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Restoring open canopy pine barrens from the ground up: Repeated burns correspond with increased soil hydraulic conductivity

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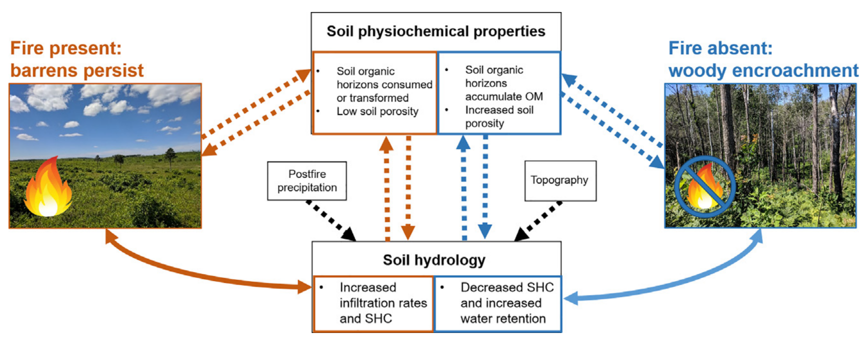
HIGHLIGHTS

- Excessively drained soils are characteristic of imperiled pine barrens habitat.
- Fire exclusion may result in changes in soils and subsequent loss of pine barrens.
- Frequently burned sites had greater SHC than long unburned sites.
- Woody fuel additions and slope position influenced SHC.
- Prescribed fire may positively impact barrens restoration and persistence.

GRAPHICAL ABSTRACT



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ABSTRACT

Prescribed fire is widely used for ecosystem restoration, yet the mechanisms that determine its effectiveness remain poorly characterized. Because soil hydrology influences ecosystem processes like erosion, runoff, and plant competition, it is important to understand how fire affects soil hydrology. A systematic approach to understanding relationships among vegetation, topography, and fire is needed to advance knowledge of how fire influences soil properties that in turn affect restoration success. Our objective was to characterize relationships among burn severity, vegetation, and soil hydrology in a heterogenous landscape under restoration management. Our study took place in a barrens-forest mosaic with recent prescribed fire history ranging from 0 to 10 burns since 1960, and additional variation in fuel loading, burn severity, vegetation cover, topography, and soils. We measured soil hydraulic conductivity (SHC) during two consecutive years, which represented control, prefire, postfire, and 1-year postfire conditions. Regression tree analysis identified an important threshold effect of antecedent soil moisture on SHC; soils with initial moisture $<$ 13% had lower SHC than soils with initial moisture $>$ 13%. Furthermore, above this threshold, sites with intermediate to high recent burn frequency (4–10 burns) had significantly greater SHC than unburned control sites. High fuel loads associated with brush cutting and piling increased SHC at barrens sites but not brush or pine sites, suggesting an interaction between vegetation cover and fire effects on SHC. At the local hillslope scale, toe-slopes had greater SHC than summits. Our results suggest that repeated prescribed fires of moderate to high frequency may enhance SHC, thereby reducing soil water retention and potentially restoring functional pine barren processes that limit woody plant growth. Prescribed fire may therefore be an important management tool for reversing mesophication and restoring a global array of open canopy ecosystems.

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1. Introduction

Fire is a keystone disturbance for many ecosystems globally, including disturbance-dependent ecosystems like savannas. The removal of fire from landscapes has consequences for ecosystem function and may result in change from open canopy systems to closed forests. For instance, a compositional shift from heliophytic, fire-adapted species to shade-tolerant, fire-sensitive species has occurred throughout eastern U.S. forests via mesophication, a process by which mesophytic species encroach fire-adapted systems in a positive feedback loop that further inhibits fire occurrence and spread (Nowacki and Abrams, 2008). As woody plants encroach in these open ecosystems and canopy cover increases, a moist and cool microclimate develops in the understory. Cumulatively, these changes drive a positive feedback loop which results in a state shift from open-canopy grasslands and savannas to closed-canopy forest. During this process the landscape shifts from fire-adapted to fire-resistant, which may result in native species decline and habitat loss. Through changes in vegetation composition, mesophication also alters leaf litter chemistry and packing ratio and, ultimately, changes decomposition rates and flammability (Scarff and Westoby, 2006; Dickinson et al., 2016). This shift occurs rapidly on mesic landscapes with fertile soils, whereas dry, nutrient-poor conditions can limit the rate at which mesophication occurs (Nowacki and Abrams, 2008). Previous studies have investigated how plant composition and litter quality contribute to mesophication (Abrams, 1990; Dickinson et al., 2016; Kreye et al., 2013), but far less is known about how changes in soil hydrology contribute to this feedback loop.

Soil properties, vegetation, and water availability (i.e. precipitation) interact to influence soil hydrology, and soil hydrologic conditions influence plant community composition by limiting the amount of water available for plant growth. Soil hydraulic conductivity (SHC) describes the ease at which water moves through soil pores and reflects the combined properties of water and the porous medium (soil), including soil structure and chemical composition (Smith, 2002). For instance, a previous study reported positive correlations between SHC and both soil porosity and sand content (Zongping et al., 2016). Similarly, organic matter accumulation may result in decreased soil bulk density, increased porosity, and increased water infiltration rates (Moody et al., 2009; Shaver et al., 2013), and one study showed that complete removal of the soil organic layer resulted in a > 50% decrease in infiltration rates of unburned *P. pinaster* forest soils (Marcos et al., 2018). In contrast, certain types of organic matter are rich in hydrophobic organic residues, which results in soil water repellency (SWR) and decreased SHC. For instance, evergreen plant species with leaves rich in waxes, resins, and aromatic compounds tend to be associated with SWR (Doerr et al., 2000). Vegetation cover may also indirectly influence SWR via plant associations with certain fungi and microorganisms (Chan, 1992; Czarnes et al., 2000). Fire can therefore affect SHC via its effects on soil chemical composition and structure, although these relationships are likely to be dependent on the soil and vegetation types present in a landscape.

Among disturbances, fire is unique because heat-induced transformations influence both the quantity and quality (i.e. chemical composition) of soil nutrient pools. Depending on burn intensity and duration, soils may become enriched or depleted in nutrient elements following fire. Carbon and nitrogen, for instance, are volatilized at relatively low temperatures (200–500 °C), but cations have higher volatilization temperatures (> 800 °C) and tend to concentrate in ash (DeBano, 1991; DeBano et al., 1998). Organic matter (OM) stored in live and decomposing plant biomass contained in the forest floor is partially to completely combusted during fire, and cumulative OM losses tend to decrease both rainfall interception and soil absorptive capacity (Baker, 1988). Fire may also transform OM into a spectrum of pyrogenic materials, collectively referred to as pyrogenic carbon, or PyC. Pyrogenic carbon (PyC) ranges from partially charred biomass to carbon-dense soot, and the degree of C-condensation is positively related to chemical aromaticity (Bird et al., 2015; Hedges et al., 2000; Masiello, 2004). Ash is the particulate residue deposited on the soil surface after fire, and, like PyC, exists along a spectrum of dark C-rich ash to light mineral-rich ash (Bodi et al., 2014). After fire, fine particulate ash (white ash) generally becomes intermixed with soil, while larger ash particles will remain on the soil surface (Stoof et al., 2010).

