

SOIL MOISTURE DYNAMICS IN A DISTURBANCE
MEDIATED FOREST, SAVANNA AND
GRASSLAND ECOTONE

By

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All we need is love. Sometimes, a second chance!

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Abstract: The Pushmataha Forest Habitat Research Area in southeastern Oklahoma provides a unique opportunity to improve the knowledge of the relationships between soil moisture dynamics, plant community structure and aboveground net primary production (ANPP) in tree-grass systems. This long-term experiment contains treatments reflecting a full range of vegetation structure that can be found across the forest-grassland transition zone due the interactions of initial harvesting practices with different prescribed fire intervals. To compare vegetation structural influences on soil moisture dynamics, measurements of soil moisture, understory ANPP, tree basal area, woody species canopy openness, and soil structure were assessed. Periodic mean volumetric water content (VWC) ranged between 4.9 and 6.6 %. The highest individual VWC value was 41.9 % and the lowest VWC was 0.7%. The VWC₀ (water content 24 hours following the end of the rainfall event) was significantly related to point-level structural covariates. The final model explained 72% of the residual error variance compared to a null model. Tree basal area was negatively related to VWC₀, although conifer BA was not. The potential evapotranspiration (PET) ranged from 0.25 to 12.2 mm per day; reaching the peak in the summer and decreasing with the end of growing season. A simple model using only meteorological covariates was able to predict growing season soil moisture loss between rainfall events and explained 43% of the residual variance compared to the null model. Including vegetation structural and plot-level environmental covariates in the soil moisture decay model, decreased residual variance by only 2.5%. The index of stoniness was significant ($p < 0.0001$) and positively related with soil moisture loss. Other vegetation structural covariates were non-significant and were dropped from the final model. Heavily forested treatments with thicker litterfall layer had the lowest upper soil moisture content. However, treatments with conifers dominance acted more similarly to open canopy grass dominated treatments. The final model used to predict soil moisture decay showed that steepness on the slope increased with basal area.

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CHAPTER I

INTRODUCTION

Savanna ecosystems and soil moisture

Savannas are plant communities or landscapes that have co-dominance of two plant components: continuous herbaceous and discontinuous woody components (Bourlière and Hadley 1970, Belsky et al. 1989, Scholes and Archer 1997). The mixture between these two components combined with distinct dry and wet seasons, regular fire and usually intense herbivory set the complex savanna structure and functions apart from others terrestrial biomes. (Belsky 1994, Scholes and Archer 1997, Higgins et al. 2000, Baldocchi et al. 2004). These tree-grass systems are common around the world in the latitudinal zone between evergreen tropical rainforest and mid-latitude deserts and comprise over 12% of the global terrestrial surface (Scholes and Hall 1996). They can be found in Africa, Australia, South and North America, and Southeast Asia (Scholes and Hall 1996, Baldocchi et al. 2004) within a broad rainfall range from 200 mm to more than 1500 mm mean annual precipitation (Scholes and Archer 1997, Jeltsch et al. 2000, Bond 2008). In North America, savanna ecosystems were historically at the transition between eastern deciduous forests and tallgrass prairie as well as areas that had been regularly burned and covered approximately 50 million ha (McPherson 1997). This landscape curved southeast from

Canadian provinces of Alberta, Saskatchewan, and Manitoba to Minnesota and Illinois, then southwest through Oklahoma and into Texas. However, because of the inconsistency in the classification and confusion over definitions among savanna ecosystems, their reported extent varies (Bourlière and Hadley 1970, Huang 2006, Hill et al. 2010).

Savannas are a major component of the world's vegetation and are important from economic and ecological perspectives (Scholes and Archer 1997, Bond et al. 2005). In addition, significant amounts of the world's surface occupied by savannas are burned frequently, by natural or prescribed fires and these events have a direct influence on the carbon and the hydrologic cycles (Chen et al. 2003, Grace et al. 2006, Huang 2006). The biome supports the largest and fastest growing human populations, as well as the most of the livestock production. They are further subject to conversion to agricultural fields (Scholes and Archer 1997, Eamus and Prior 2001, Beerling and Osborne 2006). Forest and shrub encroachment into former savanna ecosystems also continues to be a strong conversion pressure due to fire exclusion. It is estimated that 60 to 80% of historic savanna ecosystems remain in a natural or semi-natural state (Ramankutty and Foley 1999, Goldewijk 2001, Lambin et al. 2001, Brannstrom et al. 2008).

The plant community composition in an ecosystem is strongly dependent on precipitation and temporal and spatial availability of soil moisture influences the dominance of woody and herbaceous taxa. Water availability is directly affected by physical soil characteristics (soil texture, mineral composition, structure), landscape position and water inputs (e.g.: precipitation, snow and table water) (Breshears and Barnes 1999, Van Wijk and Rodriguez-Iturbe 2002, Van Langevelde et al. 2003). These variables impact ecological properties of the entire plant community, such as biomass production, nutrient cycles, biological diversity, plant-plant, and plant-animal interactions. Further, they also affect physiological properties like xylem water potential, stomatal conductance, transpiration, and photosynthesis (Hutley et al. 2000). Thus, precipitation and soil moisture are primary variables affecting plant productivity and species

community composition, and are therefore important to include in conceptual or quantitative models of savanna ecosystem structure and functions (Williams et al. 1996, House et al. 2003).

Seasonal and inter-annual variation in precipitation influence savanna ecosystems over a range of time-scales and alternately favor tree species versus grasses. This variation contributes to the coexistence of both life forms in the system (Gillson 2004). For example, with a bimodal savanna precipitation regime, summer growing season precipitation benefit shallow-rooted species and C4 grasses while winter or nongrowing season precipitation may favor deep-rooted species and C3 photosynthetic pathway plants (Weltzin and McPherson 2000). During years with low precipitation, the probability of tree establishment and survival decrease substantially (Jeltsch et al. 2000). Extreme drought may contribute to reductions in cover and productivity of both trees and grasses (McPherson 1997). Generally, small rainfall events would favor grass productivity instead of tree productivity, while large rainfall events benefit both but with greater benefit to woody components (Soriano and Sala 1984). In this way, models that include potential for between-season carryover of water resources in the lower soil profile predict a significant advantage for tree productivity, mainly in moister savannas and on areas with deeper and sandier soils (Scholes and Archer 1997).

The theory of soil moisture being used differently by woody and herbaceous components is based on niche separation theory and has been applied in several models using empirical data (Walker and Noy-Meir 1982, Knoop and Walker 1985, Lauenroth et al. 1993, Hanan and Lehmann 2011). The most classical concept is the Walter two-layer hypothesis, which suggest that trees with their deeper roots system have exclusive access to the water in the lower soil layers, and grasses with their denser root system in the upper layer of the soil are more efficient at water uptake in this layer (Walter and Mueller-Dombois 1971, Breshears and Barnes 1999, Weltzin and McPherson 2000). However, most of the models that use the two-layer hypothesis ignore the importance of soil moisture spatial distribution between areas underneath tree canopies

and between tree canopies and hence, the presence of microclimate patches surrounding woody vegetation and horizontal soil water heterogeneity in the landscape. Yet, the concept of the two-layer hypothesis applies to only a specific ratio between grasses and trees coexisting in the ecosystem. Thus, this concept does not allow a shift in the ratio, and there is no distinction regarding woody components life stage (seedlings, juvenal and adult trees) or their differences in capacity for uptake of water from the soil (Breshears et al. 1997, Breshears and Barnes 1999). The spatial distribution of soil moisture between areas underneath tree canopies and between tree canopies is likely very important for savanna vegetation dynamics and are probably more important to savannas than to forests or grassland (Breshears and Barnes 1999).

Foliar interception of precipitation and eventual direct evaporation from plant canopies also will result in differences in soil water availability, particularly for highly contrasting forest and herbaceous vegetation structures. The general pattern is that soils not directly under woody plant canopies will receive higher amounts of precipitation than otherwise due to greater canopy interception (Breshears et al. 1997). However, these patterns were generally from arid environments with a sparse or a short grass herbaceous layer. It was unclear how dense herbaceous vegetation, such as that from tallgrass prairie, would compare to under woody dominated areas. In addition, as a result of the effect of shading and litter accumulation, tree canopies may also modify soil moisture by influencing soil evaporation rates (Breshears et al. 1998). Therefore, the integration of vertical and horizontal heterogeneity concepts turns soil moisture into a crucial factor to understand savanna vegetation structure, productivity and dynamics.

Disturbances

Although water is the key resource in determining the species composition and structure of savannas ecosystems, disturbances such as fire and herbivory are also very important elements

for savannas vegetation dynamics (Scholes and Archer 1997, Higgins et al. 2000, Van Langevelde et al. 2003). These disturbances are the primary explanatory variables in non-equilibrium models to explain the coexistence of tree and grasses in the system (House et al. 2003, Gillson 2004). Fire and herbivory tree establishment, density, cover and also affect grass and forb productivity (Hanan and Lehmann 2011). Herbivory may help one plant component over another depending of its level or intensity. Increased grazing will reduce herbaceous biomass, likely leading to increased tree establishment and productivity (Walker et al. 1981); on the other hand, increased browsing will affect woody structure and recovery, which could increase grasses productivity (Van Langevelde et al. 2003).

Fire historically played an essential role in maintaining savanna ecosystems and changes on fire natural behavior (e.g., season, frequency, and severity) may alter savanna vegetation composition (Murphy et al. 2009). Many studies found strong evidence, for example, that exclusion of fire increased woody biomass among tree-grass system in various part of the world. In the south-central United States the reductions of frequency or suppression of fire led to conversion of savannas ecosystems to closed canopy forests (Johnson and Risser 1975). In contrast, increases in fires frequency contribute to herbaceous vegetation production and dramatically decrease woody plant cover, modifying savannas canopy structure to be more open and more closely resemble grasslands (McPherson 1997). Another important aspect of fire in savanna ecosystems is its interaction with climate factors, primarily with precipitation seasonality. First, precipitation is directly associated with the mean moisture content of fuels (e.g. dormant season fires and growing season fires) which has a large effect on fire intensity between seasons (Govender et al. 2006). Second, the biomass from C4 grasses produced in the wet season, which increases with more precipitation events, will intensify fire severity during the dry season and indirectly increase fire frequencies and severity in the system (Beerling and Osborne 2006, Bond 2008). These observations indicate that fire is a key factor to explain why savannas can be

found in regions with potential moisture regimes that area capable of forming closed canopy forests (Bond et al. 2005).

Southern Plains savanna ecosystems

In the south-central United States, there is a forest-prairie transition zone expressed by a mosaic of forests, grasslands and savanna systems. This ecotone is located between the eastern deciduous forest and the Great Plains (Johnson and Risser 1975). In Oklahoma, this transition zone is characterized by closed canopy forest in the eastern section, savanna ecosystem in central section and open grassland in the western section of the state (Rice 1959), following the steeply declining east–west precipitation gradient from 1200 mm to 430 mm. The savanna ecosystem occurs on soils of fairly coarse texture derived mainly from sandstone. In some places, soils are derived from limestone; they usually have a loamy texture. However, in this case, soil type and geological formation are of little importance to the maintenance of savanna (Buck 1964), but rather fire was historically the factor of greatest importance.

Prior to European settlement, the transition zone between the prairie and the forest was regularly burned by Native Americans (Abrams 1992). Burning was conducted for many reasons, including hunting, forage production, and warfare. The historic fire frequency was between one to ten years (Rice 1959, Abrams 1992). There is a bimodal precipitation regime (wet spring and drier summer) and more than half of the annual precipitation falls during the beginning of growing season. The frost-free period is approximately 300 days. This is the major difference between the north-central United States savanna ecosystems which has a frost-free period no longer than 120 days per year (e.g. Oak Savanna - Minnesota) (McPherson 1997). The woody components are normally dominated by oak-pine savanna species, such as: *Quercus stellatae* Wangenh (post oak) and *Quercus marilandica* Münchh (blackjack oak) and *Pinus echinada* Mill (shortleaf pine). The herbaceous species are similar to those found in the tallgrass prairie,

dominated by *Andropogon gerardii* Vitman (big bluestem), *Schizachyrium scoparium* (Michx.) Nash (little bluestem), *Sorghastrum nutans* (L.) Nash (Indiangrass), and *Panicum virgatum* L. (Switchgrass) (Rice 1959, Abrams 1992).

In prairie ecosystems, the spatial pattern of average aboveground net primary production (ANPP) is strongly related to the east-west precipitation gradient. The productivity is very dependent on growing season rainfall, and ANPP is linearly related to precipitation increases in this ecosystem (Sala et al. 1988, Hayden 1998). For example, a long-term plot-level experiments in a humid temperate tall-grass prairie grassland located in the Konza Prairie Natural Research Area, Kansas (39.10 N, - 96.61 W, Elevation 400 m) showed a significant relationship between ANPP and annual precipitation amount for both burned and unburned sites (Knapp et al. 1998). Likewise, in shortgrass prairie, forage production and annual precipitation are related with a coefficient of determination was 0.55 (Webb et al. 1978). However, higher coefficients could be obtained when others meteorological variables, such as when potential evaporation, temperature and solar radiation were incorporated (Knapp et al. 1998). Ungrazed and grazed grassland areas in the Great Plains had a linear increase in ANPP when growing season precipitation increases up to 500 mm and 800 mm, respectively. Similar trends could be found for annual precipitation as well (Sims and Singh 1978). Indeed, precipitation is the central driver of productivity in grasslands ecosystems. Briggs and Knapp (1995) suggested that variability in grassland primary production can be simply related to only one variable at regional scale, annual precipitation.

