IMPACTS OF MANAGEMENT ON FOREST RESPONSE TO CLIMATE VARIABILITY IN OREGON'S WESTERN CASCADES

by

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THESIS ABSTRACT

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Climate projections suggest increased droughts for the PNW region in the nearfuture, which could lead to forest die-offs. Studies indicate that drought stress and competition is reduced by forest thinning, but that effect has yet to be tested in long-term experiments. Here I examine tree rings, soil properties, streamflow, and satellite data to determine sensitivity to climate in 45 forest stands distributed across three watersheds with differing styles of management at the HJ Andrews Experimental. Specifically, I focus on three questions: First, what are the effects of management on the structure and function of Douglas-fir forests? Second, how does ecosystem function scale from dominant Douglas-fir trees to the entire watershed? Third, what are the impacts of management on forest productivity and water-yields of Douglas-fir forests? My goal is to provide mechanistic understanding of how interactions between climate and management affect the overall productivity and water use of PNW forests.

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CHAPTER I

INTRODUCTION

Climate projections suggest increased droughts for much of the Pacific Northwest region in the near-future (Mote & Salathé, 2010), which is expected to lead to large-scale forest die-offs (Anderegg et al., 2015). A recent study that observed an increased variability in carbon suggests that forests of the Pacific Northwest are turning from carbon sinks to carbon sources due to the outpacing of changes in respiration compared to those in photosynthesis (Baldocchi et al., 2018). Thus, in order to grasp the relationship of forest management and climate variability a holistic approach is needed, one that integrates spatio-temporal data in general, and in particular those related to the interactions between soils, plants, and the atmosphere.

Management practices that allow for increased stand density have been observed to intensify the impacts of drought by increasing tree mortality (Safford et al., 2012). Other management practices, such as forest thinning are known to reduce long-term stressors such as water competition, as well as increase tree resilience and resistance to drought (Navarro-Cerrillo et al., 2019). Thinning has therefore become a common forest management practice for minimizing drought vulnerability (McDowell et al., 2008), but few previous studies have considered the long-term effects of said practice upon tree growth sustainability and ecosystem health. An ecosystem is generally accepted as being healthy if there is stability in ecosystem services provided for the benefit of society, implying an ability to maintain its structure and function over time while external stressors occur. (Kruse, 2018). Fisher et al., argue that ecosystem services are the "aspects of ecosystems utilized to produce human well-being", which are intended to include ecosystem structure and functions (2009). Old growth forests have proven to be great examples of healthy ecosystems, where, despite the global-scale cooling effect observed from forests, Frey et al., found that subtle differences in forest structure moderate under-canopy temperature regimes. Thermal buffering was found to be reduced in single-species, even-aged plantations when compared to old growth forests. These older forests with increased structural and biological diversity have shown their ability to buffer climate and reduce inter-annual variability of carbon fluxes compared to younger, managed forests (2016). Given that these structural characteristics have the ability to diminish the effects of temperature increases, land management will play a critical role on the magnitude of their impacts upon biodiversity. Thus, in order to grasp the relationship of forest management and climate variability a holistic approach is needed, one that integrates spatio-temporal data in general, and in particular those related to the interactions between soils, plants, and the atmosphere.

The alterations originating from forest management practices have been observed in not only species and structural diversity, but also ecophysiological traits (Herbst et al., 2015). Water yield, a common ecophysiological trait, is typically calculated as the amount of precipitation minus evapotranspiration, where subdivision of precipitation is influenced by vegetation. A recent synthesis of streamflow response to disturbance has suggested that a decrease in water yield is more likely to occur following non-stand replacing disturbances than following stand-replacing disturbance. This decrease in streamflow is thought to be due to the increase in evapotranspiration (ET) postdisturbance, which is caused by increased transpiration of understory vegetation, increased sublimation from snowpack, or increased soil evaporation from higher amounts

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of radiation penetrating the canopy (Goeking & Tarboton, 2020). This leads to the impression that characteristics of vegetation post-disturbance are what determine water yield responses. A study by Perry and Jones found that in the Pacific Northwest, summertime streamflow was initially higher after conversion from mature forests to timber plantations, but then became lower in comparison after 15 years postharvest with the potential to remain low for multiple decades (2017). Precipitation regimes also play an important role when it comes to control on streamflow. Interannual variability in wetter ecosystems have the strongest influence upon streamflow, whereas dry regions have demonstrated that prediction strength is dominated by vegetation (Burt et al., 2015). These suggestions become less straightforward in Mediterranean climates, such as Oregon's Cascades, exhibiting cool and wet winters along with hot and dry summers. Research at HJ Andrews Experimental Forest, near Blue River OR, has revolutionized our understanding of long-term processes by creating watershed-scale experiments that provide opportunities to close gaps in the knowledge of carbon-water relations. It remains unclear, however, what the impacts of increased warming and variability of precipitation will be on ecosystem health in a heterogeneously managed landscape within the Pacific Northwest.

The present study builds on previous research at HJ Andrews Experimental Forest, as part an effort allowed by the LTER (Long-Term Ecological Research) Network. Several ecological surprises have been identified at these sites (Vucetich et al., 2020), including processes that occur very slowly on the order of decades to centuries, as well as dynamic processes that control carbon-water relations from trees to landscapes. By leveraging the vast data sources and long-established experimental treatments at HJ Andrews, this study asks to what degree the role of forest management and climate control the structure, productivity, and water use of individual trees and watersheds. Our overarching hypothesis is that a tradeoff between photosynthesis and water loss via transpiration drives spatial and temporal variation in landscape carbon accumulation and water yields. This hypothesis is supported by empirical observations as well as biological scaling theory which predicts concerted shifts in productivity from the scale of dominant trees and ecosystem level (Maxwell & Silva, 2020). Generally, we expect to find a significant relationship between certain climatic variables and productivity variables, such as annual temperatures, precipitation, tree growth, stand structure, and streamflow. The structural limits of the carbon-water tradeoff are well established for several dominant tree species, but it remains difficult to use those limits to guide forest management. Specifically, this study was designed to answer three questions: First, what are the effects of forest management (clearcut, thinned, control) on the structure and function of Douglas-fir forests? Second, how does ecosystem function response from dominant trees scale to the entire watershed? Third, what are the impacts of forest management upon water-yield of douglas-fir forests measured across scales (i.e. trees to watershed)? To answer these questions we examined 27 soil profiles (9 per watershed, 0-60 cm depth), 45 tree-ring chronologies from dominant trees (15 per watershed) collected along a replicated topographic gradient; combined with climatic, hydrologic, and remotely-sensed data (Normalized Difference Vegetation Index (NDVI) and Normalized Difference Wetness Index (NDWI)). We expected thinning to increase watershed productivity and reduce the variability of tree growth by decreasing competition for water and nutrients, as well as mitigating summer drought. We also expected the control

watershed to promote a stable positive growth trend, while also limiting variability and summertime deficits in streamflow. Finally, we expected the clearcut watershed to have lower levels of productivity, increased variability, but low water-use efficiency (WUE). Our results bring new insights on the sustainability of increased growth found in managed plantation stands, suggesting that trees in thinned or clearcut areas, even when possessing higher productivity, are less resilient to climate variability than typical oldgrowth stands.

