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**The Influence of Mature Moss Mats on Topsoil Moisture Along Temperate Forest Stream
Banks**

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Abstract

Background and Aims: Mosses (Bryophyta) are a distinct functional plant type whose influence on near-surface soil moisture dynamics in temperate riparian environments remains poorly understood. This study examines how ectohydric moss mats affect topsoil moisture content on stream banks across contrasting ecoregions.

Methods: Field experiments were conducted at 56 sites (28 per stream) along two headwater streams in contrasting ecoregions (Illinois and Virginia) over a two-year period. Four plot types were established at each site: naturally moss-covered, naturally bare, newly moss-introduced, and moss-removed. Topsoil moisture content was measured at 4, 6, and 8 cm depths across multiple seasonal sampling periods. Statistical comparisons assessed the effects of moss presence, removal, and introduction on topsoil moisture.

Results: Plots with mature moss mats had significantly lower topsoil moisture than bare plots across most sites and sampling periods. When mature moss mats were removed, soil moisture increased significantly relative to moss-covered plots, while plots with introduced moss mats had soil moisture similar to naturally bare plots, suggesting maturity and structural integrity are important in influencing soil water dynamics. Ecoregional differences in moisture responses were most pronounced during high-rainfall periods.

Conclusion: Mature ectohydric moss mats intercept precipitation, likely increase evaporative losses from their canopy surface, and thereby reduce infiltration into the mineral soil, creating drier near-surface soils. These findings establish mosses as a distinctive plant functional type that shapes plant-soil water relations in temperate riparian environments, with implications for how bryophytes modify soil moisture dynamics across ecoregions, and potential applications in nature-based riverine landscape management.

Keywords: Bryophyte; Ecology; Ectohydric moss mat; Near-surface soil moisture; Plant-soil interactions; Riparian stream bank

Introduction

Topsoil moisture is a fundamental regulator of terrestrial ecosystem processes, influencing plant establishment, microbial activity, nutrient cycling, decomposition, and stream-bank stability (Niether et al. 2017; Wang et al. 2019). Although interactions between vascular plant vegetation and soil moisture have been extensively investigated (Wang et al. 2019), comparatively little is known about the influence of bryophyte mats on near-surface soil moisture in temperate riparian ecosystems. Along forested stream banks, woody plants, graminoids, and herbaceous species frequently occur in scattered patches, leaving extensive areas of exposed mineral soil or dense lawns of mosses. These moss mats form the principal living interface between the atmosphere and the soil surface, yet their role in regulating soil moisture under natural precipitation regimes remains poorly understood (Glime 2020).

Mosses differ fundamentally from vascular plants in both structure and water relations. Most forest-floor species are long-lived, indeterminate in growth, poikilohydric, and ectohydric, relying primarily on external capillary conduction rather than roots or specialized vascular tissues for water transport (Proctor 2000; Vitt 2026 (In Press); Vitt et al. 2014). Unlike vascular plants, they lack true roots and absorb water directly across the surfaces of stems and leaves, rapidly equilibrating with atmospheric and substrate moisture conditions. In mat-forming pleurocarpous species, which dominate many temperate forest floors (Frahm and Vitt 1993; Vitt 2026 (In Press)) and comprise the majority of species on our study stream banks (Vitt et al. 2018), densely interwoven stems and closely overlapping leaves produce a continuous capillary network that intercepts rainfall, retains water, and redistributes moisture across the soil surface (Mägdefrau 1938; Zacherl 1956). Their unistratose leaves, absence of stomata in the gametophyte, and extensive exposed surface area enable exceptionally high water-holding capacities, commonly several times their dry weight (Barkman 1958; Griffiths et al. 2013). Because water is

conducted externally and water loss is largely unregulated, excess moisture stored within moss mats is gradually returned to the atmosphere by evaporation, making bryophytes an important component of ecosystem water balance (Bond-Lamberty et al. 2010; Heijmans et al. 2004). Consequently, moss mats function not simply as ground cover, but as biologically active interfaces capable of intercepting precipitation, storing and redistributing water, and modifying the timing and amount of moisture reaching the underlying mineral soil.

Recent studies have demonstrated that moss cover strongly influences near-surface hydrological processes. Greenhouse and rainfall-simulation experiments show that moss mats modify soil water storage, evaporation, infiltration, and runoff while frequently increasing moisture retention within the underlying soil (Gall et al. 2025; Hu et al. 2023; Thielen et al. 2021). Bryophytes also contribute substantially to ecosystem evapotranspiration, accounting for a significant proportion of water loss from boreal and temperate forests (Bond-Lamberty et al. 2010; Heijmans et al. 2004). Together, these studies suggest that moss mats function as dynamic water-storage layers that alter both the movement and timing of water entering the mineral soil. However, nearly all existing studies have been conducted under greenhouse conditions or simulated rainfall, leaving uncertainty about how moss mats influence soil moisture under natural precipitation in riparian environments.

Field evidence addressing this question is remarkably limited. As summarized by Glime (2020), unpublished observations by B. Scafone in a *Pinus banksiana* forest suggested that collectors placed beneath exposed soil frequently accumulated standing water, whereas those beneath adjacent moss mats often remained dry. Despite this intriguing observation, no long-term field study has directly quantified the influence of moss cover on topsoil moisture along temperate forest stream banks under natural rainfall conditions. To evaluate this relationship, we present results from field experiments conducted along two relatively undisturbed, low-order alluvial channels in different ecoregions (Figure 1). Low-order streams of this type collectively make up 70–80% of total stream length across global river networks (Downing et al. 2012; Wohl 2017), making findings from such sites broadly relevant. We ask three questions

addressed as hypotheses 1) do natural moss mats consistently alter topsoil moisture relative to adjacent bare soil, 2) do recently transplanted moss mats reproduce the hydrological behavior of naturally developed mats, and 3) does topsoil moisture under bare areas wherein moss mats have been removed differ from those with recently transplanted moss mats?

