On the Influence of Biological Soil Crusts and Bryophytes on Soil Erosion and the Soil Water Balance in Temperate Forests

Dissertation
der Mathematisch-Naturwissenschaftlichen Fakultät
der Eberhard Karls Universität Tübingen
zur Erlangung des Grades eines
Doktors der Naturwissenschaften
(Dr. rer. nat.)

vorgelegt von
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Tübingen
2023

Gedruckt mit Genehmigung der Mathematisch-Naturwissenschaftlichen Fakultät der Eberhard Karls Universität Tübingen.

Tag der mündlichen Qualifikation: 08.05.2023
Dekan: Prof. Dr. Thilo Stehle
1. Berichterstatter: Prof. Dr. Thomas Scholten
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Abstract

Soil erosion is a serious threat to the soil because it impairs the provision of important ecosystem services such as filtering water, providing nutrients and habitat for biology activity, storing carbon, and producing biomass. This also plays a crucial role in forest ecosystems where natural and anthropogenic disturbances expose bare soil to erosion. An important countermeasure is the rapid recolonization by vegetation. Especially in arid regions, biological soil crusts (biocrusts) are known to be pioneer colonizers of disturbed soils and to reduce soil erosion. Bryophytes also protect the soil and can have a positive effect on the soil water balance. However, the influence of bryophytes and biocrusts on soil erosion and the soil water balance in temperate forests is largely unexplored.

This thesis investigated how biocrusts and bryophytes influence soil erosion and the soil water balance in skid trails of a temperate forest ecosystem in the Schönbuch Nature Park in South Germany. This included in-situ studies of soil erosion in the skid trails during vegetation succession and ex-situ studies of the influence of combinations of soil substrates and moss species (soil-moss combinations) on soil erosion. In addition, the water absorption and evaporation patterns in the soil-moss combinations were examined, also taking into account the structural traits of the moss species.

Within this thesis, it was shown that bryophyte-dominated biocrusts significantly affected soil erosion and that bryophytes not only contributed more to erosion reduction than vascular vegetation, but also positively influenced the soil water balance. Surface runoff and soil erosion were decreased with moss covers, while the amount of percolated water was increased; however, these processes were superimposed by desiccation cracks and water repellency. Moss treatments exhibited lower water contents over time compared to bare treatments, highlighting the strong influence of moss covers and desiccation cracks on the soil water balance. Mosses were no barrier for infiltration in case of high precipitation rates and they did not store much of the applied water themselves, but passed it on to the soil. During desiccation, mosses with high leaf area index (LAI) had lower evaporation rates than mosses with low LAI, and they prevented desiccation of the soil substrates, although even dense moss covers did not completely seal the surface.

Zusammenfassung

Bodenerosion stellt eine ernsthafte Bedrohung für den Boden dar, da sie die Bereitstellung wichtiger Ökosystemleistungen wie die Filterung von Wasser, die Nährstoffversorgung und die Schaffung von Lebensraum für biologische Aktivitäten, die Kohlenstoffspeicherung und die Erzeugung von Biomasse beeinträchtigt. Dies spielt auch in Waldökosystemen eine entscheidende Rolle, wo natürliche und anthropogene Störungen den brachen Boden der Erosion aussetzen. Eine wichtige Gegenmaßnahme ist die schnelle Wiederbesiedlung durch Vegetation. Vor allem in trockenen Regionen sind biologische Bodenkrusten (Biokrusten) dafür bekannt, dass sie gestörte Böden als Pioniere besiedeln und die Bodenerosion verringern. Auch Moose schützen den Boden und können sich positiv auf den Bodenwasserhaushalt auswirken. Der Einfluss von Moosen und Biokrusten auf die Bodenerosion und den Bodenwasserhaushalt in gemäßigten Wäldern ist jedoch weitgehend unerforscht.

In dieser Arbeit wurde untersucht, wie Biokrusten und Moose die Bodenerosion und den Bodenwasserhaushalt in Rückegassen eines gemäßigten Waldökosystems im Naturpark Schönbuch in Süddeutschland beeinflussen. Dazu gehörten In-situ-Untersuchungen der Bodenerosion in den Rückegassen während der Vegetationssukzession und Ex-situ-Untersuchungen des Einflusses von Kombinationen von Bodensubstraten und Moosarten (Boden-Moos-Kombinationen) auf die Bodenerosion. Darüber hinaus wurden die Wasseraufnahme- und Evaporationsmuster in den Boden-Moos-Kombinationen untersucht, wobei auch die strukturellen Merkmale der Moosarten berücksichtigt wurden.

Im Rahmen dieser Arbeit wurde gezeigt, dass von Moosen dominierte Biokrusten die Bodenerosion erheblich beeinflussen und dass Moose nicht nur stärker zur Erosionsminderung beitragen als Gefäßpflanzen, sondern auch den Wasserhaushalt des Bodens positiv beeinflussen. Oberflächenabfluss und Bodenerosion wurden durch den Moosbewuchs verringert, während die Menge des versickernden Wassers erhöht wurde; diese Prozesse wurden jedoch durch Austrocknungsrisse und wasserabweisende Eigenschaften überlagert. Die Moos-Treatments wiesen im Laufe der Zeit niedrigere Wassergehalte auf als die brachen Treatments, was den starken Einfluss der Moosbedeckung und der Austrocknungsrisse auf den Wasserhaushalt des Bodens verdeutlicht. Moose stellten bei hohen Niederschlagsmengen kein Hindernis für die Infiltration dar und sie speicherten selbst nicht viel von dem aufgebrachten Wasser, sondern gaben es an den Boden weiter. Während der Austrocknung wiesen Moose mit hohem Blattflächenindex (LAI) geringere Verdunstungsraten auf als Moosen mit geringem LAI und sie verhinderten die Austrocknung der Bodensubstrate, obwohl selbst dichte Moosdecken die Oberfläche nicht vollständig versiegelten.

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List of abbreviations

AS	Skid trail on / soil substrate of Angulatensandstein-Formation
BB	Soil substrate of Bernburg-Formation
Biocrust	Biological soil crust
BWP	Biocrust wetness probe
EC	Electrical conductivity
GAM	Generalized additive model
IQR	Interquartile range
LAI	Leaf area index
LS	Skid trail on / soil substrate of Löwenstein-Formation
MWD	Mean weight diameter
N_t	Total nitrogen
PT	Skid trail on / soil substrate of Psilonotenton-Formation
RH	Relative humidity
ROP	Runoff plot
SOC	Soil organic carbon
TS	Skid trail on / soil substrate of Trossingen-Formation
WDPT	Water drop penetration time
WSC_{max}	Maximum water storage capacity

List of publications

Published manuscripts

Manuscript 1:

GALL, C.; OHAN, J.; GLASER, K.; KARSTEN, U.; SCHLOTER, M.; SCHOLTEN, T.; SCHULZ, S.; SEITZ, S. & KURTH, J. K. (2022): Biocrusts: Overlooked hotspots of managed soils in mesic environments. *Journal of Plant Nutrition and Soil Science*, 185 (6), 745-751. DOI: 10.1002/jpln.202200252.

Manuscript 2:

GALL, C.; NEBEL, M.; QUANDT, D.; SCHOLTEN, T. & SEITZ, S. (2022): Pioneer biocrust communities prevent soil erosion in temperate forests after disturbances. *Biogeosciences*, 19, 3225–3245. DOI: 10.5194/bg-19-3225-2022.

Manuscript 4:

THIELEN, S. M.; **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. *Journal of Hydrology and Hydromechanics*, 69 (4), 421-435. DOI: 10.2478/johh-2021-0021.

Manuscripts in preparation

Manuscript 3:

GALL, C.; NEBEL, M.; SCHOLTEN, T.; THIELEN, S. M. & SEITZ, S. (in preparation): On the impact of soil-moss combinations on surface runoff, percolation, soil erosion, and temporal dynamics of soil water content.[*]

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[*] This manuscript has been published in a modified version as a preprint with the following citation: GALL, C.; NEBEL, M.; SCHOLTEN, T.; THIELEN, S. M. & SEITZ, S.: Water's path from moss to soil Vol. 2: How soil-moss combinations affect the soil water balance and soil erosion, 30 November 2023, Preprint (Version 1) available at Research Square. https://doi.org/10.21203/rs.3.rs-3268666/v1.

1 Introduction

Soils are the elementary basis for life on Earth (FAO, 2015), as they filter and store water, provide nutrients, store carbon, provide habitat for biological activity, and produce biomass (VOGEL et al., 2019). Given this wide range of ecosystem services, soils play a central role for human security (AMUNDSON et al., 2015), and soil health is crucial to achieving the Sustainable Development Goals of the United Nations (LAL et al., 2021). However, soil health is threatened by human activities, leading to imbalanced soil cycles that alter soils in ways that risk the provision of their ecosystem services (AMUNDSON et al., 2015). Soil erosion, in particular, is a serious threat to the soil because it removes the most productive soil layers (BORRELLI et al., 2017b; SCHOLTEN & SEITZ, 2019). Global soil erosion due to water is estimated at 20 to 30 gigatons per year, which exceeds the rate of soil formation by many orders of magnitude (FAO & ITPS, 2015). As land use and climate change continue, soil erosion will intensify in the future, requiring the rapid development of effective soil conservation strategies (OLSSON et al., 2019; BORRELLI et al., 2020).

Agricultural land is the land use type that contributes most to global soil erosion (BORRELLI et al., 2017b; BORRELLI et al., 2020). For instance, BORRELLI et al. (2017b) estimated that cropland accounts for 50.5 % of the total predicted soil erosion in 2012, although it represented only 11.2 % of the total land. In comparison, forests covered more than 28 % of the global land and were responsible for about 1.7 % of the total soil erosion estimates (BORRELLI et al., 2017b). For this reason, soil erosion in forests has received little scientific attention so far. However, forest disturbances have the potential to drastically increase soil losses (BORRELLI et al., 2017a). Even disturbances at a smaller scale such as forest road systems or skid trails can cause increased soil erosion (SHERIDAN & NOSKE, 2007; ZEMKE, 2016). In addition to these anthropogenic forest disturbances, natural forest disturbances due to climate change are likely to become more frequent in the future (SEIDL et al., 2017; ANDEREGG et al., 2022).

In forests, it is not primarily the canopy that protects the soil against erosion, but rather an intact forest floor (SEITZ et al., 2015; SHINOHARA et al., 2019). Undisturbed forest soil is usually covered by leaf or conifer litter from surrounding trees or by vegetation. This also includes cryptogamic vegetation such as bryophytes, which under certain conditions can also occur as biological soil crusts (biocrusts). Biocrusts are described as an association of soil particles and organisms such as cyanobacteria, algae, lichens, bryophytes, bacteria, and fungi that occupy the first millimetres of topsoil and form a crusted coherent layer on the soil surface (WEBER et al., 2016b; WEBER et al., 2022). So far, biocrusts have been studied mainly in arid and semi-arid regions, where they are effective in reducing soil erosion (BELNAP & BÜDEL, 2016) and considerably influence the soil water balance (ELDRIDGE et al., 2020; LI et al., 2022b).

However, the ecohydrological effects of biocrusts in temperate regions are largely unexplored (CORBIN & THIET, 2020; KIDRON et al., 2022b), especially in environments with sufficient water supply, referred to as mesic. Moreover, bryophytes are widely distributed in temperate forests, and there little is known about their ecohydrological role in general (HEDENÄS, 2007; LINDO & GONZALEZ, 2010; MEDINA et al., 2011).

1.1 Soil erosion in skid trails

Soil erosion in forests can be locally severe due to management intensities and tree species composition (SEITZ et al., 2016; SHINOHARA et al., 2019). Small-scale disturbances of the forest floor can already have a large impact on sediment discharge. In skid trails, for example, the forest floor is heavily disturbed by the direct overpassing with forestry equipment, resulting in the removal of the protective organic layer and soil compaction (DEMIR et al., 2007), which in turn increases the possibility of runoff formation (ZEMKE et al., 2019). For this reason, soil erosion in skid trails is also significantly higher than in undisturbed forest soil (SAFARI et al., 2016; ZEMKE, 2016). SAFARI et al. (2016) reported a 14-fold increase in erosion rates for bare wheel tracks of skid trails (301.65 ± 236.97 g m^{-2} h^{-1}) relative to undisturbed forest floor (21.83 ± 33.13 g m^{-2} h^{-1}). In comparison, ZEMKE (2016) showed that skid trails already covered with vegetation contributed significantly less to soil erosion, these skid trails had a 5-fold higher sediment yield compared to undisturbed forest soils. This clearly demonstrates that vegetation has an important erosion-reducing effect in skid trails. Several studies have also confirmed that soil erosion on skid trails was highest in the first year after logging and decreased significantly thereafter, mainly due to revegetation (BAHARUDDIN et al., 1995; JOURGHOLAMI et al., 2017). Thus, the most important measure to counteract negative effects of soil erosion on the upper soil layer after skidding is a quick restoration of the soil surface by vegetation (ZEMKE, 2016; MCEACHRAN et al., 2018).

1.2 Effect of biocrusts and bryophytes on soil erosion

Biocrusts are known to reduce soil erosion, but there are differences in the extent to which they decrease erosion with respect to the predominant biocrust type or their developmental stage (BELNAP et al., 2012; CHAMIZO et al., 2017). In particular, bryophyte-dominated biocrusts can significantly reduce soil erosion; BU et al. (2015) found, for example, an 81 % reduction in soil erosion compared to bare soil. Furthermore, SEITZ et al. (2017) observed that a bryophyte-dominated biocrust cover of more than 50 % significantly reduced soil erosion in a subtropical, early-successional Chinese forest plantation. Similar results were reported by SILVA et al. (2019) after a wildfire in eucalyptus plantations in central Portugal. Bryophyte-dominated biocrusts are hypothesized to increase their erosion-reducing effects as they develop into mature bryophyte covers.

To date, there are few studies that have measured sediment discharge beneath mature bryophyte covers. For instance, PARSAKHOO et al. (2012) investigated the differential effects of the bryophyte *Philonotis marchica* (Hedw.) Brid. and the shrub *Rubus hyrcanus* L. on soil erosion from forest road cutslopes. They found that *Philonotis marchica* significantly reduced soil erosion by 61 % compared to bare soil, but less significantly than *Rubus hyrcanus,* resulting in an 81 % mitigation of soil erosion. In general, both biocrust and bryophyte covers significantly reduce soil erosion, although the extent depends on the stage of development (CHAMIZO et al., 2017), the respective species, its life form (TU et al., 2022), and other still unknown factors.

1.3 Overlooked biocrust habitats in mesic environments (Manuscript 1)

Biocrusts and their beneficial ecosystem functions have primarily been described in arid and semiarid regions (WEBER et al., 2016b). However, biocrusts are also prevalent in temperate regions, where most studies have been carried out especially on bare soils or on soils with minimal vascular plant cover. Similar to arid soils, these soils are often of poor quality for vascular plant establishment and growth, with high salinity and/or low nutrient and water availability (CORBIN & THIET, 2020). Temperate environments in which biocrusts have been studied are, for example, coastal areas (THIET et al., 2014; KHANIPOUR ROSHAN et al., 2021), inland dunes (THIET et al., 2005; FISCHER et al., 2010b), sand plains and pine barrens (HAWKES & FLECHTNER, 2002; GILBERT & CORBIN, 2019), reclaimed lignite open-cast mining sites (FISCHER et al., 2010a; GYPSER et al., 2015), and potash tailings piles (SOMMER et al., 2020; PUSHKAREVA et al., 2021). While low vascular plant cover is common in these environments, that is not reflective of most temperate regions.

Most temperate ecosystems are characterized by an adequate water supply, which is referred to as mesic. In such mesic environments, vascular-plant growth is generally unrestricted, making it more difficult for biocrusts to compete. However, recent studies also found biocrusts in mesic environments that are anthropogenically impacted such as disturbed areas in forests (KURTH et al., 2021; GALL et al., 2022) or agricultural lands (NEVINS et al., 2020, 2021; Figure 1). The essential requirements for biocrust development include bare soil and a minimum amount of light, which can be created by disturbing or removing layers of vegetation and/or litter. These conditions serve as a starting point for the establishment and succession of biocrusts, which develop rapidly in mesic environments and are ephemeral unless the disturbance is persistent (SZYJA et al., 2018).

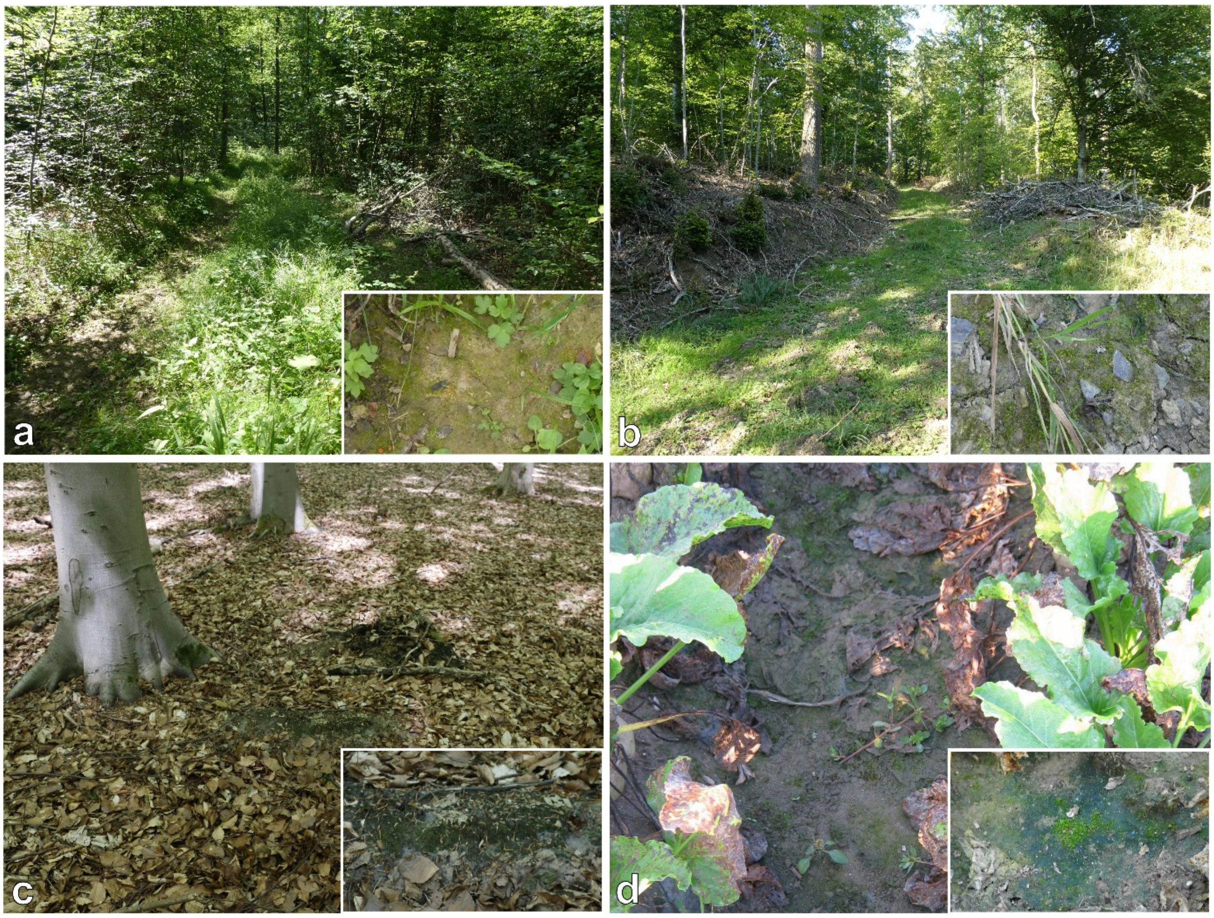


Figure 1: Overview of biocrusts on managed soils in mesic environments. (a) and (b) Early-successional bryophyte-dominated biocrusts on skid trail wheel tracks in a deciduous forest. (c) Bryophyte-dominated biocrust under leaf litter (Photograph: Julia K. Kurth). (d) Bryophyte- and cyanobacteria-dominated biocrusts on arable land between sugar beet crops (Photograph: Julia K. Kurth).

In forests, disturbances that cause bare soil can be natural (e.g. pest insects, disease, heavy storms, drought stress) or human-induced (e.g. clearcutting, forest roads, or skid trails). The total area of naturally and anthropogenically disturbed forests amounts to 39 million hectares, or 17 % of the total area of all European forests (SENF & SEIDL, 2021). Biocrusts are visible in the field as green cover (BAUMANN et al., 2017; KURTH et al., 2021; GLASER et al., 2022) and are found in both coniferous and deciduous forests (Figure 1 a-c). They are characterized by highly diverse photo- and heterotrophic microbial communities (GLASER et al., 2018; GLASER et al., 2022) or may consist of protonemata, green cell filaments which indicate the initial stages of bryophyte development. Subsequently, biocrusts develop into bryophyte covers and their biocrust characteristics disappear with succession of vascular plants (GALL et al., 2022). However, there is a smooth transition between biocrusts and mature bryophyte covers (BELNAP et al., 2001a; WEBER et al., 2022).

Biocrusts also occur on agricultural soils (Figure 1 d), often in conjunction with copiotrophic microorganisms (NEVINS et al., 2020, 2021, 2022). Agricultural practices such as plowing or other methods of tillage create large amounts of bare soil that provides niches for biocrust development until crops shade the soil. Additionally, many crops such as potatoes, sugar beet, and maize, are grown in rows which allow for solar radiation to reach the soil during the entire growing season. In Europe, this results in 12.4 million hectares of potential biocrust cover, or approximately 12.6 % of the total arable land (EUROSTAT, 2020).

In summary, biocrusts can cover large areas on managed soils in mesic environments, and it is very likely that beneficial ecosystem functions can be attributed to them here as well, similar to those in arid areas (WEBER et al., 2016b). Biocrusts are known to reduce soil erosion (SEITZ et al., 2017), and there is great potential for this effect to occur on managed soils in mesic environments as well. Additionally, there are no exemplary measurements for mesic environments for the controversial effects of biocrusts on surface runoff, infiltration, and evaporation (KIDRON et al., 2022a; KIDRON et al., 2022b). For a better understanding of these water-related effects of biocrusts in mesic environments, it is necessary to monitor the occurrence of biocrusts in disturbed areas and investigate their erosion-reducing potential, their runoff contribution, and their overall impact on the soil water balance at different developmental stages by field measurements.

1.4 Impact of bryophytes on the soil water balance in forests

Bryophytes are often overlooked, although they are very important to the soil water balance (MÄGDEFRAU & WUTZ, 1951; PRICE et al., 1997). With about 20,000 species, they are the second largest group of land plants, which includes mosses, liverworts, and hornworts (FREY et al., 2009; SÖDERSTRÖM et al., 2016). In this thesis, the term "bryophytes" is used when all or part of the three groups of bryophytes occur, while the term "mosses" is used when only mosses are considered. Contrary to vascular plants, bryophytes cannot actively regulate their water content, but are poikilohydric, i.e., bryophytes do not transpire via stomata or cuticle, and their internal water content is in equilibrium with ambient humidity (GREEN & LANGE, 1994). For bryophytes, water is available mainly by rain, dew, and fog (GLIME, 2021). Bryophyte water content is influenced by many factors that depend on both the habitat and the species itself in terms of structure and life form (DILKS & PROCTOR, 1979; OISHI, 2018), i.e., the form of individual shoots that grow together and are considered as an ecologically functional unit (BATES, 1998). Overall, bryophytes can absorb a great amount of water, reaching maximum water storage capacities of 108 % to 2070 % of their dry weight (PROCTOR et al., 1998), with some Sphagnum species even achieving over 5000 % of their dry weight (WANG & BADER, 2018).

An intact forest floor with understory vegetation plays a crucial role in the water balance of temperate forest ecosystems (LANDUYT et al., 2019; BALANDIER et al., 2022). There, the forest floor is often covered by bryophytes, which are particularly important for the water balance of the forest (MÄGDEFRAU & WUTZ, 1951). Previous research by PRICE et al. (1997) in a Canadian boreal forest found that bryophyte covers can retain 16.8 mm of water, or about 21 % of precipitation. In addition, OISHI (2018) discovered that soil moisture increases with bryophyte cover and bryophytes with high water storage capacity also have a larger impact on soil moisture. Finally, LIU & SHE (2020) determined a linear decrease in soil evaporation with increasing bryophyte biomass, using laboratory-cultivated bryophytes. Overall, the forest floor water balance is influenced by the amounts of throughfall rain, the processes inside bryophyte covers, and the processes at the bryophyte-soil interface (PRICE et al., 1997). However, little is known about the water fluxes from bryophytes to soil and vice versa (GLIME, 2021), indicating the need to quantify the impact of bryophytes on the soil water balance (VOORTMAN et al., 2014).

1.5 Bryophyte water storage capacity as a function of structural traits

In bryophytes, water absorption occurs mainly through external capillaries (ectohydric), but in some species it also occurs through internal movement (endohydric). Endohydric transport works either cell by cell or with the help of special water-conducting cells (hydroids). In comparison, ectohydric transport occurs through spaces between adjacent shoots, leaves, leaves and stems, leaves and rhizoids and capillary systems such as leaf bases, revoluted leaf margins, grooves or networks of capillary channels (GIORDANO et al., 1993; GLIME, 2021). These capillary spaces are characterized by a number of structural properties such as leaf shape, leaf arrangement, leaf orientation, detailed leaf anatomy (e.g. surface ornamentation), branch arrangement, nature of cortical cells, and presence of rhizoids or paraphyllia (SCHOFIELD, 1981). As a result, the water storage capacity of bryophytes varies significantly depending on the respective species (PROCTOR et al., 1998; WANG & BADER, 2018). Moreover, it can be assumed that a high water storage capacity also entails a high water retention capacity, which means that bryophytes that can absorb a lot of water take longer to dry out (WANG & BADER, 2018). However, it is still unclear which are the main structural traits that most influence water storage capacity and water retention of bryophytes.

Many bryophytes are able to dry out without dying, i.e., they can withstand the loss of free intracellular water and resume their normal functions, such as photosynthesis and growth, when water is available (PROCTOR et al., 2007). Factors influencing this water loss by evaporation are microclimatic conditions (PROCTOR, 1990), life form characteristics (MÄGDEFRAU & WUTZ, 1951; NAKATSUBO, 1994; ZOTZ et al., 1997; ELUMEEVA et al., 2011), and canopy structural properties such as surface roughness, shoot density and cushion height

(RICE et al., 2001; RICE & SCHNEIDER, 2004; GOETZ & PRICE, 2015; RICE et al., 2018). Bryophytes can increase the water content at the soil surface (SUN et al., 2021; LI et al., 2022a), and presumably this effect is more pronounced in bryophytes with high water storage capacity (OISHI, 2018), which is in turn determined by their structural traits. Due to future challenges related to climate change and especially dealing with droughts in forest ecosystems, a better understanding of these interrelationships is indispensable.

1.6 Objectives

This thesis was part of the DFG project "MesiCrust: Mechanisms of Soil Erosion under Forest – The Role of Biological Soil Crusts" (DFG SE 2767/2-1), which investigated how biocrusts and bryophytes influence soil erosion and the soil water balance in skid trails of a temperate forest ecosystem. This included both in-situ investigations of soil erosion in the skid trails during the natural process of vegetation succession (Manuscript 2; GALL et al., 2022) and ex-situ investigations of the influence of combinations of soil substrates and moss species (soil-moss combinations) on soil erosion (Manuscript 3). Additionally, water absorption and evaporation patterns in the soil-moss combinations were examined during and after watering, considering moss structural traits as well (Manuscript 4; THIELEN et al., 2021).

Thus, this thesis provides an overview of the water-related interactions between soils and bryophytes, from the site level of skid trails to the microscopic level of individual structural traits of bryophytes. Specifically, the following objectives were pursued:

i. Monitoring of the occurrence and succession of biocrusts and bryophytes in the skid trails of a temperate forest (Manuscript 2)

ii. Investigating the impact of biocrusts and bryophytes on soil erosion processes in the skid trails of a temperate forest (Manuscript 2)

iii. Examining the influence of soil-moss combinations on surface runoff, percolation and soil erosion (Manuscript 3)

iv. Monitoring of the temporal dynamics of water content in soil-moss combinations during soil erosion measurements (Manuscript 3)

v. Investigating the maximum water storage capacity of different moss species and to what extent it is influenced by their structural traits (Manuscript 4)

vi. Analysing the effect of soil-moss combinations on temporal dynamics of water content during watering and subsequent desiccation (Manuscript 4)

In Manuscript 2, the hypothesis was tested that biocrusts occur as pioneer vegetation in skid trails of temperate forests and that biocrusts and bryophytes are a major factor in mitigating soil erosion following disturbances.

Additionally, in Manuscript 3, it was hypothesized that moss covers reduce surface runoff as well as soil erosion and increase percolation, also affecting the temporal dynamics of soil water content.

Finally, Manuscript 4 addressed the hypothesis that the water storage capacity of bryophytes is determined by their total surface area and that bryophytes have a positive effect on the soil water content during watering and subsequent desiccation.

2 Material and methods

2.1 Study sites

The studies took place in the Schönbuch Nature Park in south-western Germany (Figure 2), which is a low-altitude (highest peak, Bromberg, is 583 m above sea level), hilly (69 % with slopes ≤ 3 ° and 14 % with slopes > 15 °), and almost completely forested (86 %) area in the sub-Atlantic temperate climate zone (Arnold, 1986; Einsele & Agster, 1986). Mean annual temperature is 8.3°C and average precipitation is 740 mm (mean annual values from 1979 to 1984 at the climate station in Herrenberg; DWD Climate Data Center, 2021a), which is comparable to the long-term average for Germany (DWD Climate Data Center, 2021b, c). The Schönbuch Nature Park is located in Triassic hills consisting of sandstones, marlstones, and claystones with abundant limestones and a few Lower Jurassic shales, sandstones, and limestones on the hilltops, which are often covered with a loess layer (Einsele & Agster, 1986).

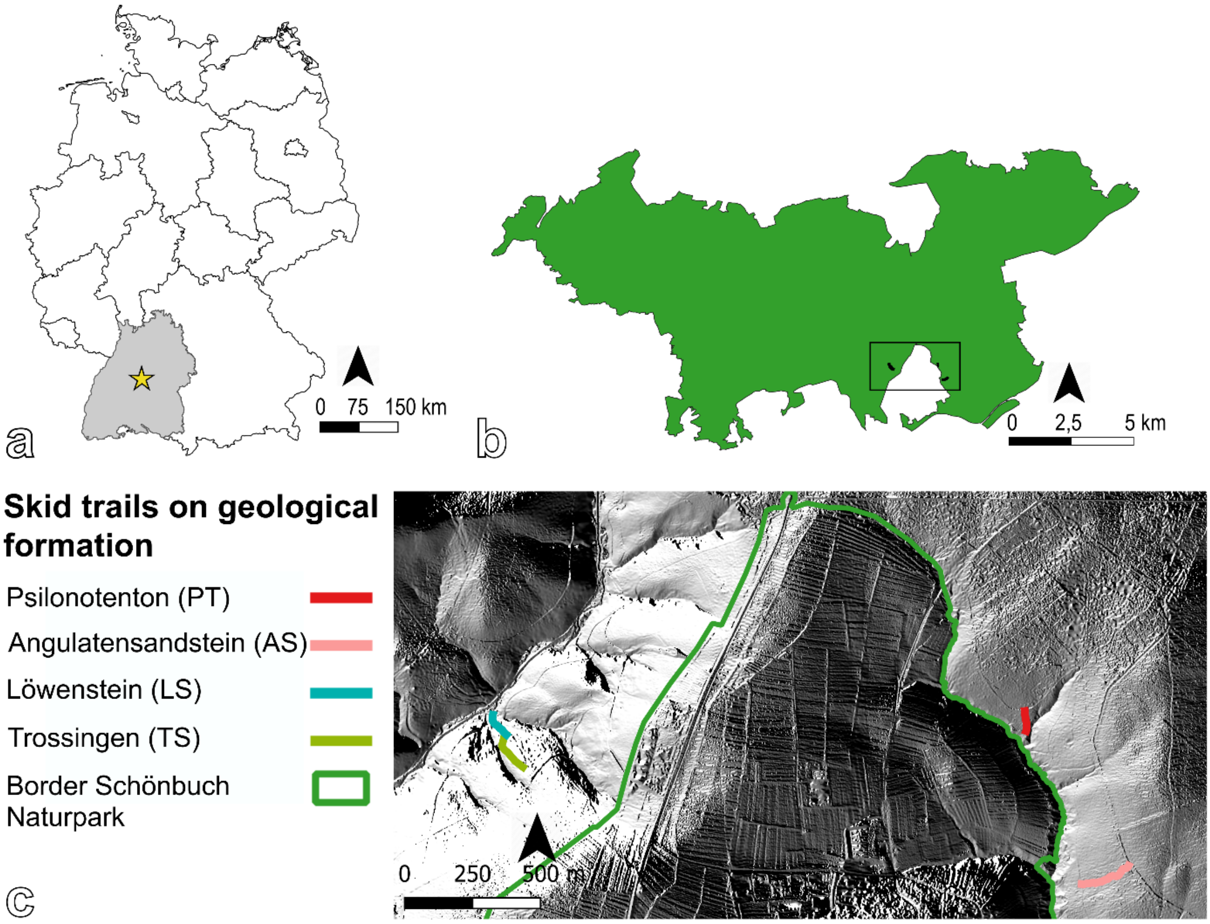


Figure 2: Overview of the study area. (a) Location of the Schönbuch Nature Park in Germany. (b) Location of the selected skid trails inside the Schönbuch Nature Park. (c) Location of the four skid trails on a hillshade raster (Landesamt für Geoinformation und Landentwicklung Baden-Württemberg, https://www.lgl-bw.de).

Four unfortified skid trails newly created in winter 2018/19 with different geological substrates, soil properties, and vegetation characteristics were selected for this study (Table 1). They were generated during logging operations of the State Forestry Administration of Baden-Württemberg (ForstBW) and consisted of two wheel tracks and a centre track in between (Figure 3). The skid trails were named according to their location in the respective geological formation: Angulatensandstein (AS), Psilonotenton (PT), Löwenstein (LS), and Trossingen (TS). AS is composed of thin, platy, fine-grained sandstones containing unweathered limestone; PT consists of pyrite-bearing shale clay interstratified by beds of limestone; TS is comprised of firm, fractured, unstratified claystones with lime nodules; and LS forms medium- to coarse-grained banked sandstones interrupted by reddish marls (EINSELE & AGSTER, 1986). However, the in-situ geological formation is not necessarily the same as the parent material of soil formation, since the hills of the Schönbuch are extensively covered by periglacial slope deposits with varying proportions of loess (BIBUS, 1986).

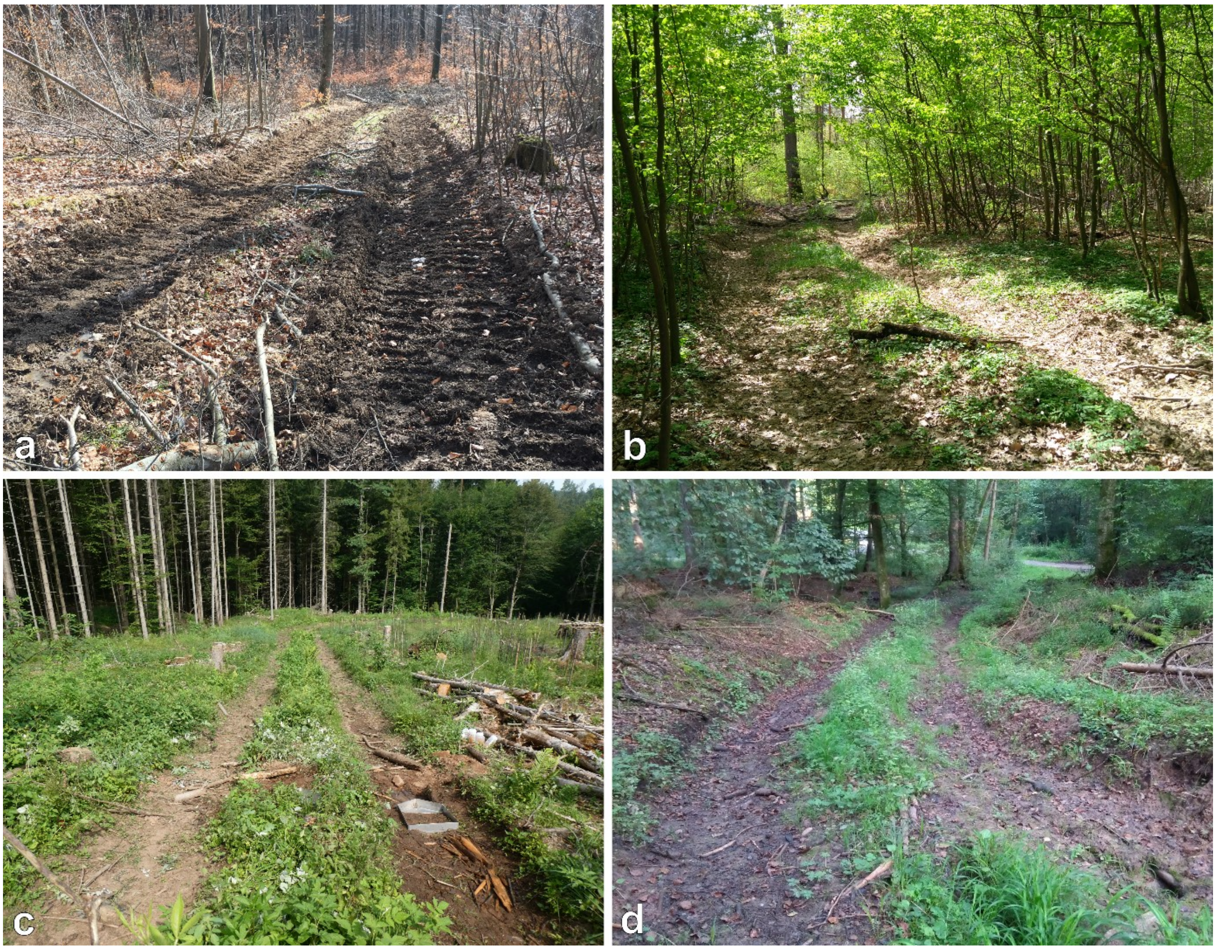


Figure 3: Overview of the skid trails in the Schönbuch Nature Park. (a) Skid trail on Psilonotenton-Formation (PT) in February 2019. (b) Skid trail on Angulatensandstein-Formation (AS) in April 2019. (c) Skid trail on Trossingen-Formation (TS) in July 2019. (d) Skid trail on Löwenstein-Formation (LS) in September 2019.

Table 1: Characteristics of the four studied skid trails. They are named according to their location in the respective geological formation: Psilonotenton (PT), Angulatensandstein (AS), Löwenstein (LS), and Trossingen (TS).

	PT	**AS**	**LS**	**TS**
Location of the skid trails	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
Forest characteristics	Deciduous forest (*Fagus sylvatica*)	Deciduous forest (*Quercus petraea*, *Fagus sylvatica*, *Carpinus betulus*)	Mixed coniferous and deciduous forest (*Pinus sylvestris*, *Picea abies*, *Fagus sylvatica*, *Carpinus betulus*)	Coniferous forest (*Picea abies*)
Series	Lower Jurassic	Lower Jurassic	Upper Triassic	Upper Triassic
Formation	Psilonotenton (PT)	Angulatensandstein (AS)	Löwenstein (LS)	Trossingen (TS)
Parent material	Shale clay	Sandstone	Sandstone	Claystone
Slope	7.2°	4.6°	10°	11.3°
Aspect	South	Southwest	West	Northwest
Soil type in skid trail wheel track (IUSS WORKING GROUP WRB, 2015)	Calcaric Albic Planosol (Clayic, Ochric, Raptic)	Dystric Leptosol (Ochric, Siltic, Stagnic)	Calcaric Cambisol (Humic, Loamic, Protovertic)	Eutric Cambisol (Geoabruptic, Clayic, Ochric, Protovertic)
Soil type in surrounding forest (IUSS WORKING GROUP WRB, 2015)	Eutric Calcaric Amphistagnic Cambisol (Loamic, Ochric)	Dystric Stagnic Regosol (Ochric)	Eutric Cambisol (Ochric)	Eutric Cambisol (Geoabruptic, Clayic, Ochric, Raptic, Protovertic)
Humus form in surrounding forest	Mull-like moder	L mull	Typical moder	Mull-like moder
Soil texture	Silty clay loam • Sand: 6.67 % • Silt: 56.49 % • Clay: 36.86 %	Silt loam • Sand: 6.89 % • Silt: 67.99 % • Clay: 25.33 %	Clay loam • Sand: 25.91 % • Silt: 40.78 % • Clay: 33.20 %	Silty clay loam • Sand: 11.46 % • Silt: 50.70 % • Clay: 37.81 %
Soil organic carbon (SOC)	5.22 %	4.08 %	5.52 %	7.95 %
Total nitrogen (N_t)	0.31 %	0.24 %	0.27 %	0.40 %
pH in 0.01 M $CaCl_2$ (pH_{Ca})	6.9	5.6	6.9	5.4

2.2 Field experiments

2.2.1 Rainfall simulations with small-scale runoff plots

Small-scale runoff plots (ROP) were used in combination with rainfall simulations to investigate interrill soil erosion processes (Zemke, 2016; Seitz et al., 2019), i. e., sediment discharge in thin sheets between rills due to shallow surface runoff (Blanco & Lal, 2008). The ROPs are 40 x 40 cm stainless-steel metal frames (surface: 0.16 m²) connected to a triangular surface runoff gutter and driven into the topsoil (Figure 4). A total of four ROPs were installed in each right wheel track, and another four in the centre track at each of the four skid trails. Two additional ROPs were placed in the undisturbed forest soil adjacent to each skid trail, yielding a total of 40 ROPs per rainfall simulation. Surface runoff and sediment discharge were collected in 1 L sample bottles attached to the outlet.

