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Water's path from moss to soil Vol. 2: how soil-moss combinations affect soil water fluxes and soil loss in a temperate forest

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Abstract

Mosses are key components of many ecosystems and particularly related to water cycling. In principle, the importance of mosses for water-related processes is known; however, their influence is rarely quantified in scientific studies. To fill this research gap, this study concentrates on the influence of mosses of different species on surface runoff, the amount of percolated water, soil loss, and the temporal dynamics of soil water content. For this purpose, an experimental approach consisting of an ex situ rainfall simulation (45 mm h^{-1} for 30 min) with infiltration boxes equipped with biocrust wetness probes was applied. On average, mosses significantly reduced surface runoff by 91% and soil loss by almost 100%, while the amount of percolated water was increased by 85% compared with bare soils. These processes were superimposed by desiccation cracks, and partly water repellency, with the result that the respective influences could not be quantified individually. However, by simultaneously measuring the water content in the substrates during rainfall simulations, we were able to achieve a better understanding of the water flows in the substrates. For instance, water content at 3 cm substrate depth was higher under mosses than in bare soils, implying that mosses facilitated infiltration. In this study, we were able to demonstrate that mosses play an important role in soil hydrology and in protecting the soil from erosion, and it is imperative that further experiments will be conducted to elucidate the apparently underestimated effects of mosses and their specific traits on soil water fluxes and sediment transport.

Keywords Bryophytes · Rainfall simulation · Soil erosion · Soil water content · Surface runoff

Introduction

Mosses have a strong impact on the soil water fluxes in many ecosystems (Turetsky et al. 2012; Liu et al. 2022). They are capable of absorbing large amounts of water, with water storage capacities ranging from 100 to 5000% of their dry weight, depending on the moss species (Proctor et al. 1998; Wang and Bader 2018; Thielen et al. 2021), and they can form dense moss covers depending on the ecosystem (Lindo and Gonzalez 2010). Consequently, mosses lead to relevant changes in important water-related parameters such as surface runoff, infiltration and soil water content compared to bare soils, which in turn also have an influence on soil erosion (Bu et al. 2015; Seitz et al. 2017; Sun et al. 2021).

However, most studies on the influence of mosses on parameter of the water cycle and soil erosion deal exclusively with biological soil crusts (biocrusts) dominated by mosses (Eldridge et al. 2020). Biocrusts are formed by a close association of soil particles and organisms such as bryophytes, lichens, cyanobacteria, algae, bacteria or fungi that colonize the upper millimeters of the soil (Belnap et al. 2001; Weber et al. 2016b), and are characterized by regular desiccation, forming a cohesive and hardened soil layer (Weber et al. 2022). Especially in temperate mesic ecosystems, which are defined by adequate water availability, the environmental conditions cause biocrusts to occur ephemerally, i.e. they are either overgrown by vascular plants or

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develop into a mature moss cushion (Gall et al. 2022b). The mature moss cushion stage is reached when most of the moss biomass has grown above the soil's surface, so that there is no longer an encrustation (Weber et al. 2022). Thus, due to the different surface structure, different hydrological and erosion mitigating properties between moss-dominated biocrusts and moss cushions can be assumed. For example, in the case of biocrusts, there is no clear direction of influence on surface runoff; various studies resulted in either a decrease or an increase (Kidron et al. 2022b). In comparison, studies on mosses solely indicate a reducing influence on surface runoff (Parsakhoo et al. 2012; Tu et al. 2022; Juan et al. 2023).

Irrespective of the moss cover, the formation of surface runoff, infiltration of water into the soil, and soil loss depend on numerous edaphic factors such as soil texture, soil organic carbon, aggregate stability, microtopography, and soil moisture, as well as environmental factors such as rainfall intensity, raindrop kinetic energy, rainfall temperature, slope, vegetation coverage, and human activities (Le Bissonnais and Singer 1993; Le Bissonnais et al. 1995; Morgan 2005). These factors also influence the type of surface runoff that occurs: Either rainfall intensity exceeds the infiltration capacity of the soil, which is known as Hortonian overland flow, or the soil is water-saturated and cannot absorb any more water, which is known as saturation overland flow (Horton 1933; Kidron 2021). Hortonian overland flow can be caused by the presence of a water-impermeable layer in or on the soil, e.g. due to hydrophobicity, pore clogging or differences in texture (Le Bissonnais 1996; Doerr et al. 2000; Kidron et al. 2022a). These complex relationships must be taken into account when measuring soil water fluxes.

Overall, there have been very few studies that measured surface runoff, infiltration, and soil erosion under mosses. For instance, Parsakhoo et al. (2012) investigated the effects of the moss *Philonotis marchica* (Hedw.) Brid. on surface runoff, infiltration and soil erosion from forest road cutslopes using rainfall simulations in combination with small-scale runoff plots. They found that *Philonotis marchica* significantly reduced surface runoff by 67%, increased infiltration by 39% and also reduced soil erosion by 61% compared to bare soil. Likewise, Tu et al. (2022) recently demonstrated in a soil trough approach under simulated rainfall that mosses significantly reduce surface runoff, while infiltration was increased or decreased depending on the moss species compared with bare soils. By considering different moss species and demonstrating species-specific effects on infiltration, the importance of moss structural traits is underlined (Tu et al. 2022). Recently, Juan et al. (2023) showed that soils covered with the moss *Racomitrium japonicum* significantly reduced surface runoff, mean flow velocity, and soil loss compared to bare soils, although the surface roughness of these two treatments did not differ significantly. Although this major role of functional traits in the contribution of mosses to ecosystem services is now recognized, it has still not been adequately described and only few studies have compared species, so important species-specific effects are poorly known (Eldridge et al. 2023).

Mosses not only influence the movement of water onto and into the soil, but also soil water storage processes. Earlier research by Price et al. (1997) showed that moss layers from boreal forests in Canada can retain 16.8 mm of water, equivalent to about 21% of precipitation, and likely also has a strong influence on net soil water inputs. In this context, Siwach et al. (2021) also observed higher moisture contents under moss compared with bare soil in a temperate forest of the Indian Garhwal Himalaya during the monsoon, which was reversed in winter with far less precipitation. Recently, Hu et al. (2023) showed that more water can be stored in soils under moss than in soils without moss cover, with increases in water storage capacity of up to 57%, an even higher increase was measured in the plant-available water content (110% increase compared with no moss cover). These positive effects on soil water retention were primarily attributed to better pore distribution and the accumulation of organic matter under mosses (Hu et al. 2023).

Even though it has been known for a long time that mosses have a considerable influence on the soil water fluxes (Oltmanns 1884; Mägdefrau and Wutz 1951), there are still few studies that quantify this influence and many vegetation zones have been disregarded so far. To help fill this research gap, this study focuses on the influence of moss covers of different species on surface runoff, the amount of percolated water, soil loss, and the temporal dynamics of soil water content. The following hypotheses were tested for a temperate forest ecosystem:

1. Mosses reduce surface runoff, soil loss and increase percolation, with the effect depending on the moss species.
2. Mosses increase soil water content during rainfall simulations compared to bare soil.

The experimental design consisted of an ex situ rainfall simulation with infiltration boxes which were equipped with biocrust wetness probes (BWP) at the surface and in 3 cm soil substrate depth to continuously record the soil water content for a duration of 30 min. In addition, we considered antecedent soil moisture in the experiments by performing rainfall simulations both with and without moss covers in both dry and wet conditions.

Materials and methods

Properties of studied moss species and soil substrates

Soil substrates were collected from the wheel tracks of four skid trails as described in Gall et al. (2022a) in the Schönbuch Nature Park in southwest Germany and distinguished according to their geological formation: Angulatensandstein (AS), Psilonotenton (PT), Löwenstein (LS) and Trossingen (TS) (Einsele and Agster 1986). Furthermore, we included a sandy substrate from the Palatinate Forest, which differs considerably from the other substrates in terms of its properties (Table 1). The designation of this substrate was also based on the geological formation: Bernburg (BB). Samples were taken from the topsoil to a depth of 10 cm and mixed topsoil samples were also collected for laboratory analysis.

