

Tree and stand transpiration in a Midwestern bur oak savanna after elm encroachment and restoration thinning

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Abstract

Oak savannas, once common in the Midwest, are now isolated remnants within agricultural landscapes. Savanna remnants are frequently encroached by invasive trees to become woodlands. Thinning and prescribed burning can restore savanna structure, but the ecohydrological effects of managing these remnants are poorly understood. In this study, we measured sap flow (J_s) to quantify transpiration in an Iowa bur oak (*Quercus macrocarpa*) savanna woodland encroached by elms (*Ulmus americana*), and in an adjacent restored savanna after thinning to remove elms, during summer 2004. Savanna oaks had greater mean daily J_s ($35.9 \text{ L dm}^{-2} \text{ day}^{-1}$) than woodland oaks ($20.7 \text{ L dm}^{-2} \text{ day}^{-1}$) and elms ($12.4 \text{ L dm}^{-2} \text{ day}^{-1}$). The response of J_s to vapor pressure deficit (D) was unexpectedly weak, although oaks in both stands showed negative correlation between daily J_s and D for $D > 0.4 \text{ kPa}$. An earlier daily peak in J_s in the elm trees showed a possible advantage for water uptake. As anticipated, the woodland's stand transpiration was greater (1.23 mm day^{-1}) than the savanna's (0.35 mm day^{-1}), yet the savanna achieved 30% of the woodland's transpiration with only 11% of its sapwood area. The difference in transpiration influenced water table depths, which were 2 m in the savanna and 6.5 m in the woodland. Regionally, row-crop agriculture has increased groundwater recharge and raised water tables, providing surplus water that perhaps facilitated elm encroachment. This has implications for restoration of savanna remnants. If achieving a savanna ecohydrology is an aim of restoration, then restoration strategies may require buffers, or targeting of large or hydrologically isolated remnants. © 2007 Published by Elsevier B.V.

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1. Introduction

Plants have an important hydrologic function by transpiring water from the soil to the atmosphere, accounting for a significant portion of evaporative losses from terrestrial ecosystems (Körner, 1994). Water uptake capacities and dynamics vary among plant species and functional groups. Generally, total water uptake is greater for woody plants compared to herbaceous plants, and for perennial plants compared to annual plants (Brye et al., 2000; Zhang et al., 2001; Huxman et al., 2005). Consequently, land use activities that convert perennial vegetation to annual crops can alter plant water cycling functions and, in turn, the hydrologic balance at a

site. This trend is exemplified in the upper Midwestern U.S., where landscape-scale conversion of the native perennial prairie and savanna vegetation to annual crops has greatly increased surface runoff and baseflow (Schilling and Libra, 2003) and, subsequently, the loss of nutrients and sediment into rivers and estuaries (Burkhart and James, 1999; Rabalais et al., 2002).

Efforts to mitigate environmental effects of agriculture have often focused on including perennial plants in agricultural systems through conservation practices such as riparian buffers and contour strips (Lowrance et al., 2002). Yet hydrologic interactions between agricultural lands and remnant patches of native or restored native plant communities are not generally recognized. Oak savanna ecosystems, characterized by an open canopy of widely dispersed oak trees and a continuous herbaceous layer in the understory, historically comprised a significant component of the native vegetation in the

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Midwestern U.S. (Anderson, 1998). Most of the savanna remnants that remain on the landscape today have been heavily encroached by shade-tolerant, fire-sensitive species due to fire suppression and removal of grazing pressures, thereby converting them to dense woodlands (Nuzzo, 1986; Anderson, 1998; Asbjornsen et al., 2005). Many of these remnants are scattered in locations poorly suited to farming; e.g., depressions, riparian zones, and hilltops.

While research to quantify effects of conservation practices on nutrient and sediment loss has been widely published (Udawatta et al., 2002; Dosskey et al., 2002 and references therein), relatively little work has examined water use patterns by small patches of perennial vegetation within agricultural landscapes. The hydrologic functioning of these remnants will vary depending on tree density (Bréda et al., 1995; Meinzer et al., 1996), species (Swank et al., 1988; Hornbeck et al., 1997; Veneklaas and Poot, 2003), rooting depth (Huxman et al., 2005), and edge effects on microclimate and advective heat energy (Rider et al., 1963; Brakke et al., 1978). Much of the remaining non-agricultural vegetative cover in the Midwest is transitioning from open systems (prairies, savannas, abandoned pastures) to more closed woodlands, altering both stand structure and species composition. Efforts to restore these woodlands to their former savanna or prairie compositions are being initiated, through tree removal and re-introduction of a fire regime. Given the isolation and rarity of these savanna remnants, there are few opportunities to conduct research on restoration efforts. The success of these restorations may depend on their hydrological effects, which are not well understood.

In this study, we used sap flow measurements to assess water uptake by trees in an elm-encroached remnant oak savanna compared to an adjacent area undergoing savanna restoration treatment initiated by removal of encroaching trees. Our main objectives for the study were to: (1) determine the difference in sap flow between oak trees growing in the savanna restoration and the untreated encroached savanna woodland; (2) compare absolute rates and diurnal patterns of sap flow between the elm and oak trees in the woodland; (3) characterize effects of climatic factors (e.g., vapor pressure deficit, radiation, wind, precipitation) on sap flow for each species and stand; (4) estimate the difference in daily stand transpiration between the savanna and woodland. The ecohydrological implications of the findings from this study for agricultural landscapes in humid temperate climates where small patches of woodlands or savannas are embedded within a dominant matrix of annual cropping systems are discussed.