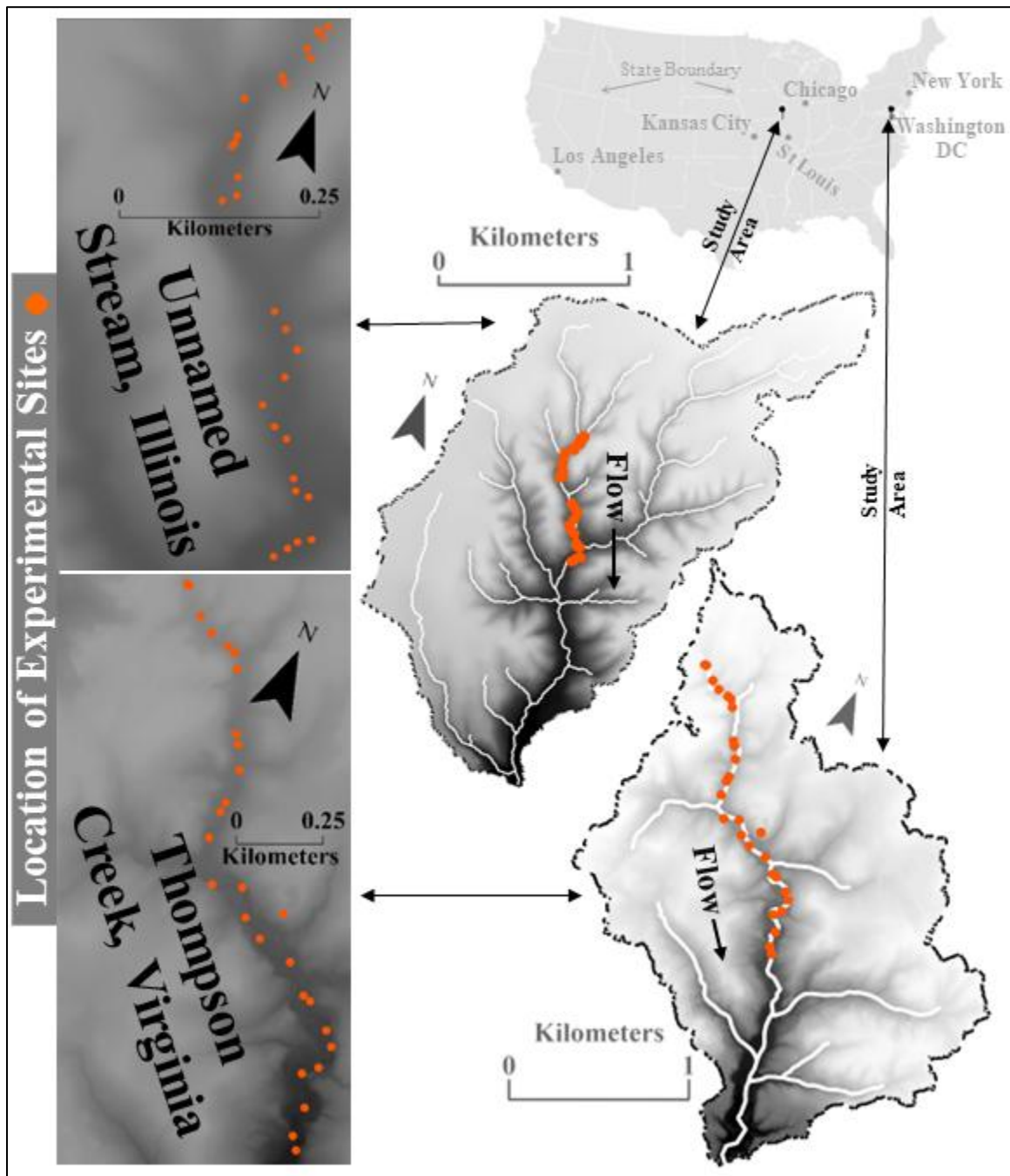


Figure 1. Location of study sites in Illinois and Virginia

Study Area

The two streams are protected areas with mature forest cover and minimal human impact (Figure 1). Thompson Creek is located in northern Virginia, in Fairfax County, approximately 64 kilometers south of Washington DC (38°40'22"N; 77°12'07"W). It is managed as the Meadowood Recreation Area by the Bureau of Land Management. The second stream is an unnamed waterway located in west-central Illinois, in McDonough County (40°25'55"N; 90°53'35"), within the Ira and Reatha T. Post Wildlife Sanctuary—managed by Western Illinois University and commonly known as Vishnu Springs. For the purposes of this study, we refer to this stream as Vishnu Springs. Forest cover at both sites has developed with minimal disturbance and is characteristic of mature eastern deciduous woodland, although the two canopies differ in composition. American beech (*Fagus grandifolia*) is the dominant canopy species in Virginia, occurring alongside sweetgum (*Liquidambar styraciflua*), tulip poplar (*Liriodendron tulipifera*), ash (*Fraxinus* spp.), mockernut hickory (*Carya alba*), sugar maple (*Acer saccharum*), and chestnut oak (*Quercus prinus*); American holly (*Ilex opaca*) forms a thin understory beneath this canopy. The Illinois canopy, by contrast, is led by several oak species—white, red, and black oak (*Quercus alba*, *Q. rubra*, *Q. velutina*)—together with American basswood (*Tilia americana*), hickory (*Carya* spp.), and American sycamore (*Platanus occidentalis*). The streambank at Thompson Creek in Virginia is dominated by 13 species of moss, whereas the streambank at Vishnu Springs in Illinois is dominated by 16 species of moss, with variable occurrences of each species along both streams (Vitt et al. 2018). Two species, *Thuidium delicatulum* and *Bryoandersonia illecebra*, account for most of the moss cover in Virginia; in Illinois, this role falls primarily to *Plagiomnium cuspidatum* and *Oxyrrhynchium hians*. Mosses at both sites tend to establish where fallen leaves do not accumulate heavily enough to smother them, a condition

met more often near the channel itself, where the ground sits slightly higher and the canopy thins (Vitt 2019; Vitt et al. 2018); a fuller accounting of site conditions and the bryophyte taxa recorded in the research plots can be found in Vitt et al. (2018). While Thompson Creek is a tributary of the Potomac River, Vishnu Springs drains into the LaMoine River, part of the Illinois River–Mississippi River system. Climate of the two study areas is similar, with long-term annual precipitation and mean annual temperature varying from 97 cm and 11.6°C in Illinois to 101 cm and 13.6°C in Virginia, respectively (NOAA 2024).

Methods

Field surveys and data collection. Twenty-eight sites along the bank of each of the two streams were selected for field experiments (Total = 56). Each site included 4 circular plots located close to each other (Figures 2 and 3): Control Moss (CM) where moss was naturally present, Control Bare (CB) where the stream bank was naturally bare, Treatment Moss (TM) where moss cover was introduced on a previously bare surface, and Treatment Bare (TB) where moss was removed from the bank surface. Each plot was 15 centimeters in diameter (Figure 3). In order to minimize the possible effects of local topography, local atmosphere, vegetation cover, and soil texture on the soil moisture content (Entin et al. 2000; Teuling and Troch 2005; Western et al. 1999), different plots for each site were located within a two meter distance from each other. Control Moss and Treatment Bare plots were, in all cases, centered within a continuous moss mat.

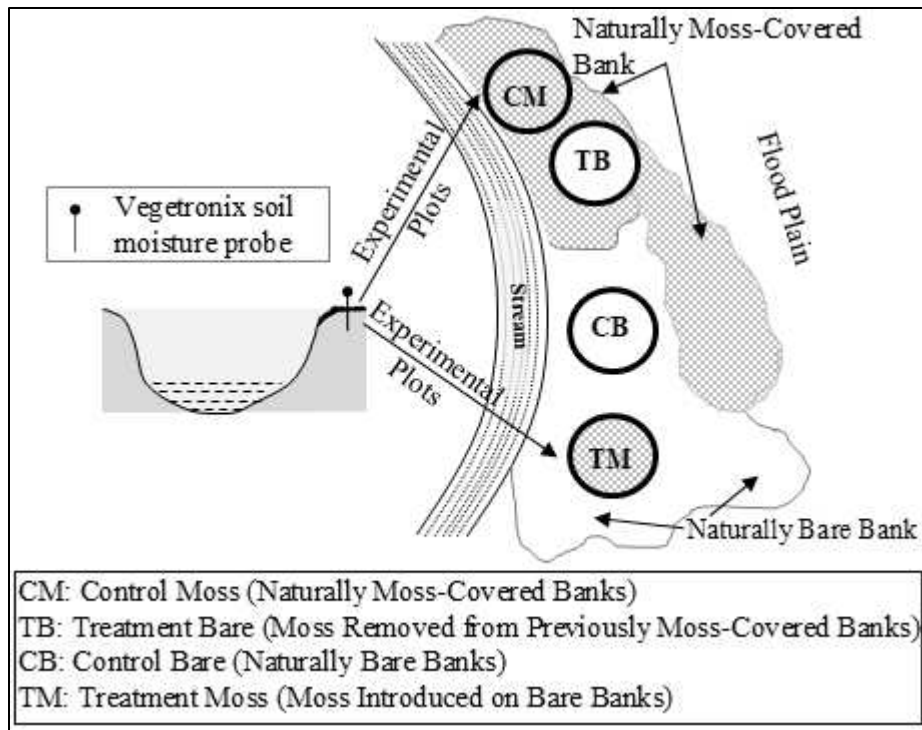


Figure 2. A schematic diagram of experimental plots



Figure 3. Representative photographs of experimental field plots showing Control Bare (CB), Control Moss (CM), Treatment Moss (TM), and Treatment Bare (TB) plots along Thompson Creek.

