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Key Points:

- Peat hydraulic conductivity is well explained by a small number of simple, easy-to-measure descriptors
- Horizontal and vertical hydraulic conductivity possess subtly different controls that reflect contrasting roles in peatland water budgets
- Generalizable models of peat hydraulic conductivity using simple descriptors may be attainable through meta-analysis of published data

Supporting Information:

- Supporting Information S1
- Data Set S1

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Controls on Near-Surface Hydraulic Conductivity in a Raised Bog

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Abstract Shallow water tables protect northern peatlands and their important carbon stocks from aerobic decomposition. Hydraulic conductivity, K , is a key control on water tables. The controls on K , particularly in degraded and restored peatlands, remain a subject of ongoing research. We took 29 shallow (~50 cm) peat cores from an estuarine raised bog in Wales, UK. Parts of the bog are in close-to-natural condition, while other areas have undergone shallow peat cutting for fuel and drainage, followed by restoration through ditch blocking. In the laboratory we measured horizontal (K_h) and vertical (K_v) hydraulic conductivity. We fitted linear multiple regression models to describe \log_{10} -transformed K_h and K_v on the basis of simple, easy-to-measure predictors. Dry bulk density and degree of decomposition were the strongest predictors of K_h and K_v . Perhaps surprisingly, the independent effect of hummocks was to produce higher- K_v peat than in lawns; while the independent effect of restored diggings was to produce higher- K peat than in uncut locations. Our models offer high explanatory power for K_h (adjusted $r^2 = 0.740$) and K_v (adjusted $r^2 = 0.787$). Our findings indicate that generalizable predictive models of peat K , similar to pedotransfer functions for mineral soils, may be attainable. K_h and K_v possess subtly different controls that are consistent with the contrasting roles of these two properties in peatland water budgets. Our near-surface samples show no evidence for the low- K marginal peat previously observed in deeper layers at the same site, indicating that such structures may be less important than previously believed.

1. Introduction

1.1. Background

Northern peatlands are organic-rich wetlands that are thought to store up to a third of all global soil carbon (Gorham, 1991; Yu, 2011). The persistence and gradual accumulation of peat owes much to shallow water tables that limit the rate of microbial respiration, thereby preserving plant detritus. Peatland carbon and water budgets are intrinsically linked, and depth to water table is a first-order control on peatland plant productivity and ecosystem respiration (Belyea & Clymo, 2001; Moore & Dalva, 1993; Roulet et al., 2007). Peat hydraulic properties govern water retention through a variety of mechanisms (Ingram, 1982; Waddington et al., 2015) and are therefore of central importance to the maintenance of these valuable ecosystems. One of the most commonly measured peat hydraulic properties is saturated hydraulic conductivity, K (dimensions of L/T; throughout, we use the terms permeability and hydraulic conductivity interchangeably).

Peat hydraulic properties sometimes exhibit strong vertical gradients. Previous studies have observed that K can decline by several orders of magnitude from fresh, open peat at the surface, to highly decomposed, barely permeable material just a few tens of centimeters below (e.g., Clymo, 2004; Fraser et al., 2001; Kneale, 1987; Moore et al., 2015; Waddington & Roulet, 1997). However, some studies have reported no consistent depth variation in K (Chason & Siegel, 1986). Strong relationships have also been reported between K and degree of decomposition (e.g., Grover & Baldock, 2013; Ivanov, 1981), dry bulk density (e.g., Boelter, 1969), and various combinations of these predictors (e.g., Branham & Strack, 2014; Morris et al., 2015; Päivänen, 1973). Human modification of peatlands, particularly drainage, can lead to increased aeration and decomposition in near-surface layers, causing a constriction of pore spaces and so reduced K (e.g., Silins & Rothwell, 1998); while long-term flooding through the construction of dams and berms can lead to increasingly buoyant peat with more open, conductive pore structures (Moore et al., 2015).

Strong horizontal gradients in K have been reported at a range of scales. Modeling (Lapen et al., 2005) and observational (Baird et al., 2008) studies suggest the possibility of a low- K margin in raised bogs, while Lewis

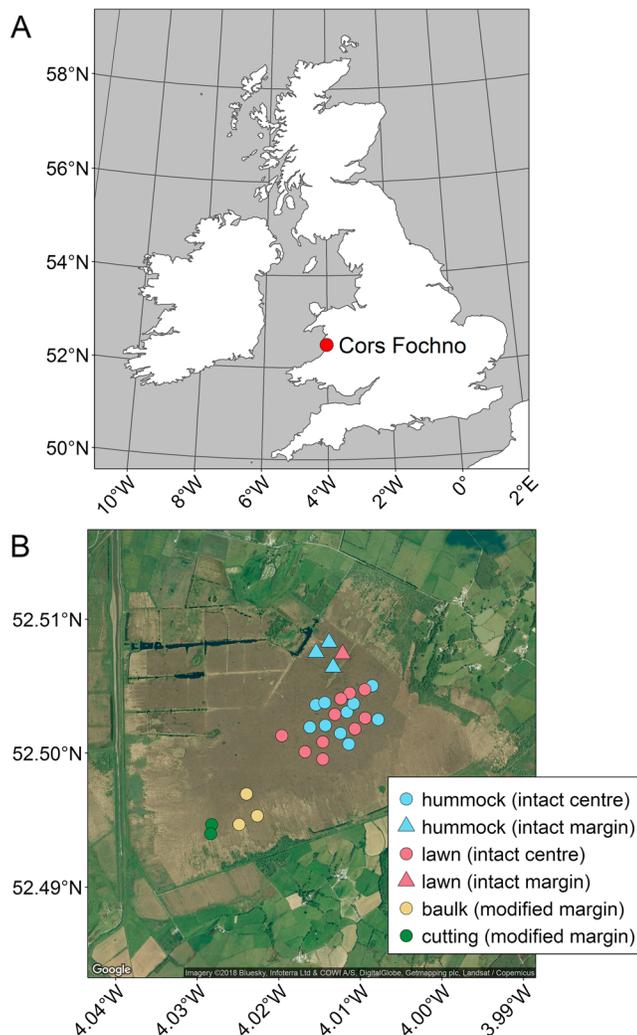


Figure 1. Details of the study site, Cors Fochno, showing: (a) location within British Isles; and (b) site-scale aerial photography overlain with sampling locations. Aerial photography and map data shown in Figure 1: Google, Bluesky, Infoterra Ltd & COWI A/S, DigitalGlobe, Getmapping plc, Landsat/Copernicus.

et al. (2011) observed a similar phenomenon in blanket peat. Such structures may act as barriers to lateral flow and thus help to retain water, with feedbacks to peat decomposition and accumulation. However, Morris et al. (2015) found no evidence for any such low- K margin in shallower layers (< 0.5 -m depth) of a Swedish bog, so it remains unclear whether such marginal structures are common features. At smaller spatial scales of a few meters, K can sometimes vary by more than an order of magnitude between adjacent plant microhabitat types such as hummocks, lawns, and hollows (e.g., Baird et al., 2016; Ivanov, 1981). However, the evidence for strong lateral variability in K at such small spatial scales is mixed. For example, Branham and Strack (2014) found differences in K between microhabitat types to be secondary to depth variation across a range of Canadian sites; while Baird et al. (2016) found that strong horizontal gradients in K at depths of 0.5 m were much less evident at depths of 0.9 m.