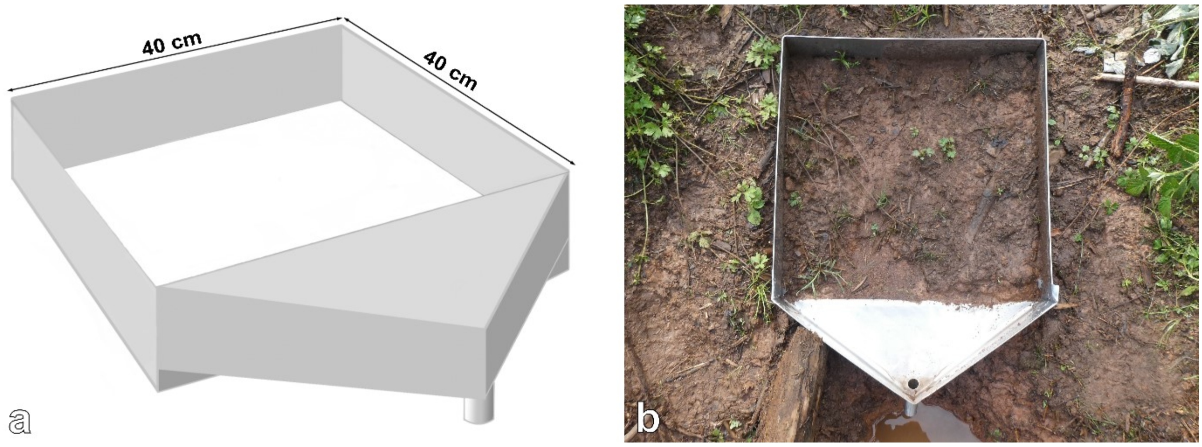


Figure 4: Illustration of a runoff plot (ROP). (a) Technical drawing of a ROP with dimensions (Illustration: Julia Dartsch). (b) A ROP installed in the field.

Rainfall simulations were performed with the Tübingen rainfall simulator (Iserloh et al., 2013; Seitz et al., 2015) equipped with a Lechler nozzle 460.788.30 and set to a falling height of 3.5 m (Figure 5). The sprinkle area was protected from outside influences by a lightweight portable tent. Rainfall simulations with an intensity of 60 mm h^{-1} were conducted for a duration of 30 minutes, which refers to a regional rainfall event with a recurrence interval of 20 years (DWD Climate Data Center, 2021d). Drop size spectrum and intensity were calibrated with a "Laser Precipitation Monitor" by Thies (Lanzinger et al., 2006) to obtain homogeneous properties. Rainfall simulations were conducted at four times (March, July, October 2019, and February 2020) in the skid trails and at two times (October 2019 and February 2020) in the undisturbed forest soil, yielding a total of 144 measurements. Prior to each rainfall simulation, soil moisture was determined adjacent to each ROP using a ThetaProbe ML2 in combination with an HH2 Moisture Meter (both Delta-T Devices, Cambridge, UK). Slope was measured on both sides of each ROP using an inclinometer. Additionally, water repellency of the skid trails was investigated using water drop penetration time (WDPT) test (Dekker et al., 2009).

Figure 5: The Tübingen rainfall simulator with protective tent. (a) The Tübingen rainfall simulator inside the tent. (b) The protective tent in the field (2 x 2 m ground area, 4 m height).

Following soil erosion measurements, the total surface runoff of a ROP was read on the millimetre measuring scale of the sample bottles. To determine sediment discharge, the runoff water was evaporated from the sample bottles in a compartment drier at 40°C. Subsequently, the dried sediment remaining in the sample bottle was weighed.

2.2.2 Vegetation survey

The development of vegetation cover and species composition per ROP was determined during vegetation survey campaigns at five times (April, June, July, October 2019, and February 2020) together with soil erosion measurements. Total vegetation and bryophyte cover were surveyed for each ROP, and the Braun-Blanquet cover-abundance scale was used to determine coverages at the species level (BRAUN-BLANQUET, 1964). Vascular-plant cover was calculated as the difference between total vegetation and bryophyte cover. Classification of vascular plants and bryophytes was carried out at the species level, and performed either by eye or with a stereomicroscope (SteREO Discovery.V8, Carl Zeiss Microscopy Deutschland GmbH, Oberkochen, Germany) or a microscope (Leitz SM-Lux, Ernst Leitz GmbH, Wetzlar, Germany) using the following plant identification literature: JÄGER & WERNER (2005), NEBEL et al. (2000, 2001, 2005), and MOSER (1963). Additionally, perpendicular photographs were taken of each ROP using a digital compact camera (Panasonic DC-TZ91, Osaka, Japan) to assess total vegetation cover with a photogrammetric survey. The photographs were processed with the grid quadrat method with a 100-division digital grid (BELNAP et al., 2001b), in which bare soil and vegetation cover were separated by hue distinction.

2.2.3 Rainfall simulations with infiltration boxes

To investigate surface runoff, sediment discharge and temporal dynamics of soil water content in five soil substrates with different coverages and moisture conditions during erosion processes, an ex-situ rainfall simulation was performed with infiltration boxes equipped with biocrust wetness probes (BWP, UP GmbH, Cottbus, Germany). Infiltration boxes are 40 x 30 x 15 cm stainless-steel containers with a triangular surface runoff gutter at the top and an outlet at the bottom to collect percolated water (Figure 6). They were filled with soil substrates from the topsoil of the skid trail wheel tracks (0-10 cm) up to a height of 6.5 cm from the top edge by installing a substructure of perforated metal.

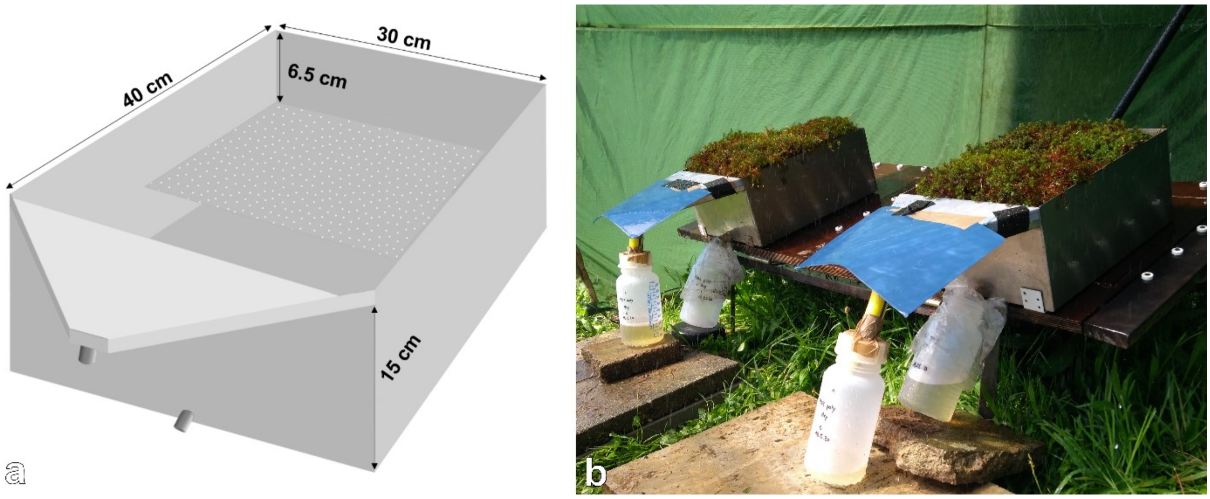
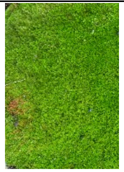


Figure 6: Illustration of an infiltration box. (a) Technical drawing of an infiltration box with dimensions (Illustration: Julia Dartsch). (b) Infiltration boxes during rainfall simulations.

The soil substrates were previously air-dried and sieved to 6.3 mm. In addition, we selected a sandy substrate from the Lower Triassic of the Palatinate Forest to include a substrate that has distinctly different properties compared to the other substrates of the Schönbuch Nature Park (Table 2). The designation of this substrate was also based on the geological formation: Bernburg (BB). Four treatments according to moisture condition and cover type were distinguished: bare & dry, bare & wet, moss & dry, and moss & wet. Six moss species (*Amblystegium serpens* (Hedw.) Schimp., *Brachythecium rutabulum* (Hedw.) Schimp., *Eurhynchium striatum* (Hedw.) Schimp., *Oxyrrhynchium hians* (Hedw.) Loeske, *Plagiomnium undulatum* (Hedw.) T.J.Kop., and *Polytrichum formosum* (Hedw.) G.L.Sm.) were selected. *Amblystegium serpens* was cultivated in the laboratory and we considered both a lab-grown and a field-collected sample of *Oxyrrhynchium hians*. The following soil-moss combinations were generated: *P. undulatum* (Field) + PT (n = 4), *O. hians* (Field) + AS (n = 2), *O. hians* (Lab) + AS (n = 2), *B. rutabulum* (Field) + LS (n = 2), *A. serpens* (Lab) + LS (n = 2), *E. striatum* + TS (n = 4), and *P. formosum* + BB (n = 4; Table 2).

Table 2: Characteristics of the studied soil-moss combinations. The names refer to the geological substrate from which they were collected: Psilonotenton (PT), Angulatensandstein (AS), Löwenstein (LS), Trossingen (TS), and Bernburg (BB).

	PT	**AS**	**LS**	**TS**	**BB**
Sampling location for soil substrates	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
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
Photos of the soil substrates before applying the moss samples					
Soil texture	Silty clay loam • Sand: 6.88 % • Silt: 56.28 % • Clay: 36.93 %	Silty 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 (SOC)	5.25 %	4.34 %	4.39 %	8.02 %	4.93 %
Total nitrogen (N_t)	0.30 %	0.25 %	0.19 %	0.40 %	0.20 %
pH in 0.01 M $CaCl_2$ (pH_{Ca})	7.0	5.8	7.0	5.6	3.4
Moss species for the soil-moss combinations	4 x *P. undulatum*	2 x *O. hians* (lab-grown; left photo) 2 x *O. hians* (field-collected; right photo)	2 x *B. rutabulum* (left photo) 2 x *A. serpens* (lab-grown; right photo)	4 x *E. striatum*	4 x *P. formosum*
Photos of the moss samples growing on the substrate (March 2020)		 	 		

For the rainfall simulations with the Tübingen rainfall simulator (see section 2.2.1), two infiltration boxes were placed on a table with 20° slope (Figure 6 b). Surface runoff, sediment discharge and percolated water were collected in 1 L sample bottles and treated as previously described (see section 2.2.1). To measure water content during rainfall simulations, two BWPs per infiltration box were installed at 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), that recorded electrical conductivity (EC) every five minutes at the substrate surface and every two minutes at 3 cm substrate depth. These inconsistent logging intervals are due to a technical error and were later interpolated to intervals of one minute for each measurement.

First, rainfall simulations were performed for bare substrates in air-dried condition (n = 4 per substrate; 20 measurements). 24 hours later the same infiltration boxes were irrigated once again in wet condition (20 measurements). Second, moss samples were placed onto substrates and stored in a shady place outdoors to adapt and grow on the substrate (December 2019), until the next rainfall simulations were conducted five months later (May 2020). Moss-covered infiltration boxes were also measured in dry and wet condition (40 measurements). Altogether, 80 rainfall simulations were carried out.

2.2.4 Greenhouse experiment with infiltration boxes

A greenhouse experiment was set up to investigate water absorption and evaporation patterns in soil-moss combinations during and after watering. For this purpose, the following soil-moss combinations in infiltration boxes were selected from those described above, leading to six treatments with two replicates each: *P. undulatum* (Field) + PT, *O. hians* (Field) + AS, *O. hians* (Lab) + AS, *B. rutabulum* (Field) + LS, *A. serpens* (Lab) + LS, and *E. striatum* + TS. Here, three BWPs were installed per infiltration box in different positions: in 3 cm substrate depth, in the first 5 mm of the substrate surface and in the moss cover. Each sample was watered for one hour (6 L h^{-1}) with a garden sprayer, split into 500 mL every 5 minutes (Figure 7). This corresponds to a precipitation amount of 122 mm, which occurs less frequently than once in a hundred years in Germany (DWD CLIMATE DATA CENTER, 2021d). During watering and subsequent desiccation, EC was recorded every 10 seconds for 72 hours with BWPs connected to a GP2 Data Logger. At the same time, air temperature and relative humidity (RH) were monitored (Tinytag Plus 2 – TGP-4500, Gemini Data Loggers, Chichester, UK). During desiccation, evaporation rates were calculated using the following formula

$$E = \frac{WC_0 - WC_x}{t_x - t_0},$$

where WC_0 is the maximum gravimetric water content in the examined time period, WC_x is the gravimetric water content at time point x, and t_x and t_0 are the respective time points (ROBINSON et al., 2000).

Figure 7: Overview of the greenhouse experiment setup. (a) Biocrust wetness probe (BWP) in 3 cm substrate depth before refilling with another 3 cm substrate layer. (b) BWP at the substrate surface and in the moss cover. (c) Experimental setup with moss-covered substrate inside the infiltration box and sprayer.

2.3 Laboratory experiments

2.3.1 Basic soil properties

Topsoil samples (0-5 cm) were collected in the surroundings of each ROP, oven-dried at 40°C, and sieved to 2 mm to determine basic soil properties. Grain size distribution was obtained using an X-ray particle size analyzer (SediGraph III, Micromeritics, Norcross, GA, US), and aggregate size was measured by wet sieving, which served as a basis for calculating the mean weight diameter (MWD) of soil aggregates (VAN BAVEL, 1950). Soil pH was measured in 0.01 M $CaCl_2$ solution with a pH meter and SenTix 81 electrodes (WTW, Weilheim, Germany), while soil organic carbon (SOC) and total nitrogen (N_t) were determined using an elemental analyzer (Vario EL III, Elementar Analysensysteme GmbH, Hanau, Germany). Core samples (100 cm^3) were collected to determine bulk density of the topsoil using the mass-per-volume method (BLAKE & HARTGE, 1986).

2.3.2 Maximum water storage capacity of soil substrate and moss samples

After completing rainfall simulations and the greenhouse experiment, moss and soil substrate samples were taken from the infiltration boxes to assess their maximum water storage capacity (WSC_{max}). Mosses were detached from the substrate, dried at 30°C in a dehydrator (Dörrex 0075.70, Stöckli, Netstal, Switzerland) and weighed on a precision balance (Mettler Toledo MS603S, Mettler Toledo, Columbus, US). Soil substrate samples were taken using a 100 cm^3 core cutter, dried at 105°C in a compartment drier, and weighed. Subsequently, both moss and soil substrate samples were saturated with water. Mosses were saturated by immerging them in water for 5 minutes between two soil sieves with 52 µm mesh size at the bottom and 250 µm at the top, then drained for 2 minutes, and weighed using the same precision balance. To saturate the soil substrates, they were placed into a tub of water until the surface was wet, and then weighed (BLUME et al., 2011).

2.3.3 BWP calibration

As BWPs measure EC, they were calibrated to gravimetric water content according to WEBER et al. (2016a). For this purpose, moss and soil samples were water saturated as described above (see section 2.3.2) and their weight loss and EC were measured simultaneously for at least 65 hours under laboratory conditions (average air temperature: 19.1 ± 1.2°C; average RH: 45.8 ± 5.9 %; recorded with Tinytag Plus 2 at 5-minute intervals). Samples were placed on a precision balance (Kern EW 620-3NM, Kern & Sohn GmbH, Balingen, Germany) and equipped with three BWPs per sample to record EC and weight loss at 10-second intervals. A temperature correction was then applied to the EC values, the gravimetric water content was derived from the weight data, and an individual calibration curve was generated for each sample. For more information on BWP calibration and an overview of all calibration curves, see THIELEN et al. (2021).

These calibration curves were used for the greenhouse experiment with the infiltration boxes (see section 2.2.4), but were not applicable for BWP measurement during rainfall simulations (see section 2.2.3). Although the same infiltration boxes were used in both experiments, we obtained partially negative values for the water content during rainfall simulations using the calibration curves, which was probably caused by the high temperature differences between the measurements of bare and moss treatments (December 2019 and May 2020). For this reason, we here used the simplified linear calibration procedure described in WEBER et al. (2016a) and already applied by LÖBS et al. (2020).

2.3.4 Moss structural traits

After WSC_{max} assessment, the following structural traits were determined for each moss species: total surface area, leaf area, leaf frequency, leaf area per shoot length, shoot length, length of a single component (sum of shoot length and length of attached branches), shoot density, and leaf area index (LAI). First, three circular samples with a diameter of 5.5 cm were taken from each moss species (sample area = 23.76 cm²), dissected into single moss shoots, and scanned using a high-definition flatbed scanner (Epson Perfection V700 Photo, Suwa, Japan). All shoots were counted to determine shoot density. Shoot and branch length were measured using ImageJ versions 1.53e and Fiji 2.1.0 (SCHINDELIN et al., 2012; SCHNEIDER et al., 2012). Second, three shoots were selected from each sample, all leaves along one centimetre of the shoot were removed, placed on a slide, and scanned either using the flatbed scanner or a digital microscope (Keyence VHX-7000 with dual zoom lens VH-ZST, Keyence, Osaka, Japan). Subsequently, leaf area was measured using ImageJ as well and formulas according to THIELEN et al. (2021) were applied to calculate total surface area and LAI.

2.4 Statistical analysis

All statistical analyses were conducted with R software (R CORE TEAM, 2021). Prior to all statistical tests, normality was proven with the Shapiro-Wilk test, and homoscedasticity was verified using Levene`s test. One-way ANOVAs combined with post-hoc Tukey`s HSD tests were used to examine significant differences in normally distributed and homoscedastic data. To detect significant differences in non-normally distributed and heteroscedastic data, Kruskal-Wallis tests were applied in combination with post hoc Games-Howell or Wilcoxon signed-rank tests for related measurements and post hoc Wilcoxon rank-sum tests for independent measurements. Generalized linear models were performed to screen for significant differences in samples with repeated measurements (using the R package “stats”). A nonparametric analysis of covariance comparing regression curves from the R package “sm” was performed to determine if there was a significant difference between vascular-plant ROPs and bryophyte ROPs in terms of sediment discharge (BOWMAN & AZZALINI, 2021).

Differences in bryophyte species composition between skid trails were identified using an analysis of similarity with 999 permutations from the R package “vegan” (OKSANEN et al., 2020). Generalized additive models (GAMs) with restricted maximum likelihood and smoothing parameters selected by an unbiased risk estimator (UBRE) criterion (R package “mgvc”) were performed to evaluate the combined effect of environmental parameters on sediment discharge and bryophyte coverage (WOOD, 2020). Significance was assessed as $p < 0.05$ in all cases. For all mean values described, the standard error was also given (mean ± standard error). Depending on the distribution of the data, either pairwise Pearson or Spearman`s Rank correlation analyses were conducted to describe relationships between different parameters.

3 Results and discussion

3.1 Influence of biocrusts and bryophytes on soil erosion in a mesic forest (Manuscript 2)

3.1.1 Vegetation succession and biocrust occurrences

A total of 24 moss, 2 liverwort and 2 fungi species occurred in the skid trails, while 13 moss species were present in the undisturbed forest soil and vegetation succession in the four skid trails was different in terms of species composition ($p = 0.001$) and coverage (Figure 8). A few weeks after skidding, protonemata of different species were observed in AS and PT in April 2019, which are the earliest developmental stage of bryophytes with green cell filaments. Parallel DNA-sequencing revealed the presence of cyanobacteria as well as coccoid and filamentous algae (e.g., Chlorophyceae and Xanthophyceae). In July 2019, the early successional stages of *Pohlia lutescens*, *Dicranella schreberiana*, and *Trichodon cylindricus* evolved from the protonemata and were found to be volatile, spreading only during summer and disappearing again at the beginning of autumn. The thallose liverwort species *Apopellia endiviifolia*, which forms shallow structures close to the soil surface in its early developmental stage, occurred in PT and LS in October 2019. However, also in this case the biocrust stage was ephemeral and the transition to a more developed thallus with narrow branching at the tips was smooth. Generally, the most abundant and persistent pioneer bryophyte species were *Brachythecium rutabulum* and *Oxyrrhynchium hians* in all skid trails.

In our study site, the occurrence of cyanobacteria as well as coccoid and filamentous algae plus bryophyte protonemata and the subsequent early developmental stage of bryophyte shoots fulfilled the definition of biocrusts by BELNAP et al. (2001a) and WEBER et al. (2022). These biocrusts occurred in the two skid trails AS an PT from April to July 2019, evolving into *Pohlia lutescens*, *Dicranella schreberiana*, and *Trichodon cylindricus,* which we included here among the temperate biocrust species. While this biocrust stage was primarily characterized by protonemata, the thallose liverwort *Apopellia endiviifolia* colonized in October 2019 and was considered a temperate biocrust species as well. However, this was only the case until *Apopellia endiviifolia* formed antler-like branches along the thallus, as described in ATHERTON et al. (2010), extending considerably above the soil surface.

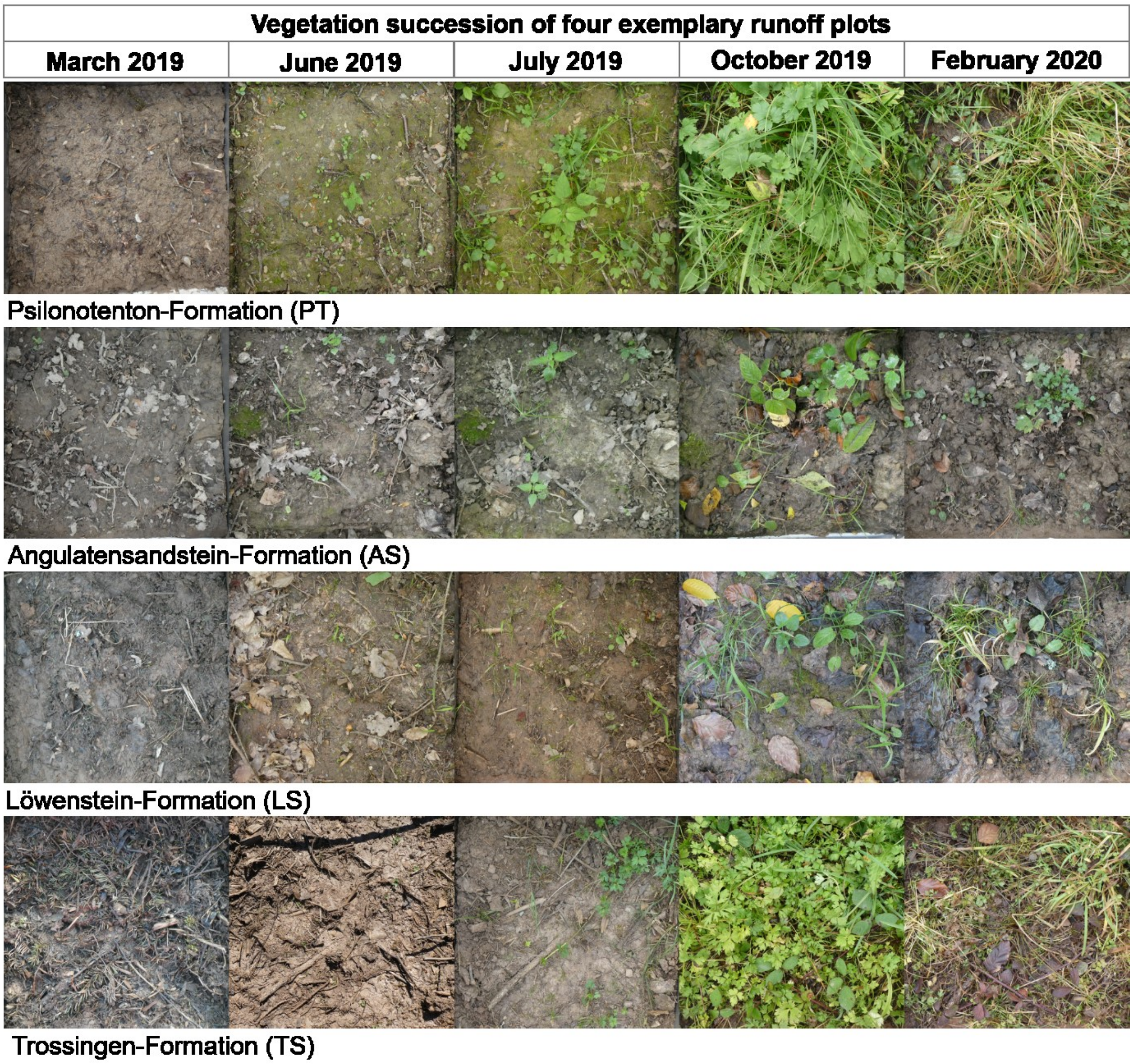


Figure 8: Vegetation succession of four exemplary runoff plots (40 x 40 cm) in wheel tracks of the skid trails in the Schönbuch Nature Park.

The development of bryophyte and total vegetation cover varied widely in the skid trails (Figure 9). In AS and LS, total vegetation cover was lower than in PT ($p < 0.001$), which was also true for bryophyte cover (for AS and PT: $p < 0.001$; for LS and PT: $p < 0.01$). Comparatively, PT and TS were rapidly overgrown by vascular plants; however, they did not replace bryophytes. This coexistence of vascular plants and bryophytes was also reflected in a positive correlation between their cover rates (Spearman`s correlation $\rho = 0.38$, $p < 0.001$). A decline in bryophyte cover was observed for the first time in autumn on deciduous, but not on coniferous sites. Using a GAM that explained 80.3 % of the deviation of bryophyte cover, pH ($p < 0.001$), SOC ($p < 0.001$), sand content ($p < 0.001$), total vegetation coverage ($p < 0.001$), and N_t ($p < 0.05$) were identified as significant influencing factors.

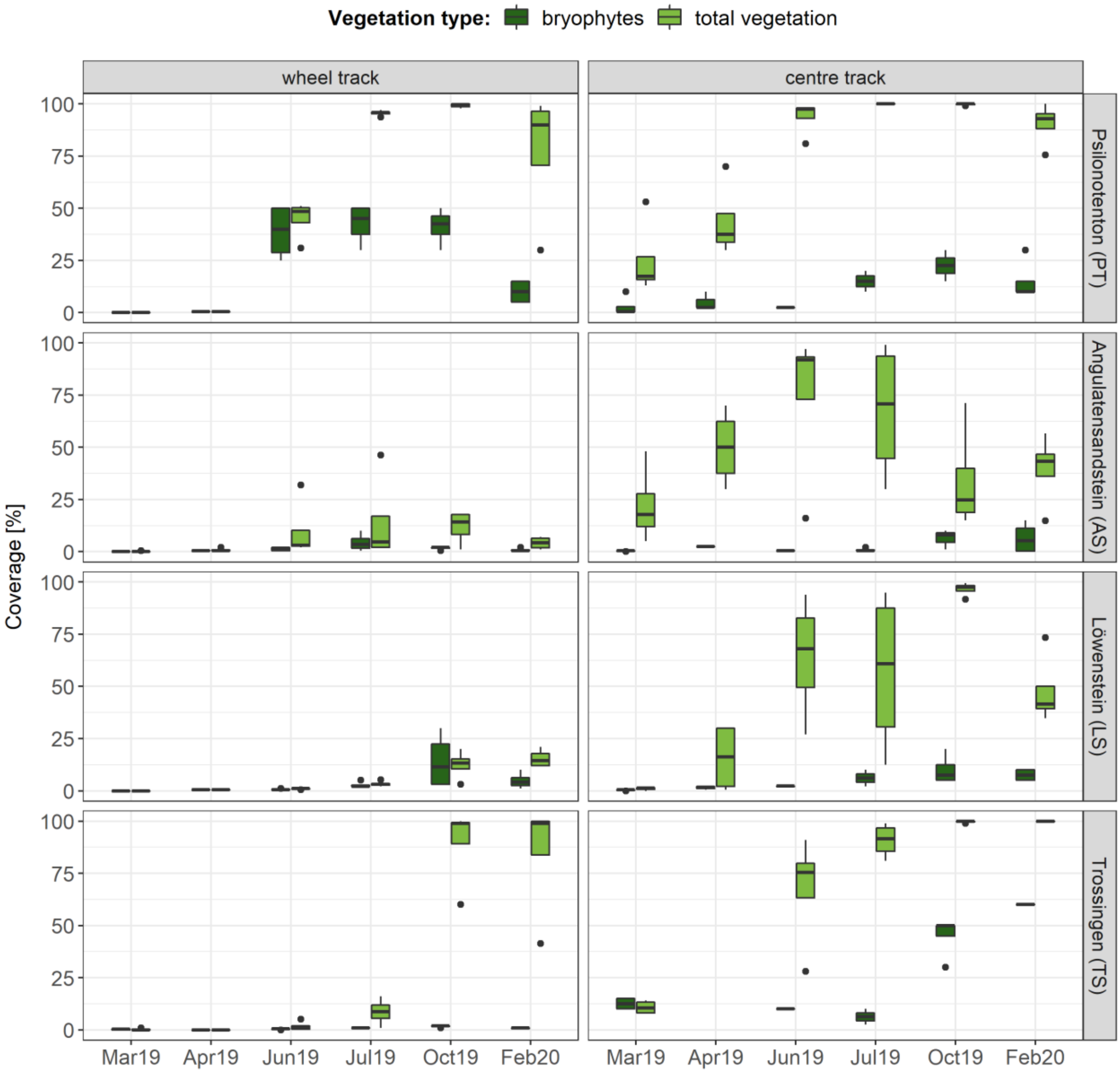


Figure 9: Development of bryophyte and total vegetation cover [%] per runoff plot (n = 4) at the individual skid trails. The bottom and the top of the box represent the first and third quartiles, and whiskers extend up to 1.5 times the interquartile range (IQR) of the data. Outliers are defined as more than 1.5 times the IQR and are displayed as dots.

Occurrence and cover of bryophytes as well as biocrusts depended on local soil properties, with pH being an important control variable for bryophyte growth. The importance of pH on the growth and species richness of bryophytes has been highlighted in several studies (LÖBEL et al., 2006; HYDBOM et al., 2012; OLDÉN et al., 2016), and this is also true for biocrusts (PONZETTI & MCCUNE, 2001). For example, in a temperate forest ecosystem comparable to our study area, ROLA et al. (2021) showed that soils with a more acidic pH promoted a larger bryophyte cover.

The time when bryophytes were overgrown by vascular plants marks the transition from biocrusts to a developed successional stage of bryophyte cover, characterized by a large proportion of the biomass being above the soil surface (BELNAP et al., 2001a). This bryophyte cover was established even in presence of vascular vegetation, contradicting observations that vascular plants limit bryophyte growth in different ecosystems (BERGAMINI et al., 2001; FOJCIK et al., 2019; CORBIN & THIET, 2020). While FOJCIK et al. (2019) explained a negative correlation between bryophyte and vascular-plant cover in a temperate forest with competition, BERGAMINI et al. (2001) attributed this effect in montane wetlands primarily to the availability of light, with a combination of optimal radiation and moisture conditions also depending on the extent of vascular-plant cover. Conversely, Ingerpuu et al. (2005) demonstrated in a grassland experiment that vascular plants could actually facilitate bryophyte growth, which was explained by a more favourable microclimate under the canopy of vascular plants. Similar effects were also reported by MÁRIALIGETI et al. (2009) and ROLA et al. (2021) for temperate forests, which are comparable to our results. ROLA et al. (2021) pointed out that species composition and density of vascular-plant cover also play an essential role.

We hypothesize that the decline of bryophyte cover in our study site was caused by leaf litter fall rather than suppression by vascular plants, as only the deciduous forest sites showed a decline of bryophyte cover in autumn. Presumably, the leaf litter resulted in excessive shading of the bryophytes so that they could not survive. This negative impact of leaf litter on bryophyte growth was also reported in other studies (MERCIER et al., 2019; ALATALO et al., 2020).

3.1.2 Impact of biocrusts and bryophytes on soil erosion

Average sediment discharge was 206.76 ± 24.53 g m^{-2} in the wheel tracks and 15.68 ± 3.84 g m^{-2} in the undisturbed forest soil ($p < 0.001$), a difference by a factor of 13.2. Centre tracks caused a mean sediment loss of 63.09 ± 10.28 g m^{-2}, being 4 times higher than in the undisturbed forest soil ($p < 0.05$). Considering only bare soil ROPs, an average soil erosion of 341.53 ± 68.20 g m^{-2} was achieved, which corresponds to a 22-fold increase compared with undisturbed forest soil. In general, mean sediment discharge in the skid trails was highest in March 2019 (201.80 ± 39.82 g m^{-2}) and was significantly decreased in July 2019 (74.13 ± 16.16 g m^{-2}; $p < 0.01$; Figure 10). Subsequently, sediment discharge increased in October 2019 (97.77 ± 21.16 g m^{-2}; $p < 0.05$) and rose again in February 2020 (165.03 ± 29.75 g m^{-2}; $p < 0.001$). This charateristic trend of soil erosion occurred in PT, AS and LS, but not in TS. We found a difference for sediment discharge between the measurement times for PT and LS, but not for AS and TS. While PT showed a 89 % decrease of sediment discharge from March 2019 to July 2019, LS had 59 % reduction over the same period. A GAM explained 71.9 % of the deviation of sediment discharge, with surface runoff ($p < 0.001$) and total vegetation cover ($p < 0.001$) being significant.

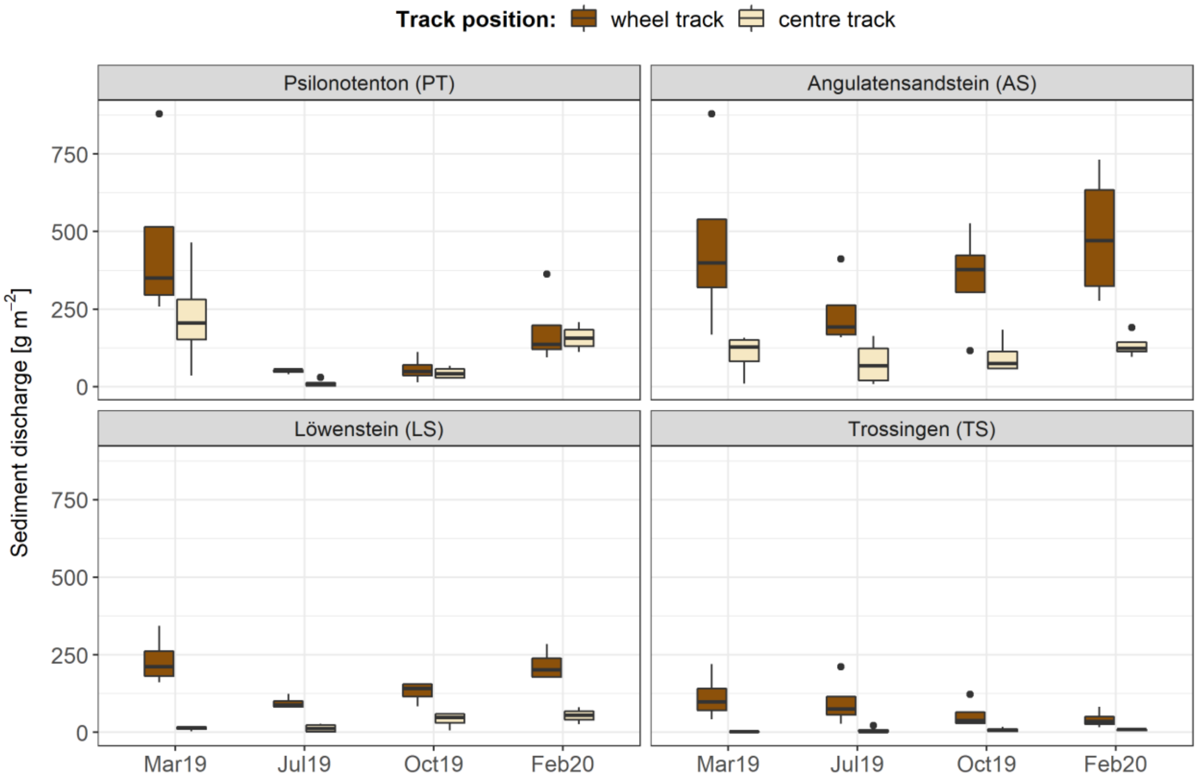


Figure 10: Sediment discharge during simulated rainfall in the wheel track (n = 4) and centre track (n = 4) of the four skid trails for every rainfall simulation. The bottom and the top of the box represent the first and third quartiles, and whiskers extend up to 1.5 times the interquartile range (IQR) of the data. Outliers are defined as more than 1.5 times the IQR and are displayed as dots.

Our findings highlight that skid trails are a key driver of soil erosion in temperate forest ecosystems and that wheel tracks in particular increased sediment discharge, which has also been demonstrated in previous studies (SAFARI et al., 2016; ZEMKE, 2016). This is primarily due to soil compaction and disturbance of the forest floor by timber-harvesting machines, which enhances surface runoff, and in turn leads to an increase in soil erosion (ZEMKE et al., 2019). The amount of sediment discharge clearly depended on the particular site, indicating an important effect of parent material on soil erosion, as also demonstrated by RODRIGO-COMINO et al. (2018). Highest reduction in soil erosion was achieved in PT in July 2019, when biocrusts dominated by protonema and early-successional bryophytes were abundant. Such an erosion-mitigating effect of protonema- and bryophyte-dominated biocrusts was also observed by SEITZ et al. (2017) in a subtropical forest plantation.

Surprisingly, sediment discharge increased again in autumn and winter despite a high vegetation cover in all skid trails except TS. Several erosion studies on skid trails already emphasized vegetation cover as one of the key control variables of soil erosion (ZEMKE, 2016; MCEACHRAN et al., 2018), with sediment discharge often being highest one year after skidding and declining as vegetation cover increased (BAHARUDDIN et al., 1995; JOURGHOLAMI et al., 2017; MALVAR et al., 2017). Similar to our results, MARTÍNEZ-ZAVALA et al. (2008) demonstrated a seasonality in their erosion measurements on forest backslopes in southern Spain. They discovered high soil erosion rates in winter despite vegetation cover and attributed this to higher soil moisture, although this effect did not occur with vegetation cover above 30 %. In our case, vegetation cover was significantly higher and there was no clear relationship between soil erosion and antecedent soil moisture.

Sediment discharge was negatively affected by total vegetation cover (Spearman`s correlation $\rho = -0.61$, $p < 0.001$). When considered separately, bryophyte cover showed a stronger negative relationship with sediment discharge (Spearman`s correlation $\rho = -0.54$, $p < 0.001$) than vascular-plant cover (Spearman`s correlation $\rho = -0.36$, $p < 0.001$). All cover classes exhibited different sediment discharge, with a 77 % reduction in sediment discharge measured between bare ROPs and bryophyte ROPs ($p < 0.001$) and a 59 % reduction between bare ROPs and vascular-plant ROPs ($p < 0.005$). Sediment discharge was 44 % lower in bryophyte ROPs than in vascular-plant ROPs ($p < 0.05$). When ROPs were categorized into cover classes, there was a nonsignificant trend for bryophytes to result in less sediment discharge compared with vascular plants (Figure 11).

Bryophytes can densely cover the soil of temperate mesic forests (MÄGDEFRAU & WUTZ, 1951), preventing the direct impact of raindrops on the soil surface. Depending on the life form, bryophyte cushions can convert the kinetic energy of the impacting raindrops into a bouncing motion and the raindrop is literally swallowed, so that no splash effect is caused (ROTH-NEBELSICK et al., 2022). Additionally, bryophytes can influence the soil water balance due to their high water storage capacity (OISHI, 2018), which is also related to their structural traits such as leaf frequency and leaf area (THIELEN et al., 2021). Both effects have a particular impact on soil erosion and may explain our result that bryophyte covers protect better against erosion than vascular plants. However, contrasting results were reported by PARSAKHOO et al. (2012), who found that the bryophyte species *Philonotis marchica* produced more sediment than the shrub *Rubus hyrcanus* during rainfall simulations on forest road cutslopes. On the Loess Plateau in China, BU et al. (2015) found that bryophyte-dominated biocrusts reduced soil erosion by 81.0 % compared with bare soil, though the grass *Stipa bungeana* Trin. and the shrub *Caragana korshinskii* Kom. showed a greater erosion-reducing effect (95.9 % and 99.5 %, respectively). A combination of the vascular plant species with bryophytes could increase the erosion-reducing effect by just 0.7 % and 0.3 %, respectively. Thus, there are still a number of unresolved questions regarding bryophyte-soil interactions on aspects such as water storage, infiltration, runoff generation, and therefore erosion processes.

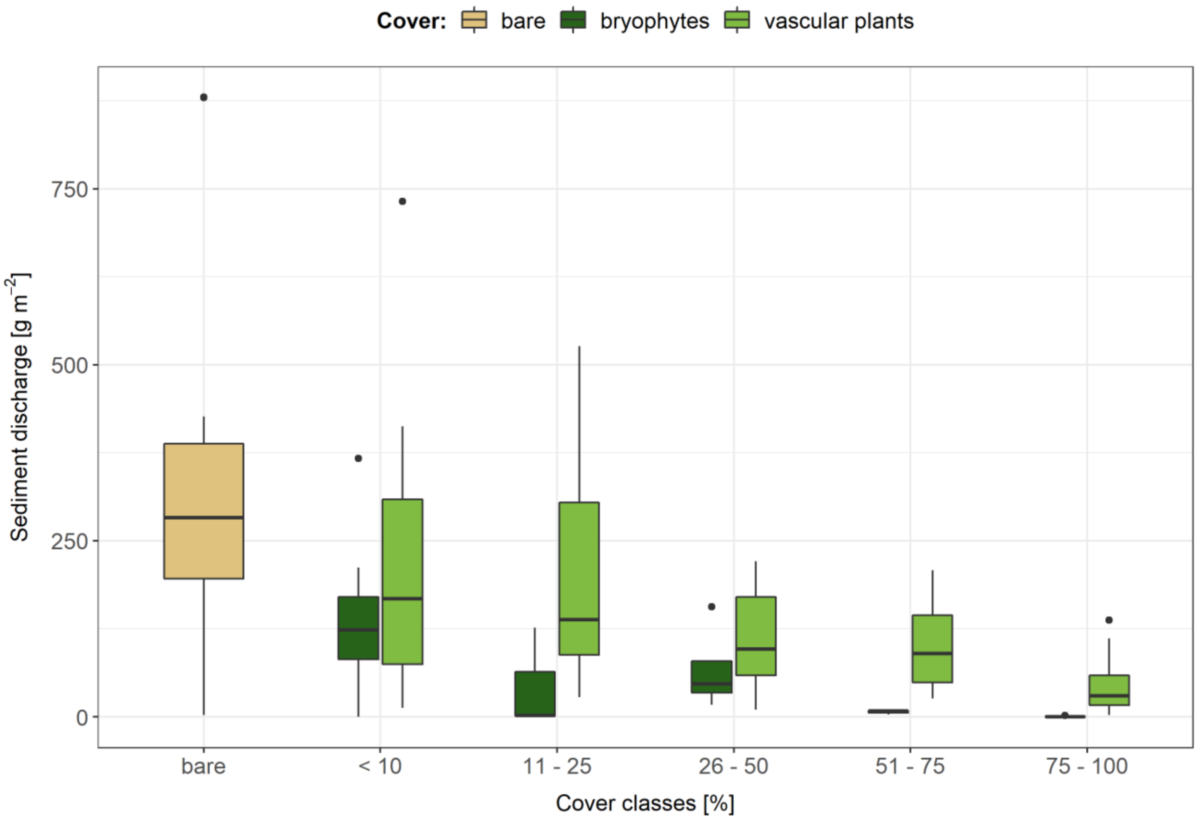


Figure 11: Sediment discharge during simulated rainfall for bare (n = 14), bryophyte (n = 27), and vascular-plant (n = 58) runoff plots (ROPs) categorized into cover classes. The bottom and the top of the box represent the first and third quartiles, and whiskers extend up to 1.5 times the interquartile range (IQR) of the data. Outliers are defined as more than 1.5 times the IQR and are displayed as dots.