CHAPTER II

METHODS

Study Site

The area of study is within HJ Andrews Experimental Forest near Blue River, OR. First established as a US Forest Service Experimental forest in 1948, HJ Andrews is home to 10 experimental watersheds. The Andrews Forest became a member of the National Science Foundation's Long-Term Ecological Research Program in 1980. According to the LTER website, the Andrews Forest is largely characteristic of the rough mountainous landscape of the Pacific Northwest and contains an abundance of examples of the region's conifer forests and associated wildlife and stream ecosystems (LTER, 2019). The experimental watersheds have undergone various forest management methods over the years and three plots were sampled in this study, all of which experienced a stand-replacing wildfire in the 1850's and are dominated by Douglas Fir (*pseudotsuga menziesii*). See **Figure 1** for a map of HJ Andrews with labeled watersheds and meteorological stations.

Watershed 6 was 100% clear-cut in 1974, 90% of logs were yarded uphill by a high-lead cable system, and the remaining 10% was yarded by tractor. The logging residue was broadcast burned in 1975 and the watershed was planted with Douglas fir seedlings in 1976. A road was constructed in 1976 that makes a traverse through watershed 6 into watershed 7. Watershed 6 will be referred to as the clearcut watershed throughout this research. Watershed 7, or the thinned watershed, was shelterwood cut in 1974, where approximately 60% of basal area was removed and 30 to 40 trees per acre

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Figure 1. Map of HJ Andrews experimental watersheds with sampling scheme indicating the approximate distribution of 15 forest stands sampled in watersheds WS06, WS07, WS08 (45 stands total) and context map adapted from *andrewsforest.oregonstate.edu*.

were left as overstory. Logs were tractor logged above the road and cable logged below the road. A broadcast burn took place below road in 1975, and district planting occurred in 1976, while the rest of the larger canopy was removed in 1984. In 2001 this watershed was thinned to 14 foot spacing, leaving 220 trees per acre. Watershed 8, or the control watershed, is the undisturbed control. No significant difference of basal area was found between watersheds 6, 7, or 8 before treatment. All three watersheds are within close proximity to each other, with similar aspect and slope. Figure 2 exhibits images of each watershed along with LiDAR profiles, giving an idea of the structural difference between management histories. Soils are derived from deep andesitic landslide deposits, which make up approximately 75% of the total area in watersheds 6, 7, and 8. Soil texture is



Max height = 78 m, profile length = 200 m Max height = 28 m, profile length = 160 m Max height = 32 m, profile length = 160 m **Figure 2.** Forest Management types with LiDAR profiles created from the center of each watershed where color indicates elevation class. LiDAR data accessed through NOAA, captured in 2008 and plotted using ArcMap version 10.5. Photos taken by Michael Farinacci (2019).

described as gravelly loam to sandy gravelly loam with gravel content ranging from 5 to 20% by volume (Dyrness and Hawk, unpublished).

Climate and hydrologic data collection

All climate data was obtained from a meteorological station within HJ Andrews, or PRISM. Two meteorological stations in particular have been active since 1957 at HJ Andrews giving daily averages of ambient temperature and total precipitation, and streamflow gauges have collected daily values of streamflow for each watershed since the 1960's. The Climatic Station at Watershed 2 (CS2MET; -122.249, 44.214735) was used for ambient temperature and total precipitation and was chosen because it contains the most complete record for both variables. The PRISM data used comes from the PRISM Climate Group (Oregon State University) where climate data is collected from a multitude of climate networks; resulting datasets incorporate numerous modeling techniques and are available for the public in various spatial and temporal resolutions. This research project utilizes regionally interpolated temperature and precipitation data from PRISM in order to compare to the records from HJ Andrews for statistical analysis. This regional data were also used to fill in gaps in the temperature record measured at HJ Andrews, where a significant relationship was found between the modeled data and actual measured. Streamflow data was measured from gauges collecting real-time data from the bottom of each watershed. The streamflow gauge at the thinned watershed did not collect any data from 1988 through 1994 due to malfunctioning equipment. A simplified version of a conceptual model for the fluxes involving moisture storage reservoirs in forested basins from Jones & Post is used for this study (2004). The model in this case assumes groundwater flux to be zero, and precipitation includes both rain and snowfall. Therefore, with the utilization of the assumptions mentioned and the fact that this study examines three watersheds with similar geological conditions, evapotranspiration (ET) can be meaningfully estimated by converting streamflow values from cubic feet per second into mm per month and subtracting precipitation. Streamflow in this case can be defined as volume per second that has been corrected for area, therefore putting it in the same unit as precipitation, or mm per month. The equations below were used for conversion of streamflow units and estimating evapotranspiration:

Equation 1:

Streamflow in mm = $(Q(cfs) * 0.0283168(ft3 to m3) * 1000(m to mm) *86400(seconds in a day) * length of days in month of observation) / Area of watershed (m^2)$

Equation 2:

Evapotranspiration = Precipitation – Streamflow \pm Groundwater (0)

Sampling design

The sampling design of this study was intended to create three transects of 100 m in length at different elevations within each watershed, as seen in the top left of **figure 1**. Transects were sampled for soil at three locations, or plots, at the middle and the two ends. Soil profiles were sampled at three depths at each sample plot, 0-20 cm, 20-40 cm, and 40-60 cm, for a total sample number of 27 per watershed. In the case of the thinned watershed, only 25 samples were collected as the lowest depth increment was inaccessible. The same transects were used to sample Douglas-Fir trees, with 5 trees sampled along each transect leading to 45 total samples. Tree-cores were collected at 1.5 meters aboveground using a wood Pressler borer. Tree-cores and soil samples were all collected between June and November 2018. At each soil profile, hemispherical photos were taken using a Nikon Coolpix 4500 camera with a Nikon FC-E8 181° hemispherical lens on a north-oriented level tripod 1.5 m above the ground. Photos were processed using Gap Light Analyzer to calculate stand-level Leaf Area Index (LAI), integrating at the 60 degree zenith angle (Frazer, 1999). LAI, in this case, excluded wood and focused only on the green portion of the canopy (see table 1 for average LAI and other stand characteristics).

