

## RESEARCH ARTICLE

# Topographic, edaphic, and vegetative controls on plant-available water

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## Abstract

Soil moisture varies within landscapes in response to vegetative, physiographic, and climatic drivers, which makes quantifying soil moisture over time and space difficult. Nevertheless, understanding soil moisture dynamics for different ecosystems is critical, as the amount of water in a soil determines a myriad ecosystem services and processes such as net primary productivity, runoff, microbial decomposition, and soil fertility. We investigated the patterns and variability in in situ soil moisture measurements converted to plant-available water across time and space under different vegetative cover types and topographic positions at the Marcell Experimental Forest (Minnesota, USA). From 0- to 228.6-cm soil depth, plant-available water was significantly higher under the hardwoods (12%), followed by the aspen (8%) and red pine (5%) cover types. Across the same soil depth, toeslopes were wetter (mean plant-available water = 10%) than ridges and backslopes (mean plant-available water was 8%), although these differences were not statistically significant ( $p < .05$ ). Using a mixed model of fixed and random effects, we found that cover type, soil texture, and time were related to plant-available water and that topography was not significantly related to plant-available water within this low-relief landscape. Additionally, during the 3-year monitoring period, red pine and quaking aspen sites experienced plant-available water levels that may be considered limiting to plant growth and function. Given that increasing temperatures and more erratic precipitation patterns associated with climate change may result in decreased soil moisture in this region, these species may be sensitive and vulnerable to future shifts in climate.

## KEYWORDS

mixed hardwoods, quaking aspen, red pine, soil moisture

## 1 | INTRODUCTION

The interactions between soil moisture, plants, landscapes, and climate have been increasingly studied (e.g., Adams, Flint, & Fredriksen, 1991; Breshears, Myers, & Barnes, 2009; Cavanaugh, Kurc, & Scott, 2011; Detto, Montaldo, Albertson, Mancini, & Katul, 2006; Rodriguez-Iturbe, D'Odorico, Porporato, & Ridolfi, 1999; Tromp-van Meerveld & McDonnell, 2006; Troch et al., 2009), yet in situ datasets that link physiographic and vegetative controls to temporal and vertical patterns in soil moisture are rare, especially in forested ecosystems. Soil moisture is an important component of the water balance in forests; evapotranspiration rates, tree growth and carbon assimilation (Bassett, 1964; Pastor & Post, 1986; Porporato, Daly, & Rodriguez-Iturbe, 2004), soil respiration (Davidson, Belk, & Boone, 1998;

Davidson, Verchot, Cattaneo, Ackerman, & Carvalho, 2000), and ecosystem resistance and resilience to disturbance (Johnstone et al., 2010) are all influenced by soil moisture. However, at the watershed scale, water storage in the form of soil moisture is heterogeneous and site-driven, leading to variability within and between sites, as well as across time (Breshears et al., 2009; Tromp-van Meerveld & McDonnell, 2006; Western & Blöschl, 1999). Because of the inherent variability, detailed quantification of soil moisture dynamics is needed both within and across different landscapes.

Within a hillslope, soil moisture is related to topography, soil texture, and vegetation cover type (Burt & Butcher, 1985; Famiglietti, Rudnicki, & Rodell, 1998; Nyberg, 1996; Tromp-van Meerveld & McDonnell, 2006; Western, Blöschl, & Grayson, 1998), yet differences between hillslopes within a watershed are complex (Francis, Thornes,

Romero Diaz, Lopez Bermudez, & Fisher, 1986). The influence of topography on hillslope soil moisture dynamics cannot be emphasized enough, as lateral subsurface flow due to gravity can significantly impact soil water storage (Burt & Butcher, 1985). Hillslope curvature can also affect its soil moisture distribution, as concave hillslopes accumulate water and generate subsurface runoff to a greater degree than convex hillslopes (Anderson & Burt, 1978).

Few studies have assessed the relationships among soil moisture and landscape-level drivers at depths beyond the near surface (>0.3 m) using field data (Breshears et al., 2009; Schulze et al., 1996; Tromp-van Meerveld & McDonnell, 2006). These studies have shown that in situ measurements of soil moisture are highly variable across space, depth, and time and can vary according to cover type as well as precipitation inputs (e.g., snow versus rain-dominated systems; Breshears et al., 2009). Additionally, soil water availability varies across topographic positions and with physical soil properties, and soil moisture levels can influence plant transpiration, creating a feedback mechanism between water availability and plant water use (Tromp-van Meerveld & McDonnell, 2006).

From an ecohydrological standpoint, soil water, or volumetric soil water content, is important because it represents the amount of water available to plants. However, the plant-available water is non-linearly related to volumetric soil water content due to its dependence on soil texture. Whereas some species may be able to access water held under a higher tension than others, converting volumetric soil water content to plant-available water is critical for understanding when, where, and why plants access water. This concept is fundamental to plant-soil water relationships and is commonly expressed in terms of “wilting point,” “permanent wilting percentage,” “available soil water,” “non-limiting water range,” or other similar terms (Kirkham, 2005; Kramer, 1983; Slayter, 1967). The point at which water is no longer available to plants is dynamic and can be influenced by a number of parameters including species, antecedent moisture conditions, and depth to water table (Kirkham, 2005), thus creating a limitation to using metrics of plant-available water. However, converting volumetric soil water content to plant-available water based on soil texture remains a useful way of describing the amount of water that is generally available to plants, allowing for better understanding of the feedback mechanisms between ecosystems and water availability (Breshears et al., 2009).

Annual precipitation and soil water availability are regarded as some of the most important controls of vegetation distribution (Köppen, 1936; Peel, Finlayson, & McMahon, 2007; Rodriguez-Iturbe et al., 1999). In general, mid-latitude forests can only be sustained in regions where precipitation inputs exceed 500 mm per year (Prentiss et al., 1992). Locations where vegetation transitions from one type to another (i.e., forests to grasslands), or tension zones, are ecologically sensitive areas (Emanuel et al., 1985) that are dependent upon climatic conditions that are changing at an alarming pace (Kirtman et al., 2013). In the United States, a prairie-forest tension zone runs through central Minnesota that is strongly correlated with a sharp decrease in mean annual precipitation (Johnson, 1995). This region has already experienced significant warming and drying of soil moisture, despite no change in annual precipitation (Dymond, Kolka, Bolstad, & Sebestyen, 2014). The changes in temperature and thus water availability in this region have the potential to push these already sensitive ecosystems

beyond their threshold of tolerance to natural climate variability. Such pressure on the forests could result in a shift of forest to prairie, resulting species loss, reduced ecosystem services, habitat loss and degradation, and economic loss (Dirnböck, Essl, & Rabitsch, 2010; Hansen et al., 2001; Parmesan & Yohe, 2003). Thus, understanding the complex dynamics between soil water availability, vegetation type, and physiography is vital for predicting the resiliency of these forested ecosystems to climate change.

