

# Water use of *Juniperus virginiana* trees encroached into mesic prairies in Oklahoma, USA

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## ABSTRACT

*Juniperus virginiana* (eastern redcedar) is encroaching into mesic prairies of the southern Great Plains, USA, and is altering the hydrologic cycle. We used the thermal dissipation technique to quantify daily water use of *J. virginiana* into a mesic prairie by measuring 19 trees of different sizes from different density stands located in north-central Oklahoma during 2011. We took the additional step to calibrate our measurements by comparing thermal dissipation technique estimates to volumetric water use for a subset of trees. Except for days with maximum air temperature below  $-3^{\circ}\text{C}$ , *J. virginiana* trees used water year round, reached a peak in late May, and exhibited reduced water use in summer when soil water availability was low. Overall daily average water use was 241 ( $\pm 21.8$  l s.d.) per tree. Trees in low density stands used more water than trees with similar diameters from denser stands. However, there was no difference in water use between trees in different density stands when expressed on a canopy area basis. Approximately 50% of variation in water use that remained after accounting for the factors site, tree, and day was explained using a physiologically-based model that included daily potential evapotranspiration, maximum vapour pressure deficit, maximum temperature, solar radiation, and soil water storage between 0 and 10 cm. Our model suggested that a *J. virginiana* woodland with a closed canopy is capable of transpiring almost all precipitation reaching the soil in years with normal precipitation, indicating the potential for encroachment to reduce water yield for streamflow and groundwater recharge. Copyright © 2013 John Wiley & Sons, Ltd.

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## INTRODUCTION

Woody plants are encroaching into grassland ecosystems throughout the world (Van Auken, 2000; Archer *et al.*, 2001), potentially transforming the biogeochemical cycles of these important ecosystems (Engle *et al.*, 2008; Knapp *et al.*, 2008). *Juniperus* spp., primarily *Juniperus virginiana*, have encroached into grasslands over large areas of the Great Plains, e.g. approximately 5 million ha in Oklahoma, as well as several million more hectares in Texas, Kansas, and Nebraska (Engle *et al.*, 2008). As one of the major genera of woody plants encroaching into grassland ecosystems in North America (Engle *et al.*, 2008), understanding water use by *Juniperus* spp. is important to quantify watershed-level hydrological changes associated with the spread of woody plants. To that end, several studies have measured *Juniperus* spp. water use directly (Owens, 1996; Leffler *et al.*, 2002; Awada *et al.*, 2012) or

estimated it using a water balance approach (Lane and Barnes, 1987; Dugas *et al.*, 1998). However, these studies were conducted mainly in semi-arid locations with karst geology or deep, sandy soil and are less relevant for locations in the eastern portion of the Great Plains, which receive greater than 600 mm precipitation per year.

The replacement of  $C_4$ , warm-season grasses by the  $C_3$ , evergreen *J. virginiana* alters phenology as well as the rates and efficiencies of physiological processes and plant water use. *J. virginiana* is physiologically active year round compared with 5 months for grasses (Knapp *et al.*, 2008). As the result of a longer growing season and greater leaf area, *J. virginiana* woodlands annually produce two to three times more aboveground biomass than native, warm-season grasslands and accumulate more than 20 times the aboveground standing biomass (Briggs and Knapp, 1995; Norris *et al.*, 2001; Lett *et al.*, 2004). *J. virginiana* is drought tolerant and maintains stomatal conductance at extremely low soil water potentials (Eggemeyer *et al.*, 2006; Willson and Jackson, 2006; Bihmidine *et al.*, 2010; Volder *et al.*, 2010). Additionally, *Juniperus* spp. generally have deeper rooting systems than most grasses and are able

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to access water at depths unavailable to grasses (Huxman *et al.*, 2005; Tennesen, 2008). *J. virginiana* exhibits flexibility by exploiting water from deeper soil layers during dry periods and from the upper soil when shallow water is available (Eggemeyer *et al.*, 2008).

Measurements of plant water use are required for accurate estimation of the ecosystem water balance. Sap flow measurements of individual trees can be scaled to the stand-level by using variables that are easy to measure such as stem diameter at breast height (DBH) (Vertessy *et al.*, 1995), basal area (Teskey and Sheriff, 1996), crown or leaf area (Hatton *et al.*, 1995), or sapwood area (Dunn and Connor, 1993). Measurement of tree water use over periods representing all different seasons and weather conditions are necessary to extrapolate tree water use to an annual basis.

Plant water use varies depending on environmental conditions and species-specific characteristics (Farmer, 1918; Oren and Pataki, 2001; Tang *et al.*, 2006; Loranty *et al.*, 2008; Heilman *et al.*, 2009). Determining water use of *J. virginiana* invading a mesic prairie will provide a better understanding of the changes in this ecosystem's water balance due to encroachment. Our objective was to quantify, scale, and predict the water use by individual *J. virginiana* trees of encroached watersheds in north-central Oklahoma by measuring sap flow density ( $\text{cm}^3 \text{H}_2\text{O cm}^{-2} \text{sapwood h}^{-1}$ ) using thermal dissipation probes (TDP) (Granier, 1985). We measured water use across a range of tree ages and diameters in low-density and high-density stands. To ensure accuracy, we calibrated the TDP technique for *J. virginiana* by comparing actual water use of cut trees with sensor-based estimates of water use, a step not previously taken in sap flux studies in *Juniperus*. We scaled results from individual trees to the stand-level and compared water use with net rainfall input during the same period. We developed and parameterized a physiological model based on Fick's law (Nobel, 1999) to determine how environmental factors affect *J. virginiana* water use.