On the other hand, the relationship between precipitation and forest ANPP in this transition zone seems to be more complex (Johnson and Risser 1973, Webb et al. 1978). Compared to grasslands, forests have greater evapotranspiration rates which influences the hydrological cycle. Field experiments and eddy covariance flux showed local-scale insight to forest-atmosphere interactions, such as the effect of leaf emergence on springtime air temperature and evapotranspiration (Bonan 2008). Furthermore, compared to grassland, woodlands usually

have greater leaf areas and roots that extend beyond the canopy, which potentially increase rainfall interception and water uptake (Scholes and Archer, 1997). Forests act as a natural water pump between soil and atmosphere (Schäfer and Dirk, 2011). Their productivity is severely constrained by low precipitation (or water availability). For example, during drought events stomatal closure occurs, limiting water fluxes and steady state conditions of water transfer may be disrupted. This may result in trees growth limitation, and ultimately can lead to tree death (Bréda et al. 2006).

Consequently, forests ecosystems are more commonly situated in areas with high annual precipitation. In Oklahoma, forests are located in the eastern area which is the wettest region of the state (Rice 1959). Forest in mesic regions of Oklahoma are formed of a mixture of deciduous and evergreen trees species. These different species assemblages function differently in the response to resource limitation. This may be particularly pronounced in adaptations to soil water availability through leaf morphology and physiology (Sternitzke and Van Sickle 1968). However, these forests usually have sufficient soil water availability and minimal water stress year-around compared to grasslands areas (Rice 1959). Thus, precipitation may have less influence when it is in excess during wetter years or wetter regions and others factors may limit ANPP (e.g., solar radiation and nutrients). Consequently, positive correlations between forest ANPP and precipitation will be more apparent in areas where productivity is water limited (Boisvenue and Running 2006).

Investigations about spatio-temporal effects of soil moisture heterogeneity in savannas ecosystems on ANPP, mainly understory productivity, are scarce and mostly focused at isolated, single-tree systems (Belsky 1994). These studies focused on understanding the coexistence of trees and grasses in the system. Thus, the influence of soil moisture dynamics on savanna structure and function is not well understood. As part of a comprehensive investigation of short- and intermediate-term carbon dynamics contrasts between grassland, restored savannas and

closed canopy forest, I undertook a study to improve the knowledge of the relationships between soil moisture dynamics, plant community structure and ANPP in tree-grass systems, focusing on restored savanna ecosystem. The study was conducted inside an approximately 35-year-old prescribed fire and forest restoration experiment in southeastern Oklahoma with treatments reflecting a full range of vegetation structure that can be found across the forest-grassland transition zone. Since all units were in the same area, I was able to evaluate the effect of soil moisture dynamics, plant community structure, and ANPP under the same climate and weather conditions.

CHAPTER II

OBJECTIVES

Landscapes along the forest-prairie transition zone may shift along the vegetation state in response to given environmental conditions, including fire frequency, temperature, and soil moisture. Climate change and management practices can highly influence these conditions. It is important to understand how these alterations may or may not affect soil moisture, as it is an important variable in aboveground net primary productivity. This study will provide data that will be used to develop and parameterize a mechanistic model describing how carbon sequestration changes in a newly restored savanna and contrast these changes to grasslands and closed canopy forest.

The objectives of the study are to improve understanding of the correlations among soil moisture dynamics, understory productivity, and plant community structure and dynamics within forest, savanna, and grassland ecosystems. To accomplish these objectives, measurements of soil moisture, understory ANPP, tree basal area, woody species canopy openness, and soil structure were assessed. The research questions included:

- 1) how vegetation structure affects soil water recharge during precipitation events;

- 2) how vegetation structure affects soil moisture dynamics due to evapotranspiration and,
- 3) sensitivity of understory aboveground annual productivity (ANPP) to soil moisture availability in the upper layer of the soil.

Hypotheses addressing the preceding objectives, are as follows:

- 1) Vegetation structure will affect soil water recharge through its influence on interception loss. Canopy storage capacity (CSC) will be the main driver of interception loss and leaf area index, tree basal area, structural complexity, and canopy species dominance will be the vegetation-dependent parameters to estimate CSC. Herbaceous vegetation interception will be significant, especially in relation to small rainfall events, and will have the highest values in its later stage of growth (Figure 1).

- 2) Evapotranspiration (ET) will be responsible for loss of water from the soil and it will be a function of stomatal conductance, leaf area index, structural complexity, canopy species dominance and within-canopy microclimate. The leaf area differences associated with tree basal area and related structural parameters are expected to be related to the rate of soil moisture loss. Plant species composition shift to C3 (woody encroachment) will decrease resource use efficiencies and hence, increase biomass productivity and water uptake (Figure 2).

- 3) Understory aboveground productivity will be highly sensitivity to soil moisture availability in the upper layer of the soil and this sensitivity will vary between forest, savanna and grassland systems (Figure 3).

CHAPTER III

METHODOLOGY

Study site

The study was conducted at Pushmataha Forest Habitat Research Demonstration Area (FHRA) located on the Pushmataha Wildlife Management Area (PWMA). The PWMA is approximately 6 km southeast of Clayton, Oklahoma (34°32'N, 95°21' W). The 29-ha FHRA was established by the Oklahoma Department of Wildlife Conservation in 1982 with the purpose to examine herbaceous and woody components responses to various traditional and non-traditional methods of forest management using different combinations of timber harvesting and prescribed fire (Masters et al. 1993) .

The climate of the region is semi-humid with hot summers and mild winters (Masters et al. 1993, Crandall and Tyrl 2006). The 30-year average annual precipitation for Clayton, OK is 1286 mm and the average over the two years of the study was 1029 mm in 2012 and 1308 mm in 2013. The 30-year average annual mean temperature for Clayton, OK is 17.2 °C. In 2012, the average was 18.3 °C and mean summer temperature was 27.8 °C. In 2013, the average was 16.0 °C, with mean summer temperature of 26.7 °C (Oklahoma Climatological Survey).

The PWMA lies in the mountainous terrain along the western edge of the Ouachita highland province in southeastern part of Oklahoma (Masters et al. 1993). The soils are derived from sandstone, belonging to the Carnasaw-Pirum-Clebit association with areas of rock outcrop. Soils are thin and drought prone, with a stony, fine, and sandy loam texture and a high proportion of surface rock (Bain and Jr 1979). The PWMA is situated near a ridge top with approximately 335 m in elevation on a southeastern aspect and between 5- 15% slope (Masters et al. 1993).

The vegetation is characterized as a mixed pine hardwood forest with overstory mostly composed of shortleaf pine, post oak, black jack oak, and mockernut hickory (*Carya tomentosa* Lam). The understory is dominated by little bluestem, big bluestem, Indiangrass, Switchgrass, *Carex* spp., *Scleria* spp., *Rhynchospora* sp. (sedges), *Panicum* spp. (panicum), *Toxicodendron radicans* (poison ivy), and *Lespedeza* spp. (legumes) (Masters et al. 1993, Crandall and Tyrl 2006). In 1982, the vegetation structure was a near uniformly closed-canopy forest, with a mature overstory approximately 60-years-old. Current vegetation composition and structure within the FHRA is different depending of the method of management applied.

Treatments

Treatments began during the summer of 1984. Merchantable pine trees were harvested, and hardwoods were selectively thinned by single stem injection using 2, 4-D in assigned treatments. Prescribed strip-head fires were applied to appropriate units in the winter of 1985 and in succeeding years at 1 through 4 year intervals (Masters et al. 2006).

Cultural treatments are summarized as follows: Control (CONT): no harvesting, no thinning, and no burning; Rough reduction burn (RRB): no harvesting or thinning and late winter prescribed burn on a 4 year interval; Harvest pine timber-no thin (HNT1): merchantable pine was harvested and late winter prescribed burn of 1 year interval; Harvest pine timber-thin hardwood (HT): merchantable pine harvested, hardwoods selectively thinned and no burning; Harvest pine

timber thin hardwood fire (HT1, HT2, HT3 and HT4): merchantable pine harvested, hardwoods selectively thinned and late winter prescribed burn of 1 through 4 year interval; clearcut loblolly pine (CCSP): clearcut, summer burn in 1985, contour rip in 1986, and plant genetically improved loblolly pine planted (*Pinus taeda*) seedlings on 2.1 x 2.4 m spacing in early spring 1986, late winter prescribed burn in 1998, thin summer 2001, and late winter prescribed burn in 2002, 2007, 2009 and 2012.

The experimental design for FHRA was completely randomized with three replications for each treatment, except HT3 (2 replications) totaling 26 units with areas varying from 0.8 to 1.6 hectare (Figure 4). Each unit had 10 permanent plots (4m x 4m) evenly arrayed on 2 random lines perpendicular to the contour of each treatment unit (Figure 5).

Understory vegetation aboveground net primary production

The understory vegetation was been measured annually between September to October since the beginning of FHRA. The data used in this study were from years 2012 and 2013. The vegetation was clipped at ground level within a quadrat of 0.25 m² (two from 2012) adjacent to each 10 permanent plots. The current-year woody growth for seedling and saplings shorter than 1.4 m; litterfall, which included dead grass, leaves, bark fragments, and twigs smaller than 2.5cm diameter was collected down to mineral soil; and herbaceous vegetation was divided as forb, panicum, legume, sedge and grass. The samples were hand separated into the categories above, dried to constant weight at 70° C in a forced air oven, and then weighed to obtain the dry matter weight per unit area (g m⁻²). To avoid bias, samples are never collected from the same point as the previous years or within the permanent plots.

Tree measurements

Basal area was estimate using a prism factor (BAF) 10 from two points around each permanent plot, centered on the 2011 clipping areas. Tree diameter and species was collected for

each tallied live tree in order to estimate density and diameter distribution. Canopy openness was measured with hemispherical photography from the center of each permanent plot in the late summer of 2013. The photos were taken 1 m above the ground level with a Nikon digital camera (Model E8400a) and fisheye lens. The pictures were taken when the sun was behind the clouds or near dusk and dawn to avoid interference of direct sunlight. The images were analyzed for percent open sky using WinScanopy Version 2006a program (Regent Instrument Inc.) with an area of 140° centered on vertical.

Soil Moisture

Soil moisture was measured during the growing seasons of 2012 and 2013, including early winter of 2013 using two periodic and continuous measurements, which vary in their spatial and temporal attributes. All the equipment used to measure soil moisture were manufactured by Campbell Scientific, (Logan, UT), based on the travel time of electronic pulse in a waveguide (probe) that is surrounded by the soil. The travel time of the electronic pulse is a function of dielectric permittivity of the medium in which the pulse is propagating. Dielectric permittivity of water is much higher than the dry soil; hence the time travel of the electronic pulse is a function of dielectric permittivity of the free water in the soil. Therefore, VWC can be estimated using calibration equation between soil water content, and dielectric permittivity (Topp et al. 1980, Topp et al. 1984). In the very stony soils in this study, I used Topp's equation parameters to calculate VWC (Topp et al. 1984).

The periodic measurements were taken in all plots in all treatment units (n=260) typically every three weeks using HydroSense II, a compact and portable display (model CS659) equipped with two 12 cm rods but with the sensing volume extending approximately 3 cm beyond the end and in a radius around each rod (www.campbellsci.com). Within each plot, VWC was measured for the areas clipped in the autumn for understory biomass calculation. The continuous measurements were taken every 30 min from 30 locations distributed across all treatments, except

for HT2, CCSP and RRB, using two types of probes (CS655) and its wireless version (CWS655). These probes were also equipped with two 12 cm rods; however, they had sensing volume extend 4.5 cm beyond the end and approximately 7.5 cm radius around each rod (www.campbellsci.com).

Soil structure

The rock fractions were estimated from all points from which the periodic and continuous soil moisture were taken by inserting a 20 cm rod into the soil 12 times at different positions inside a 0.25 m² quadrat. Measurements were taken at each plot at the same place as 2013 herbaceous ANPP. The mean vertical depth (meters) of the insertion for each quadrat was computed and converted to an index of soil stoniness since values near zero indicated a high rock fraction. The index was computed as $I_{\text{stoniness}} = \exp(-0.2 (\text{mean depth}))$ which was considered to realistically reflect the range of soil rock fractions encountered. Soil bulk density was calculated taking sample from 3 points inside each unit. The soils were collected 1.5 m west from 2013 clipping area at plots 2, 6 and 10 from all 26 units. The soil samples were dried to constant weight at 105° C in a forced air oven and then weighed. Spherical projectiles (BBs) and graduated cylinder were used to estimate the volume of the hole (10 cm in diameter and approximately 20 cm deep) of each soil sample in the field (excavation method), a similar concept to the rubber balloon method (Alberty et al. 1984). The soil core method could not be used because of the soil characteristics of the study area.

Meteorological measurements

The meteorological data were obtained from nearby Oklahoma Mesonet station 3 miles NE from Clayton – OK (www.mesonet.org). Potential evapotranspiration (PET) was computed from weather data and used to estimate evapotranspiration (ET) due to the difficulty to obtaining accurate field measurements of ET. For this study PET was associated with standardized

reference pan evaporation equation, which follows the recommendation from the United Nations Food and Agriculture Organization Irrigation and Drainage (FAO-24, 1976) (www.mesonet.org).

Precipitation events at the Clayton Mesonet station did not necessarily correspond to the PWMA. Therefore, rainfall events in PWMA were identified by their direct influence on soil moisture. Increasing VWC in a short amount of time was assumed to result from rainfall. The initial increase in VWC would follow the beginning and the peak would approximate the end of the rainfall (Zhang et al. 2008). Thus, a set of probes preferably located in open canopy areas were used to identify the initial and ending points from all precipitation events to the nearest hour.