Soil chemical transformations and inputs of PyC and ash can affect SHC by changing soil physical characteristics or by resulting in hydrophilic or hydrophobic soil conditions. Because of its high chemical aromaticity, PyC may result in SWR, a widely-reported phenomenon after wildland fires (e.g. Plaza-Alvarez et al., 2018). SWR may also result from other soil heating processes like the volatilization and subsequent condensation of hydrophobic organic compounds downward along a temperature gradient, or the physical coating of sand particles by hydrophobic organic residues (DeBano et al., 1970; Savage, 1974). However, because thermal destruction of hydrophobic OM occurs between 175 and 400 °C (Dlapa et al., 2008), fire-induced SWR results only from a narrow range of soil temperatures. In addition to PyC, ash formed during fires may also alter soil water retention, even if present in very small amounts (Stoof et al., 2010). Ash interacts with soil physical and chemical properties and may ultimately alter soil texture, porosity, bulk density, and mineralogy. When mineral-rich white ash blankets topsoil immediately postfire, surface sealing (Larsen et al., 2009), pore clogging, or the formation of a subsurface hydrophobic soil layer may result (DeBano et al., 1998). These processes each lead to decreased SHC (DeBano, 2000; Stoof et al., 2011; Woods and Balfour, 2008), but pore clogging and surface sealing are unlikely to occur in sandy soils (Stoof et al., 2016). Macroscopic PyC (e.g. char, or "black ash") may also increase water repellency because it is rich in hydrophobic aromatic compounds (Bodi et al., 2014). The temporal persistence of these pyrogenic inputs is highly variable. The effects of fine ash are transient due to the mobile nature of ash (Cerdà and Doerr, 2008), but other soil properties, such as pH and OM content, may show persistant legacy effects of fire for > 45 years (James et al., 2018).

Prescribed fire is a widely used land management tool, and burn conditions may be optimized to achieve desired restoration outcomes including effects on vegetation and soils. Burn intensity, severity, frequency, and seasonality may all influence prescribed fire effects on soils. Broadly defined, burn severity is a measure of ecosystem impacts from fire, and both ground estimates and remotely sensed severity indices may be used to estimate ecosystem response to fire, including hydrological response (Chafer et al., 2016; DeBano et al., 1998; Jain et al., 2012). For instance, remotely sensed burn severity of a wildfire in ponderosa pine (*P. ponderosa*) forest in Colorado, USA indicated a threshold effect in which soil hydraulic properties were affected at moderate to high, but not low, burn severity (Moody et al., 2016). In contrast, another study of a prescribed fire in Rocky Mountain coniferous forest reported temporary soil hydrophobicity after fire despite low burn severity (Robichaud, 2000). Thus, it is important to study SHC response to both wildfire and prescribed fire to identify similarities and differences that may arise under different burn conditions and in different forest types. Seasonality is also important for prescribed fires since fuel quantity and moisture content vary seasonally and may impact burn severity (Knapp and Keeley, 2006; Sparks et al., 2002). Finally, previous studies have reported that increased burn frequency may intensify the effects of fire on soils and suggest that repeated burns may be necessary to meaningfully alter soil conditions (James et al., 2018; Neary et al., 1999; Pellegrini et al., 2017).

Ongoing prescribed fire management in the Moquah Barrens (Wisconsin, USA) presented a unique opportunity to quantify relationships between prescribed fire and soil properties, including SHC. The Moquah Barrens includes diverse vegetation communities from semi-open savannas to closed forests, and a wide range in fuel loads resulting from variation in disturbance history, land management, and experimental fuel manipulations (i.e. woody fuel additions and removals). Fire exclusion, coupled with land use change, has resulted in significant loss of fire-adapted pine barrens throughout the Great Lakes region, and prescribed fire is one of the primary restoration tools for land managers attempting to restore pine barrens habitat. However, it is unclear how prescribed fire will affect soil conditions after an extended period (i.e. > 50 years) of fire exclusion.

In this study, we sought to understand how prescribed fire, soils, vegetation, and SHC interact in a pine barrens-forest mosaic with varying vegetation cover and fuel loads (open barrens to closed forest), burn severity (low to moderate), burn history (0–10 prescribed fires in the last 50 years), and topography. Based on previous literature, we hypothesized how each of these factors was expected to influence SHC independently (Table 1), with the predominant expectation that prescribed fire would increase SHC (See Fig. 1). Because pine barrens have declined to less than 1% of their pre-European settlement extent in the northern Great Lakes region (Wisconsin DNR, 2015), our overarching goal was to determine the degree to which prescribed fire can reverse belowground processes contributing to mesophication in this system. To test our predictions, we measured field SHC during two successive years, resulting in measurements that represent three paired burn scenarios: 1) pre and post-fire, 2) 1-year and 2-years postfire, and 3) no fire (control). Given our study design, we also aimed to investigate transient (immediate postfire) versus persistent (1–2 years postfire) responses of SHC to prescribed fire.

2. Materials and methods

2.1. Study area

Our study took place in the Moquah Wildlife Management Area (henceforth Moquah), in the Chequamegon-Nicolet National Forest (CNNF), Wisconsin, USA. Moquah was established in 1970 and includes 10 management units encompassing approximately 6000 ha (Fig. 2). Moquah is located 350 m above sea level with a mean annual temperature of 5 °C and mean annual precipitation of 780 mm yr^{-1}. Soils here are well to excessively drained Spodosols developed on collapsed outwash plains and washed till and are classified as Vilas loamy sands and Sultz sands, both Entic Haplorthods. Local topography ranges from flat to rolling hills. Moquah contains approximately 10% of Wisconsin's remaining pine barrens, a type of savanna ecosystem in which tree growth is limited by fire and edaphic conditions. Pine barrens plant communities have experienced widespread loss over the last century and are now classified as regionally and globally imperiled (Olson et al., 2006; Wisconsin DNR, 2015).

Vegetation cover varies from open-canopy pine barrens to closed-canopy forest (Fig. 3). Barrens are defined as having a tree basal area ≤ 7 m^2 ha^{-1} and shrub cover < 30%, with a dominant ground-layer vegetation of blueberry (*Vaccinium angustifoliu and V. myrtilloides*), sweet fern (*Comptonia perengrina* [L.] J.M. Coult.), and mixed grasses and forbs, and a sparse pine overstory (*Pinus banksiana* Lamb., *P. strobus* L., and *P. rubus*). Barrens occur in patches in a mosaic of shrubland, pine woodland, and deciduous forest. Shrublands consist of > 50% cover of woody shrubs (*Amelanchier laevis* Wiegand, *Corylus cornuta* Marshall, *C. americana* Walter, *Salix humilis* Marshall, and others) and tree saplings with dominant stem DBH < 12 cm. Pine woodlands include thinned plantations of red pine (*P. rubus*) and jack pine (*P. banksiana*) and sparse naturally occurring white pine (*P. strobus*) with basal area from 7 to 14 m^2 ha^{-1}. Deciduous forests are dominated by aspen (*Populus tremuloides* Michx., *P. grandidentata* Michx.), oak (*Quercus rubra* L., *Q. ellipsoidalis* E.J. Hill), and red maple (*Acer rubrum* L.) that were > 12 cm DBH, and with a basal area 7–14 m^2 ha^{-1}.