The overarching goal of this study was to examine the role of topography and cover type on plant-available water in northern Minnesota forests. Specifically, our research objectives were to (a) characterize plant-available water across cover types and landscape positions (inter-site dynamics), and (b) describe plant-available water within cover types and landscape positions (intra-site dynamics). Additionally, we determined the physiographic characteristics that best describe plant-available water throughout the soil profile.

## 2 | METHODS

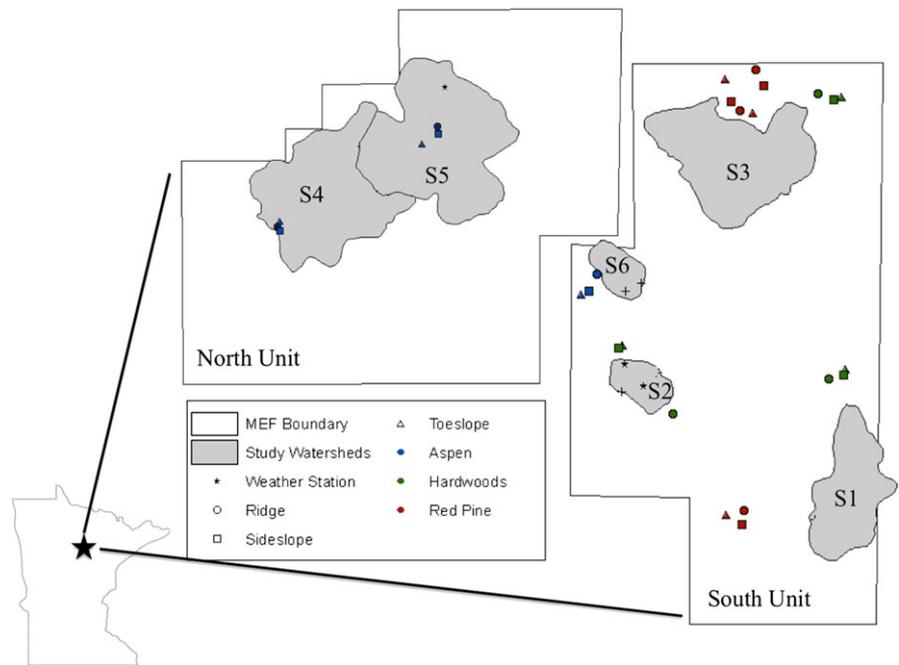
### 2.1 | Study area

The 1100 ha Marcell Experimental Forest (MEF; 47°52'N, -93°46'W) is located on the eastern edge of the Chippewa National Forest in north-central Minnesota (Figure 1). Climate is continental with warm, moist summers and cold winters (Sebestyen et al., 2011). Mean annual air temperature from 1961 to 2013 ranged from -15.0 °C in January to 18.9 °C in July. Annual precipitation is dominated by summer rainfall events and averaged 779 mm from 1961 to 2013. The MEF is in a landscape of peatland bogs and fens dominated by black spruce and tamarack (*Picea mariana* Mill. B. S. P. and *Larix laricina* [Du Roi] K. Koch) that are surrounded by uplands consisting of pine (*Pinus resinosa* Ait. and *Pinus banksiana* Lamb), aspen (*Populus tremuloides* Michx. and *Populus grandidentata* Michx.), and mixed hardwoods (*Tilia Americana* L., *Acer saccharum* Marsh, and *Acer rubrum* L.). Topographic relief at the MEF varies subtly with elevations ranging, from 412 m at the watershed outlets to 438 m in the uplands. Soils in the forest uplands are predominately sandy outwashes consisting of Menahga sands (mixed frigid and Typic Udipsamments), Graycalm loamy sands (isotic, frigid, and lamellic Udipsamments), Cutaway loamy sands (fine-loamy, mixed, superactive, and frigid oxyaquic Hapludalfs), and Sandwick loamy sands (loamy, mixed, superactive, and frigid Arenic Glossaqualfs). Approximately two thirds of the MEF contain sandy outwashes that are overlain with lay loam tills, which are classified as Warba sandy clay loams (fine-loamy, mixed, superactive, and frigid haplic Glossudalfs), Nashwauk sandy loams (fine-loamy, mixed, superactive, and frigid oxyaquic Glossudalfs), or Keewatin fine sandy loams (fine-loamy, mixed, superactive, and frigid aquic Glossudalfs; Sebestyen et al., 2011).

### 2.2 | Soil moisture monitoring network

Percent volumetric soil moisture was measured using a Troxler Series 4300 neutron probe moisture gauge (Troxler Electronic Laboratories, Inc., Research Triangle Park, North Carolina, USA) at a network of 27 sites across the MEF. The neutron probe technique was chosen so

**FIGURE 1** The Marcell Experimental Forest (MEF) is located in north-central Minnesota and has six research watersheds (S1–S6). Three soil moisture monitoring sites were located in each cover type (aspen, hardwoods, and red pine) and topographic position (summit, backslope, and toeslope) combination. Soil moisture was measured using a neutron probe from 2011 to 2013



new soil moisture measurements could be compared with historical soil moisture records at the MEF that date back to 1966 (Dymond et al., 2014, 2015; Sebestyen et al., 2011). These historical monitoring sites are predominately located in ridge aspen stands. The neutron probe works by emitting high energy neutrons from a radioactive source into the soil. These neutrons interact with hydrogen molecules in the soil, which bounce the neutrons back to a counter in the probe. The ratio of neutrons emitted to neutrons returned back to the counter is related to the abundance of hydrogen atoms in the soil, or the volumetric soil water content (Gardner, 1986). Volumetric soil moisture was measured gravimetrically from 0 to 15.2 cm in the soil profile, because moisture measured using the neutron probe technique can lead to spurious measurements due to a loss of neutrons from the soil surface (Brakensiek, Osborn, & Rawls, 1979). Calibration measurements for the soil moisture monitoring network were collected in both dry (October 2012) and wet (May 2014) soil conditions. Neutron probe measurements were collected, and gravimetric moisture analysis and bulk density were determined for each depth. Calibration curves were created for each site, and depth and raw neutron probe measurements were adjusted accordingly.