## MATERIALS AND METHODS

### *Study area description*

The research was conducted at the Cross Timbers Experimental Range (CTER), a 728-ha research and extension facility under the administration of Oklahoma Agricultural Experiment Station of Oklahoma State University. This site is located about 11 km southwest of Stillwater in Payne County, Oklahoma (36°04'N, 97°21'W) (Engle *et al.*, 2006). The climate is continental with an average growing season of 204 days. The average annual precipitation is 942 mm with 65% occurring from May to October. The temperature ranges from an average daily minimum of  $-4.3^\circ\text{C}$  in January to an average daily maximum of  $34^\circ\text{C}$  in August. The annual daily average is  $15^\circ\text{C}$  (Oklahoma Climatological Survey). Vegetation at CTER comprises cross timbers forest, savanna, and

tallgrass prairie. The cross timbers forest is dominated by hardwood species, such as post oak (*Quercus stellata*) and blackjack oak (*Quercus marilandica*) in the overstory, and hackberry (*Celtis occidentalis*) and American elm (*Ulmus americana*) in the understory. Dominant herbaceous species in the savanna and prairie areas are little bluestem (*Schizachyrium scoparium*), Indian grass (*Sorghastrum nutans*), western ragweed (*Ambrosia psilostachya*), Scribner's panicum (*Panicum oligosanthes*), purpletop (*Tridens flavus*), and lespedeza (*Lespedeza* spp.) (Ewing *et al.*, 1984). *J. virginiana* has invaded portions of the tallgrass prairie, and there are different stages of forest formation with canopy coverage approaching 100% in some locations.

Three sites of different *J. virginiana* growth patterns and canopy cover were selected from the encroached tallgrass prairie areas at CTER. Trees in the 'OG' site had an open-grown form that consisted of widely spaced trees with live branches along the entire stem. The 'CG' site had closely spaced trees with full canopy cover and trees with closed-grown form that was characterized by live branches only on the upper trunk. The 'mixed growth' site was a transition between open and closed forest and contained a mix of tree growth forms. Nineteen trees were measured with a range of diameters representing the variation at each site, five trees at the OG site, six at the CG site, and eight at the mixed growth with four each of open and closed growth form (MO and MC) (Table I).

### *Environmental data*

To relate water use to environmental conditions, meteorological variables were measured at a weather station located approximately 60, 160, and 400 m from the OG, CG, and mixed growth sites, respectively. Measurements taken at the station included air temperature and relative humidity (HMP50 Temperature/RH Probe with a 6-Plate Gill Solar Radiation Shield; Vaisala, Helsinki, Finland), wind speed and direction (03002 anemometer and vane; RM Young Company, Traverse City, MI), solar radiation (SP-110 Pyranometer; Apogee Instruments, Inc., Logan, UT), soil temperature at 5 cm depth (107-L temperature probe; Campbell Scientific, Logan UT), and precipitation (TB3 siphoning tipping bucket rain gauge with a 0.254 mm tip; Hydrological Services America, Lake Worth, FL). Data were recorded at 5-min intervals, and daily averages, maximums, and minimums were calculated (CR510 datalogger; Campbell Scientific, Logan, UT). These meteorological data were used to calculate potential evapotranspiration (PET) based on the Food and Agriculture Organization of the United Nations Penman–Monteith equation (Allen *et al.*, 1998). From February through April, PET was the reference ET based on a 'shortgrass' plant cover. From May onward, PET was the reference ET based on a 'tallgrass' plant cover.

Table I. Characteristics of *Juniperus virginiana* trees used to investigate water use for 2011 with thermal dissipation probes in encroached mesic tallgrass prairie watersheds.

Tree ID	Growth type	Age	DBH (cm)	Height (m)	Sapwood area (cm <sup>2</sup> )	Canopy area (m <sup>2</sup> )	Average (1 day <sup>-1</sup> )	Maximum (1 day <sup>-1</sup> )	Minimum (1 day <sup>-1</sup> )
OG1	Open	18	4	3	42	13	9.5	26.1	0.8
OG2	Open	26	17	8	88	12	23.5	58.9	1.7
OG3	Open	41	32	9	205	37	58.4	127.0	5.4
OG4	Open	46	23	6	276	29	61.9	142.2	9.9
OG5	Open	29	18	7	198	28	49.2	141.0	5.2
CG1	Closed	25	20	12	157	14	20.5	75.1	2.2
CG2	Closed	20	11	8	48	3	7.2	30.0	0.5
CG3	Closed	12	7	5	16	1	1.7	9.4	0.1
CG4	Closed	16	13	8	72	5	6.8	21.9	0.5
CG5	Closed	35	27	14	231	28	46.6	119.1	3.0
CG6	Closed	27	33	10	168	26	32.2	81.4	1.8
MO1	Open	35	31	8	370	67	65.6	161.4	3.8
MO2	Open	20	8	5	53	8	12.8	34.4	0.6
MO3	Open	10	2	8	10	2	1.6	8.2	0.0
MO4	Open	16	6	4	61	7	8.3	27.3	0.3
MC1	Closed	11	5	6	10	2	1.0	14.8	0.0
MC2	Closed	20	12	7	76	4	7.5	28.2	0.4
MC3	Closed	21	21	9	125	3	23.6	56.9	1.6
MC4	Closed	16	12	6	84	10	10.3	28.9	0.7

DBH is the diameter at breast height (1.37 m). Sapwood is the area of functional vascular tissue in a tree measured at height of probe insertion (between 0.5 and 1.5 m depending on the tree). Designations ‘O’, ‘C’, and ‘M’ in the tree ID refer to different sites.

Volumetric soil water content (cm<sup>3</sup> cm<sup>-3</sup>) was measured at each site with an array of frequency domain technology sensors (EC-5; Decagon Devices, Inc., Pullman, WA) consisting of four probes installed at depths of 5, 20, 45, and 80 cm. Soil moisture was measured every 15 min, and daily averages were calculated. Soil water storage was calculated for each of the four soil profile sections (0–10, 10–30, 30–60, and 60–100 cm). The distance from the soil moisture array to the trees was approximately 35, 45, and 30 m for OG, CG, and mixed growth sites, respectively. Soil water content at field capacity for the 0–10 cm layer was estimated to be 0.23 cm<sup>3</sup> cm<sup>-3</sup> by using equations provided by Saxton and Rawls (2006) based on soil texture, soil bulk density, and organic matter data.