2.2. Study design

Our study took advantage of an established study of soil heating during prescribed fires (Quigley et al., 2019, 2020). In 2015 and 2016, these study plots were established and stratified among vegetation and fuel treatment factors spanning the four management blocks in Moquah and the unburned areas immediately adjacent to Moquah (Fig. 2). The previously established study classified vegetation cover as barrens, brush, pine woodland, or deciduous forest based on the above descriptions. In areas of the management blocks with standing brush, the brush was cut prior to prescribed fires with the intention of reducing postfire woody re-sprouting. At a subset of the plots with cut brush, all 10-h and 100-h woody fuels were removed and then added to a subset of the barrens and pine woodland plots at a rate of approximately 15–25 metric tons ha^{-1} to create low and high fuel conditions, respectively. As such, the fuel factors were cut & leave brush, cut & remove brush, brush addition, and ambient (no cut brush). We used a subset of these established plots from these vegetation and fuel factors: 59 burned plots and 20 long-unburned (i.e. ≥ 50 years without fire). See Supporting Information Table S1 for the distribution of study plots among vegetation and fuel factors.

In addition to the 79 established study plots, we added 12 plots (6 barrens [3 burned, 3 control], 6 brush [3 burned, 3 control]) to investigate relationships between hillslope position and SHC. We established

Table 1
Summary of hypotheses for how individual fire, environment, and soil variables included in this study influence SHC. Direction of predicted relationships is indicated by "+" (positive relationship), "-"(negative relationship), and "+/−"(non-linear relationship).

Factor	Measure	Relationship with SHC	Description of predicted relationship
Fire	Burn severity	−	SHC is expected to decrease with increasing burn severity, although a threshold of burn severity may be needed to alter soil hydraulic properties.
	Burn intensity	−/+	Moderate temperatures may create hydrophobic PyC residues that decrease SHC, whereas high intensity fires are more likely to result in mineral-rich ash (see below).
	Burn frequency	+	Frequent fire prevents accumulation of woody debris and maintains shallow organic horizons. Repeated prescribed burns are expected to contribute to high SHC.
	Ash load	−/+	Ash can have very high infiltration rates, but is generally short-lived on the soil surface. Ash may reduce soil porosity and result in decreased SHC once intermixed with sandy soils.
Environment	Vegetation cover	−/+	Hydrophobic plant root exudates, plant-associated microbes, and litter of certain plant species are associated with soil water repellency (SWR) which can decrease SHC in the absence of fire.
	Topographic index	+	Topographic wetness index indicates where water tends to accumulate, so high values are expected to be associated with greater OM accumulation, increased porisity, and higher SHC.
	Slope position	−/+	OM and fine soil particles are expected to accumulate at footslopes and toeslopes. We predict that SHC will be lower at backslope relative to summit and toeslope positions (i.e. catena effect).
Soil	Organic matter	+	OM content is expected to be positively related to SHC because OM decreases soil bulk density and increases porosity.
	A horizon depth	+	A horizon depth indicates the extent to which humified material is intermixed with the upper mineral soil horizon and is expected to be positively related to SHC.
	Bulk density	−	High soil bulk density indicates low SOM content and low porosity, so bulk density is expected to be negatively related to SHC.

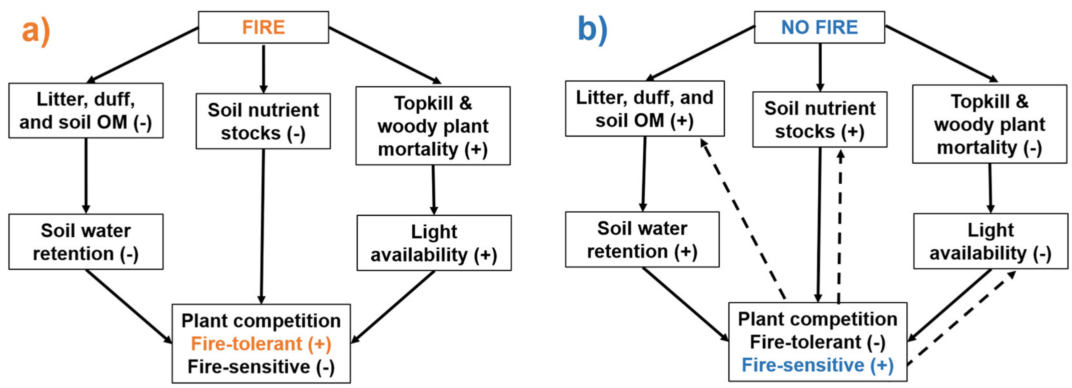

Fig. 1. Alternative scenarios for pine barrens plant community persistence in the presence of fire (a) and in the absence of prescribed fire (b). Plus signs (+) represent hypothesized increases, and minus signs (−) represent hypothesized decreases. Dashed arrows in panel b highlight positive feedbacks expected to occur during mesophication. In the presence of fire (a), soil nutrients are lost via volatilization, and consumption of soil OM maintains well-drained and highly conductive soils with poor water retention. Topkill and woody plant mortality maintain high light levels. High light availability and droughty, nutrient-poor soils allow fire-tolerant woody species to dominate. Consequently, pine barrens persist in the presence of fire. In the absence of fire (b), Topkill and woody plant mortality are low, allowing woody plants and their leaf litter to accumulate. The increased shading from the aggrading woody canopy creates a positive feedback loop whereby moist, minimally conductive, and nutrient rich soil conditions favor fire-sensitive over fire-tolerant woody plants. Consequently, this mesophication process favors woody encroachment.

3 sampling positions along hillslope plot: 1) summit, 2) backslope (~20 m downslope from summit position), and 3) toeslope. Hillslope sites were established between the South and East aspect, and average slope at the backslope location was 32%.

2.3. Prescribed fires

Dormant season prescribed fires were conducted for four management blocks (200–800 ha) of which two blocks were burned in May 2016 (n study plots = 25) and two in May 2018 (n study plots = 34). The two 2018 burn blocks were last burned in 2014, and the remaining 2016 burn blocks were last burned in 2001, 2013, or had no previous burn history (n = 20). Prescribed fires were historically applied to smaller area burn units (~50–100 ha), resulting in a heterogenous landscape of burn frequency ranging between zero and ten prescribed fires since 1963 (Fig. 2). Due to low within-level replication for burn frequency among established plots, we assigned burn frequency to qualitative classes; plots established within units with no recorded history of burns were classified as "unburned", and plots established within burned units were classified as low (1–3 burns), moderate (4–6 burns), or high (≥ 7 burns) burn frequency. Plot distribution among burn frequency classes are listed in Table S2. We took field SHC measurements in 2017 and 2018, capturing three distinct burn scenarios: 1) 1-year prefire versus ~2 months postfire, 2) 1-year versus 2-years postfire, and 3) unburned control conditions. Prior to prescribed fires, we installed aluminum tags treated with temperature-sensitive paints