2. Materials and methods

2.1. Study site

This study was conducted in an oak savanna remnant (8 ha) adjacent to agricultural fields (rotational, no-tillage corn and soybean), located at the Neal Smith National Wildlife Refuge in Central Iowa (41°33'N, 93°17'W; Fig. 1). Soils include the Ladoga (fine, smectitic, mesic Vertic Hapludalfs), Gara (fine-loamy, mixed, superactive, mesic Mollic Hapludalfs), and

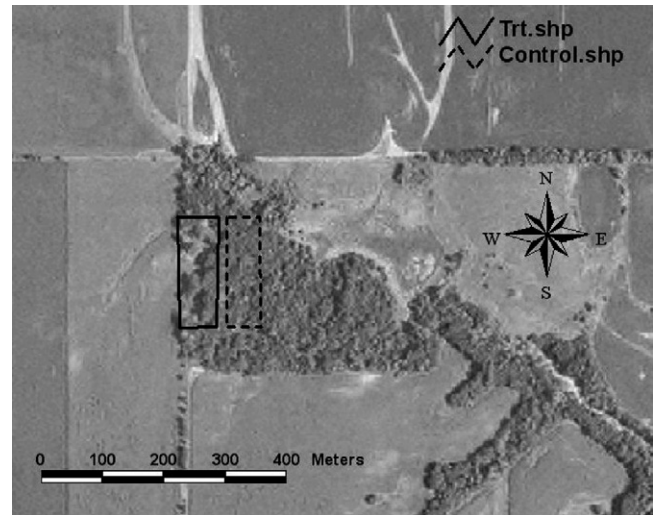


Fig. 1. Aerial photo (2004) showing the encroached woodland embedded within a matrix of agricultural fields (rotational corn and soybeans), and the boundaries of the two ~1 ha study sites with the savanna restoration treatment (solid line) and woodland control (dotted line).

Armstrong series (fine, smectitic, mesic Aquertic Hapludalfs), which formed under a mixture of deciduous trees (primarily oak and hickory) and tallgrass prairie (Nestrud and Woster, 1979). The soils developed in approximately 2 m of Wisconsin-age loess, which is underlain by glacial till of pre-Illinoian age that is capped with the Sangamon paleosol (Ruhe, 1969; Prior, 1991). The loess and till materials are fine textured, slowly permeable, and considered aquitards in terms of their saturated hydraulic properties, meaning they become saturated but yield inadequate water supplies for any type of well development (Freeze and Cherry, 1979; Rodvang and Simpkins, 2001). Annual precipitation is approximated 840 mm. This savanna remnant has no known history of grazing by domestic animals and has never been plowed, although cropped fields do surround the site (Karnitz and Asbjornsen, 2006). It has been managed by the U.S. Fish and Wildlife Service since its purchase in the mid-1990s.

The dominant overstory trees are *Quercus macrocarpa* (bur oak), which have a large, open-grown form indicative of a former savanna ecosystem. The current stand has been heavily encroached by shade-tolerant, fire-sensitive species, primarily *Ulmus americana* (American elm) and *Ulmus rubra* (slippery elm). Prominent understory shrubs include *Symphoricarpos orbiculatus* (coralberry) and *Ribes missouriense* (Missouri gooseberry). The most common understory herbaceous species are *Sanicula gregaria* (black snakeroot) and *Osmorhiza claytonii* (sweet cicely); however, over 40 understory herbs have been identified at this site.

In the winter of 2003–2004 an experimental restoration treatment was conducted that involved mechanical removal of all non-oak trees within ~1 ha of the stand (hereafter ‘savanna’), which reduced the basal area from 31.95 to 12.44 m²/ha. The basal area of the non-thinned stand was 38.27 m²/ha. The non-thinned stand served as the control (hereafter ‘woodland’) (see Asbjornsen et al., 2005 for details on restoration experiment).

Table 1

Characteristics of *Quercus macrocarpa* and *Ulmus americana* trees sampled for the sap flux density measurements (*removed due to abnormally low sap flow rates)

Species and location	dbh (cm)	dbh without bark (cm)	Sapwood depth (mm)	Sapwood area (cm ²)
Savanna oak 1	83.7	82.3	12.4	316.7
Savanna oak 2	74.5	73.1	14.2	320.4
Savanna oak 3	90.7	89.3	18.6	511.1
Woodland oak 1	71.3	70.0	17.7	378.3
Woodland oak 2*	91.4	90.1	21.2	611.3
Woodland oak 3	77.7	76.3	14.4	338.5
Woodland elm 1	15.9	15.1	29.6	112.9
Woodland elm 2	19.7	18.9	40.1	188.1
Woodland elm 3	19.1	18.3	31.6	150.4
Woodland elm 4	22.9	22.1	41.1	232.5

2.2. Microclimate measurements

A weather station (IntelimetTM Weather Station from Dynamax, Inc.¹) was located nearby, in an opening by an adjacent cornfield. Continuous data was collected for precipitation (Tipping Bucket Rain Gauge), solar radiation (R_s), temperature, relative humidity and wind direction and speed. Data were averaged or totaled on an hourly basis and stored by a data logger. Vapor pressure deficit (D , in kPa) was calculated from hourly average relative humidity (R_H) and air temperature (T_A) measurements, as described by Allen et al. (1994). To represent daily mean D as a driver for transpiration, hourly values were averaged between 09:00 and 16:00 h (the third of the day when solar radiation is at a maximum), for statistical comparison to daily sap flow.

Groundwater level (head) was monitored continuously beginning August 15, 2004 using groundwater wells (one per site) installed during the 2004 growing season and water-level data were collected using pressure transducers. Relative elevations of the wells were measured using an automatic level accurate to approximately 1 mm elevation.

2.3. Sap flow measurements

Sap flow (L H₂O dm⁻² sapwood h⁻¹) was monitored for three oak trees (savanna and woodland sites) and four elm trees (woodland site only) using thermal dissipation probes (Dynamax, Inc.) constructed after Granier (1987). Representative trees were selected to include healthy individuals (no apparent disease in their boles or crowns), of similar size within each species to minimize size effects on water uptake, and within a 50 m radius to allow for equipment connection (Table 1). The depth to active sapwood was determined by extracting two cores from each study tree and measuring sapwood depth based on visually assessment of the coloration and translucency of the wood (Pataki et al., 2000). Sensors (30 mm in length) were inserted radially at breast height to a depth of 30 mm, approximately equidistant from each other (four sensors in each oak tree and two sensors in each elm tree).

