

Ecohydrological changes in semiarid ecosystems transformed from shrubland to buffelgrass savanna

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ABSTRACT

In arid and semiarid lands worldwide, vegetation cover is being transformed to savannas dominated by exotic grasses. However, the ecohydrological and biogeochemical changes associated with this process remain little understood. For more than 3 years, we studied soil moisture dynamics in natural semiarid shrubland patches and compared those with changes in an adjacent site that had been transformed to an exotic buffelgrass (*Cenchrus ciliaris*) savanna. We found that volumetric soil moisture was higher in patches with some kind of cover. For both tree and bare patches, volumetric soil moisture and plant-available water in the 60- to 100-cm depth interval were significantly lower in the savanna than in the natural site. In buffelgrass patches, volumetric soil moisture and plant-available water were higher at almost all depths and in wet years and increased significantly during the summer monsoon season, suggesting rapid infiltration mechanisms under buffelgrass. During years with wet winters, these mechanisms also led to brief accumulations of water in the soil profile (0–200 cm). Such changes in soil profile water dynamics brought about adaptive responses in perennial plant species. The ability of species to change their patterns of soil water use in the profile may be an important mechanism enabling them to compete when novel tree–grass interactions are established by invasion of grasses. Our results provide new insights for understanding the changes caused by grass invasion in arid and semiarid lands, as well as how these changes may impact ecohydrological dynamics in global change scenarios. Copyright © 2016 John Wiley & Sons, Ltd.

KEY WORDS *Cenchrus ciliaris*; ecosystem transformation; land use change; patch dynamics; soil moisture profile; soil water availability

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INTRODUCTION

Vegetation dynamics have been studied extensively in regions undergoing encroachment by woody plants (Archer, 1995; Archer *et al.*, 1988, 2000), but the reverse disturbance process – the invasion of arid and semiarid woodland ecosystems by exotic grasses – is less well understood. While a few studies have examined how invasive grasses become established and maintained (Duniway *et al.*, 2010), almost nothing is known about how vegetation and soil water will be altered when grasses invade warm arid and semiarid ecosystems (Wilcox *et al.*, 2012). Indeed, little work has been done in these

ecosystems comparing water balance components in native shrublands with those in areas undergoing increasing dominance or invasion by grasses (Wilcox and Thurow, 2006; Wilcox *et al.*, 2012).

Arid and semiarid ecosystems are fundamentally water driven (Noy-Meir, 1973; Reynolds *et al.*, 2004), although vegetation dynamics play an important role in community structure and assemblage (Barnes and Archer, 1999; Callaway, 1995; Segoli *et al.*, 2012). Water limitation and the uncertainty and variability (Ehleringer and Mooney, 1983; Le Houérou *et al.*, 1988) of rainfall in arid environments – typically coming in small and infrequent pulse events (Ogle and Reynolds, 2004) – result in a heterogeneous landscape of patchy vegetation. This patchiness, in turn, increases the heterogeneity of water and nutrient inputs and their distribution over the landscape (Peters and Havstad, 2006). Spatial heterogeneity along a gradient of increasing patchiness of light, water and nutrients has been documented in grassland-to-woodland continuums (Aguilar and Sala, 1999; Breshears, 2006). Ecosystem transformation or invasion by exotic grasses,

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driven by changes in land use and global change, should influence vegetation patchiness as well as water inputs, losses and storage, with still unknown or unconfirmed ecohydrological ramifications (Archer *et al.*, 1995; Wilcox, 2010; Wilcox *et al.*, 2012).

Changes in evapotranspiration are the main focus of most ecohydrological studies in transformed arid lands. However, resource patchiness and heterogeneity along vertical gradients in the soil are as important, and less well known – especially for woody plant species as they tap water and resources from intercanopy spaces at different depths (Breshears *et al.*, 2009). The bare ground/vegetation patchiness pattern seen in arid and semiarid ecosystems may be enhanced by woody plants because of the concentration of resources under their canopies (Ferrante *et al.*, 2014; Newman *et al.*, 2010), and this pattern may be expected to change when grasses become predominant.

Below-ground soil moisture conditions depend on and are modified by soil texture, water availability, rooting depth activity (woody and herbaceous plant species have different rooting strategies) and seasonal variations in plant water use. Woody plant encroachment of arid and semiarid grasslands increases water use (Scott *et al.*, 2008; Scott and Huxman, 2005), as the roots of woody plants reach water stored in deeper soil layers, and some may reach the water table (Potts *et al.*, 2010). The opposite was found in Mediterranean shrublands that had been transformed into exotic grasslands: Moisture levels were higher below the rooting depth of the grasses, which changed the soil profile at the site (Davis and Mooney, 1986). Under both conditions, it is suggested that soil water availability and the moisture use patterns of shrubs become decoupled, because the root systems of woody plants are multi-layered – even drawing moisture from deeper soil layers near the water table (Scott *et al.*, 2009, 2014) – and thus these plants may be able to coexist with grasses in the same site (Davis and Mooney, 1986; Schenk and Jackson, 2002; Walter, 1971).

The transformation of many native ecosystems into savannas dominated by exotic grasses is currently a major concern, as this phenomenon appears to be a consequence of global change (Wilcox, 2010). In arid, semiarid and subtropical woodlands, savannization may involve changes in soil biogeochemistry and ecohydrology, particularly in the use and storage of water in the soil profile (Cochrane *et al.*, 1999). For example, model scenarios for cool and warm desert ecosystems predict increases in both deep water storage and shallow-depth water use (Wilcox, 2010; Wilcox and Thurow, 2006; Wilcox *et al.*, 2012). However, empirical evidence for such changes in these ecosystems is lacking (Wilcox *et al.*, 2012).

In this paper, we report on a 4-year study (2010–2013) designed to compare water use and dynamics in a native Sonoran Desert shrubland with those in a neighbouring

rangeland transformed into exotic buffelgrass savanna (with some native trees remaining on the site). By examining how soil water dynamics are modified by this type of transformation during different seasons and years, we wanted to test several ecohydrological hypotheses put forward by Wilcox *et al.* (2012) – in particular, that soil water storage will increase in response to increasing exotic grass cover. We sought to ascertain whether and how such changes in water storage and availability may lead to changes in patterns of soil water use by different plant species, an issue that has not yet been fully addressed.

STUDY AREA

The study site is located at El Churi Ranch, 54 km east of Hermosillo, Mexico (28°42'672 N latitude and –110°32'969 W longitude). The region is semiarid with a bi-seasonal rainfall regime. Data from the closest weather station (at San José de Pimas, a slightly wetter location about 15 km due east) show a mean annual temperature of 23.5 °C and annual rainfall of 425 mm for the last 12 years. During the period of study, while the mean annual temperature was 23.5 °C, rainfall recorded at that same station was only 323.5 mm. Monthly precipitation was also estimated, from rainfall gathered at the study site: from January of 2010 to July 2011 with a funnelled reservoir covered with mineral oil in the bottom to prevent water evaporation, and after July 2011 with an automatic weather station. The magnitude and seasonal distribution of annual rainfall at the site varied greatly over the 4-year period. For example, the early winter of 2011 was dry, whereas the winter of 2013 was wet; the summer of 2011 was dry, whereas the summer of 2012 was wet; and the autumn season of 2011 was unusually wet (Figure 1).