In the center of each plot, and at the beginning of the experiment, a Vegetronix soil moisture probe was inserted to obtain discrete, point-in-time measurements of soil moisture (percent) at 4 cm, 6 cm and 8 cm depths from the ground level (Vegetronix 2019), with the meter recalibrated after each reading. These data were collected twice yearly over two years; the two sites were sampled sequentially within each round (Thompson Creek: April 11-13, November 7-10, 2017; April 28-May 1, September 16-27, 2018; Vishnu Springs: May 13-18, October 15-20, 2017; May 9-10, October 2-8, 2018). The Vegetronix soil moisture probe is a portable moisture sensor to record in-situ soil moisture with an accuracy of 2% and can be operated in temperatures ranging from -40°C to 85°C. It is insensitive to salinity and non-corrosive and was calibrated before each measurement. The slender shape and size (93.76 mm long, 7.09 mm wide, and 1.4 mm thick) of the probe allows the precise measurement of soil moisture without disrupting the soil. There are other types of equipment which can measure the soil moisture at more depth; however, they are not portable and their relatively large size can disrupt the plots. Also, due to the lack of any roots and only a few centimeters height of moss plants, their immediate impacts on the soil moisture would be concentrated in the top few centimeters of the surface. Small samples of moss were identified and an inventory of moss species in both watersheds was prepared (Vitt et al. 2018). While recording the soil moisture under each plot, we also used a gas flux chamber (15 cm in diameter) to assess the overall biotic condition of moss-covered plots (Vitt 2019). A sample of bank material was collected from the middle portion of the face of the bank in relation to bankfull stage at each site. These samples were dried in ovens at the WIU-IES lab for the mechanical texture analysis. ArcGIS Pro 3.6.1 software was used to calculate the sinuosity of each stream at a longitudinal interval of 10 meters from a digital elevation model

(DEM). Using the same DEM, channel morphology at the bankfull stage was extracted for a general understanding of the channel width, depth, and cross section area from most sites along both streams.

Experimental design and hypothesis testing. Due to the non-parametric nature of the soil moisture data, a 1-Sample Wilcoxon lumped test was used to test the following hypotheses ($\alpha = 0.05$):

Hypothesis 1a-d: First, we tested whether topsoil moisture contents were similar between the two streams for each of the four experimental plot-types (CM, CB, TM, TB) over each of the four sampling periods.

Hypothesis 2 and 3: Secondly, we tested the following hypotheses: The topsoil moisture content of stream banks covered by mature moss mats (CM) is significantly lower as compared to the stream banks without moss mats (CB, TB):

$$CM_{SM} < CB_{SM} \dots\dots\dots \text{Hypothesis-2}$$

$$CM_{SM} < TB_{SM} \dots\dots\dots \text{Hypothesis-3}$$

Where:

CM: Control Moss, i.e., where moss was naturally present

CB: Control Bare, i.e., naturally bare bank

TB: Treatment Bare, i.e., where moss was removed from previously moss covered banks

$_{SM}$: Topsoil Moisture Content

Hypothesis 4: We anticipate that newly introduced moss mats will not have the structural integrity similar to mature moss mats and not affect the topsoil moisture content. Therefore, we tested what happens if moss mats are introduced on bare stream banks hypothesizing that the

topsoil moisture content of naturally moss-covered stream banks (CM) is significantly lower than the newly moss covered stream banks which were previously bare (TM):

$$CM_{SM} < TM_{SM} \dots\dots\dots Hypothesis-4$$

Where:

TM: Treatment Moss, i.e., where moss was introduced on bare banks

Hypotheses 5 and 6: The topsoil moisture content of stream banks decreases significantly if moss cover is introduced (TM) and increases if moss is removed (TB):

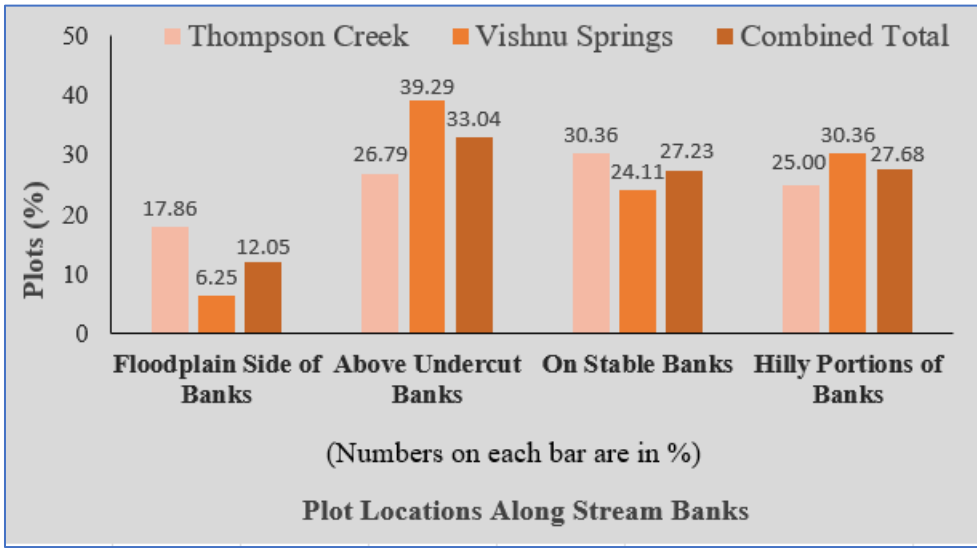
$$CB_{SM} > TM_{SM} \dots\dots\dots Hypothesis-5$$

$$TM_{SM} < TB_{SM} \dots\dots\dots Hypothesis-6$$

Results

Characteristics of the two streams. The plots in both streams represented four general local landscapes along stream banks (Figure 4), 1) the flood plain side of banks not located on active cutbanks (12%), 2) above the undercut banks (33%), 3) on stable banks (27% i.e., without any visible bank failure or undercut bank), and 4) on hilly portions of banks (28% i.e., elevated river terraces from the stream valley). The bank material in both streams was predominantly sandy and loamy sand texture (Figure 5). Both streams had minimal human impact with a majority of their watershed under mature forest cover. Both streams showed similar geomorphic characteristics ($\alpha=0.05$) except sinuosity (Table 1) that ranged from 0.1-1.30 (Median = 1.00) at Thompson Creek and 0.1-1.50 (Median = 1.01) at Vishnu Springs (Table 1).