Analysis

Periodic VWC estimates were analyzed for the site with analysis of variance (ANOVA) as:

$$\ln(VWC_{ijk}) = \mu + TRT_i + u_i + v_k + \varepsilon_{ijk}$$

where μ is the overall mean, TRT was an indicator variable for the i -th treatment, u_i , v_k were random effects assumed $\sim (0, \sigma^2)$ for sample date k and plot j , respectively; and ε_{ijk} was random error assumed normal distribution $(0, \sigma^2)$. A log transformation on VWC was used to help ensure normality and uniformly distributed residuals, and also to avoid negative VWC predictions. Since 10 samples points were made within each treatment unit, we adjusted the degrees of freedom accordingly ($df=17$) for treatment level hypothesis testing. The random effects also accounted for the hierarchical and repeated sample design, partitioning the error variance into plot, date and random components.

Precipitation interception was modeled by influence on VWC, rather than estimated directly. This was owing to the difficulty in estimating interception in grassland systems with a

high proportion of stemflow. The relative interception differences between forest and savanna structures with grassland vegetation were modeled as follows:

$$\ln(VWC_0) = \delta_0 + \delta_{1..n}(EnvCovs_{1..n})_j + u_i$$

where VWC_0 was recorded 24 hours immediately after the end of a precipitation event, $\delta_{0..n}$ were estimated parameters, $EnvCovs$ were vegetation structural and productivity variables for the sample point j for a specific year, and u_i were random effects for precipitation event ($i=1..29$). The model was structured in a way that pure grassland was the reference condition for VWC_0 , with environmental covariates modeling a proportional departure from this reference. A direct estimate of interception (e.g., 20% of precipitation) was not possible with the data on hand. Only data from the continuous measurement probes (0-12 cm depth) was used in this analysis.

The soil moisture decay beginning 24 hours after a rainfall event was modeled using a negative exponential function following (Laio et al. 2001, Teuling et al. 2006):

$$\Delta(VWC_{ij}) = \alpha_{ij} \cdot e^{-\beta_{ij} \cdot t}$$

where ΔVWC was daily moisture loss from the soil expressed as change in VWC between subsequent days with measurements taken at midnight for the i -th day at the j -th location. Variable t was the number of days between soil moisture measurements; α is a parameter fixed at VWC when t was equal to zero (VWC_0 ; 24 hours following the end of the rainfall event). β was function of meteorological and vegetation structure covariates as follows,

$$\beta_{ij} = b_1 + b_2(PET)_i + b_{3..n}(EnvCovs_{3..n})_j + u_i$$

where $b_{1..n}$ were fitted parameters, PET was potential evapotranspiration (mm d^{-1}) for the i -th day, u was a random effect modifying PET with levels of the effect corresponding to year and month combinations, and $EnvCovs$ were plot-level environmental and vegetation structural covariates corresponding to our hypotheses. The model was fitted on the log scale, with $\ln(\Delta VWC)$ as the

response variable, and where the VWC at time t were normalized to where VWC_0 equals unity, and thus $\alpha=1$. In addition, a daily time step was used so $t=1$. This formulation simplified the fitted model to,

$$\ln\left(\frac{VWC_t}{VWC_{t-1}}\right) = -\beta_{ij}$$

where the negative sign was retained for emphasis, and all terms were as defined previously. The random effects and residual errors were estimated on the log-scale, and so were assumed to have a multiplicative form. All analyses were done in SAS statistical software v9.3 (SAS Institute Inc., Cary, NC) with the Mixed procedure. Model selection and testing of meteorological and structural covariates were done with an Akaike information criterion (AIC) for random effects, and individual t-test for fixed effects.

CHAPTER IV

RESULTS

Treatments

The treatments altered the vegetation structure as consequence of the combination of timber harvesting and thinning at the start of the experiment and the prescribed fire regimes of 1 to 4 years interval. After nearly 30 years, these changes were strongly apparent between treatments, especially in tree species composition and canopy structure, creating a gradient from an open canopy prairie system (HT1) to closed-canopy forest in the controls. These differences in overstory vegetation structure have remained relatively stable over the past years. The control and unharvested treatment with 4-year fire return (RRB) retained a mature forest cover with mean canopy openness between 24.3 % and 28.3 % (Table 2). Similarly, the harvested and thinned, but never burned treatment (HT) regenerated to an even-aged closed canopy forest currently in the stem exclusion stage, with a canopy openness averaging 19.8 %. These heavily forested treatments differed substantially in the amount of hardwoods versus conifers, where the HT treatment regenerated to primarily conifer forest with conifer BA of 24.2 m² ha⁻¹ (68% of total) and scattered residual hardwoods. The RRB was similar to the CONT in tree species composition

with average density of 804 and 939 trees ha⁻¹ with 36.07% and 36.10% conifer BA, respectively. The CCSP treatment was a traditional plantation (loblolly pine), and essentially was a conifer even-aged stand forest with mean canopy openness of 29.80%.

Thinned treatments with a more frequent fire regime (HT1, HNT1 and HT2) tended to have more open canopy structure, with canopy openness directly related to the fire frequency (Figure 6). The annually burned treatments, HT1 and HNT1, were largely open prairie with scattered residual hardwoods (oaks) and occasional smaller diameter conifers. The biggest difference between the annually burned plots was that the HNT1, which was not thinned, retained scattered large residual oaks. The open savanna structure of these treatments was reflected in a low mean basal area of 4.09, 8.15 and 7.92 m² ha⁻¹ for HT1, HTN1, and HT2, respectively. However, the savanna structure changed markedly with decreasing of fire frequency. From all treatments that included burning and thinning, HT3 and HT4 had a more closed canopy cover, with average canopy openness of 68.46% and 45.21%; and HT4 the highest BA of 17.52 m² ha⁻¹.

Differences between forest, savanna and grassland structures were also seen in understory ANPP, species composition and litterfall accumulation. These differences followed the same trend for both years of this study (Table 3). The annually burned treatments had similar understory characteristics, with mainly grasses and with higher ANPP. The understory biomass productivity was inversely related to fire frequency and was close to zero in the heavily forested treatments (Figure 7). Consequently, CONT, HT and RRB treatments had the lowest understory biomass production, with mean productivity between 7.35 and 45.84 g m⁻². The species composition of the understory also differed between treatments. The heavy grass presence had negative impact of woody understory (shrubs and trees). For instance, in the HT2, HT3 and HT4 treatments the understory biomass productivity shifted toward C₃ woody plants, generally following the increasing of fire interval.

There were also substantial differences in the litter accumulation among treatments. Litterfall production, which included dead grass, leaves, bark fragments, and twigs smaller than 2.5 cm diameter, ranged from 105.1 g m⁻² on HT1 treatment to 1738.6 g m⁻² on HT treatment (Table 3). Litterfall production was higher in forested treatments and was negatively correlated to canopy openness and fire. Additionally, the time since last burn event also influenced litterfall accumulation and had the greatest impact on the non-annually burned treatments.

Periodic soil moisture measurements

Periodic VWC measurements across the study found that forested plots tended to have lower overall soil moisture (Table 4). This trend was strongly related to sample date, with the general pattern of higher VWC in the non-growing season months (Figure 8). The mean VWC ranged between 4.9 and 6.6 %, on treatments HT and HT4 respectively (Table 4). However, the periodic measurement dataset had a wide range of individual point VWC values, with the highest being 41.9 % for the treatment HT1 after a large rainfall event midwinter, and the lowest VWC was 0.7 % that occurred on the RRB treatment during the growing season (Table 4). The VWC of the forested treatments, i.e., CONT, RRB and HT were similar to one another (Figure 8) ($p < 0.10$), but lower than the non-forested treatments ($p < 0.05$). On the other hand, the highest average VWC values were observed on treatments HT1, HT2, HT3 and HT4 with no significant differences among them; although a slight increase in VWC was noticed with longer return fire interval.

The forested treatment were a distinguishable group with similar mean VWC. However, treatment CCSP and HNT1 were intermediate to the forested treatments and the savanna structures. Statistically significant differences were only noted between CCSP and HT2 and HT4, ($p = 0.008$ and 0.0014); and also, between HTNI and HT ($p = 0.007$).

Canopy interception

Interception of precipitation by the vegetation and litter was indirectly estimated through the influence on upper soil moisture content 24 hours following a precipitation event (VWC_0). The probes placement covered a broad range of vegetation structure owing the heterogeneity between and within treatments, which included areas from open canopy prairies with scattered residual trees and fully grown understory to closed canopy forests in the stem exclusion stage (Table 5). In addition, large variations in precipitation events were observed during the study period from approximately May 2012 through Dec 2013, each with different characteristics (e.g., precipitation amount, duration and intensity). Less soil recharge was associated with canopy cover and litterfall accumulation because these, were strongly related to the amount of water that reached the soil (net precipitation). Thus, the initial VWC_0 values 24 hours after a rainfall event were greater on open canopy prairies than closed canopy forest.

The VWC_0 was significantly related to several point-level structural covariates, with the final model explaining 72% of the residual error variance compared to a null model. Residual error had a CV of 14% of the average VWC_0 . The precipitation event random effect was significant ($p=0.0004$) with $\sigma_{(event)}$ 25% of the model intercept. In addition, model covariates generally corresponded to the hypothesized patterns (Table 6). Tree basal area was negatively related to VWC_0 ; however, conifer BA was not significantly related to VWC_0 . Tree density had a similar pattern as tree basal area. Of the understory variables, only litter accumulation was significant, and was negatively related to VWC_0 . Finally, soil stoniness was included to adjust point level VWC_0 data for possible soil volume influences. Results suggested that increasing stoniness was negatively related to VWC_0 . All terms were significant in the final model ($p<0.05$).

Soil moisture decay

Meteorological variables are main drivers of soil moisture loss. Potential evapotranspiration (open-pan) was used as a means for representing the soil moisture- evapotranspiration relationship (Figure 9). The PET ranged from 0.25 to 12.2 mm per day; reaching the peak in the summer and decreasing with the end of growing season. Potential evapotranspiration is always high in warm, dry, windy and clear days, but low in cold, moist and cloudy days. As expected, a simple model using only meteorological covariates was able to predict growing season soil moisture loss between rainfall events and explained 43% of the residual variance compared to the null model. For this simple model, PET was significant ($p=0.03$). Once PET was included in the model, VPD by itself was not significant ($p=0.31$). However, seasonal changes in the effect of PET and VPD were significant ($p=0.004$, and $p=0.005$) when added as random effects with the year and month combinations as levels. Estimated variances were for PET was $\sigma_{PET}=0.415$ and VPD was $\sigma_{VPD}=0.0067$ which were 158 and 353% of the estimated slope parameters for each variable, respectively. The residual error variance for the meteorological-only model was 0.0022.

Including vegetation structural and plot-level environmental covariates in the soil moisture decay model, decreased residual variance by only 2.5%. Despite that, most structural covariates were highly significant as predictors of soil moisture loss (Table 7). As expected, total basal area was significant and positively related to soil moisture decay (i.e. more negative β) in both study years; however, when considering just conifer basal area the effect was somewhat less, with identical conifer BA showing a flatter decay curve than hardwood BA, considering rain events in the growing season. For woody understory biomass productivity, the significance was detected only in the wetter year (2013) with increasing woody productivity corresponding to decreased soil moisture loss. Further, a distinct pattern was detected between total tree density and conifer density with conifer density increasing the rate of moisture loss. This pattern was

confirmed by the test of model sensitivity to basal area (Figure 10). Also as expected, the index of stoniness was significant ($p < 0.0001$) and positively related with soil moisture loss. Overall, the model fitted with meteorological and structural covariates fit the data well (Figure 11). There was some indication that the negative exponential model might not adequately fit the observed patterns immediately after rainfall events, and possibly in very dry soil conditions.

Other vegetation structural covariates (e.g., understory biomass productivity) including grass and forb productivity, and litter accumulation were investigated assuming that they would result in a better fit for the model but, these were non-significant and were dropped from the final model.

CHAPTER V

DISCUSSION

Treatments

Previous studies found similar patterns of vegetation response to treatment operations on the FHRA. They showed that canopy cover and the proportion of C₃ woody shrubs and trees in the understory layer were higher in the unburned and infrequently burned treatments. Further, that grass species production increased on treatments with more frequent fire regime (Masters and Engle 1994, Crandall and Tyrl 2006, Masters et al. 2006, Feltrin et al. 2016). These effects of fire in the understory layer were confirmed from others studies on tree-grass ecosystems around the world (Medina and Silva 1990, Abrams 1992, Govender et al. 2006, Higgins et al. 2007). These studies found that fire not only increased the total understory biomass productivity on these ecosystems, but it also markedly influenced the whole vegetation structure. In the southeastern United States the lack of fire was assumed to be the major factor of the shift from open pine-oak savanna, which was historically common across the region, to closed canopy forest (Johnson and Risser 1975, Abrams 1992, Ratajczak et al. 2012).

Similarity of vegetation structure between RRB and control treatments, however, showed that fire by itself would not readily reduce canopy cover and restore more open canopy savanna systems. Rather initial harvesting, to reduce overstory tree density and basal area prior to the start of the burning program was need (Table 2). In this way, it would be more appropriate to say that fire can maintain savanna structure by controlling forest and shrub encroachment (Peterson and Reich 2001, Higgins et al. 2007). This is demonstrated by the fact that fire frequency of three years or less is needed to prevent woody encroachment, as observed by the difference on vegetation structure between harvested and burned treatments (HT4 vs HT1, HT2, and HT3) (Table 2).

In addition, the intensity of fire also is very important and is strongly related to fuel load although, this variable was not measured in this study. An increase in grass biomass leads to more severe fires and consequently more damage to trees and shrubs. On the other hand, a decrease in grass biomass and hence fire severity, may lead to forest and shrub encroachment (Van Langevelde et al. 2003). In fact, fire behavior and biomass consumption influenced postfire community productivity and structure at the study site, resulting in a positive feedback of higher grass productivity in the frequently burned treatments (Figure 7).