Exposed portions of sensors were encapsulated in black tree wax to prevent direct contact with the atmosphere, and all probes were insulated with several layers of bubble wrap and Styrofoam and shielded with aluminum foil to minimize temperature fluctuations. When the depth of sapwood was less than 30 mm, sap flow values were corrected using formulas developed by Clearwater et al. (1999). These corrections were required for the oak trees which had sapwood lengths between 12.5 and 18.5 mm. Although these measurements were repeatable and carefully made using a hand lens, an error analysis showed that a 1 mm error in the length measurement would result in a -15 to +22% difference in J_s for the shortest of these sapwood lengths, and a -7 to +9% difference for the greatest oak sapwood thickness. When sapwood depth was greater than 30 mm (all of the elm trees), sap flow was assumed uniform over the entire depth, as documented for other Eastern deciduous forest species (Phillips et al., 1996). Continuous heat was supplied to the upper probe from direct current generated by deep cycle marine (12 V) batteries recharged by solar panels located on site. The temperature difference between the heated and reference probe was measured every 60 s and 15-min averages were recorded on a Campbell CRX-10 datalogger. Sap flow data were collected on 38 dates covering five periods between 23 June and 15 September 2004 (missing dates were due to equipment power failures). Temperature data were used to calculate sap flow, J_s , expressed in mm per second, according to the equation derived empirically by Granier (1987):

$$J_s = 0.119 \left(\frac{\Delta T_b}{\Delta T} - 1 \right)^{1.23} \quad (1)$$

where ΔT is the temperature difference between the two probes and ΔT_b is the baseline temperature difference under zero flow conditions. For reporting herein, we summed these data on an hourly basis (J_h), and hourly data were summed to provide daily values (J_d).

2.4. Stand transpiration

In order to estimate stand transpiration, the amount of active sapwood area (A_s) was estimated based on increment cores extracted from 10 trees representing the most frequent diameter size classes occurring within the study area (Fig. 2). The depth

¹ Mention of trade names is for information only and does not constitute or imply endorsement by the authors or their institutions.

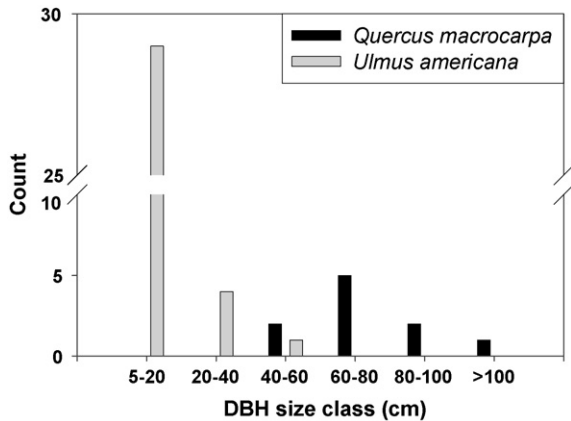


Fig. 2. Diameter at breast height (DBH) size distributions for *Quercus macrocarpa* (total $n = 10$) and *Ulmus americana* (total $n = 35$) trees used to scale sap flow from individual trees to the savanna and woodland stands.

to active sapwood was determined as described above. Regression models between tree diameter and sapwood area were developed for each species according to the equation (Vertessy et al., 1995):

$$SA = B_0 \times dbh^{B_1}$$

where SA is the sapwood area (cm^2), dbh the measured tree dbh (cm) and B_0 and B_1 are species-specific coefficients determined by the regression. These models were used to estimate sapwood area for non-cored trees within a $10 \text{ m} \times 130 \text{ m}$ transect at each site (regression coefficient: $r^2 = 0.54$ and 0.96 for oaks and elms, respectively). Due to our low sample size and high variability in measured sapwood depth in the oak trees, the strength of the relationship between sapwood and dbh was lower than that reported in other studies (e.g., r^2 values of 0.075 – 0.92 ; Wullschlegel et al., 2001; Wullschlegel and

Hanson, 2006). However, the regression was based on a sample of six trees with a range in DBH of only 20 cm. The regression result was only applied to seven non-cored individuals; we were not permitted by the Refuge management to core all the oaks in the stand. Total sapwood area to ground area ($A_s:A_g$) was extrapolated by summing all individual tree sapwood areas and converting values to $\text{m}^2 \text{ ha}^{-1}$ sapwood. Mean daily stand transpiration (E_c) was determined by dividing the geometric mean J_d (as discussed below) by $A_s:A_g$.

2.5. Statistical analyses

Statistical analyses were conducted to evaluate variation in sap flow among individual trees and days, and between oaks in the savanna and woodland. Single and multiple-factor ANOVA procedures were conducted to determine the proportion of variation in daily sap flow rates for bur oak trees due to stand (savanna versus woodland). Multiple factor ANOVA (proc GLM, SAS software: SAS Institute, 1985) was used to compare the proportion of variation in sap flow associated with the individual trees, versus that associated with day-of-year. Because variance of sap flow measurements tends to increase with flow rate, analysis was performed on natural-log transformed data. Therefore average values reported are geometric means, with standard deviations calculated according to:

$$\text{S.D.} = \sqrt{\exp(2\mu + \sigma^2)(\exp(\sigma^2) - 1)}$$

where μ and σ^2 are means and variances calculated on the transformed data (Haan, 1977).

Correlations were run to evaluate consistency of daily sap flow rates among individuals, and association of sap flow with