El Churi Ranch is a cattle ranch that has been in operation for many decades (as have most such ranches in the region), but with no evident signs of overgrazing. The natural vegetation is semiarid shrubland, the dominant species being *Olneya tesota*, *Ipomoea arborescens*, *Prosopis velutina*, *Mimosa laxiflora* and *Fouquieria macdougalli*. During wet years, a continuum cover of annual grasses (*Bouteloua aristidoides*, *Aristida ternipes*) and annuals is present. About 35 years ago, some areas of the ranch were cleared of most but not all of the woody plants (individuals of the dominant tree species *O. tesota* were left untouched to provide shade for livestock), and the exotic buffelgrass (*Cenchrus ciliaris*) was seeded, establishing a savanna-like cover in those areas. For our study, we compared canopy and intercanopy patches in the natural woodland/shrubland site with corresponding patches in the buffelgrass savanna site. The two sites are located only a couple of kilometres from each other and have similar rainfall.

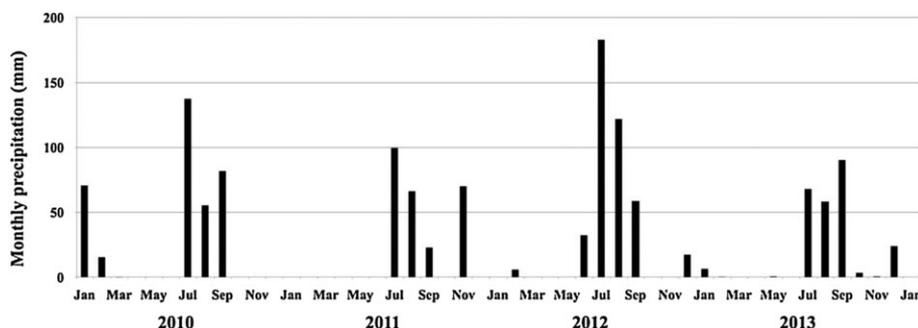


Figure 1. Monthly precipitation totals for the study area, 2010–2013. Data for the period 2010 to mid-2011 come from a nearby (± 15 km) climatological station (San José de Pimas, Sonora). Data for the period 2012 through 2013 come from a micrometeorological station on site.

METHODS

For each of the two vegetation cover sites, we delineated patches having characteristics similar to those of the other site. Within the natural vegetation cover site, we selected patches under the canopy of the dominant nurse tree species (NT) and intercanopy patches (NI). In the savanna site, we selected patches under the canopy of dominant nurse tree species (ST), intercanopy patches (SI) and patches covered with the now dominant buffelgrass (SB). Each patch type had five replicates.

Soil moisture was sampled by means of access tubes: some were arranged within the tree canopy (T), close to its edge and as far as possible from other trees of the same species; others extended from the canopy edge 2–3 m into the nearest bare intercanopy space (I), to allow tracking of changes in soil moisture within the bare intercanopies of both the natural shrubland (NI) and the savanna site (SI) up to depths of 200 and 160 cm, respectively.

To characterize soil texture, bulk density and soil moisture retention at field capacity (0.03 MPa) and permanent wilting point (1.5 MPa), we collected three soil samples from each of the five patch types; soil was taken from a depth of 20 cm at three different points within the patch, then homogenized for laboratory analysis. We obtained textural data using the Bouyoucos hydrometer technique and soil moisture retention data using the pressure plate method. Bulk density was obtained after oven-drying and weighting known volumes of undisturbed soil. The analyses were performed by the Agronomy School Soil Sciences Analysis Lab, Universidad de Sonora.

Volumetric soil moisture (VSM) was measured by means of access tubes with a TRIME-FM3 soil moisture meter and a T-3 tube probe (IMKO, Ettlingen, Germany). At both sites, we inserted a TRIME probe in 4.5-cm-diameter TECANAT polycarbonate access tubes permanently installed within each of the five different patch types (a total of ten tubes), enabling soil moisture to be measured at 10-cm intervals along the profile to a depth of 200 cm. We measured soil moisture monthly for about 4 years (January 2010–January 2014). TRIME is a TDR-type system that

uses an electromagnetic emission field to measure water bipolar states at a frequency of 0.5 to 1 GHz; within this range, most of the real part of the dielectric constant is maintained, whereas the imaginary interference part is reduced to minimum, eliminating the need for temperature correction (Stacheder *et al.*, 1997). TRIME calibration is recommended for very clayey soils because of their high organic content and dielectric properties, and in that case a simple calibration is enough (Laurent *et al.*, 2001, 2005). Most soils at our sites are sandy, and our lab calibrations were not significantly different from manufacturer specifications (Stacheder *et al.*, 1997).

To convert VSM values to soil water potential, we calculated soil water retention curves from soil textural and bulk density (D_b , $g\ cm^{-3}$) data, using pedotransfer functions (Zaccharias and Wessolek, 2007), as follows:

$$\theta(h) = \theta_r + (\theta_s - \theta_r) / [1 + (ah)^n]^m, \quad (1)$$

where θ_r is the residual water content ($m^3\ m^{-3}$), θ_s is the water content at saturation ($m^3\ m^{-3}$) and h is the soil water potential. The remaining components are empirical parameters that will be a function of the clay and sand content as well as the soil bulk density. Soil texture characteristics obtained every 10 cm to a depth of 50 cm were used to estimate soil water potential at each of those depths (Dardanelli *et al.*, 2004).

We also used the soil textural analyses to calculate plant-available water (PAW), as the difference between VSM at 0.03 MPa soil water potential and soil moisture at permanent wilting point. We did not use the standard agronomic permanent wilting point of -1.5 MPa because most of our species are known to tolerate much more negative water potentials; instead, we used a ‘plant extraction limit’ concept (Seyfried and Wilcox, 2006) and assumed this point to be close to -4.0 MPa (Schulze *et al.*, 2005). For most species, this value coincided with some of the lowest pre-dawn water potentials found during the growing season, as well as with the midday leaf water potential of the dominant species – the level at which their stomata closed (-3.8 to -5.4 MPa, measured in the summer of 2011). It also coincided well with

the lowest VSM reading obtained for each depth, via Equation 1, over the entire study period.

Seasonal PAW values were obtained from the difference between end-of-season mean soil moisture and field capacity for a given soil profile, for the depth intervals 0–10, 11–40, 41–80, 81–120, 121–160 and 161–200 cm. The soil moisture data for the period 2010–2013 came from readings in March (winter), June (spring), September (summer) and December (autumn), except for spring 2010 when May readings were used. An equipment failure in the summer of 2010 resulted in a gap in the data until the spring of 2011, when readings resumed. Plant-available water values were obtained for each depth interval but were counted only for depths at which roots of the dominant species were assumed to be present. A weighted PAW was calculated on the basis of vegetation cover percentage for each of the five patch types.

Rooting depths (R_{dp}) for the dominant species were estimated from pre-dawn leaf water potentials and VSM measurements. For each species, pre-dawn leaf water potential was assumed to be in equilibrium with the matric water potential in the soil, which was derived from the corresponding VSM obtained via Equation 1. Although some studies have found that pre-dawn leaf water potentials may not be at full equilibrium with matric water potentials when stomata remain slightly open (Donovan *et al.*, 2003), previous measurements have shown that stomata openings should be minimal in species at our site (Castellanos pers. obs.).

Throughout the study period, we used one-way ANOVA to track variances between repeat measurements of soil moisture and PAW among the five patch types. When data normality criteria were not met, we used non-parametric statistics, and when data normality was ensured, we used Tukey–Kramer post-hoc statistical test analysis with $p < 0.005$. We used JMP 11.0 for Mac (SAS Institute, Inc.) for all the statistical analyses.