As well as governing rates of shallow groundwater flow, peat K also defines the upper limit for unsaturated hydraulic conductivity, K_{unsat} . K plays an important role in determining the supply of water from the saturated zone and through the vadose zone to meet surface evaporative demand, and thus the resistance of peatland ecosystems to drought (Kettridge et al., 2016). Peat K can be highly anisotropic, with measurements in horizontal (K_h) and vertical (K_v) dimensions sometimes differing by more than three orders of magnitude for the same sample (Beckwith et al., 2003). Given the low hydraulic gradients usually seen in peatlands, K_h is most relevant to shallow groundwater flow, where horizontal fluxes dominate (Ingram, 1982). In contrast, K_v appears more relevant to describing surface-atmosphere fluxes, such as evapotranspiration and infiltration (Kettridge et al., 2016), and interactions between peat and underlying groundwater systems (Devito et al., 1997; Reeve et al., 2000). However, the two components of K are rarely reported together, and it is unclear if they possess similar controls.

1.2. Aim and Objectives

We sought to establish the controls on shallow peat hydraulic conductivity at the same study site where Baird et al. (2008) previously characterized deeper hydraulic structures. We addressed the following specific questions:

1. Does the low- K margin found by Baird et al. (2008) in deep peat also exist in near-surface layers?
2. Can a combination of simple, easily measured descriptors adequately characterize peat K and provide the basis for a reliable and generalizable predictive model?
3. Do the controls on K_h and K_v differ in ways that reflect these two properties' contrasting ecohydrological roles?

2. Materials and Methods

2.1. Study Site and Field Sampling

Cors Fochno, also known as Borth Bog, is a mostly intact estuarine raised bog in Ceredigion, west Wales (52.500°N , 4.020°W , up to 5 m above mean sea level; Figure 1a). The main dome of the bog covers approximately 440 ha and is bounded to the north by saltmarshes of the Dyfi Estuary, to the west by the canalized Afon Leri, and to the south and east by farmland and bedrock hills. Some of the bog's margins have been modified through shallow peat cutting for fuel (diggings $< \sim 0.6$ -m deep) and ditch drainage since Victorian times. The peat in the center of the bog dome is 7-m thick (Hughes & Schulz, 2001) and is uncut and in a near-natural condition. Vegetation in this intact central area comprises a mosaic of hummocks,

lawns, and hollows. The hummock vegetation comprises mostly *Calluna vulgaris*, *Eriophorum vaginatum*, and *Sphagnum capillifolium*, with some *Eriophorum angustifolium* and *Myrica gale*. Hollow vegetation is dominated by *Sphagnum pulchrum*, *Rhynchospora alba*, and *E. angustifolium*, with occasional *Erica tetralix* and *M. gale* plants. Lawns tend to have a similar vegetation to the hollows but with *Sphagnum papillosum* and *Sphagnum magellanicum* instead of *S. pulchrum* and a lower cover of *R. alba*. Marginal areas of the bog have similar vegetation to the hummocks, except the bases of former peat cuttings where the vegetation is more like that of lawns and hollows. Since 1976 the peatland has been protected as part of the Dyfi UNESCO Biosphere Reserve and is administered by Natural Resources Wales (formerly the Countryside Council for Wales) who have undertaken extensive remedial works to promote surface wetting and peat accumulation through ditch damming. Annual average temperature at the nearby Trawscoed weather station is 9.8 °C, and annual average precipitation is 1,195 mm/year (averaging period 2005 to 2015).

We collected shallow core samples from 29 locations across the site, including at 16 of the 27 locations studied by Baird et al. (2008). We collected 20 cores from the intact center of the bog dome (intact center, Figure 1b), where Baird et al. (2008) found K in deeper layers to be significantly higher than in marginal areas. We collected four cores from the northern margin of the dome (intact margin, Figure 1b), which is still relatively intact and, unlike most of the site's other margins, retains its original mosaic of hummocks, lawns, and hollows. In both the intact central and marginal areas we sampled hummock and lawn microhabitats only; peat in hollows was usually too loose and open to take intact cores from. We collected a further five cores from the heavily modified southwest margin of the bog (modified margin, Figure 1b), where the original vegetation habitats and their associated microtopographies have been replaced by a high density of former diggings, many of which have been dammed and have begun to revegetate and infill with new peat. In this modified marginal area we sampled two revegetating cuttings and three drier, uncut ridges, known as balks, in between cuttings. See Figure 1b for sampling locations.

At each coring location we used square-section polyvinyl chloride (PVC) guttering downpipe with a 0.12×0.12 m cross section to extract shallow peat cores of at least 0.4-m depth. We employed the scissor-cut method described by Green and Baird (2012) to insert the PVC pipe, before digging out each core—protected by the pipe—with a spade. The scissor-cut method and the use of the PVC sleeve minimized damage to the samples. We transported the cores in their PVC sleeves to the laboratory, where they were stored upright and refrigerated until analysis.

2.2. Hydraulic Conductivity

In the laboratory we removed the PVC sleeves and used highly sharpened, nonserrated blades to remove the top 0.03 to 0.05 m of material from each core, which we determined to be the growing surface. The growing surface consisted of living plant material and loose, poorly decomposed peat that would be unlikely to remain structurally intact during preparation for K tests. The top few centimeters of cores from the intact central and marginal areas comprised a layer of living *Sphagnum* that transitioned gradually into fresh, poorly decomposed, *Sphagnum* peat. The tops of cores from the modified marginal area exhibited a much sharper transition from new peat that represents regrowth in response to restoration efforts, to a dense, fibrous, well decomposed peat a few centimeters below. Although some of this regrowth was removed as part of the growing surface, a portion of it was retained in all cores from the modified margin. Henceforth, we report all depths relative to the base of the growing surface.