Soil sample processing

The soil samples were dried at 50 °C for 72 hours until a steady dry weight was reached. Soils were then sieved to <2 mm, while subsamples of each soil were ground to a fine powder using a roller mill to be prepared for analysis of total carbon (C) and nitrogen (N) on a Costech ECS-4010 elemental combustion analyzer (Silva Lab, University of Oregon). Below ground C stocks were calculated from approximate bulk density measurements and total soil organic carbon (SOC) percentages.

Tree-core sample processing

Tree-cores were dried in an oven at 50 °C for 72 hours, they were then mounted, sanded, and polished with 600-grit sandpaper. The cores were then digitally scanned and ring widths were measured using image-J software (National Institutes of Health). Individual ring widths were converted to annual basal area increment (BAI, cm² yr⁻¹) using the dplR package (Bunn, 2008). BAI is known as a measure of site productivity and is sensitive to climate. Assuming that annual increments are uniform along each tree-ring, it is calculated as follows:

BAI = π (R²_t-R²_{t-1}) where R is the tree radius and t is the year of tree ring formation (Biondi & Qeadan, 2008).

Watershed	Area (ha)	Max Elevation (m)	Soil Type	LAI	Origin of forest	Management History
6	878	1029	andesitic deposits	3.18 +/- 0.27	~1700-1850 AD	100% clearcut 1974
7	918	1102	andesitic deposits	3.45 +/- 0.78	~1700-1850 AD	60% overstory harvest 1974; remaining canopy removed 1984; 12% non- commercial thin 2001
8	962	1182	andesitic deposits	3.81 +/- 0.80	70% after fire ~1850, 30% ~1500 AD	Reference, no harvest

Table 1 HJ Andrews experimental watershed stand characteristics, average ground-based LAI (m^2/m^2) and standard deviations of the mean (n = 27; 9 per watershed), measured June, 2019.

NDVI/NDWI/LiDAR Data

A combination of tree ring data, used as a proxy for forest productivity, and remotely sensed variables representing ecosystem productivity and canopy moisture (normalized difference vegetation index (NDVI) and normalized difference wetness index (NDWI)), have been successfully used to gauge forest responses to climate variability in terms of magnitude and direction of ecosystem alterations. NDVI is derived from the ratio between red and near-infrared light reflected by vegetation, and is an indirect measurement of photosynthesis and forest productivity (Myneni et al., 1995). NDWI is derived from the ratio between short-wave infrared and near-infrared light reflected by vegetation and is an indirect measurement of plant water stress (Gao, 1996). Only in recent decades has research related remotely sensed parameters to direct field dendrochronological measurements, and a gap has been identified for this relationship using local specific conditions to improve the mechanistic understanding of the impact of climate and management on essential forest functions (Correa-Díaz et al., 2019). Here, surface reflectance imagery was acquired and processed through Google Earth Engine to calculate NDVI and NDWI for all images between 1984 and 2017 using 30m LANDSAT data (Google Earth Engine Team, 2015). Landsat Thematic Mapper (Landsat 5) data were used for the years 1984 through 2011, and Landsat Operational Land Imager (Landsat 8) data were used for 2013 to 2017. The year 2012 was unable to be captured due to the scan-line error associated with data from Landsat Enhanced Thematic Mapper (Landsat 7). A cloud mask was used to remove overcast days from the time series and all abnormally low values of NDVI and NDWI were removed as they do not accurately represent the productivity or canopy moisture index of the area in question. A 5x5 pixel

polygon was selected as the area to be analyzed from each watershed at HJ Andrews. The polygons were placed in the center of the watershed, away from roads and parking lot clearings. Once the raw data was filtered to each polygon, all data from Landsat 5 and Landsat 8 were homogenized to Landsat 7 values using the following equations (Su et al., 2017, Figure S3).

 $NDVI_{Landsat5}$ homogenized = $NDVI_{Landsat5} \times 1.1307 - 0.0571$

 $NDVI_{Landsat8 homogenized} = NDVI_{Landsat8} \ge 0.0167$

NDWI_{Landsat5 homogenized} = NDWI_{Landsat5} x 1.10375 - 0.0346

NDWI_{Landsat8 homogenized} = NDWI_{Landsat8} x 0.9748 - 0.0117

The final step was to export each time series to excel where area under the curve (AUC) was calculated for the NDVI and NDWI values of each year. A common geometrical method was employed to calculate AUC by using the area between data points and summing those areas to produce the annual value. Linear regressions were then run using this time series and other climate, hydrologic, and productivity variables with the understanding that the NDVI or NDWI AUC value is arbitrary compared to a normal scale of NDVI, and is recognized as the annual accumulation of productivity that represents the growing season of the forested area in polygons from each watershed (Devadas, 2009; Rahman et al., 2016).

NDVI anomaly maps were created ArcMap version 10.5 with images downloaded from USGS Earth Explorer for the years 2004 – 2019, excluding 2012 due to the scanline error in Landsat 7 data. The NDVI values were standardized by comparing a snapshot in time to a more historical average. The historical average is subtracted from the current value and divided by the standard deviation, producing a z-score that is positive or negative in relation to the historical baseline.

Canopy density was measured from three sets of LiDAR data produced for the area of interest, data was collected from the National Oceanic and Atmospheric Association (NOAA) and a time series was then created from extrapolating upon the relationship of canopy density and NDVI. The procedure for measuring density includes converting the LASer file format above ground point cloud to a raster, as well as the bare earth point cloud to raster, and then calculating a point total for each cell by summing the bare earth and above ground point clouds. Then above ground density is calculated by dividing the above ground points by the total points using the LAS Toolbar in ArcMap version 10.5. Canopy height was measured from bare earth Digital Elevation Models (DEMs) and Digital Surface Models (DSMs), where the DEM is subtracted from the DSM using the Raster Calculator tool with ArcMap.