Canopy interception

These changes in vegetation structure caused by the combinations of timber harvesting and prescribed fire affected soil moisture and as hypothesized, heavily forested treatments with thicker litter layers had the lowest upper soil moisture content across the study period (Figure 8) (Table 4). Also, due to their higher canopy and litter interception, they had the lowest VWC values 24 hours following a precipitation event (VWC_0).

Previous studies showed that tree and grass canopies differ in their ability to store and subsequently evaporate intercepted precipitation (Gash and Morton 1978, Bosch and Hewlett

1982, van Dijk and Bruijnzeel 2001, Muzylo et al. 2009). Further, interception loss is strongly dependent on precipitation intensity and duration. However, our data suggested the same trend even with a broad range of different rainfall events during the study period (Figure 9).

Forested treatments had relatively smaller changes of volumetric water content in response to precipitation events compared to treatments with more open canopy (grassland and savannas). The increase of VWC observed from the upper soil was the most straightforward method to estimate net precipitation, which was defined as the amount of rainfall that penetrates into the soil (Leonard 1961, Verry 1976). Therefore, higher VWC_0 values after a given rainfall event indicate less interception assuming surface runoff was negligible. However, our study design lacked a non-vegetated reference (i.e., bare soil), thus results were constrained to approximating the relative difference in interception rates in forest and savanna structures compared to a grassland reference condition.

Furthermore, leaf structure and configuration also affects interception loss. Generally, flat leaves from hardwoods intercept less water than conifer clumped needles (Pypker et al. 2011). Thus, the range of interception loss from hardwood forests would be expected to be lower than conifer forest, 20 to 40% and 19 to 45%, respectively (Carlyle-Moses and Gash 2011). Following these results, we hypothesized that increasing pine component in the overstory would increase interception loss. However, our results showed the reverse pattern, with conifers acting more similarly to grasslands (Table 6). Perhaps, the structural covariates used to predict interception loss during the growing season (basal area and tree density) underestimate conifers canopy storage capacity and then interception loss. In fact, the same basal area or tree density value for hardwoods or conifers forest have different canopy cover and hence different canopy storage capacity because of their differences in canopy architecture (Verry 1976).

Leaf area index (LAI) would be a better variable for comparing interception loss of different vegetation (Van Dijk and Bruijnzeel 2001) and hemispherical photography can be used to estimate LAI. However, this indirect method may underestimate canopy storage capacity as well (Mussche et al. 2001). In addition, limited hemispherical photography data was available from the study site (only from the peak of growing season), which means, for example, that canopy phenology would not be captured. Therefore, basal area was chosen because its advantage was relatively simple to measure and strongly related to canopy cover (Mitchell and Popovich 1997); and our results showed that total basal area was related to interception loss, as expected (Table 6).

Soil moisture decay

Periodic measurements could not distinguish between canopy interception effects and different evapotranspiration rates between treatments. These data nevertheless confirmed, over a much larger sample area, the general patterns found with increased interception by forested and savanna points, along with increased ET. It was somewhat surprising however, that understory vegetation productivity was non-significant for any of the vegetation taxa (or total) suggesting that even slight amounts of live vegetation were sufficient to intercept or transpire the same amount of moisture as on more productive sites. It remains to be seen whether these results hold-up across dry and wet years.

The soil moisture decay curve between rain events differ between forested treatments and grassland treatments; with savanna-like systems having a decay curve in between, as expected (Figure 2). These findings suggested that the two ecosystems (grassland and forest) may have only moderate differences in evapotranspiration rate, with forested treatment having greater ET than non-forested treatments (Zhang et al. 2001). Following our hypothesis, ET was the only

driver of soil moisture loss at least 24 hours after a rain event. We could not account for surface or sub-surface soil moisture movement.

The final model used to predict soil moisture decay showed that steepness on the slope was substantially different with increasing basal area. This trend can be explained mainly because basal area was a measurement related to trees. These differences could be due to greater total LAI in forest plots or by reduced water use efficiency of C₃ trees. Forested treatments with higher total LAI tends to have higher leaf transpiration and stomatal conductance (Bosch and Hewlett 1982). In addition, high basal area values meant treatments with dominance of C₃ photosynthetic pathway plants, with lower resource use efficiency. On the other hand, treatments with low basal area values were related to the dominance of grass species, which in our study site, were predominantly C₄ photosynthetic pathway plants with high water use efficiency. In fact, plants using the C₄ pathway of carbon metabolism are marked by greater photosynthetic water efficiencies, typically 1.5 to 4 times greater than C₃ species (Vogan and Sage 2011).

However, even with our results showing the slight differences between treatments with forested and grassland vegetation structure, the magnitude of these differences was much smaller than hypothesized. The reason can be because C₄ grasses appear to have similar water efficiency patterns than C₃ trees by stomatal response to light conditions (Huxman and Monson 2003). In an open grassland treatments, the vegetation can transpire water at higher rate because of the higher evaporative demand in direct sunlight (Amundson et al. 1995). In addition, in a non-stressed soil water condition, the treatments may have similar evapotranspiration rate driven by atmosphere demand (Hodnett et al. 1995), which was interpreted by potential evapotranspiration (PET), assumed to be equal across the study site.

REFERENCES

- Abrams, M. D. 1992. Fire and the development of oak forests. *BioScience*. 42:346-353.
- Alberty, C., H. Pellett, and D. Taylor. 1984. Characterization of soil compaction at construction sites and woody plant response. *Journal of Environmental Horticulture*. 2:48-53.
- Amundson, R., A. Ali, and A. Belsky. 1995. Stomatal responsiveness to changing light intensity increases rain-use efficiency of below-crown vegetation in tropical savannas. *Journal of Arid Environments*. 29:139-153.
- Bain, W. R., and A. W. Jr. 1979. Soil Survey of Pushmataha County, Oklahoma. US. *in D. o. Agriculture*, editor. Washington, DC., Soil Conservation Service
- Baldocchi, D. D., L. Xu, and N. Kiang. 2004. How plant functional-type, weather, seasonal drought, and soil physical properties alter water and energy fluxes of an oak–grass savanna and an annual grassland. *Agricultural and Forest Meteorology* 123:13-39.
- Berling, D. J., and C. P. Osborne. 2006. The origin of the savanna biome. *Global Change Biology*. 12:2023-2031.
- Belsky, A., R. Amundson, J. Duxbury, S. Riha, A. Ali, and S. Mwonga. 1989. The effects of trees on their physical, chemical and biological environments in a semi-arid savanna in Kenya. *Journal of Applied Ecology*. 26:1005-1024.
- Belsky, A. J. 1994. Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. *Ecology*. 75:922-932.

- Boisvenue, C., and S. W. Running. 2006. Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century. *Global Change Biology* 12:862-882.
- Bonan, G. B. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science*. 320:1444-1449.
- Bond, W., F. Woodward, and G. Midgley. 2005. The global distribution of ecosystems in a world without fire. *New Phytologist*. 165:525-538.
- Bond, W. J. 2008. What limits trees in C4 grasslands and savannas? *Annual Review of Ecology, Evolution, and Systematics*. 39:641-659.
- Bosch, J. M., and J. Hewlett. 1982. A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration. *Journal of Hydrology* 55:3-23.
- Bourlière, F. o., and M. Hadley. 1970. The ecology of tropical savannas. *Annual review of Ecology and Systematics*. 1:125-152.
- Brannstrom, C., W. Jepson, A. M. Filippi, D. Redo, Z. Xu, and S. Ganesh. 2008. Land change in the Brazilian Savanna (Cerrado), 1986–2002: Comparative analysis and implications for land-use policy. *Land Use Policy*. 25:579-595.
- Bréda, N., Huc, R., Granier, A., & Dreyer, E. (2006). Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals of Forest Science*. 63:625-644.
- Breshears, D. D., and F. J. Barnes. 1999. Interrelationships between plant functional types and soil moisture heterogeneity for semiarid landscapes within the grassland/forest continuum: a unified conceptual model. *Landscape Ecology*. 14:465-478.
- Breshears, D. D., O. B. Myers, S. R. Johnson, C. W. Meyer, and S. N. Martens. 1997. Differential use of spatially heterogeneous soil moisture by two semiarid woody species: *Pinus edulis* and *Juniperus monosperma*. *Journal of Ecology*. 85:289-299.

- Breshears, D. D., J. W. Nyhan, C. E. Heil, and B. P. Wilcox. 1998. Effects of woody plants on microclimate in a semiarid woodland: soil temperature and evaporation in canopy and intercanopy patches. *International Journal of Plant Sciences*. 159:1010-1017.
- Briggs, J. M., and A. K. Knapp. 1995. Interannual Variability in Primary Production in Tallgrass Prairie: Climate, Soil Moisture, Topographic Position, and Fire as Determinants of Aboveground Biomass. *American Journal of Botany*. 82:1024-1030.
- Buck, P. 1964. Relationships of the Woody Vegetation of the Wichita Mountains Wildlife Refuge to Geological Formations and Soil Types. *Ecology*. 45:336-344.
- Carlyle-Moses, D. E., and J. H. Gash. 2011. Rainfall interception loss by forest canopies. Pages 407-423 *Forest Hydrology and Biogeochemistry*. Springer.
- Chen, X., L. B. Hutley, and D. Eamus. 2003. Carbon balance of a tropical savanna of northern Australia. *Oecologia*. 137:405-416.
- Crandall, R. M., and R. J. Tyrl. 2006. Vascular flora of the Pushmataha Wildlife Management Area, Pushmataha County, Oklahoma. *Castanea*. 71:65-79.
- Eamus, D., and L. Prior. 2001. Ecophysiology of trees of seasonally dry tropics: comparisons among phenologies. *Advances in Ecological Research*. 32:113-197.
- Feltrin, R. P., Will, R. E., Meek, C. R., Masters, R. E., Waymire, J., & Wilson, D. S. (2016). Relationship between photosynthetically active radiation and understory productivity across a forest-savanna continuum. *Forest Ecology and Management*. 374:51-60.
- Gash, J., and A. Morton. 1978. An application of the Rutter model to the estimation of the interception loss from Thetford forest. *Journal of Hydrology*. 38:49-58.
- Gillson, L. 2004. Testing non-equilibrium theories in savannas: 1400 years of vegetation change in Tsavo National Park, Kenya. *Ecological Complexity*. 1:281-298.
- Goldewijk, K. K. 2001. Estimating global land use change over the past 300 years: the HYDE database. *Global Biogeochemical Cycles*. 15:417-433.

- Govender, N., W. S. Trollope, and B. W. Van Wilgen. 2006. The effect of fire season, fire frequency, rainfall and management on fire intensity in savanna vegetation in South Africa. *Journal of Applied Ecology*. 43:748-758.
- Grace, J., J. S. José, P. Meir, H. S. Miranda, and R. A. Montes. 2006. Productivity and carbon fluxes of tropical savannas. *Journal of Biogeography*. 33:387-400.
- Hanan, N. P., and C. E. Lehmann. 2011. *Tree-grass interactions in savannas: Paradigms, contradictions and conceptual models*. Boca Raton, FL: CRC Press.
- Hayden, B. P. 1998. *Regional climate and the distribution of tallgrass prairie. Grassland dynamics: long-term ecological research in tallgrass prairie*. Oxford University Press, New York, New York, USA:19-34.
- Higgins, S. I., W. J. Bond, E. C. February, A. Bronn, D. I. Euston-Brown, B. Enslin, N. Govender, L. Rademan, S. O'Regan, and A. L. Potgieter. 2007. Effects of four decades of fire manipulation on woody vegetation structure in savanna. *Ecology* 88:1119-1125.
- Higgins, S. I., W. J. Bond, and W. S. Trollope. 2000. Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. *Journal of Ecology*. 88:213-229.
- Hill, M. J., M. O. Román, and C. B. Schaaf. 2010. *Biogeography and Dynamics of Global Tropical and Subtropical Savannas: A Spatiotemporal View. Ecosystem Function in Savannas: Measurement and Modeling at Landscape to Global Scales*:1.
- Hodnett, M. G., L. P. da Silva, H. R. da Rocha, and R. Cruz Senna. 1995. Seasonal soil water storage changes beneath central Amazonian rainforest and pasture. *Journal of Hydrology*. 170:233-254.
- House, J. I., S. Archer, D. D. Breshears, and R. J. Scholes. 2003. Conundrums in mixed woody–herbaceous plant systems. *Journal of Biogeography*. 30:1763-1777.
- Huang, C. Y. 2006. *Understanding the ecological complexity of semi-arid savannas using remote sensing*. The University of Arizona.

- Hutley, L., A. O'grady, and D. Eamus. 2000. Evapotranspiration from Eucalypt open-forest savanna of Northern Australia. *Functional Ecology*. 14:183-194.
- Huxman, T. E., and R. K. Monson. 2003. Stomatal responses of C3, C3-C4 and C4Flaveria species to light and intercellular CO2 concentration: implications for the evolution of stomatal behaviour. *Plant, Cell & Environment*. 26:313-322.
- Jeltsch, F., G. E. Weber, and V. Grimm. 2000. Ecological buffering mechanisms in savannas: a unifying theory of long-term tree-grass coexistence. *Plant Ecology*. 150:161-171.
- Johnson, F. L., and P. G. Risser. 1973. Correlation analysis of rainfall and annual ring index of central Oklahoma blackjack and post oak. *American Journal of Botany*. 60:475-478.
- Johnson, F. L., and P. G. Risser. 1975. A quantitative comparison between an oak forest and an oak savannah in central Oklahoma. *The Southwestern Naturalist*. 20:75-84.
- Knapp, A. K., J. M. Briggs, J. M. Blair, and C. L. Turner. 1998. Patterns and controls of aboveground net primary production in tallgrass prairie. *Grassland dynamics: long-term ecological research in tallgrass prairie*. Oxford University Press, New York, New York, USA:193-221.
- Knoop, W., and B. Walker. 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. *The Journal of Ecology*. 73:235-253.
- Laio, F., A. Porporato, L. Ridolfi, and I. Rodriguez-Iturbe. 2001. Plants in water-controlled ecosystems: Active role in hydrologic processes and response to water stress: II. Probabilistic soil moisture dynamics. *Advances in Water Resources*. 24:707-723.
- Lambin, E. F., B. L. Turner, H. J. Geist, S. B. Agbola, A. Angelsen, J. W. Bruce, O. T. Coomes, R. Dirzo, G. Fischer, and C. Folke. 2001. The causes of land-use and land-cover change: moving beyond the myths. *Global environmental change*. 11:261-269.
- Lauenroth, W., D. Urban, D. Coffin, W. Parton, H. Shugart, T. Kirchner, and T. Smith. 1993. Modeling vegetation structure-ecosystem process interactions across sites and ecosystems. *Ecological Modelling*. 67:49-80.