3.2 Soil erosion and water dynamics in different soil-moss combinations (Manuscript 3)

3.2.1 Surface runoff, percolation, and soil erosion 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 the two moss 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 within bare treatments. For all substrates, surface runoff was higher than percolated water for bare treatments, and the reverse was true for moss treatments (Figure 12). The only exceptions were bare & dry treatment of PT and moss & wet treatment of BB. 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 ($p < 0.01$).

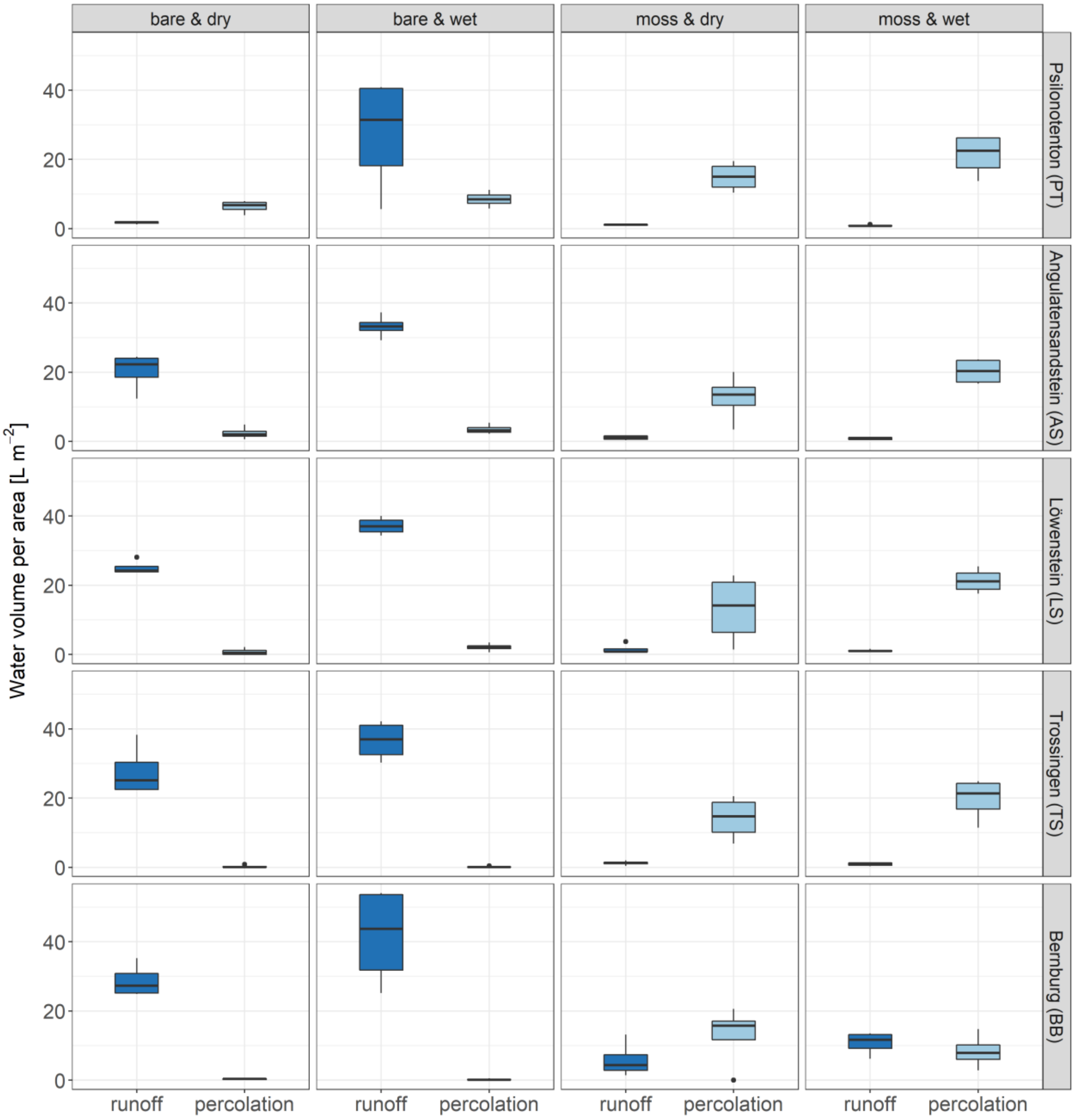


Figure 12: Surface runoff and amount of percolated water [L m^{-2}] per infiltration box with four treatments and five soil substrates (n = 4). Lines within boxplots represent median values, while bottom and top of the boxplot show the first and third quartiles. Whiskers extend up to 1.5 times the interquartile range (IQR) of the data. Outliers are defined as more than 1.5 times the IQR and are displayed as dots.

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 within the moss treatments (Figure 13). On average, there were no differences in sediment discharge between the substrates. However, 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 considerably higher compared with the other substrates. However, soil erosion for BB was still 605 times lower in moss compared with bare treatments.

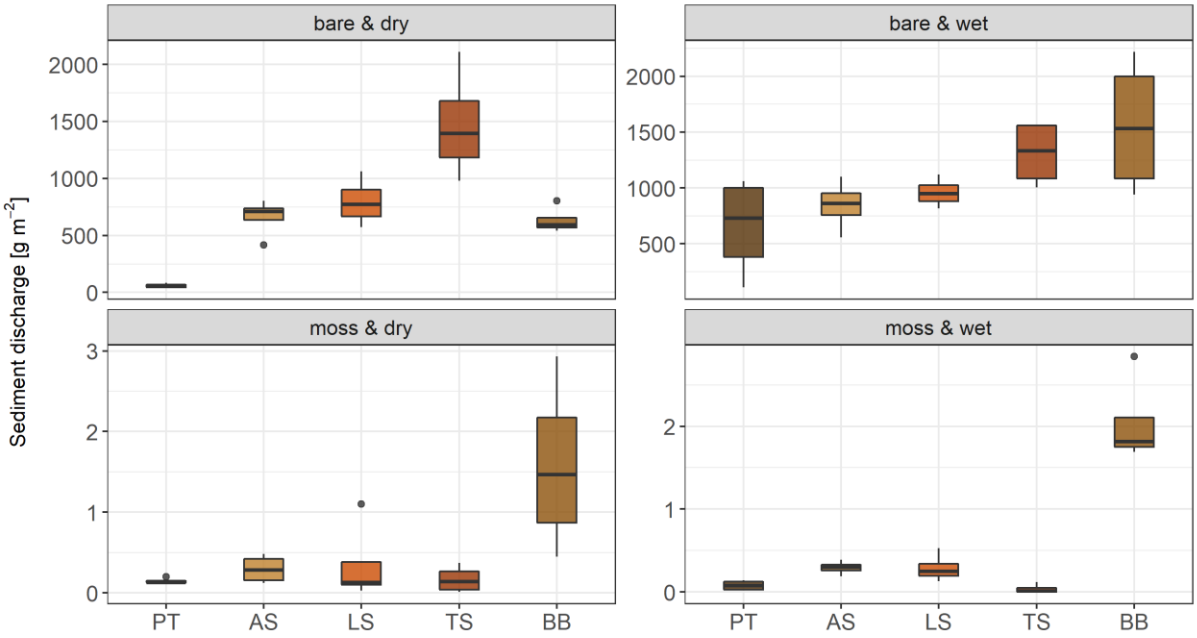


Figure 13: Sediment discharge [g m^{-2}] per infiltration box with four treatments and five soil substrates (n = 4). Lines within boxplots represent median values, while bottom and top of the boxplot show the first and third quartiles. Whiskers extend up to 1.5 times the interquartile range (IQR) of the data. Outliers are defined as more than 1.5 times the IQR and are displayed as points.

The effect of soil moisture on surface runoff and soil erosion 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 & 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 erosion 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. As a result, surface runoff was delayed, which also led to less erosion. This process occurred very quickly, usually within the first 15 minutes of the rainfall simulations, which can be explained by the fact that dry soil aggregates are more susceptible to slaking than wet aggregates (SACHS & SARAH, 2017). For this reason, many studies conclude that soil erosion resistance increases with increasing soil moisture, at least up to a certain threshold value of soil moisture content (MORAGODA et al., 2022). However, our bare & wet treatments did not have any wet soil aggregates on the surface at the beginning of the rainfall simulation, but already had a sealed soil surface due to our experimental setup with repeated measurements of the same infiltration boxes. Consequently, surface runoff and soil erosion were higher in bare & wet treatments compared with dry conditions.

Differences between substrates regarding surface runoff, amount of percolated water and soil erosion 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 & 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 soil moisture to rain temperature (SACHS & SARAH, 2017). In our experiment, the differences between the substrate 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 would be necessary to survey a larger number of different soil properties and environmental variables, but even this is difficult to concentrate in a single study due to the wide range of influencing factors.

In addition to the treatments and substrates we selected, there were two factors that strongly influenced our measurements. Firstly, due to the weather conditions during the adaption phase of moss covers, desiccation cracks occurred in all loamy substrates, but not in the sandy substrate BB. Secondly, our measurements revealed that the substrate BB was highly water repellent, which strongly affected the infiltration. Similar to the findings of TU et al. (2022), we attributed the large runoff and erosion reduction between bare and moss treatments to the moss cover, assuming that the extent of the reduction also depended on the moss species. However, this could not be demonstrated in our experiments because the desiccation cracks also had a particular influence on surface runoff and percolated water volume, and both components could not be quantified individually. The substrate BB did not form desiccation cracks, but was strongly water repellent, which generally increases surface runoff and soil erosion compared with wettable soils (LOWE et al., 2021), and resulted in bare treatments of sandy BB substrate producing more runoff than the other loamy substrates. Also, the moss treatments of BB caused significantly higher surface runoff and sediment discharge as well as lower volume of percolated water compared with the other substrates. Despite the lack of desiccation cracks and occurrence of water repellency of this sample, however, the measured parameters were significantly reduced compared to the bare treatments, indicating a high influence of moss cover.

3.2.2 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 (Figure 14). 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 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 quite similar, however, the difference between surface and 3 cm depth was less pronounced in the moss & dry treatments than in the bare & dry treatments. 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 treatment 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 minutes for the BWP at 3 cm depth to respond in AS and LS, it took about 20 minutes in PT and TS, and no water was detected in BB. It is also noticeable that the water content in the moss treatments of LS at a depth of 3 cm was considerably lower than in the bare treatments. 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 to 3 cm depth, and the water content increased in moss substrates at 3 cm depth compared to bare substrates.

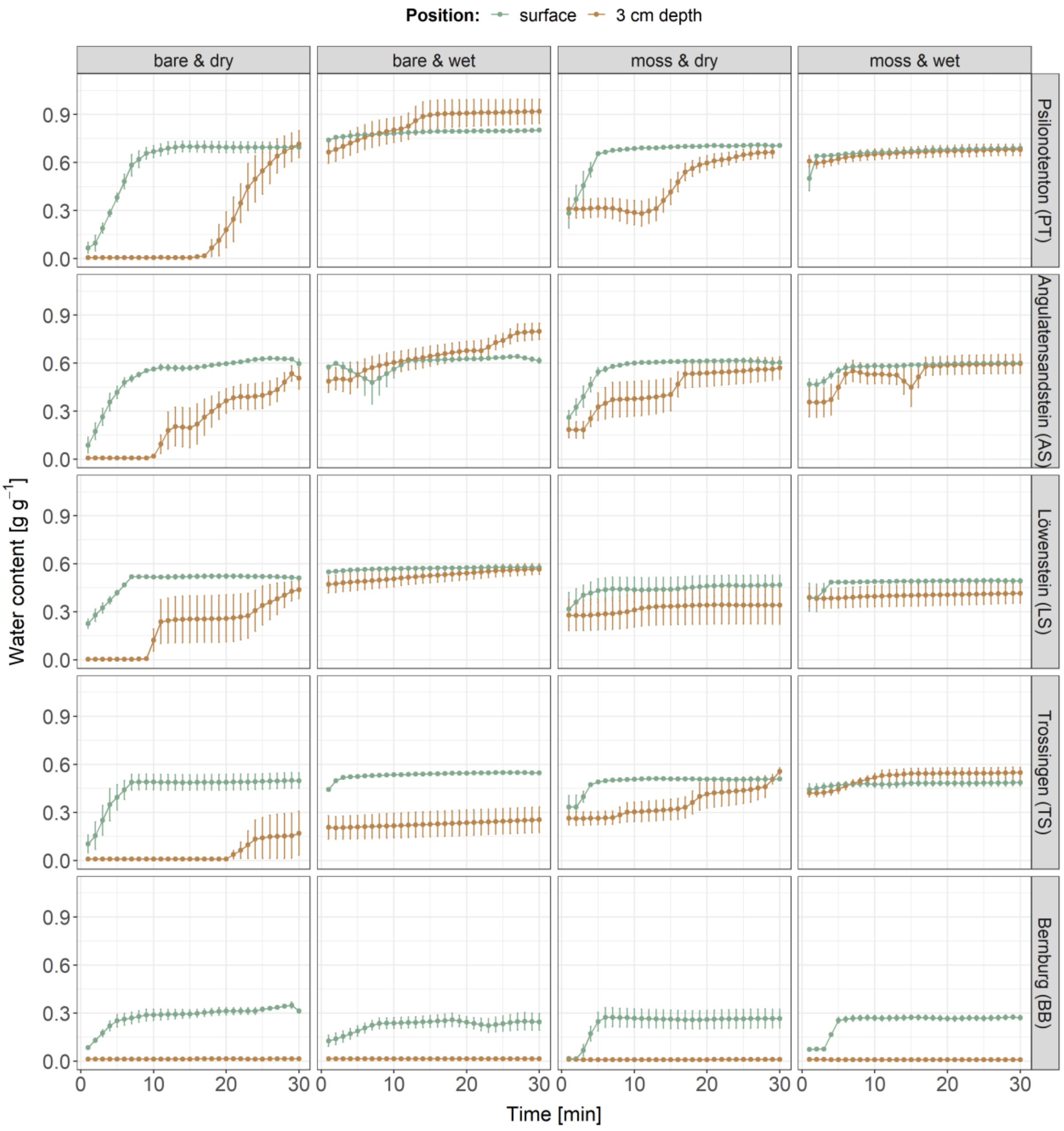


Figure 14: Temporal dynamics of water content values [g g⁻¹] of treatments and substrates during rainfall simulations. Minute averages of water content are shown as points with standard errors. Water content was measured with biocrust wetness probes (BWP) at two positions: At the substrate surface and at 3 cm substrate depth.

These findings of the temporal dynamics of water content during rainfall simulation supported our theories of surface runoff and percolated water volume described in the previous section 3.2.1. 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 increased 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 lot 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 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, less water infiltrated into the substrate. In comparison, TU et al. (2022) have 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 attributed to surface runoff, whereby these ratios depended on the respective moss species.

Another phenomenon that was particularly evident in these results was the water repellency of BB. As also described in LOWE et al. (2021), water moved across the surface in rivulets, bringing dry substrate back to the surface, so that fluctuating water contents were observed in the bare & wet treatments. It was also interesting 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. So it can be assumed that the water flowed only at the outer edge of the infiltration box as preferential flow path.

3.3 Water absorption and evaporation of soil-moss combinations (Manuscript 4)

3.3.1 Maximum water storage capacities and their influencing factors

With regard to WSC_{max} of the studied moss species, there were significant differences between *E. striatum* and *P. undulatum* ($p < 0.05$), *B. rutabulum* and *P. undulatum* ($p < 0.05$), and *A. serpens* and *P. undulatum* ($p < 0.001$). *P. undulatum* exhibits a particularly low WSC_{max}, half as high compared with *A. serpens*, although very similar total surface areas were determined for both species (Table 3). In general, there was no significant correlation between WSC_{max} and total surface area or LAI. Similarly, most of the moss structural traits did not correlate individually with WSC_{max}. A small leaf area (Spearman's correlation $\rho = -0.30$, $p < 0.05$) and a high leaf frequency (Spearman's correlation $\rho = 0.32$, $p < 0.05$) were the main traits that tended to increase WSC_{max}.

The fact that *P. undulatum* absorbed comparatively less water could be due to the endohydric water transport typical of acrocarpous moss species, i.e., water transport via internal conductive structures (RICHARDSON, 1981). Endohydric mosses often comprise a water-resistant cuticle with waxy layers (PROCTOR, 1979), inhibiting water absorption by their leaves (GLIME, 2021). Furthermore, our results showed that leaf traits, e.g., leaf area and leaf frequency, were important for the water storage capacity of mosses. For Sphagnum species, this was also proven by BENGTSSON et al. (2020). Contrary to our expectations, we found no correlation between WSC_{max} and total surface area, indicating that additional parameters must be of great importance to the WSC_{max}. One parameter could be the capillary spaces of mosses, which are very difficult to quantify and are diverse and often complex (PROCTOR, 1982). In this context, VOORTMAN et al. (2014) discussed that capillary spaces between moss leaves and branches might be more relevant for water retention than those between moss shoots. Generally, the 3D structure of the mosses, e.g., the branching of the shoots, the shape of the leaves and the position of the leaves in relation to the stems, potentially plays an important role for capillarity of bryophytes (SCHOFIELD, 1981; GIORDANO et al., 1993).

Table 3: Species-specific average values of moss structural traits and maximum water storage capacity (WSC$_{max}$) of mosses (± standard error of the mean). Listed are leaf area, leaf frequency, leaf area per shoot length, shoot length, length of a single component (sum of shoot length and length of attached branches), shoot density (shoot number per ground area), total surface area, leaf area index (LAI) and maximum water storage capacity for the studied moss species.

Species	**Leaf area [mm^2]**	**Leaf frequency [cm^{-1}]**	**Leaf area per shoot length [cm^2 cm^{-1}]**	**Shoot length [cm]**	**Length single component [cm]**	**Shoot density [n cm^{-2}]**	**Total surface area [cm^2]**	**LAI**	**WSC$_{max}$ [g g^{-1}]**
Amblystegium serpens (Lab)	0.104 ± 0.002	81.778 ± 3.929	0.085 ± 0.006	1.168 ± 0.024	1.764 ± 0.224	97.005 ± 11.786	346.204	14.572	14.097 ± 1.278
Brachythecium rutabulum	1.151 ± 0.035	39.333 ± 4.93	0.452 ± 0.064	3.791 ± 0.166	8.470 ± 0.286	3.031 ± 0.402	297.076	12.504	11.800 ± 0.805
Eurhynchium striatum	0.629 ± 0.013	91.333 ± 9.541	0.574 ± 0.06	2.018 ± 0.129	7.756 ± 0.656	2.511 ± 0.496	265.672	11.182	11.223 ± 0.615
Oxyrrhynchium hians	0.307 ± 0.006	69.889 ± 3.545	0.187 ± 0.008	2.524 ± 0.129	8.124 ± 0.702	4.714 ± 0.712	169.907	7.151	9.686 ± 1.411
Oxyrrhynchium hians (Lab)	0.393 ± 0.008	55.556 ± 2.911	0.219 ± 0.014	2.180 ± 0.092	6.198 ± 1.480	10.368 ± 2.509	333.764	14.048	9.934 ± 1.238
Plagiomnium undulatum	4.737 ± 0.129	20.111 ± 2.6	0.953 ± 0.121	3.004 ± 0.129	4.960 ± 0.571	3.087 ± 0.827	346.517	14.585	7.308 ± 0.799

Regarding the soil substrates, WSC_{max} values were 30 times less compared with WSC_{max} of the mosses (Figure 15). We found highly significant differences between PT and TS, PT and LS as well as AS and TS ($p < 0.001$) and a significant difference between AS and TS ($p < 0.05$). On one hand, these differences can be explained by soil texture, as there is a negative relationship with sand content (Spearman's correlation $\rho = -0.62$, $p < 0.001$) and a positive correlation with silt content (Spearman's correlation $\rho = 0.52$, $p < 0.001$), while the clay content seemed to be of rather minor importance for WSC_{max} (Spearman's correlation $\rho = -0.40$, $p < 0.01$). On the other hand, we found a negative correlation with bulk density (Pearson's correlation r = –0.70, t39 = –5.94, $p < 0.001$) and C/N ratio (Spearman's correlation $\rho = -0.62$, $p < 0.001$). These relationships are also reported in other studies (FRANZLUEBBERS, 2002; GONG et al., 2003; RAWLS et al., 2003; NOVÁK & HLAVÁČIKOVÁ, 2019).

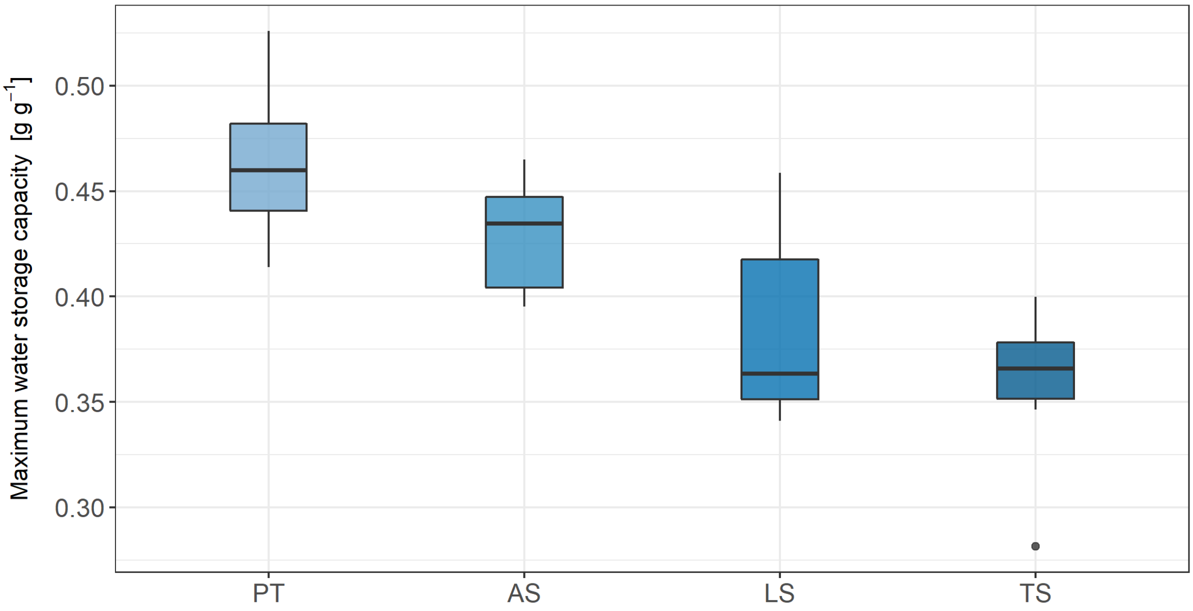


Figure 15: Maximum water storage capacity [g g^{-1}] of soil substrates. Lines within boxplots represent median values, while bottom and top of the boxplot show the first and third quartiles. Whiskers extend up to 1.5 times the interquartile range (IQR) of the data. Outliers are defined as more than 1.5 times the IQR and are displayed as points.

3.3.2 Temporal dynamics of water content in soil-moss combinations during watering

Considering the 60 minutes of watering, we observed clear differences in water content of different moss species, both in terms of temporal progression and water content level achieved (Figure 16). When watering started, all moss species had dried out, so that moss water content initially increased until an equilibrium was reached, with the two replicates of one moss species also reaching a similar equilibrium. However, there were also certain variations in the temporal progression of water content within replicate measurements (e.g., for *E. striatum* + TS), indicating a great heterogeneity within species. In general, we could not observe any clear relationships between the water absorption patterns of moss species during the watering process and their species-specific structural traits. For instance, *A. serpens* (Lab) and *P. undulatum* both maintained a low water content during watering, although they are quite different regarding most of their structural traits and are very similar only in total surface area, which did not correlate with WSC_{max}. It was also surprising that the mosses in the greenhouse experiment did not achieve their respective WSC_{max} values by far, although a considerable amount of water was applied at 122 mm h^{-1}. As an example, the WSC_{max} of *A. serpens* was 14.10 ± 1.28 g g^{-1}, which was 5 times higher than its water content after watering (2.63 ± 0.02 g g^{-1}). Most notably, it was very unexpected that the denser mosses, especially the lab-grown mosses, did not absorb much water during the greenhouse experiment.

Since similar equilibria and characteristic temporal progression of water content were obtained within one moss species measured with two replicates, it appears that moss species can be distinguished by the BWP response. The variation that nevertheless existed within the replicate measurements can probably be explained by air-filled interstitial spaces that interfere with the contact between BWP and moss cushion, and was also observed by LÖBS et al. (2020). The fact that no clear relationships between water absorption and moss structural traits could be found in the greenhouse experiment either, again indicates that other parameters, such as capillary spaces, also play an essential role here. Furthermore, no clear patterns are discernible that explain why the mosses in the greenhouse experiment do not achieve their WSC_{max} values. In general, we can deduce that the mosses are not a barrier to infiltration in case of high precipitation rates. For instance, LI et al. (2016) reported that bryophyte-dominated biocrusts reduced infiltration, but this effect was clearly reduced at higher precipitation rates and also depended on biocrust thickness. A new observation of our study is that the mosses growing on the soil do not store much of the applied water themselves, but pass it on to the soil.

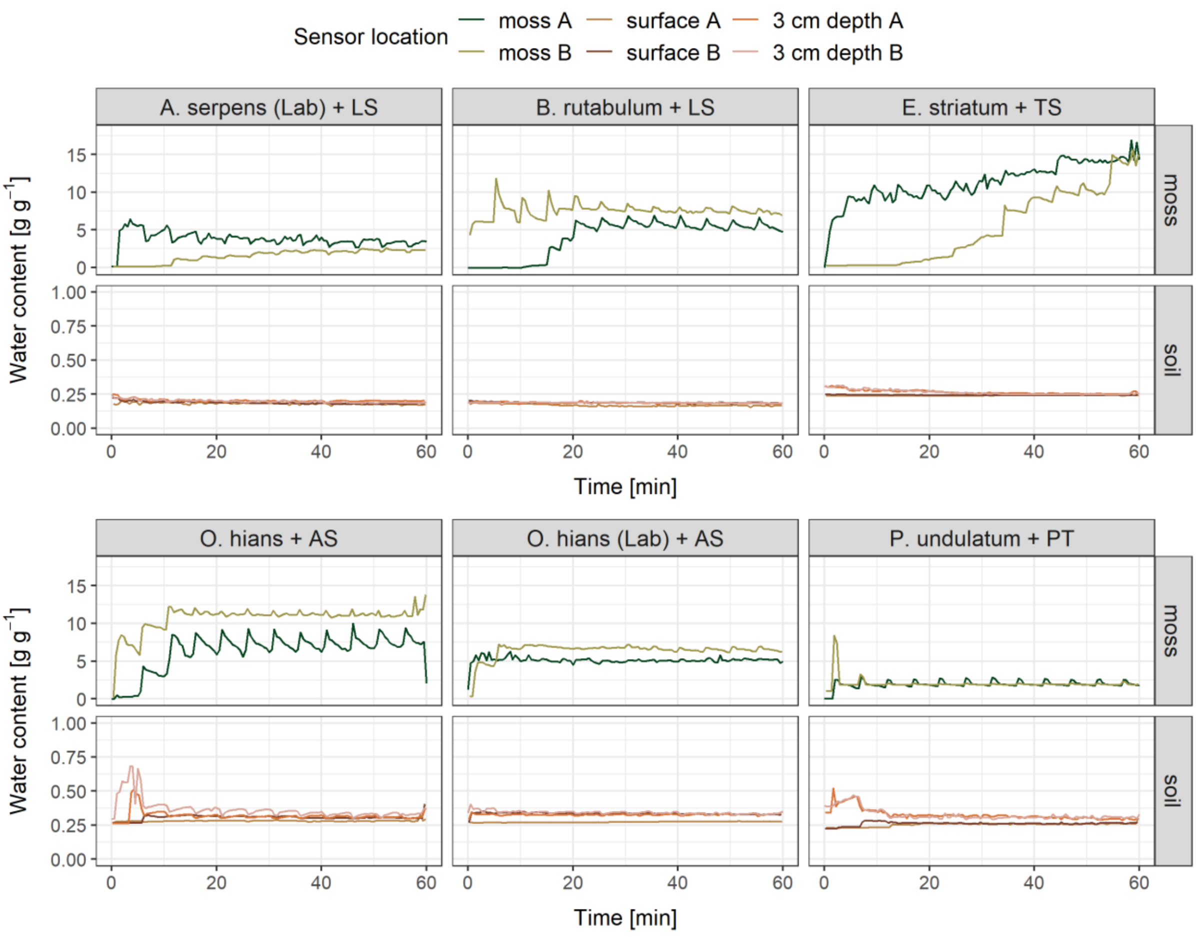


Figure 16: Temporal dynamics of water content values [g g^{-1}] of treatments during watering in the greenhouse experiment. Replicate measurements are labeled with A and B for every biocrust wetness probe (BWP) location (moss cover, substrate surface, 3 cm substrate depth). Plotted are half-minute values.

In comparison with the mosses, the soil substrates exhibited much lower water contents during the 60 minutes of watering, which was true for both surface and 3 cm substrate depth (Figure 16), and was consistent with the results on WSC$_{max}$ (see previous section 3.3.1). Since the surfaces had not completely dried out at the beginning of the experiment, the temporal progression of water content on the substrate surface started with high values at the beginning of watering and slightly decreased. Comparatively, the temporal progression of water content at 3 cm substrate depth was steady. Overall, we found substrate-specific coherences regarding the level of water content achieved.

Furthermore, we expected the soil substrates to reach their WSC$_{max}$ in the greenhouse experiment. However, water content after watering in the greenhouse was lower than the substrate-specific WSC$_{max}$, which applied to each BWP position both at the surface and at 3 cm substrate depth. Regarding the temporal progression of water content, it appeared that water had initially accumulated at the surface, causing the high initial water contents. Subsequently, the water percolated through the substrate without filling any more pores. This could be attributed to desiccation cracks in the substrate that result in preferential water flow through the substrate, which may also be the reason why substrate-specific WSC_{max} was not reached during watering in the greenhouse experiment.

3.3.3 Temporal dynamics of water content in soil-moss combinations during desiccation

During the subsequent 71-hour desiccation period, water content of mosses generally decreased, while water content at the substrate surface fluctuated with RH and remained constant at 3 cm substrate depth (Figure 17). Moss species differed in evaporation rates and their responses to climatic changes in the greenhouse. Evaporation rates calculated for the measurement period depended on the maximum water content after watering of moss species: *E. striatum* with the highest water content after watering also had the highest evaporation rates (0.181 and 0.197 g h^{-1}), while *P. undulatum* exhibited considerably lower evaporation rates (0.023 and 0.012 g h^{-1}). A group with slightly higher evaporation rates consisted of *A. serpens* (Lab; 0.056 and 0.03 g h^{-1}), *B. rutabulum* (0.046 and 0.055 g h^{-1}), *O. hians* (Lab; 0.057 and 0.078 g h^{-1}), and *O. hians* (0.06 and 0.093 g h^{-1}). We found a positive correlation between leaf frequency and evaporation rate (Spearman's correlation $\rho = 0.832$, $p < 0.001$). LAI, however, correlated negatively with evaporation rate (Spearman's correlation $\rho = -0.78$, $p < 0.001$). Furthermore, water content in moss species showed diel fluctuations, albeit to different degrees. Desiccation periods clearly aligned with declining RH and rising temperatures in *E. striatum*, *O. hians* (Lab), and to a smaller degree in *P. undulatum*, *A. serpens* (Lab), *B. rutabulum* and *O. hians*. In general, replicate measurements of moss species varied slightly from each other with respect to water content values, but showed comparable patterns over time.

The lower evaporation rates for mosses with high LAI are in line with our expectations. LAI, as a product of different structural traits, makes the formation of a multitude of capillary spaces for water storage in different hierarchical levels (leaf, shoot, and colony) more likely, overall resulting in higher water contents in moss cushions and lower evaporation rates, as also described in ELUMEEVA et al. (2011). However, this was not reflected in our results of species-specific WSC_{max}, which showed no influence of LAI (see section 3.3.1). These contradictory findings make it even more important to conduct further research on water absorption and evaporation mechanisms of mosses. Integrating new methods, such as clipping a water content sensor to moss stems as proposed by LEO et al. (2019), would be interesting to compare with BWP response in future studies. Nevertheless, the BWPs used in this study showed a high sensitivity as they could even detect that mosses reacted to increasing RH and could absorb water under conditions with high RH as also reported by LÖBS et al. (2020), which in turn can have beneficial effects on the soil water balance.

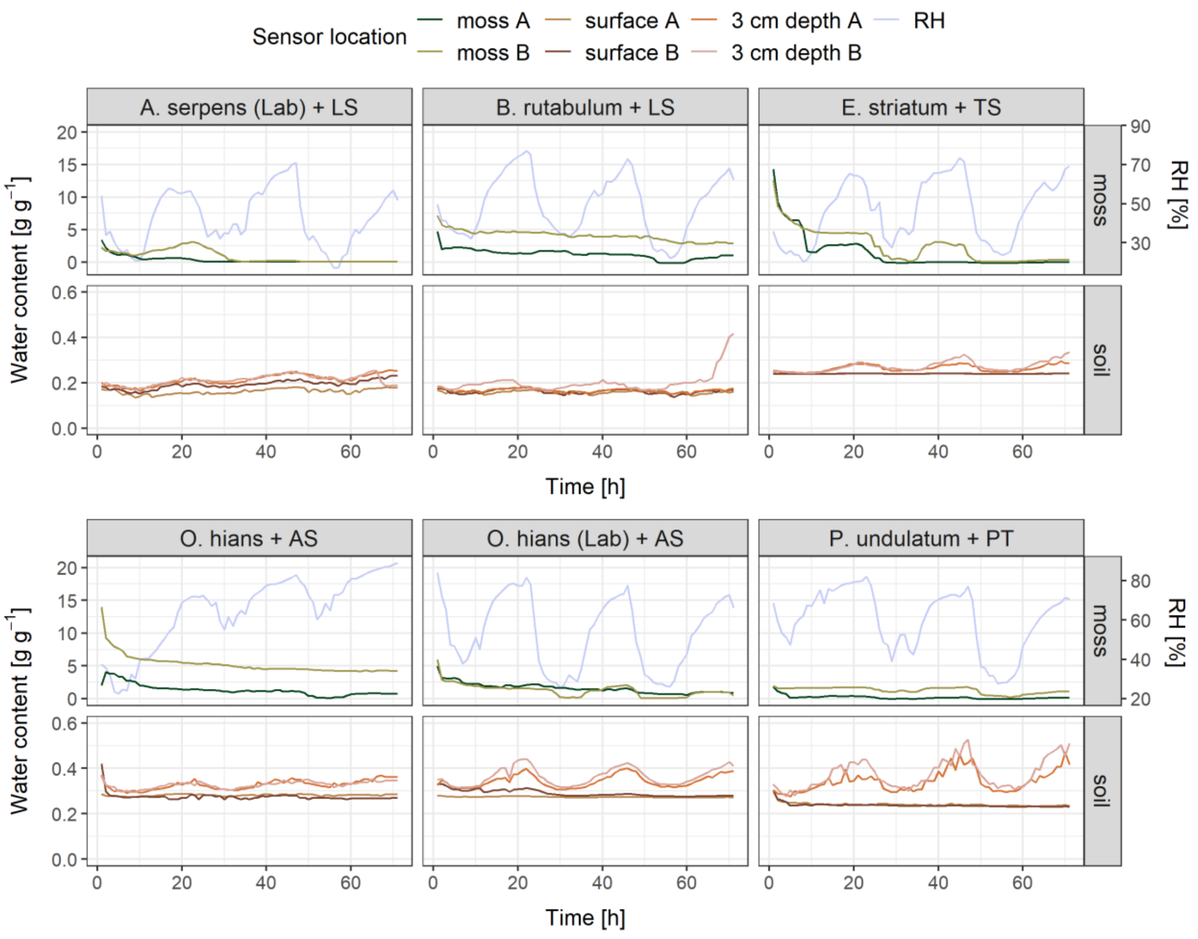


Figure 17: Temporal progression of water content values [g g^{-1}] of treatments during 71 h of desiccation in the greenhouse experiment. Replicate measurements are labeled with A and B for every biocrust wetness probe (BWP) location (moss cover, substrate surface, 3 cm substrate depth). The course of relative humidity (RH) is displayed for every measurement. Plotted are hourly values.

Soil substrates showed slightly different levels of water content in 3 cm substrate depth, which remained largely stable during the 71 hours of desiccation. In comparison, the water content at the substrate surface fluctuated diurnally depending on RH, but not at 3 cm substrate depth, with the exception of LS, where the oscillations related to RH were evident even at 3 cm substrate depth. Generally, water content at the substrate surface was higher than in 3 cm depth during desiccation, and the extent of this difference depended on the substrate: For LS, the water content in both BWP positions was very similar, but especially for PT, water content was a factor of 1.4 to 2.3 higher at the substrate surface than at 3 cm substrate depth.

Since the soil substrates did not dry out during the measuring period despite sometimes very high maximum temperatures of up to 40°C, we assume that moss covers prevented desiccation of the substrate, although it remains unclear whether the substrate received water from the mosses themselves or plainly from RH. In principle, fine pores at the substrate surface are able to absorb water from the air (HILLEL, 1998; AGAM & BERLINER, 2006), and our results show that this was not inhibited despite dense moss covers. Thus, even dense moss covers did not completely seal the substrate surface, and there was no full barrier by mosses. However, since the RH-induced fluctuations also varied depending on the density of the moss cover, i.e., the most pronounced reactions were found in the loosest moss cover *P. undulatum*, we assume that mosses mitigate soil evaporation. For low precipitation rates, prevention of soil evaporation from moss-dominated biocrusts was also reported in Li et al. (2016).

4 Conclusion and outlook

Within this thesis, it was found that bryophyte-dominated biocrusts occur in disturbance zones of temperate forests for a limited period of time and substantially reduce soil erosion during that period. Similarly, bryophyte covers contribute significantly to the mitigation of soil erosion and play an essential role in the soil water balance, the extent depending on the particular species. With regard to the objectives of this thesis, the following conclusions were drawn in detail:

i. At our study sites in the Schönbuch Nature Park, biocrusts occurred a few weeks after disturbance from April to July 2019 in two skid trails, and vegetation succession differed among the four skid trails in terms of species composition and coverage. Biocrusts were composed of cyanobacteria, coccoid and filamentous algae plus bryophyte protonemata and subsequent early developmental stages of bryophyte shoots. At the end of summer, they were rapidly overgrown by vascular plants, but not replaced. In this process, biocrusts turned into a mature bryophyte cover that coexisted with vascular plants and declined during winter probably due to leaf litter fall.

ii. The highest reduction of soil erosion was observed with the occurrence of protonema- and bryophyte-dominated biocrusts in summer. Interestingly, sediment discharge increased again in autumn and winter despite high vegetation cover, which could not be explained by antecedent soil moisture. Overall, bryophytes made a major contribution to erosion control after disturbance, even more than vascular plants. In addition, skid trail wheel tracks in particular caused high soil erosion, which was 13.2 times higher compared with the undisturbed forest soils. However, the amount of sediment discharge clearly depended on the particular site, indicating an important effect of parent material.

iii. The combinations of moss species and underlying soil substrates (soil-moss combinations) showed clear differences between bare & dry, bare & wet, moss & dry and moss & wet treatments in terms of surface runoff, percolated water volume and sediment discharge. Surface runoff and sediment discharge were highest in bare & wet treatments, as the substrate surface was already sealed compared to bare & dry measurement. In contrast, surface runoff and soil erosion in the moss treatments were significantly reduced, while the amount of percolated water was increased. This process was superimposed by desiccation cracks and water repellency, with the result that the respective influences could not be quantified individually. Nevertheless, a large influence of moss cover on surface runoff, sediment discharge and percolation was evident.

iv. Temporal dynamics of water content showed clear differences between treatments, allowing us to understand the differences in surface runoff and percolated water volume in more detail. Bare & wet treatments were already water saturated at the surface at the beginning of rainfall simulations, and at 3 cm substrate depth there was still potential to absorb water, which explained higher surface runoff and low percolated water volume. Moss treatments exhibited lower water contents over time compared to bare treatments, highlighting the strong influence of moss covers and desiccation cracks on the soil water balance. In the water-repellent substrate, the water was prevented from percolating down to a depth of 3 cm in all treatments.

v. Maximum water storage capacities (WSC_{max}) of the studied moss species varied widely, which could not be explained by total surface area or leaf area index, and higher WSC_{max} values were correlated with low leaf areas and high leaf frequency. However, there must be further factors influencing WSC_{max} that were not surveyed in this study. One such factor is assumed to be the capillary spaces of mosses, e.g., spaces between moss leaves, branches and stems, which are diverse, often complex and very difficult to quantify.

vi. During watering of soil-moss combinations, no clear relationships between water absorption and moss structural traits could be found. In general, mosses were no barrier for infiltration in case of high precipitation rates and they did not store much of the applied water themselves, but passed it on to the soil. During desiccation, mosses with high leaf area index (LAI) had lower evaporation rates than mosses with low LAI, which was surprising due to the lack of correlation with WSC_{max} and necessitates further detailed studies. Mosses prevented desiccation of the substrate, although even dense moss covers did not completely seal the surface.