The six moss species studied are native to southwest Germany (Nebel et al. 2001) and vary in terms of origin, classification and growth form. While *Amblystegium serpens* (Hedw.) Schimp., *Brachythecium rutabulum* (Hedw.) Schimp., *Eurhynchium striatum* (Hedw.) Schimp. and *Oxyrrhynchium hians* (Hedw.) Loeske are pleurocarpous (side-fruited), *Plagiomnium undulatum* (Hedw.) T.J.Kop. and *Polytrichum formosum* (Hedw.) G.L.Sm. exhibit an acrocarpous (top-fruited) growth form. Regarding the origin of the moss species, we used both field-collected and laboratory-cultivated mosses. Cultures of *A. serpens* and *O. hians* were grown in hydraulic fluid in an in vitro environment by Hummel InVitro GmbH Stuttgart, Germany. Concerning the nomenclature of the moss species, we have used Hodgetts et al. (2020). The characteristics of the studied moss species are listed in Table 2 and their allocation to the soil substrates is based on their preferred growing conditions and the availability of the laboratory-cultivated moss species. The studied soil-moss combinations are displayed in Fig. 1.

Experimental setup

Soil substrates were air dried, sieved by 6.3 mm and filled into infiltration boxes (40×30×15 cm) up to a height of 6.5 cm from the top edge by installing a substructure of perforated metal. The infiltration boxes are made from stainless steel and have a triangular surface runoff gutter at the top and an outlet at the bottom to collect percolated water (Fig. 2). During rainfall simulations with the Tübingen rainfall simulator (Iserloh et al. 2013; Seitz 2015), two infiltration boxes were placed on a table with 20° slope. Drop falling height was adjusted to 3.5 m and mean rainfall intensity was set to 45 mm h^{-1}, which was simulated for a duration of 30 min. This setting refers to a rainfall event with a recurrence interval of 5 years (DWD Climate Data Center 2021). Surface runoff, sediment and percolated water were collected in sample bottles (1 L). To measure water content during rainfall simulations, two biocrust wetness probes (BWP, UP GmbH, Cottbus, Germany) were installed per infiltration box in 3 cm substrate depth and in the first 5 mm of substrate surface. BWPs were connected to a GP2 Data Logger (Delta-T Devices, Cambridge, UK), which logged the electrical conductivity every 5 min at substrate surface and every 2 min at 3 cm substrate depth. These incongruent logging intervals were due to a technical error and were later interpolated to a one-minute interval for each measurement.

First, rainfall simulations were performed for bare soil substrates in air-dried condition, with 4 replicates for each substrate. The same infiltration boxes were watered once

Table 1 Soil substrate properties

	PT	AS	LS	TS	BB
Series	Lower Jurassic	Lower Jurassic	Upper Triassic	Upper Triassic	Lower Triassic
Formation	Psilonotenton-Formation (PT)	Angulatensandstein-Formation (AS)	Löwenstein-Formation (LS)	Trossingen-Formation (TS)	Bernburg-Formation (BB)
Parent material	shale clay	sandstone	sandstone	claystone	sandstone
Soil texture	silty clay loam sand: 6.88% silt: 56.28% clay: 36.93%	silt loam sand: 7.00% silt:67.58% clay: 25.68%	clay loam sand: 25.02% silt: 42.43% clay: 32.60%	silty clay loam sand: 10.78% silt: 50.83% clay: 38.10%	loamy sand sand: 82.63% silt: 7.20% clay: 9.80%
Soil organic carbon	5.25	4.34	4.39	8.02	4.93
Total nitrogen	0.30	0.25	0.19	0.40	0.20
pH	7.0	5.8	7.0	5.6	3.4
Water repellency class (Dekker and Jungerius 1990)	wettable	wettable	wettable	wettable	extremely water repellent
Sample site location	Tübingen 48.557425° N 9.114462° E	Tübingen 48.553054° N 9.119053° E	Tübingen 48.557527° N 9.088098° E	Tübingen 48.556036° N 9.089313° E	Kaiserslautern 49.424156° N 7.758673° E

Table 2 Characteristics of studied moss species from Thielen et al. (2021)

	Amblystegium serpens	Brachythecium rutabulum	Eurhynchium striatum	Oxyrrhynchium hians	Oxyrrhynchium hians	Plagiomnium undulatum	Polytrichum formosum
Family	Amblystegiaceae	Brachytheciaceae	Brachytheciaceae	Brachytheciaceae	Brachytheciaceae	Mniaceae	Polytrichaceae
Origin	Laboratory	Field	Field	Field	Laboratory	Field	Field
Site characteristics	-	ruderalized fertile meadow	coniferous forest	dry hedge understore	-	flood plain	coniferous forest
Growth form	pleurocarpous	pleurocarpous	pleurocarpous	pleurocarpous	pleurocarpous	acrocarpous	acrocarpous
Dry moss biomass per area [mg cm^{-2}]	34.71 ± 3.67	27.12 ± 2.71	33.37 ± 5.77	24.30 ± 3.48	28.13 ± 2.05	24.60 ± 2.07	17.23 ± 0.69
Maximum water storage capacity [mm]	4.95 ± 0.74	3.15 ± 0.31	3.34 ± 0.21	2.09 ± 0.12	2.70 ± 0.32	1.84 ± 0.29	0.76 ± 0.03

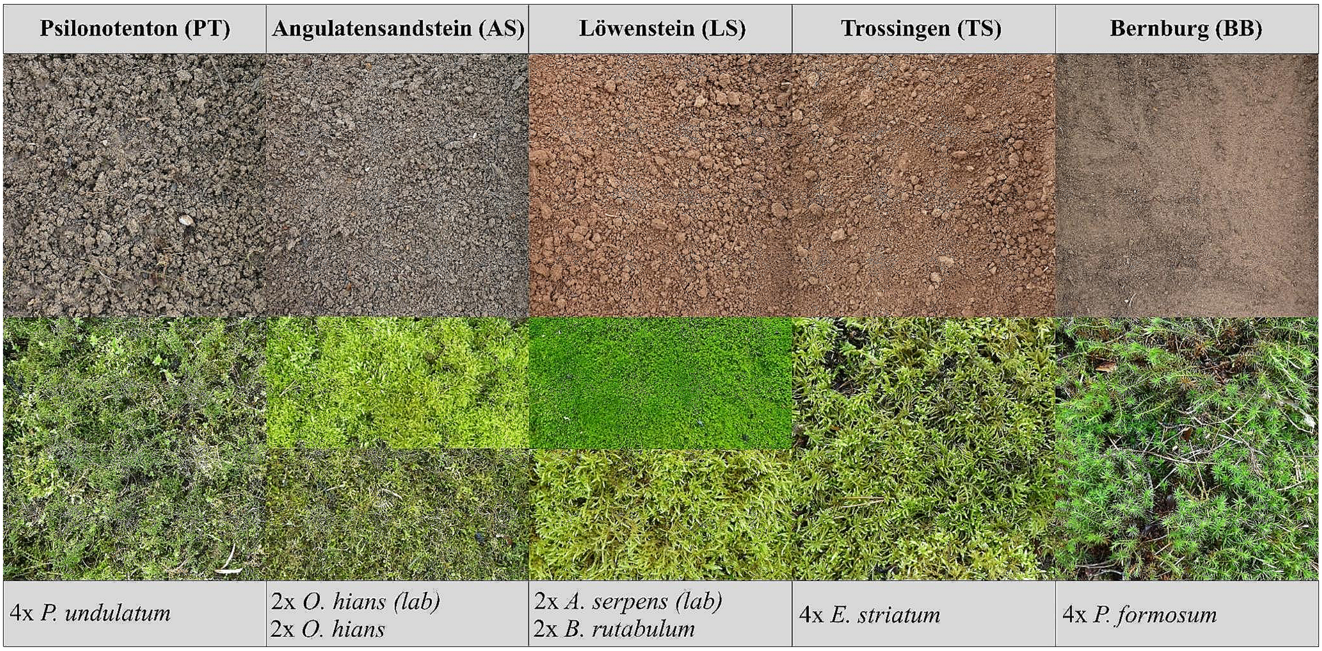

Fig. 1 Illustration of the studied soil-moss combinations

again in wet soil condition 24 h later, which yielded in a total of 40 measurements, 20 each bare & dry and 20 each bare & wet condition. Second, moss samples were placed onto the substrate-filled infiltration boxes and stored in a shady place outdoors to adapt and grow on the substrate, until the next rainfall simulations were conducted five months later. Moss-covered infiltration boxes were also measured in dry and wet condition, again leading to a total of 40 measurements with 20 each moss & dry and 20 each moss & wet condition. Altogether, 80 rainfall simulations were carried out.