RESULTS

Soil moisture

The soils from the canopy patches of both the natural and the savanna sites (NT and ST) were found to be sandy-silt with higher organic matter content than soils from the other patch types (Table I).

Measured over a 4-year period, VSM was found to be about one percent higher in the natural vegetation site ($0.086 \pm 0.03 \text{ m}^3 \text{ m}^{-3}$), apparently owing to greater variability in the buffelgrass savanna ($X^2 = 7.82$, $n = 359$; $p < 0.002$). When compared seasonally, VSM was found to be higher in the natural site only during the dry season ($X^2 = 6.53$, $n = 95$; $p < 0.01$), with no differences for the other seasons.

In these desert shrublands, some of the patches of nurse tree canopies and intercanopies are maintained after transformation of the area to buffelgrass savanna. When

Table I. Soil textural and moisture retention characteristics of patches in the natural shrubland/woodland site (NT, under tree canopy; NI, bare intercanopy) and in the buffelgrass savanna site (ST, under tree canopy; SI, bare intercanopy; SB, buffelgrass cover).

Patch type	Depth (cm)	Sand %	Clay %	Silt %	Bulk density (g m^{-3})	Organic matter %	pH
NT	30	83.3	6.7	10.0	0.97	2.59	7.42
NI	30	84.3	7.7	8.0	1.23	0.62	6.43
ST	30	79.3	8.7	12	1.0	1.59	7.04
SI	30	84.3	6.7	9.0	1.38	1.02	6.06
SB	30	87.3	5.7	7.0	1.17	0.68	5.76

such tree canopies and intercanopies patches in the two sites were compared, VSM was always about 30% higher under natural site conditions ($NT = 0.097 \pm 0.031 \text{ m}^3 \text{ m}^{-3}$; $X^2 = 44.85$, $p < 0.0001$) than in the savanna site. Soil moisture values in the buffelgrass (SB) patches were similar to those in the natural tree (NT) patches ($0.109 \pm 0.03 \text{ m}^3 \text{ m}^{-3}$) and were significantly higher than those for the NI, ST and SI patches ($X^2 = 119.19$, $n = 359$; $p < 0.0001$).

In all patch types, the most significant differences in VSM patterns were found in the shallower (0 to 40 or 50 cm) depths of the profile (Figure 2), and the greatest changes occurred at the end of the rainy season (September). The SB patches experienced the largest inter-annual changes in VSM, and those were during the summer rainy season ($X^2 = 39.25$, $p < 0.0001$; $n = 71$).

Volumetric soil moisture profile patterns up to 90 cm in the soil profile were similar for the tree and the intercanopy patches within each site. In the natural site, soil moisture in both tree and intercanopy patches increased in the 80- to 120-cm depth interval (e.g. $0.119 \text{ m}^3 \text{ m}^{-3}$; $X^2 = 15.95$, $p < 0.003$ for trees at this depth), whereas in the savanna site soil moisture in similar patches decreased at those depths (Figure 2). At both sites, below the 90-cm depth, the intercanopy patches had consistently lower VSM values than the tree patches (Figure 2). Most significant – of all patch types, the SB patches had the highest VSM values at all depths, and especially below 90 cm (Figure 2). Significant changes in VSM patterns during the wet season were found at shallower depths (Figure 2).

Water accumulation

Water accumulation, calculated in depth increments of 40 cm, differed according to patch type. Again, all patch types showed most of the changes in the uppermost 80 cm, with the greatest in the 0- to 40-cm interval. At the same time, as shown in Figure 3, NI and particularly SB patches accumulated water at 120 cm in the soil profile (even deeper in the case of SB). The largest changes in water accumulation for the SB patches happened during the

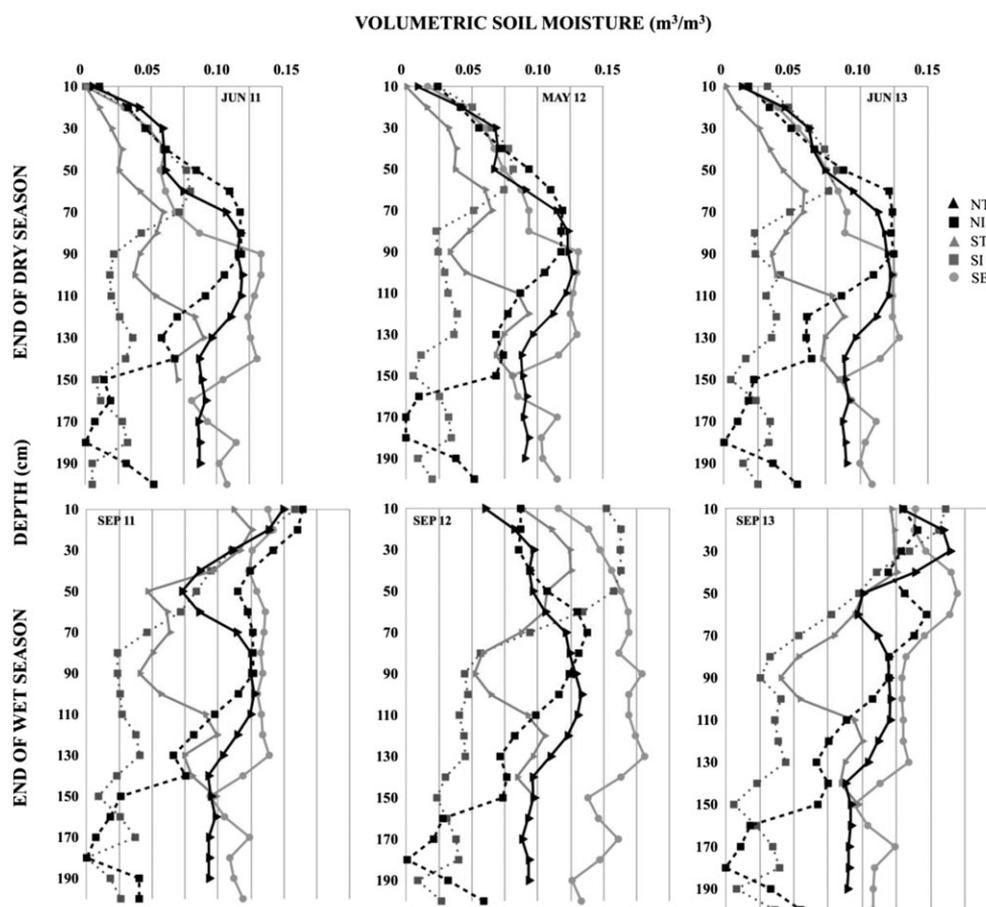


Figure 2. Volumetric soil moisture content ($\text{m}^3 \text{m}^{-3}$) for the five patch types at the end of the dry and wet seasons (2011–2013).

summer rainy season – particularly in those years when rainfall was highest (2010 and 2012) – reaching depths even lower than 180 cm (Figure 3). Water accumulation for tree patches of the savanna site (ST) was lower and seasonally much more differentiated down to the 120-cm depth interval than that for tree patches in the natural site. The same was true for intercanopy patches; in the SI patches, seasonal differences were greater down to the 80-cm depth, with almost no water found below 80 cm.

Plant-available water

Rainfall in the Sonoran Desert has a bi-seasonal pattern, with a summer monsoon as well as a winter wet period. Total rainfall amounts can be highly variable, both seasonally and annually. During the 4-year study period (January 2010–January 2014), the summers of 2010 and 2012 were the wettest of the rainy seasons. As would be expected, PAW was significantly higher during the summer monsoon season ($F=3.39, p<0.02$), followed by autumn, winter and spring (Figure 4).