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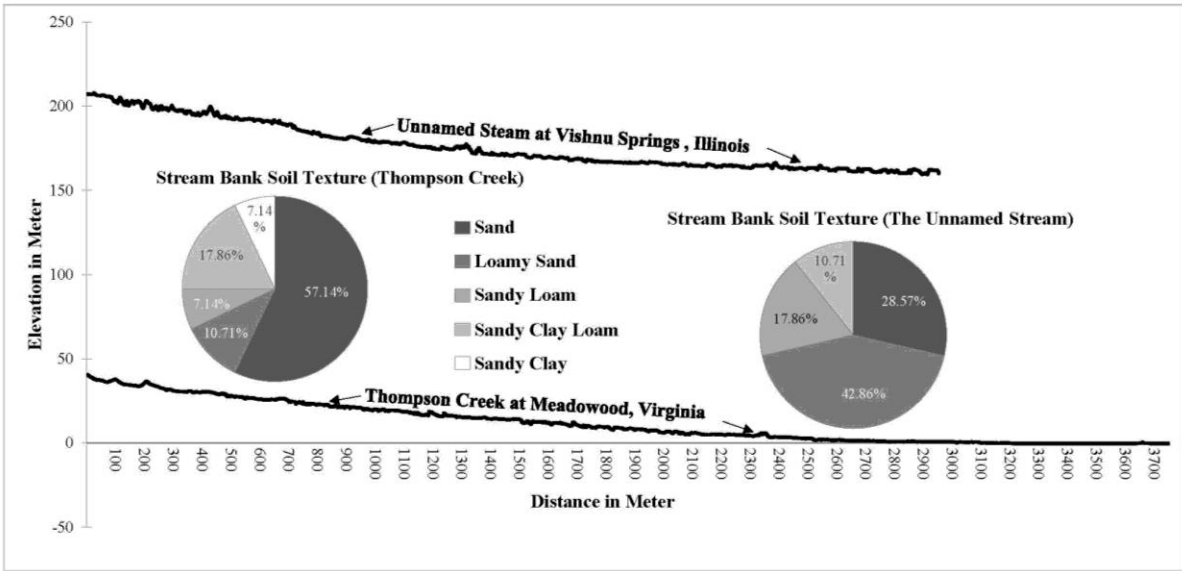


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Figure 4. General characteristics of plots and their locations along stream banks.

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Figure 5. Longitudinal profiles and soil texture of bank material of two sites.

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Topsoil moisture of similar treatment and control plots (with 3 exceptions) were not significantly different between Vishnu Springs and Thompson Creek during fall 2017, spring 2018, and fall 2018; however, during fall 2018 with the high rainfall events, similar treatment

and control plots had significantly different topsoil moisture content between the two streams (Table 2).

Climatic comparisons. Annual precipitation varied from 83.4 cm in 2017 to 122.0 cm in 2018 at Vishnu Springs, with similar values for Thompson Creek (81.8 cm for 2017 and 121.7 cm in 2018, Figures 6-7). In 2018, August and September rainfall was much greater than in 2017 – compare 11 cm in 2017 vs. 40 cm in 2018 at Vishnu Springs and 14 cm vs. 28 cm at Thompson Creek, September in particular had high rainfall at both sites (18 cm -Figures 6-7). High rainfall events occurred at Vishnu Springs on September 26, 30 and October 5-8, 2018. These produced 13.2 cm of precipitation (just before our October 2-8 sampling), while at Thompson Creek 15.6 cm of rain fell between September 7-11 and 14-27 (just before and during our September 16-27 sampling period) (NOAA 2024).

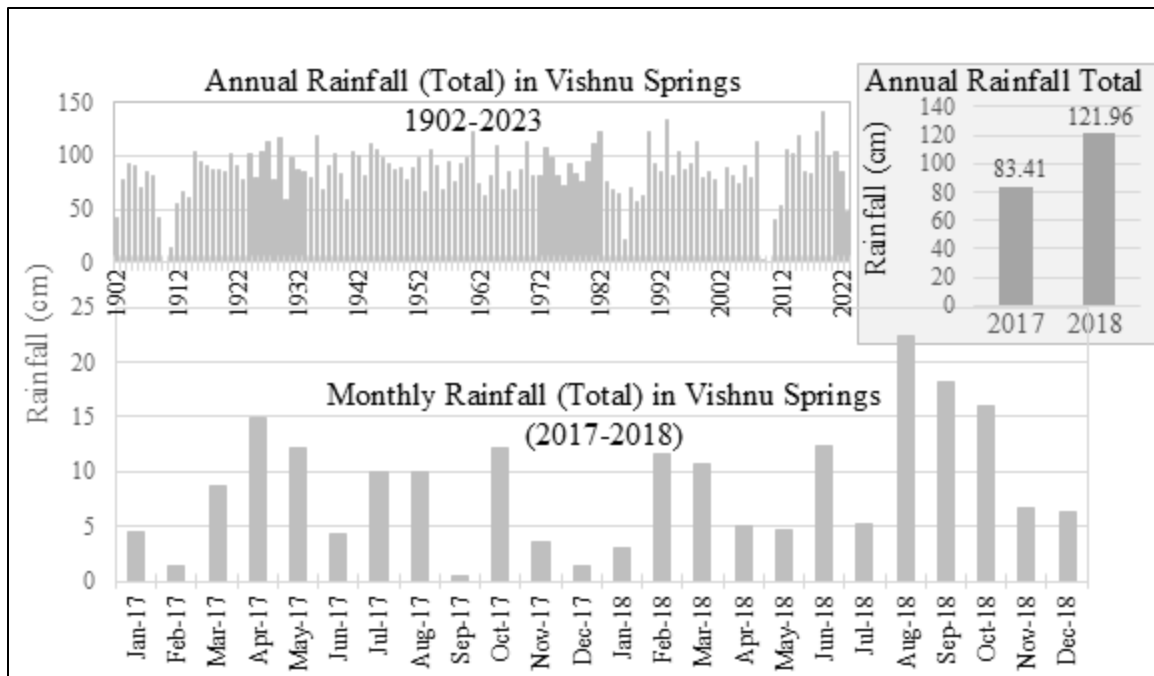


Figure 6. Rainfall data (based on daily total) over different time periods in Vishnu Springs (Source: www.noaa.gov).

