in the absolute water level asl. However, not all the strings are effective in stagnating water flow (Figure 20). Of the eight strings crossed by Transect 1, three do not affect the water level in any substantial way; at least they did not on 31 January 2005.

The small string around 314 m along the transect did not affect the water level on 31 January 2005 when the water table was at -42 cm. However, on 3 March the water table was at -50 cm and a hydraulic conductivity of 0.028 m/day was measured, which is even lower than the 0.54 m/day measured on the same day in the large string just upslope at 308 m; it is actually the lowest hydraulic conductivity measured along the transect in the string–flark complex. The string must be young and overlies loose flark peat that it easily compresses. When the water table is high, no impounding effect can be observed, but when water table is low, then even more compressed original flark peat will effectively obstruct water flow. So, there are “full-time” strings, which always obstruct water flow, and “part-time” strings that are young and only effective in reducing runoff when water tables are low enough. Yet, when they are effective, they are very much so.

Why the flark outlier at 294 m along the transect (Figure 18) has such low hydraulic conductivity is unclear.

Next to differences in features of the same type within the string–flark complex, differences exist within the mire features of the string–flark complex as well. A detailed look at the strings and flarks shows that these are asymmetric (Figure 20). The transition between the two is steeper at the upslope side of the strings. Here, the water, which flows easily through the flark upslope, collects in front of the flow-impeding string. The simulation model produces this pattern for the (strings and) flarks close to the plateau as well, where the downslope side of the flarks has highest, the upslope side only intermediate transmissivity. In the model, the dome is rising toward the plateau, but the water table in the flarks tends toward the horizontal. The result is a wet upslope and a drier downslope side of the strings. In reality, the pattern is reinforced when the peatland goes through drier times repeatedly. If water tables temporarily fall, the area immediately upslope of the string will still remain wet, whereas the area immediately downslope will become drier and thus conducive to expansion of the hummock string. Herein also lies the key to the downslope migration of the strings and flarks: A string *cannot* move upslope because it is always wet there and so it moves downslope, not because there is any pressure to do so,

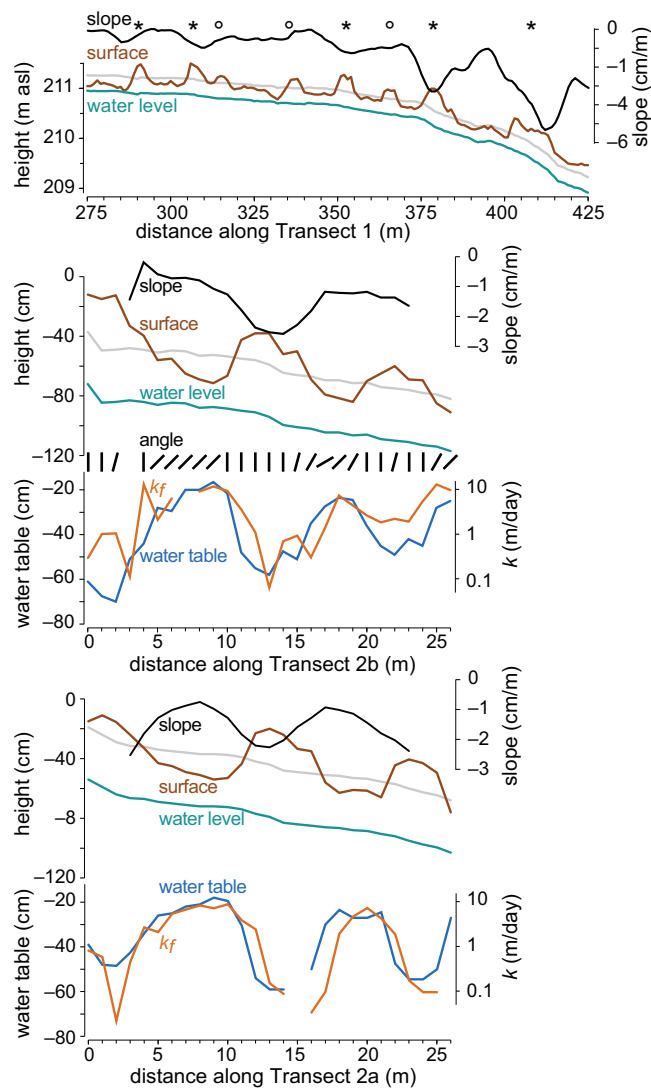


FIGURE 20 Transects through the string–flark complex, showing the height of the surface and water level above sea level (upper graph) or below a horizontal reference line and the slope in the water level. The light gray line is water level + 31 cm. If the brown line depicting the surface is above the gray line, there is a hummock; if it is below, there is a hollow. The slope dips when water level falls inside hummocks marked with an asterisk. In three hummocks along Transect 1 marked with a circle, a dip in slope did not occur. Also shown for Transects 2a and 2b are the relative water table and hydraulic conductivity k as measured 10–30 cm below the water table. For Transect 2b, the angle of *Sphagnum* stems is displayed in 15° steps

but because it is possible to move down and impossible to move up (Bogdanovskaya-Gieneff, 1928, see also Osvald, 1923).

When going downslope, the measurements along the short Transects 2a and 2b show that at the start of every hummock, string hydraulic conductivity is still high, even though water tables are already low. Similarly, at the start of every hollow flark, hydraulic conductivity is still

low, even though water tables are already high. The same phenomenon occurs along Transect 1, but the picture is blurred here because of the differences in water table at the time hydraulic conductivity was measured. Why changes in hydraulic conductivity are not fully harmonized with changes in the water table, can only be hypothesized. There are three factors decisive for hydraulic conductivity below the water table: the original sturdiness of the peat and belowground biomass material, the degree of humification, and the weight exerted by unsaturated peat above the water table.

On the upslope side of the strings, sturdy hummock peat occurs that has many (also woody) roots and stem fragments and is generally well fed with water from the flarks upslope. The peat at the upslope side of a string may be expected to be particularly sturdy, because—with the strings moving downslope—this peat has longest been deposited by dry vegetation. The relatively high and relatively stable water tables limit humification of the peat that is anyhow less prone to structural degradation following decomposition. So, both the sturdiness of the peat and the relatively high and relatively stable water table support high hydraulic conductivity at the upslope side of the strings.