Overall differences in PAW between the two sites were not significant and were due mainly to seasonal variations in rainfall and in usage by plants. However, as shown in

Table II and Figure 5, there were significant differences in PAW of similar patches during the same season ($F=61.20; p \leq 0.0001; n=4$). In other words, patch and seasonal characteristics appear to explain the vast majority of the differences in PAW between the two sites ($F=17.56; p \leq 0.0001; n=69$), particularly during the summer. The tree and intercanopy patches in the natural site had at least two and as much as three times higher PAW values ($\text{NT}=71.7 \pm 9.7$ and $\text{NI}=61.8 \pm 19.1$ mm) than the tree and intercanopy patches in the savanna site ($\text{ST}=26.3 \pm 9.2$ and $\text{SI}=39.3 \pm 27.2$ mm; $p < 0.0007$). The highest PAW levels were found for the SB patches during the summer season (191.2 ± 40.6 mm; $p > 0.0001$).

During the summer period, PAW at shallow depths in the soil profile was lower for tree patches (NT and ST) than for intercanopy patches (NI and SI) and buffelgrass (SB) patches. The greatest differences were below the 40- to 80-cm depth interval, with lower PAW in patches of the savanna site than in corresponding patches of the natural vegetation site. Changes in accumulated water and PAW in the SB patches provide evidence that water can reach greater depths at the end of the summer rainy season (Figures 3 and 5).

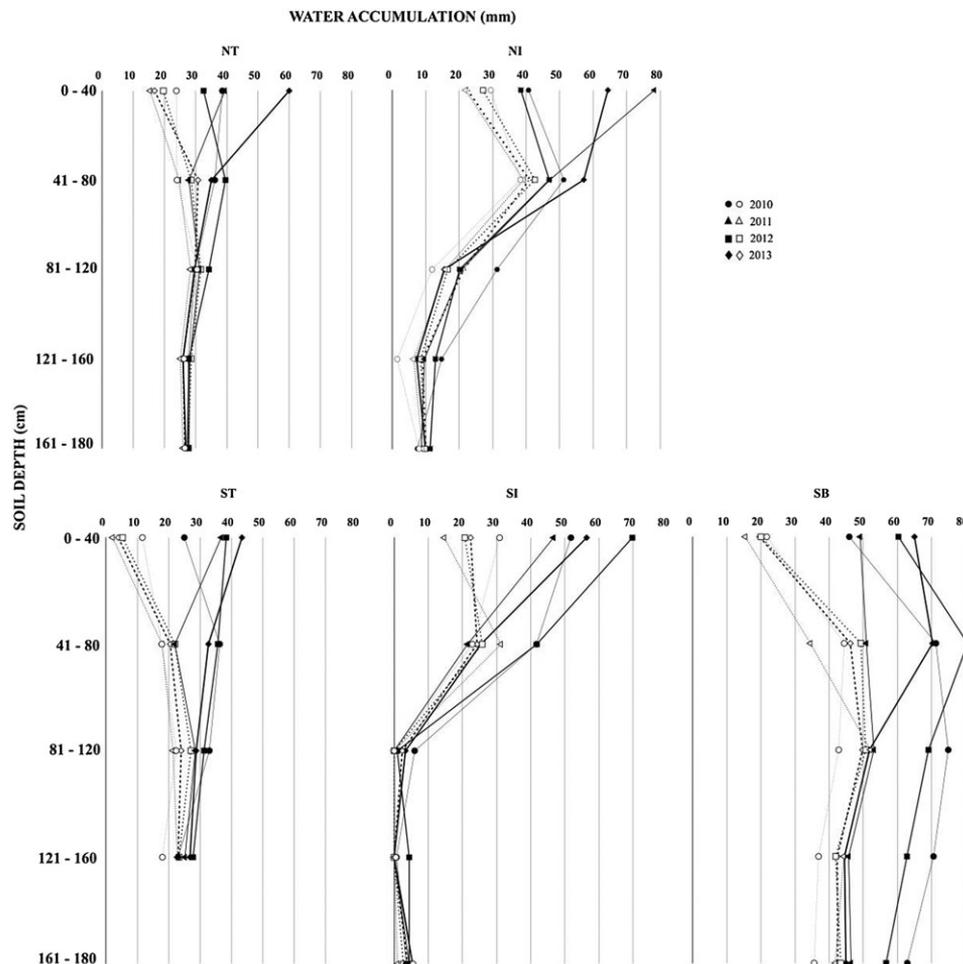


Figure 3. Water accumulation (mm) every 40 cm for each of the five patch types. Solid lines and symbols represent end of wet season, and dotted lines and open symbols represent end of dry season, 2010–2013.

Changes in rooting depth

We measured pre-dawn leaf water potentials during the summer for the dominant species (*O. tesota*) in both the natural and the savanna site. These measurements, which assumed the equilibrium of leaf and soil water potentials during the night, were compared with soil matric potentials previously calculated from VSM values (see Section on Methods). By matching pre-dawn leaf and soil water potentials, we were able to estimate the depth at which roots and leaves are in equilibrium. Our calculations provide evidence of overlapping rooting depths for buffelgrass (40–70 cm) and *O. tesota* trees (55–100 cm) in the savanna site. In contrast, at the natural site, the active rooting depth for *O. tesota* was much deeper: 145–180 cm (Table III).

DISCUSSION

Changes in climate and in land use are becoming important drivers for the increase and expansion of exotic grasses in arid (Wilcox, 2010; Wilcox and Thurow, 2006) and

semiarid lands. Buffelgrass is a notorious example, becoming widespread around the world and particularly in Australia and North America (Arriaga *et al.*, 2004; Marshall *et al.*, 2012; Miller *et al.*, 2010). Such drastic shifts in above-ground land use and plant cover would inevitably lead to a variety of ecohydrological changes. But most of our knowledge of these changes has thus far been obtained through modelling outcomes and indirect evidence (Turnbull *et al.*, 2012; Wilcox and Thurow, 2006; Wilcox *et al.*, 2012).

Our study is the first long-term, comparative monitoring effort to understand how the transformation of semiarid shrublands to buffelgrass savannas affects the amounts, patterns and availability of soil water. For almost 4 years, we compared below-ground seasonal soil moisture dynamics in tree and intercanopy patches of native semiarid shrublands with those in similar patches of a neighbouring site transformed to buffelgrass savanna. The savanna site, formerly a native semiarid shrubland, had been cleared about 35 years ago of most of its vegetation cover (except for dominant trees) and seeded with buffelgrass, which resulted in a structural and functional exotic buffelgrass savanna.