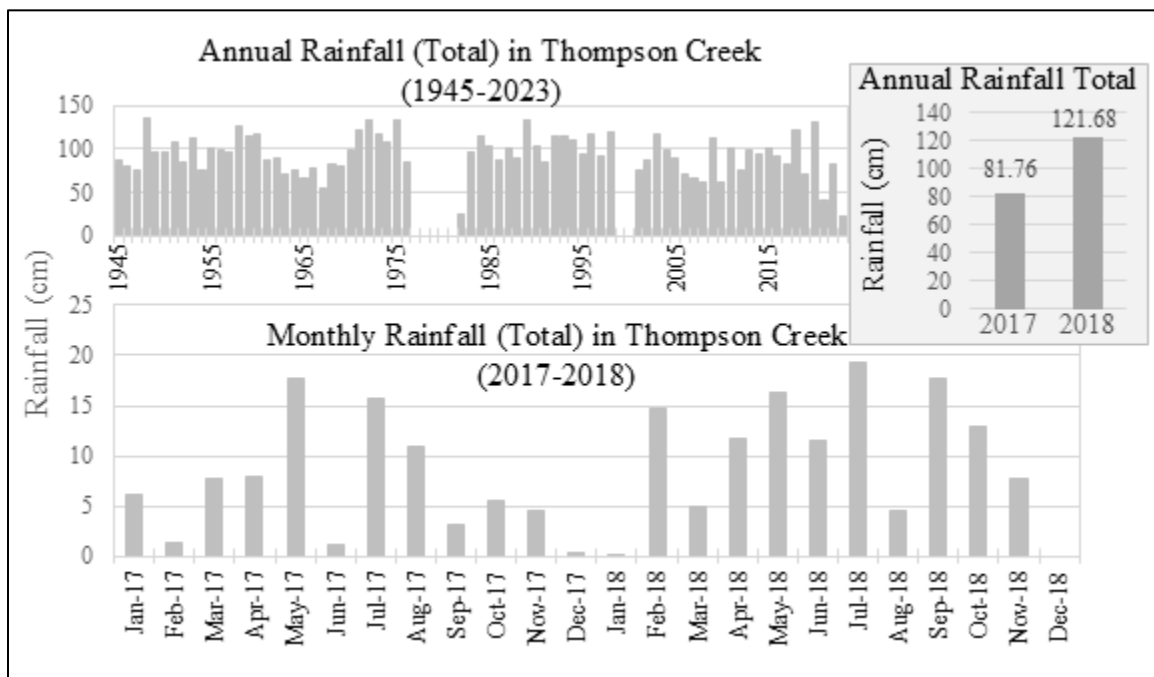


Figure 7. Rainfall data (based on daily total) over different time periods in Thompson Creek (Source: www.noaa.gov)

Topsoil moisture at 4 cm depth. Soil moisture at plots with bare soil (CB) varied from 10.8% to 15.8% moisture at 4 cm depth at Vishnu Springs (mean = 13.3%) and 14.0% to 14.6% soil moisture at Thompson Creek (mean = 14.3%) over the first three time periods increasing to 25.4% at Vishnu Springs and 45.4% at Thompson Creek in fall 2018 during high precipitation events (Table 3 and 4). Comparatively, plots with mature moss mats (CM) varied from 10.8% to 12.0% at Vishnu Springs (mean 11.6%) and 9.2% to 11.5% at Thompson Creek (mean 10.2%) over the first three time periods and from 18.0% at Vishnu Springs and 45.4% at Thompson Creek in Fall 2018. Overall, during the first three time periods within this two-year-time period, soil moisture at 4 cm in moss-covered plots was 14% lower at Vishnu Springs and 29% lower at Thompson Creek compared to plots with bare soil, and significantly lower when all plots are considered together for the entire two-year period (CM/CB-Tables 3 and 4).

During the fall 2018 high rainfall events, at Vishnu Springs, soil moisture under the plots with moss cover (CM) averaged 19% lower soil moisture (at 4 cm), while the extreme rainfall event just before our sampling at Thompson Creek saturated all plots with both moss covered plots and exposed soil plots having 45.5% soil moisture at 4 cm; this increased to 65.4% soil moisture at 6 cm depth and 76.5% at 8 cm.

Plots with the moss cover removed (TB) were significantly different from the naturally moss covered plots (CM/TB-Table 3 and 4); with mean soil moisture values higher for plots with moss cover removed (compare 11.7% (TB) vs. 11.6% (CM) at Vishnu and 13.2% (TB) vs. 10.2% (CM) at Thompson Creek for first three time periods). Thus, we accept hypotheses 2 and 3 that mature moss mats decrease near-surface moisture.

Although mean soil moisture values for bare soil plots that received new moss cover at the beginning of the experiment (TM) were somewhat lower than bare soil plots (CB -compare

TM means of 12.2% (Vishnu) and 12.0% (Thompson Creek with CB means of 13.2% at Vishnu and 14.3% at Thompson Creek) they were significantly different from bare plots only for the Spring 2017 time period (CB/TM – Table 3 and 4). Soil moisture for bare plots with transferred moss was not significantly different from those where moss mats were removed (TM/TB). Thus, we reject hypotheses 5 and 6 and conclude that newly introduced moss mats do not influence topsoil moisture.

Soil moisture at 8 cm depth. Soil moisture at 8 cm depth averaged 37.6 and 34.9% in bare plots and 32.0% and 28.9% in moss-covered plots at Vishnu Springs and Thompson Creek, respectively, a 15-17% decrease of soil moisture in moss-covered plots, except at Thompson Creek in September 2018 with high rainfall that apparently saturated the soil at the site (18 cm).

During spring and fall 2017 and spring 2018, at Vishnu Springs soil moisture in bare soil plots (CB) at 4 cm averaged 13.3% at 4 cm depth and 35.7% at 8 cm depth (37.3%); while at Thompson Creek soil moisture at 4 cm depth averaged 14.3% and at 8 cm it averaged (34.9%). For naturally moss-covered plots (CM) over this same time period, at Vishnu Springs soil moisture at 4 cm depth averaged 11.7% and 31.7% at 8 cm depth (36.9%), while at Thompson Creek it averaged 10.2 at 4 cm depth and 29.0 at 8 cm depth (35.2%). Thus, at these three time periods both bare and moss-covered plots have similar profiles with the 4 cm depth between 35% and 37% water content compared to that at 8 cm. However, at the fall 2018 time period of high rainfall at Thompson creek (in the week before and during sampling), the 4 cm differential between 4 and 8 cm depth increased to 59% in both bare and moss covered plots, with similar water contents (54.4 % at 4 cm and 76.7% at 8 cm) suggesting that after heavy rainfall, potentially saturated moss mats infiltrate water similar to that of bare areas.

Discussion

The results strongly support our central hypotheses that mature moss mats significantly influence topsoil moisture in temperate riparian ecosystems. Across two years of observation and two geographically separated stream systems, soils beneath intact moss mats consistently contained less moisture than adjacent bare soils, particularly within the upper 4 cm of the mineral soil. Although the magnitude of the response varied seasonally, the direction of the response remained remarkably consistent despite differences in regional climate, dominant tree species, stream morphology, and dominant bryophyte species. This consistency suggests that the influence of moss cover on topsoil moisture represents a general ecological property of mature riparian moss mats rather than a site-specific phenomenon.

The greatest differences occurred within the uppermost soil layer where mosses maintain intimate physical contact with the mineral soil. At deeper depths (6 and 8 cm), moisture differences remained evident, but became less pronounced, indicating that the hydrological influence of mosses is strongest at the atmosphere-soil interface and gradually diminishes with depth. This vertical pattern is consistent with the growth form of pleurocarpous forest mosses, whose densely interwoven stems and overlapping leaves form a continuous capillary layer immediately above the mineral soil (Héban 1977; Vitt 2026 (In Press)). Unlike vascular plants, mosses lack roots and most mosses regulate water movement primarily through ectohydric transport, allowing rainfall to be intercepted, temporarily stored, redistributed throughout the moss canopy, and subsequently lost through evaporation (Mägdefrau 1938; Proctor 2000; Vitt et al. 2014).

Our findings differ from several recent greenhouse and rainfall-simulation studies in which moss cover frequently increased moisture within the underlying soil (Gall et al. 2025; Hu et al. 2023; Thielen et al. 2021). Rather than representing a contradiction, these contrasting results likely reflect differences between controlled experimental systems and natural riparian environments. Greenhouse studies typically eliminate many of the physical processes operating in mature field communities, including prolonged atmospheric exposure, repeated wetting and drying cycles, heterogeneous moss architecture, and seasonal

variation in rainfall, humidity, and temperature. Under natural field conditions, intact moss mats are exposed continuously to atmospheric demand, allowing repeated cycles of interception, capillary redistribution, and evaporation that may ultimately reduce the amount of water retained within the upper mineral soil.