The string not only receives water from the flark upslope, keeping it wet, but also loses water to the flark below. The result, as shown above, is a rather steep slope in the water level asl. inside the strings (Figure 20). As the water table decreases further downslope in the string, there is increasingly more pressure on increasingly deeper, older, and more decomposed peat and hydraulic conductivity decreases rather steeply as well. With respect to the upslope side of the flarks, the inflow of water from the string upslope is limited, and in dry times, the peat will not remain saturated as at the downslope side. As a result, the peat at the upslope side of the flark underlies stronger water table fluctuations and is more decomposed (Figure 6). Consequently, hydraulic conductivity is low. Keep in mind that the general distinction between strings and flarks still holds and that the peat forming vegetation of the flarks is adapted to wet conditions and largely lacks plants with woody roots and stems.

In conclusion, there is a strong differentiation between parts with low and parts with high hydraulic conductivity in the string–flark complex. Yet, the distribution of these two conductivity modes does not coincide with the two, fully coinciding modes in water table and vegetation cover.

Picotope (mire eros)

Growth form

At the level of the picotope, we distinguish mire eros. An ero is a single plant or, in case of mosses, a single moss stem.

The *S. magellanicum* mosses of the string–flark complex show different growth forms in the wet and dry features (Figures 21 and 22). The mosses of the dry features have more branches (Figure 22) that in turn have more leaves and the mosses are overall much denser as a result. Incidental measurements of bulk density and number of capitula show a parallel trend to the number of branches (data not shown). Moreover, repeated drying of the moss capitulum can lead to adversely high concentrations of ions that then suppress apical dominance and result in more frequent bifurcation of the stem. Overall, these changes in growth form make for a denser moss stand with increased capillarity that is able to keep the capitula moist (Masing, 1984; Smolyanitsky, 1977). Their dense build makes them less prone to loss of stability upon decomposition or under weight.

In the wet flarks, the mosses are less dense and sturdy, hydraulic conductivity is higher, and water is flowing more easily, exerting horizontal pressure on the mosses. Growing mosses are known to bend in the direction of least resistance (Overbeck & Happach, 1957). As a result, the stems of the mosses can be tilted in the direction of water flow if the pressure is strong enough (Panov, 2006). Indeed, moss stems are tilted in the direction of water flow along Transect 2b (Figure 20). Bending of moss stems has also been observed in reaction to snow load in winter. After snow melt, mosses would grow straight up again and annually repeated snow loads would result in multiple bends in the stems (cf. Mironov et al., 2016; Pakarinen & Tolonen, 1977). Moreover, mosses in strings would be affected by snow load

as well, although snow loads are typically larger in flarks than in strings, of course. Instead of multiple bends, the mosses in the flarks show only a single angle. In aquatic plants, similar adaptations are known to reduce adverse effects of drag forces on the plants (Biehle et al., 1998; Miler et al., 2012; Puijalon et al., 2008).

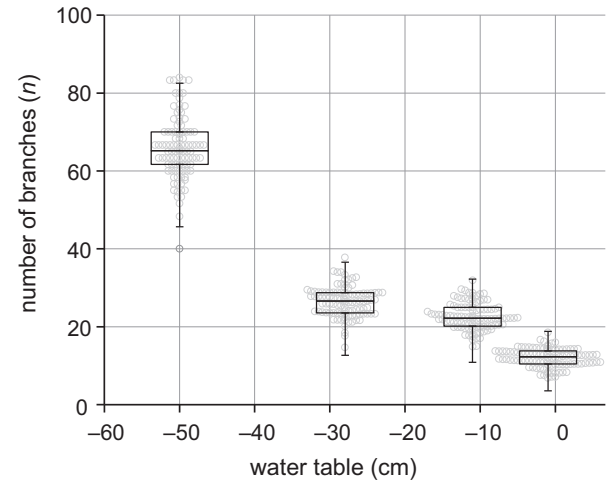


FIGURE 22 Number of branches per centimeter stem length of *Sphagnum magellanicum* collected at sites with different water tables relative to the surface. Box plots show median and quartiles, and whiskers the 1.5 interquartile range. Gray open circles show the actual measurement values ($n = 100$ for each respective water table). Differences between each of the respective water tables have $p < 10^{-10}$



FIGURE 21 Variation in growth form of *Sphagnum magellanicum*. Samples were collected in the string–flark complex where water tables were 1 cm (left) and 50 cm below the surface (right)

Genotypes

DNA analysis revealed 35 genotypes of *S. magellanicum* along Transect 1. Most of these genotypes occur only once ($n = 19$) or twice ($n = 5$). There are six genotypes that occur 13 times or more along the transect (Table 5, Figure 6). The most frequent type occurs in 50 sample spots. Meanwhile, instead of 8, 12 microsatellite markers developed for *Sphagnum* (Kyrkjeeide et al., 2016) have been amplified, which revealed 51 genotypes along the transect (Lamkowski et al., unpublished manuscript). The overall picture did not change with the more detailed analysis, however. There are still six dominant genotypes and the remainder occur only sparingly.

In light of the stark differences in growth forms, we had expected to find specific genotypes to be more dominant in wet or dry features. Yet, with the possible exception of Genotype A, none of the genotypes seems to occur more frequently in either wet or dry sites (Figure 23). Genotype A is about twice as frequent in the wet as in the dry features. Note that some strong associations with water table (high frequency of a genotype in a water table class) must be ascribed to the rarity of some water table classes. If a water table class has only one entry, there can be only one genotype associated with it and the frequency of this genotype is then necessarily 1.

If Genotype A were indeed associated with wet conditions, its occurrence in dry water table classes would be explained by mosses occurring on strings in the direct vicinity of wet flarks. Yet, it appears that the occurrence of Genotype A under dry conditions is not in the strings but rather in the lower rand (Figures 6 and 24). Genotype B may seem associated with the wet (upper and lower) plateau, but it also occurs frequently in the upper rand. Like A, Genotype C seems associated with the plateau and the flarks, but—like A—it is also frequent in the lower rand.

Rather than being associated with wet or dry sites or with specific ecotopes, single genotypes seem to occur in large patches of up to six subsequent samples along Transect 1 (i.e., over 10 m distance). The average patch size of each of the six common genotypes is clearly larger than expected on the basis of a random distribution (Table 5). Clonal growth is ubiquitous in *Sphagnum* (Cronberg, 1996; Gunnarsson et al., 2007) and would explain the patches. Genotype A happens to dominate between 240 and 290 m along Transect 1 (Figures 6 and 25), where it is only occasionally interrupted by single samples belonging to other genotypes. This stretch of the transect happens to cover the lower plateau, which consists solely of wet features. And so, Genotype A is seemingly associated with wet features.