Statistical Analysis

Shapiro-Wilks tests were performed to indicate normality of soil C, N, and C:N data; two-way anovas were then used to establish significance of the effect of predictor variables such as depth and management. Tukey post-hoc tests were run to identify means with significant differences, where P < 0.05. In the case of non-normality, the data were log transformed and again checked for normality. A Kruskal-Wallis test for significant differences was performed when variables displayed non-normality after log-transformation. Raw ring-width measurements were first detrended using a cubic smoothing spline where the frequency response is 0.5 to standardize age-growth trends. A

regional curve standardization was performed with ring widths over cambial age to assess the consistency of growth trends at similar ages. Pairwise correlations were applied to the entire dataset in order to summarize the magnitude and direction of relationships between environmental and tree ring variables (**Table S1.1, S1.2, S1.3**). Least-squares regressions were applied to describe trends in growth and climate when appropriate, and adjusted coefficients of determination (r²) and probabilities were reported. Predicted water yield was created using a mixed effect model testing management, productivity, and climate variables, with year to year variation set to random. All data presented in tables and figures are untransformed, not all data are normal, and transformations were made as stated above. All statistical analyses were performed in R using the following packages: dplR, treeClim, plyr, sjPlot, detrendeR, and agricolae.

CHAPTER III

RESULTS

Changes in climate and water budget

Figure 3 top panel demonstrates the variability of average temperature and total precipitation back to the late 1950's, when HJ Andrews forest was first being set up as a LTER station. On average, there was no significant statistical trends for local climate observations. One exception would be a small increase in precipitation during spring months, with a very small decline in temperature for the same months (Figure S1, months 4-6). The annual temperature time series does not show an increasing pattern over the past 30 years, when globally a 0.6 °C warming since 1970 has been confirmed and linked to human activity (IPCC, 2014). We suspect that this can be explained by the effect of forest cover, which has been shown to buffer climate warming below 2.5 °C on average at the site relative to the regional trend, as mentioned in the introduction from Frey et al. (2016). Regional climate inferred from interpolated PRISM data was used for comparison, displaying smoother trends than the HJ Andrews meteorological station, especially in the precipitation record as seen during years of variable precipitation. The area circled in black is a time period of particular interest in that there are several years of low precipitation followed by several years of high precipitation, which is then mirrored in the hydrologic record, albeit less pronounced. The coefficient of variation (CV) of the highly variable years, 2004 to 2018, was found to be 0.951, while the record before 2004 has a CV of 0.890, suggesting lower variation in the historical record. This increased



Figure 3. Monthly climatological and hydrological records with temperature and precipitation record in top record, streamflow and ET in bottom record. CS2.MET is data from the local meteorological station, while PRISM data is projected. The circled area represents years of variable climate that are likely influencing productivity while red dashed lines represent treatment events that affected both the clearcut and thinned stands. (n = 59 years).

variability plays an important role when it comes to interpreting climate's influence upon productivity suggested in the following sections.

The hydrologic record of water yields (seen at the bottom of **figure 3**) measured from streamflow gauges for each watershed, exhibits significant variability over time. A statistically significant relationship was found for streamflow and precipitation for all except the thinned watershed (control $r^2 = 0.706$, P < 0.001; clearcut $r^2 = 0.601$, P < 0.001; thinned $r^2 = 0.141$, P > 0.05; **Table S1**). On average, summertime landscape water yields, recorded as streamflow, have increased by 6 - 7 % across all watersheds (July – October relative to the pre-treatment summer average, **Figure S2e**). Between the years 2005 to 2017, the summertime average increase in the control watershed was approximately 2.5 to 3 mm higher than the treated watersheds with a 6 mm gain in 2008, and a 10 mm gain in 2013 in comparison to the treated watersheds. These fluctuations in streamflow deficits and gains are in concert with monthly precipitation and temperature records and the intensity of the watershed scale response to climate variability was strongly modulated by management type. As mass balance of water inputs and streamflow (Equation 2) shows that the thinned watershed has a period from 1987 – 1995 where the streamflow gauge was in disrepair, affecting both the streamflow and ET record, as seen in **figure 3**. Interestingly, treatment did not observably alter the hierarchy of streamflow regimes between these watersheds, where the clearcut had the highest streamflow amounts before and after treatment, followed by the control and then the thinned watershed. The record of estimated ET displays a very tight spread between management during winters when ET is high, but during the summer months when ET goes negative due to low precipitation the spread between watersheds widens, with the lowest amounts of ET in the clearcut followed by the control and thinned, respectively.

Changes in soil carbon and nitrogen as function of management

As seen in upper **figure 4a**, significant differences between management of total organic carbon concentration were found only in the thinned watershed at the lowest depth increment. For all watersheds, the topsoil has significantly more carbon than the lowest depth increment. Differences in response to management were only seen for the thinned watershed, where significantly less carbon was found at the deepest depth



Figure 4. Soil C and N as a function of depth and management. Panel (a) top: displays total organic carbon where significant differences shown are between management; panel (a) bottom displays total nitrogen concentration where significant differences shown are between depths. Panel (b) top: displays the C:N response ratio, where the C:N of the treated watersheds is compared to the control (red-dashed line); panel (b) bottom: displays estimated soil organic carbon stocks corrected for bulk density where significant differences shown are between management. All elemental concentrations are represented on a percent basis as a function of depth and management. In all cases, data range and error bars indicate spatial variation measured as standard deviation of 27 soil profiles sampled up to the bedrock (n = 9 per watershed).

increment in comparison to the control and clearcut watersheds. Total nitrogen generally followed the trends observed for organic carbon, but significant differences were found only between depths, where the topsoil is different from the lowest mineral horizon. Notably, the thinned watershed showed the largest variation for C and N concentrations in the top 20 centimeters (IQR = 14.04 %C, and 0.23 %N), which was not observed in the control and managed watershed. A closer look at the data (**Figure 4a**), shows that this increase in C and N was only seen in a few individual samples (20% of the total number of samples; n = 25) and was not statistically significant.