The present study did not directly measure interception, evaporation, or infiltration, and therefore cannot identify the relative importance of individual hydrological processes. Nevertheless, the observed reduction in soil moisture beneath intact moss mats is consistent with a conceptual model in which mature moss canopies modify the timing and movement of water at the soil surface. Rainfall intercepted by the moss canopy is temporarily retained within a highly porous network of stems and leaves before gradually moving downward into the mineral soil or returning to the atmosphere through evaporation (Hu et al. 2023; Thielen et al. 2021). Because bryophytes are poikilohydric and lack the ability to regulate water storage and loss (Proctor 2000; Vitt et al. 2014), evaporation proceeds largely in response to atmospheric conditions rather than physiological control. The large surface area presented by densely packed shoots therefore provides an efficient evaporative surface capable of altering near-surface water balance following rainfall events.

In contrast, transplanted moss mats on previously bare soil failed to consistently produce the reduction in soil moisture observed beneath naturally developed moss communities. This result suggests that the hydrological function of a moss mat depends upon more than the simple presence of moss biomass. Mature mats possess complex structural characteristics including continuous capillary pathways, tightly interwoven shoots, intimate contact with the mineral soil, accumulated organic material, and long-term integration with the soil surface (Hu et al. 2023; Vitt 2026 (In Press)). Some of these characteristics may continue to be evident directly after transplantation; however, the disturbance associated with removing and relocating moss populations probably disrupts capillary continuity and alters the physical architecture responsible for efficient water redistribution. Consequently, hydrological functioning appears to be an emergent property of an intact, well-developed moss community rather than an immediate consequence of moss establishment.

These observations emphasize that mosses should not be viewed simply as passive ground cover (Savile 1972). Instead, they function as biologically active regulators of the soil-atmosphere interface (Vitt and Pakarinen 1977). By intercepting precipitation, temporarily storing water, facilitating capillary redistribution, and promoting evaporation, mature moss mats influence the amount and timing of water reaching the mineral soil. Their ecological role therefore differs fundamentally from that of vascular plants, whose influence on soil moisture is mediated primarily through roots and transpiration. In riparian ecosystems where woody vegetation may be discontinuous and herbaceous cover sparse, mosses represent a distinctive plant functional type capable of exerting a disproportionate influence on near-surface hydrological processes despite their relatively small stature.

The ecological implications of these findings extend beyond the hydrology of individual moss mats. Riparian zones represent critical interfaces between terrestrial and aquatic ecosystems where soil moisture regulates microbial activity, nutrient transformations, organic matter decomposition, and the exchange of water and dissolved materials with adjacent streams (Bentrop and Kellerman 2004; Chase et al. 2016; Gregory et al. 1991). By consistently reducing near-surface soil moisture, mature moss mats may influence numerous physical and biological processes operating within these environments. Although the present study did not directly examine nutrient cycling or microbial activity, altered moisture regimes beneath moss cover have the potential to affect decomposition rates, microbial community composition, seedling establishment, and the stability of stream-bank soils (Klarenberg et al. 2022; Staunch et al. 2012; Sun et al. 2017; Turetsky et al. 2012). Because near-surface soil moisture governs the cohesive strength and detachment susceptibility of fine-grained bank material (Rinaldi and Casagli 1999; Simon and Collison 2002), the consistent moisture reduction documented here within the uppermost mineral soil may also influence the physical resistance of moss-covered bank surfaces to soil detachment, a dimension of riparian bryophyte ecology with broader implications for stream bank and riparian ecosystem management. These possibilities warrant further investigation.

Our results also suggest that mosses should be recognized as a distinct plant functional type within riparian ecosystems. Hydrological influences of vascular plant vegetation are mediated principally

through root systems that alter soil structure and remove water through transpiration. Bryophytes function differently. Lacking roots and possessing little physiological control over water loss, they modify soil moisture through interception, capillary transport, temporary water storage, and evaporation occurring immediately above the mineral soil surface. Consequently, the ecological effects of mosses are concentrated within the upper few centimeters of soil, precisely where many biological and geochemical processes are most active. This functional distinction helps explain why extensive moss cover can substantially influence topsoil moisture despite contributing relatively little biomass compared with vascular vegetation.

An important outcome of this study is that the hydrological influence of mosses was remarkably consistent despite substantial differences between the two study regions. The streams differed in dominant tree species, bryophyte composition, climate, and geographic location, yet naturally developed moss mats consistently produced lower soil moisture than adjacent bare soil. Such consistency suggests that the observed response reflects a fundamental property of mature ectohydric moss communities rather than the characteristics of individual moss species or local environmental conditions. Because pleurocarpous mosses dominate forest floors throughout much of the temperate biome (Eldridge et al. 2023; Frahm and Vitt 1993), similar plant-soil interactions may occur widely in riparian forests where extensive moss mats develop.

The contrasting response of transplanted moss mats provides additional ecological insight. Hydrological function was not restored immediately following transplantation, indicating that moss communities require time to develop the structural characteristics necessary for effective regulation of near-surface water movement. This finding suggests that moss mats should be viewed as self-organizing ecological systems whose function depends upon long-term development rather than simply the presence of living shoots. Future investigations examining the recovery of hydrological function following disturbance would contribute substantially to understanding the resilience and development of moss-dominated ground layers.

Limitations and future directions

Although the present investigation provides one of the first long-term field evaluations of moss effects on topsoil moisture in temperate riparian ecosystems, several questions remain unresolved. Soil moisture was measured directly, whereas interception, evaporation, infiltration, and capillary water movement were inferred from existing knowledge of bryophyte water relations rather than measured experimentally. Future studies combining continuous soil-moisture monitoring with direct measurements of rainfall interception, evaporative water loss, and infiltration would allow the relative importance of these processes to be quantified. Likewise, investigations spanning additional climatic regions, stream orders, and bryophyte communities would determine the generality of the relationships documented here. Experimental studies examining moss mat thickness, species composition, and how soil moisture is effected by moss mats over time after a rainfall event would further clarify the mechanisms through which mature moss communities regulate near-surface hydrology.

Conclusions

This study demonstrates that naturally developed moss mats significantly influence topsoil moisture within temperate riparian ecosystems. Across two geographically separated watersheds and over two years of field observations, soils beneath intact moss cover consistently contained less moisture than adjacent bare soils, particularly within the upper 4 cm of the mineral soil. This reduction averaged 14–29% at 4 cm depth and 15–17% at 8 cm depth across 56 field sites, establishing bryophyte cover as a quantifiable driver of near-surface water balance in riparian corridors. This hydrological influence was depth-stratified: strongest at the soil–atmosphere interface and attenuating with depth, concentrating the moss effect within the shallow mineral soil zone most directly relevant to plant establishment, microbial activity, and nutrient cycling on headwater stream banks. In contrast, recently transplanted moss mats did not produce the same response, indicating that hydrological function depends upon the development of mature, structurally integrated moss communities rather than the simple presence of moss biomass. Specifically, removal of mature moss consistently elevated bank soil moisture, whereas transplantation of

fresh moss onto bare banks produced no consistent hydrological change, a functional asymmetry indicating that the hydrological properties associated with mature moss communities are linked to structural and developmental attributes that do not arise immediately upon establishment and may require extended time to develop in newly colonizing bryophyte communities.