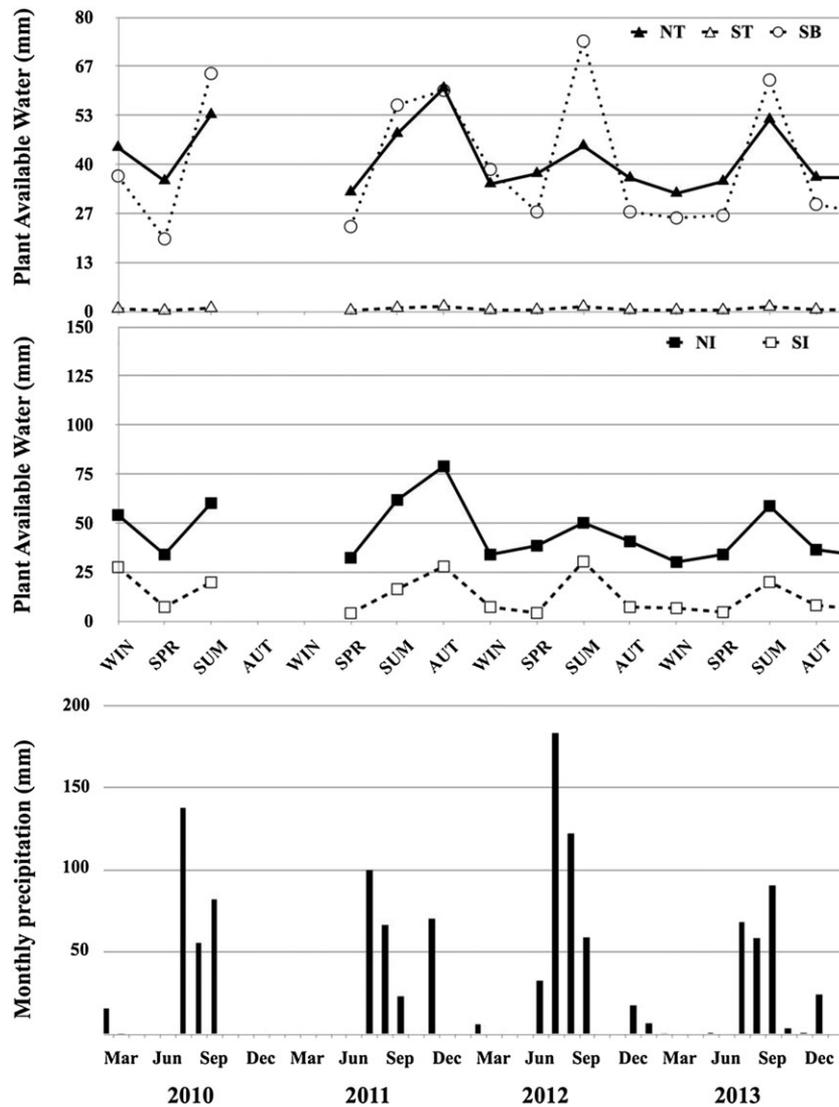


Figure 4. End-of-season plant-available water for the three canopy patch types (top graphic) and the two intercanopy patch types (middle graphic), compared with monthly rainfall data (bottom graphic). Gaps in data were due to an equipment malfunction in 2010.

Changes in soil water patterns after transformation

Transformation of the shrubland ecosystem to buffelgrass savanna decreased volumetric soil moisture, water accumulation and PAW in the soil profile of tree and intercanopy patches. The differences observed between the natural site and the savanna site – in VSM in the depth interval from

about 60–70 cm to 130 cm, in water accumulation, and in PAW patterns –under *O. tesota* trees indicate that water dynamics and availability to roots changed in those patches after land transformation (Figure 2). Assuming equilibrium between pre-dawn leaf and soil water potential measurements, shallower active rooting depths were found for *O.*

Table II. Seasonal variability in mean plant-water availability (mm) for the five patch types, 2010–2013.

	NT	NI	ST	SI	SB
Spring	44.56 ± 5.42a	20.60 ± 2.79b	3.60 ± 1.55c	11.11 ± 3.92c	93.34 ± 11.25a
Summer	71.74 ± 9.68b	61.79 ± 19.13b	26.32 ± 9.23c	39.30 ± 27.22c	191.18 ± 40.61a
Fall	67.14 ± 32.83a	45.26 ± 39.76a	18.09 ± 20.75a	28.42 ± 31.40a	127.31 ± 36.59a
Winter	42.44 ± 13.60a	14.69 ± 9.22ab	4.34 ± 0.83b	9.31 ± 4.68b	98.04 ± 21.47a

Lowercase letters indicate statistical differences ($p \leq 0.005$; Tukey–Kramer HSD test).

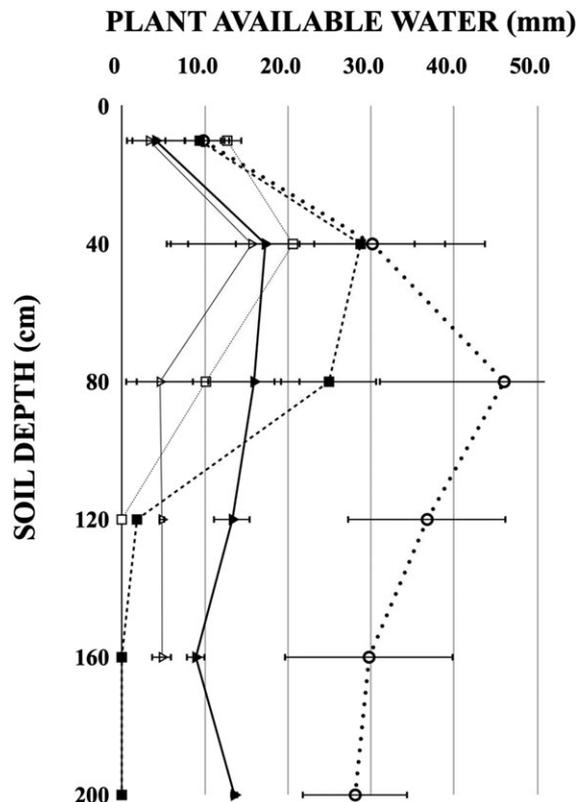


Figure 5. Summer mean plant-available water (mm) for the five patch types, 2010–2013.

tesota in the savanna than in the natural site (Table III). Stronger depletion at shallower depths in the soil profile may be indicative of higher plant use as well as evapotranspiration forcing at those depths.

Most land-transformation studies have made no assumptions about whether plant species change their rooting patterns, and this issue has not been explicitly addressed. Some studies have interpreted changes in the rooting profiles of desert plants as adaptations to outcompete neighbour species under conditions of limited water availability (Canadell *et al.*, 1996; Schenk and Jackson, 2002). Given that arid-land species allocate a substantial amount of their biomass to roots (Orians and Solbrig,

Table III. Estimated rooting depths for *Olneya tesota*, natural site versus savanna site; and for buffelgrass (*Cenchrus ciliaris*) at the savanna site.

	Growth form	Pre-dawn water potential (–MPa)	θh	Root depth (cm)
Natural				
<i>O. tesota</i>	Tree	3.85 ± 0.6	0.054	145–180
Savanna				
<i>O. tesota</i>	Tree	3.80 ± 0.1	0.055	55–100
<i>Cenchrus ciliaris</i>	Grass	5.00 ± 0.1	0.041	40–70

1977), the growth of new roots may either increase or decrease the species' success and survivorship when major ecohydrological shifts occur in the soil profile, such as those produced by changes in land use.

The lack of data on these issues highlights the need for more studies to ascertain (1) how a species is able to change its rooting patterns after land transformation; (2) what physiological and ecological cues prompt changes in root growth; and (3) whether there are any measurable effects on leaf or plant water status, above-ground growth and/or plant survivorship.

Deep water dynamics and plant neighbour interactions

Modelling studies of warm, arid shrublands transformed to grasslands have found higher soil water content deep in the soil profile and increased groundwater recharge over time (Wilcox *et al.*, 2012; Turnbull *et al.*, 2012). Most of those changes were assumed to result from lower runoff and increasing infiltration over time, combined with the negligible use of deep water by grasses. Our data showed that in the savanna site, water reached deep levels only in the buffelgrass patches – where increases in VSM deep in the soil profile resembled those found in the modelling studies. However, we observed that water infiltration changed more rapidly and reached greater depths than predicted by those studies. In some years with wetter summer seasons (such as 2012), we were able to record water pulses reaching depths of 120 cm or more, in contrast to the finding of many studies of soil moisture in arid and semiarid lands that rainfall moisture pulses do not reach depths below 100 cm (Canadell *et al.*, 1996). During such wet summer conditions, buffelgrass patches (SB) exhibited rapid infiltration, which led to water accumulation in the entire soil profile, down to 200 cm.