Looking at the water table of the sites at which the respective genotypes occur, there is a different mean

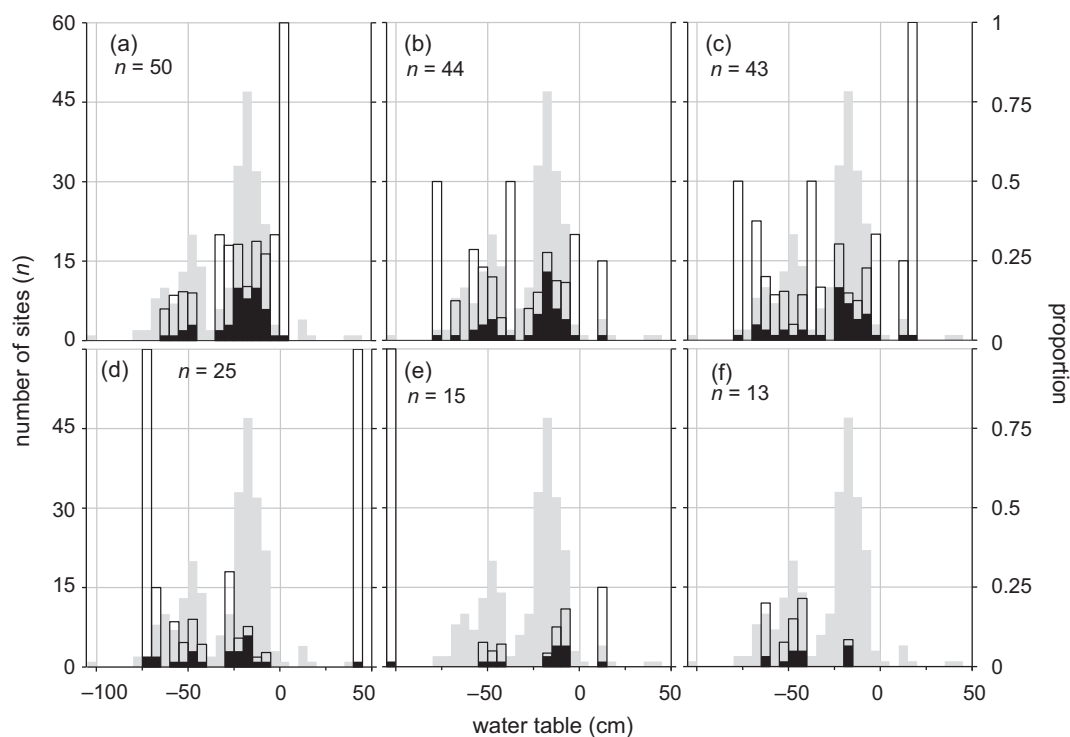


FIGURE 23 Distribution of the six common Genotypes A through F in relation to water table relative to the surface on 31 January 2005. Water table classes span 5 cm. The number of sites for each water table class is shown in gray bars; the number of sites where a particular genotype occurs in black bars; the proportion of total sites of a water table class where the genotype occurs in transparent bars

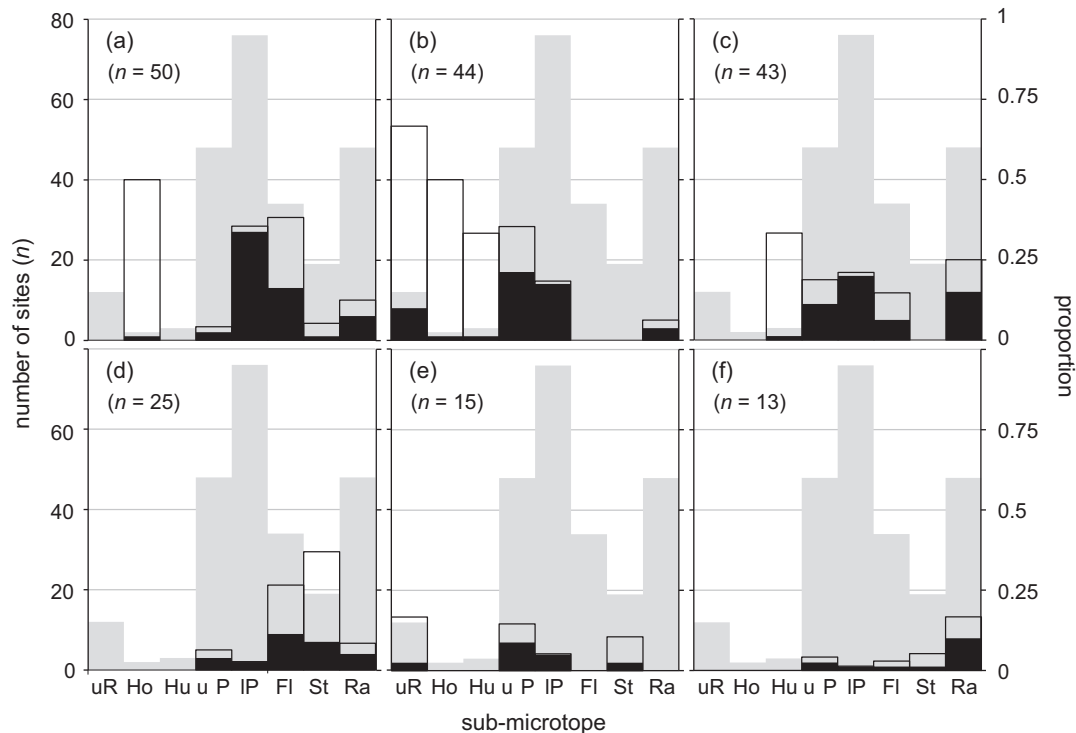


FIGURE 24 Occurrence of the six common Genotypes A through F in the different ecotopes upper rand (uR), hollow (Ho), and hummock (Hu) of the upper hummock–hollow complex, upper plateau (uP), lower plateau (IP), flarks (FI), and strings (St) of the lower string–flark complex, and the lower rand (Ra). The number of sites for each ecotope is shown in gray bars; the number of sites where a particular genotype occurs in black bars; the proportion of total sites of an ecotope where the genotype occurs in transparent bars

TABLE 5 Number of occurrences, frequency, and clustering of genotypes along Transect 1

Genotype	No. occurrences	Frequency	Cluster size		
			Observed	Random	Observed/random
A	50	0.21	1.76	1.33	1.32
B	44	0.18	1.91	1.27	1.50
C	43	0.18	1.79	1.26	1.42
D	25	0.10	1.39	1.13	1.23
E	15	0.06	1.88	1.07	1.75
F	13	0.05	1.63	1.06	1.53
Remainder	52	(0.21)	—	—	—
Total	242	1	—	—	—

Note: The size of genotype clusters is expressed as the average number of subsequent sampling sites at which the same genotype occurs. Cluster size is also given as expected for a random distribution based on the frequency of the respective genotypes. The “remainder” group of genotypes collectively represents types that each in total occur in six or fewer sampling sites; hence, cluster size characterization is omitted.

water table for each genotype and there are even “significant” differences. Yet, with randomly initiated clonal growth of a limited number of genotypes forming patches on a peatland with a clear pattern of wet and dry features it is inevitable that such differences arise.