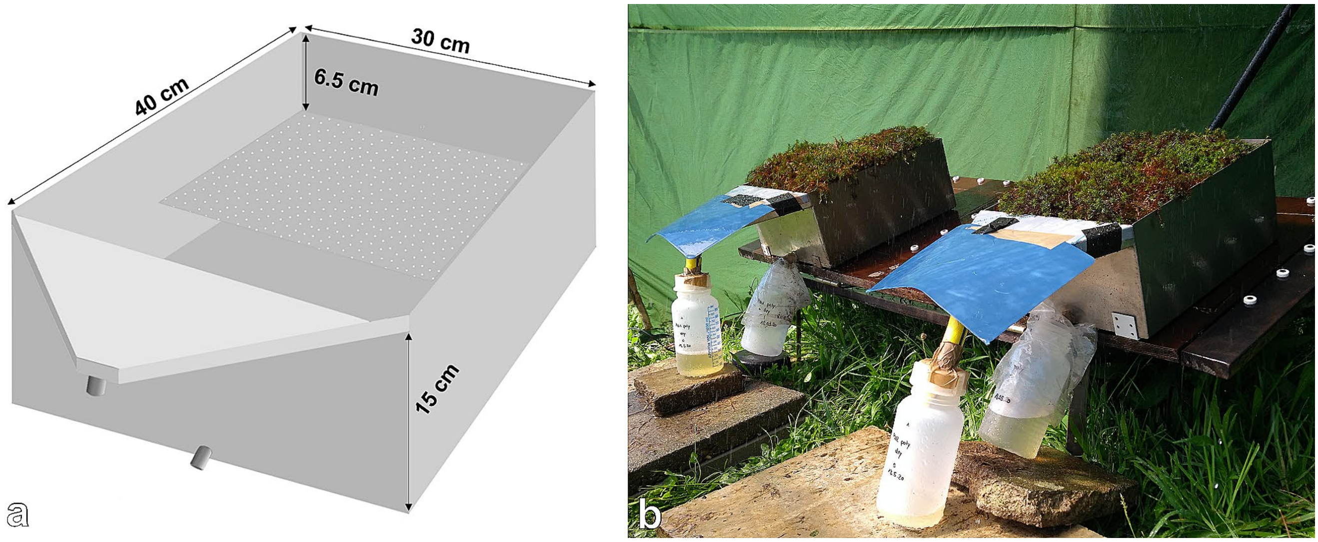

Fig. 2 Illustration of an infiltration box. (**a**) Technical drawing of an infiltration box (Illustration: Julia Dartsch). (**b**) Infiltration boxes during rainfall simulations

Laboratory analysis and BWP calibration

After rainfall simulations, the amount of surface runoff and percolated water was determined from the measuring scale of the sample bottles. Subsequently, surface runoff samples were evaporated at 40 °C in a compartment drier to weigh the eroded sediment. The following basic soil properties were determined for the mixed topsoil samples before the rainfall simulations: Grain size distribution with an x-ray particle size analyzer (Sedigraph III, Micromeritics, Norcross, GA, USA), soil pH in 0.01 M $CaCl_2$ solution with a pH-meter and Sentix 81 electrodes (WTW, Weilheim, Germany), soil organic carbon (SOC) and total nitrogen with an elemental analyzer (element analyzer Vario EL II, Elementar Analysensysteme GmbH, Hanau, Germany). Soil bulk density was determinded after rainfall simulation with 100 cm^3 core samples using the mass-per-volume method (Blake and Hartge 1986). The water drop penetration time (WDPT) according to Dekker et al. (2009) was determined when the hydrophobicity of the sandy substrate was observed during rainfall simulation.

Since electrical conductivity recorded by the BWP is temperature-dependent, a temperature correction was carried out to adjust all measurements to a temperature of 25 °C as suggested by Weber et al. (2016a). A BWP calibration was conducted as described in detail by Thielen et al. (2021) for the soil substrates studied. However, the soil substrates in the current study showed a higher variability in their water content, which would have made extensive extrapolation of the data necessary. Therefore, a simplified calibration procedure according to the example of Weber et al. (2016a) was used in this case. For this purpose, the soil samples were weighed in 100 cm^3 core cutters once in water saturated and once in dry condition (40 °C) to create linear calibration functions between minimum and maximum water content for each soil substrate.

Data analysis

All analyses were performed with R software version 4.0.4 (R Core Team 2021) on the level of individual samples. Normality was tested with the Shapiro-Wilk test prior to all statistical tests, while homoscedasticity was verified with Levene's test. Due to our sampling design with repeated measurements and the lack of normal distribution of most variables, we used Generalized Linear Models (GLM) without interactions to screen for significant differences between the treatments as independent variable (bare & dry, bare & wet, moss & dry, moss & wet) and surface runoff, amount of percolated water and soil loss as dependent variable (using the R package "stats"). Significant differences were postulated in all cases at $p < 0.05$. For all mean values described, the standard error was also given (mean ± standard error). Either Pearson or Spearman pairwise correlation analyses were performed to describe the relationships between different parameters.

Results and discussion

Surface runoff, percolation and soil loss in different soil-moss combinations

In general, average surface runoff was highest in bare & wet treatments (35.20 ± 2.34 L m^{-2}) and significantly lower in bare & dry treatments (20.71 ± 2.46 L m^{-2}, $p < 0.001$). All moss treatments had significantly lower surface runoff than bare treatments ($p < 0.001$), with no difference between moss & dry and moss & wet treatments. Conversely, the average amount of percolated water was highest in moss treatments, with significantly higher amounts for moss & wet treatments (18.17 ± 1.52 L m^{-2}) compared with moss & dry treatments (13.58 ± 1.52 L m^{-2}, $p < 0.05$). In comparison, significantly less water was percolated in bare treatments ($p < 0.001$), however, there was no difference between bare & dry and bare & wet treatments regarding the amount of percolated water. For all substrates, surface runoff was higher than percolated water for bare treatments, and the reverse was true for moss treatments (Fig. 3). The only exceptions were bare & dry treatment of PT and moss & wet treatment of BB.