This thesis contributes substantially to the investigation of the ecohydrological function of biocrusts and bryophytes in temperate forests, and raises several additional questions that need to be explored in detail in future research. First of all, there is a major need to explore the role of factors determining the occurrence of biocrusts in temperate mesic environments and to measure their potentially beneficial functions. This requires interdisciplinary physical, biological, microbiological, chemical, and applied soil science research. Among others, continuous monitoring of biocrusts on agricultural land, and measuring their impact on soil erosion would be of particular interest. This is also accompanied by the consideration of using biocrusts or bryophytes specifically as erosion control for erosion-prone soils, but this also necessitates a more detailed knowledge of the species-specific erosion mitigation effects and the structural traits that determine these patterns. Under this premise, artificial inoculation of bryophytes as erosion control on bare forest or agricultural soils should be of particular interest for future research. Our results also emphasize that some bryophytes species may develop different traits due to different cultivation sites (field vs. laboratory), raising the question of whether laboratory cultivation can confer beneficial traits to individual species, e.g., for erosion control.

In the light of climate change, however, not only erosion protection but also resistance to dry periods plays a special role. The effects of bryophytes on the soil water balance are species-specific and require more detailed studies to understand how different moss species and soil substrates interact regarding water absorption, infiltration, and evaporation. For instance, long-term drought experiments that measure water content at different soil depths under bryophyte covers of different species and continuously monitor evaporation would be promising. This also demands the availability of a climate-regulated environment with control and manipulation possibilities. Such interdisciplinary approaches of biology and soil science can provide new insights into the complexity of water-related soil-moss interactions.

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Appendix

Manuscript 1 **pp. 59 - 72**

GALL, C.; OHAN, J.; GLASER, K.; KARSTEN, U.; SCHLOTER, M.; SCHOLTEN, T.; SCHULZ, S.; SEITZ, S. & KURTH, J. K. (2022): Biocrusts: Overlooked hotspots of managed soils in mesic environments. *Journal of Plant Nutrition and Soil Science*, 185 (6), 745-751. DOI: 10.1002/jpln.202200252.

Manuscript 2 **pp. 73 - 111**

GALL, C.; NEBEL, M.; QUANDT, D.; SCHOLTEN, T. & SEITZ, S. (2022): Pioneer biocrust communities prevent soil erosion in temperate forests after disturbances. *Biogeosciences*, 19, 3225–3245. DOI: 10.5194/bg-19-3225-2022.

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Manuscript 4 **pp. 127 - 159**

THIELEN, S. M.; **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. *Journal of Hydrology and Hydromechanics*, 69 (4), 421-435. DOI: 10.2478/johh-2021-0021.

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[*] This manuscript has been published in a modified version as a preprint with the following citation: GALL, C.; NEBEL, M.; SCHOLTEN, T.; THIELEN, S. M. & SEITZ, S.: Water's path from moss to soil Vol. 2: How soil-moss combinations affect the soil water balance and soil erosion, 30 November 2023, Preprint (Version 1) available at Research Square. https://doi.org/10.21203/rs.3.rs-3268666/v1.

Manuscript 1

Biocrusts: Overlooked hotspots of managed soils in mesic environments

Journal of Plant Nutrition and Soil Science, 185 (6), 745-751

DOI: 10.1002/jpln.202200252

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Submitted: July 15, 2022

Accepted: October 12, 2022

Published: November 6, 2022

Abstract

Biological soil crusts, or “biocrusts", are biogeochemical hotspots that can significantly influence ecosystem processes in arid environments. Although they can cover large areas, particularly in managed sites with frequent anthropogenic disturbance, their importance in mesic environments is not well understood. As in arid regions, biocrusts in mesic environments can significantly influence nutrient cycling, soil stabilization, and water balance; however, their persistence may differ. We call for interdisciplinary physical, biological, microbiological, and chemical, and applied soil science research with a special focus on biocrusts of managed soils from mesic environments, to better understand their impact on overall ecosystem health and resilience, particularly with regard to climate change.

1 Overlooked biocrust habitats

Biological soil crusts (hereafter referred to as biocrusts) are hotspots of microbial activity, characterized by large amounts of microbial biomass, high nutrient turnover rates, and intensive biotic interactions. This is due to the supply of numerous bioavailable organic compounds provided by plants and/or animals (Kuzyakov and Blagodatskaya, 2015). Biocrusts develop on and a few millimeters below the soil’s surface, and modify their surroundings with organismal metabolites to create new habitats. Typical biocrust biota include algae, cyanobacteria, fungi, bacteria, archaea, protists, lichens, bryophytes, and microarthropods (Belnap et al., 2001; Weber et al., 2016; Khanipour Roshan et al., 2021; Weber et al., 2022). Biocrusts play an important ecological role in the creation and maintenance of healthy soils, and can (1) improve nutrient availability and fertility (Evans and Ehleringer, 1993; Gao et al., 2010; Li et al., 2012), (2) influence plant germination (Godinez-Alvarez et al., 2012; Zhang and Belnap, 2015; Havrilla et al., 2019), (3) increase biogeochemical cycling (Miralles et al., 2012; Xu et al., 2013; Wang et al., 2017), (4) keep and enhance water availability at the soil surface (George et al., 2003; Li et al., 2022), (5) increase soil aggregate stability (Zhang et al., 2006; Cania et al., 2020; Riveras-Muñoz et al., 2022), and (6) protect the soil surface by counteracting soil erosion from water (Chamizo et al., 2017; Seitz et al., 2017) or wind (Zhang et al., 2006; Bullard et al., 2022). However, thus far, biocrusts have primarily been studied in arid and semiarid regions (Weber et al., 2016).

Most studies of biocrusts in temperate regions have concentrated on bare soils or on soils with minimal vascular plant cover. Similar to arid soils, these soils are often too poor for vascular plant establishment and growth, with high salinity and/or low nutrient and water availability (Corbin and Thiet, 2020). Some temperate regions that biocrusts have been investigated include: coastal areas (Thiet et al., 2014; Schulz et al., 2016; Mikhailyuk et al., 2019; Khanipour Roshan et al., 2021), inland dunes (Thiet et al., 2005; Fischer et al., 2010a), sand plains and pine barrens (Hawkes and Flechtner, 2002; Gilbert and Corbin, 2019), reclaimed lignite open-cast mining sites (Fischer et al., 2010b; Gypser et al., 2015), and potash tailings piles (Sommer et al., 2020; Pushkareva et al., 2021). Corbin and Thiet (2020) focused their review on biocrusts in temperate environments with restricted vascular plant productivity due to challenging soil and/or climatic conditions. While low vascular plant cover is common in arid regions, that is not reflective of most temperate regions. These regions are largely characterized by adequate water availability and unrestricted vascular plant growth, which can also be colonized by biocrusts. Recent studies have also found biocrusts at mesic, manged sites, which are anthropogenically impacted, such as monospecific pine forests, broadleaf-mixed forests and agricultural fields (Baumann et al., 2017; Glaser et al., 2018; Nevins et al., 2020; Ngosong et al., 2020; Kurth et al., 2021; Nevins et al., 2021; Gall et al., 2022). As the study of biocrusts in mesic environments is still in its infancy, herein, we will elaborate on their dynamics, distribution and potential impacts on ecosystem services.

2 Biocrust development on disturbed silvi- and agricultural soil surfaces in mesic environments

The essential requirements for biocrust development include bare soil and a minimum amount of light. These conditions act as a starting point for biocrust establishment and succession, and can be created in mesic environments by disturbing or removing layers of vegetation and/or litter. As a result, soil is directly exposed to sunlight and biocrusts can rapidly colonize within a few weeks (Seitz et al., 2017). Recent work has described biocrusts in forests (Baumann et al., 2017; Glaser et al., 2018; Ngosong et al., 2020; Kurth et al., 2021; Gall et al., 2022) and on agricultural fields (Nevins et al., 2020; Nevins et al., 2021; Nevins et al., 2022). In these environments, biocrusts are ephemeral and do not usually persist unless the disturbance is permanent (Szyja et al., 2018).

In forests, bare soil can be natural or human induced. The total area of natural (e.g. caused by pest insects, disease, heavy storms, drought stress) and anthropogenic (e.g. clearcutting, forest roads, or skid trails) disturbance amounts to 39 million hectares, or 17 % of the total area of all European forests (Senf and Seidl, 2021). Biocrusts can be found in both coniferous and deciduous forests of mesic environments, and are visible in the field as green cover (Baumann et al., 2017; Kurth et al., 2021; Glaser et al., 2022a) (Figure 1). While they can quickly establish in disturbed areas such as skid trails, their biocrust characteristics rapidly disappear with succession of vascular vegetation (Gall et al., 2022). Other cryptogamic communities that host a large part of their biomass above the soil's surface (such as thick moss mats, which are common in coniferous forests) are not always classified as biocrusts. However, there is a smooth transition between these communities and biocrusts (Belnap et al., 2001; Weber et al., 2022).

Biocrusts have also been found on agricultural soils (Figure 1), often in conjunction with copiotrophic microorganisms (Nevins et al., 2020; Nevins et al., 2021; Nevins et al., 2022). Agricultural practices such as plowing or other methods of tillage create large amounts of bare soil. This bare soil provides niches for biocrust development until crops shade the ground (limiting the light required). Additionally, many crops such as potatoes, sugar beet, and maize, are grown in rows that allow for solar radiation to reach the ground during the entire growing season. In Europe, this results in 12.4 million hectares of potential biocrust cover, or approximately 12.6 % of total arable land (Eurostat, 2020).

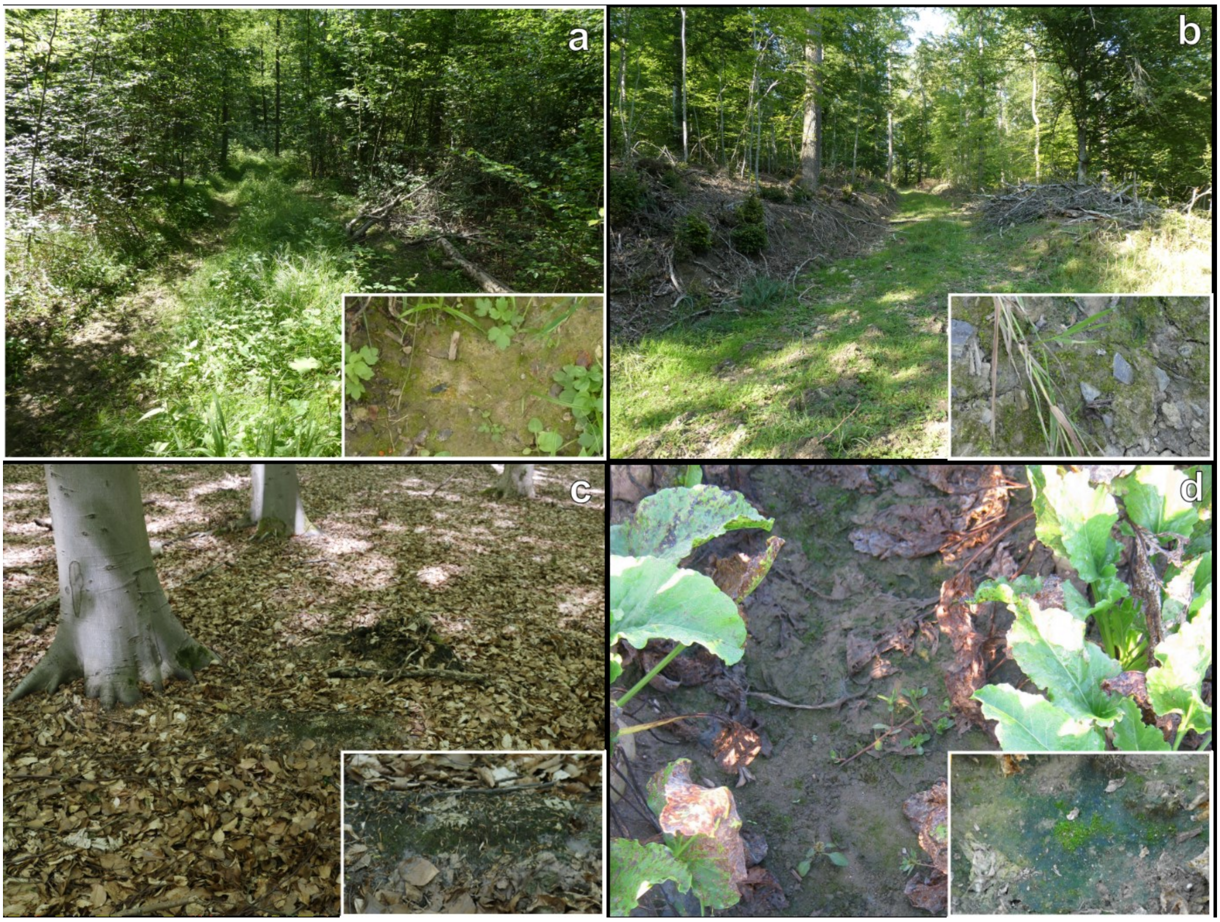

Figure 1: Overview of biocrusts on managed soils in mesic environments: (a, b) early successional bryophyte-dominated biocrusts on skid trail wheel tracks in a deciduous forest; (c) bryophyte-dominated biocrust under leaf litter; (d) bryophyte- and cyanobacteria-dominated biocrusts on arable land between sugar beet crops.

As biocrusts have been documented in forests and agricultural fields, they have the potential to colonize very large areas in mesic environments. Considering this and the fact that biocrusts are biogeochemical hotspots that can increase nutrient pools and turnover rates (Glaser et al., 2018; Nevins et al., 2020; Kurth et al., 2021), we hypothesize that they play a significant role in agri- and silvicultural soils, but this perspective has not yet been addressed.

3 Beneficial effects of biocrusts in mesic environments

A large number of beneficial ecosystem functions can be attributed to biocrust development (Weber et al., 2016). However, there are very few studies dealing with the beneficial effects of biocrusts in mesic environments, and even fewer address managed soils.

In disturbed areas, biocrusts have great potential to reduce soil erosion (Seitz et al., 2017), and in some cases are even more effective than vascular plant cover (Bu et al., 2015; Gall et al., 2022). In particular, early biocrust cover can protect against erosion immediately following timber harvest (Gall et al., 2022), a very vulnerable stage for soils. Three main erosion-reducing mechanisms in biocrusts have been described. First, the “sticky” filamentous structure of many pioneer microalgae and cyanobacteria can glue soil particles together (Glaser et al., 2018; Glaser et al., 2022a; Glaser et al., 2022b). Second, biocrusts are able to store water and reduce the kinetic energy of raindrops relative to bare soil (Zhao et al., 2014), which can reduce overland runoff (Bu et al., 2015). Third, biocrusts can increase soil organic matter (Gao et al., 2017) and improve aggregate stability by bacterial excretion of exo- and lipopolysaccharides (Cania et al., 2020). However, these effects depend on climatic conditions (Riveras-Muñoz et al., 2022; Kidron et al., 2022b) and species composition (Gypser et al., 2016). As shown in Kidron et al. (2022b), biocrust-related mechanisms of runoff generation are very complex, with significant variability documented in arid environments, and corresponding studies for mesic ecosystems are lacking.

The impact of biocrusts on the soil water balance in arid environments has been contradictory (Kidron et al., 2022a; Kidron et al., 2022b). On one hand, they can improve infiltration into the soil and increase water content while reducing evaporation – although these effects can vary depending on rainfall intensity, temperature, and soil texture (Chamizo et al., 2016). On the other hand, biocrusts may have a negative effect on the soil water balance, due to pore clogging by exopolysaccharides and/or water repellence (Xiao et al., 2019; Kidron et al., 2022b). Additionally, recent studies of biocrusts in temperate environments have primarily been conducted in challenging conditions for vascular plant growth (Thiet et al., 2005; Gypser et al., 2016), and cannot be generalized. Therefore, further studies in managed mesic environments are needed to fully characterize the potential beneficial effects of biocrusts on the soil water balance.

Biocrusts have been referred to as biogeochemical hotspots in mesic environments (Kuzyakov and Blagodatskaya, 2015). They host higher microbial biomass compared to surrounding bulk soil (Nevins et al., 2021; Kurth et al., 2021; Glaser et al., 2022a; Glaser et al., 2022b), exhibit more nutrient turnover, and can consequently impact biogeochemical cycling (Glaser et al., 2018; Kurth et al., 2021). Recent work has found a carbon enrichment from microbial biomass and plant-available nitrogen beneath biocrusts in agricultural soils (Nevins et al., 2020), and that biocrusts play a key role in the biogeochemical phosphorus cycle in forests (Baumann et al., 2017; Baumann et al., 2019; Kurth et al., 2021). Artificially cultivated biocrusts have also been found to increase carbon, nitrogen and phosphorus contents at the soil`s surface (Wu et al., 2013; Deng et al., 2020). Kheirfam (2020) observed an increase in carbon sequestration when soils were inoculated with bacteria, cyanobacteria, or both, resulting in an extrapolated removal of 3.11 – 3.93 t ha^{-1} y^{-1} of CO_2 from the atmosphere. Several other studies have primarily been concerned with the composition of biocrust soil microbial communities (Nevins et al., 2021; Kurth et al., 2021; Glaser et al., 2022a; Glaser et al., 2022b), and their changes with elevation and microclimates (You et al., 2021). However, further work will be required to determine which specific organisms or community profiles contribute to these changes in biogeochemical cycling. Additionally, future investigations could determine biocrusts’ capability to store nitrogen or phosphorus temporally in their biomass, particularly over winter when microbial activity is reduced.

Based on these ecological functions, biocrusts bear the potential as a novel tool for sustainable soil management. They have already been explored as possible avenues for the restoration of degraded soils, such as in the rehabilitation of salt heaps (Sommer et al., 2020) and felled/burned forests (Olarra, 2012; Chamizo et al., 2020). In addition to habitat restoration by loose soil particle stabilization (Grover et al., 2019), they can also serve as a "living" fertilizer in agriculture, as they biologically fix atmospheric nitrogen and retain nutrients and water (Sears and Prithiviraj, 2012; Vinoth et al., 2020). Methods to facilitate and accelerate biocrust establishment have primarily been applied in arid environments; and include the addition of chemical or physical soil stabilizers (Antoninka et al., 2020), improved light conditions (Zhao et al., 2020), irrigation (Wu et al., 2013; Zhou et al., 2020), and the inoculation of pioneer organisms with single or multi-species biocrusts to close gaps in natural biocrust cover (Bowker, 2007). We propose these could also be modified for use in mesic environments (Figure 2).

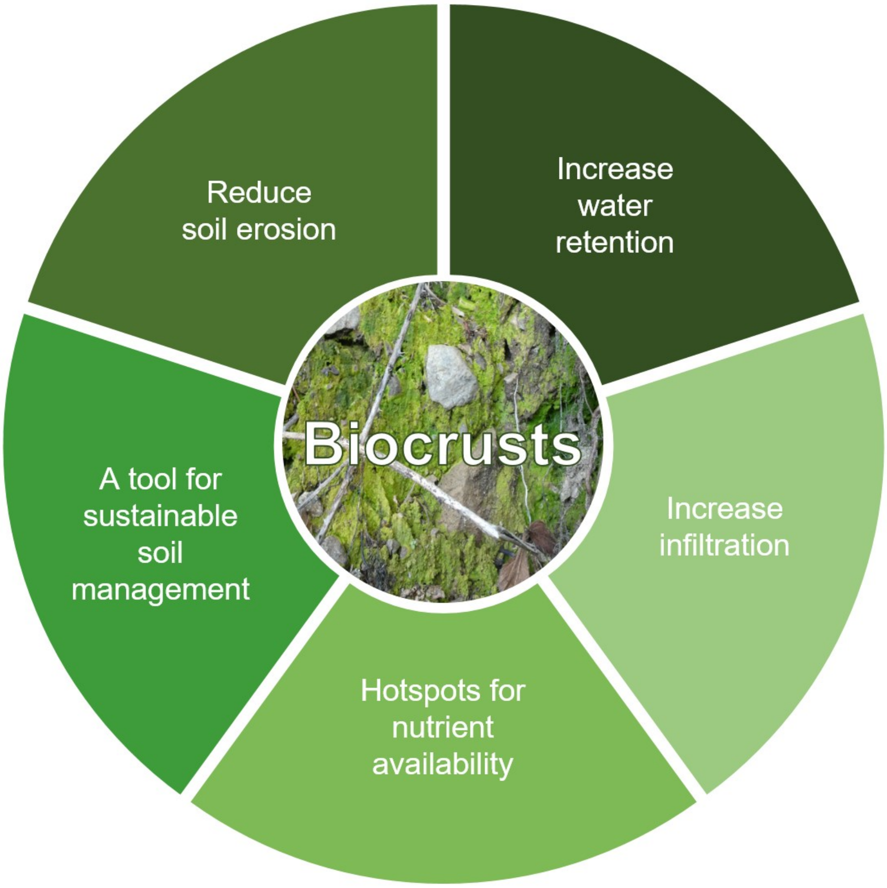

Figure 2: Summary of the potential beneficial effects of biocrusts in mesic environments (Illustration: Julia Dartsch)

4 Outlook: Biocrusts' potential to mitigate climate change in mesic environments

Global climate change is becoming increasingly visible in mesic environments, and will bring extreme weather events like heavy rain and extended drought, as well as mineral fertilizer shortages (Olsson et al., 2019). As a result, soils will be more vulnerable and require new forms of management for their protection, as stipulated by the UN's "Sustainable Development Goals". Accordingly, biocrusts could make a significant contribution. Considering the large range of biocrust colonization in managed mesic environments, and these areas` projected expansion due to climate change (Senf and Seidl, 2021; Gejdoš and Michajlová, 2022), further studies will be essential in evaluating their contribution to ecosystem services and global importance (Ferrenberg et al., 2017). Interdisciplinary physical, biological, microbiological, and chemical soil research will be indispensable in understanding the development and influence of biocrusts in mesic and anthropogenically-impacted environments. Their inoculation as an erosion control measure may be of particular importance (Cruz de Carvalho et al., 2018; Varela et al., 2021), especially as erosion rates are projected to increase due to climate change (Li and Fang, 2016). In addition, biocrusts' ability to sequester carbon could help in combating climate change in general (Kheirfam et al., 2017; Kheirfam, 2020), and applied in agriculture (Vinoth et al., 2020) or restoration (Román et al., 2018). We call for interdisciplinary research with a focus on biocrusts of managed soils in mesic environments, in order to better understand their multi-trophic interactions, consequences on chemical and physical soil properties, and impact on overall ecosystem health.

Acknowledgements

We acknowledge support from *DFG Project SE2767/2-1 "MesiCrust"* and *DFG Priority Program 1803 "EarthShape"*, as well as help provided by *Julia Dartsch, Lena Grabherr, Sonja M. Thielen, Martin Nebel* and *Michael Sauer*. Moreover, we are grateful for funding from *DFG Priority Program 1374 "Biodiversity—Exploratories" (GL909/2-3, KA899/28-1/2/3, SCHL 446/ 31-2, SCHU2907/7-3*) and the inspiring scientific community within that program, as well as by the *Leibniz ScienceCampus "Phosphorus Research Rostock"*. We acknowledge support from the Open Access Publishing Fund of the University of Tübingen.

Open access funding enabled and organized by Projekt DEAL.

Data Availability Statement

Data sharing is not applicable to this article as no new data were created or analyzed.

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Manuscript 2

Pioneer biocrust communities prevent soil erosion in temperate forests after disturbances

Biogeosciences, 19, 3225–3245
DOI: 10.5194/bg-19-3225-2022

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Submitted: December 17, 2021

Accepted: June 15, 2022

Published: July 11, 2022

Abstract

Soil erosion continues to be one of the most serious environmental problems of our time and is exacerbated by progressive climate change. Until now, forests have been considered an ideal erosion control. However, even minor disturbances of the forest floor, for example, from heavy vehicles used for timber harvesting, can cause substantial sediment transport. An important countermeasure is the quick restoration of the uncovered soil surface by vegetation. To date, very little attention has been paid to the development of nonvascular plants, such as bryophytes, in disturbed areas of temperate forests and their impact on soil erosion. This study examined the natural succession of pioneer vegetation in skid trails on four soil substrates in a central European temperate forest and investigated their influence on soil erosion. For this purpose, rainfall simulations were conducted on small-scale runoff plots, and vegetation was continuously surveyed during the same period, primarily to map the development of bryophytes and the occurrence of biological soil crusts (biocrusts).

Biocrusts appeared immediately after disturbance, consisting primarily of bryophyte protonemata and cyanobacteria as well as coccoid and filamentous algae that lost their biocrust characteristics as succession progressed. They were present from April to July 2019, with a particular expression in the skid trail that was on shale clay (Psilonotenton-Formation) and silty clay loam substrate. In general, skid trails on clayey substrates showed considerably higher bryophyte cover and species richness. Although bryophytes were subsequently overtopped by vascular plants, they managed to coexist until their growth was restricted due to leaf litter fall. *Brachythecium rutabulum* and *Oxyrrhynchium hians* were the most important and persistent pioneer bryophyte species, while *Dicranella schreberiana* and *Pohlia lutescens* were volatile and quickly disappeared after spreading in the summer. Sediment discharge was 22 times higher on disturbed bare soil compared with undisturbed forest soil and showed the largest sediment removal in the wheel tracks. Counteracting this, soil erosion decreased with the recovery of surface vegetation and was particularly reduced with growing pioneer biocrusts in summer, but it again increased in winter, when vascular vegetation became dominant. This leads to the conclusion that the role of bryophyte-dominated biocrusts in forests has been underestimated so far, and they can contribute more to soil conservation at specific times of succession than vascular plants.

1 Introduction

For decades, soil erosion has been a major environmental problem, as it degrades the most productive soil layers, which threatens, among other things, food production worldwide. Although these effects have long been known, there are still a variety of challenges to mitigating soil erosion in different ecosystems. As climate change progresses, the risk of soil loss increases, particularly due to increased rainfall intensities, making the preparation of effective solutions an urgent matter (Olsson et al., 2019; Scholten and Seitz, 2019). The most prominent soil loss occurs in agricultural environments, and thus, considerable relevant research has been conducted in these habitats (Morgan, 2005; Maetens et al., 2012). Soil erosion in forests has received comparably less attention, as undisturbed forest ecosystems generally exhibit the lowest soil erosion among all land-use types (Blanco and Lal, 2008; Maetens et al., 2012; Panagos et al., 2015b) and are seen as a successful countermeasure to prevent the soil from being eroded (Panagos et al., 2015a; Wiśniewski and Märker, 2019).

However, soil erosion in forestlands can be locally severe, due in part to management intensity and tree species composition, for example, in subtropical forest ecosystems (Goebes et al., 2015; Seitz et al., 2016). Even forest disturbances on smaller scales, such as human-induced felling and skidding of individual trees or the construction of forest trail systems on sloped terrain, have the potential to drastically increase soil loss (Blanco and Lal, 2008). Sheridan and Noske (2007) showed that unsealed forest roads accounted for 4.4 % of the total annual sediment load from a forest, even though they represented only 0.023 % of the catchment. The most important reason for this is soil compaction and reduced infiltration rates caused by heavy machines used for timber harvesting (Foltz et al., 2009; Jordán-López et al., 2009; Wemple et al., 2018; Kastridis, 2020). For instance, results from Demir et al. (2007) revealed a significantly higher soil bulk density on skid trails, where soil compaction is caused by direct overpassing with forestry equipment. In this context, Zemke (2016) measured 58 times higher erosion rates on unfortified forest roads (272.2 g m^{-2}) compared with undisturbed forest floor (4.7 g m^{-2}) in a temperate forest in western Germany. Also, already vegetated wheel tracks of skid trails showed 5-fold higher soil erosion, up to 21.4 g m^{-2}. Similarly, Safari et al. (2016) reported an increase in erosion rates of a factor of 14 for bare wheel tracks of skid trails relative to the undisturbed forest floor.

The findings of Li et al. (2019), Seitz et al. (2016), and Shinohara et al. (2019) suggest that it is not primarily the forest canopy that protects the soil against erosion, but an intact forest floor. Several studies have also confirmed that soil erosion on skid trails was highest in the first year after logging and decreased significantly thereafter, mainly due to revegetation (Baharuddin et al., 1995; Jourgholami et al., 2017). Thus, the most important measure to counteract negative effects of soil erosion on the upper soil layer after skidding is a quick restoration of the soil surface by vegetation (Zemke, 2016; McEachran et al., 2018). These protective soil covers consist of either leaf and conifer litter from surrounding trees (Li et al., 2014; Seitz et al., 2015) or understorey vascular vegetation on the forest soil (Miyata et al., 2009; Liu et al., 2018). They also include a cryptogamic cover of bryophytes, lichens, fungi, algae, cyanobacteria, and various other bacteria lineages within or on top of the first millimetres of the soil, referred to as biological soil crust (biocrust; ; Weber et al., 2016, 2022). Especially when vascular-plant growth is limited by soil conditions such as high acidity or low nutrient and water availability, biocrusts play a vital role as pioneer soil colonizers and stabilizers (Corbin and Thiet, 2020) and can persist even in temperate climates due to these harsh environmental conditions (Szyja et al., 2018).

In mesic environments not necessarily constrained by harsh soil conditions, biocrusts occur primarily as an intermediate state of succession following disturbances such as deforestation (Seppelt et al., 2016), although they may redevelop seasonally if disturbances continue (Szyja et al., 2018; Kurth et al., 2021; Weber et al., 2022). The definition of biocrusts first provided by Belnap et al. (2001a) referred to organisms that are in close contact with the soil surface and form a coherent hardening layer. In this context, all organisms with a substantial part of their biomass above the ground are excluded, e.g. large cryptogamic mats consisting of bryophytes or lichens, which are common in temperate coniferous forests. However, especially in temperate climates, the boundaries are fluid, so the distinction between biocrusts and cryptogamic covers is not always easy to make. Consequently, evidence of the occurrence of biocrusts in temperate forests is rare (Glaser et al., 2018; Corbin and Thiet, 2020).

Biocrusts in general, and especially bryophyte-dominated biocrusts, are known for their influence on hydrological processes (Eldridge et al., 2020) such as reducing surface runoff (Bu et al., 2015; Xiao et al., 2015) and, thus, decreasing sediment discharge (Silva et al., 2019). Such mitigation of soil erosion is also reported by cryptogamic covers consisting of bryophytes (Pan et al., 2006; Parsakhoo et al., 2012), which is inevitably related to their impressive water storage capacity, since bryophytes are able to absorb up to 20 times their dry weight (Proctor et al., 1998), with some *Sphagnum* species even reaching more than 50 times their dry weight (Wang and Bader, 2018). These mechanisms of water storage capacity are influenced by the complex 3D structure of bryophytes; the composition of a variety of individual functional traits, e.g. leaf area, leaf frequency, leaf area per shoot length, leaf area index, total surface area, shoot length, and shoot density; and their ability to form dense colony-level cushions (Elumeeva et al., 2011; Glime, 2021; Thielen et al., 2021). As most studies investigating the impact of biocrusts on soil erosion have been conducted in arid and semiarid regions, their influence in humid and temperate climates is largely unknown (Weber et al., 2016;

Eldridge et al., 2020). Previous studies in subtropical China proved an important erosion-reducing effect of bryophyte-dominated biocrusts within early-stage forest plantations after clear-cutting (Seitz et al., 2017). It can be assumed that similar effects also occur in humid and temperate forest conditions; however, evidence for these effects is missing.

Pioneer biocrust communities could be particularly important as erosion-controlling agents in recently disturbed forest areas, such as along skid trails, where vascular plants are presumed to grow slowly due to harsh soil conditions. To date, few studies have addressed natural plant succession and its influencing factors in skid trail recovery (DeArmond et al., 2021), and of these, the majority relate exclusively to vascular plants (Buckley et al., 2003; Wei et al., 2015). For example, Mercier et al. (2019) observed on skid trails of different forest types in southern Germany that the species composition of vascular plants and bryophytes differed markedly from the forest interior. Furthermore, these vegetation surveys showed that vascular-plant species richness benefited from soil compaction in the skid trails, while bryophyte species richness was unaffected. Overall, there are still a variety of unresolved questions regarding the temporal development of species composition; species richness; and coverage of bryophytes in temperate forest disturbance zones and how they are affected by soil properties such as soil texture, bulk density, pH, and carbon and nitrogen content. With respect to these research gaps, it is of great interest to determine at what time and under what conditions biocrust communities naturally develop after the passing over by forestry machinery and when they transition to a more developed bryophyte cover. It is also important to investigate the functional role of these temperate successional stages of bryophyte cover in soil erosion. The knowledge gained from this study can be used to implement more targeted measures of good forestry practice to prevent soil erosion, for example, by enhancing the recovery of cryptogamic vegetation in skid trails.

This study examined the natural succession of pioneer vegetation with a focus on bryophytes and the occurrence of biocrusts in skid trails at four different sites with varying substrates and soil properties in a central European temperate forest. Moreover, it investigated the influence of bryophytes and biocrusts on soil erosion processes measured in small-scale runoff plots (ROPs) with rainfall simulations while also considering the position of the tracks within the skid trails. We tested the following hypotheses:

1. Species composition of bryophytes varies depending on individual skid trails.
2. Bryophyte cover and species richness are highest in wheel tracks, and total vegetation cover and vascular-plant species richness are highest in centre tracks, but each differs depending on the individual skid trail.

3. Soil erosion is reduced with increasing vegetation cover and is higher in wheel tracks than in centre tracks.
4. Bryophytes and early-successional bryophyte-dominated biocrusts are a major factor in mitigating soil losses following disturbances in temperate forests.

2 Material and methods

2.1 Study site

This study took place in Schönbuch Nature Park in southwestern Germany (Figure A1 in the Appendix), which is situated in Triassic hills consisting of sandstones, marlstones, and claystones with abundant limestones and a few Lower Jurassic shales, sandstones, and limestones on the hilltops. The Lower Jurassic plateaus are often covered with a loess layer (Einsele and Agster, 1986). Schönbuch Nature Park represents a low-altitude (the highest peak, Bromberg, is 583 m above sea level), hilly (69 % with slopes ≤ 3° and 14 % with slopes > 15°), and almost completely forested (86 %) area in the sub-Atlantic temperate climate zone (Einsele and Agster, 1986; Arnold, 1986). While the mean annual temperature is 8.3 °C, the average precipitation is 740 mm (mean annual values from 1979 to 1984 at the climate station in Herrenberg; DWD Climate Data Center, 2021a), which is comparable to the long-term average for Germany (DWD Climate Data Center, 2021c, d).

For this research, four newly established (winter 2018/19) and unfortified skid trails in Schönbuch Nature Park with different parent materials, soil properties, and vegetation characteristics were selected (Table A1 in the Appendix). All four skid trails consisted of two wheel tracks and a centre track in between. They were created during logging operations conducted by the state forestry service of Baden-Württemberg (ForstBW) and represented an initial point of vegetation development when this study commenced.

The four skid trails were differentiated by their parent material and named according to the geological formation of the parent material: Angulatensandstein (AS), Psilonotenton (PT), Löwenstein (LS), and Trossingen (TS). AS consists of thin, platy, fine-grained sandstones containing limestone in an unweathered state; PT is composed of pyrite-bearing shale clay interstratified by beds of limestone; TS consists of firm, fractured, unstratified claystones with lime nodules; and LS forms medium- to coarse-grained banked sandstones interrupted by reddish marls (Einsele and Agster, 1986). The AS skid trail was located next to a loess deposition, which also determines soil properties. Since Schönbuch Nature Park was formed by extensive periglacial processes, the geological formation does not represent the parent rock of soil formation in every case (Bibus, 1986).

In the surroundings of LS, a reforested conifer stand was determined with approximately 70-year-old *Pinus sylvestris* and 50-year-old *Picea abies*, where the former occurred with 50 % cover and the latter with 40 % cover in the highest tree layer. Furthermore, in a second tree layer, about 20-year-old *Fagus sylvatica* and *Carpinus betulus* had colonized, covering the forest floor with leaf litter over the entire area, such that a herb layer of about 10 %–20 % was formed, which was mainly restricted to sparse areas and dominated by grasses such as *Carex sylvatica* and *Brachypodium sylvaticum*. Additionally, a soil survey was carried out based on the classification system of the German soil mapping guideline (Bodenkundliche Kartieranleitung, KA5; Ad-hoc AG Boden, 2005), and subsequently, the soil types according to the World Reference Base for Soil Resources (WRB; IUSS Working Group WRB (2015)) were derived using the WRB Tool for German Soil Data (Eberhardt et al., 2019). For LS, a Eutric Cambisol (Ochric) with typical moder was identified, and the soil surface was covered with a moss layer up to 5 % in total.

In comparison, the natural habitat of TS was dominated by young *Picea abies* (approx. 30-year-old), with 90 %–100 % of the soil surface covered with moss, and in 5 %–10 % of the area, a herb layer was formed. The soil survey revealed a Eutric Cambisol (Geoabruptic, Clayic, Ochric, Raptic, Protovertic), which was much deeper than the wheel track in the skid trail and covered with a mull-like moder humus layer.

The other two sites were characterized by deciduous tree species: while PT was formed primarily by beech trees (*Fagus sylvatica*) at different ages, developing a sparse tree layer and a very dense shrub layer, in AS, a sparse tree layer of approximately 100-year-old *Quercus petraea* and a second level of younger *Fagus sylvatica* and *Carpinus betulus* were found. In PT, a soil survey revealed a Eutric Calcaric Amphistagnic Cambisol (Loamic, Ochric) with a mull-like moder humus layer, and in the vegetation survey, a herb layer with a cover rate of less than 5 % was determined. In contrast, AS had a 20 % herb layer formed almost exclusively by *Quercus petraea* and *Carpinus betulus* seedlings, and the soil type was identified as Dystric Stagnic Regosol (Ochric) with L mull.

2.2 Field and laboratory methods

To test for particular impacts of early-successional post-disturbance forest floor vegetation on sediment discharge, rainfall simulations with micro-scale ROPs (0.4 × 0.4 m; cf. Seitz, 2015) were performed at four different times (March 2019, July 2019, October 2019, and February 2020). ROPs are stainless-steel metal frames connected with a triangular surface runoff gutter and are used to measure interrill erosion processes (Seitz, 2015; Zemke, 2016; Seitz et al., 2019), which is the discharge of sediment in thin sheets between rills due to shallow surface runoff (Blanco and Lal, 2008). A total of 4 ROPs were placed in each right wheel track, and

4 were in the centre track at each of the 4 skid trails, for a total of 32 ROPs. Two ROPs were placed in the undisturbed forest soil adjacent to every skid trail (n = 8). While rainfall simulations in the skid trails were conducted for each of the four measurement times (n = 128), in the undisturbed forest soil, they were reduced to measurements in October 2019 and February 2020 (n = 16), yielding a total of 144 measurements.

Rainfall simulations were conducted with the Tübingen rainfall simulator (Iserloh et al., 2013; Seitz, 2015) that was equipped with a Lechler 460.788.30 nozzle and adjusted to a falling height of 3.5 m. Mean rainfall intensity was set at 60 mm h^{-1}, applied over a duration of 30 min. This rainfall intensity refers to a regional rainfall event with a recurrence interval of 20 years (DWD Climate Data Center, 2021b). In each run, two ROPs (wheel and centre track) were irrigated simultaneously, with surface runoff and sediment collected in sample bottles (1 L). An overview of the experimental setup is available in Figure A2. Prior to each rainfall simulation, soil moisture was determined next to every ROP using a ThetaProbe ML2 in combination with an HH2 Moisture Meter (Delta-T Devices, Cambridge, UK).

After soil erosion measurements, the total surface runoff for each ROP was gathered from the associated sample bottles marked with a millilitre measuring scale. To ascertain sediment discharge, the sample bottles were dried at 40 °C in a compartment drier and weighed in a dry state. To determine basic soil properties, bulk soil samples of the topsoil (0–5 cm) were collected in the surroundings of every ROP. While aggregate size was obtained by wet sieving, which served as a basis for the calculation of the mean weight diameter (MWD) of soil aggregates (van Bavel, 1950), grain size distribution was determined with an X-ray particle size analyser (SediGraph III, Micromeritics, Norcross, GA, US). Soil pH was measured with a pH meter and SenTix 81 electrodes (WTW, Weilheim, Germany) in 0.01 M $CaCl_2$ solution. Additionally, soil organic carbon (SOC) and total nitrogen (N_t) were determined with an elemental analyser (vario EL III, Elementar Analysensysteme GmbH, Hanau, Germany). Core samples (100 cm^3) were taken to determine soil bulk density in the topsoil using the mass-per-volume method (Blake and Hartge, 1986). Slope was measured on both sides of every ROP using an inclinometer, while aspect for the entire sites was derived from a digital elevation model (DEM, Geobasisdaten © Landesamt für Geoinformation und Landentwicklung Baden-Württemberg, https: //www.lgl-bw.de, last access: 7 July 2022) using a geographical information system (QGIS-version 3.16.13 Hannover; QGIS Development Team, 2020). Furthermore, skid trails were examined for water repellency by applying the water drop penetration time (WDPT) test (Dekker et al., 2009).

To investigate the development of vegetation cover on the forest floor surface in every ROP, sampling campaigns took place at five measurement times (April 2019, June 2019, July 2019, October 2019, and February 2020) synchronized with in situ soil erosion measurements.

Vascular plants and bryophytes were classified by eye and identified by morphological characteristics using a stereomicroscope (SteREO Discovery.V8, Carl Zeiss Microscopy Deutschland GmbH, Oberkochen, Germany) and a microscope (Leitz SM-Lux, Ernst Leitz GmbH, Wetzlar, Germany). Classification was carried out to the species level (Table andTable), wherever possible, using the following plant identification literature: Jäger and Werner (2005), Nebel et al. (2000, 2001, 2005), and Moser (1963). In addition, total vegetation and bryophyte cover were surveyed for each ROP, while the Braun-Blanquet cover-abundance scale was used to determine coverages at the species level (Braun-Blanquet, 1964). Due to further use of the TS skid trail after the rainfall simulation in March 2019, it was not possible to survey the vegetation in the centre track in April 2019. Vascular-plant cover was calculated as the difference between total vegetation cover and bryophyte cover. Furthermore, perpendicular photographs were taken of each ROP with a digital compact camera (Panasonic DC-TZ91, Osaka, Japan) to additionally assess total vegetation cover with a photogrammetric survey and were processed with the grid quadrat method and using a digital grid overlay with 100 subdivisions (Belnap et al., 2001b). Bare soil and vegetation covers were separated by hue distinction.