- Leonard, R. E. 1961. Net precipitation in a northern hardwood forest. *Journal of Geophysical Research*. 66:2417-2421.
- Masters, R. E., and D. M. Engle. 1994. Behavior: Evaluated for Prescribed Fire Planning in Mountainous Oak: Shortleaf Pine Habitats. *Wildlife Society Bulletin*. 22:184-191.
- Masters, R. E., R. L. Lochmiller, and D. M. Engle. 1993. Effects of timber harvest and prescribed fire on white-tailed deer forage production. *Wildlife Society Bulletin*. 21:401-411.
- Masters, R. E., and J. Waymire. 2012. Developing Management Strategies from Research: Pushmataha Forest Habitat Research Area, Oklahoma Wildlife Science: Connecting Research with Management. 272:303.
- Masters, R. E., J. Waymire, T. Bidwell, R. Houchin, and K. Hitch. 2006. Influence of Timber Harvest and Fire Frequency on Plant Community Development and Wildlife. *in* T. T. R. Station, editor. *Integrated Land Management Options*
- McPherson, G. R. 1997. Ecology and management of North American savannas. University of Arizona Press.
- Medina, E., and J. F. Silva. 1990. Savannas of northern South America: a steady state regulated by water-fire interactions on a background of low nutrient availability. *Journal of Biogeography*. 17:403-413.
- Mitchell, J., and S. Popovich. 1997. Effectiveness of basal area for estimating canopy cover of ponderosa pine. *Forest Ecology and Management*. 95:45-51.
- Murphy, B. P., J. Russell-Smith, F. A. Watt, and G. D. Cook. 2009. Fire management and woody biomass carbon stocks in mesic savannas. Culture, ecology and economy of fire management in north Australian savannas, Collingwood: CSIRO Publishing:361-378.
- Mussche, S., R. Samson, L. Nachtergale, A. De Schrijver, R. Lemeur, and N. Lust. 2001. A comparison of optical and direct methods for monitoring the seasonal dynamics of leaf area index in deciduous forests. *Silva Fennica*. 35:373-384.

- Muzylo, A., P.Llorens, F.Valente, J. J. Keizer, F.Domingo, and J. H. C. Gash. 2009. A review of rainfall interception modelling. *Journal of Hydrology*. 370:191-206.
- Oklahoma Climatological Survey. 1994. Retrieved March 22, 2014 from [http://www.mesonet.org/index.php/weather/category/past data files](http://www.mesonet.org/index.php/weather/category/past_data_files).
- Peterson, D. W., and P. B. Reich. 2001. Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. *Ecological Applications*. 11:914-927.
- Pypker, T. G., D. F. Levia, J. Staelens, and J. T. Van Stan II. 2011. Canopy structure in relation to hydrological and biogeochemical fluxes. Pages 371-388 *Forest Hydrology and Biogeochemistry*. Springer.
- Ramankutty, N., and J. A. Foley. 1999. Estimating historical changes in global land cover: Croplands from 1700 to 1992. *Global Biogeochemical Cycles*. 13:997-1027.
- Ratajczak, Z., J. B. Nippert, and S. L. Collins. 2012. Woody encroachment decreases diversity across North American grasslands and savannas. *Ecology*. 93:697-703.
- Rice, E. L. 1959. The upland forests of Oklahoma. *Ecology*. 40:593-608.
- Sala, O. E., W. Parton, L. Joyce, and W. Lauenroth. 1988. Primary production of the central grassland region of the United States. *Ecology*. 69:40-45.
- Scholes, R., and S. Archer. 1997. Tree-grass interactions in savannas. *Annual review of Ecology and Systematics*. 28:517-544.
- Scholes, R., and D. Hall. 1996. The carbon budget of tropical savannas, woodlands and grasslands. SCOPE-Scientific Committee on Problems of the Environment International Council of Scientific Unions. 56:69-100.
- Schäfer, K. V.R. & Dirk, V. W. 2011. The Physical Environment Within Forests. *Nature Education Knowledge*. 2 1:5
- Sims, P. L., and J. Singh. 1978. The structure and function of ten western North American grasslands: III. Net primary production, turnover and efficiencies of energy capture and water use. *The Journal of Ecology*. 66:573-597.

- Soriano, A., and O. Sala. 1984. Ecological strategies in a Patagonian arid steppe. *Vegetatio*. 56:9-15.
- Sternitzke, H. S., and C. C. Van Sickle. 1968. East Oklahoma forests. Southern Forest Experiment Station.
- Teuling, A. J., R. Uijlenhoet, F. Hupet, and P. A. Troch. 2006. Impact of plant water uptake strategy on soil moisture and evapotranspiration dynamics during drydown. *Geophysical Research Letters* 33.
- Topp, G., J. Davis, and A. P. Annan. 1980. Electromagnetic determination of soil water content: Measurements in coaxial transmission lines. *Water Resources Research*. 16:574-582.
- Topp, G., W. Zebchuk, J. Davis, and W. Bailey. 1984. The measurement of soil water content using a portable TDR hand probe. *Canadian Journal of Soil Science*. 64:313-321.
- Van Dijk, A. I. J. M., and L. A. Bruijnzeel. 2001. Modelling rainfall interception by vegetation of variable density using an adapted analytical model. Part 1. Model description. *Journal of Hydrology*. 247:230-238.
- Van Langevelde, F., C. A. Van De Vijver, L. Kumar, J. Van De Koppel, N. De Ridder, J. Van Andel, A. K. Skidmore, J. W. Hearne, L. Stroosnijder, and W. J. Bond. 2003. Effects of fire and herbivory on the stability of savanna ecosystems. *Ecology*. 84:337-350.
- Van Wijk, M. T., and I. Rodriguez-Iturbe. 2002. Tree-grass competition in space and time: Insights from a simple cellular automata model based on ecohydrological dynamics. *Water Resources Research*. 38:18.11-15.
- Verry, E. S. 1976. Estimating water yield differences between hardwood and pine forests: an application of net precipitation data. North Central Forest Experiment Station, St. Paul, Minn.
- Vogan, P. J., and R. F. Sage. 2011. Water-use efficiency and nitrogen-use efficiency of C3-C4 intermediate species of *Flaveria* Juss. (Asteraceae). *Plant, Cell & Environment*. 34:1415-1430.

- Walker, B. H., D. Ludwig, C. S. Holling, and R. M. Peterman. 1981. Stability of Semi-Arid Savanna Grazing Systems. *Journal of Ecology*. 69:473-498.
- Walker, B. H., and I. Noy-Meir. 1982. Aspects of the stability and resilience of savanna ecosystems. Pages 556-590 *Ecology of tropical savannas*. Springer.
- Walter, H., and D. Mueller-Dombois. 1971. *Ecology of tropical and subtropical vegetation*. Edinburgh, UK, Oliver & Boyd.
- Webb, W., S. Szarek, W. Lauenroth, R. Kinerson, and M. Smith. 1978. Primary productivity and water use in native forest, grassland, and desert ecosystems. *Ecology*. 59:1239-1247.
- Weltzin, J. F., and G. R. McPherson. 2000. Implications of precipitation redistribution for shifts in temperate savanna ecotones. *Ecology*. 81:1902-1913.
- Williams, R., G. Duff, D. Bowman, and G. Cook. 1996. Variation in the composition and structure of tropical savannas as a function of rainfall and soil texture along a large-scale climatic gradient in the Northern Territory, Australia. *Journal of Biogeography*. 23:747-756.
- Zhang, J., W. C. Wang, and J. Wei. 2008. Assessing land-atmosphere coupling using soil moisture from the Global Land Data Assimilation System and observational precipitation. *Journal of Geophysical Research: Atmospheres* (1984–2012) 113.
- Zhang, L., W. Dawes, and G. Walker. 2001. Response of mean annual evapotranspiration to vegetation changes at catchment scale. *Water Resources Research*. 37:701-708.

APPENDICES

TABLES

Table 1. Summary of reps and treatments operations of Forest Habitat Research Area (FHRA).

| Treatment | Reps | Prescribed fire frequency | Harvest |
|-----------|------|---------------------------|-------------------------------------|
| Control | 3 | None | None |
| RRB | 3 | 4-yr | None |
| HT | 3 | None | Harvest pine, thin hardwoods |
| CCSP | 3 | periodic | Clear-cut, loblolly pine plantation |
| HT4 | 3 | 4-yr | Harvest pine, thin hardwoods |
| HT3 | 2 | 3-yr | Harvest pine, thin hardwoods |
| HT2 | 3 | 2-yr | Harvest pine, thin hardwoods |
| HT1 | 3 | Annual | Harvest pine, thin hardwoods |
| HNT1 | 3 | Annual | Harvest pine |

Table 2. Overall means and standard deviations of total basal area (BA) and conifer BA; total tree density and conifer density; total canopy openness; and quadratic mean diameter (QMD) from all treatments. The BA and tree density were measured in 2011 and canopy openness in midsummer 2013.

| Treatments | Total BA (m ² ha ⁻¹) | | Conifer BA (m ² ha ⁻¹) | | Total Density (tress ha ⁻¹) | | Conifer Density (tress ha ⁻¹) | | Canopy Openness (%) | | QMD (cm) | |
|------------|--|------|--|------|--|-------|--|--------|------------------------|------|-------------|------|
| | mean | s.d. | mean | s.d. | mean | s.d. | mean | s.d. | mean | s.d. | mean | s.d. |
| CONT | 29.4 | 3.6 | 16.9 | 4.9 | 939.0 | 161.3 | 338.7 | 23.0 | 24.3 | 2.2 | 22.5 | 1.7 |
| RRB | 26.5 | 4.7 | 15.4 | 2.3 | 803.1 | 458.4 | 290.0 | 72.6 | 28.2 | 1.9 | 23.9 | 2.5 |
| CCSP | 26.6 | 6.7 | 25.6 | 8.1 | 922.0 | 412.9 | 599.0 | 12.6 | 29.8 | 5.0 | 22.3 | 4.5 |
| HT | 35.3 | 4.8 | 24.2 | 10.7 | 3400.5 | 810.2 | 2011.0 | 186.0 | 19.8 | 1.1 | 12.1 | 1.7 |
| HT4 | 17.5 | 7.9 | 13.0 | 8.0 | 2264.0 | 267.6 | 1158.1 | 1012.7 | 45.2 | 14.0 | 12.1 | 0.8 |
| HT3 | 6.5 | 0.8 | 3.3 | 1.6 | 265.7 | 210.4 | 136.0 | 88.5 | 68.5 | 3.2 | 22.9 | 8.8 |
| HT2 | 8.0 | 0.8 | 3.9 | 0.9 | 310.0 | 185.5 | 148.9 | 52.3 | 66.7 | 6.3 | 22.6 | 6.9 |
| HT1 | 4.1 | 1.3 | 1.6 | 1.00 | 187.9 | 114.2 | 130.8 | 121.3 | 76.2 | 12.2 | 19.7 | 4.8 |
| HNT1 | 8.1 | 1.9 | 1.0 | 0.7 | 493.1 | 160.4 | 185.6 | 141.4 | 63.0 | 5.0 | 21.8 | 2.4 |

Table 3. Overall means and standard deviations of understory aboveground annual productivity (ANPP) and percentage of grass; litterfall accumulation; vertical depth of the probe insertion (maximum 20 cm) inside of clipping area, and year or last burn from all treatments.

| Treatment | Understory ANPP (g m ⁻²) | | Litter (g m ⁻²) | | Insertion depth (cm) | | Year Last Burned |
|-----------------|---|-------|--------------------------------|-------|-------------------------|------|---------------------|
| | mean | s.d. | mean | s.d. | mean | s.d. | |
| - 2012 - | | | | | | | |
| CONT | 14.9 | 4.9 | 1698.7 | 580.8 | 8.3 | 1.0 | |
| RRB | 45.8 | 14.3 | 1328.6 | 336.2 | 10.6 | 1.4 | 2009 |
| CCSP | 85.4 | 50.7 | 625.0 | 284.5 | 8.7 | 2.8 | 2012 |
| HT | 7.3 | 4.5 | 1738.6 | 497.3 | 11.1 | 0.8 | |
| HT4 | 98.0 | 17.9 | 751.9 | 282.2 | 8.3 | 1.1 | 2009 |
| HT3 | 234.4 | 62.7 | 258.0 | 213.8 | 7.2 | 2.1 | 2012 |
| HT2 | 331.5 | 108.2 | 315.7 | 95.2 | 10.5 | 3.3 | 2011 |
| HT1 | 260.8 | 16.6 | 169.0 | 77.7 | 9.2 | 1.9 | 2012 |
| HNT1 | 207.4 | 131.5 | 269.1 | 135.0 | 10.9 | 2.5 | 2012 |
| - 2013 - | | | | | | | |
| CONT | 18.7 | 9.4 | 1672.4 | 490.6 | 9.1 | 1.1 | |
| RRB | 25.0 | 5.8 | 1065.2 | 189.8 | 10.6 | 1.6 | 2013 |
| CCSP | 122.8 | 100.3 | 1122.0 | 559.6 | 8.3 | 1.9 | 2012 |
| HT | 12.1 | 11.1 | 1418.7 | 265.5 | 9.5 | 1.4 | |
| HT4 | 188.5 | 143.4 | 384.7 | 167.5 | 7.3 | 0.8 | 2013 |
| HT3 | 354.7 | 7.1 | 358.9 | 219.9 | 5.5 | 0.2 | 2012 |
| HT2 | 327.0 | 85.6 | 137.8 | 29.6 | 7.6 | 2.8 | 2013 |
| HT1 | 348.4 | 199.0 | 105.1 | 38.4 | 9.0 | 2.8 | 2013 |
| HNT1 | 327.1 | 58.3 | 132.7 | 69.4 | 9.1 | 2.6 | 2013 |