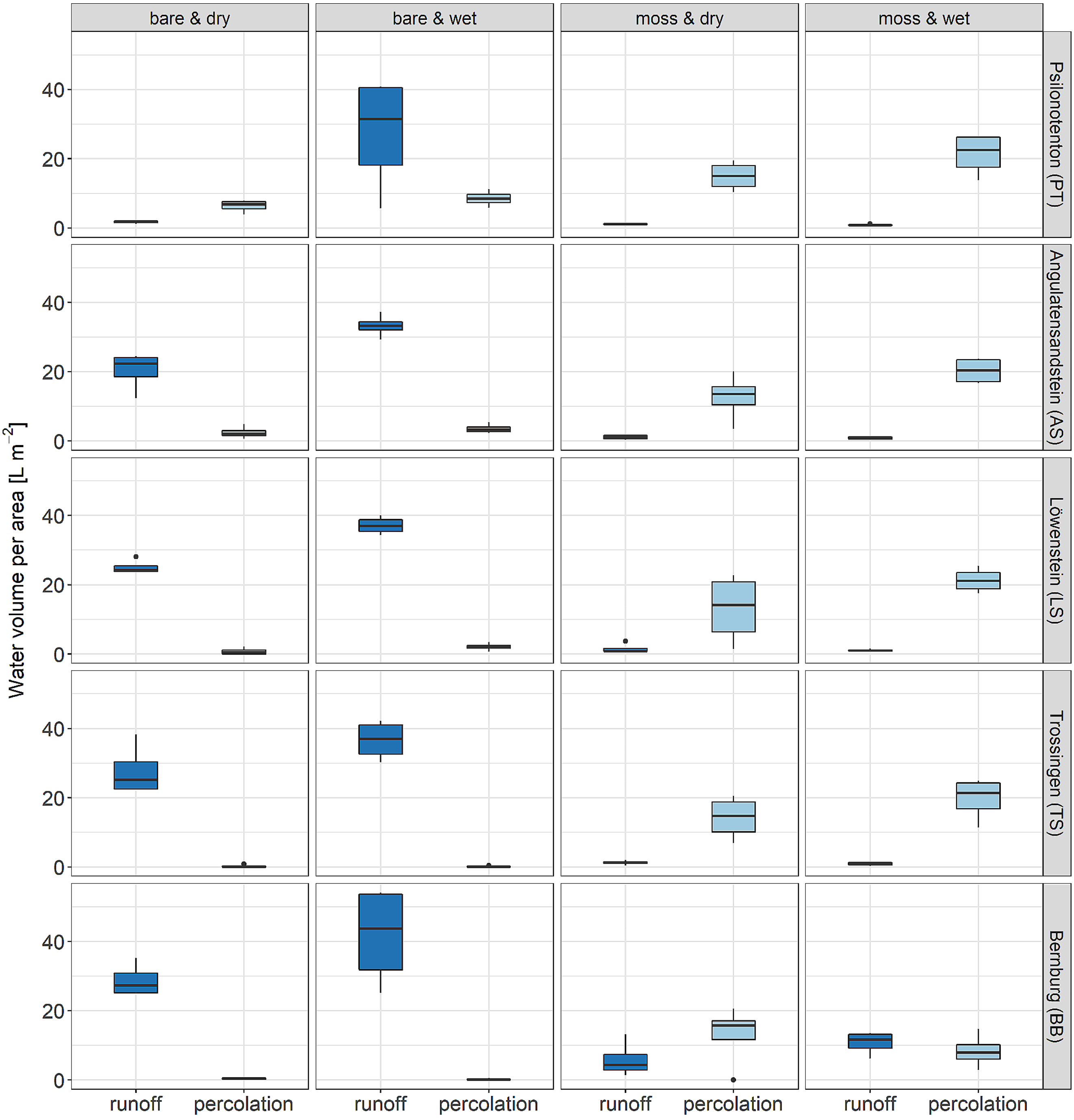

Fig. 3 Surface runoff and amount of percolated water [L m^{-2}] per infiltration box with four treatments and five soil substrates ($n = 4$). Lines within boxplots represent median values, while bottom and top of the boxplot show the first and third quartiles. Whiskers extend up to 1.5 times the interquartile range (IQR) of the data. Outliers are defined as more than 1.5 times the IQR and are displayed as points

For both surface runoff and amount of percolated water, there were no differences on average among the substrates. However, when all bare treatments were considered separately, significant differences were found: BB produced more surface runoff than PT ($p < 0.001$), TS ($p < 0.05$) and LS ($p < 0.05$). Additionally, the amount of percolated water was considerably higher in PT than in all other substrates ($p < 0.001$), and significantly more water percolated through AS than through BB ($p < 0.01$) and TS ($p < 0.01$). For the moss treatments, surface runoff was significantly higher for BB than for all other substrates, while the amount of percolated water did not differ.

The average sediment discharge was highest in bare & wet treatments (1065.01 ± 106.27 g m^{-2}), more than 2000 times higher compared with moss & dry treatments (0.51 ± 0.16 g m^{-2}). All bare treatments caused more sediment loss than moss treatments ($p < 0.001$) and while sediment discharge was significantly higher in bare & wet treatments than in bare & dry treatments (723.46 ± 114.99 g m^{-2}, $p < 0.05$), there was no difference between moss & dry and moss & wet treatments (Fig. 4). Within bare treatments, there were considerable variations in sediment discharge between the substrates: PT showed the lowest sediment discharge with a significant difference to TS ($p < 0.001$) and BB ($p < 0.01$), while TS exhibited the highest sediment discharge with a significant difference to AS ($p < 0.05$). Within the moss treatments, sediment discharge of BB was significantly higher compared with the other substrates ($p < 0.001$). However, soil loss for BB was still 605 times lower in moss compared with bare treatments.

The effect of antecedent soil moisture on surface runoff and soil loss has been intensively studied and has led to contradictory findings due to the complex interactions of a variety of influencing factors (Le Bissonnais et al. 1995; Sachs and Sarah 2017; Moragoda et al. 2022). Consistent with our results, Le Bissonnais et al. (1995) found that air-dried substrates produced less surface runoff compared with field-moist substrates, which resulted in less soil loss in dry substrates as well. Prior to our rainfall simulations, a rough soil surface composed of dry soil aggregates was visible in the bare & dry treatments of all loamy substrates, which were destroyed during the rainfall simulation, leading to pore clogging and thus sealing of the substrate surface. Therefore, we suspect that at the beginning more water was able to infiltrate into the substrates until the surface was sealed, delaying surface runoff, which also resulted in less soil loss. This process occurred very quickly, which can be explained by the fact that dry soil aggregates are more susceptible to slaking than wet aggregates (Sachs and Sarah 2017). For this reason, many studies conclude that soil loss resistance increases with increasing soil moisture, at least up to a certain threshold value of soil moisture content (Moragoda et al. 2022). However, our experimental setup involved dependent samples, so that the bare & wet treatments did not have