*Water use*

Sap flow density was measured using TDP that were 2 mm in diameter and 10 or 30 mm in length (TDP-10 and TDP-30; Dynamax, Houston, TX). One set of 10 mm probes was used in trees with ≤5 cm DBH. Two or three sets of probes, with at least one set of each length, were used in trees with DBH >5 cm. The use of probes with different lengths in trees with >5 cm DBH was to account for possible variation in xylem radial and axial water movement. Water use calculated from multiple probes within trees was averaged. For trees equipped with 30 and 10 mm probes, the average sapwood

width at point of probe insertion was 30.4 ± 5.8 mm s.d. Trees with 10 mm probes only (four trees) had average sapwood width of 11.9 ± 1.5 mm s.d. Depending on the height of live branches, the probes were placed between 0.5 and 1.5 m above the ground (below all live branches). All probes were inserted in December of 2010, and sap flux was measured for the entire 2011 calendar year.

The temperature differential between the heated upper probe and the non-heated lower probe was measured every minute, and the hourly mean was calculated and recorded by a data logger (CR1000; Campbell Scientific, Logan UT). Sap flow was calculated according to Granier (1985) by using the maximum temperature differential to calculate  $K$  [ $K = (\Delta T_{max} - \Delta T) / \Delta T$ ] and then using  $K$  to calculate sap flux velocity [ $V = 0.0119 * K^{1.231}$  (cm s<sup>-1</sup>)], and  $V$  was converted to sap flow density ( $F_s = SA \times V \times 3600$  (cm<sup>3</sup> h<sup>-1</sup>)) where  $SA$  is sapwood area in cm<sup>2</sup>.

To measure the sapwood area, the trees were cut down after the study in March of 2012. A cross section of the stem at the height where the probes were inserted was traced on a piece of paper. Because of the difference in colour between the sapwood (white) and heartwood (red), it was possible to accurately distinguish sapwood from heartwood. The portion of the paper that represented sapwood area was then measured with a LI-3000 leaf area meter (Li-Cor Inc.; Lincoln, NE). Tree height, canopy dimensions, and DBH were also measured at time of harvest.

### Calibration

Two similar methods were used to calibrate the TDP technique for *J. virginiana* trees in our study. The first calibration experiment was conducted between August and September of 2011 by using additional trees from within the study area. The nine chosen trees (8 cm DBH  $\pm$  2.3 cm s.d.) were cut as close to the ground as possible and then placed immediately in buckets filled with water. Trees were then secured in large, fully filled water reservoirs ( $\sim$ 100l). Extra probes were used for this calibration with 30-mm-long and 10-mm-long probes inserted in opposite sides in each tree. Each hour for 10 h during daylight, water was added from a graduated cylinder to fully refill the reservoir, and actual water use was calculated. After completing daytime measurements, the sapwood was severed above the probes to prevent any nighttime water movement, and temperature differentials ( $dT_m$ ) were measured until dawn the next day. To ensure we severed all the sapwood, we cut into and around the tree until sawdust turned red (heartwood in *J. virginiana* is dark red). Sapwood area of each tree was measured using the methods outlined in the previous texts.

The second calibration was conducted in March of 2012 after completion of the study. Five trees (9 cm DBH  $\pm$  5.7 cm s.d.) from the sap flow experiment were used. We measured the actual hourly water use by cutting entirely through the sapwood below the probes and placing a bucket filled with water around the tree below the incision. To put the bucket around the tree, the bucket was cut horizontally into top and bottom sections as well as vertically so that the pieces of bucket could be placed around the tree. A hole in the bottom section of the bucket was cut just large enough to fit around the stem. The day before calibration, the bottom section of the bucket was set below the location where the cut was to be made and sealed to the tree by using expanding urethane foam, silicone caulk, and water proof tape. At 0800 the next day, the cut was made through the sapwood (cut until red sawdust was produced), and the top part of the bucket was reattached to the bottom by using waterproof tape. The buckets were filled with water less than 10 min after cutting the sapwood. The buckets were refilled from a graduated cylinder every hour for 10 h starting at 0900. Sapwood above the probes was severed after the daytime measurements were completed. Sapwood area was calculated after the trees were cut down.

Tree water use values calculated using the standard Granier equation (Granier, 1985) and the TDP probe data were calibrated using the actual water use based on water additions to the reservoirs. Estimated and actual cumulative 10 h water use were divided by the tree sapwood area, and a linear regression was used to determine the correction equation that was applied to daily water use estimates (Sun *et al.*, 2012) (Figure 1).

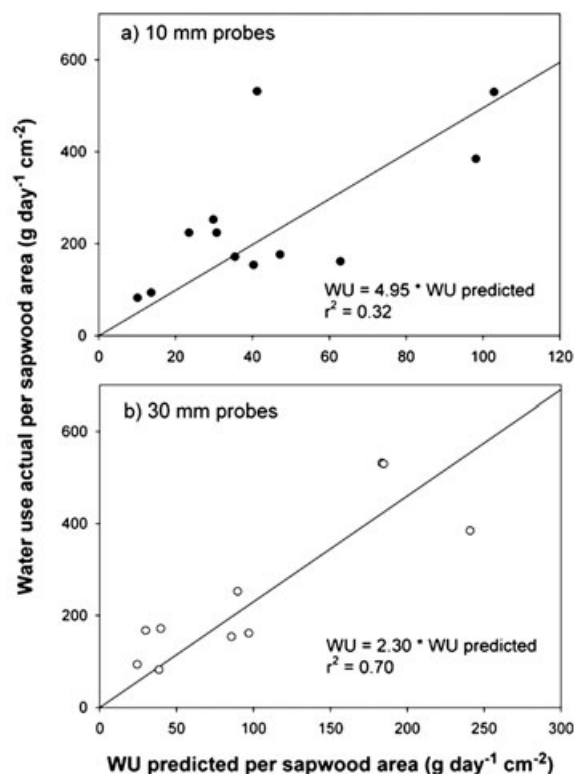


Figure 1. Relationship between *J. virginiana* actual daily water use (WU) and the predicted daily water use for 10 mm probes (a) and for 30 mm probes (b). Predicted water use for each sample tree was calculated with the original estimated parameters taken from the equation described by Granier (1985). Actual water use was measured volumetrically on cut stems.