We subsampled the remaining peat at depth intervals of 0.1 m and trimmed each subsample into a $0.1 \times 0.1 \times 0.1$ m cube. We dabbed the cubes dry using paper towel before dipping each face repeatedly in molten paraffin wax to build up a wax coating of at least 0.005 m on all sides, keeping note of the original vertical orientation (SurrIDGE et al., 2005). We measured K_h and K_v for each cube using the modified cube method described by Beckwith et al. (2003; see also SurrIDGE et al., 2005). We used a scalpel to remove opposing faces of wax from either the top and bottom faces (for K_v tests) or from two sides (K_h), which served to remove fine debris and unclog pore ends (SurrIDGE et al., 2005). Prior to the K measurements, we submerged each cube overnight in a water bath. We established a constant head gradient across each sample to generate steady state flow and calculated K using the method given by Beckwith et al. (2003). In most cases we maintained a constant head gradient of unity, but for the most permeable samples we reduced the gradient to 0.35 or 0.30 so as to reduce flow rates. We measured water temperature in each test and standardized K

measurements to 20 °C using the method of Klute (1965). In between K_v and K_h tests we resealed the exposed sides with wax, exposed alternative faces, and resaturated the cubes.

2.3. Degree of Decomposition and Dry Bulk Density

After measuring K_h and K_v , we removed all wax and determined the degree of decomposition in all samples according to the von Post classification system (Ekono, 1981). Upon visual inspection, some samples exhibited obvious horizontal banding of peat color or texture, indicating different levels of decomposition within the sample, which might have an anisotropic effect upon flow. For example, a thin, contiguous, horizontal layer of highly decomposed, low-permeability peat through a sample would be relatively unimportant to K_h , because preferential horizontal flow would occur through the less decomposed, more permeable peat above and/or below. However, the same low- K horizontal layer would present a more important barrier across the entire width of vertical flow through that sample and would likely reduce K_v . To allow for any such anisotropic effect of degree of decomposition upon K , we recorded two von Post scores: one that relates to horizontal flow and one that relates to vertical flow. Where distinct banding was apparent in a sample, we made separate von Post determinations for all horizontally contiguous layers and treated the highest of these scores (i.e., the most decomposed layer) as the most relevant to vertical flow. Our approach here is somewhat similar to calculating a harmonic mean (appropriate to flow through resistors in series). When considering horizontal flow we used the von Post score of all layers within a subsample to estimate a composite score akin to an arithmetic mean (parallel resistors). Where this led to a value in-between von Post classes we rounded up to the higher class. In samples that exhibited no clear horizontal banding, we assumed the effect of degree of decomposition upon K to be isotropic and made a single von Post determination for the entire $0.1 \times 0.1 \times 0.1$ -m cube that we applied to both the horizontal and vertical models (see below). Finally, we calculated peat dry bulk density by oven drying each $0.1 \times 0.1 \times 0.1$ -m sample at 80 °C to constant weight.

2.4. Data Analysis

2.4.1. Variables and Transformations

We fitted linear models to describe horizontal and vertical K from three continuous independent variables: depth, dry bulk density, and von Post score (see below for discussion of von Post score as a continuous variable); and two categorical variables: area (intact center, intact margin, and modified margin) and microhabitat (hummock, lawn, balk, and cutting). Our measured K_h and K_v vary across more than 5 orders of magnitude and exhibit highly nonlinear, heteroscedastic relationships with the three continuous independent variables (linear regression assumes homoscedasticity or homogenous variance of the response variable across the model domain; heteroscedasticity is the violation of this assumption, meaning that the model performs better in some parts of its domain than in others). Like Morris et al. (2015), we transformed the K_h and K_v data by taking their logarithms (base 10), which yielded linear, homoscedastic relationships, with normally distributed, unstructured residuals.

2.4.2. Interactions and Random Effects

Taking measurements at multiple depths in each core raised the possibility of a hierarchical structure in our data set, manifest as greater similarity of measurements within cores than between cores. Such a situation would violate the assumption of independent measurements required by standard multiple regression. Again like Morris et al. (2015), we fitted linear mixed effects models to both $\log_{10}(K_h)$ and $\log_{10}(K_v)$ to test for any such core-specific artifacts, grouping our measurements according to coring location (the subject variable). To begin with, we fitted all main effects (depth, dry bulk density, von Post, area, and habitat) simultaneously, without using any stepwise model building procedure. We then added interaction terms in a stepwise manner, followed by random effects individually and in combination, and at each stage tested whether any of these alterations led to a significant improvement in model performance compared to the first model, which contained fixed main effects only. No combination of random slopes and random intercept led to any significant improvements in our models' fits to either the $\log_{10}(K_h)$ or the $\log_{10}(K_v)$ data, according to the corrected Akaike Information Criterion (AIC_C ; change in AIC_C treated as χ^2 statistic with degrees of freedom equal to change in number of model parameters; $p > 0.05$ in all cases). The grouping of measurements by core therefore introduced no discernible artifact, so the assumption of independence appeared reasonable and we proceeded with linear multiple regression modeling. Unlike Branham and Strack's (2014) analysis of variance, our linear mixed effects models indicate no significant interactions between independent variables, so hereafter we consider main effects only.

2.4.3. Von Post Score as a Continuous Variable

Von Post scores occupy an ordinal scale, with 10 discrete categories across the range H1 (fresh, undecomposed peat) to H10 (entirely amorphous, highly decomposed peat). The distribution of these categories along any continuous dimension of peat decomposition is unclear, meaning that von Post scores are usually incorporated into analyses as a categorical, rather than continuous, variable. However, multiple regression is largely insensitive to uneven spacing of ordinal predictors, and it is rare for ordinal variables with a large number of categories to exhibit substantial nonlinearity (Pasta, 2009). We tested whether a continuous representation of von Post scores could be reliably incorporated into multiple regression models of $\log_{10}(K_v)$ and $\log_{10}(K_h)$. We fitted preliminary models that incorporated all five main effects: depth, dry bulk density, vegetation microhabitat, area, and either horizontal or vertical von Post score, depending on the response variable ($\log_{10}[K_h]$ or $\log_{10}[K_v]$). We compared models in which we coded von Post scores into dummy binary variables (thus treating von Post as a categorical variable) to equivalent models in which we treated von Post score as a single continuous variable. For both $\log_{10}(K_h)$ and $\log_{10}(K_v)$, continuous von Post led to models with significantly greater power (AIC_C: change in AIC_C treated as χ^2 statistic; $p < 0.001$), and greater standard and adjusted r^2 , than the categorical models. Both $\log_{10}(K_h)$ and $\log_{10}(K_v)$ respond linearly to continuous representations of von Post, regardless of any uneven spacing. Residuals in the continuous models were normally distributed and displayed no relationship to von Post score. A continuous representation of von Post score therefore satisfies the assumptions of multiple linear regression, so we proceeded with the continuous models. Doing so greatly reduced the number of independent variables and yielded a simpler, more intuitive model that is easier to interpret, while the reduction in degrees of freedom greatly increased statistical power for any given sample size. We would encourage other researchers to consider treating von Post scores as a continuous variable in similar situations.