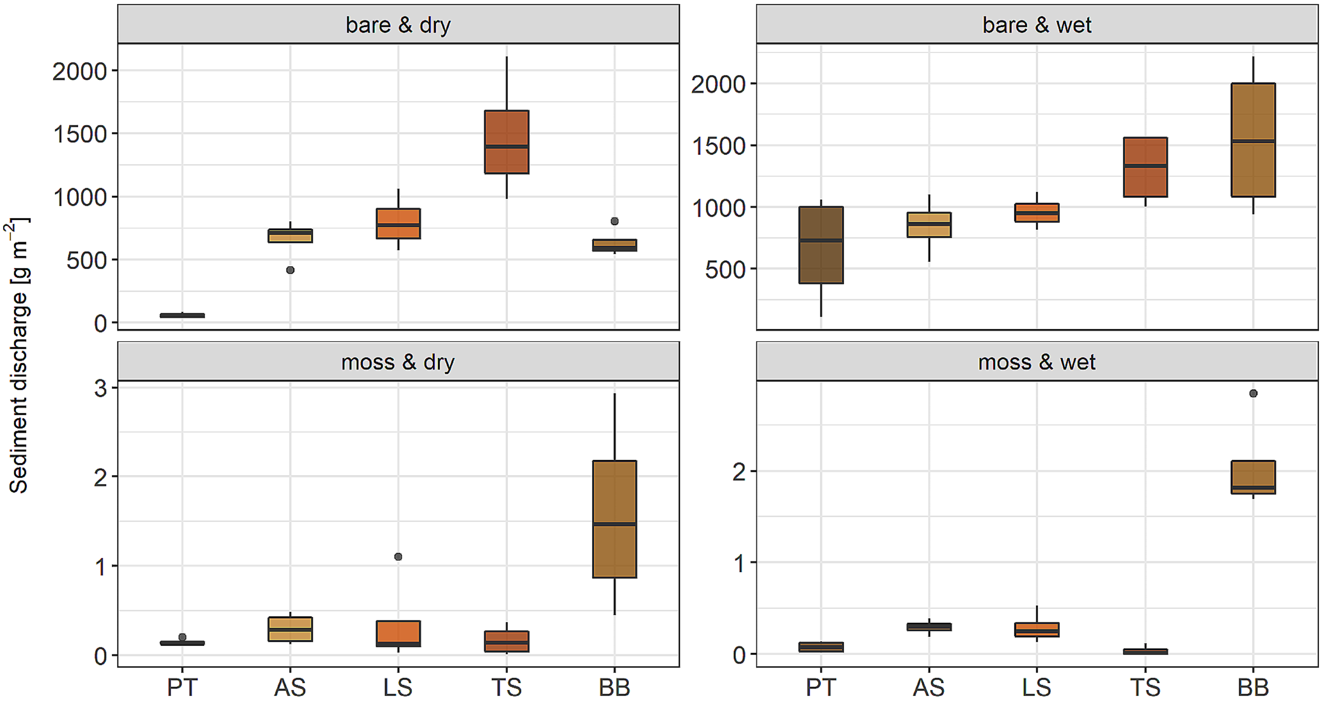

Fig. 4 Sediment discharge [g m^{-2}] per infiltration box with four treatments and five soil substrates ($n = 4$). Substrates are plotted on the x-axis with PT = Psilonotenton, AS = Angulatensandstein, LS = Löwenstein, TS = Trossingen, and BB = Bernburg. Lines within boxplots represent median values, while bottom and top of the boxplot show the first and third quartiles. Whiskers extend up to 1.5 times the interquartile range (IQR) of the data. Outliers are defined as more than 1.5 times the IQR and are displayed as points

any wet soil aggregates on the surface at the beginning of the second rainfall simulation, but were already sealed as just described. Consequently, the rainfall intensity exceeded the infiltration capacity of the soil, resulting in hortonian overland flow (Horton 1933). This caused more surface runoff and soil loss in bare & wet treatments compared with dry conditions.

Differences between substrates regarding surface runoff, amount of percolated water and soil loss were evident within the bare treatments, excluding the influence of moss covers. These soil hydrological parameters are determined by a variety of soil properties such as soil texture, SOC, aggregate stability, and many others (Le Bissonnais and Singer 1993; Le Bissonnais et al. 1995; Knapen et al. 2007). Furthermore, there are many environmental factors that influence these processes as well (Knapen et al. 2007), ranging from antecedent soil moisture to rain temperature (Sachs and Sarah 2017). In our experiment, the differences between the substrates could not be explained by the two soil properties studied, soil texture and SOC. We attribute this to the fact that all soil substrates, except BB, had very similar soil textures, and only TS had a considerably higher SOC compared with the other substrates. To fully understand these relationships, it is necessary to survey a larger number of different soil properties and environmental variables.

When preparing our experimental setup, we hypothesized that moss covers absorb a high amount of water (Wang and Bader 2018; Thielen et al. 2021) and have a strong intercepting effect (Price et al. 1997). This also means that a lot of water is stored in the capillary spaces of the mosses, which act as a runoff sink that delays runoff (Rodríguez-Caballero et al. 2012), and most likely facilitates infiltration into the soil. In addition, mosses can have a positive effect on soil structure (Hu et al. 2023), which also improves infiltration. Thus, mosses reduce surface runoff and prevent splash erosion by "swallowing" raindrops, the extent depending on the moss species (Roth-Nebelsick et al. 2022; Tu et al. 2022), both of which lead to reduced sediment discharge (Juan et al. 2023). In a previous experiment with the same soil-moss combinations (with the exception of the treatment BB + *P. formosum*) (Thielen et al. 2021), we already demonstrated that the maximum water storage capacities of the different moss species differed and were substantially shaped by their structural traits, e.g. high shoot density, high leaf frequency and low leaf area. Therefore, we suspected, similar to the findings of Tu et al. (2022), different extents of surface runoff and soil erosion reduction depending on the moss species. However, this was not reflected in our results, as no variations in soil loss and surface runoff were found between moss species with acrocarpous and pleurocarpous growth form, which was the case for maximum water storage capacities in Thielen et al. (2021). Nevertheless, surface runoff and soil loss were significantly higher in the BB treatment covered with acrocarpous *P. formosum*, which was not considered in Thielen et al. (2021). This could be partly attributed to the structural traits of *P. formosum*, as it has the lowest total surface area (124.52 cm^2), lowest shoot density (49.33 ± 11.86 shoots per cm^2), lowest leaf frequency (17.33 ± 1.34 leaves per cm shoot), and second largest leaf area (2.78 ± 0.33 mm^2) of all the moss species studied (see also Table 3 in Thielen et al. (2021), which also results in a very low maximum water storage capacity of 0.76 ± 0.03 mm (Table 2)..

In addition to the soil-moss combinations we selected, there were two main factors that strongly influenced our measurements. Firstly, due to the weather conditions, desiccation cracks occurred in the loamy substrates, i.e. all substrates except BB, during the adaptation of moss covers. Secondly, the BB substrate was highly water repellent as described in Table 1. For this reason, there was an intensified preferential flow in all loamy substrates, which caused surface runoff to be strongly reduced. This superimposition by desiccation cracks makes it impossible to determine the individual contribution of the different moss species to surface runoff and soil erosion reduction. Only the sandy BB substrate did not form desiccation cracks and its hydrophobicity (Doerr et al. 2000), which generally increases surface runoff and soil erosion compared with wettable soils (Lowe et al. 2021), resulted in higher surface runoff for bare treatments compared with the loamy substrates. Also, the water-repellent substrate showed significantly higher surface runoff and sediment discharge as well as lower volume of percolated water in the moss treatment compared with the loamy substrates. Despite the lack of desiccation cracks and occurrence of water repellency in this sample, however, the measured parameters were significantly reduced with mosses compared to the bare treatments, indicating still a high influence of the moss cover. Nevertheless, it should be taken into account that the presence of strong hydrophobic properties can modify the interaction between moss and substrate compared to bare substrates. Accordingly, a hydrophobic moss-covered substrate probably behaves differently in terms of runoff formation than a wettable moss-covered substrate. This effect requires further experimental research for a better understanding.

Temporal dynamics of water content in soil-moss combinations during rainfall simulations

The temporal progression of water content during rainfall simulations differed between treatments and substrates (Fig. 5). In principle, water content increased during rainfall simulation in all bare & dry treatments until an equilibrium was reached, with the water content at a depth of 3 cm