The causes of rapid deep water drainage could include low soil bulk density, root channelling, canopy interception and/or some other undetected biophysical mechanism present mainly in buffelgrass patches. In those patches, rapid infiltration resulted in deep storage of water only when summer rainfall was above average; and water was stored only for brief periods, not accumulated from year to year (probably because of being used by remaining active trees). Such rapid water channelling may at least partially explain why we found active roots of *O. tesota* trees at the same depths as buffelgrass roots, unlike other studies in arid lands that noted root differentiation in the soil profile (Canadell *et al.*, 1996; Schenk and Jackson, 2002). The tapping of deep stored water by remaining neighbour trees may have impeded water storage under buffelgrass, although some infiltration to deeper layers may also have occurred.

In modelling studies of grass-invaded arid ecosystems (Wilcox *et al.*, 2012), infiltration of water into deeper layers was greater in cool deserts and during the cooler months in warm deserts, when most species are inactive. In contrast,

our study showed greater accumulation of water in deep soil layers of SB patches after the summer rainy season, the most active season for plant growth, particularly in wet years (Figures 3 and 4). Some of that deep water may also be available to trees and shrubs in adjacent patches during the fall and winter seasons, limiting water storage and accumulation. How much water may have been lost to deeper layers in the soil remains unknown, but greater deep water content in the soil could be exploited by species with two-layer rooting systems remaining, leading to a stable savanna-type vegetation. Walter (1971) proposed a two-layer competitive-balance hypothesis to explain how species – particularly trees and grasses in savannas – partition soil water resources to enable coexistence in the same habitat. Working in Mediterranean-type ecosystems, Davis and Mooney (1986) found that shrub and herbaceous species coexist and avoid competition through soil moisture partitioning in the vertical profile, in accordance with the species' differing patterns of seasonal water use. Measured decreases in soil moisture in the profile may result from lack of water infiltration and/or from water use by plant species in the patch and/or other interacting species (via lateral rooting systems). Seasonal and yearly changes in VSM (below 80–100 cm) and accumulated water (80–120 cm) in patches with no deep-rooted individuals (NI, SI and SB patches) may be indicative of water use by trees and shrubs via lateral roots (Figures 2 and 3). Such water use by trees may also explain changes in deep water storage in buffelgrass patches. For example, the accumulation of water in the profile increased after the 2012 summer rainy season, but a greater depletion was noted for SB patches the next season, suggesting extensive water use by deep-rooting species.

Ecohydrological effects of transformation from shrubland to buffelgrass savanna

Our observations documented how tree species in the buffelgrass savanna were able to delay strong competitive root interactions by tapping water sources at different depths in the soil profile and beneath adjacent patches. Those strategies were a consequence of a series of physiological and structural adjustments that increased the trees' ability to use water in the vertical and horizontal soil profile – adjustments made for the new tree–grass relationships brought about by the transformation of the shrubland into a savanna-like vegetation cover. Tree–grass niche interactions in a savanna have been explained by a two-layer rooting mechanism and water use partitioning (Holdo, 2013; Ward *et al.*, 2013), although Ryel *et al.* (2010) suggest that none of the current hypotheses – niche partitioning via two-layer rooting (Walter, 1971), 'pulse-reserve' (Noy-Meir, 1973) or 'threshold-delay' (Ogle and Reynolds, 2004) – is sufficient to explain tree–grass interactions under conditions of limited water availability.

We found that of the five vegetation cover types, the buffelgrass-patch soil profiles showed the largest increases in the measured ecohydrological variables (VSM, soil water accumulation and PAW), particularly during the summer rainy season. Such increases may have come about because of changes in the above-ground and below-ground physical (textural, soil bulk density), biological/structural (canopy interception, root channelling) and physiological processes. For example, they may be related to the evidence that C₄ grasses, like buffelgrass, use water with greater efficiency than C₃ shrubs and trees (although such water economies do not always scale up to the stand level).

The tree patches in which we measured PAW in the savanna site had individuals that were already established when the site was cleared of other vegetation and seeded with buffelgrass 35–40 years ago, and there were no signs or evidence of increasing tree mortality. In the natural site, *O. tesota* acts as a nurse plant and supports a diversity of herbaceous and woody plant species, as has been documented elsewhere (Suzán *et al.*, 1996). But in the savanna, when buffelgrass establishes under *O. tesota* canopy, its shallow and high-density rooting system makes it a competitor for water at those depths (0–40 cm, Figure 2) – which explains the drier soils of the tree patches in the savanna (ST, Figure 3). Increased competition may lead to branch and tree mortality in the case of some species, e.g. *Cercidium microphyllum* and *P. velutina* (Eilts and Huxman, 2013, Castellanos, pers. obs.); however, that is less common in the case of *O. tesota*. While in some desert shrubland and savanna systems the coexistence of nurse trees and grasses has been linked to water redistribution (Hultine *et al.*, 2003; Yu and D'Odorico, 2015), we propose that changes in the active rooting patterns of *O. tesota* may also explain the increased competition for shallow water even though overall competition for scarce water in the soil profile decreases because its two-layer root system.

Concerns about the increasingly extensive distribution of exotic grasses globally led to the grass–fire hypothesis of D'Antonio and Vitousek (1992), which suggests that invasion by exotic grasses increases the risk of fire in many ecosystems, leading to dominance by fire-adapted grass species, the displacement of native species and loss of biodiversity (D'Antonio and Mack, 2001; D'Antonio and Vitousek, 1992). Although fire represents a risk and a threat to ecosystem processes, the grass–fire cycle was suggested as a primary cause that in turn led to many other biogeochemical and ecohydrological changes (D'Antonio and Mack, 2001; Levine and D'Antonio, 1999; Mack and D'Antonio, 2003; Richardson *et al.*, 2000).

We propose that after land transformation, changes in a number of biological and biophysical processes lead to ecohydrological changes at scales from patch to ecosystem, and that this process promotes the spread and dominance of

buffelgrass in arid lands. Exotic grasses continue to spread and/or increase their dominance in arid and semiarid ecosystems, but it appears that fire is not the only factor: the ability of these grasses to use limiting resources, such as water, has been a major determinant of such widespread landscape transformation (Olsson *et al.*, 2012; this study). In other words, ecohydrological changes caused by buffelgrass may be a major and relevant explanation for this exotic species' sustained spread and displacement of native species in arid and semiarid ecosystems.

The transformation of arid and semiarid shrublands to buffelgrass savannas in the Sonoran Desert and elsewhere is considered a threat because of the invasiveness potential of this exotic grass. The long-term successional trajectories and function of these transformed ecosystems are still largely unknown and are particularly difficult to study when they are determined by ecohydrological processes, rather than drastic processes such as fire. While successful grass–tree interactions are expected under conditions of ample availability of nutrients and water (Belsky, 1990; Bond, 2008), in arid and semiarid lands such as our site, the low amounts and the variability of rainfall may allow only sparse grass cover while trees and shrubs remain dominant. At some sites in the region that have undergone transformation, we have found increasing tree re-establishment and receding grass cover, with grasses mostly restricted to zones under tree canopies or to microsites with higher water availability (Castellanos *et al.*, 2010). Changes in soil water dynamics in the profile after ecosystem transformation may influence other ecohydrological and biogeochemical controls involved in the long-term successional outcome, such as those related to the species' physiological characteristics (Castellanos *et al.*, 2010), soil nutrient availability (Castellanos *et al.*, 2002; Celaya-Michel and Castellanos-Villegas, 2011; Celaya-Michel *et al.*, 2015), site functional diversity, grazing intensity and/or management strategy (Castellanos *et al.*, 2010).