2.4.4. Final Model Selection

The final models, the results of which we report below, are linear multiple regression models that describe either $\log_{10}(K_h)$ or $\log_{10}(K_v)$ from depth, dry bulk density, a continuous representation of directional von Post, and categorical representations of area and microhabitat type. Neither model represents any interaction between independent variables or any core-specific random effects. We entered all five independent variables simultaneously because we wished to test the significance of each, with no a priori assumption about their relative importance (Studenmund & Cassidy, 1987).

2.4.5. Analysis of Variance

In addition to the multiple regression models described above, we used the Kruskal-Wallis H test (one-way analysis of variance on ranks) to examine between-sample differences in $\log_{10}(K_h)$ and $\log_{10}(K_v)$ when grouped by microhabitat type and area. Where the multiple regression models (above) illustrate the independent effects of these categorical variables, Kruskal-Wallis shows the overall effect of a single independent variable across all levels of all other independent variables.

3. Results

3.1. Horizontal Hydraulic Conductivity

Measured values of K_h range between 5.00×10^{-8} and 9.78×10^{-3} m/s. The best-preserved samples with horizontal von Post scores of H1 had such open, well-connected pores that constant hydraulic head gradients could not be maintained, even when reduced to 0.3. Horizontal hydraulic conductivity therefore could not be measured for samples with horizontal von Post scores of H1, and only samples with horizontal von Post scores \geq H2 are included in the remainder of our analysis. Nonetheless, high K_h in these poorly decomposed samples agrees with the negative relationship between horizontal von Post scores and $\log_{10}(K_h)$ that was fitted to the rest of the data (see below). No samples exhibited the two highest, most decomposed horizontal von Post categories, H9 or H10.

The multiple linear regression model for our measurements of K_h indicates that $\log_{10}(K_h)$ declines strongly and highly significantly with increasing depth ($p = 0.004$), dry bulk density ($p < 0.001$), and horizontal von Post score ($p = 0.001$, Table 1 and Figure 2). The Kruskal-Wallis H test indicates no significant difference in average $\log_{10}(K_h)$ when all measurements are grouped solely by microhabitat type (albeit marginally so: $H_3 = 7.54$, $p = 0.057$) or area ($H_2 = 4.03$, $p = 0.134$; see also Figure 3). However, when considered as

Table 1
Summary of Multiple Linear Regression Model to Describe $\log_{10}(K_h)$ (m/s)

Descriptor	Level	Coefficient	Standard error	Standardized coefficient	<i>t</i>	Significance
Constant	–	–1.718	0.350	–	–4.912	< 0.001
Depth (m)	–	–3.712	1.227	–0.232	–3.025	0.004
Dry bulk density (kg/m ³)	–	–0.026	0.004	–0.715	–6.731	< 0.001
Horizontal von Post score	–	–0.199	0.056	–0.346	–3.572	0.001
Area	intact center	–	–	–	–	–
	intact margin	0.088	0.231	0.030	0.383	0.703
	modified margin	–	–	–	–	–
Microhabitat	hummock	–	–	–	–	–
	lawn	–0.360	0.197	–0.164	–1.823	0.075
	balk	0.380	0.299	0.109	1.270	0.210
	cutting	0.786	0.339	0.188	2.321	0.025

Note. The descriptors *area* and *microhabitat* are categorical, for which level indicates a dummy variable (coded 1 to represent the named condition, otherwise coded 0); the reference category for *area* is intact center, so that level is redundant; the modified margin level in the *area* predictor is also redundant; the reference category for *microhabitat* is hummock, so that level is redundant. See also Table 2. $r^2 = 0.774$, adjusted $r^2 = 0.740$, and predicted $r^2 = 0.685$.

predictors in the multiple regression model, the modified microhabitat types, balks and cuttings, exert significant independent effects upon $\log_{10}(K_h)$. Specifically, the independent effect of cuttings was to increase $\log_{10}(K_h)$ significantly compared to both hummocks ($p = 0.025$) and lawns ($p = 0.004$) of comparable depths, dry bulk densities, and levels of decomposition; while the independent effect of balks was to raise $\log_{10}(K_h)$ significantly compared to lawns ($p = 0.026$); no other pairs of microhabitat types exhibited significant independent effects on $\log_{10}(K_h)$ (Table 2). The distinction between the intact central and intact marginal areas had no significant independent effect on $\log_{10}(K_h)$ ($p = 0.703$; Table 1). The fitted model explains a large proportion of variation in $\log_{10}(K_h)$: $r^2 = 0.774$, while adjusted $r^2 = 0.740$ (see also Figure 4a). A high predicted r^2 of 0.685 indicates that the model is largely robust to the effects of individual data points, including two samples with particularly high $\log_{10}(K_h)$. The three continuous predictors (depth, dry bulk density, and horizontal von Post) are all significantly positively correlated with one another (Spearman's Rank Correlation Coefficient; $p < 0.001$ in all cases; see Figure 5). This situation, known as multicollinearity, means that estimates of coefficients and significance of individual predictors can be sensitive to random error and must therefore be treated with caution.

The three continuous descriptors, depth, dry bulk density, and horizontal von Post, differ greatly in their units and magnitudes, which hinders direct comparison of their unstandardized regression coefficients. Standardized coefficients arguably provide a more meaningful illustration of the relative effects of each descriptor upon $\log_{10}(K_h)$. Dry bulk density has the largest standardized coefficient (–0.715), followed by horizontal von Post score (–0.346), while depth has the weakest effect (–0.232, Table 1).

3.2. Vertical Hydraulic Conductivity

Measured values of K_v range between 3.00×10^{-8} and 7.28×10^{-3} m/s. In common with our horizontal measurements, samples with vertical von Post scores of H1 were so permeable in the vertical dimension that we could not attain meaningful measurements of K_v . Unlike horizontal measurements, some samples exhibited vertical von Post scores of H9, although there were still none in the highest category, H10.