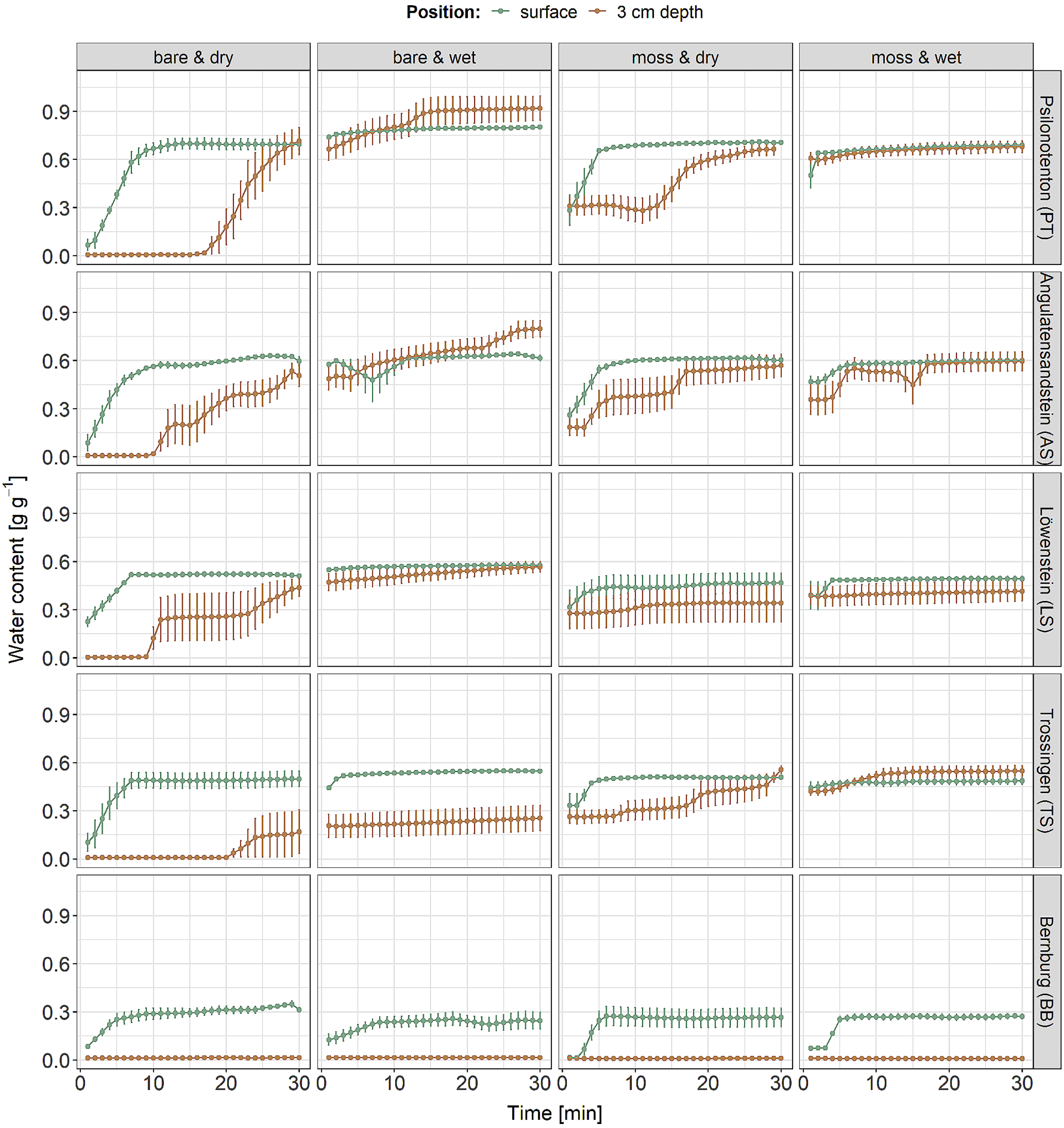

Fig. 5 Temporal dynamics of water content values [g g^{-1}] of treatments and substrates during rainfall simulations ($n = 4$). Minute averages of water content are shown as points with standard errors. Water content was measured with biocrust wetness probes (BWP) at two positions: At the substrate surface and at 3 cm substrate depth

increasing clearly later than at the surface. For the bare & wet treatments, water content at the surface remained nearly the same, while it still rose at a depth of 3 cm. The temporal dynamics of water content in the moss treatments were similar, however, the difference between surface and 3 cm depth was less pronounced in the moss & dry treatments than in the bare & dry treatments. In the substrates TS, PT and AS, the water contents at a depth of 3 cm are in fact the same as on the substrate surface or even exceed them. Furthermore, water content increased less in the moss & wet treatments at 3 cm depth and reached lower values than in the bare & wet treatments. In comparison, BB stands out due to its considerably lower water content at the surface and dry conditions at 3 cm substrate depth in all treatments. Besides, the only difference between bare and moss treatments in BB was that the water content in bare treatments fluctuated slightly over time, whereas it was continuous in the moss treatments. With regard to the substrates, there were differences in particular in the time it took for the water to percolate to a depth of 3 cm: while it took about 10 min for the BWP at 3 cm depth to respond in AS and LS, it took about 20 min in PT and TS, and no water was detected in BB. It is also noticeable that there is a tendency for lower water contents in moss treatments at 3 cm depth compared to bare treatments, which was particularly pronounced for the substrate LS. Furthermore, the water content dynamics in TS were different from the other substrates: In the bare treatments there was a clearly higher water content at the surface compared with 3 cm depth, and the water content increased in moss substrates at 3 cm depth compared to bare substrates.

These findings on the temporal dynamics of water content during rainfall simulation supported our theories of surface runoff and percolated water volume described in the previous section. For instance, surface runoff was lower in the bare & dry than in the bare & wet treatments, which we attributed to a delay in runoff due to greater initial infiltration. In combination with these results, we could see that it took several minutes for the surface to be completely moistened in all substrates and it took correspondingly longer until the soil moisture also increased at a depth of 3 cm. According to this, a high amount of water was first stored inside the substrate, which did not become effective for surface runoff. The rainfall simulation of the bare & wet treatments already began with water saturated soil surfaces, which resulted in more surface runoff. In addition, at a depth of 3 cm, there was still the potential to absorb water, and presumably at deeper levels as well, which overall resulted in no difference in percolated water volume between bare & dry and bare & wet treatments.

We attributed the tendency towards lower water contents at the substrate surface in moss treatments to the high water storage capacity of the mosses and the occurrence of desiccation cracks. Due to the desiccation cracks and the associated preferential flow, the water passed quickly through the soil and did not remain on the soil surface, which likely lead to lower water contents at the soil surface. In comparison, Tu et al. (2022) had studied the influence of moss covers on infiltration and surface runoff processes in karst bedrocks and found that more than 50% of the precipitation percolated into the ground through karst cracks and only 1–17% were dedicated to surface runoff, whereby these ratios depended on the respective moss species. Interestingly, the water content in the moss treatments was often just as high at 3 cm substrate depth as on the substrate surface, indicating that mosses promoted the infiltration of water into the soil. In contrast, Tu et al. (2022) found that average infiltration rates of bare soils were not significant different from soils covered with mosses. However, there was a clear species effect, as the moss described as *Eurohypnum* reduced infiltration rates by 6–8%. Compared to this, Xiao et al. (2011) conclude that artificially cultivated moss crusts significantly increase infiltration. Likewise, Hu et al. (2023) found that soil water retention was higher under moss covers than in bare soils, which can be attributed to differences in soil structure. For example, soil macropores were more abundant and better connected under moss covers than in bare soils, although the thickness of the moss covers also played a decisive role (Hu et al. 2023).

Another phenomenon that became particularly clear in these results was the water repellency of BB. As also described in Lowe et al. (2021), water moved across the surface in rivulets during which dry substrate was brought back to the surface, so fluctuating water contents were also observed in the bare & wet treatments. It was remarkable that although percolated water was measured in BB, there was no increase in water content at the position of the BWP in 3 cm substrate depth. It can therefore be assumed that the water flow occurs almost solely as preferential flow in the outer edges of the infiltration boxes between soil substrate and metal edge. Again, the complex relationship between desiccation, hydrophobicity, and the individual plant effects of mosses superimposed by these factors requires further experimental studies.

Conclusion and outlook

In this study, we demonstrated that mosses have a large impact on surface runoff, amount of percolated water, and soil loss. Mosses significantly reduced surface runoff by 91% and soil loss by almost 100% compared with bare soil, while the amount of percolated water was increased by 85%. On one hand, we attributed these strong impacts to the moss covers. On the other hand, these processes were superimposed by desiccation cracks and, partly, soil hydrophobicity, with the result that the respective influences of the moss species and their traits were concealed. The temporal dynamics of water content also showed clear differences between mosses and bare soil, which allowed us to understand more precisely the changes in surface runoff and percolated water volume. Moss treatments exhibited lower water contents at the substrate surface compared to bare treatments, illustrating the strong influence of desiccation cracks due to preferential flow on soil water fluxes. However, soil water content in 3 cm substrate depth was higher compared to bare soils, suggesting that mosses encourage infiltration.

Further experiments are needed to clarify the apparently underestimated effects of mosses on soil water fluxes. For example, an experimental setup with undisturbed soil samples of the same parent material covered with different moss species would be promising to study the influence of mosses on soil water fluxes under more natural conditions. This should be also accompanied by the investigation of species-specific effects and their connection with moss structural traits. Furthermore, the influence of hydrophobicity on this complex interaction system is not understood in detail. With the help of this basic research, mosses could in future be used specifically as erosion control or to improve the hydrological properties of the topsoil in anthropogenically managed soils.