As seen in the top of figure 4b, no significant differences were found between clearcut, thinned, and old-growth watersheds with respect to C:N response ratio. We suspect that this response is causally related to the unusually high concentrations of organic carbon (Figure 4a), likely resulting from multiple thinning events (years: 1974, 1984, 2001). These events could increase the spatial variation in the amount of debris added to the soil in this watershed in comparison to the other watersheds. This explanation is supported by the observation that the total C stock (corrected for variation in bulk density; Figure 4b) is significantly lower in the thinned watershed compared to other treatments. In the bottom chart of figure 4b, carbon stocks show significant differences between management in the two lower depth increments, where the clearcut and thinned watersheds were significantly different from each other. The clearcut watershed had the highest amounts of total carbon in grams per square meter. The control watershed displays less spatial and depth-dependent variability than the clearcut watershed with a smaller average interquartile range (control IQR = 2391.61 g C/m^2 , clearcut IQR = 8337.05 g C/m^2). Indeed, most of the C in the thinned watershed (71% of the total C stock) is in the topsoil layer, whereas only a small portion (38%) of the total organic C is found in the topsoil of other treatments. Taken together, these results

indicate significant and synergistic effects of both management and depth on soil C and N.

Changes in tree growth and watershed-scale growth sensitivity

There were no statistically significant differences in temporal variation for RWI across management types. All trees and years were used in this analysis (n = 45) as seen in top left **figure 5**, and no trend was found in RWI as a function of cambial age. The lower left chart displays BAI of all trees as a function of age with a low and steady positive growth rate for old-growth trees. However, the average BAI splines in the main plot exhibit markedly distinct trends for tree growth in managed watersheds over time. There are several periods of declining growth seen in all watersheds, but within the control watershed all declines are succeeded by an increase in growth and growth variation. Increased tree-to-tree variation is evident in a near 50% increase of maximum standard errors in clearcut and a 200% approximate increase in thinned forests relative to the control maximum standard error. The variation within the control plot is observably less than the variation within both managed plots, ranging from -0.84% to 3.2%, when n = 15, of the average annual growth. Another notable observation in **figure 5** is the fast initial growth displayed by the thinned and clearcut stands compared to the control plot. Trees of the same age ~ 40 years in the old-growth forests 1.5 centuries ago had much slower growth rates (Growth Rates from regression slopes: Control = 0.08, Clearcut = 0.33, Thinned = 0.84). Finally, the most important difference observed in response to treatment is that despite fast initial growth, BAI of the treated watersheds crashes (see red arrows in figure 5), the BAI of the control watershed continues to increase. A threshold



Figure 5. Individual and average tree-growth as a function of cambial age and year with top left chart showing RWI of all trees showing no trend over time (y = 0.0000x + 0.994; $r^2 = -0.00 \text{ P} > 0.05$). Bottom left chart exhibits increasing basal area increment of all trees over time (y = 0.0599x + 11.340; $r^2 = 0.10$, P < 0.001). Right chart shows the average increasing BAI over time that suggests a crash from treated watersheds that begins around 2011. (n = 45 trees; 15 trees per treatment, 3 treatments).

autoregression analysis was used to determine the point in time where this crash is occurring, and the treated stands were found to each have 2 distinct threshold values. The clearcut thresholds were found to be in 2002 and 2015, while the thinned threshold years were 2002 and 2006. Finding 2002 as a threshold year is likely due to a lag effect of the previous year's low rainfall, similarly to 2006, where the previous year received very low rainfall. The second threshold for the clearcut watershed, in 2015, falls within the years of high variability of precipitation. The crash coincides with the highly variable years of precipitation, where the CV increases in comparison to the historical record (see circled area **figure 3**).

NDVI anomlies for a dry period in comparison to a wet period (Figure S3) suggest the managed watersheds are conserving less resources during the dry period compared to the control, where little change in NDVI is seen in the clearcut and thinned watersheds in contrast to the control which displays a decrease in NDVI during years of less precipitation. The wet anomalies map suggests the managed watersheds, especially the thinned, increase their NDVI by over 50 % (z-score > 0.5), while most of the control increases its NDVI by between 15 to 50%, (z-score > 0.15). These observations disagree with the record of BAI during the same time period, where treated watersheds are decreasing. A similar comparison can be made by examining time series of remotely sensed variables (Figure S2b, c, d) where there is no recent decline in productivity found in any of the watersheds. Despite significant relationships found between NDVI/NDWI and BAI in the managed plots as shown in table S1, the general relationship of these remotely sensed variables with BAI indicates a logistic function where a saturation point is reached once full canopy closure occurs in the treated watersheds. Figure S4 displays this relationship where after canopy closure, increases in BAI no longer translate to increases in NDVI or NDWI. This loss of relationship at canopy closure is a likely explanation for the disconnect observed between remotely sensed variables and groundbased productivity as mentioned for the maps of **figure S3** and time series of **figure S2**.

A majority of the time series satellite measurements were found to be similar to BAI, where the thinned and clearcut watersheds begin with much lower values due to their age. After 10 to 15 years, they overcome the control watershed values due to their increased growth rate influenced by plantation style management. Both NDVI and NDWI have very similar trends with significant relationships found for each watershed, (control $r^2 = 0.786$, P < 0.001; clearcut $r^2 = 0.887$, P < 0.001; thinned $r^2 = 0.847$, P > 0.001; **Table S1**). This similarity is common in that measured productivity of the canopy (NDVI) is tightly coupled with canopy moisture (NDWI). The canopy density plot seen in **figure S2d** signifies the clearcut stand had canopy density values on average 1% larger than both the thinned and control watershed, except at a young age where the clearcut measured canopy density is within 1% of the control values. This observation speaks to the uncertainty of extrapolated density measurements, where a young non-thinned stand can have the same remotely measured canopy density as an old growth forest with obvious structural differences.

Relationships of productivity with hydrologic and climatic variables

Based on the correlation matrices of **table S1**, the strongest significant relationships between productivity and climate were BAI and ET/Precip in the clearcut stand. The strongest negative significant relationship was between BAI and streamflow in the thinned watershed with ($r^2 = -0.383$, P < 0.05). This does not include the relationships between RWI and BAI, NDVI and NDWI, or precipitation, streamflow, and ET, where covariation produces strong positive relationships. Of particular interest was the relationship between BAI and ET. **Figure 6a** signifies a significant exponential relationship ($r^2 = 0.3601$) was found between ET and BAI values of trees within all watersheds. Individual treatment relationships between BAI and ET were all found to be non-parametric due to several outliers in the ET trend. Represented as the amount of water used per unit of growth, the relationship of BAI and ET in **figure 6** is a basic test of WUE. The thinned watershed has the lowest WUE with BAI values for an elevated cost



Figure 6. Measured tree productivity characteristics and estimated evapotranspiration displays WUE measured from ground and canopy. (a) Estimated ET as function of BAI, showing positive exponential relationship and (b) estimated ET as a function of the annual area under NDVI curve, showing no statistical relationship. (n = 95 years, 34 years per treatment except WS07 with 7 years missing, 3 treatments).

of ET, as well as a larger spread on the chart, similarly to the BAI trend with increased variability seen in **figure 5**. The control has the highest WUE with increased BAI at a relatively lower cost of ET, while the clearcut indicates moderate-low WUE with low values of BAI and ET. There was no evidence of a significant relationship between NDVI of all watersheds and ET (**Figure 6b**). Clustering by management type is notable within relationships of both scales of growth with ET, but the pattern found with NDVI is markedly different where management has an observable influence on ET, but not NDVI. This observation is likely a relic of the weak relationship between NDVI and BAI, where

increases in BAI are no longer reflected in the NDVI time series once full canopy coverage is reached.