Our study made use of long-term integrated monitoring schemes to gain insights into how major ecohydrological processes are affected by changes in limiting resources, such as water availability and use. Our monitoring was done at multiple scales of both time (monthly, seasonally and yearly) and space (site, patch and soil profile), comparing a semiarid ecosystem having native vegetation cover with one that had undergone transformation. Work based on this approach is currently ongoing at the sites, but more investigations must be undertaken elsewhere – comparing simplified-transformed shrublands in which management strategies have reduced structural and functional complexity with ecosystems that have remained natural (Díaz *et al.*, 2003) – as a means of better understanding the functioning of arid and semiarid ecosystems undergoing biodiversity transformation.

CONCLUSIONS

We have documented how the transformation of semiarid shrublands to buffelgrass savanna has important effects on the ecohydrological dynamics of different patch types, as well as in the soil profile. Extensive transformations of this kind are currently under way in arid and semiarid ecosystems in North America and worldwide, as a consequence of range management practices using buffelgrass, which has the potential to spread widely and invade. We provide some evidence of how different plant species, patches, vegetation cover types, soil profile and seasonal water dynamics feed back to determine the many ecohydrological changes after land transformation. Additional studies of changes in the rooting habits and water use in the soil profile of dominant species and patches should be a major scientific focus, to advance our ability to understand ecohydrological changes in arid and semiarid ecosystems.

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REFERENCES

- Aguiar MR, Sala OE. 1999. Patch structure, dynamics and implications for the functioning of arid ecosystems. *Trends in Ecology & Evolution* **14**: 273–277.
- Archer S, Boutton TW, Hibbard KA (Eds). 2000. *Trees in Grasslands: Biogeochemical Consequences of Woody Plant Expansion*. Academic Press: San Diego.
- Archer S, Scifres C, Bassham CR, Maggio R. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecological Monographs* **58**: 111–127.
- Archer S, Schimel DS, Holland EA. 1995. Mechanisms of shrubland expansion: land use, climate or CO₂? *Climatic Change* **29**: 91–99.
- Archer SR. 1995. Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: reconstructing the past and predicting the future. *Ecoscience* **2**: 83–99.
- Ariaga L, Castellanos AE, Moreno E, Alarcón J. 2004. Potential ecological distribution of alien invasive species and risk assessment: a case study for buffel grass in arid regions of Mexico. *Conservation Biology* **18**: 1504–1514.
- Barnes PW, Archer S. 1999. Tree-shrub interactions in a subtropical savanna parkland: competition or facilitation? *Journal of Vegetation Science* **10**: 525–536.
- Belsky AJ. 1990. Tree/grass ratios in East African savannas: a comparison of existing models. *Journal of Biogeography* **17**: 483–489.