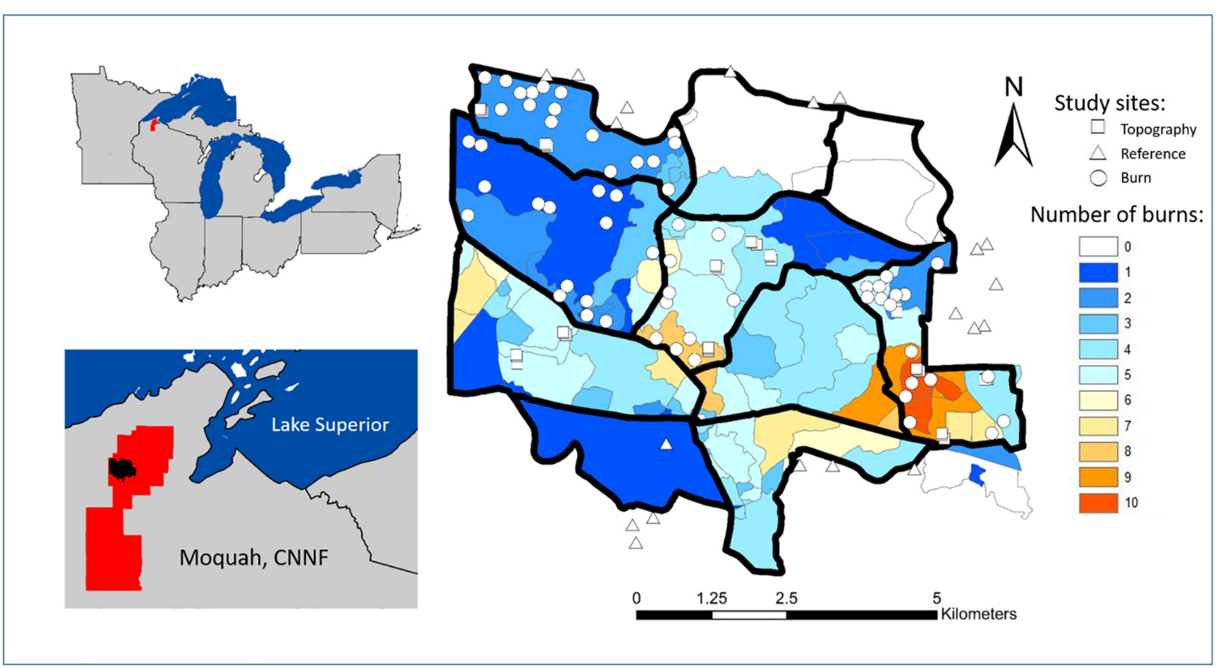

Fig. 2. Map of Moquah study sites which are located within the Chequamegon-Nicolet National Forest (Red polygon, left panels) of the Great Lakes region (Wisconsin, USA). Circles represent burn plots in current prescribed fire management blocks, triangles represent reference (unburned) plots with a long history (>60 years) of fire exclusion, and squares represent topography plots which span the summit, backslope (20 m downslope) and toeslope of individual hillslopes. Colored polygons illustrate burn frequency within historic small burn unit boundaries. Thick black polygon outlines represent current management burn blocks. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

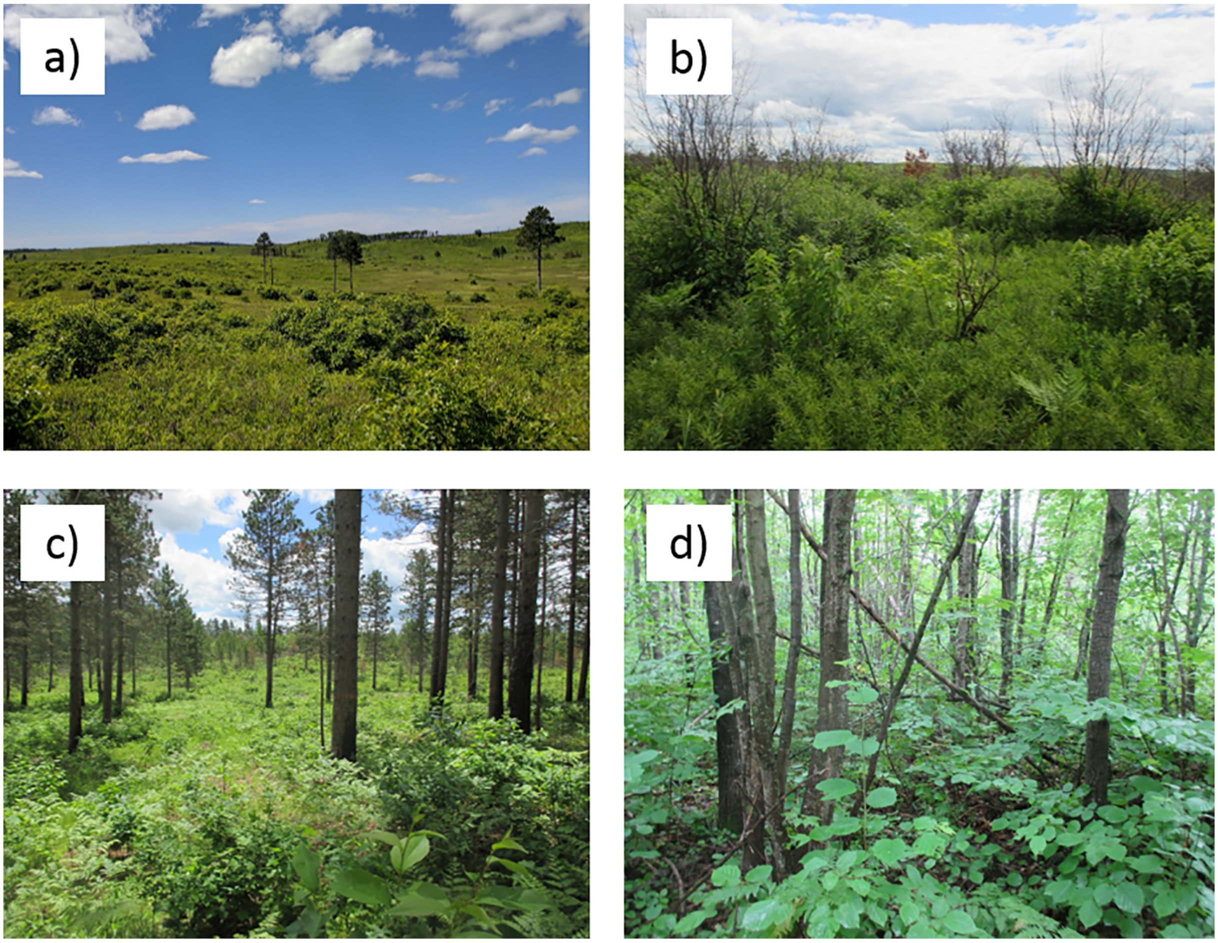

Fig. 3. Vegetation cover types included in study, from lowest to highest tree density. Pine barrens (a) are savannas maintained by fire and edaphic conditions. Brush areas (b) have shrubs and saplings exceeding 50% canopy cover. Pine woodlands (c) are thinned plantations of red and jack pine, and (d) deciduous forests are closed canopy forests dominated by oak and aspen. See text for full plant community descriptions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

at the litter surface and 20 cm above the litter surface. Paint tag temperature are positively related to fuel consumption and energy generated by combustion (Quigley et al., 2019).

2.4. Field sampling

We collected soil samples 1-year prefire, immediately (i.e. 1–2 days) postfire, and 1-year postfire within a 1m^2 quadrat near the center of each 20 m radius study plot. Forest floor, which extends from litter through the O horizon, was removed from within a 30 cm diameter sampling ring before using a soil hammer bulk density sampler to remove two 10 cm deep mineral soil cores. We assessed burn severity at the 1 m scale using the National Park Service index (NPS, 2003) within two days following burns. The NPS severity index is a substrate assessment including five qualitative classes: 'unburned', 'scorched', 'lightly burned', 'moderately burned', and 'heavily burned' (NPS, 2003).