2.3 Statistics

All analyses were conducted with R 4.0.4 (R Core Team, 2021) on the level of individual samples. To screen for significant differences, Kruskal-Wallis tests were used in combination with post hoc Wilcoxon rank-sum tests for independent measurements and Wilcoxon signed-rank tests for related measurements (using the R package “stats”). To test for significant differences between cover types, we classified ROPs as bare, bryophyte, and vascular-plant ROPs. In bare ROPs, there was neither bryophyte nor vascular-plant cover; bryophyte ROPs were mainly covered by bryophytes; and vascular plant ROPs were mainly covered by vascular plants, and, at the same time, bryophyte cover was lower than or equal to 10 %. A nonparametric analysis of covariance comparing nonparametric regression curves was performed to determine if there was a significant difference between vascular-plant ROPs and bryophyte ROPs in terms of sediment discharge (R package “sm”; Bowman and Azzalini, 2021). To determine whether bryophyte species composition differed significantly in the individual skid trails, an analysis of similarity (ANOSIM) with 999 permutations from the R package “vegan” was used (Oksanen et al., 2020). Additionally, generalized additive models (GAMs) with restricted maximum likelihood and smoothing parameters selected by an unbiased risk estimator (UBRE) criterion were performed to assess the effect of environmental parameters on soil erosion, total vegetation coverage, bryophyte coverage, and bryophyte species richness (R package “mgcv”; Wood, 2020). Prior to all statistical tests, normality was proved with the Shapiro-Wilk test, while homoscedasticity was verified using Levene’s test.

Significance was assessed as $p < 0.05$ in all cases. For all mean values described, the standard error was also given (mean ± standard error). The selected colours for Figure 1 are from the R package "wesanderson" (Karthik et al., 2018), and for Figures 3, 4, 5, and 6 they are from the R package "RColorBrewer" (Neuwirth, 2022).

3 Results and discussion

3.1 Bryophyte species composition

3.1.1 General succession of bryophyte species composition

Within the vegetation survey at five measurement times, a total of 24 moss, 2 liverwort, and 2 fungi species were found in the skid trails (Table 1), while 13 moss species occurred in the undisturbed forest soil (Table 2). The first bryophyte species to recolonize the skid trails in April 2019 after skidding were *Brachythecium rutabulum* (53.1 % of ROPs) and *Oxyrrhynchium hians* (37.5 % of ROPs). Protonemata of various species, the earliest stage of bryophyte development consisting of green cell filaments, were observed in 25 % of the ROPs. In June 2019, the percentage of ROPs occupied by *Brachythecium rutabulum* and *Oxyrrhynchium hians* increased to 75 % and 40.6 %, respectively, while protonemata were found in 31.3 % of the ROPs. Furthermore, *Plagiomnium undulatum* occurred in 25 % of the ROPs, and *Thuidium tamariscinum* occurred in 18.8 %. When the first bryophyte shoots developed from protonemata in July 2019, many occurrences could be assigned to the species *Pohlia lutescens*, *Dicranella schreberiana,* and *Trichodon cylindricus*. From July 2019 to February 2020, *Oxyrrhynchium hians*, *Brachythecium rutabulum*, and *Plagiomnium undulatum* remained the most abundant bryophyte species, and the quantity of different species increased. In comparison, 13 moss species occurred in the undisturbed forest soil (Table 2), 8 of which were also present in the skid trails.

Table 1: Percentage occurrence of bryophyte and fungi species for a total of 32 runoff plots distributed in four skid trails in Schönbuch Nature Park in southwestern Germany, based on five vegetation surveys from April 2019 to February 2020.

Species	Percentage occurrence of species in runoff plots					
	Apr 2019	Jun 2019	Jul 2019	Oct 2019	Feb 2020	Total
Liverworts						
Lophocolea bidentata (L.) Dum.	–	–	–	–	12.50	12.50
Apopellia endiviifolia (Dicks.) Nebel & D.Quandt	–	–	9.38	34.38	18.75	40.63
Mosses						
Atrichum undulatum (Hedw.) P. Beauv.	–	3.13	6.25	15.63	–	15.63
Barbula unguiculata Hedw.	–	–	3.13	12.50	3.13	12.50
Brachythecium rutabulum (Hedw.) Schimp.	53.13	75.00	59.38	62.50	71.88	93.75
Bryum pseudotriquetrum (Hedw.) P.Gaertn., E.Mey. & Scherb.	–	–	–	3.13	–	3.13
Bryum tenuisetum Limpr.	–	–	3.13	3.13	–	3.13
Calliergonella cuspidata (Hedw.) Loeske	–	–	–	–	15.63	15.63
Cirriphyllum piliferum (Hedw.) Grout	3.13	–	–	–	3.13	6.25
Dicranella schreberiana (Hedw.) Dixon	–	–	12.50	18.75	6.25	18.75
Dicranella varia (Hedw.) Schimp.	–	–	3.13	15.63	6.25	18.75
Didymodon fallax (Hedw.) R.H.Zander	–	–	–	–	3.13	3.13
Eurhynchium striatum (Hedw.) Schimp.	3.13	6.25	6.25	3.13	9.38	12.50
Fissidens taxifolius Hedw.	–	3.13	31.25	40.63	34.38	46.88
Hypnum cupressiforme Hedw. s. str.	–	–	–	3.13	3.13	6.25
Oxyrrhynchium hians (Hedw.) Loeske	37.50	40.63	50.00	78.13	81.25	93.75
Plagiomnium affine (Blandow ex Funck) T.J.Kop.	3.13	3.13	–	0.00	–	3.13
Plagiomnium undulatum (Hedw.) T.J.Kop.	9.38	25.00	40.63	68.75	56.25	71.88
Pohlia lutescens (Limpr.) H.Lindb.	–	9.38	18.75	6.25	–	18.75
Pohlia melanodon (Brid.) A.J.Shaw	–	–	3.13	12.50	9.38	15.63
Pohlia wahlenbergii (F.Weber & D.Mohr) A.L.Andrews	–	–	3.13	12.50	3.13	12.50
Pseudoscleropodium purum (Hedw.) M.Fleisch.	–	–	3.13	9.38	9.38	15.63
Rhytidiadelphus squarrosus (Hedw.) Warnst.	–	–	–	3.13	–	3.13
Rhytidiadelphus triquetrus (Hedw.) Warnst.	–	–	–	–	3.13	3.13
Thuidium tamariscinum (Hedw.) Schimp.	–	18.75	25.00	40.63	37.50	46.88
Trichodon cylindricus (Hedw.) Schimp.	–	–	15.63	25.00	6.25	31.25
Fungi						
Scutellinia kerguelensis (Berk.) Kuntze	–	–	–	3.13	–	3.13
Scutellinia umbrarum (Fr.) Lambotte	–	3.13	3.13	–	–	3.13

Table 2: Percentage occurrence of bryophyte species for a total of eight runoff plots in undisturbed forest soil in Schönbuch Nature Park in southwestern Germany, based on one vegetation survey in February 2020.

Species	Percentage occurrence of species in runoff plots in February 2020
Brachythecium rutabulum (Hedw.) Schimp.	25.00
Brachythecium salebrosum (F. Weber & D. Mohr) Schimp.	12.50
Bryum rubens Mitt.	12.50
Dicranella heteromalla (Hedw.) Schimp.	25.00
Eurhynchium angustirete (Broth.) T.J.Kop.	25.00
Euryhnchium striatum (Hedw.) Schimp.	12.50
Fissidens taxifolius Hedw.	12.50
Hylocomium splendens (Hedw.) Schimp.	25.00
Hypnum cupressiforme Hedw.	25.00
Pohlia melanodon (Brid.) A.J.Shaw	12.50
Polytrichastrum formosum (Hedw.) G.L.Sm.	25.00
Rhytidiadelphus triquetrus (Hedw.) Warnst.	25.00
Thuidium tamariscinum (Hedw.) B.S.G.	25.00

In our study area, the occurrence of cyanobacteria as well as coccoid and filamentous algae (e.g. Chlorophyceae and Xanthophyceae) plus bryophyte protonemata and the subsequent very early developmental stage of bryophyte shoots fulfilled the definition of biocrusts by Belnap et al. (2001a) and Weber et al. (2022) and occurred from April to July 2019. Since the species *Pohlia lutescens*, *Dicranella schreberiana,* and *Trichodon cylindricus* have predominantly evolved from protonemata and formed only a minor part of their biomass above the soil surface in their early developmental stages, we include these species here among the temperate biocrust species. According to the biocrust definition of Belnap et al. (2001a), we can also include the thallose liverwort *Apopellia endiviifolia* among the temperate biocrust species in our study area. Furthermore, *Brachythecium rutabulum* and *Oxyrrhynchium hians* have emerged as the most important pioneer species. Both species are widespread in Baden-Württemberg, Germany (Nebel et al., 2001) and are known to colonize a wide range of habitats (Nebel et al., 2001; Atherton et al., 2010). While *Brachythecium rutabulum* is particularly common on wood and stones, growing also on soil and gravelly ground, the habitat of *Oxyrrhynchium hians* is preferentially restricted to bare base-rich soils (Atherton et al., 2010), which renders both pioneer-friendly mosses (Nebel et al., 2001). Due to its competitive strength and broader distribution, *Brachythecium rutabulum* was even more frequent in the skid trails than *Oxyrrhynchium hians.* At a more advanced stage of succession, *Plagiomnium undulatum* and *Thuidium tamariscinum* also occurred, both of which grow mainly on forest soils (Nebel et al., 2001; Atherton et al., 2010). Furthermore, a clearly different species composition was found in the undisturbed forest soil compared with the skid trails. There, species composition showed an increased occurrence of more specialized species common in acidic woodlands, such as *Hylocomium splendens, Polytrichastrum formosum,* and *Dicranella heteromalla* (Atherton et al., 2010), which can be attributed to the lower pH in the undisturbed forest soil (mean pH = 4.54 ± 0.07) compared with the skid trails (mean pH = 6.19 ± 0.07). Mercier et al. (2019) also observed a different species composition in skid trails of different forest types in northern Bavaria compared with the forest interior during their vegetation surveys of vascular plants and bryophytes, indicating that skid trails can contribute to higher species diversity in managed forests.

3.1.2 Succession of bryophyte species composition in different skid trails

The vegetation succession developed differently in the four skid trails (see Figure 1 and 2) in terms of species composition (p = 0.001). At the beginning of vegetation succession after the disturbance due to skidding, we observed the development of protonemata in AS and PT. Whereas protonemata occurred in AS from April 2019 to July 2019 in 50 % of the ROPs, it was less common in PT but reached 50 % coverage in two ROPs in June 2019. These protonemata and their early-successional stages of *Pohlia lutescens*, *Dicranella schreberiana*, and *Trichodon cylindricus* are classified as biocrusts, which appeared in both PT and AS in April 2019 after the disturbance occurred and persisted in both skid trails until July 2019. The most abundant pioneer species were *Brachythecium rutabulum* and *Oxyrrhynchium hians* in all skid trails, but *Oxyrrhynchium hians* was absent in TS. TS was clearly dominated by *Brachythecium rutabulum*, which occurred in almost every ROP, with the coverage being up to 50 % in centre tracks, increasing constantly during the vegetation survey. *Brachythecium rutabulum* was present in all other skid trails, but with less than 5 % coverage. Furthermore, *Thuidium tamariscinum* occurred in TS in almost every ROP and in centre track plots, also with a considerably high coverage of up to 25 % in October 2019 and February 2020; it did not colonize PT or AS, but it was also abundant in LS, with cover up to 5 %. Liverwort species developed most notably in October 2019 in PT, LS, and TS, with *Apopellia endiviifolia* occurring in PT and LS and *Lophocolea bidentata* found only in TS. While *Plagiomnium undulatum* did not occur in AS, it was very common in all other skid trails, with mostly low coverage (around 5 %). Generally, *Plagiomnium undulatum* development started early in summer (June or July 2019) in PT and LS and exclusively in autumn in TS. Especially in July and October 2019, *Dicranella schreberiana* was abundant in PT and in some ROPs, up to a coverage of 50 %, while it did not grow in all other skid trails. Furthermore, *Oxyrrhynchium hians* achieved high coverage rates of up to 25 % in PT.

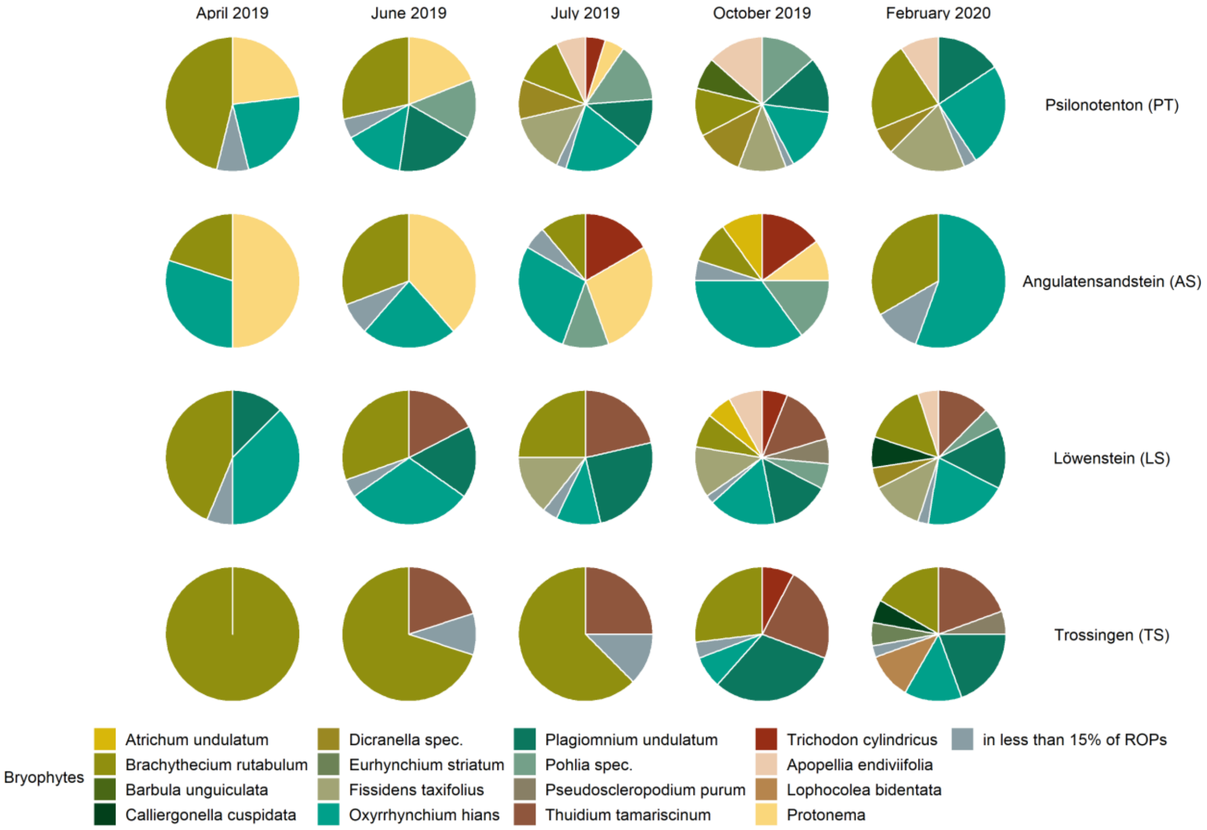


Figure 1: Bryophyte species composition in the different skid trails for each time of vegetation survey. Species from the same genera are grouped together, and species which occur in less than 15 % of the runoff plots are listed in one group.

Pioneer biocrust species were found in the three skid trails in AS, PT, and LS. It was particularly interesting that the related moss species *Dicranella schreberiana* and *Pohlia lutescens* were more volatile than expected, spreading only during the summer and disappearing again at the beginning of autumn. Temporally, the liverwort biocrust species *Apopellia endiviifolia* appeared just when the moss biocrusts disappeared. As noted by Düll (1991), *Apopellia endiviifolia* is exclusively distributed at sites with neutral-to-alkaline pH, which is why it occurred in PT and LS in our study area but not in the other two skid trails. *Brachythecium rutabulum* occurred in all skid trails as a pioneer species; however, while in PT, AS, and LS it was associated with other moss species as succession progressed, in TS it was dominant in terms of coverage. Since *Brachythecium rutabulum* is known to be stimulated in growth by eutrophication (Nebel et al., 2001), high N_t in TS could be a possible explanation for its dominant occurrence there. In addition, TS was the only skid trail in which *Oxyrrhynchium hians* did not occur. On the one hand, this can be attributed to the fact that *Brachythecium rutabulum* is very competitive, especially on eutrophic sites, and suppresses other species (Nebel et al., 2001). On the other hand, TS had a low pH of 5.4 ± 0.11, and since *Oxyrrhynchium hians* grows on base-rich soils, TS is not the preferred growing location. The absence of *Plagiomnium undulatum* in AS can be attributed to the fact that AS was clearly drier than the other sites, and according to

Nebel et al. (2001), *Plagiomnium undulatum* is a permanent moisture indicator. This moisture requirement is also shown by the fact that *Plagiomnium undulatum* occurred comparatively late in the year in TS. We assume that only the formation of a closed vegetation cover of vascular plants at this site developed a sufficiently shady and humid microclimate for *Plagiomnium undulatum* to establish itself there. In this context, Sedia and Ehrenfeld (2003) and Ingerpuu et al. (2005) demonstrated that vascular plants can promote a microhabitat that is more hospitable for moss growth. *Thuidium tamariscinum* occurred exclusively in skid trails surrounded by coniferous forests, which corresponds to its preferential distribution area (Nebel et al., 2001).

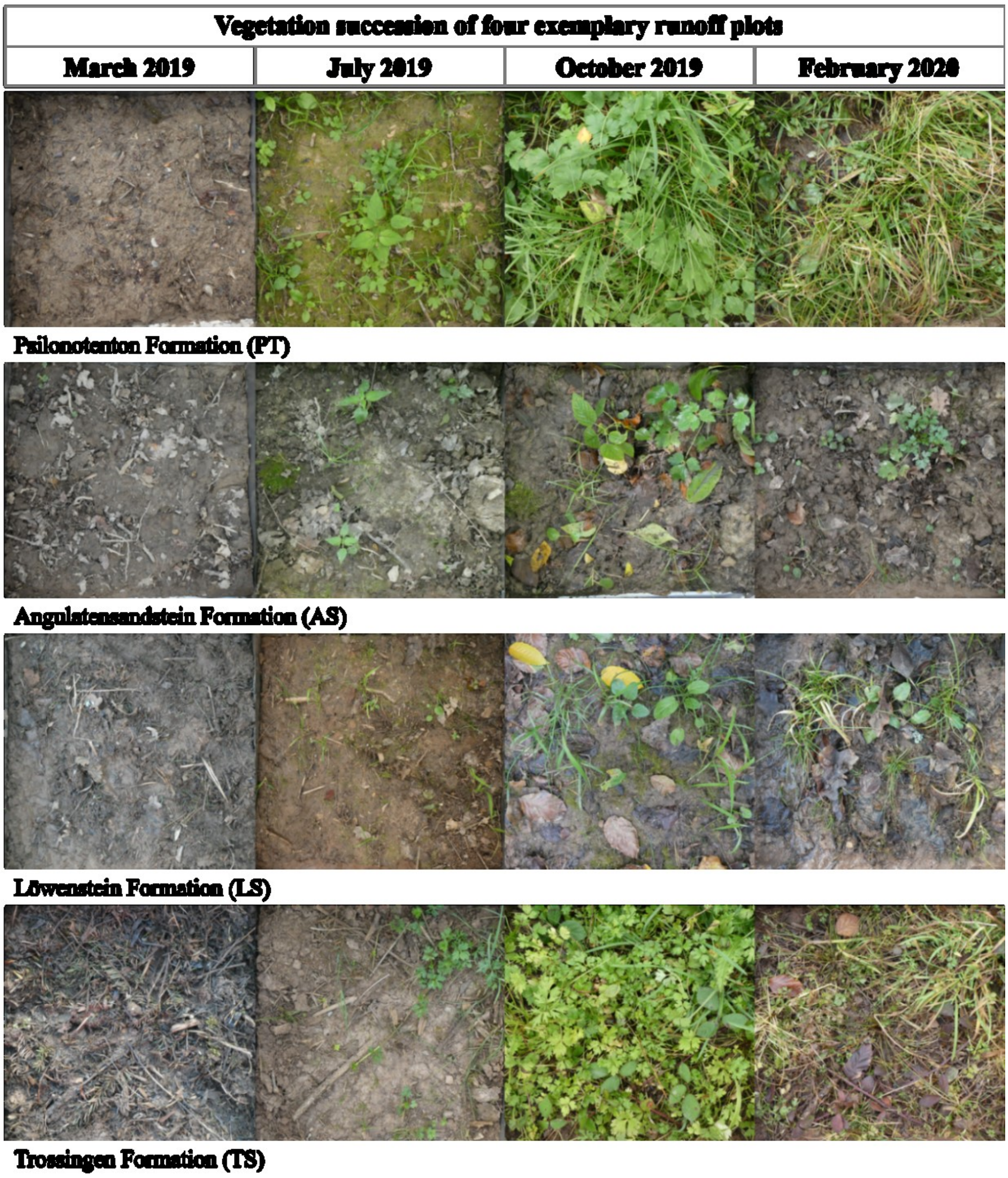


Figure 2: Vegetation succession of four examplary runoff plots in wheel tracks of the skid trails in Schönbuch Nature Park

3.2. Coverage and species richness

3.2.1 Bryophyte and total vegetation coverage

For all skid trails and vegetation surveys, bryophyte coverage was, on average, higher in centre tracks (12.01 ± 1.95 %) than in wheel tracks (7.15 ± 1.45 %; $p < 0.001$), which was also true for total vegetation coverage (centre track: 60.49 ± 3.78 %; wheel track: 24.00 ± 3.73 %; $p < 0.001$). With respect to the individual skid trails, the extent of bryophyte cover varied widely (Figure 3). In AS and LS, bryophyte coverage averaged no more than 12.00 %, while in PT it peaked at 33.33 ± 6.67 % in July 2019, and TS achieved 34.64 ± 11.95 % in February 2020, with considerable variation in cover between wheel and centre tracks in the last two skid trails. PT showed a more pronounced development of bryophyte cover in wheel tracks (up to 40 % from June to October 2019), opposite to the preferential colonization of centre tracks in TS (up to 60 % in February 2020). While bryophyte cover in PT decreased between October 2019 and February 2020, this effect did not occur in TS. Calculated in a GAM that explained 80.3 % of the deviation of bryophyte cover, pH ($p < 0.001$), SOC ($p < 0.001$), sand content ($p < 0.001$), total vegetation coverage ($p < 0.001$), and N_t ($p < 0.05$) were significant.

Generally, total vegetation and bryophyte cover developed with a higher coverage rate in centre tracks, indicating inferior soil conditions in wheel tracks compared with centre tracks. In this context, we found higher pH values in wheel tracks than in centre tracks, with the difference being significant for AS (wheel track: 5.8 ± 0.08; centre track: 5.3 ± 0.13; $p < 0.05$), TS (wheel track: 5.6 ± 0.06; centre track: 5.1 ± 0.12; $p < 0.05$), and LS (wheel track: 7.0 ± 0.04; centre track: 6.8 ± 0.05; $p < 0.05$). The importance of soil pH on the growth of vascular plants and bryophytes, as well as their composition and diversity, has also been highlighted in several studies (Löbel et al., 2006; Hydbom et al., 2012; Oldén et al., 2016). For example, Rola et al. (2021) showed that soils with a more acidic pH promoted larger bryophyte coverage, which could explain, among other things, the generally higher bryophyte cover in centre tracks in our study.

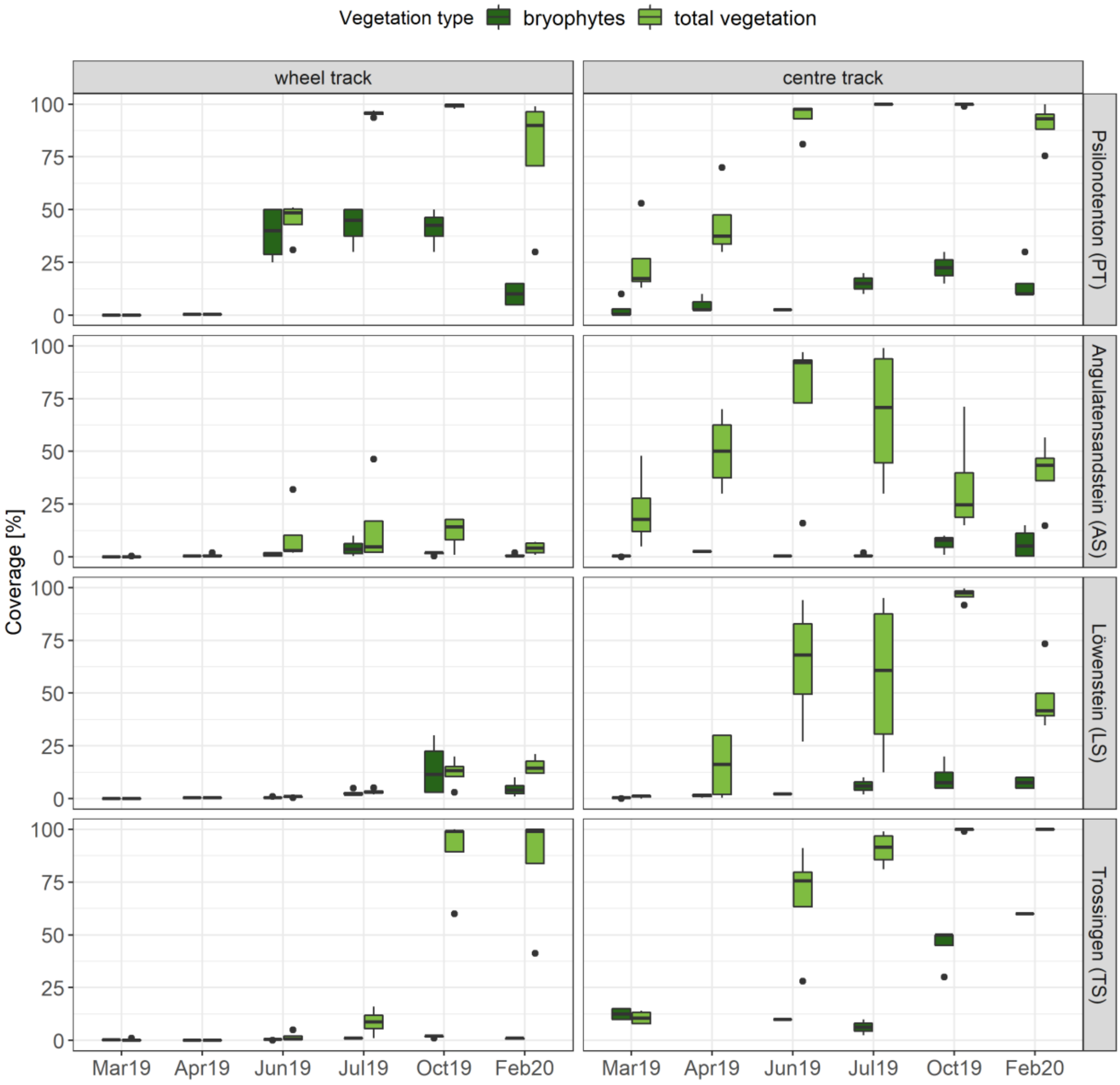


Figure 3: Development of bryophyte (n = 4) and total vegetation coverage (n = 4) per runoff plot at the individual skid trails. The bottom and top of the box represent the first and third quartiles, and whiskers extend up to 1.5 times the interquartile range (IQR) of the data. Outliers are defined as more than 1.5 times the IQR and are displayed as dots.

In AS and LS, total vegetation coverage was lower than in PT ($p < 0.001$), which was also the case for bryophyte cover (for AS and PT: $p < 0.001$; for LS and PT: $p < 0.01$). In comparison, PT and TS were rapidly overgrown by vascular plants; however, they did not displace bryophytes (see Figure 3). This coexistence of vascular plants and bryophytes was also displayed in a positive correlation between their coverage rates (Spearman's correlation $\rho = 0.38$, $p < 0.001$). Nevertheless, the overgrowth of bryophytes by vascular plants also marks the transition from biocrust to an evolved successional stage of bryophyte cover, characterized by a large proportion of the biomass being above the soil surface (Belnap et al., 2001a). While closed vegetation cover developed in PT and TS until autumn in both centre and wheel tracks, no continuous pattern of growth emerged in AS and LS, with clear differences between centre and wheel tracks. AS and LS developed a very sparse total vegetation cover in wheel tracks (about 5 %) and revealed considerably higher coverage in centre tracks.

Biocrusts reached a more developed successional stage as bryophyte cover when they were overgrown by vascular plants. This bryophyte cover could be established even with high total vegetation cover, which contradicts observations that vascular plants limit bryophyte growth in different ecosystems (Bergamini et al., 2001; Fojcik et al., 2019; Corbin and Thiet, 2020). For instance, Fojcik et al. (2019) found a negative relationship between bryophyte cover and the coverage of vascular plants in a temperate forest ecosystem, which they attributed to competition between bryophytes and vascular plants. Bergamini et al. (2001) also discovered one such negative relationship and explained it primarily in terms of light availability, with a combination of optimal radiation and moisture conditions depending on the extent of vascular-plant cover. In contrast, Ingerpuu et al. (2005) verified in a grassland experiment that vascular plants could actually facilitate bryophyte growth, explaining this by the fact that vascular plants create a more favourable microclimate under their canopy. Likewise, positive correlations between vascular plants and bryophyte cover have been reported for temperate forests, which are comparable to our results (Márialigeti et al., 2009; Rola et al., 2021). According to Rola et al. (2021), this relationship can be explained by the species composition (e.g. expansive grasses and sedges could easily eliminate bryophytes; Chmura and Sierka, 2007) and a relatively low vascular-plant cover. A decline in bryophyte cover was observed for the first time in autumn on deciduous forest sites but not on coniferous sites. For this reason, we assume that bryophyte growth in our study area was limited by leaf litter fall rather than suppression by vascular plants. A negative effect of leaf litter was also reported in several other studies (Márialigeti et al., 2009; Fojcik et al., 2019; Mercier et al., 2019; Alatalo et al., 2020; Wu et al., 2020).

3.2.2 Bryophyte and vascular-plant species richness

Regarding bryophyte and vascular-plant species richness, we observed that a greater number of vascular-plant species occurred in centre tracks (9.85 ± 0.59) than in wheel tracks (4.85 ± 0.53; $p < 0.001$), while no significant difference between tracks was found for bryophyte species richness (Figure 4). Furthermore, species richness varied in the skid trails: PT and LS showed, on average, considerably higher numbers of bryophyte species compared with AS and TS ($p < 0.01$). Concerning vascular plants, the highest species richness was achieved in PT, which was significantly higher than in AS and TS but not much higher than in LS. In comparison, AS, TS, and LS exhibited no differences in vascular-plant species richness. While bryophyte species richness was positively correlated with pH (Spearman's correlation $\rho = 0.40$, $p < 0.001$) and negatively correlated with silt content (Spearman's correlation $\rho = -0.35$, p < 0.001), we could not find any clear associations between the soil parameters surveyed and vascular-plant species richness. A GAM was used to explain 70.9 % of the deviation of bryophyte species richness, with pH ($p < 0.001$), bryophyte cover ($p < 0.001$), SOC ($p < 0.01$), and N_t ($p < 0.01$) being significant.

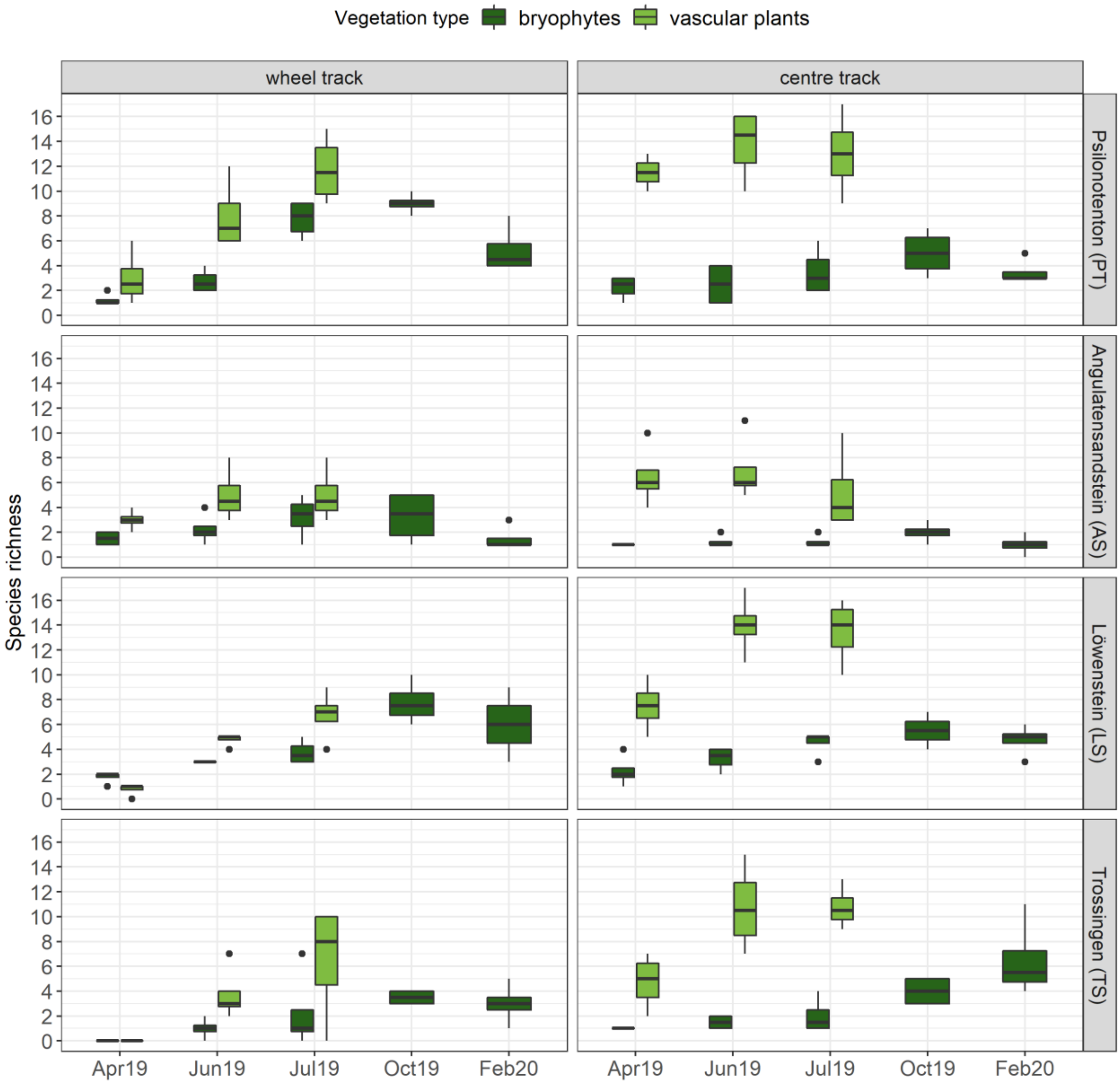


Figure 4: Species richness of bryophytes (n = 4) and vascular plants (n = 4) per runoff plot at the individual skid trails. The bottom and top of the box represent the first and third quartiles, and whiskers extend up to 1.5 times the interquartile range (IQR) of the data. Outliers are defined as more than 1.5 times the IQR and are displayed as dots.

Our results revealed not only that development of total vegetation cover was slower and less pronounced in wheel tracks but also that fewer vascular-plant species could colonize there. Contrary to our expectations, bryophyte species richness was not affected by track position. In this context, Müller et al. (2013) found that experimentally induced disturbances had no impact on bryophyte species richness, whereas the diversity of annual plants benefited from disturbances. Minor disturbances, not exceeding 12 % bare ground, could still promote bryophyte species richness, while further disturbance was detrimental. Additionally, Mercier et al. (2019) discovered that soil compaction in skid trails had a positive effect on the species richness of vascular plants, while bryophyte species richness was not affected. AS and LS, which showed particularly low levels of coverage and species richness, exhibited a different underlying substrate (sandstone) from the other two skid trails (claystone), which was also why we found different soil conditions there. Regional variations in species richness of vascular plants and bryophytes due to different soil conditions have also been confirmed in a variety of studies (Löbel et al., 2006; Klaus et al., 2013; Müller et al., 2013; Filibeck et al., 2019), with pH in particular proving to be an important positive control variable for bryophyte species richness (Hydbom et al., 2012; Oldén et al., 2016; Tyler et al., 2018). Additionally, Tyler et al. (2018) discovered a significant influence of substrate type, soil depth, and grazing intensity on overall bryophyte species richness, with pH remaining the most important factor in this study also. Further factors influencing bryophyte species richness, such as light availability, the carbon-to-nitrogen ratio, and bark water capacity, were identified by Jagodziński et al. (2018) for 30-year-old reforested areas on lignite mining spoil heaps.

3.3 Soil erosion depending on site, track position, and vegetation cover

In total, mean sediment discharge in the wheel tracks reached 206.76 ± 24.53 g m^{-2} and 15.68 ± 3.84 g m^{-2} in the undisturbed forest soil ($p < 0.001$), while centre tracks caused a sediment loss of 63.09 ± 10.28 g m^{-2}, which was 4 times higher than the undisturbed forest soil ($p < 0.05$). Considering ROPs with bare soil separately, an average soil erosion of 341.53 ± 68.20 g m^{-2} was achieved, which corresponds to a 22-fold enhancement compared with undisturbed forest soil. Additionally, sediment discharge in wheel tracks was increased by a factor of 3.3 compared with centre tracks. The main driver of sediment discharge was surface runoff (Spearman’s correlation $\rho = 0.80$, $p < 0.001$), and other important influencing soil characteristics were soil bulk density (Spearman’s correlation $\rho = 0.50$, $p < 0.001$), SOC and N_t (both with Spearman’s correlation $\rho = -0.46$, $p < 0.001$), and MWD (Spearman’s correlation $\rho = -0.46$, $p < 0.001$). Additionally, a negative correlation between soil erosion and clay content was identified (Spearman’s correlation $\rho = -0.42$, $p < 0.001$), and antecedent soil moisture and slope played a minor role in soil erosion. A GAM could explain 71.9 % of the deviation of sediment discharge, with runoff ($p < 0.001$) and total vegetation cover ($p < 0.001$) being significant.

These results show that skid trails are a major contributor to soil erosion in forest ecosystems and that compacted wheel tracks in particular significantly increased sediment discharge, which has also been demonstrated in previous studies (Safari et al., 2016; Zemke, 2016). In line with our results, Safari et al. (2016) highlighted soil texture, soil bulk density, SOC, and aggregate stability as the main soil parameters affecting runoff generation and soil erosion in skid trails. Based on these relationships, the significantly higher sediment discharge in skid trails is explained by the fact that the soil was disturbed and compacted by timber-harvesting machines, especially in wheel tracks, such that infiltration is reduced, which in turn leads to higher surface runoff and sediment transport (Zemke et al., 2019).

For all skid trails, sediment discharge was, on average, highest in March 2019 with a mean value of 201.80 ± 39.82 g m^{-2} and was considerably decreased in July 2019 to 74.13 ± 16.16 g m^{-2} ($p < 0.01$). Subsequently, sediment discharge increased significantly in October 2019 (97.77 ± 21.16 g m^{-2}; $p < 0.05$) and rose again to 165.03 ± 29.75 g m^{-2} in February 2020 ($p < 0.001$). Considering the time progression of soil erosion individually in the skid trails, different erosion mechanisms and sediment loads were evident (Figure 5). Average sediment discharge was highest in AS with 243.63 ± 37.30 g m^{-2} and lowest in TS with 42.83 ± 10.34 g m^{-2}, which represented a difference of a factor of 5.7 ($p < 0.001$). While all skid trails differed from each other in terms of sediment discharge, no significant difference was detected between PT (151.62 ± 32.57 g m^{-2}) and LS (99.26 ± 15.76 g m^{-2}). With respect to the time progression of soil erosion in the skid trails, we found a difference between the measurement times for PT and LS but not for AS and TS. In both cases, sediment discharge was significantly reduced from the bare soil condition in March 2019 to an early-successional stage of biocrust and vascular-plant vegetation in July 2019: PT showed a decrease of 89 %, and LS had a reduction of 59 %. The same pattern of soil erosion over the year was also observed in AS but could not be statistically demonstrated. While the correlation between surface runoff and sediment discharge was particularly high on average for the first rainfall simulation (Spearman's correlation $\rho = 0.89$, $p < 0.001$), the influence was distinctly reduced in the other simulations and especially in October 2019 (Spearman's correlation $\rho = 0.51$, $p < 0.01$). In the subsequent rainfall simulations, vegetation cover was an additional factor influencing soil erosion: the negative relationship between total vegetation cover and sediment discharge increased considerably from the first to the third simulation in October 2019 (first simulation in March: Spearman's correlation $\rho = -0.45$, $p < 0.01$; third simulation in October: Spearman's correlation $\rho = -0.86$, $p < 0.001$), and the highest reduction in sediment discharge occurred in July 2019.