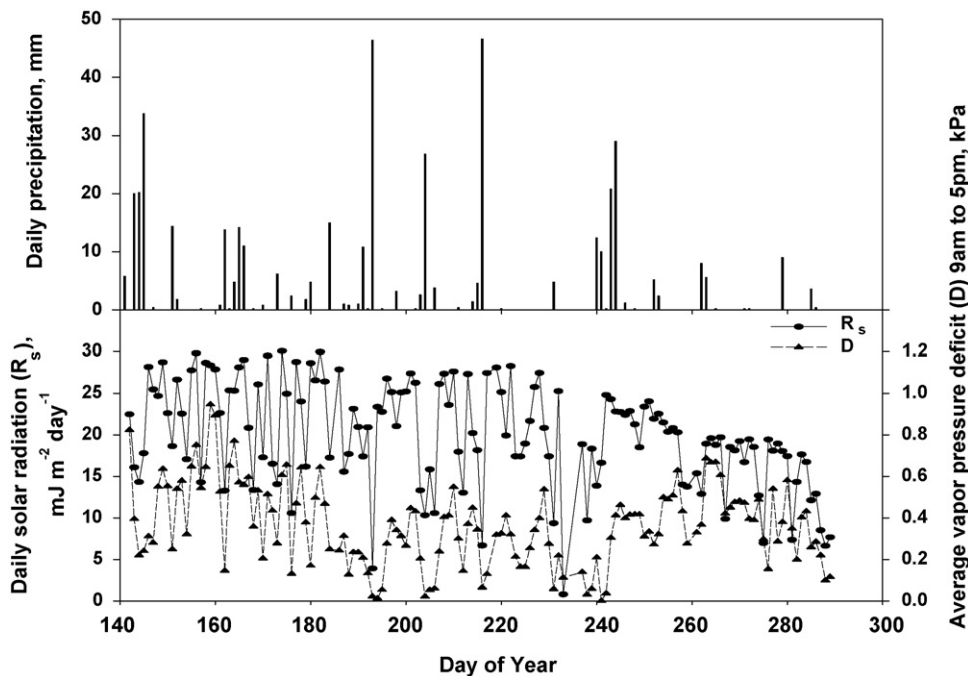


Fig. 3. Daily precipitation (mm), solar radiation, R_s (J m^{-2}), and vapor pressure deficit, D (kPa) during daylight hours (9 a.m.–5 p.m.) during the study period.

environmental variables including daytime D , daily R_s , daily wind run, recent precipitation, and daylength.

More detailed statistical analyses were conducted to assess the proportion of variation in hourly (10:00–18:00) and daily sap flow that could be attributed to weather and day-length conditions using multiple linear regressions. Independent variables were day of year (quadratic), R_s , D (linear and quadratic), wind run, average temperature, and an interaction between D and R_s . Due to generally low correlations, a backward variable selection process was used (PROC REG, SAS ver. 8.1), with a 0.1 p value used for variable retention in the model. From the final regression models, we identified and tabulated the single variable that accounted for the most variation in sap flow (type 2 sums of squares). The purpose of this analysis was to identify which variables had dominant influence on sap flow, and whether there was a shift in these variables during the day.

3. Results

3.1. Climate

A total of 267 mm of precipitation were recorded during the 3-month study period (Fig. 3). The largest three events (47, 46, and 27 mm) accounted for nearly half this total. Solar radiation averaged 0.88 (range 0.16–1.25) MJ m^{-2} , and D averaged 0.31 MPa (range 0.66–0.00 MPa). The weather was typical of this humid region, with recurrent convective storms and occasional periods (up to 10 days) without significant rainfall.

3.2. Sap flow

Continuous J_s data were available for five distinct time periods, and used to calculate J_d (Fig. 4). One of the oak trees in the woodland stand (woodland oak #2) had abnormally low J_d beginning in July and continuing through September and eventually died the following spring. Daily sap flow rates among all five healthy oaks were strongly correlated ($R = 0.67$ – 0.88), whereas Oak #2's daily transpiration was not significantly correlated with any of the other oak trees, and its R varied from 0.16 to 0.29. Early in the season (6/23–29), the daily sap flow for Oak #2 was 92–132% of the average of the other two woodland oaks. However, by July the sap flow rate of Oak #2 dropped substantially to less than 30% of the average of the other two oaks, and these low rates continued through the September sampling period. These data strongly suggest that this tree was in the process of dying during our study period, and therefore we excluded data for Oak #2 from the data analysis. Day-to-day variability among J_d values was high; however, values recorded for individual trees of the same species were strongly correlated ($0.67 < R < 0.88$ for oaks; $0.49 < R < 0.78$ for elms; Table 2), indicating good consistency in the data. Correlations between individuals of differing species were weaker, and not significant in 7 of 15 cases. Average oak sap flow rates in woodland and savanna were strongly correlated, but average elm sap flow rates were weakly (though significantly) correlated with oaks in both stands

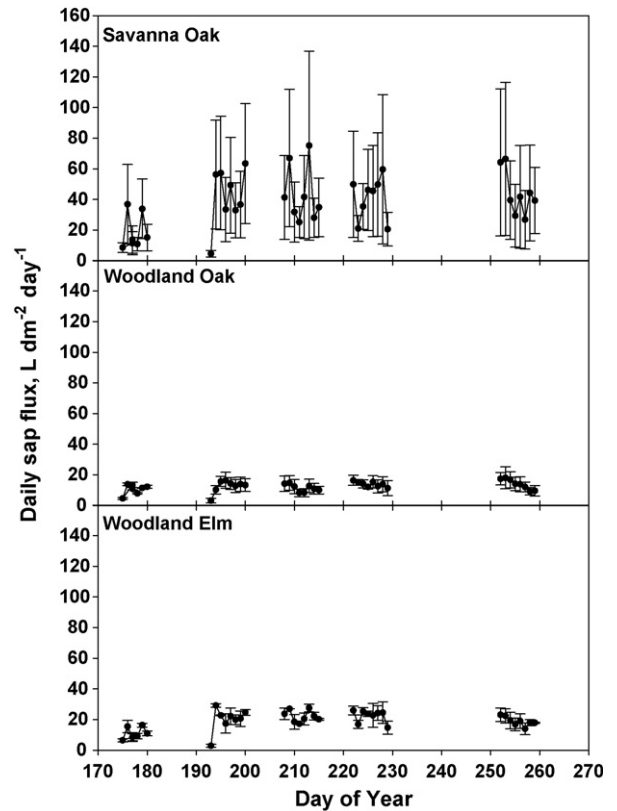


Fig. 4. Total daily sap flow (J_d , $\text{L dm}^{-2} \text{ day}^{-1}$) by species and plot (savanna: *Quercus macrocarpa*; woodland: *Quercus macrocarpa* and *Ulmus americana*), showing data collected during five time periods in 2004. Error bars indicate standard deviation.

(Table 2). Coefficients of variation among the sensors within each tree were greatest when J_s was at a minimum, i.e., at night. During daylight hours when J_s was at a maximum, the coefficient of variation was usually in the range of 20–40% (data not shown), which is slightly higher than values reported in other studies (e.g., Loustau et al., 1996 and references therein).