We recorded triplicate measurements of cumulative infiltration from within 1 m of the soil collection quadrat in 2017 and 2018 using a tension infiltrometer (Meter Group® Mini Disk infiltrometer). The infiltrometer is comprised of a plastic cylinder (32.7 cm long, 3.1 cm diameter) containing a 95 mL water reservoir, a bubbling chamber with adjustable suction (0.5–7 cm), and a 3 mm thick porous sintered stainless steel disk (4.5 cm diameter) which is placed in contact with the soil surface. Infiltration measurements taken under tension produce SHC values characteristic of the soil matrix by eliminating macropore flow. We used a suction rate of 1 cm, which prevents the filling of large macropores and soil structural features. The litter layer was carefully removed to expose the surface of the O_e horizon of soil (e.g., corresponding to the upper surface of forest duff layer where present) and to improve contact between soil and the porous disk. The infiltrometer was held in place with a ring stand and clamp, and volume was measured at 30 s time intervals for a minimum of 180 s or until no change in volume was observed for 5 continuous measurements. Antecedent volumetric moisture content was estimated using a digital time-domain reflectometer (Field Scout TDR 300, Spectrum Technologies, Aurora, IL) with 7.9 cm probes. SHC and TDR measurements were taken concurrently between July 7 and August 24 in 2017 and between July 31 and September 6 in 2018.

2.5. Lab measurements

We transported mineral soil cores to a laboratory, where we measured wet weight and depth of the A horizon to the nearest mm. The A horizon is the uppermost mineral soil horizon which includes intermixed humified organic matter. Each mineral soil core was separated into 0–5 cm and 5–10 cm depth increments, and dried to constant mass at ambient temperature. Bulk density was calculated as dry mass (g) divided by soil core volume (cm^3). We then composited the duplicate samples within depth increment prior to laboratory analysis. Each composited sample was analyzed for soil organic matter content (SOM) using loss on ignition, using a muffle furnace for two hours at 360 °C (Schulte and Hopkins, 1996).

2.6. Calculations and statistical analysis

Unsaturated soil hydraulic conductivity was calculated based on the infiltration model proposed by Zhang (Zhang, 1997) in an Excel macro provided by Meter®. Briefly, parameters relating to soil sorptivity (C_1) and hydraulic conductivity (C_2) were obtained by fitting cumulative infiltration (I) measurements vs. time (t) using Eq. (1):

$$I = C_1 t^{1/2} + C_2\, t \tag{1}$$

Field hydraulic conductivity (k) was then calculated using Eq. (2):

$$k = C_2 / A \tag{2}$$

where C_2 is the slope of the curve of cumulative infiltration versus the square root of time (from Eq. (1)) and A is a coefficient derived from the Van Genuchten parameters for a given soil texture class, suction rate, and infiltrometer disk radius (A = 2.79 for: loamy sand, 1 cm suction rate, and disk radius of 2.25 cm). A sample plot calculation is provided in the supporting information file (Fig. S1). This equation can occasionally produce negative C1 values, which are not physically realistic; we excluded negative values from analysis (see discussion).

We used the SpatialAnalyst tool in ArcMap to estimate aspect, slope, flow direction, and flow accumulation at each site from a 10-m scale digital elevation map (DEM). Next, we calculated a topographic wetness index (TWI) as: $\ln(a_s / \tan\beta)$, where a_s is the DEM resolution-corrected flow accumulation, and β is the local slope in radians (Beven and Kirkby, 1979). We obtained the detailed small unit burn history of all prescribed fires conducted in Moquah from 1963 – present from the Washburn Ranger District (USDA-FS).

We performed all statistical analyses in the R statistical computing environment (R Core Team, 2018) version 3.5.1 and used the 'dichromat' package to produce colorblind-friendly figures (Lumley, 2013). Prior to analysis, we confirmed normality and homogeneity of variance, and identified outliers using the 'boxplot.stats' function in base R. Soil hydraulic conductivity showed a right-skewed distribution, so these data were log normal transformed prior to statistical analysis. Statistical significance was determined at $p < 0.05$, unless otherwise noted.

We used linear models to test specific univariate hypotheses presented in Table 1. First, we used paired t-tests to compare 2017 and 2018 SHC measurements for each of the three burn scenarios 1) pre versus postfire (short term fire response), 2) 1-year versus 2-years postfire (postburn recovery), and 3) unburned controls. We used one-way ANOVAs to test whether SHC varied according to prescribed fire frequency classes (unburned, low, moderate, and high). For burned plots, we also used one-way ANOVAs to determine whether postfire SHC was related to NPS burn severity index. We used the 'TukeyHSD' command in base R to conduct posthoc tests for statistically significant pairwise differences among groups. For plots burned in 2016, we also used ordinary least squares (OLS) regression to investigate whether SHC was related to estimates of maximum temperatures (paint tag data) or to the amount of surface ash generated during prescribed fires (Quigley et al., 2019). We used t-tests to determine whether fuel additions (barrens, pine) and fuel removals(cut brush) influenced SHC and one-way ANOVAs and Tukey's tests to determine whether SHC varied among vegetation cover types without fuel manipulations (barrens, brush, pine, and deciduous) or hillslope positions (summit, backslope, and toeslope). Finally, we used OLS regression to test for linear relationships between continuous soil properties (organic matter, bulk density, and A horizon depth) and SHC.

To evaluate potential non-linear relationships between SHC and fire, environment, and soils, we used classification and regression tree (CART) analysis on the complete dataset (all burn scenarios, both study years). CART modeling was performed using the "rpart" package (Thernau and Atkinson, 2015) with SHC as the response variable, and the following explanatory variables: burn frequency class, fuel manipulations, volumetric soil moisture, slope, TWI, historic vegetation cover, current vegetation cover, A horizon depth, OM, and bulk density. To prevent over-fitting, we pruned the regression tree to include the number of nodes to the cost complexity parameter associated with the minimum cross-validation error (De'Ath and Fabricius, 2000).

3. Results

Cumulative infiltration consistently fit the second order polynomial regression, with a mean coefficient of regression of 0.99, and 98% of samples had an $R^2 > 0.90$. Negative C_1 values (i.e. slope from Table S2) were obtained at 9 plots, and a Welch's t-test indicated that negative C_1 values were associated with low soil moisture ($t = 2.6$, $p = 0.02$; mean = 9.19 for positive C_1 values, 5.88 for negative C_1 values). Because these values represent physically impossible conditions, we removed them from the dataset prior to subsequent analysis (see Discussion for possible explanations of negative values). After eliminating negative values and measurement lengths of < 180 s, we retained paired 2017–2018 SHC measurements for 62 of our 79 study sites.

3.1. Fire and SHC

Prescribed fires resulted in a limited range of NPS burn severities, and most sites were categorized as scorched or lightly burned, and no sites were categorized as severely burned (NPS, 2003). SHC was consistently lower in 2018 than in 2017, regardless of burn scenario (Fig. 4). For the 1-year to 2-year postfire comparison (i.e. plots burned in 2016), plots showed a 79% reduction in SHC ($t = 3.39$, df = 21, $p < 0.01$). For the pre vs. postfire comparison SHC was also reduced but this difference was not statistically significant ($p = 0.69$). Interestingly, we also observed a 72% decrease in SHC at our unburned control plots from 2017 to 2018 ($t = 2.93$, df = 12, $p = 0.01$). Substrate burn severity estimates at our study plots within the burned blocks were constrained between 'scorched' and 'moderately burned', and none of the plots within burn blocks were classified as 'unburned' or 'heavily burned' postfire. ANOVA suggested that there was no relationship between burn severity class and postfire SHC or 1-year postfire SHC. Similarly, there was no relationship between paint tag maximum temperature and SHC. There was, however, a positive relationship between prescribed fire frequency and SHC (Fig. 5), which was statistically significant for soils with antecedent soil moisture above the threshold identified in our regression tree analysis ($F = 6.7_{3,62}$, $p < 0.01$; see "CART model" section below). Sites with high and moderate burn frequency had significantly greater SHC than unburned plots (both $p < 0.01$), and sites with high burn frequency also had greater SHC than sites with low burn frequency ($p = 0.04$). A general pattern of increasing SHC with increasing burn frequency was also observed at plots with soil moisture < 13%, but post-hoc tests indicated no statistically significant differences between pairs (all $p > 0.05$). Mean and standard error for all vegetation cover types by burn frequency class are reported in Table S2. No relationship was observed between ash load and SHC.