In June 2011, 25 additional 3.8-cm-diameter aluminium access tubes were installed at the MEF along topographic gradients consisting of a ridge, backslope, and toeslope position. Sites were clustered and replicated within each of three cover types: red pine, aspen, and mixed hardwoods (Figure 1; Table 1). These cover types represent the most dominant upland vegetation types at the MEF. Access tubes were installed to a depth of approximately 300 cm using a compact excavator outfitted with a soil auger. Soil samples were collected from 0 to 15.2 cm and thereafter every 30.2 cm during the installation process and were subsequently analysed for soil texture using the hydrometer method for particle size analysis (Gee & Bauder, 1986). Soils were sandy, with textures ranging from sands to sandy clay loams (Figure 2; Appendix A). Soil moisture measurements were collected bi-weekly at eight measured depths (0–15, 15–46, 46–76, 76–107,

107–137, 137–168, 168–198, and 198–229 cm) at both the historical and expanded soil moisture networks throughout the 2011–2013 growing seasons (approximately May to November). These depths match the original depth increments of 1 foot (30.2 cm) used at the historical soil moisture monitoring sites. Total annual rainfall was lower than average in 2011 and 2013 (727 and 748 mm, respectively), and mean July temperatures were higher than normal in 2011 and 2012 (21 °C and 22 °C, respectively). Instrument error occurred during all three sampling seasons, creating dataset gaps during August 2011, June to early July 2012, and July 2013.

### 2.3 | Conversion to plant-available water

We estimated thresholds at which volumetric soil moisture was no longer available to plants based on soil characteristic curves that relate volumetric soil moisture (%) to soil water potential (MPa); similar methods were used by Breshears et al. (2009). For each soil texture identified within our data, soil water-release curves (Figure 3) were generated by converting volumetric water content to soil water potential (Equation 1; Cosby, Hornberger, Clapp, & Ginn, 1984):

$$\Psi = \Psi_s (\Theta / \Theta_s)^b \tag{1}$$

where  $\Psi$  is the matric potential of the soil in question,  $\Psi_s$  is the “saturation” matric potential,  $\Theta$  is the volumetric moisture content of the soil,  $\Theta_s$  is the saturated moisture content, and  $b$  is the slope of the retention curve.  $\Psi_s$ ,  $\Theta_s$ , and  $b$  are a function of soil texture (Equations 2–4):

$$\Psi_s = -1.58s - 0.63c + 2.17 \tag{2}$$

$$\Theta_s = -14.2s - 3.7c + 50.5 \tag{3}$$

$$b = -0.3s + 15.7c + 3.10 \tag{4}$$

where  $s$  and  $c$  are the percent sand and percent clay fractions, respectively.

**TABLE 1** Site characteristics for the 27 sites in the soil moisture monitoring network at the Marcell Experimental Forest as well as mean plant-available water (PAW) and standard deviation (SD) for 0 to 228 cm in the soil profile.

Site ID	Cover type	Landscape position	Soil texture	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	H'	Mean % PAW (SD)
AB01	Aspen	Backslope	Sandy clay loam	21.3	0.08	6.8 (4.6)
AB02	Aspen	Ridge	Sandy clay loam	21.3	0.98	8.7 (4.6)
AB03	Aspen	Toeslope	Sandy clay loam	16.3	0.77	7.6 (4.2)
AB04	Aspen	Ridge	Sandy loam	20.4	0.85	9.0 (5.7)
AB05	Aspen	Toeslope	Sandy clay loam	30.2	0.67	7.9 (3.8)
AB06	Aspen	Backslope	Sandy clay loam	22.5	0.75	8.6 (4.8)
AB07	Aspen	Ridge	Sandy loam	18.8	0.73	6.2 (5.3)
AB08	Aspen	Backslope	Sandy clay loam	22.3	0.78	9.9 (5.8)
AB09	Aspen	Toeslope	Sandy clay loam	21.2	0.47	5.6 (4.1)
NH01	Hardwoods	Ridge	Sandy clay loam	20.3	0.97	8.6 (6.1)
NH02	Hardwoods	Ridge	Sandy clay loam	31.3	1.62	9. (5.5)
NH03	Hardwoods	Backslope	Sandy loam	22.8	1.11	7.0 (6.1)
NH04	Hardwoods	Toeslope	Sandy loam	21.7	1.03	17.9 (10.6)
NH05	Hardwoods	Backslope	Sandy clay loam	39.8	1.08	11.8 (5.1)
NH06	Hardwoods	Toeslope	Sandy loam	30.3	1.44	15.0 (8.5)
NH07	Hardwoods	Ridge	Loamy sand	35.8	1.92	14.1 (10.6)
NH08	Hardwoods	Backslope	Loamy sand	27.9	0.63	9.4 (8.8)
NH09	Hardwoods	Toeslope	Sandy loam	30.7	1.15	16.6 (10.6)
RP01	Red pine	Ridge	Sandy loam	25.3	0.15	5.2 (4.5)
RP02	Red pine	Backslope	Sand	53.6	0.50	4.3 (3.2)
RP03	Red pine	Backslope	Sand	45.6	0.44	5.8 (5.5)
RP04	Red pine	Toeslope	Sand	28.1	0.69	8.9 (4.5)
RP05	Red pine	Ridge	Sand	49.5	0.62	5.5 (4.3)
RP06	Red pine	Toeslope	Sand	46.0	0.65	4.2 (3.1)
RP07	Red pine	Ridge	Sand	39.6	0.00	5.7 (4.6)
RP08	Red pine	Backslope	Sand	43.0	0.76	10.6 (4.9)
RP09	Red pine	Toeslope	Sandy loam	44.2	0.30	6.6 (6.6)

The permanent wilting point is the soil water potential at which water is held so tightly by the soil matrix that it is unavailable to plants; the permanent wilting point is commonly estimated as  $-1.5$  MPa. Using this value as a threshold, we determined the volumetric water capacity at which soil water becomes limiting to plant growth for each soil texture (Table 2). In situ volumetric soil moisture measurements were subsequently converted to plant-available water by subtracting the volumetric water threshold for the designated soil texture from the measurement for each location, depth, and time. In the cases where the threshold value exceeded soil moisture measurements, the plant-available water was set to zero.