The multiple linear regression model for $\log_{10}(K_v)$ (Tables 3 and 4) is broadly similar to that for $\log_{10}(K_h)$, albeit with some important differences. As with the horizontal model, \log_{10} -transformed K_v declines strongly and highly significantly with increasing vertical von Post score ($p < 0.001$) and dry bulk density ($p < 0.001$). Unlike the horizontal model though, depth is a nonsignificant descriptor of $\log_{10}(K_v)$, albeit marginally so ($p = 0.055$, see also Figure 2b). As with the horizontal measurements, Kruskal-Wallis H test indicates no significant difference in average $\log_{10}(K_v)$ when all measurements are grouped solely by microhabitat type ($H_3 = 4.89$, $p = 0.180$) or area ($H_2 = 3.84$, $p = 0.146$; see also Figure 3), but in the multiple regression model most microhabitat types exert significant independent controls over $\log_{10}(K_v)$. The distinction between cuttings and balks has no significant independent effect on $\log_{10}(K_v)$, but the

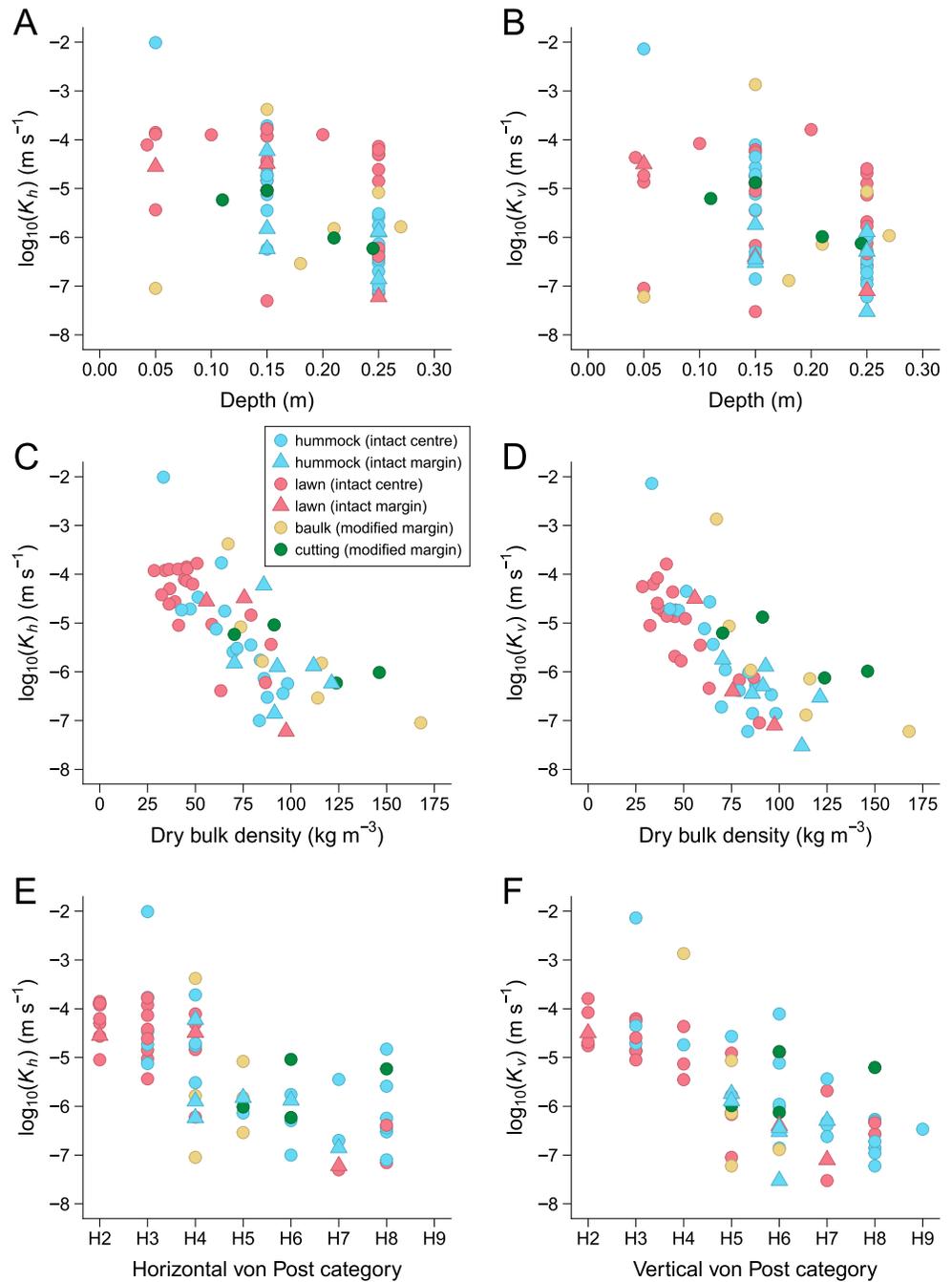


Figure 2. Response of $\log_{10}(K_h)$ (left column) and $\log_{10}(K_v)$ (right column) to depth (top row), dry bulk density (middle row), and von Post score (bottom row).

independent effect of both of these modified habitat types is to increase $\log_{10}(K_v)$ significantly in the model compared to intact hummocks, while the independent effect of lawns is to reduce $\log_{10}(K_v)$ significantly compared to samples from all other habitat types (Table 4; with comparable values of depth, dry bulk density, and vertical von Post score). As with $\log_{10}(K_h)$, the distinction between the intact center and intact margin has no significant independent effect upon $\log_{10}(K_v)$ ($p = 0.946$, Table 3). The vertical model possesses greater explanatory power than the horizontal model: $r^2 = 0.815$ and adjusted $r^2 = 0.787$ (see also Figure 4b). Like the horizontal model, the vertical model is robust to