### Sap flux data analyses

Daily water use (each 24 h period) for each tree was calculated for the 2011 calendar year by summing hourly observations and then applying the appropriate calibration equation for each sensor length. The effects of growth form, i.e. open and closed, on the relationship between DBH and canopy area and daily water use were determined using regression analysis.

For the time period 18 February 2011 to 31 December 2011, we parameterized an environmentally based model to examine which factors influenced tree water use. We lacked the full suite of environmental variables between 1 January and 17 February so this time period was not included in our model. The basis of the model was Fick's law, whereby water loss is a product of the diffusion gradient between the canopy and the atmosphere and the conductance of water from the canopy (Nobel, 1999). In our model, the diffusion gradient was represented by PET, and the conductance of water from the canopy was represented by the environmental factors that affect canopy conductance ( $G$ ), namely, solar radiation, temperature, vapour pressure deficit (VPD), and soil water status (e.g., Lloyd *et al.*, 1995; Taiz and Zeiger, 1998; Lambers *et al.*, 2000). Although VPD and solar radiation are used to calculate PET, they also have direct effects on

stomatal conductance, so were included in both terms. Likewise, temperature has a direct effect on stomatal conductance that is usually strongest at lower temperatures (Lloyd *et al.*, 1995).

The model developed to predict water use was

$$W_{ijk} = \alpha(PET)_i(G)_i \quad (1)$$

where  $W_{ijk}$  was cumulative daily sap flux per unit sapwood area ( $1 \text{ day}^{-1} \text{ cm}^{-2}$ ) for the  $i$ -th day of the  $j$ -th tree at the  $k$ -th site, PET was potential evapotranspiration ( $\text{mm day}^{-1}$ ),  $G_i$  was canopy conductance, and  $\alpha$  was a simple scaling parameter. While  $PET_i$  was estimated from meteorological data, we characterized  $G_i$  on the basis of environmental parameters as

$$G_i = (ASOL)_i(VPD_{max}^{-0.5})_i(T_{max})_i(D)_i \quad (2)$$

where ASOL was daily solar radiation ( $\text{MJ m}^{-2} \text{ day}^{-1}$ ),  $VPD_{max}$  was maximum daily VPD (kPa),  $T_{max}$  was maximum air temperature ( $^{\circ}\text{C}$ ), and  $D$  was soil moisture ( $\text{mm H}_2\text{O}$  in upper 10 cm).

A log–log transformation of the model [Equation (1)] was used to retain the multiplicative form but allows each variable to scale as a power function, e.g.  $PET_i^{\beta}$ , where  $\beta$  was a parameter to be estimated. We also partitioned the error term into random site and tree components, adding these as random effects in a mixed effects linear model.

The fitted model we assessed was

$$\ln(W_{ijk}) = \alpha + u_i + v_j + w_k + \beta \ln(PET)_i + \delta \ln(ASOL)_i + \gamma \ln(VPD_{max}^{-0.5})_i + \theta \ln(T_{max})_i + \rho(T_{max})_i + \tau \ln(D)_i \quad (3)$$

where  $\alpha, \beta, \delta, \gamma, \theta, \rho,$  and  $\tau$  were fitted parameters for the fixed effects;  $u_i, v_j,$  and  $w_k$  were random effects for day, tree, and site, respectively; and all other variables were as previously defined. Temperature effects were evaluated as a monotonic power function or as  $(T_{max})_i^{\theta} e^{\rho(T_{max})_i}$  (shown on the back-transformed scale), which allows an ‘S’-shaped response. Different soil moisture storage variables were assessed on the basis of fit, including the top 10 cm, as well as combinations of the different depths. All models were fitted using the mixed procedure in SAS v 9.2 (SAS Institute Inc., Cary, NC).

For reference, a null model (i.e. intercept only) was fitted as a mixed effects model including site, tree, and day random effects to the entire dataset. This null model was used to assess the extent that inclusion of meteorological and soil moisture data reduced the different variance components. In addition, the environmental components of the model [Equation (3)] were fitted to each tree separately to determine how well daily variation in tree water use could be explained by environmental conditions.

There were 12 days at the OG site, 12 days at the CG site, and 8 days at the mixed growth site when anomalously

high daily water use occurred relative to adjacent days. Most of these days were associated with cold temperatures in January and February. In addition, data for 1 day was eliminated because of heavy rainfall and a severe storm that caused anomalous readings at all three sites (24 April 2011), and one further day was eliminated (6 December 2011) where daily maximum temperature did not exceed  $0^{\circ}\text{C}$ . Three individual probes often had anomalous readings on days with rainfall greater than 5 cm presumably because of stemflow interfering with the temperature gradient between the upper and lower probes. For these trees, data from seven to ten individual dates were eliminated. To calculate total annual water use, data for missing dates were filled with the average of the day before and after the absent value. Estimated values were not included in modelling analyses.