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Author contributions CG, StS and MN designed the experiment. CG and StS carried out field measurements. CG was responsible for laboratory analyses, while CG and SMT conducted data analyses. CG prepared the manuscript with contributions from all other co-authors.

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Data availability The dataset compiled and analysed in this study is available on figshare at https://doi.org/10.6084/m9.figshare.23965386.v1 (Gall et al. 2023).

Code Availability The codes used in this study are available upon request.

Declarations

Competing interests The contact author has declared that none of the authors has any competing interests.

References

Belnap J, Büdel B, Lange OL (2001) Biological Soil Crusts: Characteristics and Distribution. In: Belnap, J., and Lange, O. L. (Eds.) Biological Soil Crusts: Structure, Function, and Management, Springer Berlin Heidelberg, Berlin, Heidelberg, ISBN 9783642564758

Blake GR, Hartge KH (1986) Bulk density. In: Arnold, K. (Ed.) Methods of Soil Analysis, Part 1: Physical and Mineralogical Methods, American Society of Agronomy, Inc. and Soil Science Society of America, Inc., Madison, ISBN 9780891180883

Bu C, Wu S, Han F, Yang Y, Meng J (2015) The combined effects of moss-dominated biocrusts and vegetation on erosion and soil moisture and implications for disturbance on the Loess Plateau, China. PLoS ONE 10(5):e0127394. https://doi.org/10.1371/journal.pone.0127394

Dekker L, Jungerius P (1990) Water repellency in the dunes with special reference to The Netherlands. In: Bakker, T. W., Jungerius, P. D., and Klijn, A. J. (Eds.) Dunes of European Coasts; Geomorphology - Hydrology - Soils, Catena-Verlag, Cremlingen-Destedt, Germany, ISBN 9783923381234

Dekker LW, Ritsema CJ, Oostindie K, Moore D, Wesseling JG (2009) Methods for determining soil water repellency on field-moist samples. Water Resour Res 45(4):1–6. https://doi.org/10.1029/2008WR007070

Doerr S, Shakesby R, Walsh R (2000) Soil water repellency: its causes, characteristics and hydro-geomorphological significance. Earth Sci Rev 51(1–4):33–65. https://doi.org/10.1016/S0012-8252(00)00011-8

DWD Climate Data Center (2021) Grids of return periods of heavy precipitation (design precipitation) over Germany (KOSTRA-DWD) (version 2010R), DWD [dataset], https://opendata.dwd.de/climate_environment/CDC/grids_germany/return_periods/precipitation/KOSTRA/KOSTRA_DWD_2020/asc/ (last access: 19.02.2024)

Einsele G, Agster G (1986) Überblick zur Geologie und Morphologie des Schönbuchs. In: Einsele, G. (Ed.) Das landschaftsökologische Forschungsprojekt Naturpark Schönbuch: Wasser- und Stoffhaushalt, Bio-, Geo- und Forstwirtschaftliche Studien in Südwestdeutschland, VCH Verlagsgesellschaft, Weinheim, ISBN 3527271228

Eldridge DJ, Reed S, Travers SK, Bowker MA, Maestre FT, Ding J, Havrilla C, Rodriguez-Caballero E, Barger N, Weber B, Antoninka A, Belnap J, Chaudhary B, Faist A, Ferrenberg S, Huber-Sannwald E, Issa M, Zhao O, Y (2020) The pervasive and multifaceted influence of biocrusts on water in the world's drylands. Glob Change Biol 26(10):6003–6014. https://doi.org/10.1111/gcb.15232

Eldridge DJ, Guirado E, Reich PB, Ochoa-Hueso R, Berdugo M, Sáez-Sandino T, Blanco-Pastor JL, Tedersoo L, Plaza C, Ding J, Sun W, Mamet S, Cui H, He J-Z, Hu H-W, Sokoya B, Abades S, Alfaro F, Bamigboye AR, Bastida F, de los Ríos A, Durán J, Gaitan JJ, Guerra CA, Grebenc T, Illán JG, Liu Y-R, Makhalanyane TP, Mallen-Cooper M, Molina-Montenegro MA, Moreno JL, Nahberger TU, Peñaloza-Bojacá GF, Picó S, Rey A, Rodríguez

A, Siebe C, Teixido AL, Torres-Díaz C, Trivedi P, Wang J, Wang L, Wang J, Yang T, Zaady E, Zhou X, Zhou X-Q, Zhou G, Liu S, Delgado-Baquerizo M (2023) The global contribution of soil mosses to ecosystem services. Nat Geosci 16(5):430–438. https://doi.org/10.1038/s41561-023-01170-x

Gall C, Nebel M, Quandt D, Scholten T, Seitz S (2022a) Pioneer biocrust communities prevent soil erosion in temperate forests after disturbances. Biogeosciences 19:3225–3245. https://doi.org/10.5194/bg-19-3225-2022

Gall C, Ohan J, Glaser K, Karsten U, Schloter M, Scholten T, Schulz S, Seitz S, Kurth JK (2022b) Biocrusts: overlooked hotspots of managed soils in mesic environments. J Plant Nutr Soil Sci 185(6):745–751. https://doi.org/10.1002/jpln.202200252

Gall C, Nebel M, Scholten T, Thielen S, Seitz S (2023) Water's path from moss to soil 2. https://doi.org/10.6084/m9.figshare.23965386.v1. [dataset]

Hodgetts NG, Söderström L, Blockeel TL, Caspari S, Ignatov MS, Konstantinova NA, Lockhart N, Papp B, Schröck C, Sim-Sim M, Bell D, Bell NE, Blom HH, Bruggeman-Nannenga MA, Brugués M, Enroth J, Flatberg KI, Garilleti R, Hedenäs L, Holyoak DT, Hugonnot V, Kariyawasam I, Köckinger H, Kučera J, Lara F, Porley RD (2020) An annotated checklist of bryophytes of Europe, Macaronesia and Cyprus. J Bryology 42(1):1–116. https://doi.org/10.1080/03736687.2019.1694329

Horton RE (1933) The Rôle of infiltration in the hydrologic cycle. Eos, Transactions American Geophysical Union 14 (*1*): 446–460, https://doi.org/10.1029/TR014i001p00446

Hu X, Gao Z, Li X-Y, Wang R-Z, Wang Y-M (2023) Structural characteristics of the moss (bryophyte) layer and its underlying soil structure and water retention characteristics. Plant Soil. https://doi.org/10.1007/s11104-023-06079-3

Iserloh T, Ries J, Arnáez J, Boix-Fayos C, Butzen V, Cerdà A, Echeverría M, Fernández-Gálvez J, Fister W, Geißler C (2013) European small portable rainfall simulators: a comparison of rainfall characteristics. CATENA 110:100–112. https://doi.org/10.1016/j.catena.2013.05.013

Juan J, Dongdong L, YuanHang F, Pu L (2023) Combined effects of moss colonization and rock fragment coverage on sediment losses, flow hydraulics and surface microtopography of carbonate-derived laterite from karst mountainous lands. CATENA 229:107202. https://doi.org/10.1016/j.catena.2023.107202

Kidron GJ (2021) Comparing overland flow processes between semiarid and humid regions: does saturation overland flow take place in semiarid regions? J Hydrol 593:125624. https://doi.org/10.1016/j.jhydrol.2020.125624

Kidron GJ, Fischer T, Xiao B (2022a) The ambivalent effect of biocrusts on evaporation: can the contradictory conclusions be explained? A review. Geoderma 416:115805. https://doi.org/10.1016/j.geoderma.2022.115805

Kidron GJ, Lichner L, Fischer T, Starinsky A, Or D (2022b) Mechanisms for biocrust-modulated runoff generation– A review. Earth Sci Rev 231:104100. https://doi.org/10.1016/j.earscirev.2022.104100