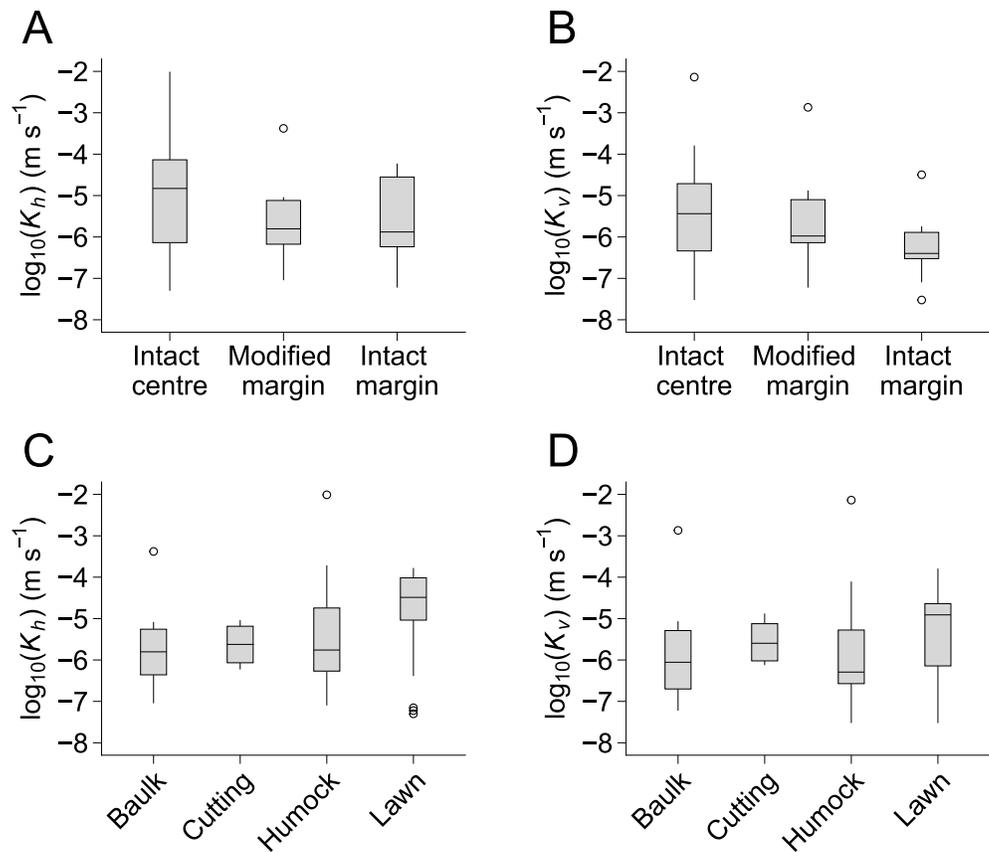


Figure 3. \log_{10} -transformed horizontal (a, c) and vertical (b, d) hydraulic conductivity grouped by area (a, b) and microhabitat type (c, d). Centerlines indicate sample medians; top and bottom of boxes indicate upper and lower quartiles, respectively; whiskers extend to values no further than 1.5 times the interquartile range beyond the upper and lower quartiles; remaining observations indicated by open circles. No groupings exhibited significant differences (Kruskal-Wallis H test, $p > 0.05$ in all cases).

individual data points (predicted $r^2 = 0.731$). As in the horizontal model, the three continuous predictors are all significantly positively correlated with one another (Spearman's Rank Correlation Coefficient; $p < 0.01$ in all cases; see Figure 5), again indicating that individual coefficients must be treated cautiously.

Standardized regression coefficients for the vertical model follow a similar pattern to those for the horizontal model. The standardized coefficients for dry bulk density (-0.793) and vertical von Post score (-0.393) in the vertical model are slightly larger than their equivalents in the horizontal model, while depth is weaker (-0.138 , Table 3).

Table 2
Regression Coefficients (p Values in Brackets) for Independent Effects of Categories in the Microhabitat Descriptor From the Multiple Linear Regression Model for $\log_{10}(K_h)$

Effect category	Reference category			
	Hummock	Lawn	Balk	Cutting
hummock	–	–	–	–
lawn	-0.360 ($p = 0.075$)	–	–	–
balk	0.380 ($p = 0.210$)	0.740 ($p = 0.026$)	–	–
cutting	0.786 ($p = 0.025$)	1.146 ($p = 0.004$)	0.406 ($p = 0.281$)	–

Note. Positive coefficients indicate that effect category causes an increase in $\log_{10}(K_h)$ compared to the reference category. Significant effects are shown in bold ($p < 0.05$ threshold). See Table 1 for details of other descriptors.

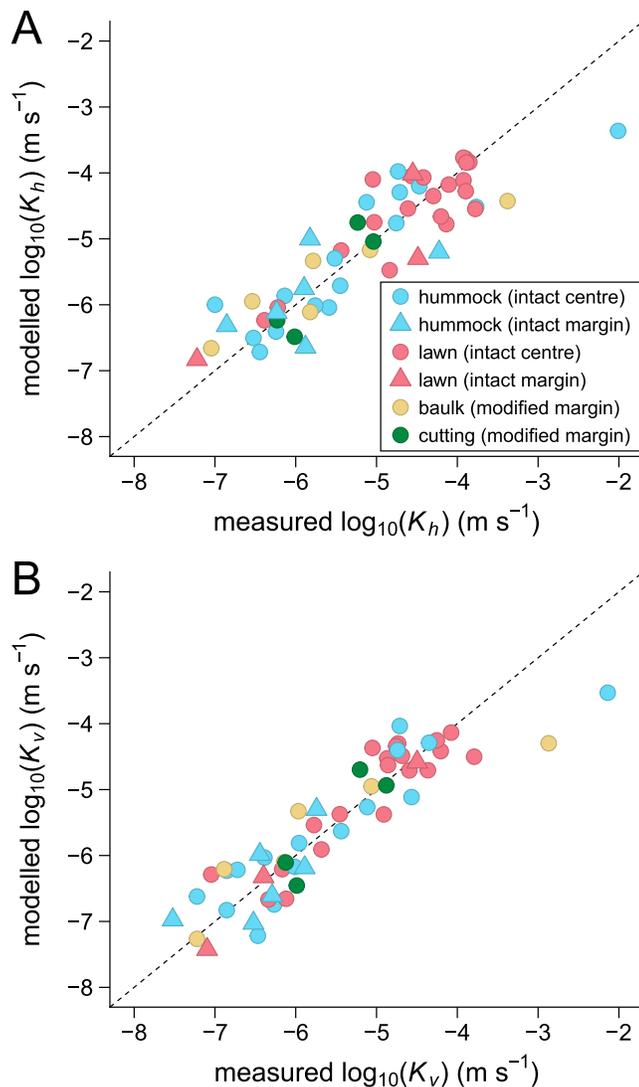


Figure 4. Performance of multiple linear regression models in predicting (a) $\log_{10}(K_h)$ and (b) $\log_{10}(K_v)$ compared to measured values. Broken lines indicate 1:1 relationships between measured and modeled values.

4. Discussion

4.1. Horizontal Permeability

The low K measured by Baird et al. (2008) in the deep peat of our study site's intact margin is not apparent in shallow layers, with differences between intact central and intact marginal areas highly nonsignificant. Morris et al. (2015) were similarly unable to find any evidence for a low- K margin in shallow layers of an intact raised bog in Sweden, so at this stage we may conjecture that, if such features are common, then they may be restricted to deeper layers. Near-surface layers are likely to dominate lateral fluxes due to their higher permeability, meaning that the low- K in deep marginal peat at Cors Fochno may be less important than previously thought. Given that the low- K of deep, marginal peat does not appear to originate in shallow layers, it may represent the legacy of some past episode of peat development at the site.

Dry bulk density is by far the strongest control on $\log_{10}(K_h)$, as evidenced by its large standardized coefficient, indicating an important role for compression in determining pore geometry. The strong, significant effect of horizontal von Post score is independent of depth and dry bulk density, meaning that loss of pore connectivity through the breakdown of pore structures can be important regardless of the degree of compression.

