Woodo plant encroachment enhances soil infiltrability of a semiarid karst savanna

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Keywords: ecohydrology, rangelands, runoff, Juniperus pinchotii, Beerkan, macropore flow, saturated hydraulic conductivity

Abstract

Semiarid karst landscapes are often the source areas for regionally important groundwater supplies. Like savannas across the globe, these landscapes are experiencing an increase in woody plant cover—often referred to as woody plant encroachment. Although this phenomenon is commonly viewed as leading to increased transpiration and reduced groundwater recharge, this may not be true of all ecosystems. For example, in the Edwards Plateau region of central Texas—where the underlying geology is karst—dramatic increases in baseflows have occurred concurrently with the expansion of woody plants. It has been suggested that in this context woody plants, especially juniper (Juniperus spp.), are partially responsible for boosting recharge by improving soil infiltrability, but this hypothesis has not been systematically evaluated. Our study examined the effects of an important encroaching shrub (Redberry juniper) on soil infiltrability in the Edwards Plateau. We carried out a large number of infiltration tests to determine soil infiltrability and used a dye tracer followed by soil profile excavation to estimate the potential for deep percolation. Tests were performed at increasing distances under juniper shrubs of five size classes, ranging from young seedlings to mature shrubs. We found that in soils underlying shrubs, infiltrability was quintupled and percolation depth almost tripled compared with soils in intercanopy zones. Surprisingly, shrub size was not a significant factor. Even the soils beneath the smallest shrubs had much higher infiltrability than intercanopy soils, showing that these woody plants modify soil properties at very early stages. We also found that both infiltrability and percolation depth gradually increased with proximity to the trunk and showed a strong correlation with litter thickness. Our results provide support for the hypothesis that in semiarid karst landscapes, woody plant encroachment—especially the invasion of juniper—can play an important role in enhancing groundwater recharge by improving the soil infiltrability.

Introduction

Trees and shrubs are the quintessential ecohydrological machines. They have the potential to profoundly alter water, energy, and biogeochemical cycles, and these changes are manifested from local to regional and even global scales (Brantley et al 2017). Woody plants have the potential to directly alter water fluxes through the processes of interception and transpiration (National Academy of Sciences 2008) as well as to influence the energy budget by modifying latent energy, shading, and albedo (Bonan 2008). An indirect—and less appreciated—influence of woody plants is the alteration of soil infiltrability via the input of organic material and root action (Tobella et al 2014).

The question of how and to what extent trees and shrubs influence water, energy, and biogeochemical cycling is especially germane for the world’s grasslands and savannas, which have been and continue to be radically transformed by woody plant encroachment (WPE) (Barger et al 2011, Eldridge and Soliveres 2014).
Historically, grasslands and open savannas had been maintained largely by fire and, to some extent, herbivory (Bond and Parr 2010); but under European colonization during the mid to late 1800s, the fire regimes in many grassy biomes in the Americas, Africa, and Australia were dramatically altered by overgrazing and active fire suppression (Walker and Janssen 2002), setting the stage for WPE in many rangelands across the globe.

The Southern Great Plains region of the United States has been profoundly affected by WPE (Barger et al 2011), but the timing and particulars of the grassland-to-woodland conversion differ across the region (Wilcox et al 2018). In Texas, the conversion began in the early 20th century, when the area was being settled and livestock grazing was unregulated (Box 1967). In Oklahoma and Kansas, WPE is more recent—probably because much of that area was cultivated following settlement, then eventually returned to grassland when cultivation proved unsustainable. In the past few decades, WPE has been advancing at an accelerated rate and currently represents a serious threat to the remaining tall- and mixed-grass prairies, including the plants and animals endemic to them (Briggs et al 2005, Wang et al 2018).