Knapen A, Poesen J, Govers G, Gyssels G, Nachtergaele J (2007) Resistance of soils to concentrated flow erosion: a review. Earth Sci Rev 80(1):75–109. https://doi.org/10.1016/j.earscirev.2006.08.001

Le Bissonnais Y (1996) Aggregate stability and assessment of soil crustability and erodibility: I. Theory and methodology. Eur J Soil Sci 47(4):425–437. https://doi.org/10.1111/j.1365-2389.1996.tb01843.x

Le Bissonnais Y, Singer MJ (1993) Seal formation, runoff, and interrill erosion from seventeen California soils. Soil Sci Soc Am J 57(1):224–229. https://doi.org/10.2136/sssaj1993.03615995005700010039x

Le Bissonnais Y, Renaux B, Delouche H (1995) Interactions between soil properties and moisture content in crust formation, runoff and interrill erosion from tilled loess soils. CATENA 25(1):33–46. https://doi.org/10.1016/0341-8162(94)00040-L

Lindo Z, Gonzalez A (2010) The Bryosphere: an integral and influential component of the Earth's biosphere. Ecosystems 13(4):612–627. https://doi.org/10.1007/s10021-010-9336-3

Liu Z, Chen R, Qi J, Dang Z, Han C, Yang Y (2022) Control of Mosses on Water Flux in an Alpine Shrub Site on the Qilian Mountains, Northwest China. Plants 11(22):3111. https://www.mdpi.com/2223-7747/11/22/3111

Lowe M-A, McGrath G, Leopold M (2021) The impact of soil water repellency and slope upon runoff and erosion. Soil Tillage Res 205:104756. https://doi.org/10.1016/j.still.2020.104756

Mägdefrau K, Wutz A (1951) Die Wasserkapazität der Moos- und Flechtendecke des Waldes. Veröffentlichung des Botanischen Instituts der Forstlichen Forschungsanstalt München 70:103–117. https://doi.org/10.1007/BF01815956

Moragoda N, Kumar M, Cohen S (2022) Representing the role of soil moisture on erosion resistance in sediment models: challenges and opportunities. Earth Sci Rev 229:104032. https://doi.org/10.1016/j.earscirev.2022.104032

Morgan RPC (2005) Soil Erosion and Conservation. Blackwell Publishing, Oxford, ISBN 140514467X

Nebel M, Philippi G, Ahrens M, Sauer M, Schäfer-Verwimp A, Schoepe G (2001) Die Moose Baden-Württembergs, Band 2: Bryophytina II, Schistostegales bis Hypnobryales. Eugen Ulmer Verlag, Stuttgart, ISBN 9783800135301

Oltmanns F (1884) Über die Wasserbewegung in der Moospflanze und ihren Einfluss auf die Wasservertheilung im Boden [Dissertation], Kaiser-Wilhelms-Universität Strassburg

Parsakhoo A, Lotfalian M, Kavian A, Hosseini S, Demir M (2012) The effects of *Rubus hyrcanus* L. and *Philonotis marchica* (Hedw.) Brid. on soil loss prevention from cutslopes of a forest road. J for Sci 58:337–344. https://doi.org/10.17221/9/2012-JFS

Price AG, Dunham K, Carleton T, Band L (1997) Variability of water fluxes through the black spruce (*Picea mariana*) canopy and feather moss (*Pleurozium schreberi*) carpet in the boreal forest of Northern Manitoba. J Hydrol 196(1):310–323. https://doi.org/10.1016/S0022-1694(96)03233-7

Proctor MCF, Nagy Z, Csintalan Z, Takács Z (1998) Water-content components in bryophytes: analysis of pressure-volume relationships. J Exp Bot 49:1845–1854. https://doi.org/10.1093/jxb/49.328.1845

R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing [code], https://www.R-project.org/ (last access: 19.02.2024)

Rodríguez-Caballero E, Cantón Y, Chamizo S, Afana A, Solé-Benet A (2012) Effects of biological soil crusts on surface roughness and implications for runoff and erosion. Geomorphology 145:81–89. https://doi.org/10.1016/j.geomorph.2011.12.042

Roth-Nebelsick A, Konrad W, Ebner M, Miranda T, Thielen S, Nebelsick JH (2022) When rain collides with plants - patterns and forces of drop impact and how leaves respond to them. J Exp Bot 73(4):1155–1175. https://doi.org/10.1093/jxb/erac004

Sachs E, Sarah P (2017) Combined effect of rain temperature and antecedent soil moisture on runoff and erosion on Loess. CATENA 158:213–218. https://doi.org/10.1016/j.catena.2017.07.007

Seitz S (2015) Mechanisms of soil erosion in subtropical chinese forests - Effects of species diversity, species identity, functional traits and soil fauna on sediment discharge [Dissertation], Universitätsbibliothek Tübingen

Seitz S, Nebel M, Goebes P, Käppeler K, Schmidt K, Shi X, Song Z, Webber CL, Weber B, Scholten T (2017) Bryophyte-dominated biological soil crusts mitigate soil erosion in an early successional Chinese subtropical forest. Biogeosciences 14(24):5775–5788. https://doi.org/10.5194/bg-14-5775-2017

Siwach A, Kaushal S, Baishya R (2021) Effect of mosses on physical and chemical properties of soil in temperate forests of Garhwal Himalayas. J Trop Ecol 37(3):126–135. https://doi.org/10.1017/S0266467421000249

Sun F, Xiao B, Li S, Kidron GJ (2021) Towards moss biocrust effects on surface soil water holding capacity: soil water retention curve analysis and modeling. Geoderma 399:115120. https://doi.org/10.1016/j.geoderma.2021.115120

Thielen SM, Gall C, Ebner M, Nebel M, Scholten T, Seitz S (2021) Water's path from moss to soil: a multi-methodological study on water absorption and evaporation of soil-moss combinations. J Hydrology Hydromechanics 69(4):421–435. https://doi.org/10.2478/johh-2021-0021

Tu N, Dai Q, Yan Y, Peng X, Meng W, Cen L (2022) Effects of Moss overlay on soil patch infiltration and runoff in karst rocky desertification slope land. Water 14(21):3429. https://doi.org/10.3390/w14213429

Turetsky MR, Bond-Lamberty B, Euskirchen E, Talbot J, Frolking S, McGuire AD, Tuittila E-S (2012) The resilience and functional role of moss in boreal and arctic ecosystems. New Phytol 196(1):49–67. https://doi.org/10.1111/j.1469-8137.2012.04254.x

Wang Z, Bader MY (2018) Associations between shoot-level water relations and photosynthetic responses to water and light in 12 moss species. AoB Plants 10(3):ply034. https://doi.org/10.1093/aobpla/ply034

Weber B, Berkemeier T, Ruckteschler N, Caesar J, Heintz H, Ritter H, Braß H, Freckleton R (2016a) Development and calibration of a novel sensor to quantify the water content of surface soils and biological soil crusts. Methods Ecol Evol 7(1):14–22. https://doi.org/10.1111/2041-210x.12459

Weber B, Büdel B, Belnap J (2016b) Biological Soil Crusts: An Organizing Principle in Drylands. Springer, Dordrecht, ISBN 9783319302126

Weber B, Belnap J, Büdel B, Antoninka AJ, Barger NN, Chaudhary VB, Darrouzet-Nardi A, Eldridge DJ, Faist AM, Ferrenberg S, Havrilla CA, Huber-Sannwald E, Issa M, Maestre O, Reed FT, Rodriguez-Caballero SC, Tucker E, Young C, Zhang KE, Zhao Y, Zhou Y, Bowker X, M. A (2022) What is a biocrust? A refined, contemporary definition for a broadening research community. Biol Rev 97:1768–1785. https://doi.org/10.1111/brv.12862

Xiao B, Wang Q-h, Zhao Y-g, Shao M-a (2011) Artificial culture of biological soil crusts and its effects on overland flow and infiltration under simulated rainfall. Appl Soil Ecol 48(1):11–17. https://doi.org/10.1016/j.apsoil.2011.02.006