No sporophytes were observed, although we did not actively search for them. Considering that each of the genotypes can cover the whole width of the different

niches and associated phenotypes, clonal growth seems a more efficient way to reproduce. Moreover, the closed cover of *S. magellanicum* hardly offers any room for the germination of spores (Sundberg & Rydin, 2002). If one of the genotypes currently present had established and expanded only later in an already existing *S. magellanicum* stand, it should have been more competitive than the mosses already present. One would then expect

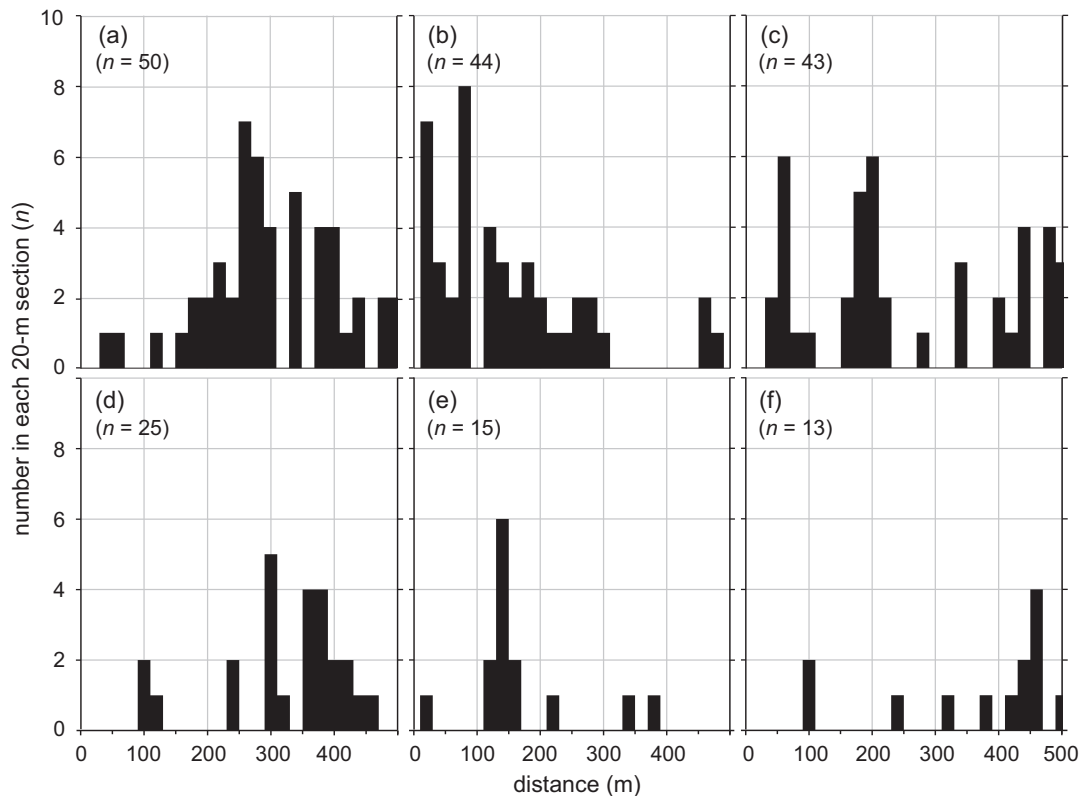


FIGURE 25 Occurrence of the six common Genotypes A through F in classes each spanning 20 m along Transect 1

it to be associated with a particular growth form and niche. It is more likely that the different genotypes have been present from the onset of the raised bog phase at least 2000 years ago. Shaw and Srodon (1995) arrive at the same conclusion in their study on *Sphagnum rubellum* genotypes in a North American bog. To explain the presence of seven genotypes, they suggest that as many as seven colonization events could have occurred and that at least four (plus interbreeding) are required.

INTEGRATIVE INTERPRETATION

Having presented the various—often correlating—patterns in plants, water, and peat on multiple scale levels, we will place our observations in the framework of a self-regulating and self-organizing raised bog. Bog *Sphagna* are *ecosystem engineers* that change their environment to their own advantage, which involves various feedbacks in which the presence of bog *Sphagna* stimulates the expansion of bog *Sphagna* (Van Breemen, 1995). Here, we focus on hydrological feedbacks. Hydrological self-regulation of a raised bog is based on three principles (Joosten & Couwenberg, 2019; cf. Joosten, 1993; Waddington et al., 2014): (1) regulating evaporation, (2) following the water level, and (3) changing

transmissivity and storativity. The measurements in the Valle de Andorra bog focus on the third principle. Before we address them, we will briefly turn to the other two.

Regulating evaporation

Regulating evaporation is important, because it constitutes by far the biggest loss item in the water balance of raised bogs. On an annual basis, about two-thirds of total precipitation is commonly lost through evaporation (Eggelsmann, 1990; Ingram, 1983; Romanov, 1968). Regulation of evaporation occurs on two different scale levels and with two different speeds. First of all, evaporation decreases promptly when water tables sink too low to uphold capillary water supply (Hayward & Clymo, 1982; Kettridge & Waddington, 2014; Romanov, 1968). On the picotope level, changes in the albedo of *Sphagnum* mosses and of dwarf shrubs may occur and on the nanotope level shifts in plant cover.

When water in the hyalocytes in *Sphagnum* capitula is replaced by air, the color of the chlorocytes manifests itself much less. The result is a lighter color—or an increase in albedo—leading to a reduction in evaporation (Eggelsmann, 1963; Hayward & Clymo, 1982; Harris, 2008). A similar change in albedo is achieved when the leaves of typical bog dwarf shrubs such as *Andromeda polifolia* or *Oxycoccus*

palustris under dry conditions change orientation, contract against the stem, and show their lighter underside. The dwarf shrubs growing in the Valle de Andorra bog do not show this feature, however. The bleaching of *Sphagnum* and dwarf shrubs functions very rapidly: If conditions become dry, the change occurs immediately. Of course the albedo of dry surfaces is in general higher than of wet ones (Ångström, 1925), which also applies to bogs (Kurbatova et al., 2002).