Table 4. Overall means, standard deviations, maximums and minimums of volumetric water content (VWC) from periodic measurements of 260 sample points during the study period. Means and standard errors were back-transformed from the log-scale for reporting.

| Treatments | Volumetric Water Content (%) | | | |
|------------|------------------------------|----------|------|-----|
| | mean | std err. | max | min |
| CONT | 5.1 | 1.2 | 30.8 | 0.9 |
| RRB | 5.0 | 1.2 | 38.2 | 0.7 |
| CCSP | 5.4 | 1.2 | 25.9 | 1.0 |
| HT | 4.9 | 1.2 | 41.0 | 0.8 |
| HT4 | 6.6 | 1.2 | 26.6 | 0.8 |
| HT3 | 6.2 | 1.2 | 28.1 | 1.1 |
| HT2 | 6.3 | 1.2 | 40.7 | 1.2 |
| HT1 | 6.1 | 1.2 | 41.9 | 1.0 |
| HNT1 | 5.8 | 1.2 | 39.1 | 0.8 |

Table 5. Overall means, standard deviations, maximums and minimums of vegetation characteristic from the 30 VWC probe locations used for modeling soil moisture decay. Understory biomass productivity data were from October 2013.

| Variable | mean | s.d. | minimum | maximum |
|---|-------|--------|---------|---------|
| Total basal area (m ² ha ⁻¹) | 15.8 | 13.5 | 13.5 | 45.0 |
| Conifer basal area (m ² ha ⁻¹) | 10.0 | 11.7 | 0 | 33.0 |
| Trees per hectare | 890.7 | 1459.3 | 0 | 7152.0 |
| Conifer per hectare | 690.4 | 1326.5 | 0 | 6321.5 |
| QMD (cm) | 21.0 | 11.5 | 0 | 55.1 |
| Canopy openness (%) | 50.5 | 25.6 | 18.3 | 91.7 |
| Stoniness (cm) | 8.6 | 4.7 | 0 | 17.4 |
| Grass (g m ²) | 203.3 | 196.4 | 0 | 679.6 |
| Forb (g m ²) | 4.8 | 13.6 | 0 | 54.0 |
| Legume (g m ²) | 1.0 | 2.7 | 0 | 13.2 |
| Panicum (g m ²) | 7.9 | 29.6 | 0 | 160.4 |
| Sedge (g m ²) | 0 | 0 | 0 | 0 |
| Woody (g m ²) | 21.4 | 42.2 | 0 | 150.0 |
| Litter (g m ²) | 688.5 | 800.3 | 0 | 2374.8 |

Table 6. Statistical analysis results of canopy interception prediction model.

| Effect | Estimate | Standard error | Pr> t |
|--------------------------|----------|----------------|--------|
| Intercept | 2.7971 | 0.09069 | <.0001 |
| Total BA | -0.00264 | 0.000883 | 0.003 |
| Conifer BA | 0.004707 | 0.00911 | <.0001 |
| Total Density | -0.00099 | 0.000196 | <.0001 |
| Conifer Density | 0.000742 | 0.000209 | 0.0004 |
| I _{stoniness} * | -0.02945 | 0.01232 | 0.0172 |
| Litter | -0.00044 | 0.00008 | <.0001 |

* Index of stoniness

Table 7. Statistical analysis results of soil moisture decay predictor model.

| Effect | Year | Estimate | Standard Error | Pr> t |
|--------------------------|------|----------|----------------|--------|
| Intercept | | -0.04252 | 0.004471 | <.0001 |
| PAN | | -0.2608 | 0.1128 | 0.0344 |
| VDEF | | 0.001966 | 0.0001832 | 0.2983 |
| I _{stoniness} * | | -0.00399 | 0.000855 | <.0001 |
| QMD | | 0.00013 | 0.000025 | <.0001 |
| BA*year | 2012 | -0.0004 | 0.000062 | <.0001 |
| BA*year | 2013 | -0.00037 | 0.00006 | <.0001 |
| Conifer BA | | 0.000518 | 0.000061 | <.0001 |
| Total Density | | 0.000038 | 0.000013 | 0.0042 |
| Conifer Density | | -0.00004 | 0.000014 | 0.0015 |
| Woody*year | 2012 | -0.00005 | 0.000055 | 0.3153 |
| Woody*year | 2013 | 0.000405 | 0.000114 | 0.0004 |

* Index of stoniness

FIGURES

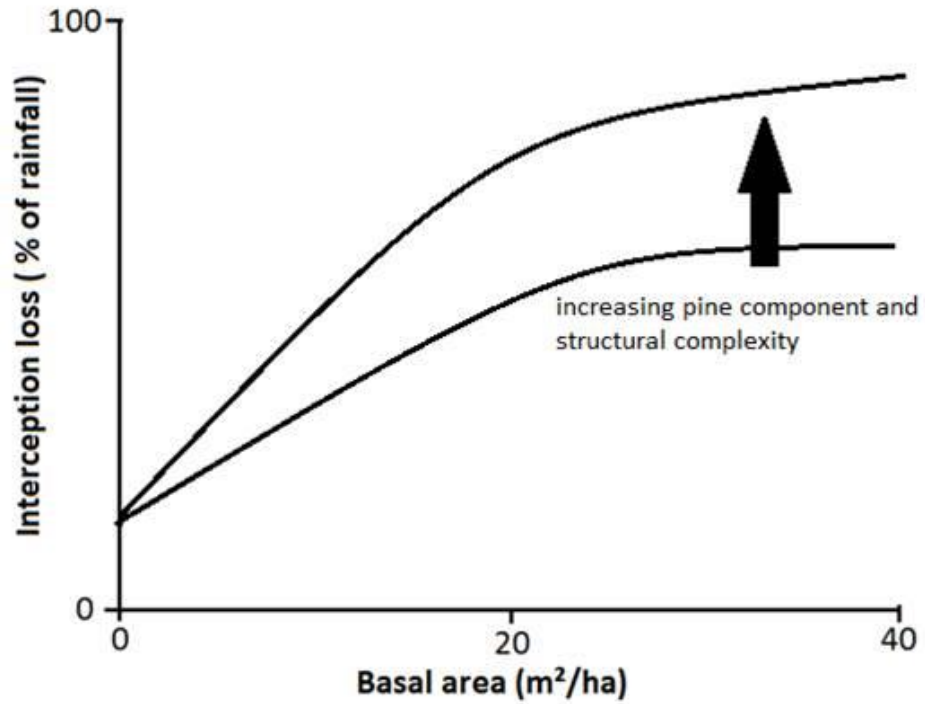


Figure 1. Hypothetical relationship between interception loss (% of rainfall) and basal area (m² ha⁻¹) inside the grassland-forest ecotone during a moderate rainfall event in the middle of the growing season. Hypothesized effects of secondary parameters (i.e.: structural complexity and canopy species dominance) on interception loss are shown.

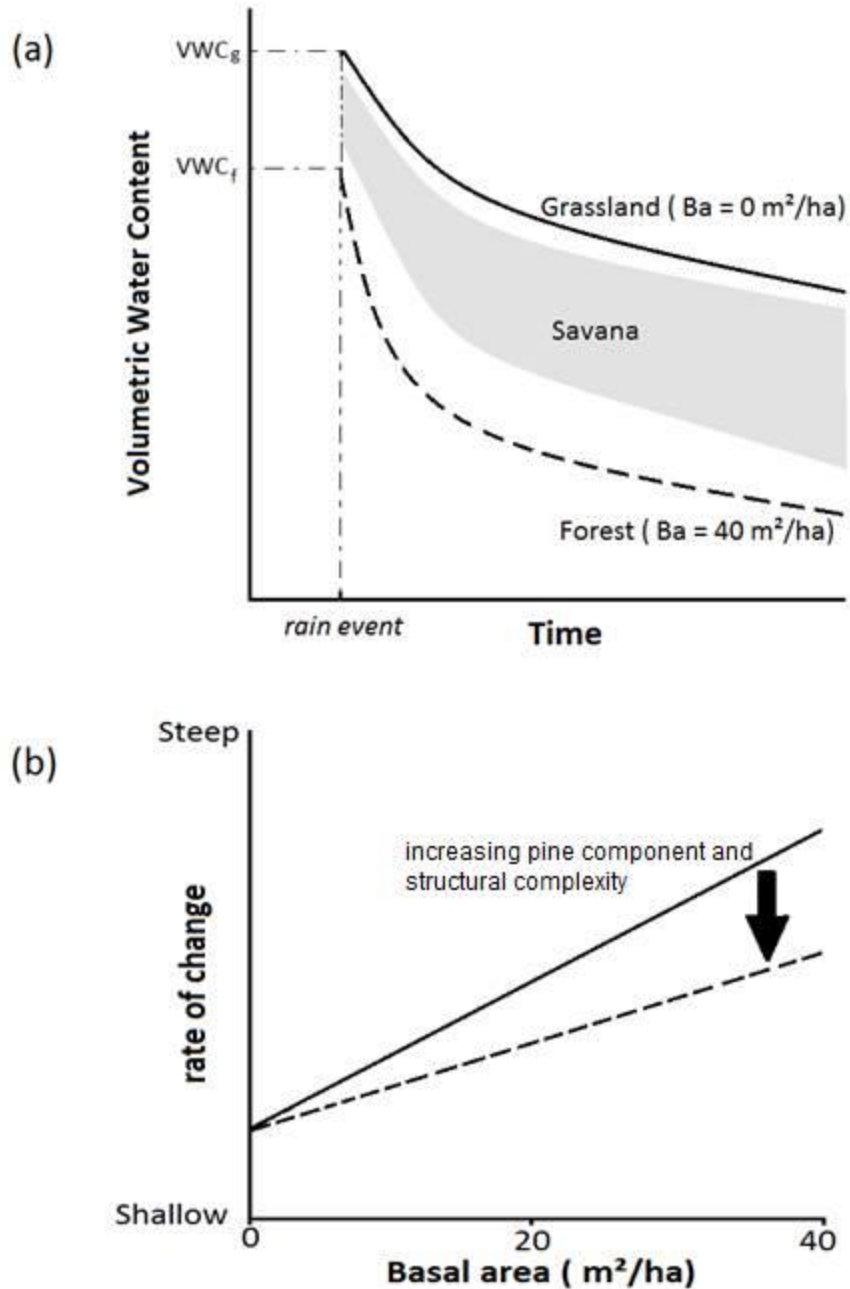


Figure 2. Model showing the soil water dynamics after a rainfall event in the middle of the growing season. The points *rain event*, VWC_g and VWC_f indicate the instant the rain has ceased and the peak volumetric water content for prairie and forest, respectively (a); and a diagram showing the relationship between the rate of change in the soil water content and basal area (m² ha⁻¹). Hypothesized effects of secondary parameters (tree age, canopy species composition (pine vs. oak), leaf area index and canopy architecture) on soil moisture dynamic (b).