These findings identify mosses as an important, but frequently overlooked component of riparian plant-soil interactions. Unlike vascular plant vegetation, whose influence on soil moisture is mediated primarily through roots and transpiration, ectohydric mosses modify near-surface hydrology through interception, temporary water storage, capillary redistribution, and evaporation occurring at the soil-moss-atmosphere interface. Although the relative importance of these individual processes remains to be quantified, together they provide a plausible mechanistic explanation for the consistent reduction in soil moisture observed beneath mature moss mats.

Recognition of mosses as a functional regulator of riparian soil moisture broadens our understanding of how ground-layer vegetation contributes to ecosystem processes. Because soil moisture influences nutrient cycling, decomposition, microbial activity, and stream-bank stability, the widespread occurrence of moss mats in temperate forests suggests that their ecological significance has been underestimated. The consistency of this effect across contrasting ecoregions, dominant canopy assemblages, and bryophyte species compositions establishes it as a spatially generalizable process property of temperate mossy stream banks rather than a site-specific phenomenon. Incorporating bryophytes into studies of riparian hydrology and plant-soil interactions should therefore improve our understanding of ecosystem function and may ultimately contribute to more comprehensive approaches for managing and restoring forested stream corridors.

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Figure Captions

Figure 1: Location of study sites in Illinois and Virginia

Figure 2: A schematic diagram of experimental plots

Figure 3: Representative images of experimental field plots showing Control Bare (CB), Control Moss (CM), Treatment Moss (TM), and Treatment Bare (TB) plots along Thompson Creek

Figure 4: General characteristics of plots and their location along stream banks

Figure 5: Longitudinal profiles and soil texture of bank material of the two sites

Figure 6: Rainfall data (based on daily total) over different time periods in Vishnu Springs

(Source: www.noaa.gov)

Figure 7: Rainfall data (based on daily total) over different time periods in Thompson Creek

(Source: www.noaa.gov)

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Table 1. General geomorphic characteristics of Field Sites in Thompson Creek in Virginia and Vishnu Springs in Illinois

	Unnamed Stream, Illinois				Thompson Creek, Virginia				Comparison	
									($\alpha=0.05$) Hypothesis: VS $\neq$ TC	
	Minimum	Maximum	Average	Median	Minimum	Maximum	Average	Median	n	<i>p</i> value
Width*	1.48	7.24	4.16	4.31	0.70	6.81	3.49	3.03	26	0.243
Thalweg*	0.13	1.18	0.38	0.35	0.03	0.79	0.36	0.34	26	0.684
Average Depth*	0.05	1.56	0.43	0.32	0.03	2.80	0.76	0.53	26	0.046
Cross-section Area*	0.25	8.57	1.72	1.27	0.02	3.64	1.43	1.32	26	0.919
Bank Slope Angle	28.75	81.76	55.32	52.23	18.79	84.83	49.47	51.65	24	0.084
Sinuosity	0.1	1.5	1.03	1.01	0.1	1.3	1.02	1.00	329	<0.01
*At Bankfull Stage (Meter) VS: Unnamed Stream at Vishnu Springs in Illinois; TC: Thompson Creek in Virginia n: Total number of transects/sample size from each stream included in the statistical analysis (1-Sample Lumped Wilcoxon test). Where n < 28 (i.e. the number of sites), missing values reflect sites where field measurements could not be obtained.										

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590 Table 2. Statistical comparison of topsoil moisture content among streams in two different eco-regions (Hypothesis 1 a-d).

Depth from the Top Surface	Hypothesis ($\alpha=0.05$)		Spring 2017		Fall 2017		Spring 2018		Fall 2018	
			n	p value	n	p value	n	p value	n	p value
4cm	a	$^{VS}CM_{SM} \neq ^{TC}CM_{SM}$	22	<0.001	22	0.178	18	0.082	19	<0.001
	b	$^{VS}CB_{SM} \neq ^{TC}CB_{SM}$	22	0.846	21	0.424	14	0.060	14	<0.005
	c	$^{VS}TM_{SM} \neq ^{TC}TM_{SM}$	25	0.778	22	0.112	17	0.795	15	<0.005
	d	$^{VS}TB_{SM} \neq ^{TC}TB_{SM}$	24	0.710	23	0.773	16	0.088	12	0.010
6cm	a	$^{VS}CM_{SM} \neq ^{TC}CM_{SM}$	27	0.674	24	0.721	19	0.031	19	0.013
	b	$^{VS}CB_{SM} \neq ^{TC}CB_{SM}$	22	0.399	21	0.375	14	0.024	15	<0.005
	c	$^{VS}TM_{SM} \neq ^{TC}TM_{SM}$	26	0.046	24	0.493	17	0.227	15	<0.005
	d	$^{VS}TB_{SM} \neq ^{TC}TB_{SM}$	24	0.932	24	0.648	16	0.171	13	0.008
8cm	a	$^{VS}CM_{SM} \neq ^{TC}CM_{SM}$	27	0.216	25	0.545	20	0.059	19	<0.005

	b	$^{VS}CB_{SM} \neq ^{TC}CB_{SM}$	22	0.249	21	0.543	15	0.112	15	<0.005
	c	$^{VS}TM_{SM} \neq ^{TC}TM_{SM}$	26	0.304	24	0.668	16	0.877	15	<0.005
	d	$^{VS}TB_{SM} \neq ^{TC}TB_{SM}$	24	0.658	24	0.920	15	0.094	13	<0.005
^{VS} : Vishnu Springs, ^{TC} : Thompson Creek, CM : Control Moss, CB : Control Bare, $_{SM}$: Topsoil Moisture n: Total number of plots included in the statistical analysis (1-Sample Lumped Wilcoxon test). The increase in sample size for some comparisons in Fall 2018 reflects one site that was unavailable in Spring 2018.										

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Table 3. Descriptive Statistics of topsoil moisture content (%) at different depths from the top surface of Vishnu Springs, Illinois

		TM			TB			CM			CB		
		Depth			Depth			Depth			Depth		
		4cm	6cm	8cm	4cm	6cm	8cm	4cm	6cm	8cm	4cm	6cm	8cm
Spring 2017	Mean	11.94	26.74	36.13	13.46	25.00	35.33	12.04	22.33	32.91	15.75	28.73	40.68
	Median	12.00	30.00	43.00	12.00	24.00	43.00	9.00	22.00	35.50	15.50	30.00	42.00
	Maximum	25.00	46.00	64.50	34.00	47.50	64.00	33.00	48.00	71.00	37.00	54.00	83.00
	Minimum	4.00	6.00	6.00	4.00	3.00	3.00	3.00	5.00	6.00	6.00	6.00	7.00
	Standard Deviation	5.28	12.20	17.84	6.71	14.57	18.48	7.38	12.20	15.40	8.47	15.47	20.60
	n	27	27	27	27	27	27	27	27	27	22	22	22
Fall 2017	Mean	14.73	26.21	34.98	12.95	25.07	36.00	11.94	22.06	32.78	13.17	26.25	36.67
	Median	13.00	25.25	37.00	10.00	23.75	40.00	10.00	19.00	34.00	10.50	25.50	38.50
	Maximum	38.00	53.00	72.00	29.50	47.00	69.00	30.00	46.00	63.00	32.00	49.00	74.50
	Minimum	6.00	6.00	6.00	7.00	7.00	6.00	4.00	3.00	1.00	5.00	5.00	6.00
	Standard Deviation	8.58	15.00	19.98	6.37	12.66	16.23	6.29	12.55	16.78	6.98	12.50	16.28
	n	26	26	26	28	28	28	27	27	27	24	24	24