On a slower timescale, evaporation can also be influenced by changes in plant cover. If the site becomes drier over a longer period of time, plant cover will respond, in Northern Hemisphere bogs, for example, by a change in *Sphagnum* species. Individual *Sphagnum* mosses can hardly regulate their evaporation, but different species have a different evapotranspiration rate, also at identical water tables, because of different stand densities and canopy roughness (Clymo & Hayward, 1982; Overbeck & Happach, 1957; Rice et al., 2001). Moreover, shading by higher plants, which can regulate evapotranspiration, will reduce these losses (Rydin, 1993). Dwarf shrubs such as *E. rubrum* or *P. pumila*, but also *Marsippospermum grandiflora* of the Juncaceae family and the dwarf form of *N. antarctica*, which occur under dry conditions all have xeromorphic features that minimize evapotranspiration. Dead, dried leaves of *Marsippospermum* with their light color are strewn across the surface where they reflect radiation.

Following the water level

Like any porous medium, peat can shrink and swell, depending on the forces exerted on it. At every depth in the peat, there is a balance between the weight of the layers above, the strength of the skeleton of the porous medium, and the water pressure in the pores (Glaser, 1987). Hydraulic conductivity, which directly relates to pore space, decreases drastically when the water table drops and the now unsaturated top layer of peat is no longer supported by water pressure in the pores and thus becomes weight on the peat below. The effect was stronger in the wet than in the dry features because the skeleton is stronger in the latter. When the water table rises, the mosses and upper peat layers are carried by water again and no longer weigh down on the deeper peat layers. These changes also affect peat at a greater depth (Schothorst, 1977). Kellner and Halldin (2002) found that 40% of changes in water storage were related to compression and swelling of peat below 40 cm.

As the peat layers shrink and swell, this leads to an oscillation of the peat surface. This bog oscillation (or Mooratmung—bog breathing) commonly has an amplitude of a few centimeters per year (Fritz et al., 2008;

Ingram, 1983; Weber, 1902). In the Valle de Andorra mire, we measured surface oscillation between 2 and 8.5 cm, but these measurements were made in an unsystematic way. An oscillating surface dampens water table fluctuations relative to this surface (Kulczyński, 1949) and conditions remain more stable and conducive to peat accumulation. The effectiveness of bog oscillation depends on the thickness and elasticity of the peat deposit. A thicker, less humified peat layer can buffer more variation in water supply than a thinner and more strongly humified layer. As a result, bog oscillation differs between mire sites (Fritz et al., 2008) and is more effective in the plateau than in the rand. Considering its thick layer of only slightly humified *Sphagnum* peat, the capacity of the Valle de Andorra mire for oscillation will be relatively large. Yet, in the stable climate of the valley, this regulation mechanism is hardly called upon.

Changing transmissivity and storativity

As a self-organizing system, a raised bog finds a compromise between small pore space that limits runoff and large pore space that enables water storage and it does so on multiple levels (Couwenberg & Joosten, 1999). We distinguish a total of 16 self-regulation mechanisms in this category, numbered [1] to [16] below. Self-regulation mechanisms maintain the status quo; they are negative feedbacks that dampen or constrain changes to the system.

The most important self-regulating mechanism of a raised bog is the **acrotelm** [1]. The acrotelm consists of the upper few decimeters of living plants and the recently formed upper peat layer. Its most important property is that it shows a steep decrease in pore space with depth. If the water table is below the surface, aerobic decomposition of the dead plants and peat can proceed rather rapidly. The resulting loss of dead plant and peat material also leads to a loss of pore space. Yet, this lost pore space is continuously replenished from above by new plant material. As the older material below has been subject to more decomposition and longer pressure from unsaturated layers above, a distinct gradient in pore space results (Figure 14).

The steep gradient in pore space forces lateral runoff of water, which creates new options for regulation (Ingram, 1982; Ivanov, 1981). The ease with which the water flows depends on the transmissivity of the peat, which is the integral of hydraulic conductivity over depth. The steep gradient in pore space means that when the water table rises, lateral water flow is increasingly through layers with an increasingly higher hydraulic conductivity. As a result, excess water flows off quickly but diffusely without causing erosion. When the water table drops, lateral flow is more and more restricted to thinner

layers with less and less hydraulic conductivity. If the water table has dropped sufficiently, lateral discharge may even stop completely (Van der Schaaf, 1999; Verry, 1984).

Because the *Sphagnum* growing on top replenishes the pore space that is lost due to decomposition and compaction, the storativity of the acrotelm remains large and water table fluctuations are well buffered: The water table remains within decimeters from the surface. The peat below—the catotelm—remains permanently water saturated.

The acrotelm fulfills two tasks: It offers high storativity combined with transmissivity that it regulates as needed. It covers the entire raised bog, and it is the only regulation mechanism that works through an existing pattern, namely, the vertical gradient in pore space. Other regulation mechanisms are subordinate to the acrotelm. They *change* the vertical gradient of the acrotelm in time or *split* its tasks in space. In the following, we will first address how the vertical gradient is flexed in time in reaction to changes in the water table, then at how it diversifies in space as the mire adapts to local conditions, which expresses itself in higher organizational levels.

The acrotelm function of limited transmissivity when water tables are low is reinforced by mechanical changes in porosity of plants and peat. To start with, weight of unsaturated surface layers of peat can decrease saturated hydraulic conductivity. This **mechanical change in acrotelm porosity** [2] can surpass the effect of decomposition and compaction with age by a large factor (Figure 18 vs. Figure 14). This mechanism depends on the stiffness of the peat and plants, and is therefore particularly strong in the wet features (see below). A change in water table furthermore results in an immediate change in the porosity of *Sphagnum* mosses. As part of the **mechanical change in the plant porosity** [3], the pendulous branches of *Sphagnum* mosses contract against the stem and later also the leaves against each other, which increases capillary water supply to the moss capitula (Clymo & Hayward, 1982). The mechanical changes in acrotelm transmissivity are associated with the bog oscillation described above. As noted, compression and swelling affect the lower catotelm peat as well. If the water table drops, compaction, or **mechanical change in catotelm porosity** [4], reduces the permeability of the entire peat under the water table, reducing infiltration and outflow.