The significant control of depth upon $\log_{10}(K_h)$ mirrors that found by Morris et al. (2015) in similarly shallow layers of their Swedish study site, although our fitted slope coefficient is half that found by Morris et al. (2015), and depth is the weakest of the three continuous descriptors (Table 1). Such site-specific differences illustrate that any attempts to generalize fitted relationships beyond the study sites for which they were developed must be made with caution.

Although significant controls from von Post, depth and dry bulk density have all been observed before, they are rarely combined into multiple regression (although see Päivänen, 1973). The high explanatory power (adjusted $r^2 = 0.740$) and apparent robustness (predicted $r^2 = 0.685$) of these three simple variables when considered simultaneously provides encouragement that generalizable models of peat K_h may indeed be attainable (see below). Nevertheless, in light of our remarks above about site-specific variations, large, multisite data sets would likely be required to produce such generalizable models.

Although Kruskal-Wallis H test indicates no significant difference between microhabitats, the significant independent effect of cuttings in the regression model nonetheless indicates the important, albeit subtle, role of microhabitat type in determining horizontal permeability. Given that this effect is independent of the other predictors—particularly depth, dry bulk density, and von Post score, all of which could conceivably contribute to determining total pore volume and pore size distribution—we are left to surmise that pores in cutting infill peat are more interconnected than that formed by other microhabitats. However, small sample sizes in the modified margin and multicollinearity of predictors both mean that care should be exercised at this stage of interpretation.

4.2. Vertical Permeability

Differences in the responses of horizontal and vertical permeability to their environmental controls highlight the distinct ecohydrological roles played by these two variables and the need to consider them separately in future modeling and measurement efforts. The nonsignificance of depth as a descriptor of $\log_{10}(K_v)$ is marginal ($p = 0.055$), so we are cautious not to overinterpret it. Nonetheless, the weaker relationship between depth and vertical permeability could be interpreted in a variety of ways. First, vertical compression may lead primarily to a shortening of vertical conduits, rather than constriction as appears to be

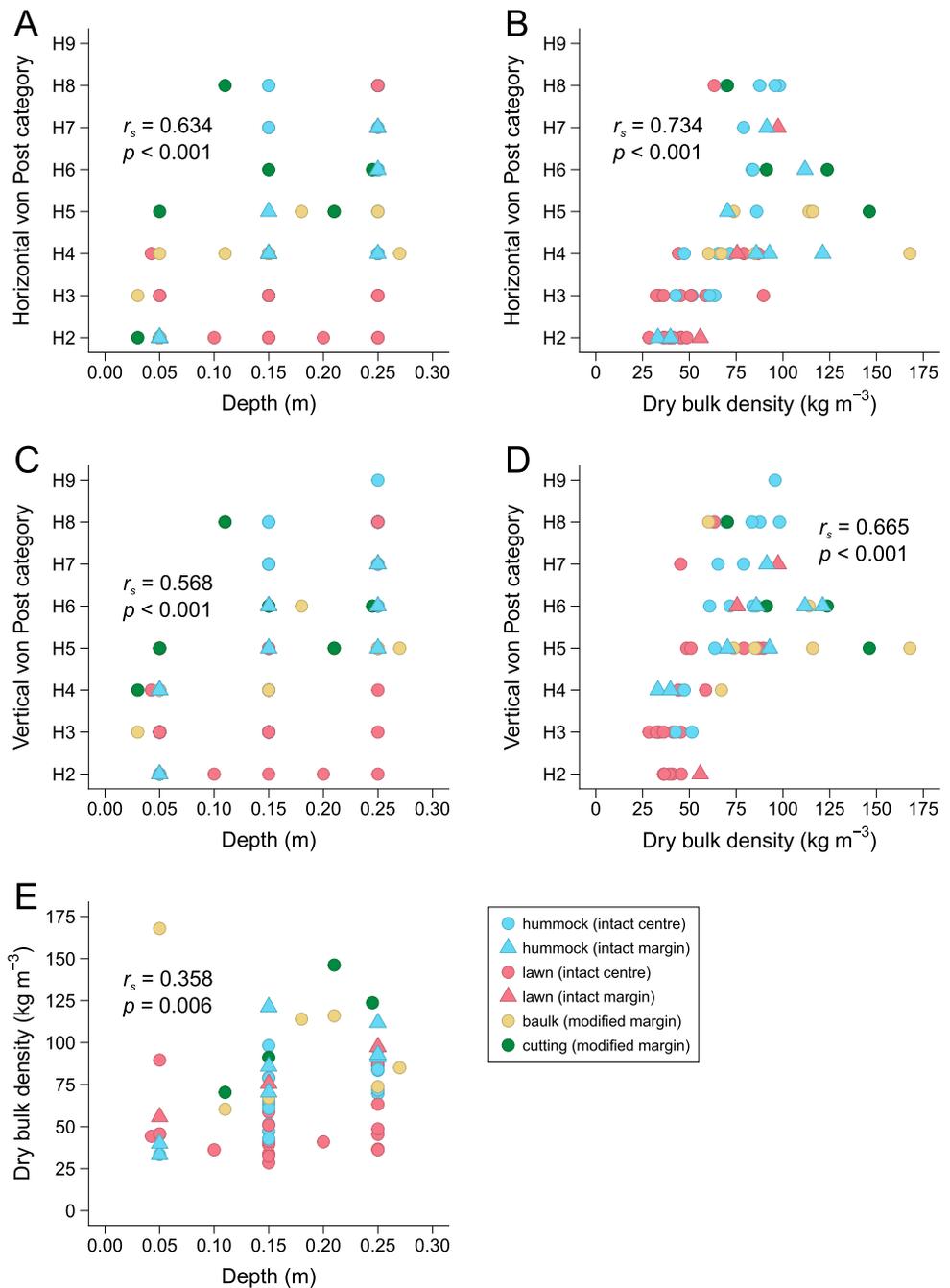


Figure 5. Scatterplots showing multicollinearity between pairs of predictor variables; r_s is Spearman's Rank Correlation Coefficient. Some data points, particularly in Figures 5a and 5c, are obscured by overwriting.

the case in K_h , which relies on horizontally aligned conduits. Alternatively, vertical permeability may be dominated by macropores associated with ericaceous shrub roots, particularly those of *Calluna vulgaris*, *Erica tetralix*, and *Myrica gale*, which are abundant at the study site. Vertical permeability of the peat matrix may indeed decline with increasing depth, but vertical macropores may preserve a high bulk K_v . The strong independent influence of microhabitat on $\log_{10}(K_v)$ contrasts with the weaker, less significant effects of microhabitat in the horizontal model, and is consistent with the hypothesis of ericaceous macropores dominating vertical permeability in shallow layers.