Table 2

Correlation coefficients for daily sap flow among individual trees for two species growing in two different stands (e.g., savanna stand: oak = *Quercus macrocarpa*; woodland stand: oak = *Quercus macrocarpa*; elm = *Ulmus americana*)

	Woodland			Savanna				
	Oak1	Oak3	Elm1	Elm2	Elm3	Oak4	Oak5	Oak6
Oak1	1			0.47				0.87
Oak3	0.75	1						
Elm1	0.58	0.25 ^x	1					0.50
Elm2	0.70	0.22 ^x	0.78	1				
Elm3	0.52	0.24 ^x	0.49	0.68	1			
Oak4	0.67	0.85	0.33 ^x	0.30 ^x	0.27 ^x	1		
Oak5	0.81	0.77	0.44 [*]	0.50	0.53	0.81	1	
Oak6	0.72	0.69	0.33 ^x	0.47	0.46	0.87	0.88	1

Above the diagonal (1 values), the correlations are for averages calculated from the individual trees belonging to the three stand-species groups (e.g., average transpiration rates for oaks in the woodland and those in the restored savanna have a correlation coefficient of 0.87). All correlations are significant at $p < 0.01$, except * indicates $p < 0.05$, and ^x indicates $p > 0.05$.

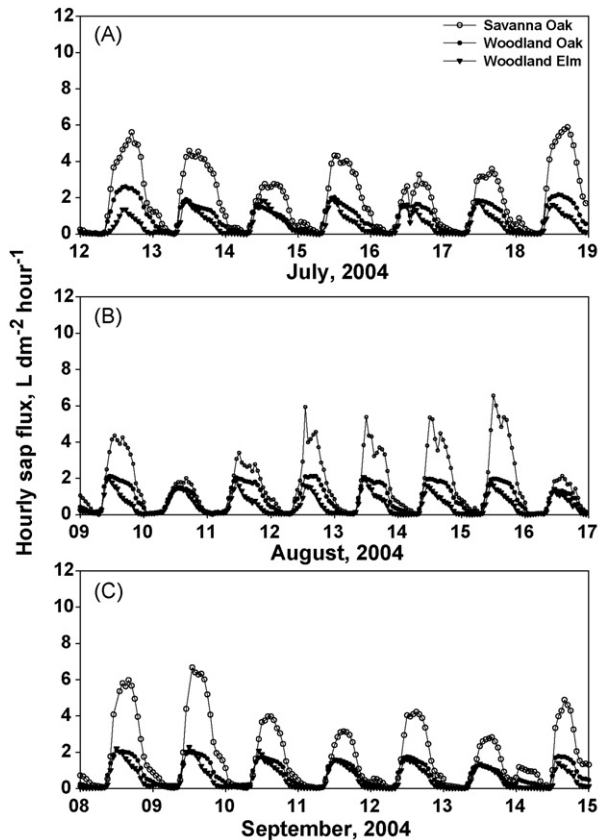


Fig. 5. Hourly mean sap flow (J_h , $L\ dm^{-2}\ day^{-1}$) during monitoring periods in July (A), August (B), and September (C), by species and plot (savanna: *Quercus macrocarpa*; woodland: *Quercus macrocarpa* and *Ulmus americana*).

Diurnal patterns in hourly sap flow data (Fig. 5) reflect a trend in which savanna oaks consistently had greater mean J_d values compared to the woodland oaks, while sap flow rates were least for the elms. The diurnal patterns in sap flow varied distinctly between the oak and elm trees: whereas J_d in elms peaked during the early morning hours then quickly declined, J_d in oaks also increased in the morning, but were then sustained at relatively high rates into the late afternoon. Mean J_d for the savanna oaks ($35.9\ L\ dm^{-2}\ day^{-1}$) was significantly greater than for the woodland oaks ($20.7\ L\ dm^{-2}\ day^{-1}$), whereas the elms had significantly lower mean J_d ($12.4\ L\ dm^{-2}\ day^{-1}$) compared to the oaks (Table 3). Maximum (peak) J_h values averaged $4.3\ L\ dm^{-2}\ h^{-1}$ for savanna oaks, $1.8\ L\ dm^{-2}\ h^{-1}$ for woodland oaks, and $1.7\ L\ dm^{-2}\ h^{-1}$ for woodland elms.

3.3. Correlation of sap flow with climatic variables

Mean J_d was significantly correlated (positive) with radiation for both stands and species (Table 4). There was

Table 3
Geometric means and standard deviations of daily sap flow rates on 32 dates of measurement during summer 2004

Stand	Species	Mean ($L\ dm^{-2}\ day^{-1}$)	S.D.
Savanna	<i>Quercus macrocarpa</i>	35.9	27.7
Woodland	<i>Quercus macrocarpa</i>	20.7	5.0
Woodland	<i>Ulmus americana</i>	12.4	4.3

Table 4

Correlation coefficients between daily average (geometric mean) sap flow rates, grouped by species and plot, and environmental variables

	Woodland oak	Woodland elm	Savanna oak
D	-0.11	0.19	-0.13
D (when $>0.4\ kPa$)	-0.84**	-0.13	-0.71*
R_s	0.41*	0.51**	0.38*
Average wind	-0.41*	-0.28	-0.32
Daylength	0.17	-0.18	0.02
Recent precipitation (3 days)	-0.02	-0.12	0.02

Significance: * $p < 0.05$; ** $p < 0.01$.

also a consistent negative correlation of J_d with wind run, which was only significant for the woodland oaks. Exponential curves fit between J_d and D ($J_d = a(1 - \exp(-kD))$) were not significant for individual trees nor average daily values. This can be attributed to: (1) high sap flow occurred on two dates that followed the largest (47 mm) rainfall, and had high R_s (about $0.95\ MJ/m^2$), and fair winds; (2) for the oaks in both stands, sap flow actually decreased at $D > 0.4\ kPa$ for both the savanna and woodland oaks (Fig. 6, and Table 4). Quadratic curves could be fit to the data but resulted in small r^2 values, between 0.14 and 0.16 (data not shown). Multiple ANOVA conducted on J_d for species-stand groupings showed variation among individual trees comprised 20–68% of the variability, with large sap-flow values from one oak savanna individual causing the 68%