In a related way, on a landscape scale a raised bog massif that grows upward over a fen will lose more water toward the subsoil as the height difference increases. Yet, with its enormous pressure of approximately 1000 kg/m² for every meter of peat, the water saturated bog compresses the underlying, originally

loose layers of fen peat so strongly that they become very compact and scarcely permeable; a phenomenon seen in Valle de Andorra as well.

If a feature is very wet and located on a slope, high transmissivity will result in flowing water that may bend the mosses in the direction of flow. This change in **moss stem orientation** [5] is an adaptation that reduces drag forces on the mosses. It enables faster runoff without damaging the moss plants. This response is a negative feedback that sets in only when water tables are (very) high and water already flows rather quickly. The feedback then allows for quick but still diffuse removal of the excess water that prevents even higher water tables that might cause a catastrophic water breakout.

Lower water tables lead to **stronger humification** [6], which reduces transmissivity. This increased humification mainly takes place in the acrotelm, but because all acrotelm peat eventually becomes catotelm peat—it will affect deeper peat as well. One might expect that prolonged drier periods in the order of decades—or steeper slopes—would create a steeper pore space gradient in the acrotelm, but this is not necessarily the case as dryness induces biochemical changes that make *Sphagnum* more recalcitrant (Sytiuk et al., 2021), and other changes occur simultaneously as well (see below). *Sphagnum* growth is sensitive to water content in the capitulum (Bengtsson et al., 2020; Jassey & Signarbieux, 2019), and in reaction to prolonged lower water tables, the growth form of the *Sphagnum* mosses becomes denser (see section “*Picotope [mire eros]*”). Like the mechanical change in plant porosity, this **biological change in plant porosity** [7] improves capillarity and keeps the capitula moist. Moreover, the plants and peat become more compact, which reduces transmissivity. Conversely, *Sphagnum* plants become more “open” under wetter conditions and their growth form and resulting peat more permeable (Früh & Schröter, 1904; Hayward & Clymo, 1983). These changes occur in single mosses, but their effect is expressed particularly at the higher nanotope level of the mire features.

A more lasting response is achieved when the **plant cover changes** [8]. In northern peatlands, such changes involve shifts in *Sphagnum* species, of which some are better adapted to drier, others to wetter conditions. Their adaptations in growth form primarily involve maximizing competitive growth while securing moisture provision to the capitula (e.g., Andrus, 1986; Clymo, 1973; Clymo & Hayward, 1982; Overbeck & Happach, 1957; Robroek et al., 2007). The specialized growth forms of the different species then consolidate the dry or wet character of the mire feature. Yet, in the Valle de Andorra mire all niches are occupied by *S. magellanicum*, which shows a broad plasticity—

apparently even independent of genetic differences. Still, once the growth form changes, it will reflect in the peat as well and the changes are not immediately reversible and may thus consolidate (see above).

Moreover, the cover of higher plants will change as well. Drier conditions are associated with a denser cover of dwarf shrubs in particular. The shrubs provide a scaffold for *Sphagnum* to grow up (Weber, 1902), and woody debris is incorporated in the peat. The dense form of the mosses and the higher degree of humification is counteracted by more sturdy components that prevent the gradient in hydraulic conductivity from becoming too steep. Pore-space gradients are actually similar whether conditions are wet or dry (Figure 14).

Until a couple of thousands of years ago, a percolation mire covered the Andorra valley (cf. Loisel & Bunsen, 2020; cf. Figure 3), which was then progressively overgrown by a *Sphagnum* raised bog. The bog gradually formed the dome shape it has now. In the beginning, its surface simply followed the underlying fen relief. As the dome rose, its slopes became steeper. Steeper slopes will drain more readily, initiating the development of a dry rand. The dry features of a rand per se are not more effective in obstructing water flow than those found in strings (Figures 14 and 18), but just as a string is more effective than a single hummock in obstructing water flow, the rand—like an oversized string—is even more so. In the rand, the compromise between small and large pore space or between limited transmissivity and maximum storativity has shifted in favor of smaller pore space. The lack of storativity in the rand is somewhat compensated by water supply from its large internal catchment. A larger dome supports not only a steeper slope, but also a flatter center further away from this slope (cf. Clymo, 2017). A central plateau will develop where the compromise shifts in favor of larger pores and storativity. On the level of the mesotope, the “tasks” of the acrotelm are thus spatially divided between dry and wet mire sites.

The steeper the dome, the wider and less permeable the rand (see simulation results in Couwenberg & Joosten, 2005). Upslope of the rand water tables is determined by the input of runoff water from the bog interior (internal catchment), the slope, and the (im)permeability of the rand. As the dome expands, the internal catchment grows, the rand steepens and widens. At one point, runoff is no longer sufficient and water will accumulate in the area just above the rand and stimulate the development of wet features. This initial flark with its high transmissivity will in turn drain the area directly upslope where a string develops that in turn will obstruct runoff from the area directly upslope where a flark develops, and so on. A more or less regular striping pattern results

as long as the slope, the amount of water, and the difference in transmissivity between dry and wet features are large enough (Couwenberg, 2005; Couwenberg & Joosten, 2005; Swanson & Grigal, 1988).

A division of the acrotelm tasks between wet and dry elements at higher levels of organization—from the nanotope upward—opens up new ways for feedbacks and regulation. Let us first turn to the hummock–hollow complex. The hummocks are associated with low transmissivity, and the hollows with high storativity. The hummocks act mainly to reduce runoff, while the hollows account more for the storage of water. The shape of hummocks (wide at the bottom and narrow at the top) and hollows (narrow at the bottom and wide at the top) mirrors the pore space gradient of the acrotelm. This correspondence strengthens the acrotelm: When water tables are low, runoff is even further reduced because it is through more narrow stretches of hollow and when water tables are high runoff is further increased because it is through more narrow stretches of hummock.

The transmissivity and storage of the hummock–hollow complex depends on the porosity of the constituent dry and wet features, or how the acrotelm expresses itself in each of these features (see above). In addition, on a higher level it also depends on the ratio of dry to wet features [9], their shape [10], and their orientation and arrangement [11].