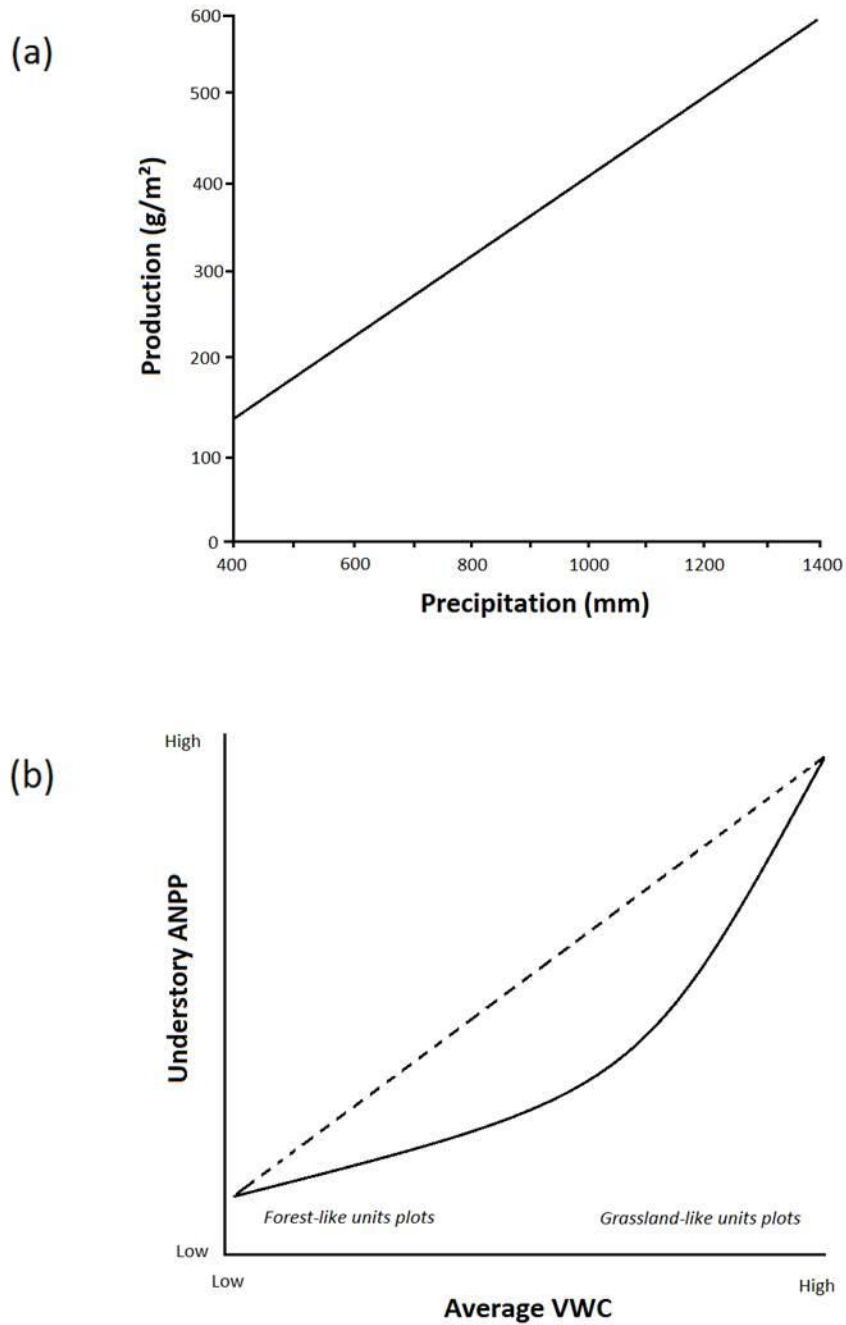


Figure 3. Hypothetical relationship between mean annual precipitation (mm) and mean understory aboveground net primary production ANPP (g m^{-2}) for grassland-like units plots based on Sala et al. (1988) (a); and a diagram showing the relationship between understory ANPP and average of volumetric water content VWC across all units plots. Dashed line indicates the water-stress only hypothesis (b).

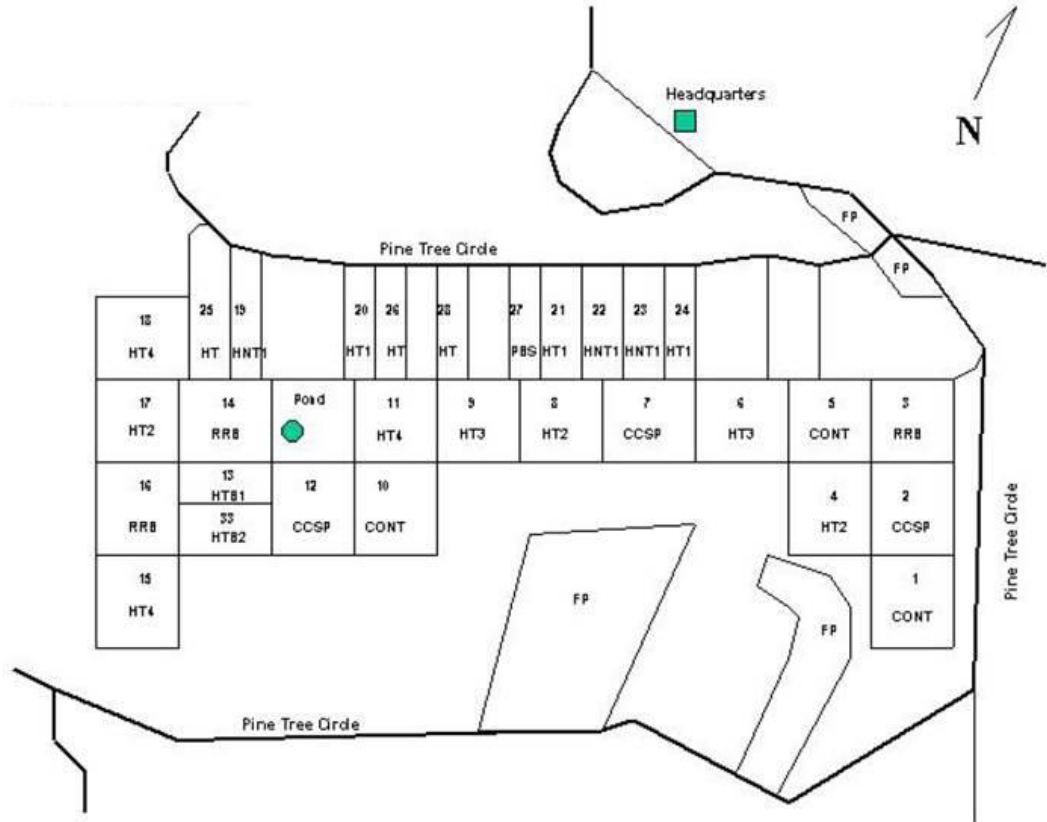


Figure 4. Map of the Forest Habitat Research Area (FHRA) with treatments and replications. Forage production (FP), pond and # 13, 27, 33 units were not used in this study.

UNIT 1:28

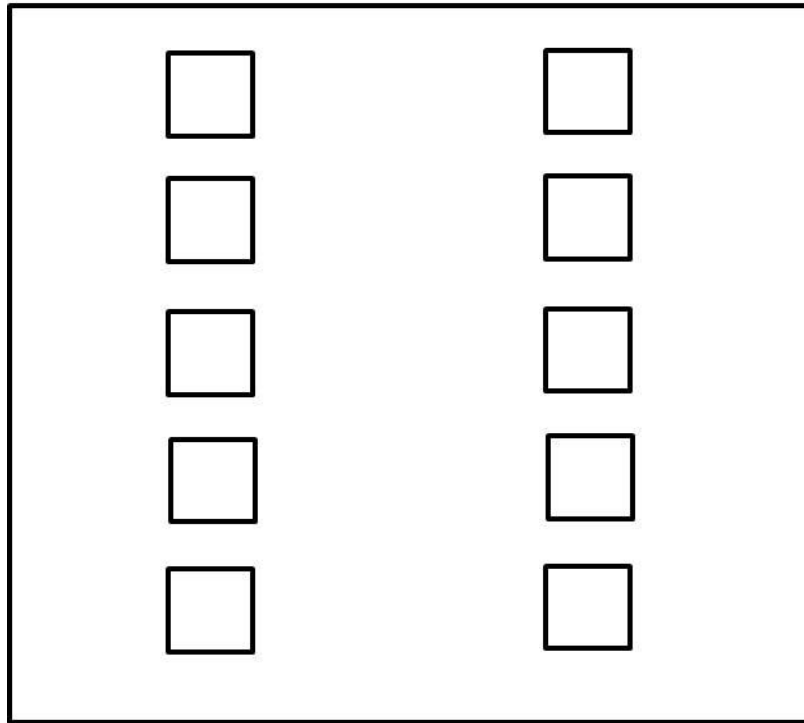


Figure 5. Diagram showing the 10 permanent plots (4x 4 meters) arrangement inside of each unit (0.8 to1.6 hectare).

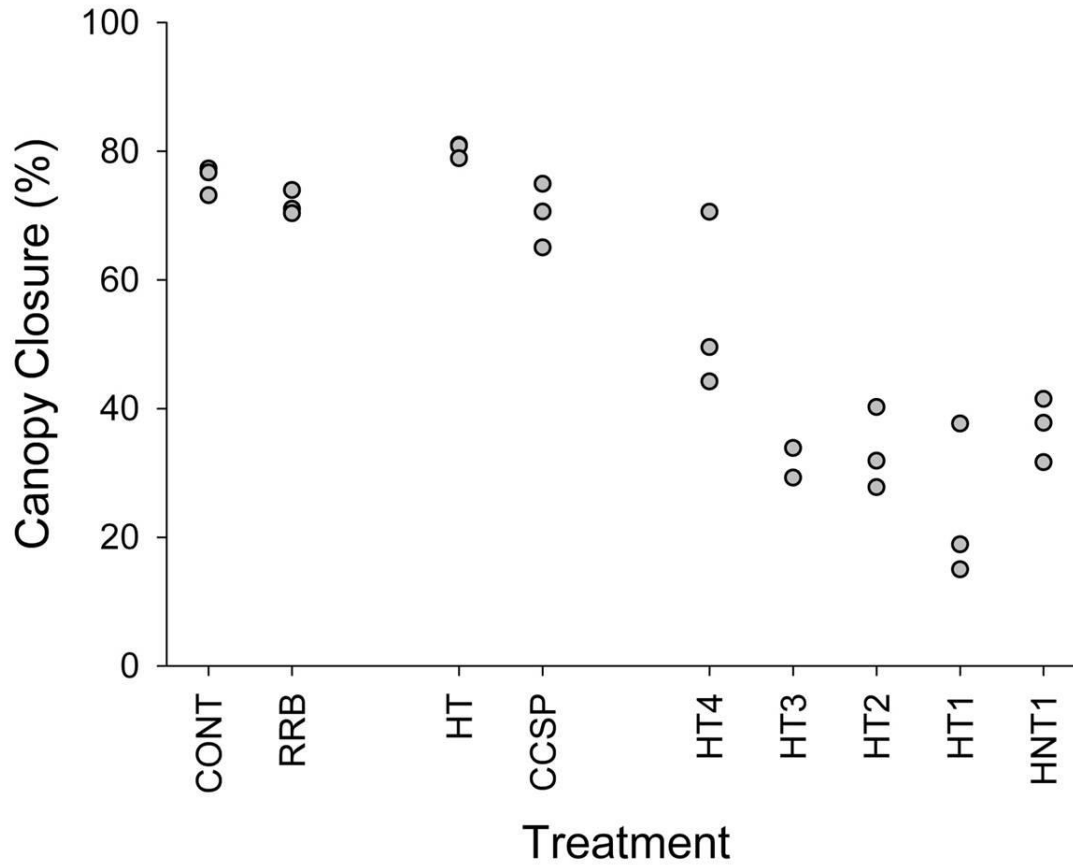


Figure 6. Canopy structure in terms of canopy closure (%) across all treatments. Each dot represents overall mean from each treatment unit. Treatment HT3 had just two replications.

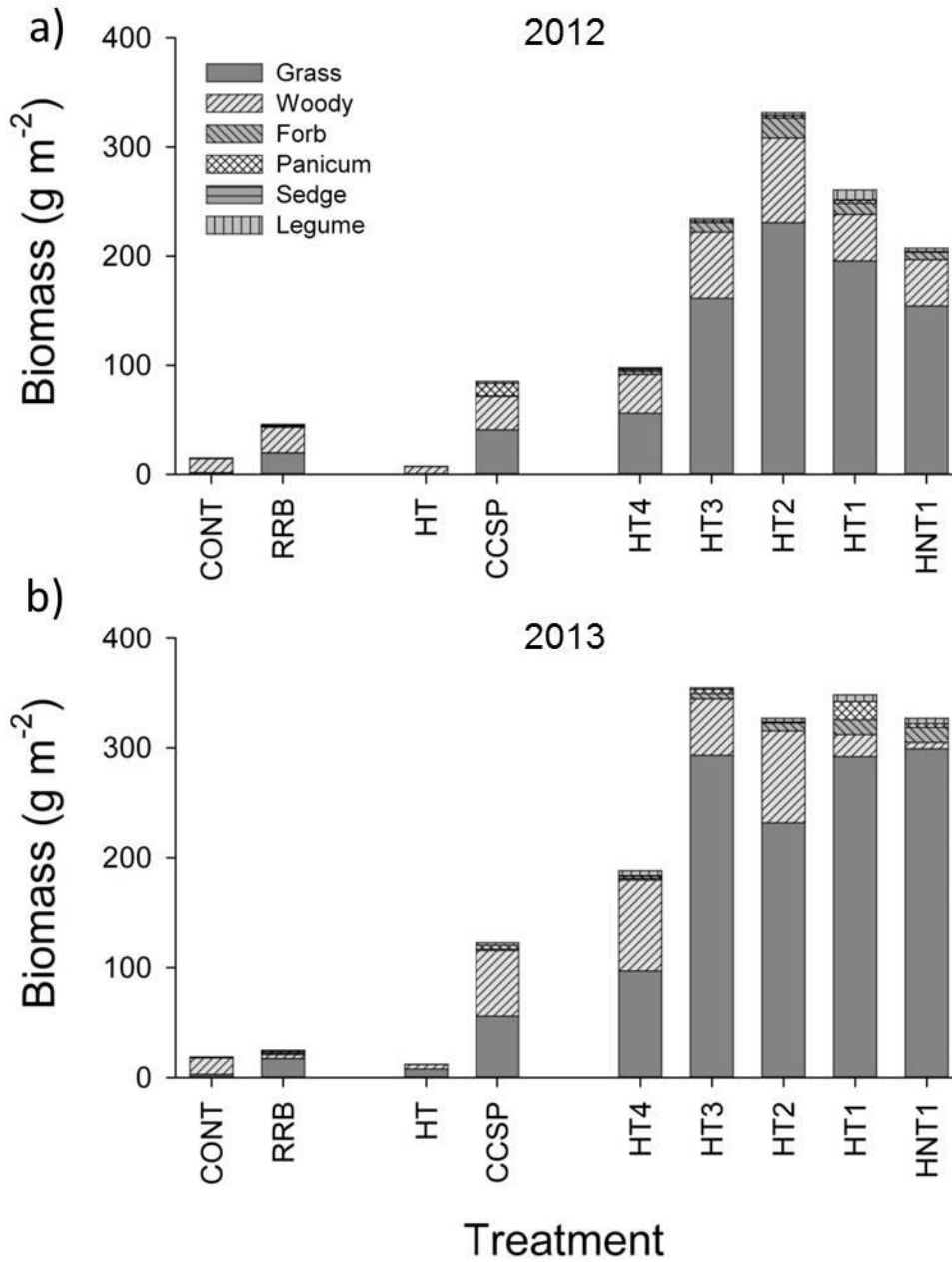


Figure 7. Understory biomass productivity separated by plants functional groups across all treatments from 2012 (a) and 2013 (b).