- Bond WJ. 2008. What limits trees in C4 grasslands and savannas? *Annual Review of Ecology, Evolution, and Systematics* **39**: 641–659.
- Breshears DD. 2006. The grassland-forest continuum: trends in ecosystem properties for woody plant mosaics? *Frontiers in Ecology and the Environment* **4**: 96–104.
- Breshears DD, Myers OB, Barnes FJ. 2009. Horizontal heterogeneity in the frequency of plant-available water with woodland intercanopy–canopy vegetation patch type rivals that occurring vertically by soil depth. *Ecohydrology* **2**: 503–519.
- Callaway RM. 1995. Positive interactions among plants. *Botanical Review* **61**: 306–349.
- Canadell J, Jackson RB, Ehleringer JR, Mooney HA, Sala OE, Schulze E-D. 1996. Maximum rooting depth of vegetation types at the global scale. *Oecologia* **108**: 583–595.
- Castellanos AE, Bravo LC, Koch GW, Llano JM, Lopez D, Mendez R, Rodriguez JC, Romo JR, Sisk T, Yanes G. 2010. Impactos Ecológicos por el Uso del Terreno en el Funcionamiento de Ecosistemas Áridos Semi-Áridos de Sonora. In *Diversidad Biológica del Estado de Sonora*, Molina-Freaner F, Van Devender TR (eds). CONABIO-UNAM: Mexico, D. F.; 157–186.
- Castellanos AE, Yanes G, Valdéz-Zamudio D. 2002. Drought-tolerant exotic buffel-grass and desertification. In *Weeds Across Borders*, Tellman B (ed). Arizona-Sonora Desert Museum: Tucson, AZ.
- Celaya-Michel H, Castellanos-Villegas AE. 2011. Mineralización de nitrógeno en el suelo de zonas áridas y semiáridas. *Terra Latinoamericana* **29**: 343–356.
- Celaya-Michel H, García-Oliva F, Rodríguez JC, Castellanos-Villegas AE. 2015. Cambios en el almacenamiento de nitrógeno y agua en el suelo de un matorral desértico transformado a sabana de buffel (*Pennisetum ciliare* (L.) Link). *Terra Latinoamericana* **33**: 79–93.
- Cochrane MA, Alencar A, Schulze MD, Souza CM, Nepstad DC, Lefebvre P, Davidson EA. 1999. Positive feedbacks in the fire dynamic of closed canopy tropical forests. *Science* **284**: 1832–1835.
- D'Antonio CM, Mack M. 2001. Exotic grasses potentially slow invasion of an N-fixing tree into a Hawaiian woodland. *Biological Invasions* **3**: 69–73.
- D'Antonio CM, Vitousek PM. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* **23**: 63–87.
- Dardanelli JL, Ritchie JT, Calmon M, Andriani JM, Collino DJ. 2004. An empirical model for root water uptake. *Field Crops Research* **87**: 59–71.
- Davis SD, Mooney HA. 1986. Water use patterns of four co-occurring chaparral shrubs. *Oecologia* **70**: 172–177.
- Díaz S, Symstad AJ, Chapin FS, Wardle DA, Huenneke LF. 2003. Functional diversity revealed by removal experiments. *Trends in Ecology and Evolution* **18**: 140–146.
- Donovan LA, Richards JH, Linton MJ. 2003. Magnitude and mechanisms of disequilibrium between predawn plant and soil water potentials. *Ecology* **84**: 463–470.
- Duniway MC, Snyder KA, Herrick JE. 2010. Spatial and temporal patterns of water availability in a grass-shrub ecotone and implications for grassland recovery in arid environments. *Ecohydrology* **3**: 55–67.
- Ehleringer JR, Mooney HA. 1983. Productivity of desert and Mediterranean-climate plants. In *Physiological Plant Ecology IV*, Lange OL, Nobel PS, Osmond CB, Ziegler H (eds), Encyclopedia of Plant Physiology New Series **12-D**. Springer-Verlag: Berlin; 205–231.
- Eilts JA, Huxman TE. 2013. Invasion by an exotic, perennial grass alters responses of a native woody species in an arid system. *Journal of Arid Environments* **88**: 206–212.
- Ferrante D, Oliva GE, Fernández RJ. 2014. Soil water dynamics, root systems, and plant responses in a semiarid grassland of Southern Patagonia. *Journal of Arid Environments* **104**: 52–58.
- Holdo RM. 2013. Revisiting the two-layer hypothesis: coexistence of alternative functional rooting strategies in savannas. *PLoS ONE* **8** (e69625): 69621–69612.
- Hultine KR, Cable WL, Burgess SSO, Williams DG. 2003. Hydraulic redistribution by deep roots of a Chihuahuan Desert phreatophyte. *Tree Physiology* **23**: 353–360.
- Laurent J-P, Ruelle P, Delage L, Zaïri A, Nouna BB, Adjmi T. 2005. Monitoring soil water content profiles with a commercial TDR system: comparative field tests and laboratory calibration. *Vadose Zone Journal* **4**: 1030–1036.
- Laurent JP, Ruelle P, Delage L, Béda N, Chanzy A, Chevallier C. 2001. On the use of the TDR TRIME-tube system for profiling water content in soils. *Proceedings TDR* **1**: 1–10.
- Le Houérou HN, Bingham RL, Skerbek W. 1988. Relationship between the variability of primary production and the variability of annual precipitation in world arid lands. *Journal of Arid Environments* **15**: 1–18.
- Levine JM, D'Antonio CM. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* **87**: 15–26.
- Mack MC, D'Antonio CM. 2003. Exotic grasses alter controls over soil nitrogen dynamics in a Hawaiian woodland. *Ecological Applications* **13**: 154–166.
- Marshall VM, Lewis MM, Ostendorf B. 2012. Buffel grass (*Cenchrus ciliaris*) as an invader and threat to biodiversity in arid environments: a review. *Journal of Arid Environments* **78**: 1–12.
- Miller G, Friedel M, Adam P, Chewings V. 2010. Ecological impacts of buffel grass (*Cenchrus ciliaris* L.) invasion in central Australia – does field evidence support a fire-invasion feedback? *The Rangeland Journal* **32**: 353–365.
- Newman BD, Breshears DD, Gard MO. 2010. Evapotranspiration partitioning in a semiarid woodland: ecohydrologic heterogeneity and connectivity of vegetated patches. *Vadose Zone Journal* **9**: 561–572.
- Noy-Meir I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* **4**: 25–51.
- Ogle K, Reynolds JF. 2004. Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds, and delays. *Oecologia* **141**: 282–294.
- Olsson AD, Betancourt MP, McClaran MP, Marsh SE. 2012. Sonoran desert ecosystem transformation by a C₄ grass without the grass/fire cycle. *Diversity and Distributions* **18**: 10–21.
- Orians GH, Solbrig OT. 1977. A cost-income model of leaves and roots with special reference to arid and semiarid areas. *American Naturalist* **111**: 677–690.
- Peters DPC, Havstad KM. 2006. Nonlinear dynamics in arid and semi-arid systems: interactions among drivers and processes across scales. *Journal of Arid Environments* **65**: 196–206.
- Potts DL, Scott RL, Bayram S, Carbonara J. 2010. Woody plants modulate the temporal dynamics of soil moisture in a semi-arid mesquite savanna. *Ecohydrology* **3**: 20–27.
- Reynolds JF, Kemp PR, Ogle K, Fernandez RJ. 2004. Modifying the 'pulse-reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia* **141**: 194–210.
- Richardson DM, Allsopp N, D'Antonio CM, Milton SJ, Rejmánek M. 2000. Plant invasions – the role of mutualisms. *Biological Reviews* **75**: 65–93.
- Ryel RJ, Leffler AJ, Ivans C, Peek MS, Caldwell MM. 2010. Functional differences in water-use patterns of contrasting life forms in Great Basin steppelands. *Vadose Zone Journal* **9**: 548–560.
- Schenk HJ, Jackson RB. 2002. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology* **90**: 480–494.
- Schulze E-D, Beck E, Müller-Hohenstein K. 2005. *Plant Ecology*. Springer-Verlag: Berlin.
- Scott RL, Cable WL, Huxman TE, Nagler PL, Hernandez M, Goodrich DC. 2008. Multiyear riparian evapotranspiration and groundwater use for a semiarid watershed. *Journal of Arid Environments* **72**: 1232–1246.
- Scott R. L., Huxman T. E. 2005 Comparing ecosystem water and carbon exchange across a riparian Mesquite invasion gradient. In: USDA, pp 320–323.
- Scott RL, Huxman TE, Barron-Gafford GA, Jenerette GD, Young JM, Hamerlynck EP. 2014. When vegetation change alters ecosystem water availability. *Global Change Biology* **20**: 2198–2210.
- Scott RL, Jenerette GD, Potts DL, Huxman TE. 2009. Effects of seasonal drought on net carbon dioxide exchange from a woody-plant-encroached semiarid grassland. *Journal of Geophysical Research* **114**: G04004.
- Segoli M, Ungar ED, Giladi I, Arnon A, Shachak M. 2012. Untangling the positive and negative effects of shrubs on herbaceous vegetation in drylands. *Landscape Ecology* **27**: 899–910.
- Seyfried MS, Wilcox BP. 2006. Soil water storage and rooting depth: key factors controlling recharge on rangelands. *Hydrological Processes* **20**: 3261–3275.

- Stacheder M, Fundinger R, Koehler K. 1997. On-site measurement of soil water content by a new time domain reflectometry (TDR) technique. In *Field Screening Europe*, Gottlieb J, Hötzl H, Huck K, Niessner R (eds), Proceedings of the First International Conference on Strategies and Techniques for the Investigation and Monitoring of Contaminated Sites. Kluwer Academic Publishers: Netherlands; 425.
- Suzán H, Nabhan GP, Patten DT. 1996. The importance of *Olneya tesota* as a nurse plant in the Sonoran Desert. *Journal of Vegetation Science* **7**: 635–644.
- Turnbull L, Wilcox BP, Belnap J, Ravi S, D'Odorico P, Childers D, Gwenzi W, Okin G, Wainwright J, Caylor KK, Sankey T. 2012. Understanding the role of ecohydrological feedbacks in ecosystem state change in drylands. *Ecohydrology* **5**: 174–183.
- Walter H. 1971. Natural savannahs as transition to the arid zone. In *Ecology of Tropical and Subtropical Vegetation*, Burnett JH (ed). Oliver & Boyd: Edinburgh; 238–265.
- Ward D, Wiegand K, Getzin S. 2013. Walter's two-layer hypothesis revisited; back to the roots!. *Oecologia* **172**: 617–630.
- Wilcox BP. 2010. Transformative ecosystem change and ecohydrology: ushering in a new era for watershed management. *Ecohydrology* **3**: 126–130.
- Wilcox BP, Thurow TL. 2006. Emerging issues in rangeland ecohydrology: vegetation change and the water cycle. *Rangeland Ecological Management* **59**: 220–224.
- Wilcox BP, Turnbull L, Young MH, Williams CJ, Ravi S, Seyfried MS, Bowling DR, Scott RL, Germino MJ, Caldwell TG, Wainwright J. 2012. Invasion of shrublands by exotic grasses: ecohydrological consequences in cold versus warm deserts. *Ecohydrology* **5**: 160–173.
- Yu K, D'Odorico P. 2015. Hydraulic lift as a determinant of tree-grass coexistence of savannas. *New Phytologist* **207**: 1038–1051.
- Zaccharias S, Wessolek G. 2007. Excluding organic matter content from pedotransfer predictors of soil water retention. *Soil Science Society of America Journal* **71**: 43–50.