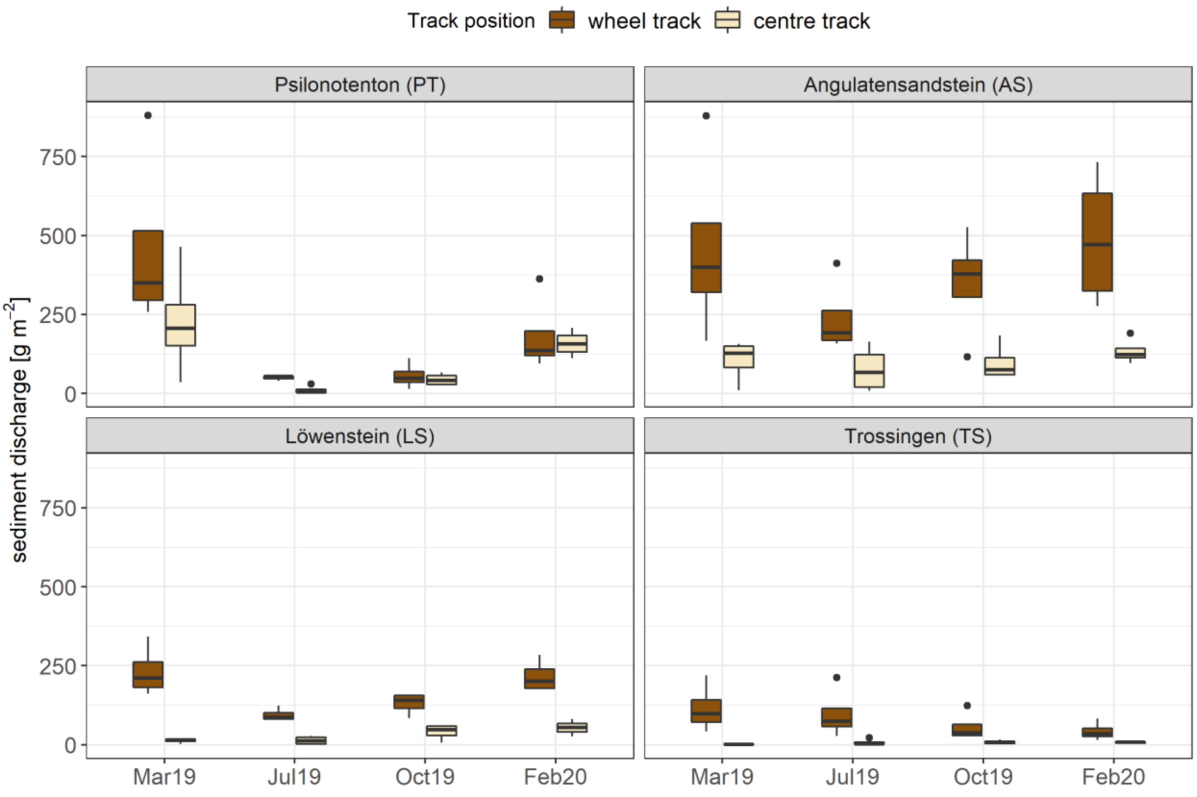


Figure 5: Sediment discharge during simulated rainfall in the wheel track (n = 4) and centre track (n = 4) of the four skid trails for every rainfall simulation time. The bottom and top of the box represent the first and third quartiles, and whiskers extend up to 1.5 times the interquartile range (IQR) of the data. Outliers are defined as more than 1.5 times the IQR and are displayed as dots.

Overall, the amount of discharged sediment clearly depended on the particular site, likely indicating an important effect of parent material on soil properties and adjunct vegetation development and, thus, on soil erosion. A high influence of parent material on soil erosion was confirmed by Rodrigo-Comino et al. (2018). Regardless of the amount of sediment discharge, three skid trails showed comparable trends in soil erosion over time: in general, soil erosion was highest on bare soil; was reduced during the vegetation period, by the most with pioneer vegetation in July 2019, where biocrusts predominated; and then increased again in winter. This general trend was not observed in TS, which is probably related to the ecological structure of TS, since it was the only skid trail located in a clearing and was therefore clearly distinguished from the other skid trails in terms of vegetation succession. In addition, forest residues, such as bark, small branches, and needles were added to the topsoil in TS as a result of forestry use, which also had a stabilizing effect and certainly contributed to the low sediment discharge in this skid trail. The erosion-reducing effect of these types of mulching with forest residues has already been demonstrated in various studies (Prats et al., 2016; Prosdocimi et al., 2016), and Vinson et al. (2017) recently demonstrated that mulching strategies could also significantly reduce erosion rates in skid trails.

Several erosion studies on skid trails have already emphasized vegetation cover as one of the key control variables of soil erosion (Zemke, 2016; Malvar et al., 2017; McEachran et al., 2018). Soil erosion was often observed to be highest in the first year after skidding and decreased thereafter with increasing vegetation cover (Baharuddin et al., 1995; Jourgholami et al., 2017; Malvar et al., 2017). Martínez-Zavala et al. (2008) also reported a seasonality in their erosion measurements on forest road backslopes in southern Spain, with higher soil loss rates in winter despite vegetation cover, primarily attributed to higher soil moisture. However, they further found that this seasonal effect did not occur above a vegetation cover of 30 %. Thus, we hypothesize that, among other factors, higher soil moisture may have influenced increased winter soil erosion in our case as well, although we have not found significant correlations to support this theory.

3.4 Influence of bryophyte cover and early-successional bryophyte-dominated biocrusts on soil erosion

Sediment discharge was distinctly negatively affected by total vegetation cover (Spearman's correlation $\rho = -0.61$, $p < 0.001$). Furthermore, we discovered a stronger negative correlation between bryophyte cover and sediment discharge (Spearman's correlation $\rho = -0.54$, $p < 0.001$) than between vascular-plant cover and sediment discharge (Spearman's correlation $\rho = -0.36$, $p < 0.001$). For these correlations, all undisturbed forest soil ROPs that were covered with leaf litter were extracted because we assume that litter-covered soils have a different protective mechanism than soils with bryophytes or vascular plants (Silva et al., 2019; Wang et al., 2020). All cover classes differed significantly from each other in terms of sediment discharge, with a reduction of 77 % being observed between bare ROPs and bryophyte ROPs ($p < 0.001$) and a reduction of 59 % being observed between bare ROPs and vascular-plant ROPs ($p < 0.005$). Bryophyte ROPs showed 44 % less sediment discharge than vascular-plant ROPs ($p < 0.05$). When ROPs were categorized into different cover classes, there was a nonsignificant trend for bryophytes to result in less sediment discharge compared with vascular plants (Figure 6). Especially with a cover of more than 50 %, the erosion-reducing effect of bryophytes was more pronounced compared with vascular plants; for example, the mean sediment discharge of bryophyte ROPs was 3.27 ± 1.50 g m^{-2}, while vascular-plant ROPs still reached an average of 57.82 ± 12.47 g m^{-2}, an 18-fold difference.

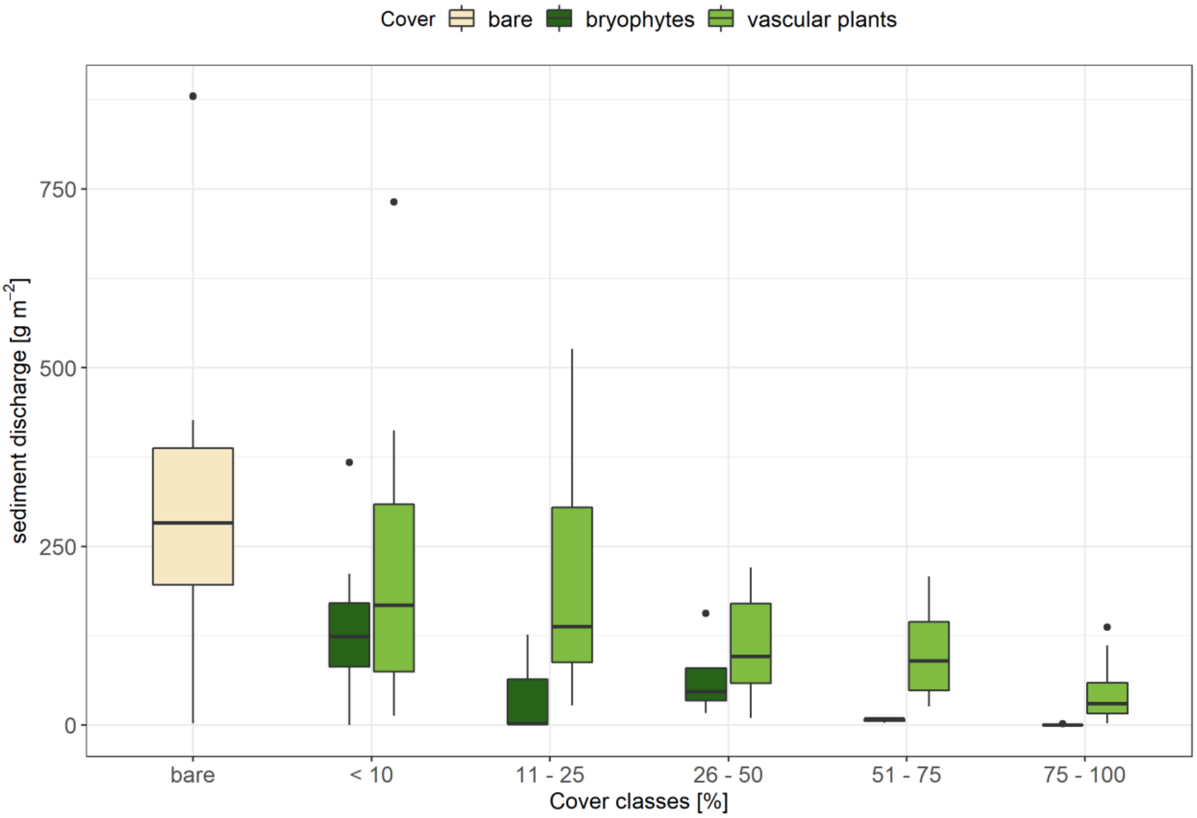


Figure 6: Sediment discharge during simulated rainfall for bare (n = 14), bryophyte (n = 27), and vascular-plant (n = 58) runoff plots (ROPs) categorized into cover classes. The bottom and top of the box represent the first and third quartiles, and whiskers extend up to 1.5 times the interquartile range (IQR) of the data. Outliers are defined as more than 1.5 times the IQR and are displayed as dots.

Bryophyte covers in temperate forest are known to stabilize soil surfaces and, thus, act as a protective agent against soil erosion (Mägdefrau and Wutz, 1951; Belnap and Büdel, 2016; Seitz et al., 2017). The same applies to covers of vascular plants (Zuazo Durán and Rodríguez Pleguezuelo, 2009); however, it is assumed that bryophyte communities have a stronger erosion-reducing effect than vascular plants (Casermeiro et al., 2004; Bu et al., 2015) due to their large water absorption capacity (Thielen et al., 2021) and the soil stabilizing effect of their rhizoids (Mitchell et al., 2016). In this context, the biocrust characteristics were demonstrated in this study at the initial successional stage, with communities of bryophytes, their protonemata, cyanobacteria, and algae, for example, seeming to further enhance the erosion-reducing effect. Thus, the erosion-reducing effect appears to be stronger than that of communities dominated by vascular plants in the later stages (Figure 5); this might be due to a combination of different complementary plant traits. Likewise, Seitz et al. (2017) attributed a positive effect to bryophyte protonemata in erosion control in mesic ecosystems. On the Loess Plateau in China, Bu et al. (2015) found that bryophyte-dominated biocrusts achieved a reduction in soil erosion of 81 % compared with bare soil, while a mixture of vascular plants and bryophytes contributed significantly less to erosion control (a 0.7 %–0.3 % reduction depending on plant species). Furthermore, Casermeiro et al. (2004) discovered during rainfall simulations in Spain that scrubs are more effective at mitigating soil erosion when they are underlain with a cover of bryophytes. However, contrasting results were reported for a very specific setup by Parsakhoo et al. (2012), who found that bryophyte-covered ROPs produced more sediment than ROPs with *Rubus hyrcanus*. Thus, there are still a number of unresolved questions regarding bryophyte–soil interactions on aspects such as water absorption, storage, and therefore erosion processes (Thielen et al., 2021), as well as on the development of biocrusts in mesic and forested areas, which need to be tackled in future research.

4 Conclusions

This study examined the initial development of pioneer nonvascular- and vascular-plant cover, composition, and species richness in temperate forest disturbance zones and their influence on soil erosion. Regarding our hypotheses, the following conclusions were drawn:

(1) The succession of bryophytes and their composition varied at every site. Generally, *Brachythecium rutabulum* and *Oxyrrhynchium hians* were the most important and persistent pioneer bryophyte species, while *Dicranella schreberiana* and *Pohlia lutescens* formed covers that quickly disappeared after spreading in summer. Biocrust communities occurred immediately after disturbance from April to July 2019, consisting primarily of bryophyte protonemata and cyanobacteria as well as coccoid and filamentous algae.

(2) Skid trails on clayey substrates showed considerably higher total vegetation cover and species richness, which applied to bryophytes and vascular plants. While vascular plants were more abundant in centre tracks than wheel tracks in terms of both cover and species richness, there was no clear difference in bryophyte species richness in this regard. Although bryophytes were quickly overtopped by vascular plants during vegetation succession, they managed to coexist until the end of the vegetation period and were then limited, most likely due to leaf litter fall.

(3) The total amount of sediment discharge and the general mechanisms of soil erosion were clearly site dependent. Soil erosion was reduced, especially with the occurrence of pioneer biocrust vegetation in summer, and again increased in winter, when vascular vegetation became dominant. Sediment discharge was 13.2 times higher in wheel tracks than in undisturbed forest soil, and bare soil ROPs produced a 22-fold greater sediment discharge than undisturbed forest soil.

(4) Bryophytes made a major contribution to erosion control after disturbances in this temperate forest ecosystem. They contributed more to mitigating soil erosion than vascular plants. Since soil erosion was especially low when bryophytes occurred within biocrusts,

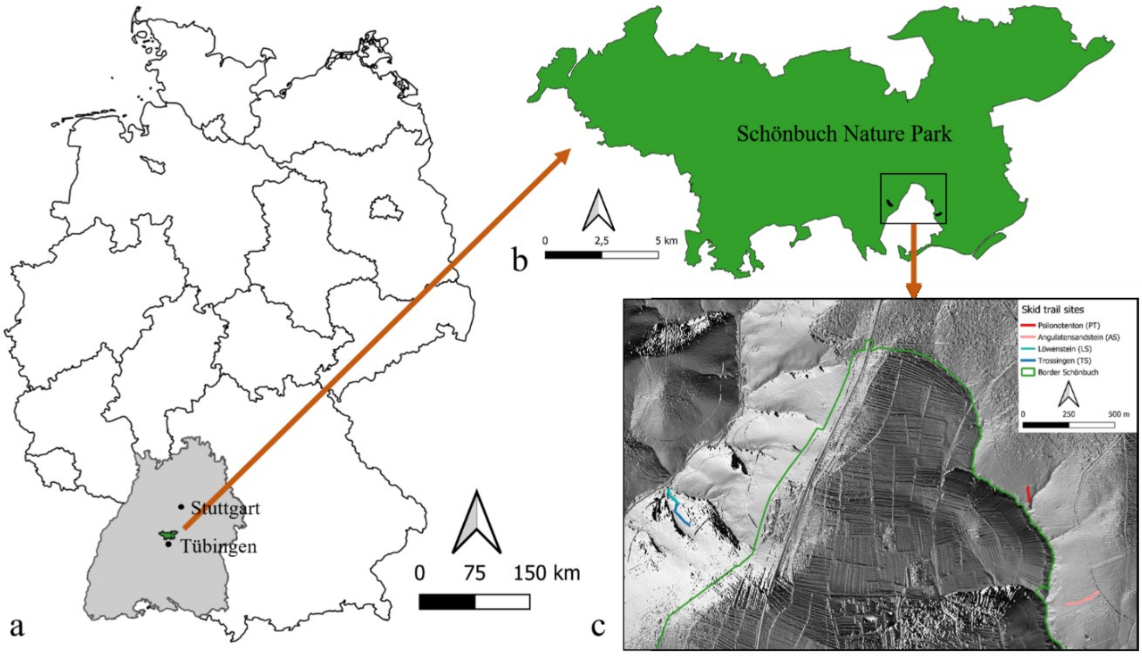
we assume that bryophyte-dominated biocrusts, in particular, are of utmost importance for preventing soil degradation, even in mesic environments.

Based on these results, artificial inoculation of bryophytes as erosion control on bare forest soils is assumed to be of particular interest for future research. In this context, Varela et al. (2021) recently published an approach to establish moss cultures from the laboratory, which could be applied for environmental studies. Moreover, the question arises as to whether bryophytes reduce soil erosion primarily through their protective-layer effect on splash and runoff, or whether they also improve soil properties, such as aggregate stability, which further enhance erosion control (Riveras-Muñoz et al., 2022). Within this framework, it continues to be of special interest whether there are different mechanisms of erosion control depending on particular bryophyte species and which of their structural traits affect soil erosion patterns the most.

Appendix A

Table A1: Characteristics of studied skid trails.

	AS	**PT**	**LS**	**TS**
Series	Lower Jurassic	Lower Jurassic	Upper Triassic	Upper Triassic
Formation	Angulatensandstein (AS)	Psilonotenton (PT)	Löwenstein (LS)	Trossingen (TS)
Parent material	Sandstone	Shale clay	Sandstone	Claystone
Soil type (Ad-hoc AG Boden, 2005)	Braunerde-Pseudogley	Pseudogley	Braunerde-Pelosol	Braunerde-Pelosol
Soil type (IUSS Working Group WRB, 2015)	Dystric Leptosol (Ochric, Siltic, Stagnic)	Calcaric Albic Planosol (Clayic, Ochric, Raptic)	Calcaric Cambisol (Humic, Loamic, Protovertic)	Eutric Cambisol (Geoabruptic, Clayic, Ochric, Protovertic)
Soil texture	Silt loam Sand: 6.89 % Silt: 67.99 % Clay: 25.33 %	Silty clay loam Sand: 6.67 % Silt: 56.49 % Clay: 36.86 %	Clay loam Sand: 25.91 % Silt: 40.78 % Clay: 33.20 %	Silty clay loam Sand: 11.46 % Silt: 50.70 % Clay: 37.81 %
SOC	4.08 %	5.22 %	5.52 %	7.95 %
N_t	0.24 %	0.31 %	0.27 %	0.40 %
C/N	17	17	21	19
pH_{Ca}	5.6	6.9	6.9	5.4
Slope	4.6°	7.2°	10°	11.3°
Aspect	Southwest	South	West	Northwest
Sample site coordinates	Tübingen 48.553054° N 9.119053° E	Tübingen 48.557425° N 9.114462° E	Tübingen 48.557527° N 9.088098° E	Tübingen 48.556036° N 9.089313° E



(Geobasisdaten © Landesamt für Geoinformation und Landentwicklung Baden-Württemberg, www.lgl-bw.de)

Figure A1: Overview of the study area. a) Location of Schönbuch Nature Park in Germany. b) Location of the selected skid trails inside Schönbuch Nature Park. c) Location of the four skid trails on a hillshade raster (Geobasisdaten © Landesamt für Geoinformation und Landentwicklung Baden-Württemberg, www.lgl-bw.de).

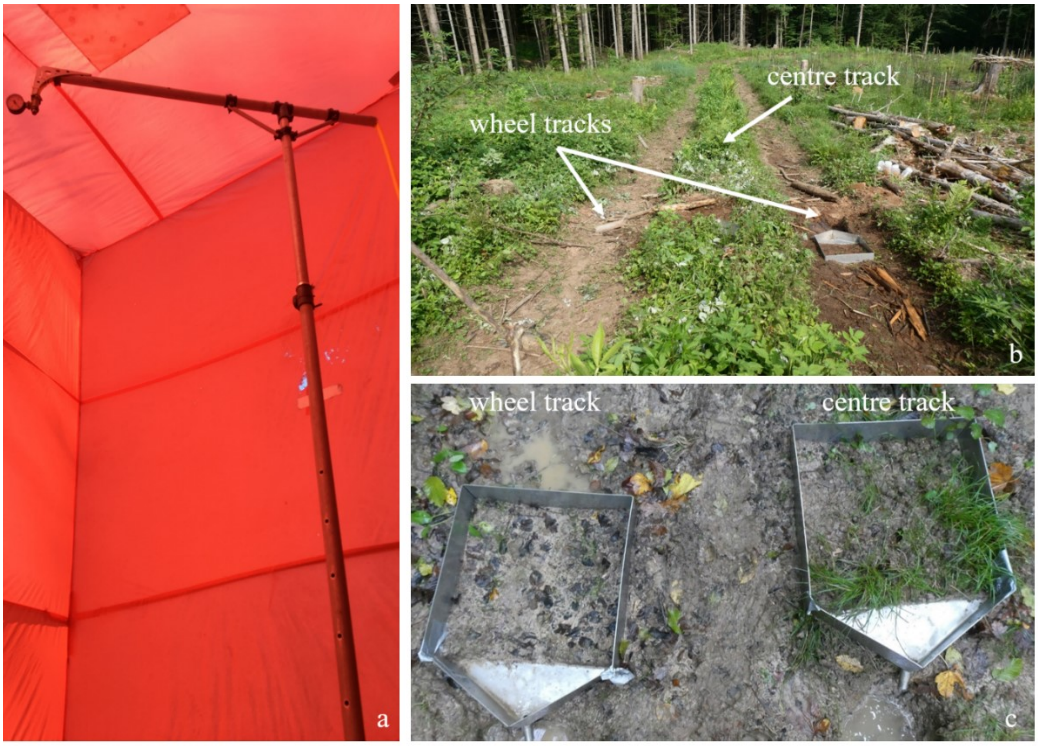


Figure A2: Experimental setup. a) Tübingen rainfall simulator inside the protective tent. b) Skid trail in the Trossingen Formation (TS) in July 2019. c) Runoff plots in the wheel track and the centre track in the Angulatensandstein Formation (AS) in October 2019.

Code availability

The codes used in this study are available upon request.

Data availability

The dataset compiled and analysed in this study is available on figshare at https://doi.org/10.6084/m9.figshare.17206835.v3 (Gall et al., 2021).

Author contribution

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

Competing interests

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

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Financial Support

This research has been supported by the Deutsche Forschungsgemeinschaft (gran no. SE 2767/2-1, “MesiCrust”).

Review Statement

This paper was edited by Steven Bouillon and reviewed by Bettina Weber and two anonymous referees.

Acknowledgements

This research would not have been possible without the exceptional support of Michael Sauer during vegetation surveys. His enthusiasm and knowledge of moss identification was an inspiration and we thank him for his great contribution to this work. We would also like to express our sincere gratitude to Laura Bindereif, Lena Grabherr, Helena Obermeier, Antonia Tertelmann, Philipp Gries, Delia Maas, Stefanie Gotterbarm, Giulia König, Nicolás Riveras-Muñoz, Sascha Scherer, Matthew A. Bowker, Daniel Schwindt and all students of GEO51 in winter semester 2019/20 for their help with field and lab work. Many thanks also to Sabine Flaiz, Rita Mögenburg and Peter Kühn for always being available to help us with questions regarding lab work. Furthermore, we thank the state forestry service of Baden-Württemberg (ForstBW) for supporting the MesiCrust project. We are grateful to Bettina Weber, further two anonymous reviewers and the students and tutor of the course “Critical Thinking in Ecological and Environmental Sciences” at the University of Edinburgh for a very constructive and helpful review.

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Manuscript 3

On the impact of soil-moss combinations on surface runoff, percolation, soil erosion, and temporal dynamics of soil water content*

(in preparation)

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* This manuscript has been published in a modified version as a preprint with the following citation: GALL, C.; NEBEL, M.; SCHOLTEN, T.; THIELEN, S. M. & SEITZ, S.: Water's path from moss to soil Vol. 2: How soil-moss combinations affect the soil water balance and soil erosion, 30 November 2023, Preprint (Version 1) available at Research Square. https://doi.org/10.21203/rs.3.rs-3268666/v1.

Introduction

For decades, soil erosion has been a major environmental problem as it degrades the most productive soil layers, which threatens, among other things, food production worldwide. Although these effects have been known for a long time, there are still a variety of challenges to mitigating soil erosion in different ecosystems. As climate change progresses, the risk of soil loss increases, making the preparation of effective solutions very urgent (OLSSON et al., 2019; SCHOLTEN & SEITZ, 2019). A current research focus is on the restoration of a protective soil cover following disturbances in the vegetation layer, e.g., through the reestablishment of biological soil crust communities. These are often dominated by bryophytes in temperate climates.

To date, there are few studies that have measured surface runoff and sediment discharge beneath mature bryophyte covers. For instance, PARSAKHOO et al. (2012) investigated the differential effects of the bryophyte *Philonotis marchica* (Hedw.) Brid. and the shrub *Rubus hyrcanus* L. on soil erosion from forest road cutslopes. They found that *Philonotis marchica* significantly reduced soil erosion by 61 % compared to bare soil, but less significantly than *Rubus hyrcanus,* resulting in an 81 % mitigation of soil erosion. In general, both biocrust and bryophyte covers significantly reduce soil erosion, although the extent depends on the stage of development (CHAMIZO et al., 2017), the respective species, its life form (TU et al., 2022), and other still unknown factors.

This study investigated the influence of different combinations of moss species and underlying soil substrates (soil-moss combinations) on surface runoff, percolation, soil erosion and the temporal dynamics of soil water content. 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 record the soil water content. We distinguished between 4 treatments according to moisture conditions and cover type: bare & dry, bare & wet, moss & dry, moss & wet. The following hypotheses were tested:

1. Moss covers reduce surface runoff as well as soil erosion and increase percolation.
2. The temporal dynamics of soil water content differ significantly in the selected treatments.

Material and methods

Properties of studied moss species and soil substrates

Soil substrates were collected from the wheel tracks of four skid trails described in GALL et al. (2022) in the Schönbuch Nature Park in Southwest Germany. They were sampled from the topsoil of the skid trail wheel tracks to a depth of 10 cm and distinguished according to their geological formation: Angulatensandstein (AS), Psilonotenton (PT), Löwenstein (LS) and Trossingen (TS) (EINSELE & AGSTER, 1986). Furthermore, we included a Lower Triassic substrate from the Palatinate Forest, which differs considerably from the other substrates in terms of its properties. The designation of this substrate was also based on the geological formation: Bernburg (BB).

Table 1: Soil substrate properties.

	AS	**PT**	**LS**	**TS**	**BB**
Series	Lower Jurassic	Lower Jurassic	Upper Triassic	Upper Triassic	Lower Triassic
Formation	Angulatensandstein-Formation (AS)	Psilonotenton-Formation (PT)	Löwenstein-Formation (LS)	Trossingen-Formation (TS)	Bernburg-Formation (BB)
Parent material	sandstone	shale clay	sandstone	claystone	sandstone
Soil texture	silty loam sand: 7.00 % silt: 67.58 % clay: 25.68 %	silty clay loam sand: 6.88 % silt: 56.28 % clay: 36.93 %	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 %
SOC	4.34	5.25	4.39	8.02	4.93
N_t	0.25	0.30	0.19	0.40	0.20
pH_{Ca}	5.8	7.0	7.0	5.6	3.4
Sample site location	Tübingen 48.553054° N 9.119053° E	Tübingen 48.557425° N 9.114462° E	Tübingen 48.557527° N 9.088098° E	Tübingen 48.556036° N 9.089313° E	Kaiserslautern 49.424156° N 7.758673° E
Associated moss samples	2x *O. hians* (lab-grown) 2x *O. hians* (field-collected)	4x *P. undulatum*	2x *B. rutabulum* 2x *A. serpens*	4x *E. striatum*	4x *P. formosum*

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. With regard to 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, and we also included field-collected samples of the latter to investigate intraspecific differences between field and cultivated mosses.

Experimental setup

Soil substrates were air dried, sieved by 6.3 mm and filled into infiltration boxes (40 x 30 x 15 cm) up to a height of 6.5 cm. 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 (Figure 1). 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 in each run of 30 minutes. Drop falling height was adjusted to 3.5 m and mean rainfall intensity was set to 60 mm h^{-1}, which was simulated for a duration 30 minutes. These settings refer to a regional rainfall event with a recurrence interval of 20 years (DWD CLIMATE DATA CENTER, 2021). Surface runoff, sediment and percolated water were collected in sample bottles (1 L). To measure water content (WC) 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 (EC) every 5 minutes at substrate surface and every 2 minutes at 3 cm substrate depth. These incongruent logging intervals are due to a technical error and were later interpolated to a minute interval for each measurement.

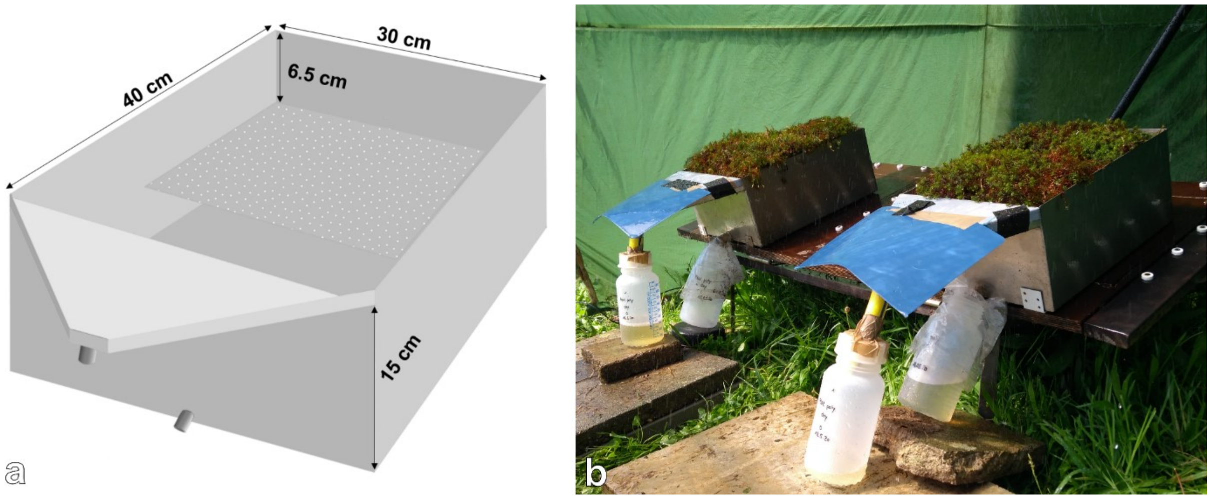

Figure 1: Illustration of an infiltration box. (a) Technical drawing on an infiltration box (Illustration: Julia Dartsch). (b) Infiltration boxes during rainfall simulations.

First, rainfall simulations were performed for bare soil substrates in air-dried condition, with 4 replicates for each substrate. 24 hours later the same infiltration boxes were irrigated once again in wet condition, 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 for adaption, 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.

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. Furthermore, the following basic soil properties were determined: 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 (N_t) with an elemental analyser (element analyzer Vario EL II, Elementar Analysensysteme GmbH, Hanau, Germany) and soil bulk density in 100 cm³ core samples using the mass-per-volume method (BLAKE & HARTGE, 1986).

Since EC values recorded by the BWP are temperature-dependent, a temperature correction was carried out to adjust all measurements to a temperature of 25 °C as suggested by WEBER et al. (2016). Following the example of WEBER et al. (2016), a BWP calibration was also conducted, which has already been described in detail in THIELEN et al. (2021) for the soil substrates studied. However, the soil substrates in the current study showed a higher variability in their WC, so extensive extrapolation of the data would have been necessary, which would not have been appropriate in this experiment. Therefore, a simplified calibration procedure according to the example of WEBER et al. (2016) was used in this case. For this purpose, the soil samples were weighed in 100 cm³ core cutter once in water saturated and once in dry condition (40 °C) to create linear calibration functions between minimum and maximum WC 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 measures, we used Generalized Linear Models (GLM) to screen for significant differences between treatments (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 erosion 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 the two moss 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 within bare treatments. For all substrates, surface runoff was higher than percolated water for bare treatments, and the reverse was true for moss treatments (Figure 2). The only exceptions were bare & dry treatment of PT and moss & wet treatment of BB. 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 ($p < 0.001$) and the same was true for 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 ($p < 0.01$).

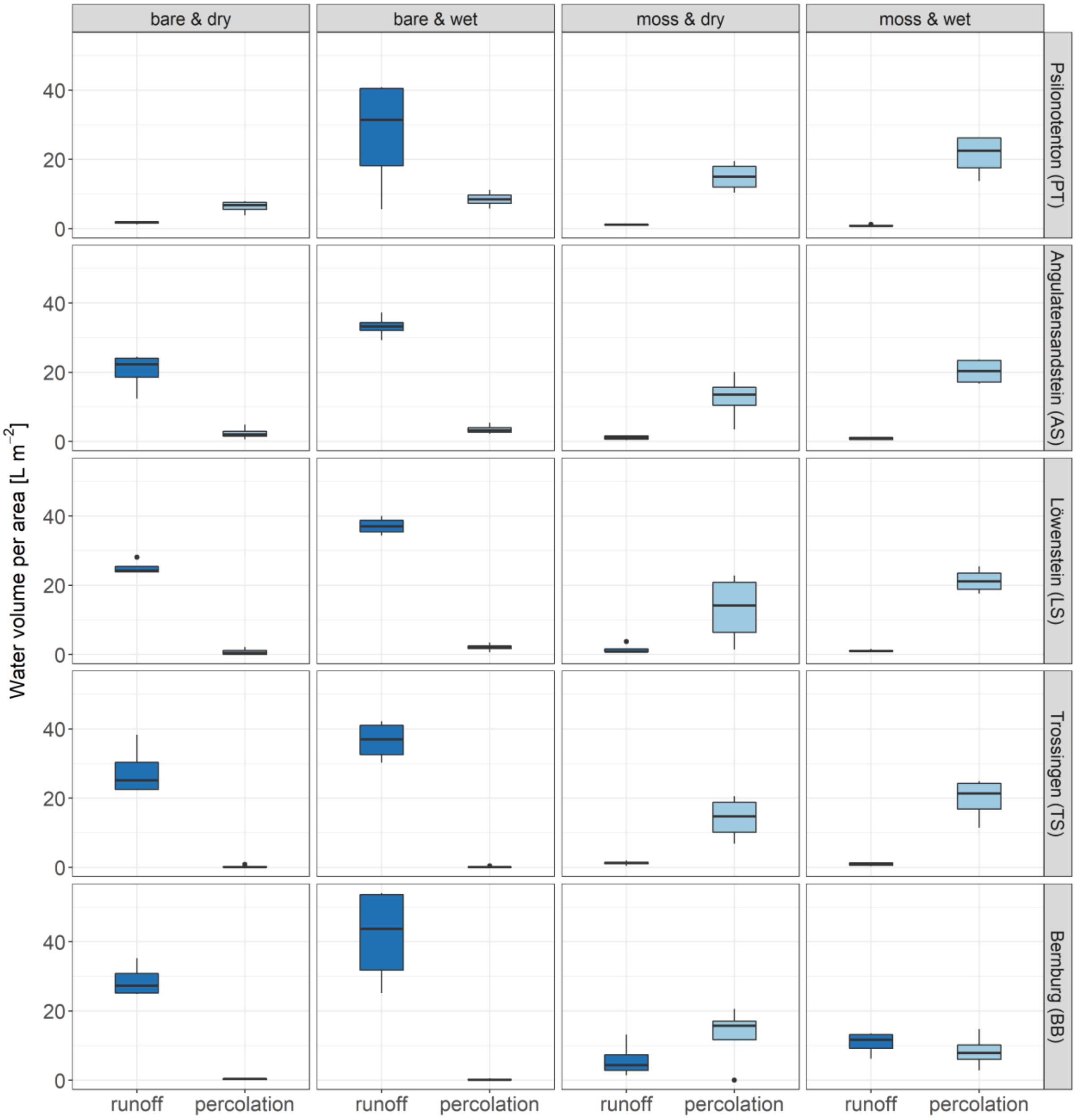

Figure 2: Surface runoff and amount of percolated water [L m⁻²] per infiltration box with four treatments and five soil substrates (n = 4). Lines within boxplots represent median values, while bottom and top of the boxplot show the first and third quartiles. Whiskers extend up to 1.5 times the interquartile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

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 within the moss treatments (Figure 3). On average, there were no differences in sediment discharge between the substrates. However, 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 considerably higher compared with the other substrates. However, soil erosion for BB was still 605 times lower in moss compared with bare treatments.

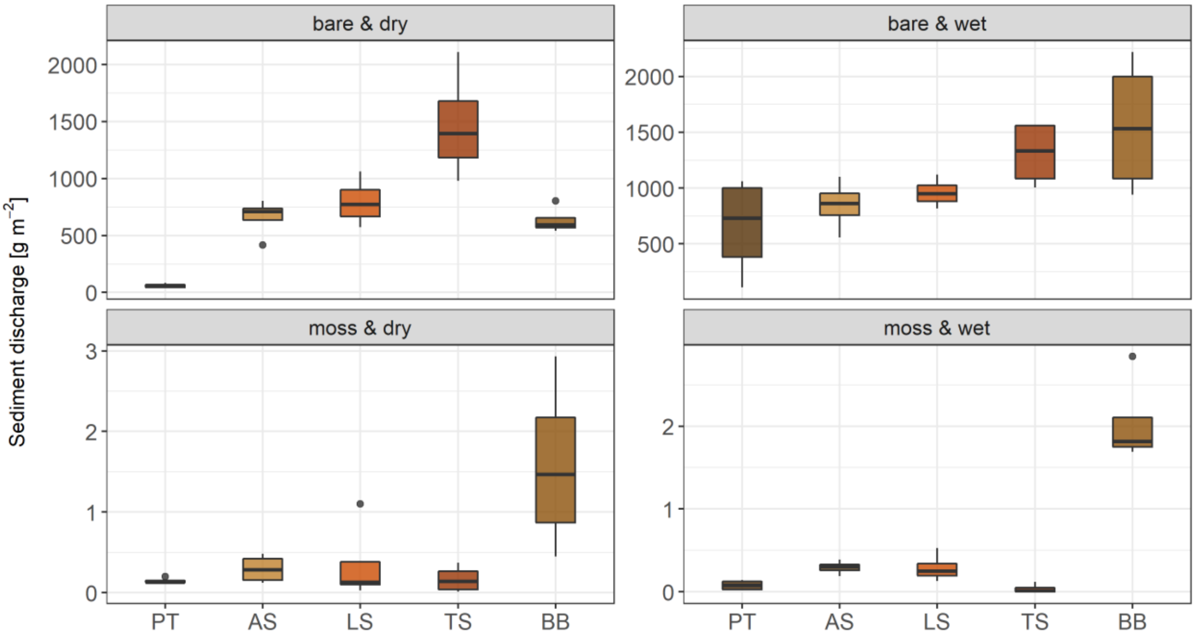

Figure 3: Sediment discharge [g m^{-2}] per infiltration box with four treatments and five soil substrates (n = 4). Lines within boxplots represent median values, while bottom and top of the boxplot show the first and third quartiles. Whiskers extend up to 1.5 times the interquartile range (IQR) of the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

The effect of antecedent soil moisture on surface runoff and soil erosion 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 & 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 erosion 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 erosion. 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 & SARAH, 2017). For this reason, many studies conclude that soil erosion 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 any wet soil aggregates on the surface at the beginning of the second rainfall simulation, but were already sealed as just described. Consequently, surface runoff and soil erosion were higher in bare & wet treatments compared with dry conditions.

Differences between substrates regarding surface runoff, amount of percolated water and soil erosion 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 & 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 & SARAH, 2017). In our experiment, the differences between the substrate 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 would be necessary to survey large number of different soil properties and environmental variables, but even this is difficult to concentrate in a single study due to the large number of influencing factors.

In addition to the treatments and substrates 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 (see section 2.2.4). Secondly, our measurements revealed that the BB substrate was highly water repellent. In preparing our experimental setup, we hypothesized that moss covers absorb a lot of water (WANG & BADER, 2018; THIELEN et al., 2021) and have a strong intercepting effect (PRICE et al., 1997), thus reducing surface runoff (TU et al., 2022) and preventing splash erosion (ROTH-NEBELSICK et al., 2022), both of which lead to reduced sediment discharge. In part, we attributed the large runoff as well as erosion reduction between bare and moss treatments to the moss cover and suspected, similar to the findings of TU et al. (2022), different extents of reduction depending on moss species. However, this could not be demonstrated in our experiments because the desiccation cracks also had a particular influence on the formation of surface runoff and the percolated water volumes, and both proportions cannot be quantified individually. The substrate BB did not form desiccation cracks, but was strongly water repellent, which generally increases surface runoff and soil erosion compared with wettable soils (LOWE et al., 2021), and resulted in bare treatments of sandy BB substrate producing more runoff than the other loamy substrates. Also the moss treatments of BB caused significantly higher surface runoff and sediment discharge as well as lower volume of percolated water compared with the other substrates. Despite the lack of desiccation cracks and occurrence of water repellency in this sample, however, the measured parameters were significantly reduced compared to the bare treatments, indicating a high influence of moss cover.

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 (Figure 4). 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 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 quite similar, however, the difference between surface and 3 cm depth was less pronounced in the moss & dry treatments than in the bare & dry treatments. 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 treatment 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 minutes for the BWP at 3 cm depth to respond in AS and LS, it took about 20 minutes in PT and TS, and no water was detected in BB. It is also noticeable that the water content in the moss treatments of LS at a depth of 3 cm was considerably lower than in the bare treatments. 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.