Spring 2018	Mean	9.93	24.40	33.90	8.50	15.26	22.92	10.75	19.70	29.28	10.75	19.70	29.28
	Median	10.00	25.00	41.00	7.50	11.00	24.00	6.00	11.00	19.00	9.00	14.50	30.50
	Maximum	16.00	40.00	48.00	26.00	40.00	47.00	23.00	35.00	54.00	34.00	55.00	77.50
	Minimum	0.00	5.00	7.00	1.00	1.00	5.00	1.00	5.00	4.00	4.00	5.00	9.00
	Standard Deviation	3.83	10.52	13.55	6.06	10.50	14.17	4.32	8.26	15.60	7.52	12.55	17.06
	n	21	21	21	18	18	18	23	23	23	20	20	20
Fall 2018	Mean	21.44	33.56	43.28	22.47	34.47	43.94	17.95	26.86	32.86	25.35	34.75	43.45
	Median	21.50	34.50	41.50	23.00	39.00	44.00	14.00	27.00	35.00	26.00	36.50	40.00
	Maximum	42.00	50.00	68.00	48.00	49.00	66.00	44.00	46.00	52.00	40.00	55.00	72.00
	Minimum	7.00	7.00	6.00	4.00	7.00	13.00	7.00	7.00	9.00	9.00	17.00	16.00
	Standard Deviation	11.67	13.11	16.84	11.67	12.31	15.19	10.10	12.02	12.98	8.90	11.46	15.93
	n	18	18	18	17	17	17	21	21	21	20	20	20
TM: Treatment Moss, TB (Treatment Bare), CM (Control Moss), CB (Control Bare)													

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607 **Table 4.** Descriptive Statistics of topsoil moisture content (%) at different depths from the top surface of Thompson Creek, Virginia

		TM			TB			CM			CB		
		Depth			Depth			Depth			Depth		
		4cm	6cm	8cm	4cm	6cm	8cm	4cm	6cm	8cm	4cm	6cm	8cm
Spring 2017	Mean	11.87	20.67	31.31	14.60	25.25	35.12	11.45	20.25	26.96	14.63	22.75	31.29
	Median	10.00	18.00	33.50	10.00	24.00	32.75	9.00	16.00	24.50	9.00	19.75	31.25
	Maximum	31.00	42.00	54.50	45.00	44.00	59.50	29.00	43.00	52.00	46.50	60.00	61.50
	Minimum	3.00	6.00	9.00	6.00	9.00	7.00	3.00	6.00	8.00	4.00	5.00	7.00
	Standard Deviation	6.16	10.78	13.84	9.63	11.80	13.97	6.91	13.02	15.13	11.20	13.37	12.39
	n	27	27	27	26	26	26	28	28	28	28	28	28
Fall 2017	Mean	11.94	23.68	35.80	12.90	26.81	37.52	9.15	19.69	29.58	14.02	23.90	34.66
	Median	11.00	25.00	39.00	10.50	26.50	39.50	8.50	21.00	30.00	10.00	20.00	37.00
	Maximum	23.00	38.00	49.00	37.00	45.00	59.00	22.00	37.00	48.00	61.00	44.00	56.00
	Minimum	6.00	5.00	3.00	6.00	11.00	15.00	2.00	2.00	2.00	6.00	9.00	9.50
	Standard Deviation	4.48	8.97	11.65	6.74	8.78	10.69	3.74	8.93	12.27	10.99	10.87	12.92

	n	25	25	25	24	24	24	26	26	26	25	25	25
Spring 2018	Mean	12.15	22.96	34.87	12.08	23.17	35.50	9.80	20.20	30.04	14.43	27.39	38.57
	Median	9.00	18.00	35.00	8.00	19.50	35.50	9.00	21.00	33.00	10.00	28.00	41.00
	Maximum	38.00	46.00	60.00	30.00	53.00	71.00	27.00	45.00	56.00	37.00	48.00	66.00
	Minimum	1.00	8.00	9.00	4.00	7.00	5.00	3.00	4.00	4.00	7.00	9.00	15.00
	Standard Deviation	7.78	11.80	13.21	8.05	13.88	16.47	5.26	12.02	16.00	8.62	11.88	13.68
	n	23	23	23	24	24	24	25	25	25	23	23	23
Fall 2018	Mean	48.59	68.50	83.32	45.50	63.70	77.90	45.35	65.04	76.74	45.35	65.04	76.74
	Median	45.00	66.50	86.00	45.00	64.00	83.00	42.50	53.50	73.50	47.00	66.00	80.00
	Maximum	84.00	100.00	100.00	77.00	100.00	100.00	68.00	88.00	100.00	72.00	99.00	100.00
	Minimum	20.00	37.00	45.00	9.00	12.00	36.00	17.00	18.00	30.00	10.00	42.00	20.00
	Standard Deviation	17.30	15.81	15.82	15.55	20.35	19.81	14.05	16.74	21.02	14.05	16.74	21.02
	n	22	22	22	22	22	22	24	24	24	23	23	23
TM: Treatment Moss, TB (Treatment Bare), CM (Control Moss), CB (Control Bare)													

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Table 5. Statistical comparisons between experimental plots.

Depth from the Top Surface	Hypothesis ($\alpha=0.05$)		Spring 2017		Fall 2017		Spring 2018		Fall 2018	
			n	p value	n	p value	n	p value	n	p value
4cm	2	$CM_{SM} < CB_{SM}$	49	<0.001	39	0.044	35	<0.005	37	<0.005
	3	$CM_{SM} < TB_{SM}$	44	<0.001	44	0.008	35	0.016	37	<0.005
	4	$CM_{SM} < TM_{SM}$	44	<0.001	50	<0.005	38	<0.005	33	0.013
	5	$CB_{SM} > TM_{SM}$	48	<0.005	45	0.600	32	0.216	32	0.839
	6	$TM_{SM} < TB_{SM}$	45	0.152	46	0.635	35	0.856	32	0.709
6cm	2	$CM_{SM} < CB_{SM}$	45	0.005	43	0.039	36	<0.005	37	<0.005
	3	$CM_{SM} < TB_{SM}$	52	0.056	49	<0.005	36	0.104	33	0.012
	4	$CM_{SM} < TM_{SM}$	51	0.016	47	0.006	38	<0.005	32	<0.005
	5	$CB_{SM} > TM_{SM}$	47	0.546	44	0.546	35	0.259	31	0.962
	6	$TM_{SM} < TB_{SM}$	45	0.152	48	0.397	37	0.948	31	0.808
8cm	2	$CM_{SM} < CB_{SM}$	49	<0.005	44	0.076	37	0.006	35	<0.005
	3	$CM_{SM} < TB_{SM}$	50	0.034	49	<0.005	37	0.061	32	0.016
	4	$CM_{SM} < TM_{SM}$	54	0.077	46	0.019	39	<0.005	32	<0.005
	5	$CB_{SM} > TM_{SM}$	49	0.066	44	0.556	33	0.401	31	0.967
	6	$TM_{SM} < TB_{SM}$	52	0.392	49	0.565	37	0.833	27	0.835
n: Total number of plots included in the statistical analysis (1-Sample Lumped Wilcoxon test) <i>CM</i>: Control Moss, <i>CB</i>: Control Bare, <i>TM</i>: Treatment Moss, <i>TB</i>: Treatment Bare <i>SM</i>: Topsoil Moisture										

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