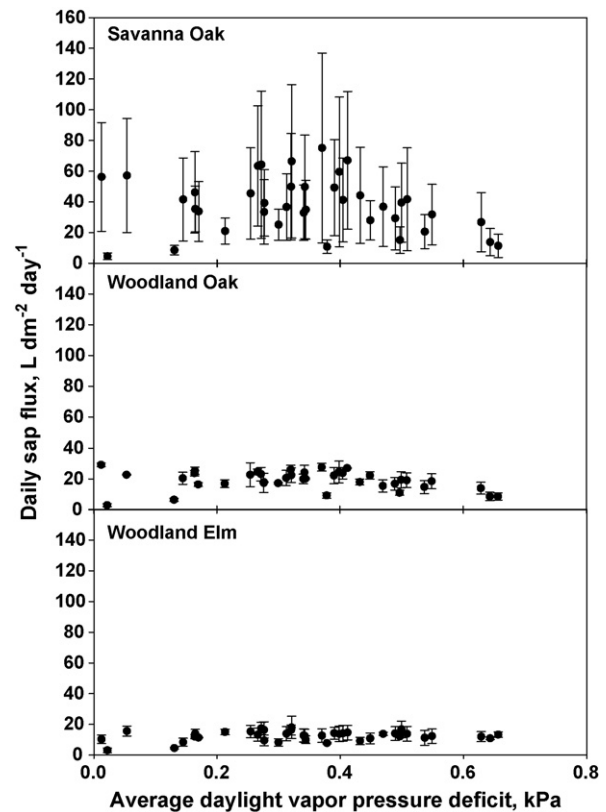


Fig. 6. Daily accumulated sap flow plotted against vapor pressure deficit, for trees in the savanna (*Quercus macrocarpa*) and woodland (*Quercus macrocarpa*; *Ulmus americana*) during the measurement period.

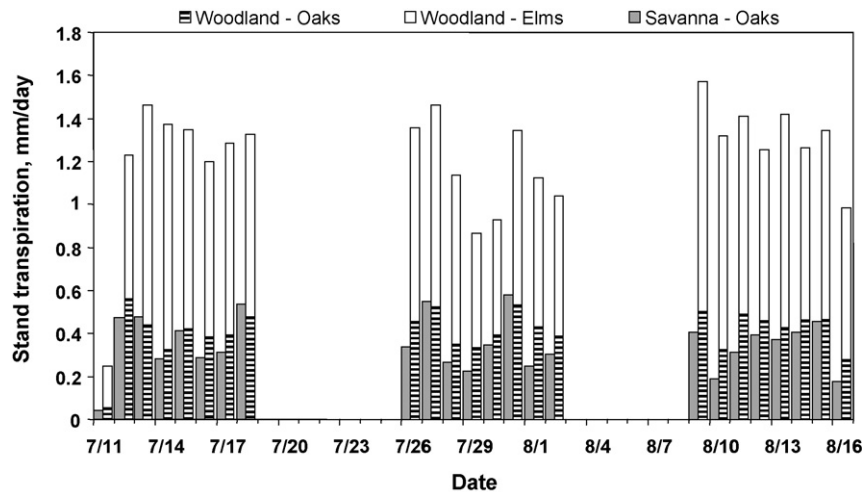


Fig. 7. Stand transpiration (E_c , mm day^{-1}) by the dominant species in the savanna (*Quercus macrocarpa*) and the woodland (*Quercus macrocarpa* and *Ulmus americana*), for three measurement periods in 2004 (July 7/11–7/18, 7/26–8/2, and 8/9–8/16).

proportion in that group. Day-to-day variation comprised most remaining variation (28–63%), as influenced by climate, with non-ascribed error sources comprising the remainder (4–17%).

Our multiple regressions on sap flow values for individual trees, segregated by hour of day, showed that R_s explained more variation in J_h than other weather or day-length variables in 66% of the regression equations. Vapor pressure deficit (D), including either linear, quadratic, or interaction (with R_s) terms, was the most significant variable in 18% of the equations, while wind, temperature, and daylength showed less frequent dominance. The D terms were dominant during early afternoon hours, whereas R_s was dominant during mornings.

Daily sap flows averaged among individual trees in the stand-species groupings showed that daylength, D (quadratic or interaction with R_s), and R_s combined to explain about half the variation (r^2 between 0.046 and 0.55) in sap flow. R_s was most important in the woodland, and R_s and D (quadratic term) were of essentially equal importance in determining savanna oak sap flow.

3.4. Stand transpiration

Total sapwood area in the woodland was $8.58 \text{ m}^2 \text{ ha}^{-1}$, of which $1.94 \text{ m}^2 \text{ ha}^{-1}$ consisted of oak trees and $6.64 \text{ m}^2 \text{ ha}^{-1}$ consisted of encroaching elms. In contrast, total sapwood area in the restored savanna was only $0.95 \text{ m}^2 \text{ ha}^{-1}$. Estimated mean daily E_c of the tree stratum, based on sap flow observations, was 1.23 mm day^{-1} in the woodland, compared to only 0.35 mm day^{-1} in the savanna (Fig. 7). Elms comprised 77% of the woodland's sapwood area, and contributed about 67% of the transpiration. The savanna only had 11% of the total sapwood area of the woodland, yet contributed nearly 30% of its transpiration rate.

3.5. Groundwater

Water table depth at the end of the study (August 15 to September 15) was shallower for the savanna (2 m) compared

to the woodland (6.5 m; data not shown). This water table head gradient is considerable, given surface elevations are similar, and that piezometers are within about 50 m of one another. Groundwater monitoring observations at other locations within the Neal Smith NWR do not show such large head gradients (K. Schilling, unpublished data). The difference in head, we conclude, is largely due to the difference in vegetation. Were the observed differences in stand-level water uptake to occur for 90 days, and effectively cause the observed difference in water table depths, that would equate to a specific yield of the glacial till aquitard of 0.02, which is within the range suggested by Freeze and Cherry (1979) for aquitard deposits. Greater canopy interception and therefore lower throughfall and recharge in the woodland could also have contributed to the lower water table elevations recorded for the woodland compared to the savanna.

4. Discussion

Few studies have quantified the effects of land use change and restoration on ecohydrology as determined by individual tree species' physiologies related to water uptake within grassland-savanna-woodland transition zones (Huxman et al., 2005). In this study, we present evidence suggesting that forest structure (open savanna versus closed woodland canopies) and co-occurring species (oak and elm) have different water uptake patterns that in turn affect site water balance. Before discussing these results in greater detail, several limitations to the study are acknowledged. First, depth to which the sap flow sensors were inserted (30 mm) exceeded sapwood depth in the oaks and were less than the sapwood depth in the elms, which may have introduced errors, especially when scaling to the stand level (discussed in detail in Clearwater et al., 1999; Nadezhdina et al., 2002). Second, the number of sample trees utilized for sap flow measurements was relatively small and given the high degree of variability among trees, estimates of stand scale transpiration are regarded as approximate. However, despite these limitations, the data do reveal consistent patterns of water use for the study stands and species, providing insights into the effects of restoration on

plant water uptake for a rare savanna ecosystem as well as the implications for landscape ecohydrology.