3.2. SHC relationships with vegetation, topography, and soils

After excluding sites with manipulated fuel loads, SHC did not vary systematically according to vegetation cover. Barrens sites were, however, affected by woody fuel additions. SHC doubled at barrens with brush fuels added ($t = -2.88$, df = 26, $p < 0.01$) (Fig. 6b), although fuel manipulations did not affect SHC at pine sites with fuel additions or at cut brush sites with fuel removals (Fig. 6a, c). SHC showed no relationship with slope, aspect, or topographic wetness index (TWI), even when data were subsetted according to the soil moisture threshold identified in the regression tree (see CART model, below). However, investigation of the hillslope study sites indicated slope position explained variation in TWI, where TWI was significantly higher at toeslopes than summits (Fig. 7a). Furthermore, we observed a pattern of increasing SHC toward the bottom of slopes, but this pattern was only marginally significant ($F = 2.8_{2,36}$, $p = 0.07$) (Fig. 7b).

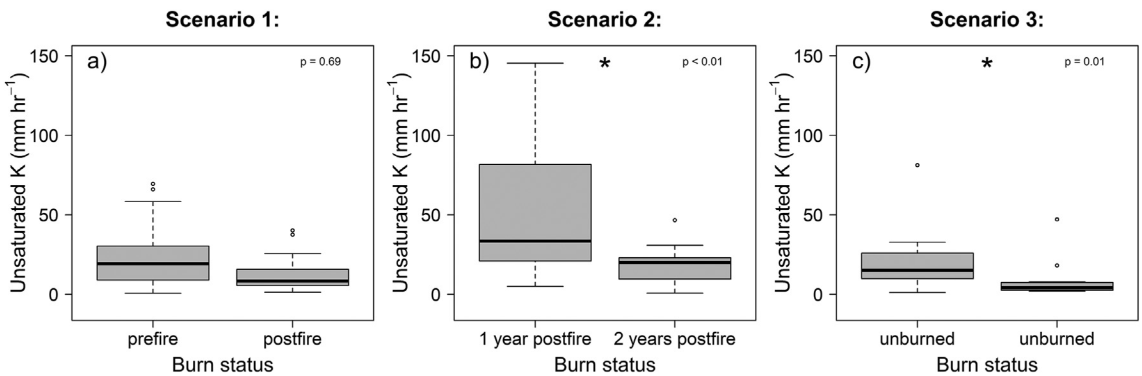

Fig. 4. Variation in unsaturated soil hydraulic conductivity (*K*) over two years at burned (a, b [2018 and 2016 prescribed burns, respectively]) and unburned (c) sites in a pine barrens ecosystem in Wisconsin USA. SHC consistently decreased between study years, and this difference was statistically significant for burn scenario 2 (1-year vs. 2-years postfire) and for burn scenario 3 (unburned control plots). Asterisks indicate statistically significant difference at the $\alpha = 0.05$ level. Two outliers > 150 are not shown in the middle panel, but were retained in statistical analyses.

3.3. SHC and soil characteristics

There were no linear relationships observed between SHC and soil organic matter, bulk density, or A horizon depth (all $p > 0.05$). Average ($\pm$ s.e.) A horizon depth was 2.65 cm (0.14), average organic matter concentration was 4.2% (0.2), and average bulk density was 0.93 g cm^3 (0.02).

3.4. CART model

Our pruned regression tree retained only one split based on soil volumetric moisture, and the tree had an overall R^2 of 0.29. The soil moisture split in the tree suggested that plots with antecedent soil moisture ≥ 13% were associated with the greater SHC (mean = 38 mm hr^{-1}) than those with < 13% volumetric moisture. The full (unpruned) regression tree is provided in supporting information (Fig. S2).

3.5. Potential limitations of field-based SHC estimates

Field measurements of cumulative infiltration which produced erroneous negative K values were generally clustered at sites with low soil moisture. A previous study noted that negative values may arise from measurement error or the mathematical equation used to derive S_1 (Moody et al., 2009). Measurement error may arise from visual determination of water volume (accurate to $\pm$ 0.5 mL), but this is unlikely since our time resolution was coarse (30 s). Alternatively, gravity may be more significant than vertical or lateral capillary terms at low soil moisture content, which would violate assumptions associated with derivation of K and suggests that an alternative model may be needed to estimate unsaturated SHC of dry soils (Moody et al., 2009).

4. Discussion

4.1. SHC and prescribed fire

SHC recorded in this prescribed fire study (mean $\pm$ std. error = 37 $\pm$ 7 mm hr^{-1}) was similar to postfire SHC at the Harvard Experimental Forest (20–36 mm hr^{-1}) and Rocky Mountain coniferous forests (10–89 mm hr^{-1}) (Moody et al., 2009; Robichaud, 2000). Although we expected SHC to decrease with increasing burn severity (Table 1), the absence of high burn severity in this study likely explains why no relationship was observed. For instance, a previous study failed to identify quantitative relationships between remotely sensed burn severity (dNBR, normalized burn ratio) and soil hydraulic conditions below a threshold of burn severity in ponderosa pine forests (Moody et al., 2016). Furthermore, we may have missed an ephemeral signal of burn severity since pyrogenic soil inputs like ash and charcoal may have been homogenized by wind, precipitation, or other environmental agents in the

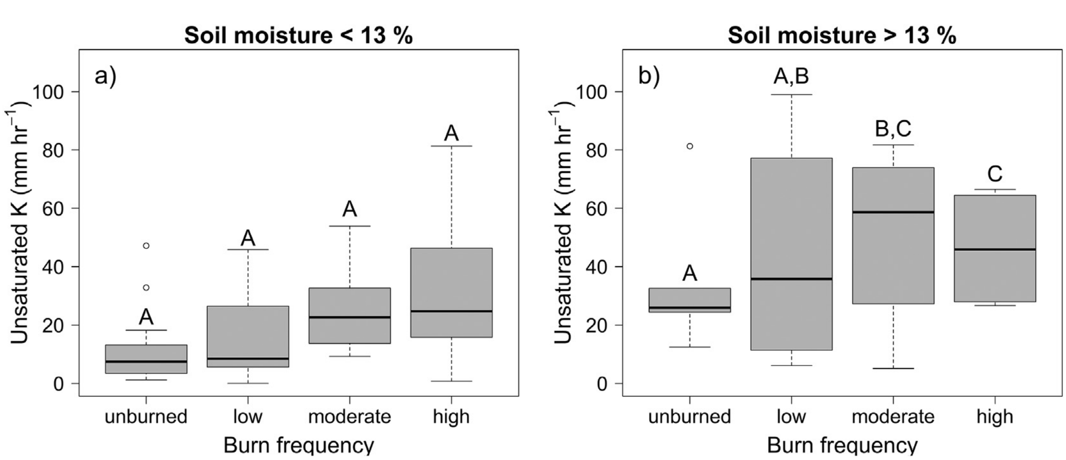

Fig. 5. Effect of recent prescribed fire frequency on soil hydraulic conductivity (*K*). No pairwise differences were observed for sites with soil moisture < 13% (a). For measurements with antecedent soil moisture > 13% (b), high and moderate burn frequency sites had greater SHC than unburned study sites, and moderate burn frequency sites had greater SHC than unburned sites. Capital letters indicate statistically different groups indicated by Tukey's Honestly Significant Difference test at the $\alpha = 0.05$ significance level. Four outliers of $K > 100$ are not displayed.