Pedo-transfer functions, such as the one used above, are commonly used to convert soil water content to soil water potential based on soil texture (e.g., Cosby et al., 1984; Saxton, Rawls, Romberger, & Papendick, 1986; Schaap, Leij, & van Genuchten, 2001; van Genuchten, 1980). Many of these methods use soil organic carbon and bulk density in the transformation (Saxton, Rawls, Romberger, & Papendick, 1986; Schaap et al., 2001; van Genuchten, 1980); however, we did not have these measurements throughout our soil profile at each site. Therefore, our pedo-transfer functions may be prone to additional error associated with omitting these measurements.

## 2.4 | Inter- and intra-site dynamics

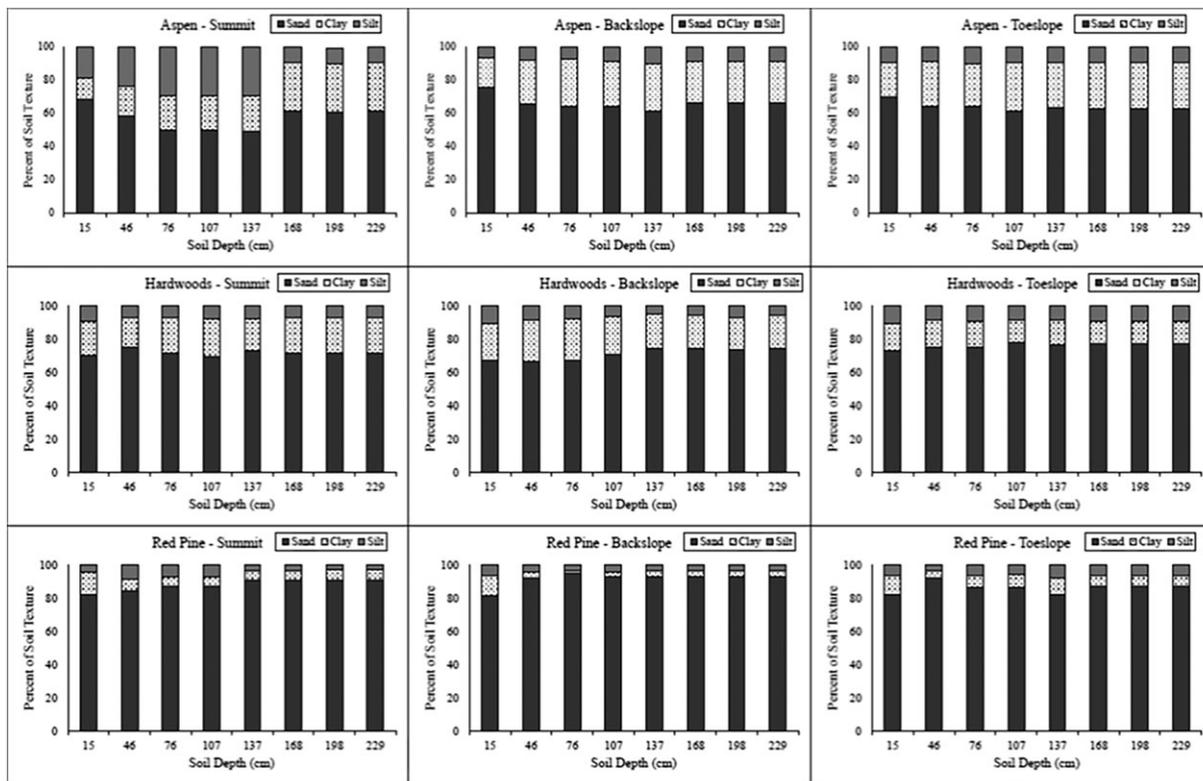
Comparisons among different sites were done using data calculated from the 27 plots within the soil moisture monitoring network from 2011 to 2013 (Table 1). In addition to soil moisture measurements, 1/20th ha circular plots were established around the access tubes at each site. Within each plot, slope and aspect were recorded. Tree species, height, diameter at breast height (DBH), crown class, azimuth, and distance from plot centre were collected for all within plot trees greater than 10 cm DBH. Stand-level basal area (m<sup>2</sup> ha<sup>-1</sup>) was calculated to determine the differences in tree density between each plot (Equation 5).

$$BA = \sum \frac{0.00007854^* DBH^2}{A} \quad (5)$$

where  $BA$  is the stand-level basal area in m<sup>2</sup>,  $DBH$  is the diameter at breast height in cm, and  $A$  is the plot area in ha. Tree species diversity at each plot was calculated as Shannon's Diversity Index ( $H'$ ):

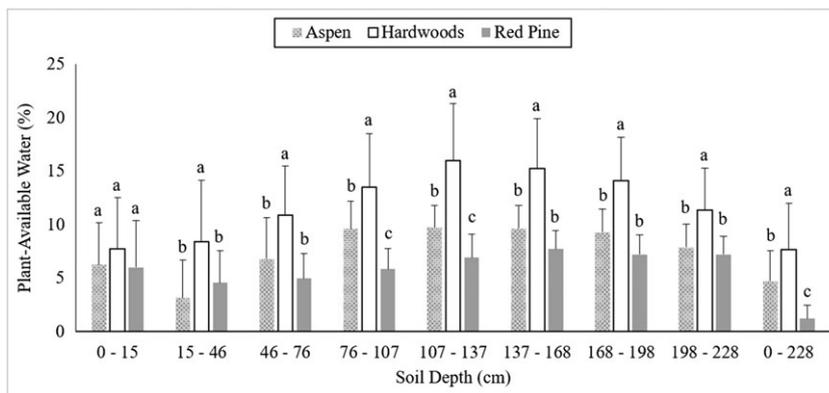
$$H' = \sum_{i=1}^N p_i \times \ln(p_i) \quad (6)$$

where  $N$  is the number of species within a plot and  $p_i$  is the relative proportion of each species by number of stems.