Another major ecosystem function, watershed streamflow, was successfully predicted using a mixed model combining management, tree-level productivity (BAI), and climate (total annual precipitation). Management in this case inherently includes soil characteristics and treatment history. **Figure 7** displays the fitness of the predicted streamflow in comparison to actual streamflow values, along with a table highlighting the significant variables as mentioned. Similar to the relationship of productivity and evapotranspiration, remotely sensed variables were not found to be significant predictors of these functions. Comparing the management clusters of **figure 7** to the clustering in **figure 6** exemplifies a closing of the water-budget for each watershed. The thinned watershed has the lowest predicted values of streamflow, which agrees with the low WUE, the control has moderate level of streamflow where its efficiency was highest, and the clearcut has high streamflow as a factor of its decreased ET and growth in comparison to the control and thinned watersheds.



CS2-Tavg (C°) 1 1 26.5 0.6210802 0.4376 CS2-Ptot (mm) 1 1 26.3 21.688162 <.0001* 2 2 184.81613 <.0001* Management 67.9 Figure 7. Actual and predicted streamflow of each treatment using a mixed effects model where variables indicated with arrows in the table are significant predictors. (n = 95

years, 34 years per treatment except the thinned watershed with 7 years missing, 3 treatments).

CHAPTER IV

DISCUSSION

The data presented here span multiple spatio-temporal scales, from trees to watersheds and from seasons to centuries. Overall, we found partial support for the overarching hypothesis that carbon-water tradeoffs within an ecosystem are dependent upon land-use. Specifically, in response to Question 1, we found that treatment has impacted the translocation of soil nutrients at lower depth increments, as well as increasing the rate of growth and variability of dominant Douglas-fir trees. In response to Question 2, the relationship between BAI and NDVI reaches a saturation point, thereby affecting the ability of watershed scale productivity to predict ecosystem function response such as WUE and streamflow. In response to Question 3, hydrologic functions were affected by treatment where the thinned had the most significant negative impacts. As expected, under the same climatic conditions, thinned forests were more productive than clearcut or control watersheds. Also expected was the faster growth rates of trees in managed forests. However, we also found multiple surprises. One unexpected response was the increased variation and decline in BAI found in both the thinned and clearcut watersheds. Another unexpected response was the poor prediction strength of remotely sensed variables of ecosystem functions, such as WUE and streamflow. Taken together, we found evidence for previously theorized carbon-water relations scaling rules that can inform the sustainability of forests ecosystems, but quantitative prediction of those rules requires consideration of field and remotely sensed data. The following sections depict those responses in more granular detail and contrast our findings with those from previous experiments and observations conducted at a smaller spatio-temporal scale.

Effects of management upon soil carbon and nitrogen

Dynamics in the deeper mineral horizons have the ability to influence the overall balance of SOC, and few studies have tested for retention of C and N stocks after harvest in coniferous forests. Alteration of soil organic matter can have large ecological implications due to its influence upon biogeochemical processes (Grand & Lavkulich, 2012). The results of this study indicate there are significant impacts from management upon concentrations and stock of SOC, but not N. Most of the significant differences were found in the lower horizons, 40-60 cm deep. Due to the consistent nature of these watersheds in characteristics that typically affect soil nutrient retention, such as elevation, geology, and fire history, it is likely that these differences observed are induced by the varying disturbance regimes of forest management. Measured concentrations of the elevated values of C and N in the top-layer of the thinned watershed provide evidence they are natural and not part of the litter layer. The increased variation of the thinned watershed, as seen in **figure 4a**, is likely a function of the increased disturbance received over time in comparison to the other watersheds. C:N response ratios stipulate how the relationship of C:N has been influenced by management in comparison to a control. Undisturbed soils tend to have a lower C:N ratio due to the stability found through a lack of disturbance, which allows for mineralization and translocation processes to occur. The top chart of figure 4b indicates that the control was indeed lower in its C:N ratio, but this cannot be stated with statistical confidence. One unexpected finding was the increased SOC stock in the clearcut stand at bottom of figure 4b, while the thinned stand was significantly lower in the two lower depth increments (20-40 cm and 40-60cm). This suggests that the type of management and disturbance intensity will affect the potential of soil to store SOC, where watersheds with short harvest cycles are more likely to experience detrimental effects upon these stocks.

Another consideration to be made is the limitation of tree growth in typical Douglas Fir forests from N fixation (Perakis et al., 2015), and decomposition of the symbiotic N-fixing lichen Lobaria pulmonaria adds N to these otherwise N-limited soils. Due to a preference for open sites, more mature forests tend to obtain the symbiotic relationship with the lichen (Ivanova, 2015), management areas with short harvest cycles are less likely to ever obtain that relationship. Repetition of short harvest cycles followed by replanting will affect the quality of litterfall and lead to significant changes in C and N stocks that are critical for maintaining forest productivity (Winsome et al., 2017). As the watersheds in HJ Andrews have not undergone multiple cycles of harvest and replanting, significant changes in N are not yet observed. We expect the act of thinning and increased disturbance upon the soil does not allow for the input of nitrogen in the top layer of soil to mineralize and translocate to the deeper soil horizons. Therefore, future studies should focus on regenerative plots that have undergone multiple harvest cycles to test for its effect upon N availability at the mineral horizons.