## RESULTS

Compared with the 30-year average annual rainfall of 942 mm at the study site, 2011 was a dry year with total precipitation of 677 mm. There were 81 days with precipitation, and more occurred in May (14 events) than any other month. Forty-six events were smaller than the average 8.2 mm ( $\pm 8.8 \text{ mm s.d.}$ ), and 22 events were larger than 10.0 mm with the largest event (52.6 mm) occurring in September (Figure 2). The summer of 2011 (June–August) in Oklahoma was the hottest on record since 1954 and the third driest on record since 1936 (NOAA, 2012). The soil volumetric water content at 5 and 20 cm reached a peak in February, decreased sharply in late February–March, increased again and was highly variable in May until it decreased again in the summer (Figure 2). During the summer and fall, volumetric water content at 5 and 20 cm increased in response to individual rainfall events but quickly decreased following the event until November and December when soil moisture recovered. Volumetric soil water content was relatively constant measured at 45 and 80 cm. During 2011, the daily average temperature and average VPD showed predictable seasonal trends and were lowest in February and highest in August (Figure 2). Average solar radiation was 11.7, 20.5, 23.7, and  $12.3 \text{ MJ m}^{-2}$ , and average daily PET was 2.1, 5.1, 6.9, and 2.7 mm for winter, spring, summer, and fall, respectively.

*Juniperus virginiana* daily water use fluctuated with seasonal and short-term weather patterns. For instance, there were distinct patterns of water use that corresponded to air temperature, precipitation, and soil water content (Figure 3). All trees used water year round with the lowest water use in January and December when temperature and VPD were low. Daily water use decreased in April and July during periods of reduced volumetric soil water content in the upper soil layers (Figure 3).

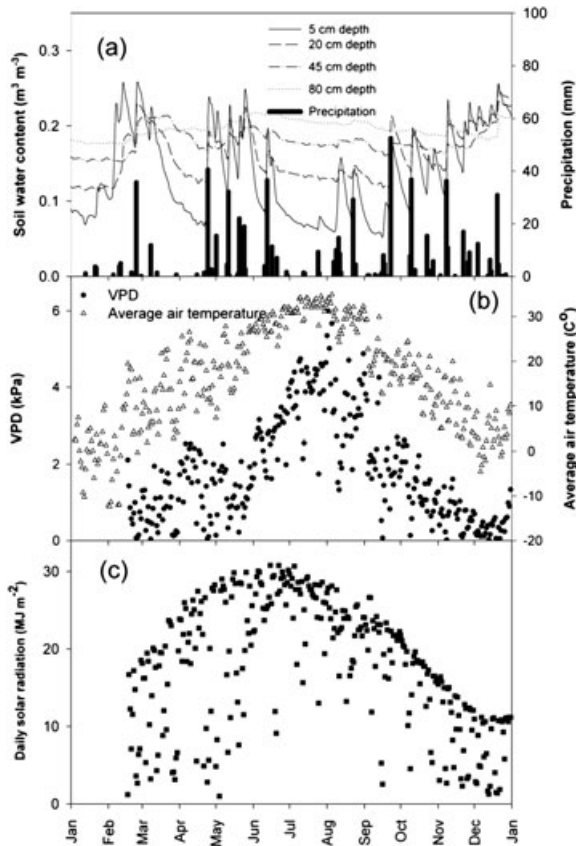


Figure 2. Daily precipitation and volumetric soil water content averaged across sites measured at 5, 20, 45, and 80 cm (a); daily average air temperature and daytime vapour pressure deficit (b); and daily solar radiation (c) for 2011 measured at the study site in north-central Oklahoma.

Tree age ranged from 10 to 46 years, height from 3 to 14 m, DBH from 2 to 33 cm, sapwood area from 10 to 370 cm<sup>2</sup>, and canopy area from 2 to 67 m<sup>2</sup> (Table I). Tree water use increased in relation to tree DBH [Figure 4(a)] and canopy area [Figure 4(b)]. Open-grown trees used more water for a given DBH than closed-grown trees ( $p=0.0003$ ). When expressed on a canopy area basis, however, water use per unit of canopy area was similar for both growth types ( $p=0.82$ ). Averaged across the entire year, annual daily water use varied from 1 to 661 depending on tree size (mean =  $23.6 \pm 21.8$  l s.d.) (Table I). The minimum daily water use among trees ranged from 0 to 9.91, and the maximum daily water use among trees ranged from 8.2 to 161.41.

To estimate annual water use on a larger scale, we assumed 100% canopy cover and extrapolated the relationship between average daily water use and canopy area [Figure 4(b)] to a hectare (10 000 m<sup>2</sup>). We calculated total water use of  $4\,308\,817\text{ l ha}^{-1}\text{ y}^{-1}$ , equivalent to 431 mm rainfall. On the basis of measured canopy interception of 36.1% within closed canopy *J. virginiana* woodlands (Caterina, 2012), 433 mm of the 677 mm of precipitation reached the soil surface as net rainfall.

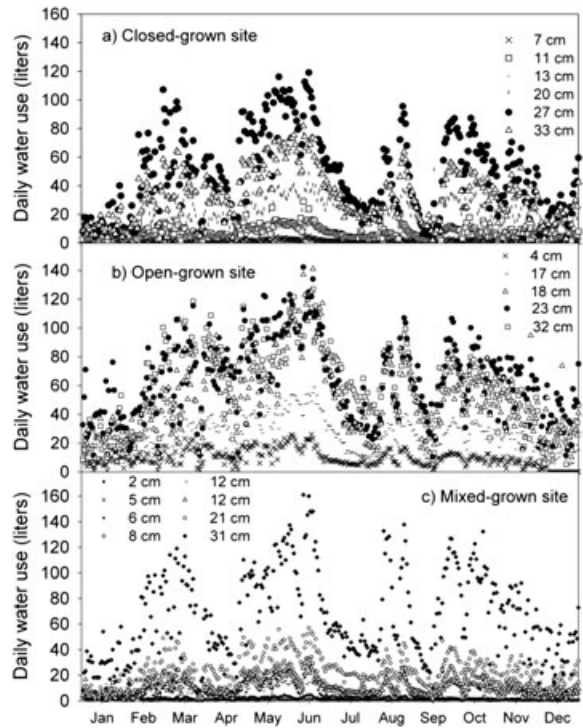


Figure 3. Daily water use measured during 2011 for *Juniperus virginiana* trees with different diameter at breast height from the (a) closed-grown, (b) open-grown, and (c) mixed-grown sites.