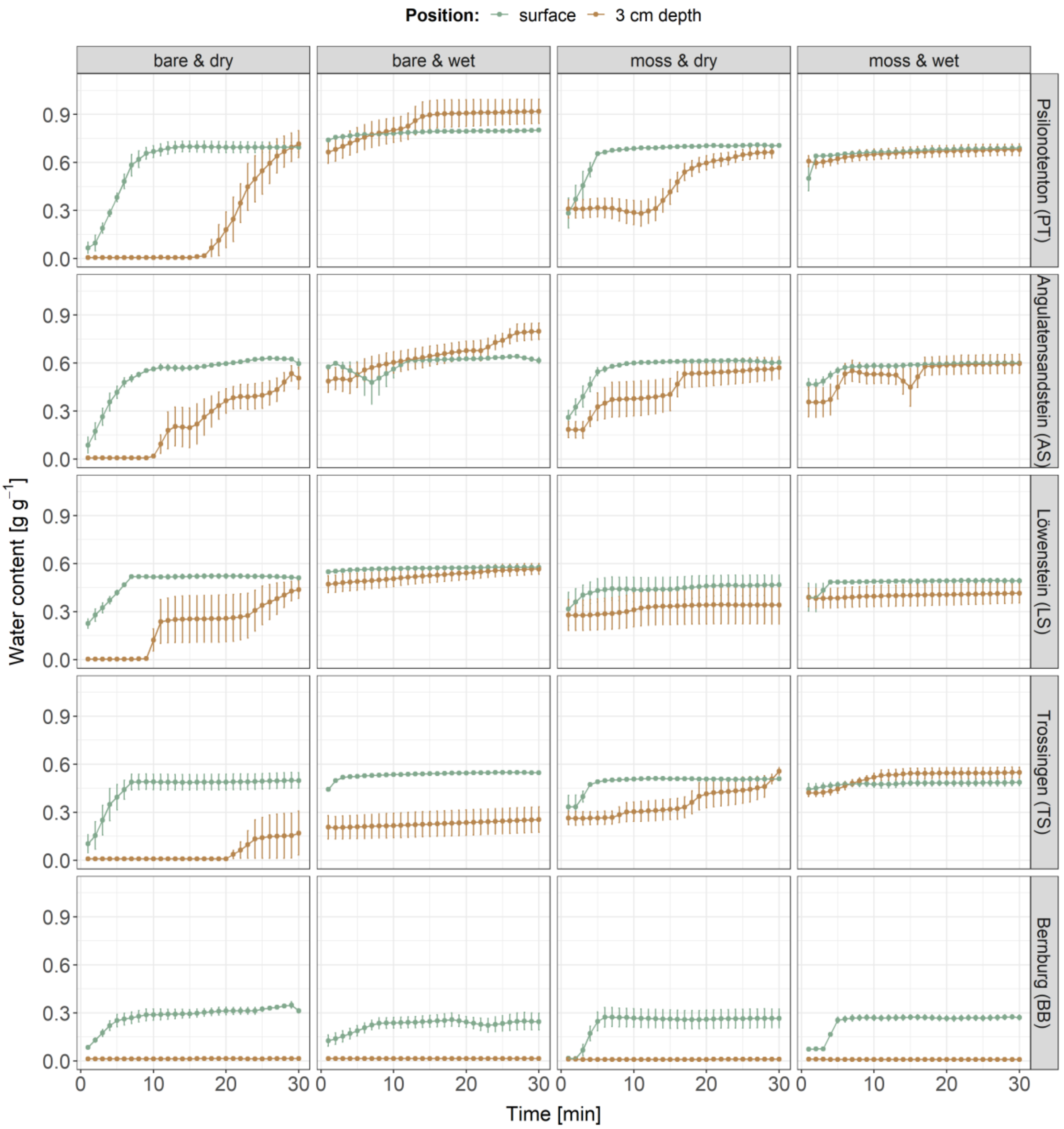

Figure 4: Temporal dynamics of water content values [g g^{-1}*] of treatments and substrates during rainfall simulations. Minute averages of water content are shown as points with standard errors. Water content was measured with biocrust wetness probes (BWP) at two positions: At the substrate surface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

These findings of 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 increased 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 lot 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 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, less water infiltrated into the substrate. In comparison, TU et al. (2022) have 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% was dedicated to surface runoff, whereby these ratios depended on the respective moss species. Another phenomenon that was particularly evident 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 also impressive 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. So it can be assumed that the water only flows at the outer edge of the infiltration box as preferential flow.

Conclusion

The combinations of moss species and underlying soil substrates (soil-moss combinations) showed clear differences between bare & dry, bare & wet, moss & dry and moss & wet treatments in terms of surface runoff, percolated water volume and sediment discharge. Due to our experimental design with repeated measurements, highest surface runoff and sediment discharge was observed in bare & wet treatments, as the soil surface was already sealed compared to bare & dry measurement. In comparison, surface runoff and soil erosion in the moss treatments were significantly reduced, while the amount of percolated water was increased. On the one hand, we attributed this to the high water storage capacity of mosses. On the other hand, this process was superimposed by desiccation cracks and water repellence, with the result that the respective influences could not be quantified individually. Therefore, further experimental setups are needed to clarify the apparently underestimated effects.

Temporal dynamics of water content also showed clear differences between treatments, allowing us to understand the differences in surface runoff and percolated water volume in more detail. Bare & wet treatments were already water saturated at the surface at the beginning, and at 3 cm substrate depth there was still potential to absorb water, which explained higher surface runoff and low percolated water volume. Moss treatments exhibited lower water contents over time compared to bare treatments, highlighting the strong influence of moss covers and desiccation cracks on the soil water balance. In the water-repellent substrate, the water was prevented from percolating down to a depth of 3 cm in all treatments.

Acknowledgements

We sincerely thank Michael Sauer for his support and expertise in collecting moss samples and Lena Grabherr, Alexander Maurer, Gesche Weiß and Daniel Schwindt for their help with field and lab work. Many thanks also to Sabine Flaiz, Rita Mögenburg and Peter Kühn for always being available to help us with questions regarding lab work. We are also grateful to the Plant Ecology group of the University of Tübingen for the space provided in their greenhouse. Furthermore, we thank the state forestry service of Baden-Württemberg (ForstBW) for supporting the MesiCrust project. This study was funded by the German Research Foundation (DFG SE 2767/2-1 “MesiCrust”).

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Water's path from moss to soil: A multi-methodological study on water absorption and evaporation of soil-moss combinations

Journal of Hydrology and Hydromechanics, 69 (4), 421-435
DOI: 10.2478/johh-2021-0021

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Submitted: March 31, 2021

Accepted: June 9, 2021

Published: November 15, 2021

Abstract

Mosses are often overlooked; however, they are important for soil-atmosphere interfaces with regard to water exchange. This study investigated the influence of moss structural traits on maximum water storage capacities (WSC_{max}) and evaporation rates, and species-specific effects on water absorption and evaporation patterns in moss layers, moss-soil-interfaces and soil substrates using biocrust wetness probes. Five moss species typical for Central European temperate forests were selected: field-collected *Brachythecium rutabulum*, *Eurhynchium striatum*, *Oxyrrhynchium hians* and *Plagiomnium undulatum*; and laboratory-cultivated *Amblystegium serpens* and *Oxyrrhynchium hians*.

WSC_{max} ranged from 14.10 g g^{-1} for *Amblystegium serpens* (Lab) to 7.31 g g^{-1} for *Plagiomnium undulatum* when immersed in water, and 11.04 g g^{-1} for *Oxyrrhynchium hians* (Lab) to 7.90 g g^{-1} for *Oxyrrhynchium hians* when sprayed, due to different morphologies depending on the growing location. Structural traits such as high leaf frequencies and small leaf areas increased WSC_{max}. In terms of evaporation, leaf frequency displayed a positive correlation with evaporation, while leaf area index showed a negative correlation. Moisture alterations during watering and desiccation were largely controlled by species/substrate-specific patterns. Generally, moss cover prevented desiccation of soil surfaces and was not a barrier to infiltration. To understand water's path from moss to soil, this study made a first contribution.

Introduction

Bryophytes occur in a wide range of ecosystems, from arctic and boreal enviroments to temperate and tropical forests, drylands, and even deserts (Hedenäs 2007; Lindo & Gonzalez 2010; Medina, Draper & Lara 2011). They often form community assemblages with other organisms such as lichens, fungi, algae, cyanobacteria and bacteria, which form what are termed biological soil crusts (biocrusts) (Belnap, Weber & Büdel 2016). With approximately 20000 species, they are the second biggest group of land plants, comprising mosses, liverworts and hornworts (Frey, Stech & Fischer 2009; Söderström *et al.* 2016). Moss layers fulfill crucial functional roles in a variety of ecosystems regarding water and nutrient fluxes (Cornelissen *et al.* 2007; Bond-Lamberty *et al.* 2011; Gundule, Deluca & Nordin 2011) as well as soil physical properties (Soudzilovskaia, van Bodegom & Cornelissen 2013). In contrast to vascular plants, mosses do not actively regulate their water content, but are poikilohydric, meaning their internal water content is in equilibrium with ambient humidity (Green & Lange 1994). For mosses, water is primarily available via rain, dew and fog (Glime 2017) and moss moisture is influenced by many factors, depending on the habitat as well as the species itself in regard to structure and life form (Dilks & Proctor 1979; Proctor 1982; Proctor 2000; Proctor

& Tuba 2002; Oishi 2018), i.e. the form of individual moss shoots growing together, which is considered an ecologically functional unit (Mägdefrau 1982; Bates 1998).

Water absorption occurs mainly via the external capillaries (ectohydric), but in some species also via internal (endohydric) movement. While the latter is achieved cell by cell or through special water conducting cells (hydroids), the ectohydric movement of water is through spaces between adjacent shoots, leaves, leaves and stems, leaves and rhizoids and capillary systems such as leaf bases, revoluted leaf margins, grooves or networks of capillary channels determined by papillae (Giordano *et al.* 1993; Glime 2017). According to Schofield (1981), capillary spaces are influenced by numerous structural parameters such as leaf shape, leaf arrangement, leaf orientation, detailed leaf anatomy (e.g. surface ornamentation), branch arrangement, nature of cortical cells, and presence of rhizoids or paraphyllia. Nevertheless, there is still limited data on moss structural traits and water relations (Elumeeva *et al.* 2011). Overall, mosses achieve maximum water storage capacities of 108 % to 2070 % of their dry weight (Proctor *et al.* 1998), with some *Sphagnum* species even reaching over 5000 % of dry weight (Wang & Bader 2018).

Many mosses are capable of drying out without dying, which means they can endure losing all free intracellular water and recover their ordinary functions afterwards, such as photosynthesizing and growing when water is available (Proctor *et al.* 2007). Due to their high surface to volume ratios, rapid drying is generally facilitated (Proctor *et al.* 2007). Typically, moss cells are either completely turgid or desiccated, with relatively short transitions in between (Proctor *et al.* 2007). Factors influencing this water loss by evaporation are microclimatic conditions (Proctor 1990), life form characteristics (Mägdefrau & Wutz 1951; Nakatsubo 1994; Zotz *et al.* 1997; Elumeeva *et al.* 2011) and canopy structural properties such as surface roughness, shoot density and cushion height (Rice, Collins & Anderson 2001; Rice & Schneider 2004; Goetz & Price 2015; Rice, Gagliardi & Krasa 2018). As an example of cushion life forms, Zotz *et al.* (2000) and Rice and Schneider (2004) found that evaporation rates decrease with moss cushion size.

For water balance of forest ecosystems, an intact forest floor cover such as leaf litter covers or moss layers play a crucial role (Mägdefrau & Wutz 1951; Sayer 2006; Gerrits & Savenije 2011; Acharya, Stebler & Zou 2017). In mid- and high-latitude coniferous forests, moss layers often form at ground level (Elbert *et al.* 2012). As forest ecosystems have suffered from drought in recent years (Senf *et al.* 2020) and mosses are also increasingly threatened by global warming (He, He & Hyvönen 2016), it is particularly important to investigate their hydrological effects in these environments. Previous research by Price *et al.* (1997) in Canadian boreal forests showed that moss layers could retain 16.8 mm of water, which was approximately 21 % of the precipitation input. Furthermore, Carleton and Dunham (2003) found that mosses in a boreal forest could not be fully hydrated by capillary water movement from the forest floor or dewfall, but rather from vapour from the forest floor condensing on the moss surface. Liu and She (2020) investigated a linear decrease of soil evaporation with increasing moss biomass, using moss that was previously cultivated in the laboratory. Overall, the forest floor water balance is influenced by the amounts of throughfall rain, the processes in the moss carpet, and the processes at the moss-soil interface (Price *et al.* 1997). However, little is known about how much water mosses release into the atmosphere and how much is transported from the soil to the moss and vice versa (Voortman *et al.* 2014; Glime 2017). In particular, the influence of different moss species on water movement through moss layers into the soil has been largely disregarded in this context, but has in turn shown great effects on e.g. erosion control (Seitz *et al.* 2017).

With this study, we aim to shorten this knowledge gap in an interdisciplinary approach (cf. Liu and She (2020)). To do so, we examined water absorption and evaporation patterns in moss-covered soil substrates typical for a Central European temperate forest during and after watering. We hypothesize that:

1. Maximum water storage capacities (WSC_{max}) of mosses are species-specific and positively affected by their surface area.
2. Differences in the temporal dynamics of water content during watering and subsequent desiccation depend largely on the combination of moss species and the underlying soil substrates.

To test our hypotheses, we set up a greenhouse experiment with five moss species and four soil substrates, whereby artificially cultivated mosses of the same species were also included. We used biocrust wetness probes (Weber *et al.* 2016) for high-resolution monitoring of water content in moss layers, on the soil surface, and in a soil depth of 3 cm. Furthermore, we investigated the selected mosses in terms of their structural traits and their maximum water storage capacities.

Material and methods

Moss and soil characteristics

Five moss species native to Southwest Germany (Nebel *et al.* 2001) differing in origin, classification and growth form were chosen for the study (Table 1). *Oxyrrhynchium hians* (Hedw.) Loeske, *Eurhynchium striatum* (Hedw.) Schimp., *Plagiomnium undulatum* (Hedw.) T.J.Kop. and *Brachythecium rutabulum* (Hedw.) Schimp. were collected in the field at different sites within the Ammer and Neckar valley. Cultures of *Amblystegium serpens* (Hedw.) Schimp. and *Oxyrrhynchium hians* were grown in a hydraulic fluid in an in vitro environment by Hummel InVitro GmbH in Stuttgart, Germany. The latter was selected a second time to study intraspecific differences between field and cultivated mosses. With regard to the position of the sporophytes, all selected mosses were pleurocarpous (side-fruited), except *P. undulatum*, which was acrocarpous (top-fruited).

Soil substrates were chosen according to common growing conditions of selected moss species and sampled from four different sites in the Schönbuch Nature Park in Southwest Germany. Sampling sites were located in the geological series of the Lower Jurassic, with shale clay, interstratified by beds of pyrite and fine grained sandstone, as well as in the Upper Triassic, where claystone with fine lime nodules and fine to coarse grained sandstone is present (Einsele & Agster 1986). The substrates varied with regard to parent material, soil texture, and pH as well as the C/N ratio (Table 2). They were sampled from the topsoil to a depth of 10 cm and sieved by 6.3 mm. Below, we distinguish the substrates according to their geological formation: Angulatensandstein (AS), Psilonotenton (PT), Löwenstein (LS) and Trossingen (TS) (Einsele & Agster 1986).

Table 1: Characteristics of studied moss samples

	Amblystegium serpens	*Brachythecium rutabulum*	*Eurhynchium striatum*	*Oxyrrhynchium hians*	*Oxyrrhynchium hians*	*Plagiomnium undulatum*
Family	Amblystegiaceae	Brachytheciaceae	Brachytheciaceae	Brachytheciaceae	Brachytheciaceae	Mniaceae
Origin	Lab	Field	Field	Field	Lab	Field
Site characteristics	-	ruderalized fertile meadow	pinewood	dry hedge understore	-	flood plain
Growth form	pleurocarpous	pleurocarpous	pleurocarpous	pleurocarpous	pleurocarpous	acrocarpous
Sample site coordinates	-	Tübingen 48.544917° N 9.043309° E	Tübingen 48.546194° N 9.036407° E	Reusten 48.541665° N 8.914316° E	-	Pliezhausen 48.566723° N 9.216494° E

Table 2: Characteristics of studied soil substrates

	AS	PT	LS	TS
Series	Lower Jurassic	Lower Jurassic	Upper Triassic	Upper Triassic
Formation	Angulatensandstein-Formation (AS)	Psilonotenton-Formation (PT)	Löwenstein-Formation (LS)	Trossingen-Formation (TS)
Parent material	sandstone	shale clay	sandstone	claystone
Soil texture	silty loam sand: 7.00 % silt: 67.58 % clay: 25.68 %	silty clay loam sand: 6.88 % silt: 56.28 % clay: 36.93 %	clay loam sand: 25.02 % silt: 42.43 % clay: 32.60 %	silty clay loam sand: 10.78 % silt: 50.83 % clay: 38.10 %
C/N	17.54	17.36	23.12	20.05
pH	5.8	7.0	7.0	5.6
Sample site coordinates	Tübingen 48.553054 N 9.119053 E	Tübingen 48.557425 N 9.114462 E	Tübingen 48.557527 N 9.088098 E	Tübingen 48.556036 N 9.089313 E

Greenhouse experiment

With a greenhouse experiment, we investigated water absorption patterns in moss covers and corresponding soil substrates during and after watering. To do this, we filled the substrates into infiltration boxes (40 × 30 × 15 cm) up to a height of 6.5 cm. Infiltration boxes are stainless steel containers with a triangular surface runoff gutter and an outlet on the bottom to capture percolated water. In December 2019, moss species were placed onto substrate-filled infiltration boxes, leading to 6 treatments with 2 replicates each: *P. undulatum* (Field) + PT, *O. hians* (Field) + AS, *O. hians* (Lab) + AS, *B. rutabulum* (Field) + LS, *A. serpens* (Lab) + LS, *E. striatum* + TS; yielding a total number of 12 boxes. Infiltration boxes were subsequently stored in a shady place outdoors for adaptation, until we began the greenhouse experiment in July 2020.

To measure water content (WC), we installed three biocrust wetness probes (BWP, UP GmbH, Cottbus, Germany) per infiltration box in different positions: in 3 cm soil depth, in the uppermost 5 mm of the soil surface and in the moss layer (Fig. 1). BWPs were specifically developed to quantify WC of soil surfaces as well as biocrusts by deriving WC from electrical conductivity measurements; they provided reliable data in several experiments under different field conditions (Weber *et al.* 2016; Gypser *et al.* 2017; Tucker *et al.* 2017; Löbs *et al.* 2020). Samples were irrigated for one hour with a sprayer (Comfort Sensitive Plant, Gardena, Ulm, Germany) with 6 $L \cdot h^{-1}$ of water, split into 500 ml every 5 min, corresponding to a precipitation amount of 122 mm (extremely heavy rainfall event). All BWPs were installed underneath the centre of the sprayer, whereby we ensured that the BWP in the moss layer was completely encased by moss shoots. During this watering and subsequent desiccation process in the greenhouse, the electrical conductivity of the samples was logged every 10 seconds for 72 hours with the BWPs connected to a GP2 Data Logger (Delta-T Devices, Cambridge, UK). Additionally, air temperature and relative humidity (RH) in the greenhouse were monitored (Tinytag Plus 2 – TGP-4500, Gemini Data Loggers, Chichester, UK) for the same time slots. Soil WC was determined before and after watering as well as after 71 hours of desiccation applying two methods: first, we used a gravimetrical approach with a heavy-duty precision balance (KERN FCB 30K1, Kern & Sohn GmbH, Balingen, Germany), and second, we used a Thetaprobe ML2 in combination with a HH2 Moisture Meter (Delta-T Devices, Cambridge, UK).

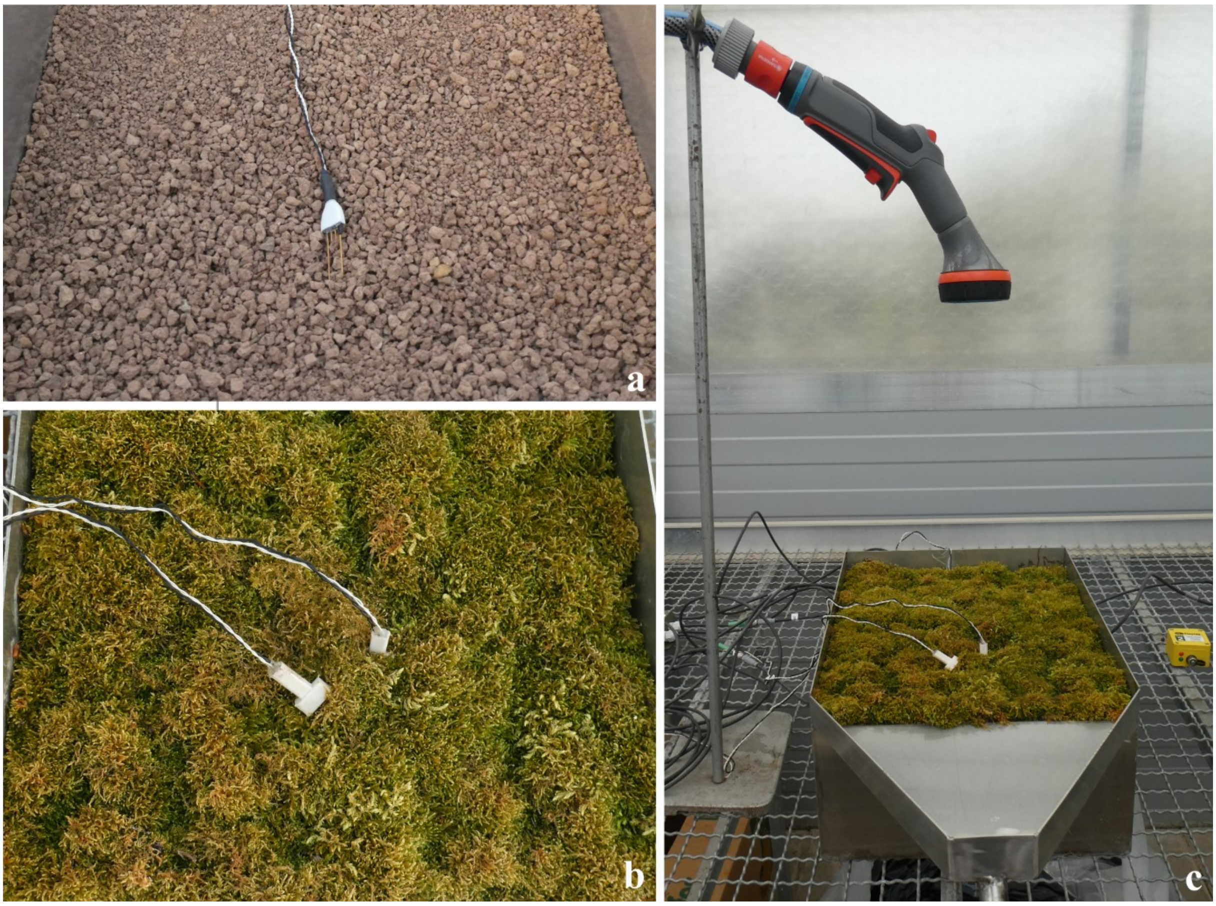

Figure 1: Overview of the greenhouse experiment setup. a) Biocrust wetness probe (BWP) in 3 cm soil depth, b) BWP in soil surface and moss cover, c) experimental setup with moss-covered soil substrate inside the infiltration box and sprayer installed at uniform height.

To consider evaporation effects during the period of desiccation, we calculated the evaporation rate of this time span for all samples using the formula

$$E = \frac{WC_0 - WC_x}{t_x - t_0} ,$$

where WC_0 is the maximum gravimetric WC in the examined time period, WC_x is the gravimetric WC at time point x, and t_x and t_0 are the respective time points (Robinson *et al.* 2000).

Laboratory BWP calibration

To calibrate the BWP to gravimetric WC, we monitored weight loss and electrical conductivity (EC) simultaneously for all samples under laboratory conditions for at least 65 hours (average air temperature: 19.1 °C, sd = 1.2; average relative humidity (RH): 45.8 %, sd = 5.9). Samples were water saturated using the immersion technique described in the following section. Afterwards, they were placed on a balance (Kern EW 620-3NM, Kern & Sohn GmbH, Balingen, Germany) and three BWPs were installed in each sample. Two samples were measured in parallel, using two precision balances of the same type. BWP and weight data were recorded at an interval of 10 seconds, while temperature and relative humidity were logged in 5 min intervals with Tinytag Plus 2 (see above).

During monitoring of weight loss, the scales generated individual error values, which required a filtering of data. Since the scales only measured stable values, we had irregular time intervals in the recording of weight losses. To be able to combine weight and BWP as well as RH and temperature values, we performed a linear fashion interpolation with both weight values and climate measurements.

As EC is affected by temperature, we conducted a temperature correction and derived the WC for a specific value of the BWP as described in Weber *et al.* (2016). According to Slatyer (1967), the formula

$$WC = \frac{(WW - DW)}{DW}$$

was used, where *WC* is the gravimetric *WC* (g g^{-1}), *WW* is the wet weight (g) and *DW* is the dry weight (g) of the soil or moss sample.

The last step of calibration included curve fitting, where we used the mean of the three BWP values and the calculated WC. We found linear relationships which can be characterized as WC = a · EC_t + b., For non-linear relationships we used non-linear least-square regressions expressed by the equation WC = exp(a · EC_t) · b · EC_t + c, as recommended in Weber *et al.* (2016). Furthermore, some relationships could be better described with the equation WC = exp(a + b · EC_t). While the moss samples could be dried from saturation to desiccation, soil samples did not dry out completely during the laboratory calibration. Therefore, an extrapolation of data for the calibration BWP values was necessary for the soil samples. An overview of all calibration curves is shown in Table S1 in the supporting information.

Maximum water storage capacity

For a detailed characterisation of moss species and adjunct soil substrates with regard to their maximum water storage capacity (WSC_{max}), further laboratory experiments were conducted with samples from the infiltration boxes. Therefore, we detached the mosses from the soil, dried them at 30 °C in a dehydrator (Dörrex 0075.70, Stöckli, Netstal, Switzerland) and weighed the dry samples (Mettler Toledo MS603S, Mettler Toledo, Columbus, USA). Soil samples were taken with 100 cm^3 metal core cutters from every infiltration box, dried at 105 °C in a compartment drier and weighed in dry state. Afterwards both moss species and soil substrates were saturated, using two different methods for the mosses: spray and immersion technique. For the spray technique, we moistened the mosses that had been placed in a petri plate with a spray bottle from above until samples could no longer absorb water. The excess water was removed with a pipette and volume was determined with a 25 ml measuring cylinder.

By weighing the spray bottle before and after spraying we estimated the amount of water added to the mosses (in average 3.45 mm). The wet mosses were weighed again with the same balance. In contrast, with the immersion technique we moistened the mosses by submerging them in water for 5 min between two soil sieves with 52 µm mesh size on the bottom and 250 µm on the top, then drained them for 2 min, and then weighed them. We decided to use these two approaches, as we observed that some mosses were still dry on the bottom after a rainfall event, which was also described in Glime (2017). Therefore, we expected different mechanisms of water absorption in the two techniques, with the spray technique probably being more similar to the greenhouse watering process. The soil samples were placed into a tub of water until the surface was wet and afterwards we measured the wet weight. To ensure that the soil substrate remained in the core cutter during rewetting, we attached a thin water permeable fleece to the bottom of the core cutter (Blume, Stahr & Leinweber 2011).

Moss structural trait measurements

To determine the surface areas of the studied moss species, we measured the following structural traits: leaf area, leaf frequency, shoot length, length of a single component (sum of shoot length and length of attached branches), shoot density (Table 3). We determined the surface areas of the studied species using the following formula, which we adapted for our experiment following Simon (1987), Niinemets and Tobias (2014) and Niinemets and Tobias (2019):

$$A_{bryo} = L\, N_{shoot}\, \frac{A_{leaf}}{1\ cm\ shoot}$$

where A_{bryo} is moss surface area, L is the average length of a shoot with its attached branches, N_{shoot} is mean number of measured shoots, and A_{leaf} is mean leaf area. Leaf area index (LAI) was then calculated with the formula

$$LAI\ = \frac{A_{bryo}}{sample\ area}$$

In the first step, three circular samples with a diameter of 5.5 cm (sample area) were taken from each species. Moss samples were then dissembled into single moss shoots. Due to the very dense structure and consequent long time duration, only half of the circular area of *A. serpens* was considered. Next, detached shoots were scanned using a high definition flatbed scanner (Epson Perfection V700 Photo, Suwa, Japan) and shoot numbers of all samples were counted to determine the shoot number per unit sample area. Afterwards, if sample size enabled it, 50 shoots were randomly chosen for length measurements, using ImageJ versions 1.53e and Fiji 2.1.0 (Schindelin *et al.* 2012; Schneider, Rasband & Eliceiri 2012). Next to shoot length, we also determined the length of branches that were attached to the measured shoots. Then, from each sample three shoots were randomly selected and all leaves were carefully removed along one centimeter of the shoot. The removed leaves were put on slides and were either scanned with the flatbed scanner or a digital microscope (Keyence VHX-7000 with dual zoom lens VH-ZST, Keyence, Osaka, Japan). Leaf area was subsequently measured with ImageJ as well.

Additionally, we determined the volume of the moss cushions for all moss samples used in the WSC_{max} experiment. Therefore, we photographed all moss samples using a Nikon D5100 (Chiyoda, Japan), equipped with an AF-S DX Micro NIKKOR 40mm f/2.8G lens to identify the individual sample area with ImageJ. The height of the moss cushions was measured at four sites with a calliper and mean values were calculated for every cushion. The moss cushion density was derived from the quotient of dry weight and cushion volume.

Data analysis

All analyses were conducted with R software versions 3.6.3 and 4.0.2 (R Core Team 2021) on the level of individual samples. To examine significant differences, we used one-way ANOVAs in combination with post-hoc Tukey's HSD tests when variables showed homogeneity of variances. In other cases, we performed post-hoc Games-Howell or Wilcoxon signed-rank tests. Previously, homoescedasticity was verified with the Levene's test. To test for differences of the means between two samples we used Welch's t-test. Significance was assessed at $p < 0.05$ in all cases.

Furthermore, we performed pairwise Pearson as well as Spearman's Rank correlation analyses to screen for relationships between WSC_{max} as well as evaporation rates of the studied samples and parameters of sample characteristics. In advance of all analyses, we used the Shapiro- Wilk Test to examine the samples for normal distribution. Additionally, generalized additive models (GAM) with restricted maximum likelihood and smoothing parameters selected by an unbiased risk estimator (UBRE) criterion were performed to assess the effect of soil substrate or moss species characteristics on WSC_{max}. Firstly, we fitted moss WSC_{max} from the spray and immersion techniques against mean shoot number, mean leaf surface area, LAI, moss cushion height as well as moss cushion density. Secondly, WSC_{max} of soil substrates were fitted against soil bulk density, sand, silt and clay contents as well as total carbon and nitrogen content.

Results and discussion

In order to discuss and answer the hypotheses presented, we first analyzed the differences in structural traits of the studied moss species and investigated their relationship with WSC_{max}. As we assumed that the temporal progression of WC in the greenhouse experiment could be explained by the structural traits of moss species, we further examined whether our samples showed similar patterns of properties in the different experiments.

Moss structural traits

A wide range of structural trait characteristics for the moss species used in this study were determined to explain moss water relations (Table 3). The average individual leaf area of the studied species ranged almost fivefold from 0.104 mm² in *A. serpens* (Lab) to 4.737 mm² in *P. undulatum*. Accordingly, average leaf area per shoot length varied elevenfold between 0.085 cm² cm^{-1} in *A. serpens* (Lab) to 0.953 in *P. undulatum*. Leaf frequency was the smallest in *P. undulatum* at 20.111 and ranged up to 91.333 in *E. striatum*. We found the longest shoots in *B. rutabulum* (3.79 cm on average) and the shortest shoots in *A. serpens* (Lab) (1.16 cm on average). After adding the length of attached branches to the respective shoot length, *B. rutabulum* still had the longest shoots with 8.47 cm, and *A. serpens* (Lab) had the shortest shoots with 1.764 cm. However, *A. serpens* (Lab) had the highest shoot density (97 shoots per cm^2), whereas *B. rutabulum*, *E. striatum*, *O. hians* and *P. undulatum* had much lower densities between 2.5 to 4.714 shoots per cm^2. Interestingly, shoot density of *O. hians* (Lab) was twice as high as for *O. hians* collected in nature, which might be due to missing competition with other species in a laboratory setting, as well as different light and water regimes, since moss structure is highly affected by water and light availability (Mägdefrau 1982). This raises the question of whether field-collected *A. serpens* also has similarly high shoot densities as determined for *A. serpens* (Lab) in this study. While *A. serpens* (Lab) grew in dense and more voluminous lawns, *A. serpens* occurs more often intermingled with other species in nature. The nutrient-loving species prefers semi-shady, rather moist sites that are also preferred by many other species that are often more vigorous and thus overgrow the delicate prostrate *A. serpens* (Nebel *et al.* 2001). The dense, extensive tall lawns of *A. serpens* (Lab) therefore contradict the species' occurrence in nature and its interspersed growth with other mosses, that can be attributed to the low competitiveness of *A. serpens*.

Table 3. Species-specific average values (± standard error of the mean) of leaf area, leaf frequency, leaf area per shoot length, shoot length, length of a single component (sum of shoot length and length of attached branches), shoot density (shoot number per ground area), total surface area, leaf area index (LAI), moss cushion height, volume and density for the studied moss species.

Species	Leaf area (mm^2)	Leaf frequency (cm^{-1})	Leaf area per shoot length (cm^2 cm^{-1})	Shoot length (cm)	Length single component (cm)	Shoot density (n cm^{-2})	Total surface area (cm^2)	LAI	Cushion height (cm)	Cushion volume (cm^3)	Cushion density (g cm^{-3})
Amblystegium serpens (Lab)	0.104 ± 0.002	81.778 ± 3.929	0.085 ± 0.006	1.168 ± 0.024	1.764 ± 0.224	97.005 ± 11.786	346.204	14.572	1.322 ± 0.091	107.058 ± 10.623	0.026 ± 0.002
Brachythecium rutabulum	1.151 ± 0.035	39.333 ± 4.93	0.452 ± 0.064	3.791 ± 0.166	8.470 ± 0.286	3.031 ± 0.402	297.076	12.504	1.536 ± 0.116	139.856 ± 19.366	0.018 ± 0.001
Eurhynchium striatum	0.629 ± 0.013	91.333 ± 9.541	0.574 ± 0.06	2.018 ± 0.129	7.756 ± 0.656	2.511 ± 0.496	265.672	11.182	2.119 ± 0.092	182.071 ± 18.683	0.016 ± 0.002
Oxyrrhynchium hians	0.307 ± 0.006	69.889 ± 3.545	0.187 ± 0.008	2.524 ± 0.129	8.124 ± 0.702	4.714 ± 0.712	169.907	7.151	1.65 ± 0.13	132.174 ± 15.278	0.015 ± 0.002
Oxyrrhynchium hians (Lab)	0.393 ± 0.008	55.556 ± 2.911	0.219 ± 0.014	2.180 ± 0.092	6.198 ± 1.480	10.368 ± 2.509	333.764	14.048	1.353 ± 0.136	114.336 ± 18.998	0.022 ± 0.003
Plagiomnium undulatum	4.737 ± 0.129	20.111 ± 2.6	0.953 ± 0.121	3.004 ± 0.129	4.960 ± 0.571	3.087 ± 0.827	346.517	14.585	1.394 ±0.08	100.778 ± 6.649	0.018 ± 0.001

Compared to the other five studied species, *O. hians* had a low LAI of 7.151. *B. rutabulum* and *E. striatum* were similar in their LAI of 12.504 and 11.182, respectively, and highest LAI values were determined for *A. serpens* (Lab) (14.572), *O. hians* (Lab) (14.048) and *P. undulatum* (14.585). Interestingly, *P. undulatum* and the two lab-grown mosses are very different in terms of leaf area, leaf frequency and shoot density, but all have similar LAI values. Considering the moss cushion density, *A. serpens* (Lab) was significantly denser than *E. striatum* ($p < 0.001$), *O. hians* ($p < 0.001$) and *P. undulatum* ($p < 0.01$). Furthermore, we found significant differences in regard to moss cushion density between *O. hians* (Lab) and *E. striatum* ($p < 0.01$), *O. hians* (Lab) and *O. hians* ($p < 0.05$), *B. rutabulum* and *E. striatum* ($p < 0.05$) and *E. striatum* and *P. undulatum* ($p < 0.05$).

Maximum water storage capacity

Mean values of WSC_{max} from the immersion technique (representing complete soaking) varied between 14.10 g g^{-1} for *A. serpens* (Lab) and 7.31 g g^{-1} for *P. undulatum*, with the difference being highly significant ($p < 0.001$) (Fig. 2 and Table S2 in the supporting information). Further significant differences were found between *E. striatum* (11.22 g g^{-1}) and *P. undulatum* as well as between *B. rutabulum* (11.80 g g^{-1}) and *P. undulatum* ($p < 0.05$). Thus, with regard to the WSC_{max}, there were strong differences between the mosses with different growth forms, but none within the group of pleurocarpous mosses. The fact that *P. undulatum* absorbed comparatively less water could be explained by its endohydric water transport, and many acrocarpous mosses are endohydric (Richardson 1981). Since the surface of endohydric mosses comprises a water-resistant cuticle with often waxy layers (Buch 1945; Proctor 1979a; Proctor 1979b), water absorption through their leaves is inhibited (Glime 2017). However, as we only measured one acrocarpous moss, this finding requires further investigation.

Although the most significant difference in WSC_{max} was shown between the visibly densest and loosest growing moss species, this relationship could not be substantiated by the surveyed traits for surface area and cushion characteristics. WSC_{max} was not affected by total surface area or LAI. Furthermore, neither height of the moss cushions, nor volume or density correlated individually with WSC_{max}. The combination of leaf area and leaf frequency seemed to have a higher influence on WSC_{max}: with a small leaf area (Spearman's correlation rho = -0.30, $p < 0.05$) and high leaf frequency (Spearman's correlation rho = 0.32, $p < 0.05$), the WSC_{max} increased. Shoot density might be another influencing factor, but due to small sample size further studies are recommended. In this context, Voortman *et al.* (2014) also discussed that capillary spaces between moss leaves and branches might be more relevant for water retention than those between moss shoots. For *Sphagnum* species, Bengtsson *et al.* (2020) also found a high influence of leaf traits on water retention.

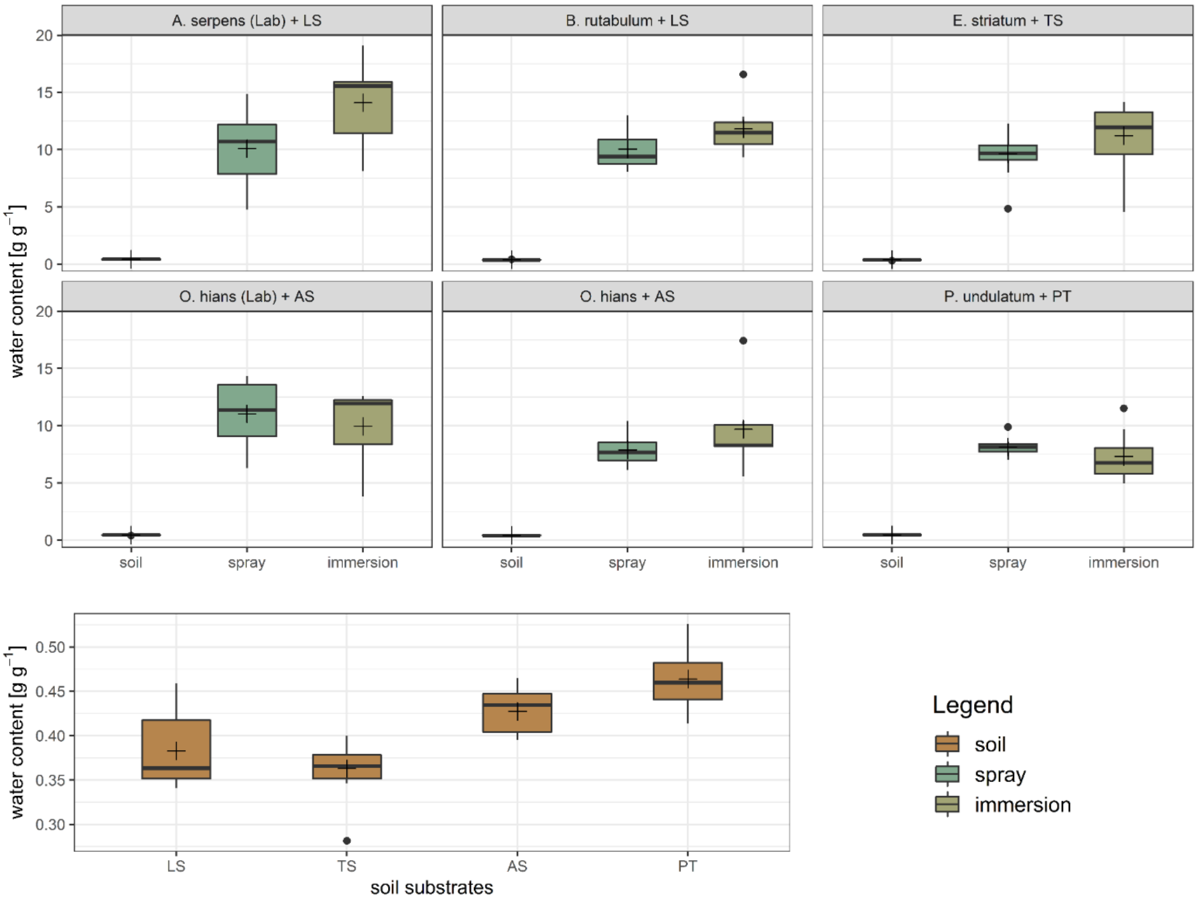

Figure 2: Maximum water storage capacity (g g^{-1}) of treatments (moss species + soil substrate). For moss species both spray and immersion technique are illustrated. Crosses represent mean values and lines within boxplots median values. The bottom and top of the box represent the first and third quartiles, and 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.

Calculated in a GAM explaining 54.1 % of the deviance, moss cushion density highly influenced WSC_{max} ($p < 0.001$), while the effects of mean leaf area ($p < 0.01$) and mean shoot density ($p < 0.05$) were smaller, but also significant. Therefore, we assume that additional parameters must be also of great importance to the WSC_{max}. Such parameters are assumed to be, for example, the capillary spaces of mosses, which are very difficult to quantify and are diverse and often complex (Proctor 1982). According to Proctor (1982), capillary conducting systems such as spaces between overlapping leaves, between shoots, in sheathing leaf bases or amongst rhizoid tomentum and paraphyllia can be 10 - 100 µm large. In addition, interspaces of a few µm can be found in interstices between papillae as well as in furrows between plicae and ridges on leaves and stems (Proctor 1982). In this context, the 3D structure of the mosses, e.g. the branching of the shoots, the shape of the leaves and the position of the leaves in relation to the stems, potentially plays an important role for capillarity of bryophytes (Schofield 1981; Giordano *et al.* 1993).

In contrast to the immersion technique, the range of mean values of WSC_{max} for the spray technique, which was intended to simulate moistening of mosses by a rainfall event, was considerably smaller (Fig. 2). Here, we found a variation of 11.04 g g^{-1} for *O. hians* (Lab) to 7.90 g g^{-1} for *O. hians* from the field. However, we could not find any significant differences between species or significant correlations between the WSC_{max} and the ascertained individual moss structure parameters, and the adjunct GAM could explain 46.5 % of the deviations. The greatest influence was due to moss height ($p < 0.01$), with LAI having a smaller effect ($p < 0.05$). Interestingly, the greatest difference in WSC_{max} was discovered within the same species*, O. hians*. Although they belong to the same species, *O. hians* collected in the field and *O. hians* grown in the laboratory displayed strong differences in structure. While *O. hians* grows as loose lawn in the field, the laboratory variety forms very dense moss cushions, which is also reflected in the higher shoot density (*O. hians*: 4.714 shoots per cm^2 and *O. hians* (Lab): 10.368 shoots per cm^2), and the larger total surface area (*O. hians*: 169.907 cm^2 and *O. hians* (Lab): 333.764 cm^2). This finding indicates that the WSC_{max} of mosses is dependent on life form. In a further chain of thought, this also implies that single species can obtain more advantageous properties through laboratory cultivation, e.g. for erosion control.