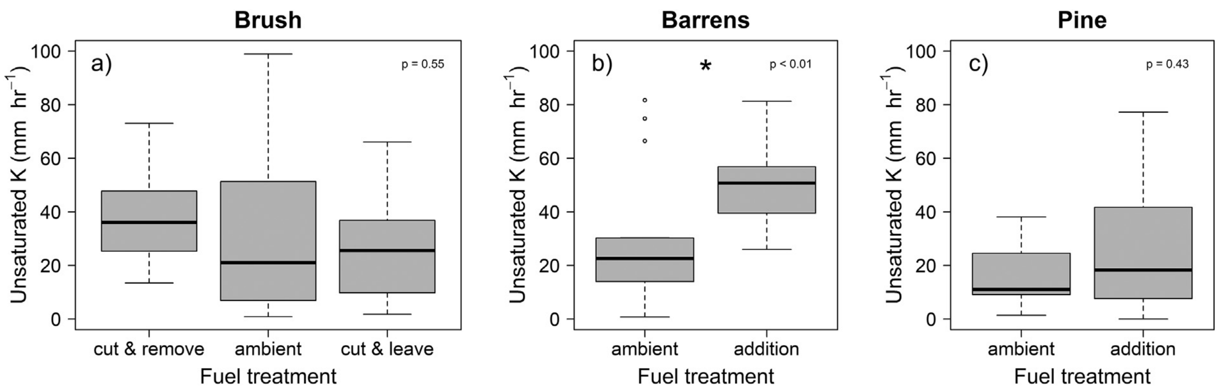

Fig. 6. Effects of fuel treatments on soil K at brush (a), barrens (b), and pine sites (c). K more than doubled at barrens sites with fuel additions (b), but fuel manipulations had no significant effect on K at pine and cut brush sites, respectively (a, c). Asterisks indicate statistically different groups determined by paired *t*-tests, at the $\alpha = 0.05$ significance level.

2–3 months between burns and field-based infiltration measurements. Similarly, it is likely that the reason we did not observe a relationship between maximum paint tag temperature (which is related to fire energy) and SHC may be due to the a skewed distribution of paint tag temperatures (67% of observations in two of the ten possible paint melt ranges; 343–426 and 426–660 °C) and the ephemeral nature of fire-induced changes in SHC.

A previous study concluded that repeated fires in conifer forests minimize accumulation of fine woody debris and maintain a shallow layer of duff, or partially decomposed plant litter, in the forest floor (Drobyshev et al., 2008). This may explain our finding that moderate and high burn frequency sites (≥ 4 burns) had greater SHC than unburned control sites (Fig. 5). Moquah prescribed fires were conducted during late spring, when the duff layer remains cool and wet, and duff consumption is inversely related to duff moisture content (Garlough and Keyes, 2011; Hartford and Frandsen, 1992; Little et al., 1986). It is therefore likely that several growing season burns, or a burn period when the soil temperature is relatively warm and fuels are dry, would be required to achieve significant reductions in duff depth at brush and forested sites. Similarly, in pine barrens repeated prescribed fires could prevent the development of organic-rich soil horizons with high water retention, subsequently maintaining excessively well drained soils that support drought-adapted barrens plant communities (Fig. 1). It is difficult to interpret whether the high SHC observed at moderate to high burn frequency sites was due to burn frequency or some combination of vegetation cover and burn frequency since vegetation cover types were not evenly distributed among burn frequency categories (see Table S1). Although our high burn frequency group was skewed toward barrens sites, we expect to observe a similar pattern of decreased SHC with high burn frequency in brush and forested sites as surface fuels are consumed and duff layers become increasingly susceptible to heating and consumption. Continued monitoring of woody vegetation cover types following subsequent burns is necessary to support this hypothesis.

Mean SHC more than doubled at barrens sites with woody fuel additions, which is most likely associated with very high fuel consumption and ash production at these sites. A previous study reported very high near-saturation hydraulic conductivity of ash collected following a wildfire, with K_f values ranging from 160 mm hr^{-1} for fine ash (< 0.06 mm diameter) to 1900 mm hr^{-1} (coarse ash) (Moody et al., 2009). Barrens sites have little to no organic horizon, so ash generated during fire can rapidly infiltrate the mineral soil. In coarse soils like the glacial outwash sands present at Moquah, we suspect that ash inputs caused the observed increase in SHC relative to sites without fuel additions. A recent study in the Moquah Barrens reported that woody fuel additions significantly increased ash production in barrens, but not in pine woodlands, which supports our hypothesis that differences in ash loads may explain the observed increase in SHC at barrens sites with brush fuel additions (Quigley et al., 2019).

4.2. Vegetation cover and SHC

We observed no significant differences in SHC for barrens versus woodland or forest sites, despite droughty (i.e. high SHC) soils being considered an important factor in maintaining pine barrens habitat relative to forested habitats (Heikens and Robertson, 1994; Hole, 1976). It is possible that hydrophobic root exudates may influence SHC, and plant species present at both woodland and barrens sites (i.e., *Pinus banksiana, P. resinosa*, *P. strobus*, *Arctostaphylus* spp., and *Vaccinium* spp.,) are known to produce hydrophobic root exudates (Doerr et al.,

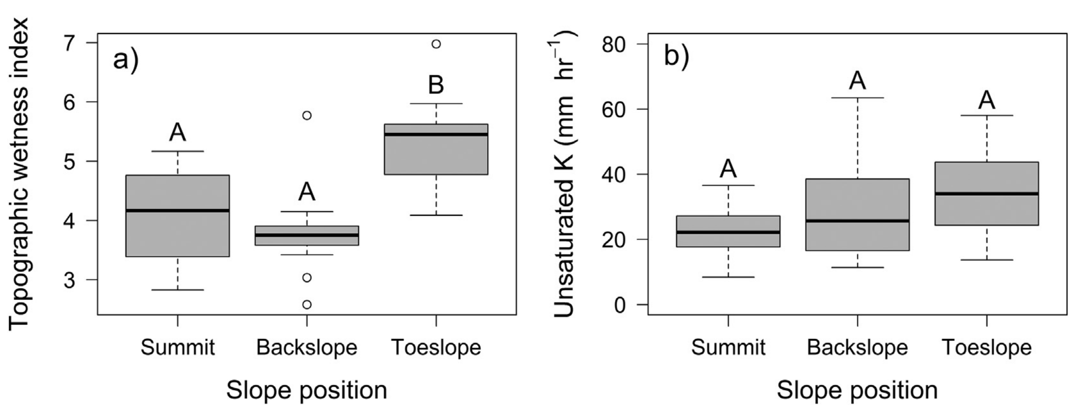

Fig. 7. Variation in TWI and soil hydraulic conductivity (K) according to slope position. At our 12 hillslope study sites, toeslopes had consistently higher TWI than backslope and summit positions (a). K increased toward the bottom of hills, but ANOVA indicated that these differences were marginally non-significant (panel b, $p = 0.07$). Capital letters indicate statistically different groups indicated by Tukey's Honestly Significant Difference test at the $\alpha = 0.05$ significance level.