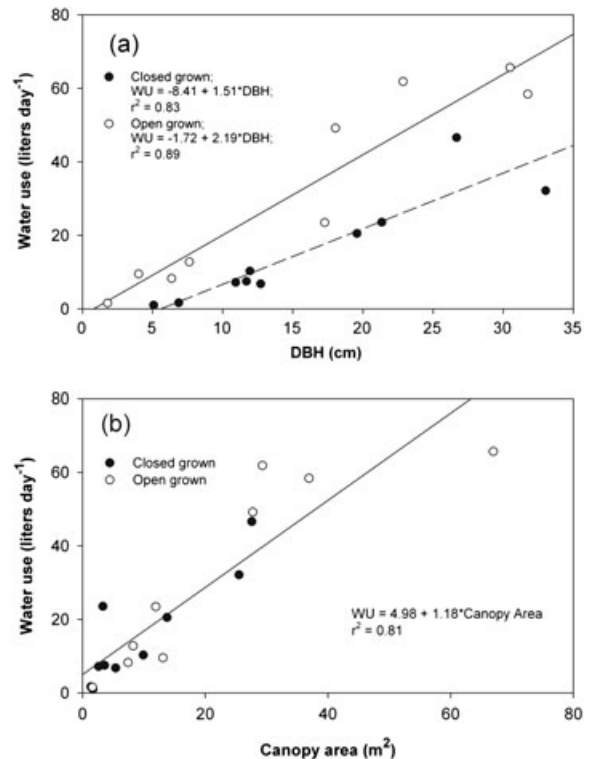


Figure 4. Relationship between 2011 daily average water use for *Juniperus virginiana* trees and diameter at breast height (DBH) (a) and canopy area (b).



Therefore, a stand with complete canopy closure of *J. virginiana* trees could completely transpire (99.5%) net precipitation during the dry, hot year we measured.

When examined using the physiologically based mixed model, the temperature effects were best expressed (on the basis of reduction of residual variance component) by a monotonically increasing power function. An inflective relationship was also fitted as  $(T_{max})_i^{\theta} e^{\rho(T_{max})_i}$ ; however, the parameter  $\rho$  was non-significant ( $p=0.12$ ), and the overall form of the function was quite similar, so only the power function was retained in the final model. Water storage in the top 10 cm of soil was chosen for the model because it reduced the residual variance component more than other depths or combination of depths.

For individual trees, the fitted models explained an average of 56% ( $\pm 13$  s.d.) of daily variation in water use (Table II). For the null model fitted to the entire dataset, the estimated variance components were for site  $\sigma_k^2=0.117$  ( $p=0.20$ ), tree  $\sigma_j^2=0.114$  ( $p=0.003$ ), day  $\sigma_i^2=0.310$  ( $p < 0.001$ ), and residual variance  $\sigma_e^2=0.127$ . For the model that included environmental variables, the estimated variance components were for site  $\sigma_k^2=0.107$  ( $p=0.20$ ), tree  $\sigma_j^2=0.114$  ( $p=0.003$ ), day  $\sigma_i^2=0.117$  ( $p < 0.001$ ), and residual variance  $\sigma_e^2=0.127$ . Including environmental variables in the model decreased the variance component for day by 63% but had virtually no impact on the other variance components or the residual error. The fitted parameters for the final model [Equation (3)] were all

significant ( $p < 0.0001$ ), with the parameter estimates (s.e. in parentheses):  $\alpha = -6.326$  (0.382);  $\beta = 0.360$  (0.126);  $\delta = 0.314$  (0.097);  $\gamma = 1.016$  (0.160);  $\theta = 0.717$  (0.081); and  $\tau = 0.483$  (0.034). The parameter  $\gamma$  was not significantly different from 1.0, indicating that the inverse square root function applied *a priori* to  $VPD_{max}$  was sufficient.

DISCUSSION

With the exception of the coldest days of winter, *J. virginiana* used water all year. The coldest 7 days with average temperature below  $-9^{\circ}\text{C}$  and maximum air temperatures below  $-3^{\circ}\text{C}$  were eliminated from our dataset as they had anomalously high estimates of water use. We assume this was due to frozen soil or frozen stems and that little or no transpiration occurred on those days. This was similar to Awada *et al.* (2012) who measured transpiration in *J. virginiana* as long as maximum air temperature was close to  $0^{\circ}\text{C}$ . Water use by *J. virginiana* trees was substantially reduced but never ceased during the hot and dry summer of 2011. *J. virginiana* is a drought-tolerant species and is able to maintain physiological functions under low xylem and soil water potentials (Bahari *et al.*, 1985; Eggemeyer *et al.*, 2006; Bihmidine *et al.*, 2010; Volder *et al.*, 2010) without incurring xylem cavitation (Willson and Jackson, 2006). The evergreen nature of *J. virginiana* and its ability to transpire water in

Table II. Individual regression models of *Juniperus virginiana* daily tree water use per sapwood area ( $\text{ld}^{-1} \text{cm}^{-2}$ ).