4.1. Savanna restoration treatment effects on individual tree sap flow

Removal of encroaching shade-tolerant species from the woodland to restore the former savanna structure resulted in an increase by approximately 42% in mean J_d in the remaining oak trees relative to oak trees in the unthinned encroached savanna woodland. Results suggest that elm encroachment has led to competition for water between the overstory oaks and the elms, and reduced water uptake by the oaks. Certainly this result was expected. These results agree with other studies documenting increased sap flow following thinning (Bréda et al., 1995) and in stands with lower tree densities (Meinzer et al., 1996). This is further supported by isotopic data indicating that woodland oaks and elms obtained water from deeper depths in the soil profile compared to savanna oaks (Asbjornsen et al., 2007). Therefore, direct competition for water between these species and extension of root systems to access deeper water supplies likely contributed to observed differences in sap flow rates between the two study stands.

Among the microclimate variables examined in this study (D , R_S , wind run, recent precipitation, daylength), the strongest positive correlation was recorded between J_d and R_S for all tree species ($r^2 = 0.38–0.51$). Further, when considering the microclimate controls on hourly sap flow rates, R_S was also the main driver, whereas D only became of critical influence in the early afternoon hours. Although plant transpiration studies generally report D as being the most important controlling factor influencing sap flow (Ewers et al., 2002; Pataki and Oren, 2003), our data suggest that under the hazy, humid climatic conditions characteristic of Central Iowa and much of the Midwest (for example, maximum D recorded in our study was 0.68 kPa, compared to $D > 2.0$ kPa commonly reported for other deciduous forests; Wullschleger et al., 2001; Pataki and Oren, 2003), solar radiation may be a more important control on transpiration, through its regulation of photosynthesis. We also detected a negative correlation between J_d and wind run, especially for the woodland oaks, which was probably associated with stomatal closure in response to moisture stress. Pataki and Oren (2003) reported that solar radiation was more important in controlling stomatal conductance of *Liquidambar styraciflua*, a shade intolerant species of bottomland eastern deciduous forests, compared to that of four shade tolerant species, which showed stronger correlations with D . Wullschleger et al. (2000), working in an upland oak forest in Tennessee, reported that sap flow in canopy dominant and codominant *Acer rubrum* was strongly correlated with both R_S and D . We are aware of no other studies that have measured sap flow in oak savanna ecosystems in the Midwestern U.S.

4.2. Variation in species' response to microclimate

Across a broad range of species and ecosystems, the relationship between sap flow and D is best depicted as a non-

linear curve, with sap flow initially increasing, eventually reaching saturation (plateau) and often declining at high D as a result of stomatal closure (Pataki et al., 2000; Pataki and Oren, 2003; Ewers et al., 2002). In our study, although this relationship was not significant across the full range of D , both savanna and woodland oaks exhibited a significant negative correlation between J_d and D for $D > 0.4$ kPa. This diminished sap flow at high D suggests oak trees in both stands experienced moisture stress, and closed their stomates to reduce transpiration. On a daily basis, elms maintained lower and relatively constant sap flow rates across the entire range of D . Diurnally, elm sap flow peaked early in the day, and this may have allowed them to maintain a relatively constant J_d during the least humid conditions of this study.

The degree and rate of stomatal closure in response to changing environmental conditions varies greatly among tree species depending on their particular physiological characteristics (Tenhunen et al., 1987; Oren et al., 1999). Response of sap flow to changes in microclimate has been found to vary among co-occurring species for a range of ecosystems (Pataki et al., 2000; Oren and Pataki, 2001; Ewers et al., 2002; Pataki and Oren, 2003). Early and mid-successional species tend to have lower stomatal resistances and greater rates of leaf transpiration than late successional species due to more conservative resource use and growth rates by the latter (Abrams, 1988, 1990; Hornbeck et al., 1997). This pattern was observed in our study, with the late successional elms tending to rapidly increase transpiration rates during early morning hours when D was still low, but unable to sustain high sap flow during the day once D increased. In contrast, *Q. macrocarpa*, which in savanna ecosystems is one of the first tree species colonizing open grasslands during fire-free intervals, maintained relatively high sap flow throughout mid-day and late afternoon hours (Fig. 5). High transpiration rates in elm trees in the early morning hours may also be related to increased water availability due to hydraulic lift (*sensu* Richards and Caldwell, 1987) by the oak trees. Bur oak trees are known to have exceptionally deep rooting habit (Weaver and Kramer, 1932), and data suggesting that hydraulic lift is occurring at this site were presented in a complementary study (Asbjornsen et al., 2007).

More drought tolerant species are generally capable of maintaining higher turgor pressure at low water potentials, thereby sustaining higher transpiration rates under conditions of moisture stress or high vapor pressure deficit (Bahari et al., 1985; Abrams and Knapp, 1986; Abrams, 1990; Ni and Palardy, 1991). Greater drought tolerance of *Q. macrocarpa* compared to the later successional and more mesic *U. americana* (Abrams, 2003) may have contributed to the oaks' higher and more sustained sap flow in our study. Similarly, studying co-occurring species having different drought tolerances in a Western subalpine forest, Pataki et al. (2000) reported that the most drought tolerant species (*Populus tremuloides*) had greater and more sustained increases in sap flow under increasing D compared to less drought tolerant *Pinus contorta* and *Abies lasiocarpa*.