**FIGURE 2** Percent sand, clay, and silt fractions for each depth as averaged across the three cover types and topographic positions at the Marcell Experimental Forest

**FIGURE 3** Differences between plant-available water for three cover types at different depths within the soil profile at the Marcell Experimental Forest. Different letters denote significant differences in plant-available water within each depth increment ( $\alpha = .05$ )



**TABLE 2** Volumetric soil water content thresholds (wilting point) based on soil moisture characteristic curves generated using Equation 1

Soil texture	Mean sand fraction (%)	Mean clay fraction (%)	Volumetric soil water content threshold (%)
Sandy clay loam	60.0	27.0	15
Sandy loam	67.5	10.0	8
Loamy sand	83.5	4.0	4
Loam	42.5	18.0	14
Sand	93.0	2.0	3

### 2.5 | Analyses

A Tukey test of means ( $\alpha < .05$ ) was used to determine significant differences in plant-available water across the different cover types

and topographic positions. The relationship with landscape-level parameters (cover type, topographic position, dominant species, soil texture, BA, and H') on plant-available water at the eight measured depths (0–15, 15–46, 46–76, 76–107, 107–137, 137–168, 168–198, and 198–229 cm) as well as across the entire soil profile (0–229 cm) was analysed with repeated measures analysis of variance using PROC MIXED in SAS Version 9.0 (SAS Institute Inc., Cary, North Carolina, USA). We used an unstructured covariance matrix of the gamma-distributed data, which allows for the covariance to be different for each term. Percent slope and aspect did not vary enough across the sites to be included in the analysis. Analyses of variance were run for each depth with plot as a random variable to understand landscape-level dynamics both across and within different cover types.

### 3 | RESULTS

#### 3.1 | Vegetative differences in plant-available water

When averaged across topographic positions, mean plant-available water varied with vegetation and with depth (Figures 3 and 4). Across the soil profile, plant-available water was significantly higher under the hardwoods (12%), followed by the aspen (8%) and red pine (5%) cover types (0–228.6 cm depth). This pattern held true from 15 cm depth throughout the soil profile (Figure 3). From 0 to 15 cm, there was no significant difference in plant-available water across the three cover types; mean plant-available water was 6%, 8%, and 6% for the aspen, hardwood, and red pine cover types, respectively. From 15 to 76 cm depth, aspen and red pine plant-available water was similar, and these sites were significantly drier than the hardwood sites. Both the aspen and hardwood sites had low plant-available water in the upper 46 cm of soil, with plant-available water more abundant from 46 to 198 cm in the profile. Plant-available water decreased for both of these cover types below 198 cm in the profile. Plant-available water in the red pine stands was extremely low across time and depth and the low numbers made it difficult to identify biologically meaningful variation in soil moisture.

#### 3.2 | Topographic differences in plant-available water

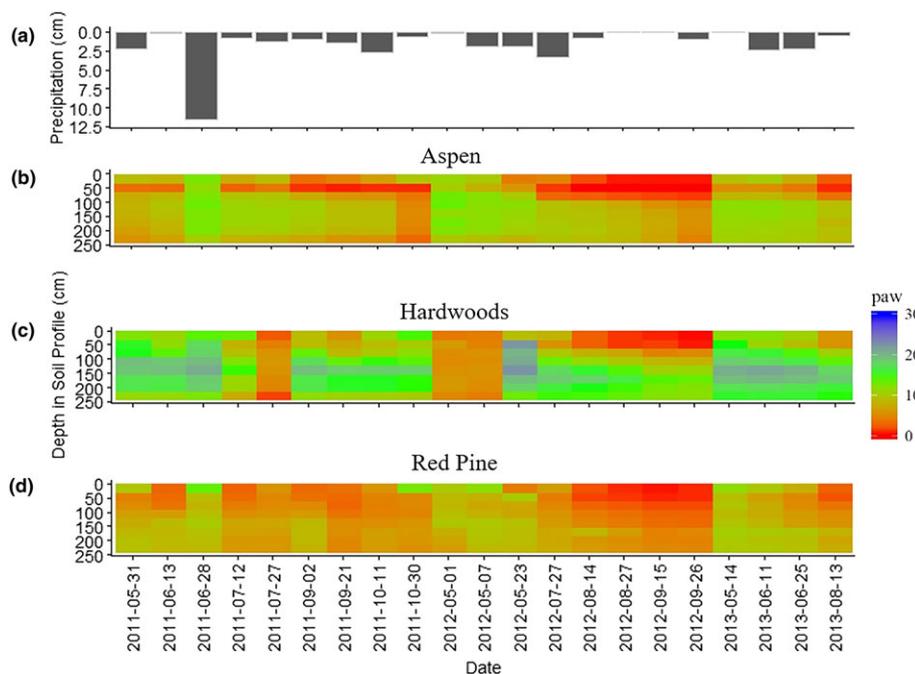
When averaged across the entire soil profile, toeslopes were wetter (mean plant-available water = 10%) than ridges and backslopes (mean plant-available water was 8%; Figure 5). However, there were no significant differences in plant-available water across the topographic gradient from 0 to 76 cm in the soil profile. Differences began to parse out at soil depths >76 cm, with toeslopes generally containing more

plant-available water than the ridges and backslopes. The ridge and toeslope topographic positions show decreasing trends in soil moisture throughout the growing season, with small pulses of increased plant-available water seen at sampling times when there was higher rainfall in the week prior to sampling (Figure 6). The exception was the backslope position, which had low plant-available water at the beginning of 2012, followed by a period of wetter soils that gradually dried out toward the end of the year (Figure 6).