Tree ID	Intercept	ln PET	ln ASOL	ln $VPD_{max}^{-0.5}$	ln $T_{max}$	ln $D_{0-10\text{cm}}$	$r^2$
OG1	-6.36	0.581*	0.296*	0.592*	0.382*	0.871*	0.63
OG2	-5.98	0.849*	0.074	0.751*	0.423*	0.869*	0.65
OG3	-5.94	0.252*	0.533*	0.639*	0.585*	0.481*	0.73
OG4	-4.95	0.678*	0.179	0.775*	0.213*	0.644*	0.56
OG5	-4.63	0.925*	-0.133	0.899*	0.361*	0.604*	0.46
CG1	-6.67	0.022	0.356*	0.373*	0.786*	0.496*	0.59
CG2	-8.06	0.279	0.275*	1.088*	1.072*	0.799*	0.56
CG3	-6.70	0.425*	0.074	0.828*	0.550*	0.811*	0.36
CG4	-7.31	0.432*	0.428*	0.398*	0.382*	0.823*	0.62
CG5	-7.45	0.519*	0.322*	0.785*	0.650*	0.994*	0.63
CG6	-6.12	0.543*	0.252*	0.460*	0.378*	0.807*	0.68
MO1	-6.78	0.355*	0.293*	0.392*	0.482*	0.900*	0.60
MO2	-7.07	0.412*	0.118	0.603*	0.718*	1.029*	0.58
MO3	-8.83	0.545*	0.097	1.042*	0.972*	1.169*	0.53
MO4	-9.04	0.674*	0.001	1.363*	1.072*	1.190*	0.49
MC1	-7.62	-0.366	0.605*	0.943*	1.039*	0.321*	0.17
MC2	-9.33	0.273	0.223	0.827*	1.005*	1.156*	0.52
MC3	-6.86	0.319*	0.257*	0.302*	0.591*	0.869*	0.71
MC4	-8.26	0.242	0.319*	0.725*	0.849*	0.935*	0.55

PET, potential evapotranspiration; ASOL, daily solar radiation; VPD, vapour pressure deficit. Variables used were selected on the basis of the underlying principle that transpiration rate is a function of atmospheric demand and stomatal conductance. The atmospheric demand was represented by daytime potential evapotranspiration (PET; mm); stomatal conductance is influenced by daily solar radiation (ASOL;  $\text{MJ m}^{-2}$ ), max vapour pressure deficit ( $VPD_{max}$ ; kPa), daily maximum temperature ( $T_{max}$ ;  $^{\circ}\text{C}$ ), and soil water storage between 0 and 10 cm depth ( $D_{0-10\text{cm}}$ ; mm). Designations 'O', 'C', and 'M' in the tree ID refer to different sites.

\*Variables statistically significant to the model ( $p \leq 0.05$ ).

cold weather as well as drought conditions translates into water use for 350–360 days per year in the southern Great Plains. In contrast, warm-season herbaceous species that dominate tallgrass prairie ecosystems are mostly dormant from October to April depending on the timing of frost and will undergo early senescence in response to drought (Eggemeyer *et al.*, 2006).

During a drought year, we calculated that *J. virginiana* in north-central Oklahoma can consume 100% of the precipitation that reaches the soil surface. Our tree-based measurements of water use are supported by the lack of runoff (measured using gauged flumes) from the encroached watersheds and little net change in soil water content between January and December (Zou *et al.*, ). For the water years 2009, 2010, and 2011, the annual runoff coefficients for the *J. virginiana* watersheds averaged 2.1%, in contrast to 10.6% for the grassland watersheds; although, there was little runoff from either the grass or *J. virginiana* watersheds in 2011, which was a drought year (Zou *et al.*, ). The potential capacity for *J. virginiana* to use all incoming precipitation and lower measured runoff from encroached areas compared with grassland areas emphasizes the transformative effect that *J. virginiana* encroachment is having on watershed-level water cycling and budgets across the southern Great Plains and its likely role in decreasing water yield. Without prescribed fire or other active management to prevent encroachment, the conversion of tallgrass prairie to *J. virginiana* woodlands can occur in less than 50 years (oldest tree we measured was 46 years old). Our scaling of tree-based measurements to the watershed included several uncertainties. For instance, canopy coverage never fully reaches 100% over larger scales, and we did not account for litter interception in our estimates. However, paired with the lack of runoff, the stand-level water use values we calculated are reasonable.

The 2011 drought resulted in only 72% of annual average precipitation. To estimate the potential water use by *J. virginiana* during years with greater soil water availability, we set soil water content in the upper 10 cm to field capacity ( $0.23 \text{ cm}^3 \text{ cm}^{-3}$ ) for each day of the year in the fitted model [Equation (3)]. On the basis of this calculation, *J. virginiana* has the potential to use 573 mm, which equates to approximately 896 mm of precipitation after including canopy interception. This estimate is a simplification as it assumes that the soil is continuously at field capacity, that throughfall never exceeds infiltration capacity, and that the temperature, the humidity, and the solar radiation are the same in a wet year as they were during the hot and dry 2011. In any case, closed-canopy stands of *J. virginiana* have the potential to use more water than we measured during a drought year and may consume as much as 95% of incoming precipitation during years with normal precipitation (942 mm).

While often limited by soil water availability, *Juniperus* spp. have the potential to consume large quantities of water. In a riparian area where soil water was not limiting, a 15-cm DBH *J. virginiana* tree used between 48 and  $621 \text{ day}^{-1}$  (Landon *et al.*, 2009). Even though both were located in semiarid environments, a *Juniperus occidentalis* tree of 44 cm basal diameter used up to  $1321 \text{ day}^{-1}$  (Eddleman and Miller, 1991), and *Juniperus ashei* trees with an average of  $23 \text{ m}^2$  canopy area used between 20 and  $1251 \text{ day}^{-1}$  (Owens, 1996).

The study most similar to ours measured water use for a planted forest of *J. virginiana* in the Sand Hills of Nebraska, USA, (Awada *et al.*, 2012). In that study, dominant *J. virginiana* trees used approximately  $201 \text{ day}^{-1}$  compared with  $50\text{--}601 \text{ day}^{-1}$  for the largest trees in our study. Even though their forest received more precipitation during the year of study (750 vs 677 mm), the greater water use in our study could be expected because of larger dominant trees ( $\sim 30$  vs  $\sim 15$  cm DBH) and larger sapwood areas of the dominant trees ( $\sim 250$  vs  $\sim 100 \text{ cm}^2$ ) in our study and perhaps also because of greater soil water holding capacity (sandy loam vs sand). Although tree size and forest structure differed among the two studies, Awada *et al.* (2012) calculated that *J. virginiana* consumed 95% of incoming precipitation, a number similar to our estimate.