Effects of management and climate variability on productivity from multiple scales

Forest structure has been palpably impacted by management in these experimental watersheds based upon measured differences of stand density, canopy density, basal area, and height between watersheds. Thinning initiated a positive effect on growth, agreeing with other studies that test its effect relative to a control or clearcut (unthinned) stand of Douglas-fir (pseudotsuga menziesii) (Briggs & Kantavichai, 2018). The increased

variation found in the managed watersheds compared to the control watershed, however unexpected, is further evidence that old-growth trees create a climate buffer and are less vulnerable to extreme events such as droughts, as mentioned previously. That being said, the increased variability in the precipitation record that occur during the same time period as the drop in BAI is a likely explanation for this crash in productivity. An alternative explanation is the concept that forests reach peak growth early in stand development which is then followed by an age-dependent decline in productivity after canopy closure (He et al., 2012). This statement disagrees with the previous assertion from Weiner and Tomas, that purports the typical response of BAI in mature stands is to increase continually until senescence begins (2001). In order to obtain a more complete understanding of what occurred in the treated watersheds, the tradeoffs between carbon and water need to be considered.

Anomaly maps of NDVI can offer a unique perspective to canopy productivity and its relationship to water-use, where in this case the control watershed is observed conserving its resources during both dry and wet years in comparison to the treated watersheds. The maps also provide evidence that an opposite response in productivity is observed remotely in relation to ground-based measurements. The time-series trends in **figure S2** agree with this difference between spatial scales, which is partially explained by the relationship between remotely sensed NDVI/NDWI and BAI, found in **figure S4**. The loss of a relationship once full canopy coverage is reached in the treated watersheds does not account for a physiological explanation of this disconnect between stem and canopy growth. Where NDVI/NDWI are measured from surface reflectance, they measure productivity of the canopy, and BAI measures productivity of stem growth. This

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suggests that while BAI may show a decrease in productivity, it may be caused or countered by an increase in canopy foliage. Carbon allocation to other pools, such as nonstructural carbohydrates, induced by water-stress could be an explanation for these observed growth dynamics between stem and canopy, where nonstructural carbon allocation is known to create time lags between carbon uptake and stem growth (Griebel et al., 2017). According to Coulthard et al., productivity measured from the stem and the canopy are loosely tied and are dependent upon the state of water-stress and management history (2017). As such, the nuances around these processes are not well understood, but are playing a significant role here in conjunction with increased precipitation variability during the unexpected crash in productivity of the treated watersheds.

Effect of management and climate variability on water-yield

Because wood formation is the leading process for long-term carbon capture in forests, and continental water fluxes are largely influenced by forest evapotranspiration, the impacts of management and climate change upon the budgets of water and carbon need to be well understood (Camarero et al., 2018). The significant relationship found between ET and BAI of treated watersheds in **figure 6a** suggests that structure at tree-level (basal area) is able to predict function (ET). A recent study by Wharton and Falk supports this statement of structure predicting function with evidence for the effect of stand age on interannual variability of carbon fluxes in temperate rain forests. Results from this study indicated that old Douglas-Fir forests of Washington had greater inter-annual variability of net ecosystem exchange by 64% in comparison to younger, even-aged forests of British Columbia (Wharton & Falk, 2016). **Figure 6** also displays WUE,

an important ecosystem function and service, where High WUE in the control watershed is less surprising due to steady positive growth at a low water-cost. Decreased WUE was found in the clearcut and thinned watershed, which does not align with Vernon et al., where findings suggest thinning activities in northern California increases drought resistance where larger trees were less resistant than younger, thinned trees. The climate of this study site is much dryer than what is found at HJ Andrews, but both Douglas-fir and ponderosa pine were tested and gave similar results for increased drought resistance (Vernon et al., 2018). These differences imply that water-carbon trade-offs depend upon tree characteristics, species-level response, ecosystem type and other geographical constraints when it comes to understanding the benefits of certain forestry practices.

Further evidence of the trade-offs that arise between management practices are seen in **figure 7**, where we see how management has impacted the water-budget differently for each watershed. This demonstrates that predicted streamflow can be accurately predicted when a combination of effects is considered, but more notably it displays the difference in streamflow between treatment groups. Closing the water-budget using **equation 2** for each watershed succinctly indicates that growth comes at a higher water-cost in the treated watersheds in comparison to the control. A recent study found that decreased gross primary productivity (GPP) of Douglas-fir forests within the Pacific Northwest are linked to rising climatic water deficit and vapor pressure deficit. With climatic water deficit calculated as potential evapotranspiration minus actual evapotranspiration, it provides a climate index of the interaction of water and energy (Restaino et al., 2016). As these climatic factors increase into the future as predicted, ecosystem health of temperate conifer forests is at risk due to the link between

sustainable growth rates and carbon sequestrion, biodiversity, and ecosystem resilience, suggesting that Douglas-fir trees within treated watersheds will face increased vulnerability to mortality than older, larger trees with less intense management histories.

The lack of a significant relationship between NDVI/NDWI and ET is evidence that productivity was able to predict ET at tree-level, but not stand-level. The mixed model of **figure 7** agrees with this as neither NDVI nor NDWI were found to be significant predictors of streamflow. It was found that remotely sensed variables were not able to predict forest functions, which could have implications for the applicability of current remote sensing procedures upon studies regarding ecosystem health. The NDVI/NDWI data used in this study were chosen based upon maximizing temporal resolution at the cost of spatial resolution. Further experiments of this type should increase spatial resolution to test for a significant relationship between variables such as NDVI and ET.

CHAPTER V

CONCLUSION

The main findings of this research include significant differences in forest carbon and water balances as a function of management and climate variability. Industrial forestry treatment methods (i.e. clear-cut and thinning) reduced climate resiliency in Douglas-fir forests in comparison to old-growth stands in a control watershed. Young trees grew rapidly in clear-cut stands during the establishment phase, but tree growth plateaued after ~20 years or growth (below the basal area increments of old-growth trees) and declining in response to recent drought events. Thinning maintained rapid tree growth (beyond the basal area increments of old-growth trees), but decreased streamflow yields as a cost for increased tree growth, leading to increased vulnerability to fluctuations in climate, as manifested in a recent drought-induced tree growth decline. Soil properties are likely modulating tree growth response to climates. Significant differences existed for soil organic carbon and nitrogen concentrations across treatments, probably due to the impact of management on residue deposition and organic matter turnover. This finding should be further investigated in future studies to assist with decisions involving methods that might be beneficial for trees but could end up depleting soil resources and water-yields, and thus affecting the long-term productivity of trees and forests.