2000). Future studies investigating trade-offs between the influences of fire-influenced versus plant root-derived hydrophobicity on SHC will help further characterize the mechanisms of soil response to fire.

Despite the lack of a direct relationship between SHC and vegetation cover, vegetation cover may indirectly influence SHC via effects on fuel quality and quantity. For instance, high fuel load and high SHC were related in barren sites (Fig. 6). Fuel loads can be managed by brush cutting followed by a period of fuel curing (drying) to increase fuel loads above ambient fuel conditions in preparation for a prescribed fire. The aim of brush cutting is often to deter or eliminate woody encroachment. In our study, we intentionally piled additional fuels in brush cut plots to experiment with extremely high fuel loads. While this manipulation is not practical at management scales, it does highlight the potential role of fuel load management to support pine barren soils functional processes, such as promoting high SHC.

The hypothesis that vegetation may indirectly influence SHC is also supported by our fuel manipulation results (Fig. 6a-c) which suggest that extreme changes in fuel loads and fuel consumption (i.e. ash production) may influence SHC. Brush cutting and fuel manipulations significantly altered ash loads in Moquah (Quigley et al., 2019), and natural variation in surface fuel quantity is likely to create similar heterogeneity in ash production and SHC. Although we did not observe a linear relationship between ash load and SHC, consumption of contrasting vegetation cover types results in ash with differing organic and mineral composition, which may also influence SHC since mineral and organic components of ash vary in their absorptive capacity (Bodi et al., 2014; León et al., 2013; Quigley et al., 2019). Further, fine ash deposits can increase runoff on bare soil but may actually decrease runoff in the presence of soil microaggregates < 0.250 mm (Thomaz, 2018). Finally, although high ash inputs may result in surface sealing under specific conditions, this scenario is unlikely for sandy soils (Stoof et al., 2016). We did not observe surface sealing after the prescribed fires at our study site.

4.3. Topographic effects

Although no direct relationships were observed between coarse-scale topography extracted from GIS (slope, aspect, TWI) and SHC, we were able to detect a signal of variation in TWI according to local slope positions along individual hills (Fig. 7). While not statistically significant, we also observed a pattern of increasing SHC toward the bottom of individual hills which supports our expectation that SHC would be greatest where sediment and fine particles accumulate at toeslopes (Schimel et al., 1985) (Table 1). Topographic variability is limited in Moquah, but our results suggest that even small hills may contribute to important landscape-scale variation in SHC. Time since fire may also impact the relative of importance of fire versus topography as explanatory predictors of soil properties, including SHC. For instance, a previous study in boreal forests in China revealed that wildland fire explained most variation in soil properties one year postfire, but that topography was a better predictor of soil properties 11 years postfire (Kong et al., 2019).

4.4. Soil properties

Our regression tree indicated that antecedent soil moisture provided the greatest explanation of overall variation in SHC across vegetation cover, burn status and fuel treatment groups (Fig. S2). Similarly, a previous study reported that antecedent soil moisture determined the formation of stable vs. unstable wetting fronts in a water repellent sandy soil (Ritsema et al., 1998). Antecedent moisture conditions also provides explanation for the consistent decline in SHC between 2017 and 2018, since contrasting precipitation patterns occurred during these two study years. The 2017 field season was characterized by frequent, low-quantity rainfall events. In contrast, most of the 2018 postfire rainfall occurred during a single 3-day storm event (160 mm, June 16–18) which was followed by dry conditions for the remainder of summer (National Oceanic and Atmospheric Administration, 2018). Individual precipitation events are becoming more intense throughout North America (Prein et al., 2017). In Wisconsin, the frequency of heavy rainstorms (> 75 mm rainfall) increased by more than 200% between 1961 and 2011 (Janowiak et al., 2014). An extreme wetting event, such as a 1000-year storm, could result in a burst of fungal activity with potential downstream effects including hydrophobic conditions and decreased SHC, especially in cases where rapid soil drying occurs (Doerr et al., 2000; Zhang et al., 2007). Alternatively, an extreme postfire precipitation event may redistribute highly mobile pyrogenic materials along topographic gradients.

Although we observed no direct relationships between SHC and additional soil physicochemical properties, soil structure and bulk density may be modified when soils are heated to high temperatures, with subsequent effects on soil hydraulic properties (DeBano et al., 1998; Badía and Martí, 2003). Because the prescribed fires in this study resulted in only light to moderate burn severity and soil heating was minimal (mean soil/duff temperature rise = 75 °C), temperature-induced transformations in mineral soil were unlikely. SOM was the primary driver of soil water retention differences recorded between burned and unburned sites after a high severity wildfire in Colorado montane forest dominated by aspen, fir (*Abies* spp.), and pine, and loss of SOM during fire homogenized landscape-scale hydraulic conditions within burned areas (Ebel, 2012). Similarly, patterns of decreasing forest floor C and N pools with increasing burn severity were observed following a wildfire in a North American boreal forest (Kolka et al., 2017). However, the range of observed SOM was constrained to very low values at Moquah relative to these other studies (3–4% SOM versus 3–40% SOM), and this likely explains why SOM could not be related to SHC. A recent prescribed fire study in Mediterranean pine forests supports this explanation, since low burn severity conditions resulted in minimal soil organic matter loss and no difference was observed between SHC of burned and unburned sites (Plaza-álvarez et al., 2019). Therefore, it seems likely that relationships between SOM and SHC depend on both the underlying range of variation in SOM as well as burn conditions (intensity, severity).

5. Conclusion: implications for pine barrens management

Factors such as fire exclusion, habitat fragmentation, and climate change have influenced the links between fire and soil hydrology. Thus, it is important that we better understand these links to develop sustainable fire management approaches to maintain ecosystem function. In eastern U.S. forests, a compositional shift referred to as mesophication has occurred in which fire-sensitive woody plants that tolerate shade, but not fire (e.g., red maple), invade open, dry landscapes in the absence of fire (Nowacki and Abrams, 2008). Similarly, grasslands and savannas are susceptible to habitat loss via woody encroachment when natural fire disturbance regimes are suppressed (Leach and Givnish, 1996). Fire management, particularly exclusion, in pine barrens of central Wisconsin has been linked to forest succession, canopy closure, and biotic homogenization (Li and Waller, 2015), and belowground soil hydraulic conditions are likely an overlooked factor contributing to aboveground changes in plant competition and community composition. Although we did not observe appreciable differences in SHC among vegetation cover types, we found that moderate and high burn frequency sites had greater soil hydraulic conductivity than long-unburned sites. This suggests that repeated prescribed fires may aide in maintaining barrens habitat by 1) encouraging dry soil conditions that favor fire-tolerant plant species and 2) by increasing topkill and plant mortality that create open canopy conditions. In addition, our experimentation with fuel loads suggests that artificially increasing fuel load through brush cutting and piling may promote droughty soils with high SHC that support pine barrens persistence. In the future, coupling soil hydrologic response to fire with soil nutrient response to fire may help managers better understand how belowground conditions contribute to mesophication in pine barrens systems and, potentially, how mesophication can be reversed.

CRediT authorship contribution statement

KQ and JM conceived the study. KQ collected field data with assistance from field technicians Wildt and Raschke. KQ analyzed data, and KQ, JM, RK, and BS interpreted the results. KQ wrote the first draft of the manuscript, and all coauthors contributed significantly to manuscript revisions.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.144258.

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