Table 3
Summary of Multiple Linear Regression Model to Describe $\log_{10}(K_v)$ (m/s)

Descriptor	Level	Coefficient	Standard error	Standardized coefficient	<i>t</i>	Significance
Constant	–	–1.740	0.329	–	–5.285	< 0.001
Depth (m)	–	–2.267	1.153	–0.138	–1.966	0.055
Dry bulk density (kg/m ³)	–	–0.029	0.004	–0.793	–7.806	< 0.001
Vertical von Post score	–	–0.233	0.054	–0.393	–4.339	< 0.001
Area	intact center	–	–	–	–	–
	intact margin	0.015	0.216	0.005	0.068	0.946
	modified margin	–	–	–	–	–
Microhabitat	hummock	–	–	–	–	–
	lawn	–0.638	0.182	–0.283	–3.516	0.001
	balk	0.687	0.290	0.192	2.373	0.022
	cutting	1.221	0.317	0.285	3.858	< 0.001

Note. The descriptors area and microhabitat are categorical, for which level indicates a dummy variable (coded 1 to represent the named condition, otherwise coded 0); the reference category for area is intact center, so that level is redundant; the modified margin level in the area predictor is also redundant; the reference category for microhabitat is hummock, so that level is redundant. See also Table 4. $r^2 = 0.815$, adjusted $r^2 = 0.787$, and predicted $r^2 = 0.731$.

Differences in K_v between the intact and modified parts of the bog are more pronounced than for K_h . Notwithstanding limitations arising from small sample sizes in the modified margin, and multicollinearity between predictors, the vertical regression model suggests that both balks and cuttings cause independent increases in K_v , compared to intact hummocks or lawns. Again, given that these effects are independent of depth, dry bulk density and vertical von Post score, they would appear to indicate greater vertical connectivity of pores in these modified areas than elsewhere on the bog. Vertical permeability in balks may be dominated by root casts from ericaceous shrubs, which were once common in this drained area of the bog before restoration efforts caused rewetting. The independent effect of intact hummocks in raising K_v compared to intact lawns is consistent with similar findings between hummocks and hollows in the Swedish site studied by Morris et al. (2015).

4.3. Opportunities and Challenges for Further Research

The high explanatory power exhibited by simple descriptors, both in the present study and previously (e.g., Boelter, 1969; Branham & Strack, 2014; Ivanov, 1981; Moore et al., 2015; Päivänen, 1973), suggests the possibility of developing generally applicable models to estimate K_h and K_v from easily measured proxies alone, which ultimately may obviate the need for expensive, laborious direct measurements. Such models might be attainable by utilizing the wealth of published data on K and other hydraulic properties from peatlands. Pedotransfer functions are used to predict hydraulic properties in mineral soils based on simple metrics such as grain size fractions, dry bulk density, and organic matter content (e.g., Clapp & Hornberger, 1978; Cosby et al., 1984; Wösten et al., 1999, 2001). However, these schemes are inapplicable to peat because they feature only a single variable to describe organic matter content and thus cannot incorporate important predictors such as the degree of decomposition; additionally, metrics of grain size distribution are rarely definable for

Table 4
Regression Coefficients (*p* Values in Brackets) for Independent Effects of Categories in the Microhabitat Descriptor From the Multiple Linear Regression Model for $\log_{10}(K_v)$

Effect category	Reference category			
	Hummock	Lawn	Balk	Cutting
hummock	–	–	–	–
lawn	–0.638 (<i>p</i> = 0.001)	–	–	–
balk	0.687 (<i>p</i> = 0.022)	1.325 (<i>p</i> < 0.001)	–	–
cutting	1.221 (<i>p</i> < 0.001)	1.860 (<i>p</i> < 0.001)	0.534 (<i>p</i> = 0.122)	–

Note. Positive coefficients indicate that the effect category causes an increase in $\log_{10}(K_v)$ compared to the reference category. Significant effects are shown in bold ($p < 0.05$ threshold). See Table 3 for details of other descriptors.

peat. In common with their existing mineral soil equivalents, pedotransfer functions for peats might also be used to predict some unsaturated hydraulic parameters, such as those from van Genuchten's (1980) widely applied model. Our measurements, and so the applicability of our fitted regression models, are restricted to near-surface peat layers. Meta-analysis of published peat K data might seek to extend our approach into deeper layers.

Several obstacles lie in the path of such an endeavor. First, published measurements of K have been collected using a wide variety of measurement techniques (e.g., piezometer slug tests and laboratory tests such as ours) and quality control procedures, which have the potential to introduce large artifacts to estimates (cf. Baird et al., 2004; Beckwith et al., 2003). Second, site-specific factors such as the distinction between bogs and fens, levels of modification and degradation, and degree of afforestation have the potential to introduce large, significant effects on peat hydraulic properties. Although some of these effects may be expressed through other predictor variables such as dry bulk density and von Post score, others may need to be represented explicitly as factors in any predictive model. Site-specific differences may reduce the predictive power of any general model compared to the high explanatory power of our site-specific models. Third, K exhibits highly non-linear, heteroscedastic relationships to its main predictors, which precludes the use of linear regression on untransformed data. Linear models fitted to transformed data (e.g., Päivänen, 1973; Morris et al., 2015; the current study) contain systematic bias when back-transformed, and require empirical correction before they can be used to predict on an untransformed scale (Ferguson, 1986). Nonlinear models fitted to untransformed data (e.g., Morris et al., 2015) avoid such bias but still suffer from heteroscedasticity, particularly for high values of K that exhibit the greatest variability and are the most important to determining flow rates. Finally, any such meta-analysis must incorporate a sound strategy to deal with multicollinearity of predictors, such as seen in our data.

5. Conclusions

We found that combinations of simple, easily measured descriptors, particularly depth, dry bulk density, and von Post score, explain much of the variation in \log_{10} -transformed values of both horizontal and vertical peat hydraulic conductivity. Controls on vertical and horizontal hydraulic conductivity are broadly similar, although vertical hydraulic conductivity responded much less strongly to depth than did horizontal hydraulic conductivity. Macropores associated with ericaceous roots may serve to maintain high vertical permeability at depth, despite low horizontal permeability. The low-permeability margin previously observed in deeper peat layers at this site and elsewhere is not evident in shallow peat. Simple, generalizable models of peat hydraulic conductivity, and possibly other parameters, may be attainable through meta-analysis of published data, so long as sufficient data can be gathered to characterize between-site variability.

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