The importance of understanding the effects and possible strategies for dealing with climate change should not be underestimated, and integrative studies such as this will further our ability to grapple with such wicked problems. Future research stands to gain valuable information from the characterization of ecophysiological mechanisms that incorporate soil biogeochemical processes to predict or mitigate climate change impacts. The observed impacts of management could become problematic under drier conditions or in areas where plantation rotation cycles are short. Less invasive practices, such as ecological forestry, might be necessary to improve climate resiliency in those areas. In the Pacific Northwest, ecological forestry attempts to replicate early-seral ecosystems by removing small amounts of trees and allows for longer harvest cycles to promote carbon sequestration and overall forest health (Franklin et al., 2018). The observed increase in old-growth forest productivity, sustained for centuries despite significant fluctuations in climate, serves as further evidence of feasibility for ecological forestry.

This finding benefits from previous studies of whole-system processes operating in the critical zone, which are possible because of long-term records and collaborative research conducted in LTER sites such as HJ Andrews. In addition to the new data reported here, the paired watershed experiment at HJ Andrews provides a vast catalog of data with a multitude of measurements and variables from ecological and environmental aspects of the whole ecosystem, which benefit researchers and managers. This project certainly benefited from previous studies at LTER, which helped explain ecological surprises that can advance our understanding of the interaction of processes that remain a mystery.

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APPENDIX A

SUPPLEMENTARY FIGURES



4-6, where a small increase in precipitation and small decrease in temperature were found as suggested by P-values < 0.05. (n = 59 years)



Figure S2. (a) Annual BAI values from each watershed from the period 1984-2017, (b) annual area under NDVI curve, (c) annual area under NDWI curve, (d) annual canopy density, (e) Summer Flow difference in comparison to pre-treatment average. (n = 34 years).



Figure S3. NDVI Anomalies shown for three dry years on left (2008 – 2010) in comparison to historical average, and two wet years (2011 and 2013) in comparison to the same historical average, which excludes years of early growth in managed watersheds.



Figure S4. Regressions of productivity variables from multiple scales displaying a logistic function where the positive relationship is lost once trees from the treated watersheds reach full canopy closure, as indicated by the dashed line. (n = 95 years, 34 years per treatment except WS07 with 7 years missing, 3 treatments).

APPENDIX B

SUPPLEMENTARY TABLES

Table S1.1. Correlation matrix of watershed 6 variables including average temperature and total precipitation. Variable units are as follows RWI = unitless, $BAI = cm^2$, NDVI/NDWI = unitless, $SF = ft^3/second$, ET = mm, T avg = °C, P tot = mm.

	Year	RWI	BAI	NDVI	NDWI	SF	ET	T avg	P tot
Year		- 0.028	0.884**	0.436**	0.485**	-0.161	0.508**	- 0.27 5	0.313
RWI	-0.028		0.166	-0.117	-0.123	0.123	0.349*	0.06 4	0.351*
BAI	0.884**	0.166		0.415*	0.479**	-0.124	0.519**	- 0.17 0	0.345*
NDVI	0.436**	- 0.117	0.415*		0.887**	0.030	0.000	- 0.01 3	0.016
NDW I	0.485**	- 0.123	0.479**	0.887**		0.172	0.001	- 0.15 1	0.102
SF	-0.161	0.123	-0.124	0.030	0.172		0.019	- 0.24 8	0.601**
ET	0.508**	0.349	0.519**	0.000	0.001	0.019		- 0.21 9	0.810**
T avg	-0.275	0.064	-0.170	-0.013	-0.151	-0.248	-0.219		-0.320
P tot	0.313	0.351	0.345*	0.016	0.102	0.601**	0.810**	- 0.32 0	

Table S1.2. Correlation matrix of watershed 7 variables including average temperatureand total precipitation. Variable units are as follows RWI = unitless, $BAI = cm^2$,

	Year	RWI	BAI	NDVI	NDWI	SF	ET	T avg	P tot
Year		0.12 3	0.948**	0.722**	0.771**	- 0.430 *	0.207	- 0.27 5	0.313
RWI	0.123		0.250	0.134	0.149	0.078	0.203	- 0.05 2	0.171
BAI	0.948** *	0.25 0		0.661**	0.722**	- 0.383 *	0.221	- 0.25 3	0.355*
NDVI	0.722**	0.13 4	0.661**		0.847**	- 0.248	0.065	- 0.10 3	0.137
NDW I	0.771**	0.14 9	0.722**	0.847**		_ 0.159	0.132	0.27 3	0.297
SF	-0.430*	0.07 8	-0.383*	-0.248	-0.159		0.151	0.27 1	0.141
ET	0.207	0.20 3	0.221	0.065	0.132	0.151		- 0.27 4	0.871**
T avg	-0.275	0.05 2	-0.253	-0.103	-0.273	0.271	-0.274		-0.320
P tot	0.313	0.17 1	0.355*	0.137	0.297	0.141	0.871**	- 0.32 0	

NDVI/NDWI = unitless, $SF = ft^3$ /second, ET = mm, T avg = °C, P tot = mm.

Note: * = p < .05, ** = p < .01, *** = p < .001

Table S1.3 Correlation matrix of watershed 8 variables including average temperatureand total precipitation. Variable units are as follows RWI = unitless, $BAI = cm^2$,

	Year	RWI	BAI	NDVI	NDWI	SF	ET	T avg	P tot
Year		0.401*	0.667**	0.252	0.059	0.108	0.348*	- 0.27 5	0.313
RWI	0.401*		0.913**	0.166	0.042	0.004	0.325	- 0.09 0	0.246
BAI	0.667**	0.913**		0.208	0.103	0.051	0.310	- 0.18 6	0.256
NDVI	0.252	0.166	0.208		0.786**	-0.055	-0.086	0.02 6	-0.092
NDW I	0.059	0.042	0.103	0.786**		0.128	-0.206	- 0.20 5	-0.099
SF	0.108	0.004	0.051	-0.055	0.128		0.343*	- 0.32 4	0.706**
ET	0.348*	0.325	0.310	-0.086	-0.206	0.343*		- 0.23 3	0.907**
T avg	-0.275	-0.090	-0.186	0.026	-0.205	-0.324	-0.233		-0.320
P tot	0.313	0.246	0.256	-0.092	-0.099	0.706**	0.907**	- 0.32 0	

NDVI/NDWI = unitless, $SF = ft^3$ /second, ET = mm, T avg = °C, P tot = mm.

Note: * = p < .05, ** = p < .01, *** = p < .001

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