When water tables are low for a prolonged period of time (years to centuries), dry features will expand at the expense of wet ones. When water tables are high, the opposite occurs (Barber, 1981; Casparie, 1972). The runoff of water is regulated by such changes in the **relative proportion of dry and wet features** [9]. During occasional dry periods, the wet features are actually very effective in reducing runoff (Figure 18), but they will adapt their growth form if dry conditions continue. Most obviously, they will do so at the transition to the dry features, making existing dry elements larger. Next to expansion of existing features, a new hummock was seen to originate along Transect 1 (see “*Sub-nanotope*”). This “part-time” hummock was very effective in obstructing runoff when water tables were low. Over time, the peat below this new dry feature will no longer have been formed under predominantly wet conditions, but be an expression of the dry feature itself. It can then consolidate and expand.

Note that the very effective reduction in transmissivity of the wet flarks when water tables drop is related to their large porosity, which could not exist on its own on a slope. It is the limited transmissivity of the strings that enables the presence of the flarks with their large porosity. The flarks primarily fulfill the task of storing water, but not at the cost of the ability to reduce runoff when

needed. Also the “part-time” hummock can only be effective because it is embedded between “full-time” strings.

In reaction to larger water table *fluctuations*, the more compact dry features also become higher and steeper: The **shape of the features** [10] changes. A higher dry feature has lower transmissivity, because the water flows deeper below the surface; a steeper dry feature retains more of its low transmissivity when the water table rises (see above). Larger water table fluctuations are associated with peak flow and overall larger runoff losses than when the water table would remain stable at an average depth. Changes toward higher and steeper dry features counteract these increased losses. A gradient from higher and steeper hummocks at the rand to lower and flatter ones in the center has been described for the Boertangerveen by Venema (1855; see Joosten et al. 2017, p. 35). Such a gradient is not seen in the Valle de Andorra mire. We do see a very steep edge where the rand meets the Arroyo Grande River at the end of Transect 1. Here, the peat is subject to the erosional forces of a river meander. Yet, the peat has been compacted to such an extent that the rand apparently remains stable.

Not only the amount of dry and wet features is important, but also the **orientation and arrangement of mire features** [11]. From a hydrological point of view, the surface elements are most effective when oriented perpendicular to the direction of water flow. Indeed, if the slope, the amount of water and the difference in transmissivity between dry and wet features are sufficient, such an orientation organizes itself (Couwenberg & Joosten, 2005). If the direction of water flow changes, the pattern will adapt, but the new pattern will take decades to establish and the old one will linger (Masing, 1982). Where slopes are gentler the organizing force of the water flow will be too weak and dry and wet elements will be randomly arranged. The resistance to water flow will be lower, which stimulates removal of excess water.

The oriented hummock strings and hollow flarks function on the higher level of the microtope. Next to the string–flark complex, a rand and a plateau can be discerned. In the rand, the pore space compromise is clearly tilted toward small transmissivity, in the plateau to high storativity, and the string–flark complex locally manages a combination of the two. At this mesotope level, changes in the **extent and spatial distribution of mire sites** [12] offer an additional regulation mechanism. The shape of a raised bog dome necessarily results in combinations of always a rand with a plateau when the dome is wetter or flatter and also a string–flark complex when a certain combination of wetness and flatness is met (Couwenberg & Joosten, 2005). While growing in width and height, raised bogs will develop flatter centers and steeper slopes (Clymo, 1984; Glaser et al., 2004), with shifts in the mire

sites as a result (Couwenberg & Joosten, 2005; Glaser & Janssens, 1986; Masing, 1984).

The increasingly flatter center of the raised bog is partly self-reinforcing (a positive feedback), because under wet conditions productivity decreases. At one point, open water **pool formation** [13] will occur, in which peat degradation exceeds production (Boatman, 1977; Foster et al., 1988; Glaser & Janssens, 1986; Loopmann, 1988). Pools are at the extreme end of the porosity compromise where storativity is maximized and transmissivity is not regulated at all.

For larger raised bogs, in particular, it is important to lose the excess water. The amount of precipitation received by a bog increases quadratically with its radius, whereas its perimeter increases only linearly. The larger the bog becomes, the more water has to leave the bog per unit perimeter. The result is the development of **preferential watercourses** [14], the so-called “Rüllen” (Weber, 1902), which break through the perimeter (Masing, 1984). They allow for fast removal of excess water without the risk of erosion. Large and effective bog streams may result in a **bog division** [15], in which a large bog is split into two (or more) lobes, considerably reducing the wetness of the total system (Masing, 1984).

The increase in the proportion of wetter, weaker features (hollows, pools, and plateau) in an ever larger bog threatens the stability of the peat body. In extremely wet periods, when the wet center can no longer be held by the rand, a **bog burst** [16] can occur (Früh & Schröter, 1904). Bog bursts are the ultimate negative feedback (Schreiber, 1927) that can reset large parts of the bog to allow for renewed growth (Caseldine & Gearey, 2005; Casparie, 1972; Dupont, 1986; Ivanov, 1981; Stastney et al., 2018; Van Geel et al., 2014).

Self-regulation mechanisms in space and time

In response to allogenic (climate) and autogenic (peat growth) hydrological changes, changes occur in the hydrologically active structures of a raised bog on all possible spatial scales: from microscopic plant tissue and pore structures to the enormous bog complexes such as the Hudson Bay Lowlands (Glaser et al., 2004; Sjörs, 1959), the Red Lake Peatlands (Glaser et al., 1981; Heinselman, 1963), or the Great Vasyugan Mire (Katz & Neustadt, 1963; Kirpotin et al., 2021) where raised bog domes alternate with fens and lakes (Tables 1 and 6).

The hydrological self-regulation mechanisms that we identified each work on their own respective spatial and temporal scale. We created a tentative overview of the spatiotemporal extent of each mechanism (Figure 26). Other mechanisms may exist, and we do not claim to

TABLE 6 Raised bog elements focusing on minimum pore space that stagnate water flow and elements focusing on maximum pore space that store water on various spatial scales

Organizational level	Indicative spatial scale (m ²)	Water stagnating elements	Water storing elements
0	10 ⁻⁸	Plant tissue	Pores
Picotope	10 ⁻²	Individual plants	Spaces between plants
Nanotope	10 ⁻¹ –10 ⁹	Acrotelm and catotelm	Acrotelm
Microtope	10 ¹ –10 ⁶	Hummocks and strings	Hollows, flarks, and pools
Mesotope ^a	10 ² –10 ⁷	Rand	Hummock-hollow complex
Macrotope	10 ⁵ –10 ⁹	Raised bog domes	Fen matrix

Note: The indicative scales overlap to differing amounts.