#### 3.3 | Landscape drivers of plant-available water

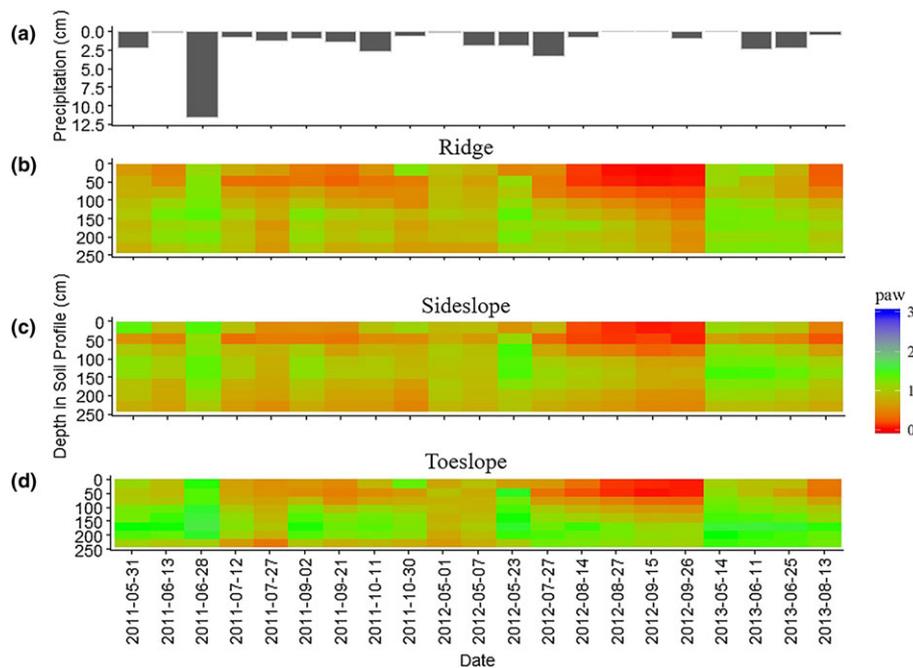
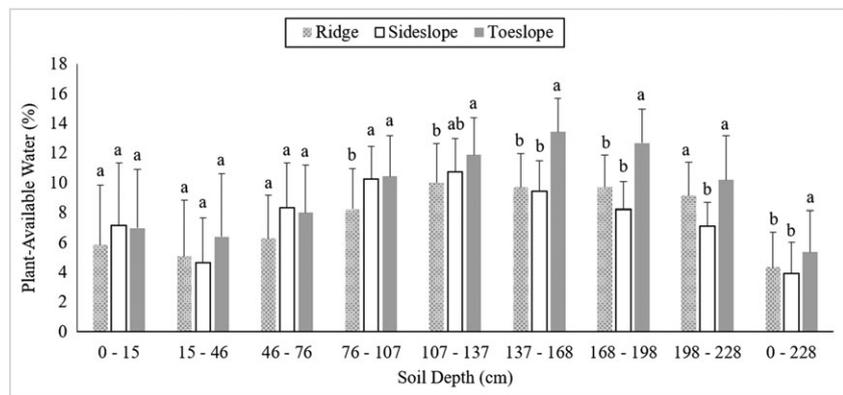
When examined across the entire dataset, plant-available water was found to be a function of the cover type, time, depth, and soil texture (Table 3). Topography was not a significant driver of plant-available water (Figure 7), nor were the stand basal area, dominant species in the stand, or Shannon's  $H'$  (plots not shown). Similar to the Tukey's tests, the mixed model results show that topographic differences in plant-available water are more substantial at deeper soil depths (Figure 7). Plant-available water also increased with increasing soil depth across all three cover types, with the effect of soil depth being less important for red pine stands (Figure 7).

Mixed models were also run for different seasons to determine if the significant landscape drivers of plant-available water were consistent over time. Three seasons were grouped into 3-month blocks: spring (March, April, and May), summer (June, July, and August), and fall (September, October, and November). The model results were similar to the model for the entire dataset, with cover type, time, depth, and soil texture all being significant factors in determining plant-available water. Although the individual measurement of plant-available water matters, the larger landscape-level patterns remain relatively consistent regardless of the season (Figure 8).



**FIGURE 4** (a) Hyetograph of total precipitation for the 1 week prior to taking soil moisture measurements. (b–d) Heat graphs of plant-available water throughout the soil profile for the three cover types sampled at the Marcell Experimental Forest

**FIGURE 5** Differences between mean plant-available water across topographic gradients at different depths within the soil profile at the Marcell Experimental Forest. Different letters denote significant differences in plant-available water within each depth increment ( $\alpha = .05$ )



**FIGURE 6** (a) Hyetograph of total precipitation for the 1 week prior to taking soil moisture measurements. (b–d) Heat graphs of plant-available water (PAW) throughout the soil profile for the three topographic positions sampled at the Marcell Experimental Forest

**TABLE 3** Significant variables describing plant-available water at the 27 forested sites at the Marcell Experimental Forest

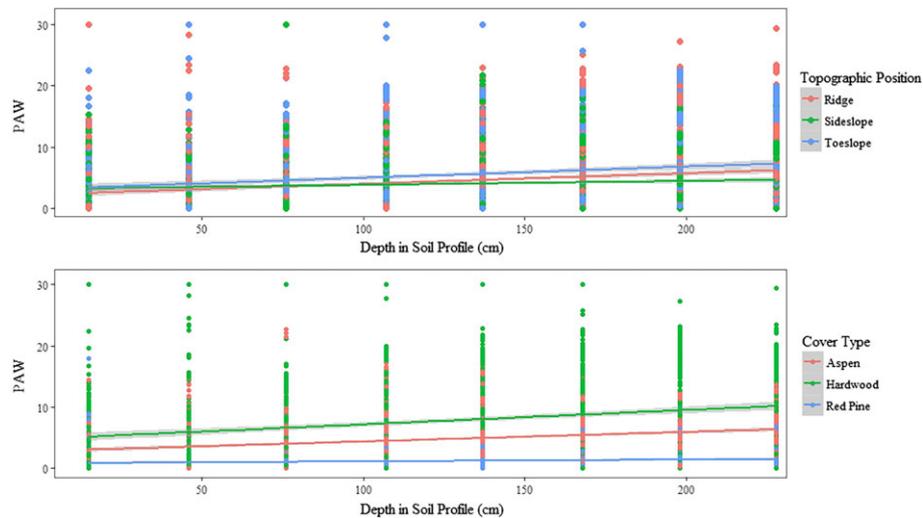
Variable	F statistic	Degrees of freedom	p value
Cover type	13.22	2	<0.0001
Time	52.24	20	<0.0001
Depth	88.58	7	<0.0001
Soil texture	41.91	4	<0.0001
Cover*time	20.97	40	<0.0001
Cover*depth	17.22	14	<0.0001
Depth*texture	14.05	22	<0.0001
Cover*time*depth	1.61	420	<0.0001

## 4 | DISCUSSION

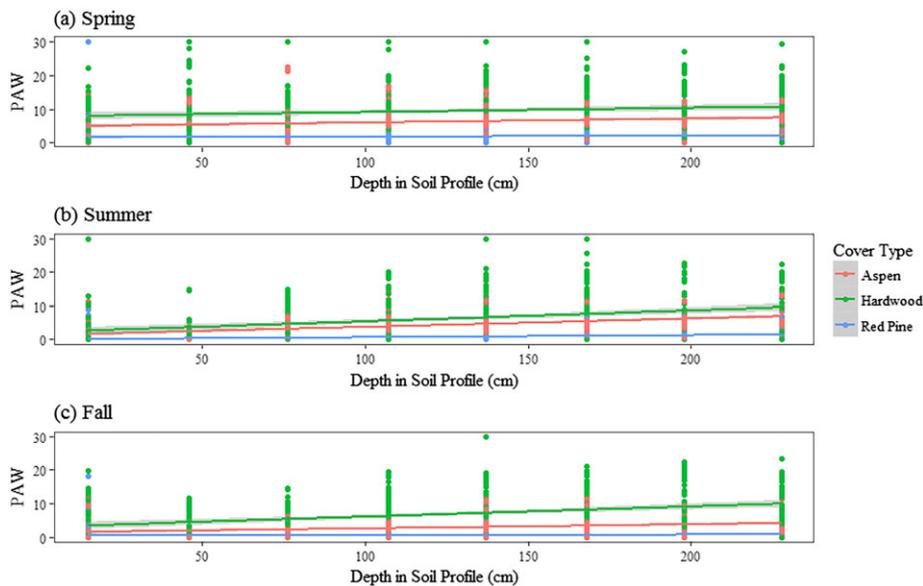
### 4.1 | Absence of topography in driving plant-available water