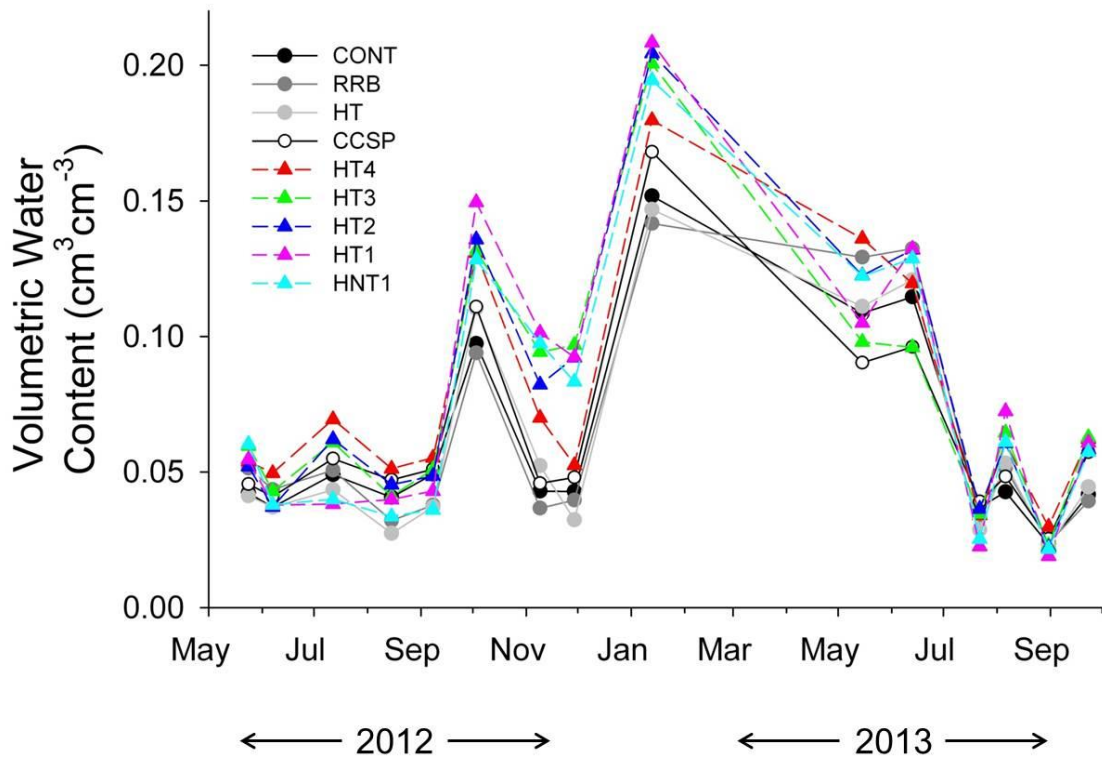


Figure 8. Mean volumetric water content in the upper 15 cm of the soil layer on 15 occasions across all 260 sample points during the study period.

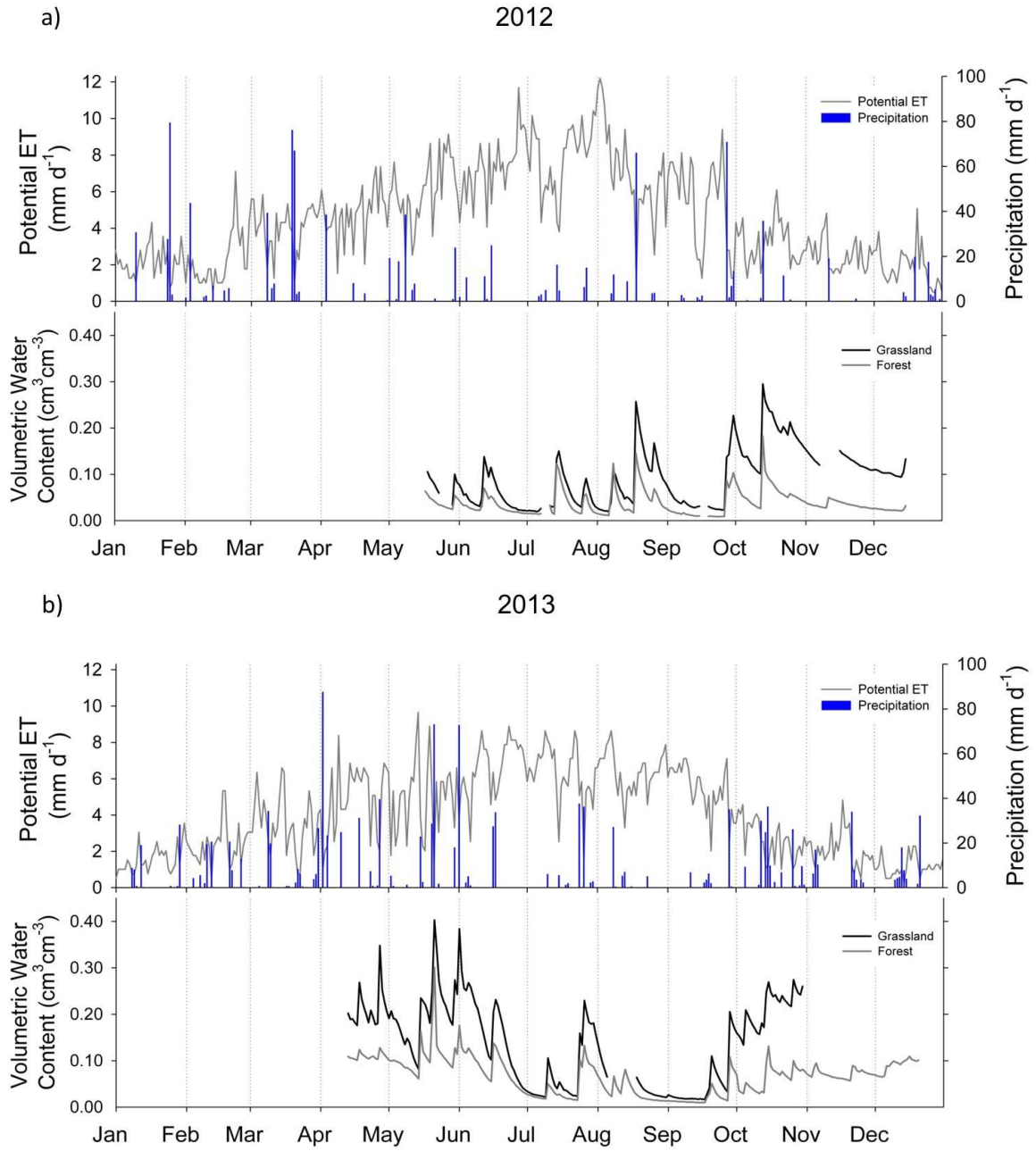


Figure 9. Daily potential evapotranspiration (open-pan) and precipitation observations on top panels; soil moisture observations from late growing season in the upper 15 cm soil layer on bottom panels. Two representative VWC probes were chosen from grassland (HT1) and conifer forest (HT) treatments. Year 2012 (a) and 2013 (b).

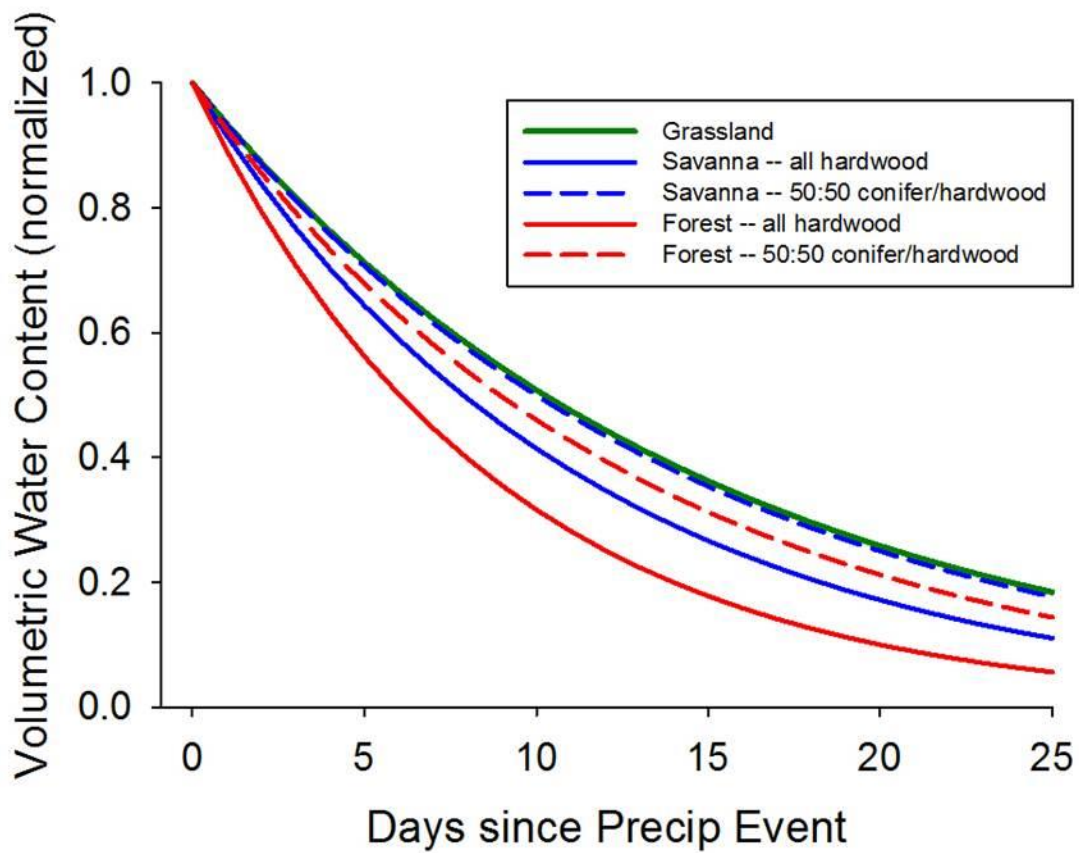


Figure 10. Soil moisture decay rate model predictions relative to tree basal area for grassland, savanna and forest. Basal area was set to $32 \text{ m}^2 \text{ ha}^{-1}$ in the forest, $16 \text{ m}^2 \text{ ha}^{-1}$ in the savanna, and zero in the grassland. Potential ET was set at an average summer value. Other parameters in the model were constant across structures or were proportional in the case of tree density.

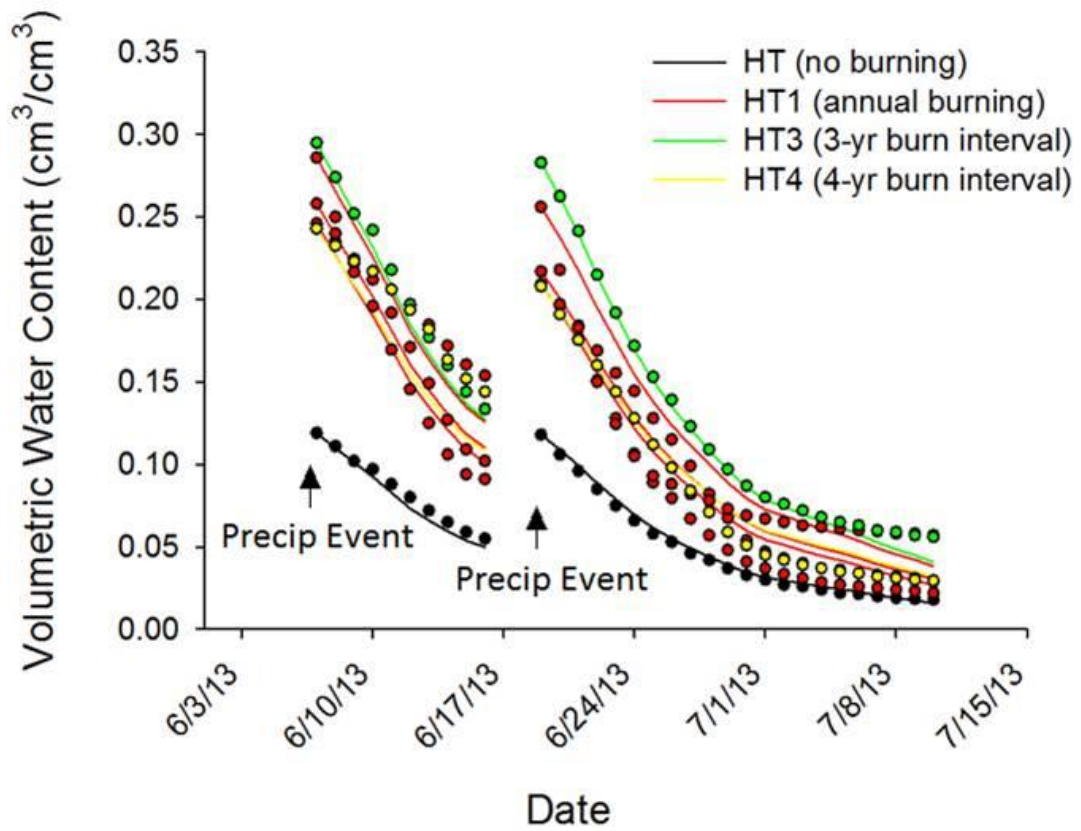


Figure 11. Modeled (lines) and observed daily volumetric water content (points) from 4 example VWC probes from different vegetation structures, and during two consecutive precipitation events.

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