^aAt the mesotope level, the hummock-hollow complex falls somewhere in between water stagnating and water storing.

know the exact limits of each mechanism. There is a conspicuous lack of mechanisms in the combined small spatial and large temporal scale realm (upper left corner in Figure 26). Here, we would situate evolution of genetically different peat mosses with distinct phenotypic expression. We do not see ourselves fit to place a box here. The lack of habitat-related genetic differences in the Valle de Andorra mire may indicate that selective forces and consequent genetic evolution may work—at least concerning *S. magellanicum*—over longer time scales.

The various mechanisms that were identified overlap in both space and time, which means there is redundancy in the self-regulation of the system. As in the case of surface oscillation in the Valle de Andorra mire, redundancy may exist within a single mechanism as well and may be almost complete. Not all mechanisms were analyzed in detail in this respect, but it is likely additional redundancy exists. Raised bogs, when in a natural state, are among the most resilient ecosystems known—resilience that is provided by feedbacks and backup systems to these feedbacks. Note that the reaction time of the self-regulation mechanisms differs from their buildup time. For surface oscillation for example, thousands of years may be needed to build up a peat body of sufficient thickness for it to “breathe” effectively. Once such a peat body exists, however, surface oscillation reacts instantaneously to changes in water supply.

OUTLOOK

The interconnections are all very clear in the simple world of the Valle de Andorra mire, but they exist elsewhere too. It may take the right search image to see them, however. Although they differ in their practical workings, similar feedbacks have been described for the physiognomically very different tropical domed peat swamps of Southeast Asia (Dommain et al., 2010).

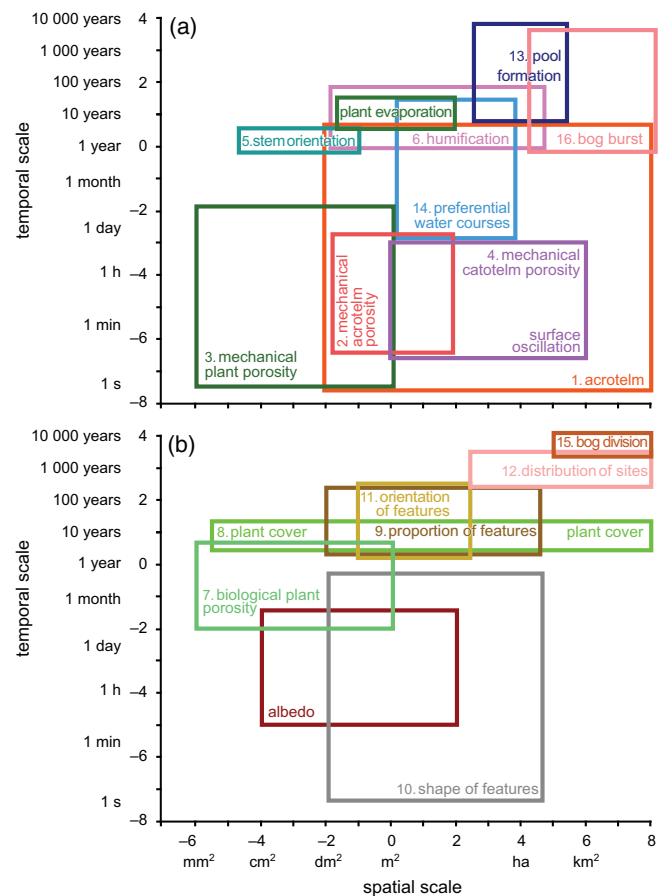


FIGURE 26 Tentative overview of hydrological self-regulation mechanisms of a raised bog in space and time. On the horizontal axis, the surface over which the mechanisms work, and on the vertical axis, the reaction time with which they react to changes. Note the logarithmic scale of the axes as also indicated by the orders of magnitude. To reduce clutter, the figure has been split in two (a, b)

Ombrotrophic peatlands with hardly any or markedly fewer self-regulation mechanisms exist as well. However, they are restricted to climates with abundant and very regular rainwater supply, like the “blanket bogs” in

highly oceanic areas (Lindsay, 1995) and the “percolation bogs” in the extremely humid warm-temperate climate of Colchis, Transcaucasia (Krebs et al., 2017). In more “normal” climates with intermittent rainfall, however, self-regulation mechanisms must be achieving the “critical compromise” between transmissivity and storativity.

In the *Sphagnum*-dominated peatlands of the Northern Hemisphere and Tierra del Fuego, only a handful of *Sphagnum* species seem to have the right characteristics to shape that critical compromise on various levels of organization (Joosten, 1993), and in this paper, we illustrate that it can even be done with only one of these *Sphagnum* species, even without genetic diversity. The comparatively wide distribution of such *Sphagnum* “acrotelm” raised bogs (named after the dominant regulation mechanism, Couwenberg & Joosten, 1999), from the subarctic to the temperate continental climate zone (cf. Moen et al., 2017), shows the impressive effectiveness of this strategy.

CONCLUSIONS

A raised bog is extremely poor in nutrients; lacks alkalinity, which makes it very acidic; and consists largely of pore space. The first two properties result in the selection of hardy species and in only limited rates of decomposition. Accordingly, they in fact facilitate the effective dealing with porosity—limiting transmissivity without losing too much storativity. This compromise is on any spatial scale crucial to the origin and survival of a raised bog. The pore space gradient in the acrotelm is the inevitable consequence of decomposition combined with replenishment of lost pore space from above. Lateral water flow is the inevitable consequence of the existence of an acrotelm. The domed shape of a bog is the consequence of simple physical processes. As the dome grows, the steep rand becomes drier with a consequent smaller pore space in the plants and peat, which reduces transmissivity and thus water losses. The mechanical response is immediate, and the biological response of a changing plant cover is slower, just like the biochemical reaction of increased decomposition. The dry rand exists in contrast to a wet plateau, creating a higher level of organization. On this level, the compromise shifts toward limited transmissivity in the rand and toward maximum storage in the plateau. Other surface patterns such as the string-flark complex follow from similar rules of self-organization and create similar shifts in the compromise. In a growing raised bog local conditions are always changing. Whenever the critical compromise can locally not be met anymore, the bog—through self-organization—apparently creates new structural elements on a higher level with new options to meet the necessary

compromise on this new level, with consequences for every level below.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

John Couwenberg and Hans Joosten conceived the study, to which Martin Baumann contributed. Martin Baumann carried out most of the field work along Transect 1. Paul Lamkowski collected and analyzed the DNA samples. John Couwenberg and Martin Baumann analyzed the bulk of the data. John Couwenberg and Hans Joosten wrote the paper, to which Martin Baumann and Paul Lamkowski contributed.

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