Previous studies have found that topography can significantly influence soil moisture (Burt & Butcher, 1985; Litaor, Williams, &

Seastedt, 2008; Tromp-van Meerveld & McDonnell, 2006; Voepel et al., 2011). We found slight differences in plant-available water across topographic positions, but only at depths greater than 76 cm in the soil profile. In general, toeslope positions were wetter than ridges and backslopes, which may demonstrate the importance of texture and rooting depth on determining plant-available water. At shallower layers, water either percolates through the soil matrix or is taken up by plant roots, regardless of initial soil moisture conditions. The result is a similar level of plant-available water across all topographic positions, at least in soils <76 cm deep. Root access and thus plant-water uptake decreases with depth, leaving more plant-available water that is driven by topographic lateral flow pathways that may develop as a result of differences in surficial soil texture. Although large differences in soil texture with depth were not evident in the data averaged across our sites (Figure 2), some specific sites did have impeding clay layers that may have influenced shallow subsurface pathways. Additionally, evidence of interflow above the impeding clay layers has been previously documented at the MEF (Verry & Timmons, 1982).



**FIGURE 7** Bivariate plots of plant-available water (PAW) across soil depth for the different topographic positions (top) and cover types (bottom). Linear regression lines with 95% confidence intervals are shown. The close proximity of the lines in the top plot suggests that the effects of topography on PAW are not significantly different between topographic positions. In contrast, PAW was significantly different across the three cover types, and this difference remained significant at each soil depth



**FIGURE 8** Bivariate plots of plant-available water (PAW) across soil depth by cover type for (a) spring (March, April, and May), (b) summer (June, July, and August), and (c) fall (September, October, and November). Linear regression lines with 95% confidence intervals are shown. Cover type was a significant factor in describing PAW, regardless of the season

Despite small differences in plant-available water with topographic position deep in the soil profile, topography was not a significant driver of plant-available water in our mixed model. Elevations at the MEF only range 20 m, and although these differences may be critical in distinguishing peatlands from the surrounding uplands, it is likely that both the horizontal and vertical distances between ridges and toeslopes were not great enough to generate significant differences in plant-available water as might be expected in steeper terrain.

#### 4.2 | Plant-available water across different cover types

Soil moisture levels often co-vary with vegetative characteristics (Adams et al., 1991; Francis et al., 1986; Hollinger & Isard, 1994), and

our results corroborate these findings, at least in shallow soil layers. Comparisons between cover types showed that at depths greater than 15 cm in the soil profile, plant-available water was highest at hardwoods sites, followed by aspen and red pine sites. The differences between aspen and hardwoods sites was not anticipated, given that the hardwoods sites had greater basal area (Table 1), which could lead to greater evapotranspiration rates and depleted plant-available water. The hardwoods and aspen sites had similar soil textures (Table 1), and no significant differences in volumetric water content were found at any depth (data not shown). These results may demonstrate that aspen stands are more effective at accessing soil water than hardwoods stands, particularly in deeper soil layers. Quaking aspen have been known to develop extensive heartroot systems that can reach depths of 2.9 m in sandy loam soils (Gifford, 1966; Perala, 1990) and may also

translocate water and nutrients via clonal integration (Stuefer, Gómez, & van Mólken, 2004). Additionally, aspen is unique in that it has photosynthetically active bark, which may lead to higher plant-water use (Foote & Schaedle, 1978; Grant & Mitton, 2010).

Throughout the study period, red pine had significantly less plant-available water than the hardwoods and aspen sites. The red pine sites were almost all classified as sands, which have higher infiltration rates and lower water-holding capacity (Saxton, Rawls, Romberger, & Papendick, 1986) than the hardwoods and aspen sites, which had higher clay contents. Plant-available water under the red pine canopies was lower from 15 to 107 cm than at the soil surface (0 to 15 cm) and deeper depths. The lower plant-available water in these depths might be due to increased uptake by plant roots in these soil layers. Red pine can develop extensive root systems, but lateral roots are typically most prolific in the upper 10–46 cm of the soil profile (Rudolf, 1990), and anecdotally, we did not see many red pine roots extending beyond 46 cm during sampling.

### 4.3 | Temporal dynamics in plant-available water

Across the MEF, plant-available water was highly influenced by the time that the measurement occurred, and the interaction between time and site characteristics in relation to plant-available water highlights the complexity of plant–soil water dynamics (Table 3). Percent soil moisture was highest in the early spring, followed by a long drawdown during the summer months. Small pulses of plant available water were evident across the record; in 2011, 7.1 cm of rain had fallen 2 days prior to the June 28th measurement. The May 2012 measurement occurred in the middle of a 36-hr event that resulted in 4.3 cm of precipitation. In early 2012, wet conditions were evident in the aspen and red pine sites, yet northern hardwoods sites were dry early in the growing season and did not show signs of wetness until later in the year.

Despite having a coarse temporal resolution, there was evidence of recharge of spring soil moisture followed by a summer drawdown (Figures 4 and 6). These soil moisture dynamics, which occurred under all forest types, are common for soils in the upper Midwestern United States (Baker, Nelson, & Kuehnast, 1979). Temporal variability was the highest in the spring and for the hardwoods cover types. The hardwoods sites also exhibited the highest species diversity (Table 1), which could lead to larger variability among sites and across depths. Additionally, the hardwoods sites may be experiencing hydraulic redistribution of deep soil water (Dawson, 1993), although verification of this phenomenon at the MEF would require further testing.