*Juniperus* spp. are morphologically and physiologically different from most species used in previous sap flux studies as they have narrow, thick-walled tracheid cells (Willson *et al.*, 2008). Even though some studies support the universal application of Granier's empirical equation (Loustau *et al.*, 1996; Braun and Schmid, 1999; McCulloh *et al.*, 2007), others found that it varies with species (Lu *et al.*, 2004; Bush *et al.*, 2010; Steppe *et al.*, 2010; Sun *et al.*, 2012). Using the general approach of Sun *et al.* (2012), our calibration of sap flux for *J. virginiana* was very important, without which we would have underestimated daily water use by two to five times. Given the size of calibration correction needed in our study, previous studies of sap flux in *Juniperus* spp. may have underestimated water use. However, the need for calibration certainly depends on tree age, size, and growth conditions as well as specifics of the technique employed. In any case, our results indicate that calibration is a step that should be undertaken to ensure accuracy.

We did not account for nighttime water movement in the stem associated with nighttime transpiration or rehydration, or the canopy. Because there were long periods during the exceptionally hot and dry summer of 2011 where nighttime temperature never approached dewpoint (up to 30 consecutive nights), we could not reasonably substitute the maximum temperature differentials from nights where temperate reached dewpoint for nights where it did not (Oishi *et al.*, 2008). As such, our estimates of annual canopy transpiration may be underestimated. In a study from North Carolina, including maximum temperature



differentials from nights with  $VPD > 0$  caused an under-estimation of water use by up to 15% (Oishi *et al.*, 2008). Monthly minimum VPD at our study site ranged from 0.03 kPa in December to 0.67 kPa in July. We assume that in our study, the extremely drought-tolerant *J. virginiana* minimizes night time transpiration, which will decrease the error associated with nonzero nighttime minimum VPD.

Sapwood area and foliage biomass generally increase with tree DBH. Therefore, it was no surprise that we found a positive relationship between DBH and water use. However, open-grown trees transpired larger volumes of water than closed-grown trees of the same DBH. Trees growing in denser stands tend to grow more slowly and are often older than open-grown trees with the same diameter, which results in a higher percentage of heartwood (Lykins, 1995). In our study, sapwood for the open-grown was greater per unit of DBH than for closed-grown trees (open-grown sapwood =  $9.64 * DBH - 6.19$ , Closed-grown sapwood =  $7.24 * DBH - 17.79$ ). Also, open-grown trees have more branches, larger canopies, and greater foliage weight than closed-grown trees of the same DBH (Lykins, 1995). Water use on a canopy area basis was similar among growth types probably indicating a functional relationship between canopy size, leaf biomass, and water use. This relationship permits scaling water use on the basis of percent canopy cover. Canopy cover can be easily obtained from aerial photographs and does not require more intensive ground-based measurements of canopy structure, e.g. stand density, growth form, and stem size.

We chose a physiologically based approach to the analysis, rather than strictly hypothesis testing for sap flux differences among the different treatment variables. The advantage of the approach was to allow fitting the different parameters simultaneously, while also accounting for treatment, tree, and day effects. This allowed us to account for co-varying effects of the explanatory variables, in order to isolate the effect of another. For example, parameter estimates from a simple regression of sap flux on  $\ln(VPD)$  are expected to be strongly biased when VPD and ASOL are strongly correlated. In this case, you cannot assign the parameter effect solely to VPD. A similar situation arises with different tree effects, and these were included to isolate these specific effects from the environmental ones. Thus, the simultaneous fitting approach, with a physiologically-based model form, was expected to provide more robust parameters estimates.

Our approach, based on Fick's law, used PET as the driving force for ET and then solar radiation, temperature, VPD, and soil moisture to represent canopy conductance based on their influence on stomatal aperture. The coefficients associated with PET, solar radiation, maximum temperature, and soil moisture were positive but less than one, indicating monotonically increasing curvilinear relationships that begin to plateau at higher values of these

variables. Further, the coefficient associated with the transformed variable  $\ln(VPD^{-0.5})$  was 1.02, indicating a decay function whereby water use initially decreases rapidly as VPD increases and approaches a minimum at higher VPD. The shapes of the water use versus VPD and water use versus temperature relationships were similar to the modelled relationships for stomatal conductance used by Lloyd *et al.* (1995). Our modelling approach can be applied to other sap flux studies and allows manipulation of environmental variables to estimate how variation in weather or climate might affect tree water use.

On the basis of the model when applied to individual trees, smaller trees had less direct relationships between water use and the measured environmental variables. In particular, the two smallest, closed-grown trees had poor relationships, i.e. MC1 (5 cm DBH,  $r^2 = 0.17$ ) and CG3 (7 cm DBH,  $r^2 = 0.36$ ). Smaller trees, particularly those within closed-canopy forests, may have poor relationships with measured environmental variables because shading by larger trees might confound estimates of radiation. In addition, temperature and VPD in the subcanopy (suppressed trees) will differ from temperature and VPD measured in the open, which is experienced by trees growing in the main canopy.

Encroachment of *J. virginiana* into tallgrass prairie across the southern Great Plains is transforming millions of hectares from warm season grasslands to evergreen forests. This change radically alters biogeochemical cycles, biodiversity, and ecosystem services such as cattle forage, wildlife habitat, carbon sequestration, and of course, water yield. With increasing societal demand for fresh water and uncertainty regarding future precipitation patterns in the southern Great Plains, the high rate of water use by *J. virginiana* has the potential to exacerbate future water shortages.

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