The lower transpiration capacity of the elms compared to the oaks and lack of a saturation effect in their sap flow may also be

attributed to their canopy position. The encroaching mid-story elm trees did not have exposure to direct sunlight and wind, whereas the dominant overstory oak trees were fully exposed to solar radiation and wind and therefore experienced greater evaporative demand. Martin et al. (1996), working in an *Abies amabilis* forest, also documented that dominant and co-dominant trees transpired for longer periods during the day and contributed disproportionately to total stand transpiration compared to trees in the smaller size classes and having lower canopy positions. Other studies that have reported an absence of a saturation effect in sap flow in response to D were primarily for trees growing under extremely high moisture availability, such as in wetlands in northern Wisconsin (Ewers et al., 2002), a mature floodplain forest in Amazonia (Oren et al., 1996), and cypress wetlands in Florida (Brown, 1981). However, one exception is a study by Wullschleger et al. (2000), which reported no indication of a plateau in the relationship between E_c and average daily D for *Acer rubrum* in Tennessee.

4.3. Effects of savanna restoration on stand transpiration

Mean daily E_c recorded in our study for the woodland (1.2 mm day^{-1}) is within the range of values reported for other deciduous forests, which typically range from $0.2\text{--}3.0 \text{ mm day}^{-1}$ for deciduous forests (Bréda et al., 1995; Oren and Pataki, 2001; Roberts et al., 2001; Wullschleger et al., 2001; Ewers et al., 2002). Mean daily E_c for the savanna (0.4 mm d^{-1}) was lower than values reported for Mediterranean and African savannas ($2\text{--}3 \text{ mm day}^{-1}$; Allen and Grime, 1995; David et al., 2004), perhaps due to the more humid climate and lower vapor pressure deficits in the Midwestern U.S.

This study documented the effect of woody encroachment of elms within an oak savanna on stand-level water uptake, as daily mean E_c was more than fourfold greater in the woodland relative to the savanna site. The greater water uptake in the woodland was at least partly sourced from groundwater, which was about 4 m deeper under the woodland relative to the savanna. The dense, glacial-till subsoils at this site would provide very little water per unit elevation drop in the water table, and given low hydraulic conductivities (and hence lateral flow rates) expected for these materials (Rodvang and Simpkins, 2001), the difference in water table elevations is not surprising. Thus, shifts in stand densities and species composition resulting from woody encroachment and savanna restoration were found to significantly alter site water balance in these remnant oak savannas, as has been reported elsewhere (Trousdel and Hoover, 1955).

4.4. Hydrologic implications of woody encroachment and restoration in oak savannas

Ecological theory posits that savannas are maintained within transitional zones between grasslands and woodlands by a combination of disturbances (fire, drought, grazing), in the absence of which woody encroachment often occurs (van Langevelde et al., 2003). Woody encroachment can also be facilitated during climatic periods with high rainfall (da Cunha

and Junk, 2004). Our study offers another potential driving mechanism for woody encroachment. Where remnant savannas are isolated within landscapes dominated by annual crops, hydrologic alterations resulting from land use change (i.e., increased base flow and higher water tables; Schilling, 2005) may facilitate woody encroachment by increasing water availability above levels that historically occurred in perennial-dominated landscapes. Thus, surplus moisture could hamper restoration of oak savannas from encroached woodlands in the Midwest by maintaining conditions that favor encroachment processes. This could increase the frequency of management interventions (e.g., fire) needed to deter encroachment, increasing costs and logistical requirements of restoration.

Restoration efforts also need to consider the potential trade-offs with respect to water uptake, biodiversity, and ecosystem resilience. On one hand, conversion of encroached woodlands to savanna through restoration will reduce their total water uptake, thereby decreasing any attenuation of hydrologic alterations of the larger landscape that woodland water use may provide. On the other hand, restoration of savannas would increase the biodiversity within agricultural landscapes, particularly native savanna species that are presently rare (Leach and Givnish, 1999). Further, the resilience of savannas to climate change and extreme climatic events may be greater due to the diverse assemblage of species and functional groups occurring in mixed grass-tree savanna systems and the stabilizing influence of frequent fire (Anderson and Brown, 1986; Scholes and Archer, 1997; Jeltsch et al., 2000). It is important to note that opportunities to restore these remnants are very rare as they occupy a fraction of a single percent of their original extent in this region of the US.

5. Conclusion

This study demonstrated large differences in stand-level transpiration and water table levels between a restored savanna and an elm-encroached oak woodland. Differences in diurnal water use between species were clear, and there was a strong effect of the thinning treatment on increasing sap flow in savanna oaks relative to the woodland oaks. Savanna oaks had greater mean daily J_s ($35.9 \text{ L dm}^{-2} \text{ day}^{-1}$) than woodland oaks ($20.7 \text{ L dm}^{-2} \text{ day}^{-1}$) and elms ($12.4 \text{ L dm}^{-2} \text{ day}^{-1}$). Although the woodland's stand transpiration was greater (1.23 mm day^{-1}) than the savanna's (0.35 mm day^{-1}), the savanna achieved 30% of the woodland's transpiration with only 11% of its sapwood area. High intra-specific and within-plot correlations for daily sap flow suggest that these trees were responding to the same drivers for transpiration. However, low correlations for daily transpiration rates between species reflect their differing physiological controls on water uptake patterns. Correlations performed with microclimate variables indicated that R_S was the strongest driver of transpiration for both species. Oaks were more sensitive to D than elms, exhibiting diminishing daily sap flow at high D . Differences in species' patterns of sap flow and climate controls were attributed to their

physiological strategies, successional status, drought tolerance, and canopy position.

In the Midwestern U.S., woody encroachment of former savanna ecosystems results in greater stand density and shifts in species composition. Our study suggests that greater water uptake by the vegetation accompanies this transition. These shifts have occurred while, across the wider landscape, dominance by annual crops has decreased plant water use. This has provided surplus water that may support species transitions in native ecosystem remnants. Conservation and restoration of remnants of native savannas within agricultural landscapes can help retain the region's biodiversity, but the hydrologic functioning of these areas are affected by restoration and surrounding land uses. Savanna restoration efforts should consider the potential for reestablishing the hydrologic conditions of a site, for example, by targeting of larger remnants or hydrologically isolated sites (e.g., hilltops), or by buffering of smaller remnants. If the management goal is to enhance hydrologic regulation of agricultural landscapes experiencing excess runoff and nutrient loss, then maintenance of woodlands supporting high transpiration rates may be desirable. Further study is needed to better understand the effects of woody encroachment and savanna restoration on their hydrologic functions, including infiltration, water storage potential, hydraulic lift, and the role of different species and plant functional groups on stand transpiration.

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