### 4.4 | Implications for vegetation

Plant-available water reached low levels during the growing season, regardless of cover type or topographic position. Red cells (Figures 4 and 6) indicate times and depths in which plant-available water was close to or exceeded the pre-determined threshold where volumetric soil moisture becomes limiting to plant growth (Table 2). Thus, these times and depths indicate moisture levels where plants may experience some level of moisture stress. In the aspen sites, plant-available water was continuously low in the upper 50 cm of the soil profile. For red pine sites, plant-available water was low throughout the entire profile,

regardless of time of year. Our interpretation of plant-available water is based upon our threshold values (Table 2), so they are not perfect representations of the true amount of water availability in a system. Although we saw no evidence of plant-water stress among the different cover types (Dymond et al., 2015), our results are in-contrast with those that have been modelled. In a simulation of soil moisture in northern Minnesota, Pastor and Post (1986) found that levels rarely dipped below wilting points during the growing season. However, it is likely that soil moisture dynamics in the region have changed due to increased warming over the past three decades (Dymond et al., 2014).

The low levels of plant-available water under red pine and aspen stands may have implications for regeneration of these species. Red pine seeds need a suite of environmental conditions that are favourable for germination, such as moderate-severity fire, temperatures ranging from 21 °C to 30 °C, and precipitation exceeding 100 mm in May, June, and July (Cheyney, 1942; Rudolf, 1990; van Wagner, 1970). Quaking aspen need considerably moist soils to germinate via seed, as a water potential exceeding  $-0.4$  MPa is required (Perala, 1990). This water potential is close to our designated plant-available-water threshold capacity for loamy sands and sandy loams ( $-0.7$  MPa for both textures). Therefore, plant-available water in the upper soil horizon might not be sufficient enough to culminate in aspen regeneration via seed at the MEF (Figure 4). However, aspen regenerate via clonal ramets following a disturbance event, thereby increasing its chances of propagating despite climate extremes.

Recent dieback and mortality of quaking aspen has been well-documented across its North American range (Michaelian et al., 2010; Worrall et al., 2008), with studies attributing the tree loss to drought and climatic effects (Worrall et al., 2013). More recently, studies have shown that the linkage between climate and tree growth is dynamic over time, with periods of increased stress on trees following drought or insect outbreaks (Itter, Finley, D'Amato, Foster, & Bradford, 2016). Given increasing temperatures and decreasing soil moisture levels at the MEF (Dymond et al., 2014), plant-available water levels may drop even further in the region. An increase in dry periods and thus low water availability could have profound impacts on ecosystem productivity and health in the region (Briggs & Knapp, 1995; Graumlich, 1993). This is especially true given the relationship between annual tree growth and water availability. Dymond et al. (2015) found that red pine productivity increased with high levels of June and July potential evapotranspiration, which is driven by high summer temperatures. In general, aspen productivity declined with warm July temperatures and needed high precipitation in the fall prior to the growing season to sustain growth the following year (Dymond et al., 2015). Some studies have suggested that warmer temperatures are causing an increase in plant water demand, yet the impacts of a warming climate on tree productivity remain uncertain (Jung et al., 2010; Pastor & Post, 1988; Robock et al., 2000).

## 5 | CONCLUSIONS

Topography is usually a key driver in soil moisture dynamics. However, in the northern Great Lakes region, where there generally

is low topographic relief, we found little evidence that topography drives plant-available water over time. Instead, we found that plant-available water was related to vegetative cover type, soil texture, depth, and time of the measurement. Average plant-available water was variable across depth and time but was generally lowest for red pine, followed by aspen and hardwoods cover types. During the 3-year study period, plant-available water reached levels that could be considered detrimental to plant growth, particularly for red pine and quaking aspen species, though we did not observe any evidence of plant water stress. Given that tree growth is connected to climate and water availability, our results have important implications for forest productivity in the region. Soil moisture levels at the MEF have been decreasing over time, presumably due to an increase in temperatures that are driving potential evapotranspiration (Dymond et al., 2014). If these trends continue, soil moisture or plant-available water may limit productivity of forests in the region, leading to increased susceptibility of the forests to disease, mortality, and fire or possibly a shift from forested ecosystems to more drought-resistant grassland species.

## ACKNOWLEDGEMENTS

Funding for this research was provided by the USDA Forest Service Northern Research Station. We would like to thank Laura Nelson, Matt Hoveland, and Paul Klockow for their assistance in field and laboratory work, as well as Deacon Kyllander for his help in repairing and maintaining the neutron probe. We would also like to thank the anonymous reviewers who have helped to improve the manuscript. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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**How to cite this article:** Dymond SF, Bradford JB, Bolstad PV, Kolka RK, Sebestyen SD, DeSutter TM. Topographic, edaphic, and vegetative controls on plant-available water. *Ecohydrology*. 2017;e1897. <https://doi.org/10.1002/eco.1897>

## APPENDIX A

## MEAN PERCENT SOIL SIZE FRACTIONS FOR THREE TOPOGRAPHIC POSITIONS (RIDGE, SIDESLOPE, AND TOESLOPE) AND COVER TYPES (ASPEN, NORTHERN HARDWOODS, AND RED PINE) AT DIFFERENT DEPTHS FOR 27 SITES AT THE MARCELL EXPERIMENTAL FOREST

Cover type	Soil depth	Ridge			Sideslope			Toeslope		
		Sand	Clay	Silt	Sand	Clay	Silt	Sand	Clay	Silt
Aspen	0-15	69	13	18	76	18	6	70	21	9
	15-46	58	18	23	65	27	8	64	27	9
	46-76	50	21	29	64	28	7	64	26	10
	76-107	50	21	29	64	27	9	62	29	10
	107-137	50	21	29	62	29	10	63	27	10
	137-168	61	29	9	66	25	8	63	28	9
	168-198	61	29	9	66	25	8	63	28	9
	198-229	61	29	9	66	25	8	63	28	9
Northern hardwoods	0-15	70	21	9	67	22	11	73	16	11
	15-46	75	18	7	67	25	8	75	16	9
	46-76	71	22	7	67	25	8	75	16	9
	76-107	69	23	8	71	23	7	78	14	9
	107-137	73	20	8	74	20	5	77	15	9
	137-168	72	21	7	74	20	6	77	14	9
	168-198	72	21	7	73	20	7	77	14	9
	198-229	72	21	7	74	20	6	77	14	9
Red pine	0-15	82	14	4	82	12	7	82	11	6
	15-46	84	7	9	92	4	4	92	5	4
	46-76	87	6	7	95	2	3	87	7	6
	76-107	87	6	7	93	3	4	86	8	6
	107-137	90	6	4	93	4	4	82	10	8
	137-168	91	6	3	93	4	4	87	7	6
	168-198	91	6	3	93	4	4	87	7	6
	198-229	91	6	3	93	4	4	87	7	6