Overall, we suppose that for both the immersion technique and the spray technique, the capillary spaces between moss shoots as well as between leaves and shoots are more important for WSC_{max} than surface parameters such as LAI or total surface area. Finally, it can be concluded that a further development and standardization of the spray technique is required to be able to gather more reliable data on this important moss characteristic.

Regarding the soil substrates, WSC_{max} values varied on average between 0.46 g g^{-1} for PT and 0.36 g g^{-1} for TS, which is 30 times less compared to the WSC_{max} of the mosses (Fig. 3). Within soil substrates we found highly significant differences between PT and TS, PT and LS as well as AS and TS ($p < 0.001$) and a significant difference between AS and TS ($p < 0.05$). On one hand, these differences can be explained by soil texture, as there is a negative relationship with sand content (Spearman's correlation rho = -0.62, $p < 0.001$) and a positive correlation with silt content (Spearman's correlation rho = 0.52, $p < 0.001$), while the clay content seemed to be of rather minor importance for WSC_{max} (Spearman's correlation rho = -0.40, $p < 0.01$). On the other hand, we revealed a negative correlation with bulk density (Pearson's correlation r = -0.70, $t_{39} = -5.94$, $p < 0.001$) and C/N ratio (Spearman's correlation rho = -0.62, $p < 0.001$). Additionally, we tested for a joint impact on soil WSC_{max} using a GAM with soil bulk density, sand, silt and clay contents as well as total carbon and nitrogen content as fixed effects and were able to explain 84.7 % of the deviance with this model. The results also showed a high relevance of bulk soil density as well as total carbon content ($p < 0.001$), which is consistent with the results of the individually tested correlations and an influence of the clay content ($p < 0.01$). These relationships are also reported in other studies (Franzluebbers 2002; Gong, Cao & Sun 2003; Rawls *et al.* 2003; Novák & Hlaváčiková 2019).

Greenhouse experiment

Watering process

Focusing on the 60 minutes of watering, we observed clear differences in WC of different moss species, regarding temporal progression as well as the level of WC achieved (Fig. 3). At the beginning of the watering, all moss species were desiccated, so that the WC initially increased until an equilibrium was reached. Moss species were classified in terms of WC in equilibrium: (a) low WC (0 - 5 g g^{-1}) for *A. serpens* (Lab) and *P. undulatum*, (b) medium WC (5 - 10 g g^{-1}) for *B. rutabulum*, *O. hians* and *O. hians* (Lab), (c) high WC (10 – 15 g g^{-1}) for *E. striatum.* This classification shows the possibility of distinguishing between moss species based on the BWP response. Surprisingly, *A. serpens* (Lab) and *P. undulatum* both reached a low WC during irrigation, although they are quite different regarding their structural traits. While *A. serpens* (Lab) forms very dense moss cushions (shoot density: 97.005 ± 11.786 shoots per cm^2), *P. undulatum* is more likely to grow single shoots (shoot density: 3.087 ± 0.827 shoots per cm^2). Although *O. hians* and *O. hians* (Lab) were both assigned to medium WC, we recognized a distinct difference, with *O. hians* tending to weigh 10 g g^{-1} and *O. hians* (Lab) tending to weigh 5 g g^{-1}. Since *O. hians* (Lab) grows considerably denser than *O. hians* with a shoot density twice as high (*O. hians* (Lab) = 10.368 ± 2.509 shoots per cm^2, *O. hians* = 4.714 ± 0.712 shoots per cm^2) and a higher cushion density (*O. hians* (Lab) = 0.022 ± 0.003 g cm^{-3}, *O. hians* = 0.015 ± 0.002 g cm^{-3}), we expected that *O. hians* (Lab) would also absorb more water during watering. The fact that this expectation was not fulfilled could be attributed to *O. hians* having a comparatively high leaf frequency with small leaf area, which had already been highlighted as important factors for water absorption in previous chapters.

Furthermore, almost all moss species showed a certain variation in WC at equilibrium within replicate measurements, illustrating a great heterogeneity within species. Overall, we noticed that the variations between replicate measurements were smaller for denser moss cushions than for looser ones, with *P. undulatum* being an exception in this case. This could be attributed to the fact that denser mosses establish better contact with the sensor without forming air spaces (Löbs *et al.* 2020).

Some moss species demonstrated a more pronounced response to the watering pulses than others. This might also be related to denser moss cushions with less air-filled interstitial spaces (Löbs *et al.* 2020), as it was the case for *A. serpens* (Lab) and *O. hians* (Lab), which both form the densest cushions. To examine moss intraspecific differences regarding water absorption in detail, higher replication is necessary in future studies.

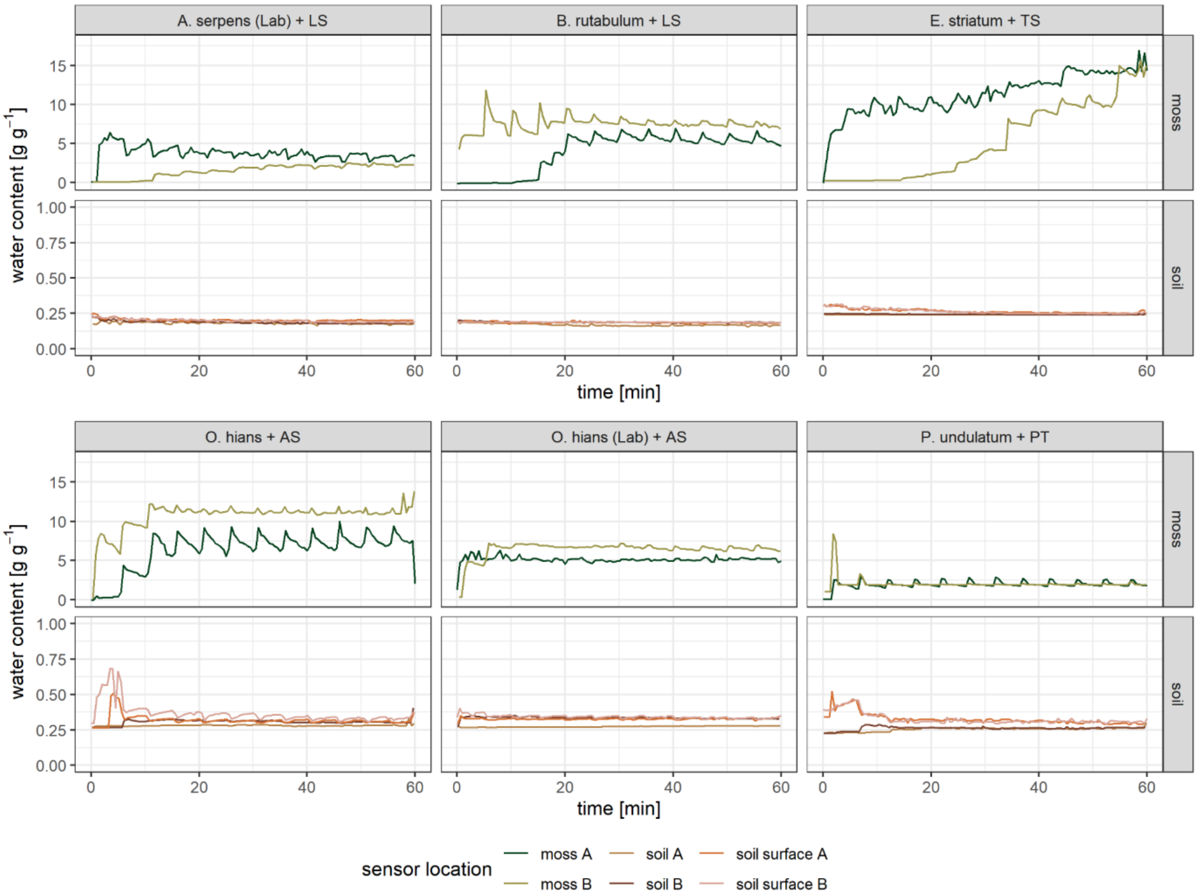

Figure 3: Temporal progression of water content values (g g^{-1}) of treatments during watering in the greenhouse experiment. Replicate measurements are labelled with A and B for every biocrust wetness probe (BWP) location (moss cover, soil surface, 3 cm soil depth). Plotted are half-minute values.

Because of the water volume applied to the samples in the greenhouse, we speculated that the moss species would reach their WSC$_{max}$ within the watering time in the greenhouse, especially when compared with the achieved WSC$_{max}$ using the spray technique. To go into more detail, we compared the WC values directly after watering (means of WC for all values between 60th and 65th minute) with the WSC$_{max}$ determined in the lab. For most of the species the WC after watering was considerably lower than the WSC$_{max}$, for both spray and immersion technique. As an example, the maximum WC for *A. serpens* using the immersion technique was 5 times higher than the WC after watering (WSC$_{max}$ (immersion) = 14.10 g g^{-1}, SE = 1.28, WC after watering = 2.63 g g^{-1}, SE = 0.02), while the spray technique showed almost a fourfold difference (WSC$_{max}$ (spray) = 10.10 g g^{-1}, SE = 1.25). Additionally, we found an almost fivefold difference from the immersion technique, respective fourfold difference from the spray technique, and higher WSC$_{max}$ compared to the WC after watering in *P. undulatum* (WSC$_{max}$ (immersion) = 7.31 g g^{-1}, SE = 0.80, WSC$_{max}$ (spray) = 8.15 g g^{-1}, SE = 0.32, WC after watering = 1.76 g g^{-1}, SE = 0.01). Based on these results, no clear patterns are discernible that would explain the different intraspecific mechanisms of water absorption comparing greenhouse and laboratory experiments. Above all, it was very surprising that especially the denser mosses, most notably the lab-grown mosses, did not absorb much water during the greenhouse experiment. In general, we can deduce that the mosses are not a barrier to infiltration in case of high precipitation rates, as also reported in Li *et al.* (2016). A new observation of our study is that the mosses growing on the soil do not store much of the applied water themselves, but pass it on to the soil.

Compared to the mosses, the soil substrates showed a much lower WC during the 60 minutes of watering, which is true for both the surface and 3 cm soil depth (Fig. 3). Overall, mosses adjusted their equilibrium in the range between 2.5 – 15.0 g g^{-1} of WC, while soil substrates varied between 0.15 – 0.35 g g^{-1}. The fact that mosses can absorb more water than soil substrates could be attributed to a larger surface area of mosses. Additionally, capillary effects in mosses might contribute to higher water absorption rates compared to soil substrates.

Since the soil surfaces were not completely dried out at the beginning of the experiment, they showed a relatively high starting value of WC in comparison with the later reached equilibrium. The temporal progression of WC on the soil surface started with higher values at the beginning of watering and slightly decreased over time. Regarding infiltration into the soil surface, it appeared that water had initially accumulated on the surface, causing the high WC.

When considering WC at 3 cm soil depth, temporal progression of WC was almost steady, which was also due to the already wet soil substrate at the beginning of the experiment. For two substrates (AS and PT) we observed an increase of WC during the first 10 minutes of irrigation, indicating percolation of water through the substrate. Additionally, WC tended to be lower at 3 cm soil depth than on the soil surface during irrigation. Overall, with respect to the temporal progression of WC values on soil surface and in 3 cm soil depth, we generally found substrate-specific coherences regarding the level of WC achieved.

Furthermore, we expected that the soil substrates show a similar response due to WSC_{max} in the lab and in the greenhouse experiment. However, the WC after watering in the greenhouse, which we expected to be the maximum WC reached in the greenhouse (means of WC for all values between 60th and 65th minute), were lower than the WSC_{max} measured in the lab, which was true for every substrate both for surface as well as in 3 cm soil depth. For example, PT achieved a WSC_{max} of 0.46 g g^{-1} and only showed a WC of 0.31 g g^{-1} on the surface and 0.27 g g^{-1} in the soil after one hour of watering in the greenhouse, which means a deviance of 32.61 %. In comparison, LS reached only 50% of the WSC_{max} under *A. serpens* (Lab) (WC after watering = 0.19 g g^{-1}, WSC_{max} = 0.46 g g^{-1}) and 52% under *B. rutabulum* on the surface (WC after watering = 0.18 g g^{-1}), WC values in 3 cm soil depth were even lower (WC after watering

(*A. serpens* (Lab)) = 0.18 g g^{-1}; WC after watering (*B. rutabulum*) = 0.17 g g^{-1}). Altogether, soil substrates did not show the same patterns of water absorption in the lab as in the greenhouse.

Desiccation process

During the subsequent desiccation process of 71 hours, moisture in the moss layers generally decreased, while moisture at the soil substrate surface as well as in 3 cm soil substrate depth remained at the same levels (Fig. 4). However, moss species differed in maximum WC, evaporation rates and their responses to climatic changes in the greenhouse. Sample replicates slightly differed from each other in regard to WC values, but generally showed comparable patterns. We observed the highest WC values directly after watering in *E. striatum* with a mean WC of almost 15 g g^{-1}, while mean WC of *B. rutabulum*, *O. hians* and *O. hians* (Lab) ranged between 5 - 10 g g^{-1}, and mean WC of *A. serpens* (Lab) and *P. undulatum* did not exceed 5 g g^{-1}. The low WC of *P. undulatum* might be related to its delicate and loose structure with a low leaf frequency and large leaf areas, and leaves that stand off the shoot. Especially compared to a branched structure with high leaf frequencies and densely attached leaves, few capillary spaces for water storage are formed in *P. undulatum* (Mägdefrau & Wutz 1951). Furthermore, leaf surfaces of mosses from the Mniaceae family often have a water-resistant cuticle, reducing their ability to absorb water via the leaves (Proctor 2000; Glime 2017). Additionally, we observed that leaves and stems of *P. undulatum* were twisting and curling during the desiccation process, which might result in altered measurement conditions for the sensor. Clipping the sensor to moss stems of such species as *P. undulatum*, as proposed in Leo *et al.* (2019), would be interesting to compare with BWP response in future studies. Nevertheless, the BWP used in this study proved to be successful in all moss species, as also confirmed in Löbs *et al.* (2020).

A. serpens (Lab) had dried out after 30 hours, whereas the other species generally remained moist longer than 40 hours, and did not desiccate completely during the measurement. A more stabilized, steady evaporation was observed in *B. rutabulum*, *O. hians*, *O. hians* (Lab) and *P. undulatum*. Evaporation rates calculated for the measurement period corresponded to maximum WC: *E. striatum* with the highest maximum WC after watering also had the highest evaporation rates (0.181 – 0.197 g h^{-1}). Evaporation rates for *P. undulatum* were considerably smaller (0.023 and 0.012 g h^{-1}). A group with slightly higher evaporation rates consisted of *A. serpens* (Lab) (0.056 and 0.03 g h^{-1}), *B. rutabulum* (0.046 and 0.055 g h^{-1}), *O. hians* (Lab) (0.057 and 0.078 g h^{-1}) and *O. hians* (0.06 and 0.093 g h^{-1}). We found a positive relationship between leaf frequency and evaporation rate (Spearman's correlation rho = 0.832, $P < 0.001$). LAI, however, correlated negatively with evaporation rate (Spearman's correlation rho = -0.78, $P < 0.001$); this was congruent with our expectations of lower evaporation rates for moss species with a high LAI, which, as a product of different structural traits, makes the formation of a multitude of capillary spaces for water storage in different hierarchical levels (leaf, shoot, and colony) more likely, overall resulting in wetter moss cushions and lower evaporation rates, as also described in Elumeeva *et al.* (2011).

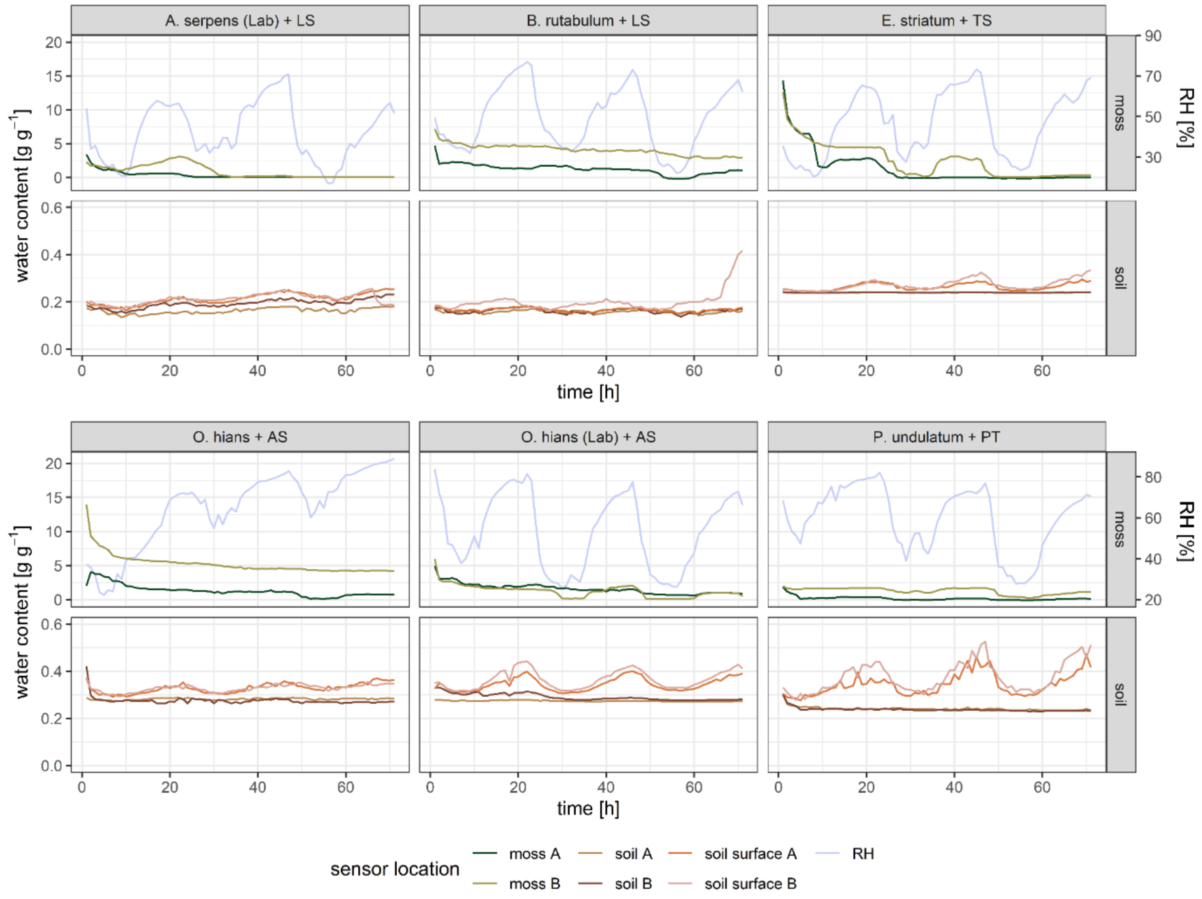

Figure 4: Temporal progression of water content values ($g\ g^{-1}$) of treatments during 71 h of desiccation in the greenhouse experiment. Replicate measurements are labelled with A and B for every biocrust wetness probe (BWP) location (moss cover, soil surface, 3 cm soil depth). Mean temperature and mean relative humidity ± standard deviation: Amblystegium serpens (Lab) + Löwenstein-Formation (LS) 25.93 °C ± 6.13, 42.67 % ± 14.39; Brachythecium rutabulum + Löwenstein-Formation (LS) 26.35 °C ± 5.38, 49.45 % ± 15.22; Eurhynchium striatum + Trossingen-Formation (TS) 24.70 °C ± 5.78, 46.31 % ± 16.15; Oxyrrhynchium hians + Angulatensandstein-Formation (AS) 20.30 °C ± 3.89, 64.72 % ± 18.45; Oxyrrhynchium hians (Lab) + Angulatensandstein-Formation (AS) 23.10 °C ± 6.07, 53.37 % ± 18.38; Plagiomnium undulatum + Psilonotenton-Formation (PT) 20.96 °C ± 4.31, 59.92 % ± 15.35. Plotted are hourly values.

WC in moss species showed diel fluctuations, albeit to different degrees. Desiccation periods clearly aligned with declining RH and rising temperatures in *E. striatum*, *O. hians* (Lab), and to a smaller degree in *P. undulatum*, *A. serpens* (Lab), *B. rutabulum* and *O. hians*. Comparably high RH and low temperatures contributed to the quite stable WC of *O. hians* throughout the measurement and to the fact that the moss did not dry completely. We observed slight reactions of WC towards RH changes in all samples, confirming that mosses reacted to increasing RH and could absorb water under conditions with high RH, as also described in Löbs *et al.* (2020).

Climatic conditions cannot explain intraspecific variation of WC, since the replicates were measured in parallel at the same time. A possible explanation could be that moss structure at the sensor locations differed in regard to surface roughness, altering boundary layer resistance and thus resulting in different evaporation velocities (Proctor 1982). Further experiments in a climate-controlled environment with closer control and manipulation possibilities could determine if moss reactions are species-specific.

The different soil substrates had slightly different mean WC values in 3 cm depth: LS 0.16-0.18 g g^{-1}, TS 0.24 g g^{-1}, AS 0.28 g g^{-1} and PT 0.24 g g^{-1}. In LS, a slight reaction to rising RH (due to night-day-shifts) was recognizable, and LS did not desiccate, despite high temperatures above 40 °C during the measurement period. We assume that the moss cover prevented desiccation of the substrate, but it remains unclear whether the substrate receives water from the moss cushion itself or plainly from RH. For low precipitation rates, prevention of soil evaporation from moss-dominated biocrusts was also reported in Li *et al.* (2016).

WC at the soil surface fluctuated diurnally depending on RH as also described in Tucker *et al.* (2017), especially in AS and PT and less pronounced in LS. Moreover, we found that oscillations related to RH were visible at the soil surface but not in 3 cm soil depth, which showed that fine pores at the surface were capable of adsorbing water out of the air (Hillel 1998; Agam & Berliner 2006). So even dense moss cushions were not completely sealing the soil surface and there was no full barrier by bryophytes. However, since the RH-induced fluctuations varied depending on the density of the moss cover, i.e. the most pronounced reactions were found in the loosest moss cover *P. undulatum*, we assume that mosses mitigate soil evaporation.

Generally, WC at the soil surface was higher than in 3 cm depth during desiccation. This could be ascribed to the fact that the soil surface had a finer texture due to clogging of the pores as an influence of splash effects (Morgan 2005), which allows for a higher WC (Dodd & Lauenroth 1997). A further influencing factor to explain this observation might be the initial soil WC. As we measured a high soil WC before watering, the matrix potential is reduced, resulting in a lower and less deep infiltration (Novák & Hlaváčiková 2019).

Differences between WC values of surface and 3 cm depth depended on the substrate: for LS, the values were very similar, but especially for PT, WC values at substrate surface were higher than in 3 cm depth by a factor of 1.4 to 2.3. In AS, there was either an influence by the moss cover, or by the climatic conditions during the measurement: AS covered with *O. hians* showed a smaller difference between surface and soil WC and not very pronounced oscillations with

RH. In contrast, AS covered with *O. hians* (Lab) displayed strong day-night oscillations and WC values during nights were up to 1.5-times higher in the surface than in 3 cm depth. Since RH remained above 50% after 20 hours during the measurement of AS with *O. hians*, but dropped from 75% in the nights to 25% RH during the days in the measurement of AS with *O. hians* (Lab), we cannot exclude a strong influence of these fluctuations on the different oscillation patterns in the AS measurements. To determine the effect of moss layers itself on soil substrate moistness and evaporation, an experiment with different moss species on similar substrates and control samples without moss is necessary.

Conclusion and outlook

This study found that five moss species from Central European temperate forests can exhibit different water absorption and evaporation patterns in response to rainfall. In some cases, the target moss species also showed significant intraspecific variability in rainwater interception. With regard to our hypotheses, the following conclusions were drawn:

Contradictory to our hypothesis, total surface area did not affect maximum water storage capacity (WSC_{max}). Results further indicate that a combination of structural traits (high shoot density, high leaf frequency, and low leaf area) may increase WSC_{max} during immersion. Generalized additive models (GAM) revealed that cushion density also can influence WSC_{max}. A combination of different structural traits tested in a GAM showed that WSC_{max} determined using the spray technique was affected by leaf area index (LAI) and moss height. Overall, soil substrates absorbed around 30 times less water compared to mosses and an effect of bulk density, grain size distribution and total carbon content on WSC_{max} was found.

Both moss species and soil substrates showed species/substrate-specific patterns in regard to changes of moisture during watering as well as desiccation. Since soil substrates did not desiccate despite high temperatures, yet water content at the surface responded to relative humidity changes, we hypothesize that the moss cover prevented desiccation without sealing the soil. Because the humidity-induced fluctuations varied depending on the density of the moss cover, we further hypothesize that mosses mitigate soil evaporation. Among moss species, differences were also observed between replicates, primarily related to the moistening until an equilibrium in water content was reached, as well as in the process of desiccation. Similar WSC_{max} values (to immersion and spray) were not achieved in greenhouse experiments during watering, indicating different mechanisms of water absorption for both soil substrates and moss species, which could not be explained by clear patterns. In general, we can deduce that the mosses growing on the soil may not store much of the applied water themselves, but pass it on to the soil. Leaf frequency correlated positively with evaporation rates, while LAI showed a negative relationship with evaporation rates.

Although not explicitly mentioned in our hypotheses, the results underscore that some species can develop different morphologies due to different growing locations (field vs. laboratory). This can lead to a heterogeneous expression of the same traits and raises the question of whether beneficial traits can be conferred to individual species by laboratory cultivation, e.g. for erosion control. Thus, the interplay of individual moss structure traits appears to be very complex, such that further detailed investigations especially on the 3D structure of individual species are urgently needed. In this context, more information on moss capillary spaces would help to achieve a higher level of accuracy regarding the mechanisms of water absorption in mosses. It should be noted that the methodology also needs further improvement and the exact determination of individual species effects can be seen as non-trivial.

Further research is required to understand the details of how different moss species and soil substrates interact regarding water absorption and evaporation. A multi-method approach to measure water content in different layers is recommended, using biocrust wetness probes as well as clip sensors for the moss cover as introduced by Leo *et al.* (2019). This approach should be combined with the use of a climate-regulated greenhouse and expanded to include control samples without moss cover and large number of replicates in order to cover the existing complexity as well as possible. This complexity is also the major challenge in the investigation of "water’s path from moss to soil", to the understanding of which this study has made a further contribution.

Acknowledgements

We thank Michael Sauer for his assistance and expertise during moss sample collection, Lena Grabherr and Sarah Fodor for their support in measuring moss structural parameters, Daniel Schwindt for helpful comments and Matthew Hughes for improving the language of the manuscript. We are also grateful to the Plant Ecology group of the University of Tübingen for the space provided in their greenhouse. This study was funded by the German Research Foundation (DFG SE 2767/2-1 “MesiCrust”) and the Federal Ministry for Economic Affairs and Energy (AiF 19808 N).

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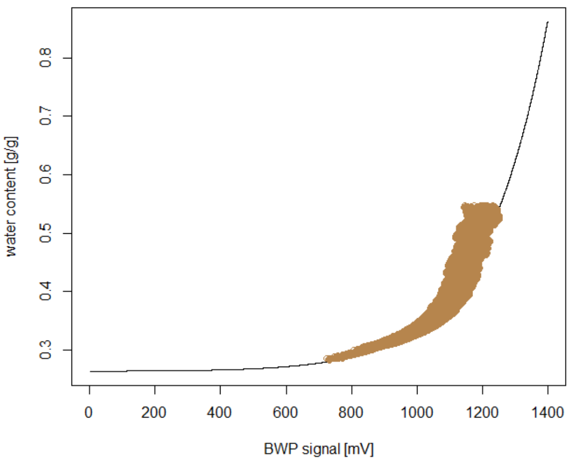
Supporting information

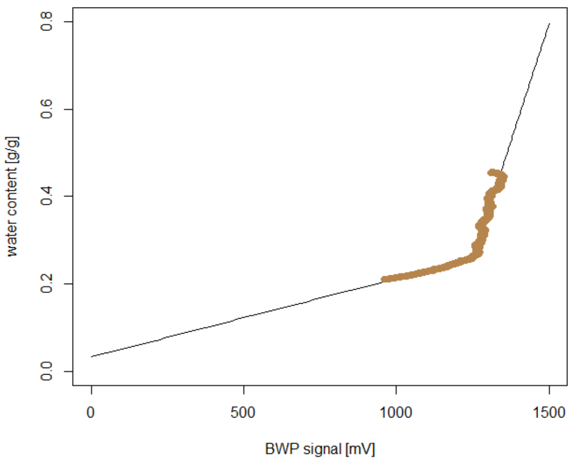
Table S1: Equations of calibration curves for studied soil substrates and moss species. The fit quality is assessed by the root mean square error (RMSE) and the determination coefficient (R^2) between measured and modeled water content.

Sample	Calibration equation	a	b	c	d	e	RMSE	R²
Angulatensandstein-Formation	$y = \exp(a \cdot x) \cdot b \cdot x + c$	0.0043	$9.125e^{-07}$	0.264			0.027	0.928
Löwenstein-Formation	$y = a \cdot x + b$ (BWP < 1250 mV) $y = a \cdot x + b$ (BWP > 1250 mV)	0.00018 0.00215	0.0322 -2.437				0.002 0.016	0.990 0.954
Psilonotenton-Formation	$y = \exp(a \cdot x) \cdot b \cdot x + c$	0.0038	$2.055e^{-06}$	0.221			0.031	0.926
Trossingen-Formation	$y = \exp(a \cdot x) \cdot b \cdot x + c$	0.0065	$3.218e^{-08}$	0.238			0.010	0.990
Aamblystegium serpens (Lab)	$y = (a + b \cdot x)$	-2.555	0.0045				0.703	0.979
Brachythecium rutabulum	$y = a \cdot x + b$	0.0096	-0.401				0.229	0.996
Eurhynchium striatum	$y = a \cdot x + b$	0.0194	-0.617				0.205	0.995
Oxyrrhynchium hians	$y = a \cdot x + b$	0.0127	-0.414				0.200	0.993
Oxyrrhynchium hians (Lab)	$y = \exp(a \cdot x) \cdot b \cdot x + c$	0.0008	0.0036	-0.057			0.133	0.998
Plagiomnium undulatum	$y = a \cdot x^4 + b \cdot x^3 + c \cdot x^2 + d \cdot x + e$	$-3.141e^{-11}$	$7.996e^{-08}$	$-6.066e^{-05}$	0.0198	-0.5402	0.223	0.994

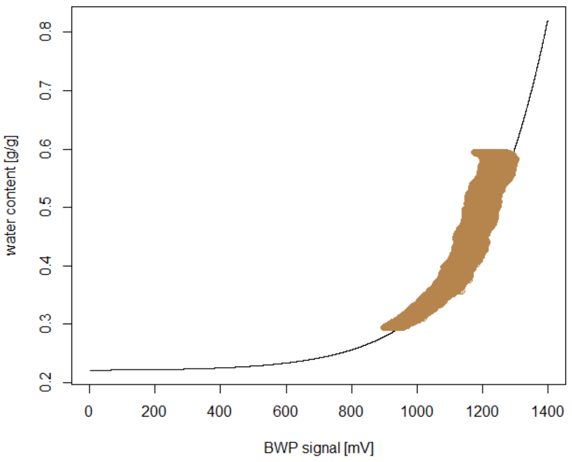
Calibration curve of AS



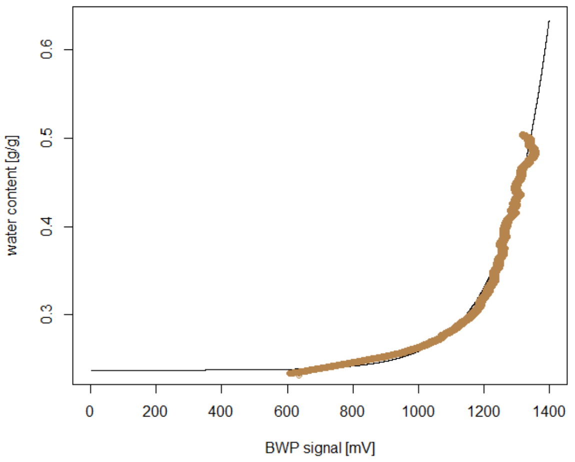
Calibration curve of LS



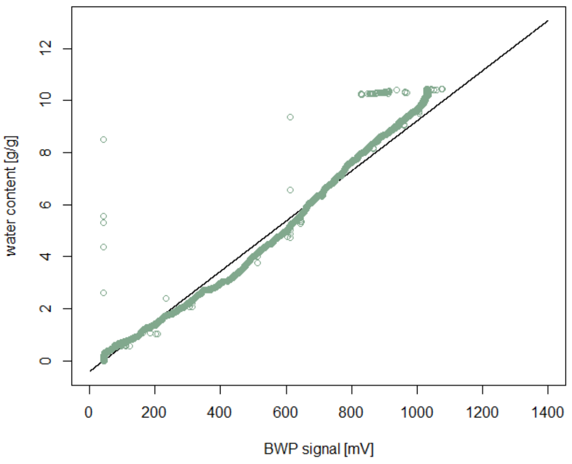
Calibration curve of PT



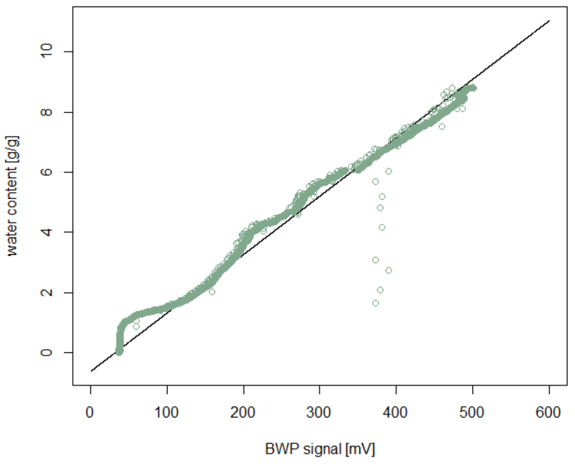
Calibration curve of TS

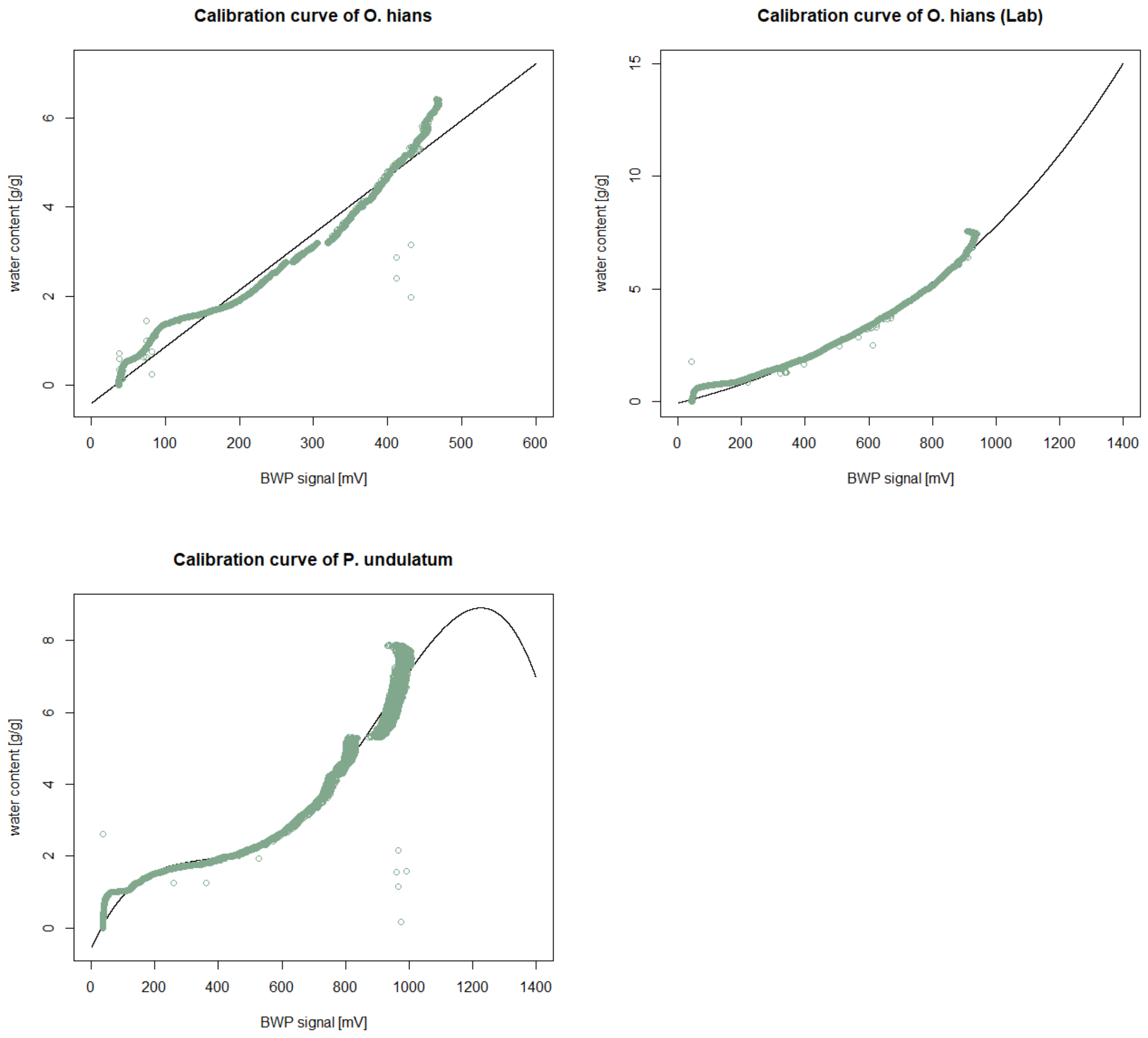


Calibration curve of B. rutabulum



Calibration curve of E. striatum





Figures S1-S10: Plots of calibration curves for studied soil substrates and moss species. Measured water contents for soil substrates are illustrated in brown and for moss species in green.

Table S2: Maximum water storage capacity values (WSCmax) and sample sizes of the studied moss species for immersion and spray technique as gravimetric WSCmax (g g-1), percentage WSCmax (%) and WSCmax per unit area (mm), ± standard error of the mean.

Moss species	Sample size	WSC_{max} immersion (g g^{-1})	WSC_{max} spray (g g^{-1})	WSC_{max} immersion (%)	WSC_{max} spray (%)	WSC_{max} immersion (mm)	WSC_{max} spray (mm)
Amblystegium serpens (Lab)	8	14.097 ± 1.28	10.082 ± 1.25	1409.668 ± 127.82	1008.176 ± 125.09	4.947 ± 0.74	3.144 ± 0.23
Brachythecium rutabulum	8	11.800 ± 0.81	10.049 ± 0.66	1179.965 ± 80.52	1004.919 ± 65.74	3.152 ± 0.31	2.712 ± 0.25
Eurhynchium striatum	17	11.223 ± 0.62	9.629 ± 0.40	1122.260 ± 61.55	962.943 ± 39.78	3.342 ± 0.21	2.820 ± 0.18
Oxyrrhynchium hians	7	9.686 ± 1.41	7.880 ± 0.57	968.598 ± 141.08	787.973 ± 56.90	2.094 ± 0.12	1.945 ± 0.09
Oxyrrhynchium hians (Lab)	7	9.934 ± 1.24	11.038 ± 1.23	993.381 ± 123.82	1103.796 ± 122.86	2.703 ± 0.32	2.448 ± 0.21
Plagiomnium undulatum	8	7.308 ± 0.80	8.146 ± 0.32	730.792 ± 79.89	814. 613 ± 31.58	1.841 ± 0.29	1.870 ± 0.13

Acknowledgements

First of all, I would like to thank Dr. Steffen Seitz, who offered me the opportunity to do my PhD in his DFG project "MesiCrust" and who supported me at all times during my PhD. Thank you for countless fruitful and inspiring discussions, your constructive and helpful feedback, and all the time you spent supporting me in field work, lab work, and paper writing!

I am very grateful to Prof. Dr. Thomas Scholten that I could ask him for advice at any time and that I can be part of his working group, which is a great experience for me. Furthermore, I would like to express my gratitude to Prof. Dr. Yvonne Oelmann for reviewing this thesis.

I gratefully acknowledge the financial support of the Deutsche Forschungsgemeinschaft and I am also indebted to ForstBW for the opportunity to work in the Schönbuch Nature Park.

This thesis would not have been possible without the exceptional support of Martin Nebel and Michael Sauer during vegetation surveys. Your enthusiasm and wide knowledge of mosses has been an inspiration to me, and I would like to thank you for teaching me so many new things.

In particular, I would like to thank the student assistants in the MesiCrust project Lena Grabherr, Laura Bindereif and Julia Dartsch. Without your valuable help with field and lab work, this thesis would not have been realized. Many other helping hands were needed to carry out the field work for this thesis with numerous rainfall simulations, including Helena Obermeier, Antonia Tertelmann, Philipp Gries, Delia Maas, Stefanie Gotterbarm, Giulia König, Nicolás Riveras-Muñoz, Sascha Scherer, Matthew A. Bowker, Daniel Schwindt, Alexander Maurer, Gesche Weiß, Kerstin Rau and the students of GEO 51 in winter semester 2019/20. Thank you all so much for helping me and being so motivated despite the sometimes terrible weather conditions. Also many thanks to Sabine Flaiz, Rita Mögenburg, and Peter Kühn for always being available to help me with questions regarding lab work. A special thank goes to Sonja Thielen for the best teamwork I have ever experienced!

For proofreading and very helpful comments on my thesis, I would like to thank Daniel Schwindt, Tobias Rentschler, Sonja Thielen, and Philipp Gries.

Additionally, I would like to thank the working group of Soil Science and Geomorphology for the very pleasant working atmosphere. I appreciated that all of you always supported me, but also distracted me with coffee breaks and sweets, Feierabend beers in the garden and table football (aka. Babyfoot or Taca taca) when needed. Especially, I enjoyed our Wednesday Stammtisch at Darko's place or during Corona our Online-Stammtisch. Thank you, Philipp, Tobi, Arne, Steffen, Sonja, Nico, Kerstin, Sandra, Sascha, Carla, Mathias, and Tara for so many funny evenings!

Thank you all for making the time during my PhD such a great and exciting experience!