The invasive woody plants in the Southern Great Plains are typically native but are expanding in their range and abundance. Of particular importance are woody plants in the *Juniperus* genus. Eastern red cedar (*Juniperus virginiana*) has expanded steadily northward from Texas into Oklahoma, Kansas, and Nebraska (Engle et al 2008, Twidwell et al 2016). To the south, in the Edwards Plateau and Rolling Plains areas of Texas, both Ashe juniper (*Juniperus ashei*) and Redberry juniper (*Juniperus pinchotii*) have become pervasive (Ansley and Ueckert 1995). Detailed analyses of long-term streamflow records (1915–2010) for rivers in these two areas show dramatic changes in streamflow (Wilcox et al 2008a, Wilcox and Huang 2010): floods have declined in magnitude and baseflows have increased. In the Edwards Plateau, an enormous karstic formation in Central Texas, baseflow from four perennial rivers is now twice as high as it was between 1915 and 1965. Wilcox and coauthors argue that this change is the result of increased soil infiltrability—both because stocking rates are much lower now than in the past (Wilcox et al 2012), resulting in less bare ground and more herbaceous vegetation, and because of the increase in woody plants (particularly juniper species). Although there is some evidence that infiltration rates are higher under juniper canopies than in the intercanopy in the Edwards Plateau (Wilcox et al 2008b), this hypothesis has not been systematically evaluated.

The objective of this study was to compare and contrast the soil infiltrability of Redberry juniper (*Juniperus pinchotii*) canopy zones with that of intercanopy zones and to evaluate how infiltrability is affected by shrub size, distance from shrub trunks, soil cover, and depth of litter.

**Study site**

Field data for this study were collected between January and April of 2018 at the Texas A&M Research Station near Sonora, Texas, on the southwestern border of the Edwards Plateau ecological region. This region is characterized by karst geology and rolling, stony topography with shallow and rocky soils. Woody vegetation cover is around 40% (Twidwell et al 2014). Annual precipitation is highly variable, ranging between 156 and 1054 mm (median of 557 mm) and occurring mostly between May and October. Short-duration and high-intensity convective storms are common; 15 min intensities of 90 mm h⁻¹ and 120 mm h⁻¹ are estimated to have return periods of 2 and 5 years, respectively (Cleveland et al 2015), and will likely become more frequent because of climate change (Dominguez et al 2012).

For our study, we selected an area of approximately 2.5 ha with gentle slopes (1%–2%). This area was selected because of its abundance of shrubs of multiple sizes and its sparse rock cover facilitating the insertion of ring infiltrometers. The soils are shallow and classified as Typic Calciustolls. A characteristic pedon will have a clay-textured A horizon from 0 to 12 cm in-depth, and 5% fragments or large slabs of limestone rock; a Bw horizon from 12 to 33 cm, with dark brown clay (10YR 3/3) and 5% fragments or large slabs of limestone rock; a Bk horizon from 33 to 56 cm, with a yellowish-brown (10YR 5/4) extremely gravelly clay, 90% of which consists of limestone slabs; and an R horizon consisting of indurated, fractured limestone bedrock (USDA–Natural Resource Conservation Service 2016).

The vegetation of this area is savanna/parkland with Ashe juniper (*Juniperus ashei*), Redberry juniper (*Juniperus pinchotii*), and live oak (*Quercus virginiana*) the dominant shrubs. Most of the Ashe juniper are large individuals (>3 m tall) growing near rock outcrops along with mottes of live oaks. The Redberry juniper shrubs are of various sizes and far more abundant, occurring throughout the area. Individuals or clusters of woody species are interspersed within a matrix of bare soil and grasses that includes Curly mesquite (*Hilaria spp.*), Sideoats gramma (*Bouteloua curtipendula*), Threawns (*Aristida spp.*), and Texas wintergrass (*Nassella leucotricha*).

Grazing pressure on the site is very light and has been for several decades. The area has been lightly browsed by a small herd of goats during a few months of the year and year-round by deer. Prescribed fires were commonly used as a management tool to control WPE, but at the time of the study the area had not been burned for approximately 10 years.
**Methods**

**Measuring soil infiltrability**

We used field saturated hydraulic conductivity (Kfs), as estimated by the Beerkan procedure (Lassabatere et al 2006), as a proxy for soil infiltrability. Saturated hydraulic conductivity is a key soil hydraulic property, and is ideal for comparisons between soils with different vegetation covers or land uses (Zimmermann et al 2006, Niemeyer et al 2014, Basant et al 2020).

The Beerkan procedure has been extensively tested and evaluated with good results (Aiello et al 2014, Di Prima et al 2018). It consists of inserting small-diameter (10 cm) rings to a shallow depth (1 cm) and carefully pouring small volumes of water (75 ml) into each ring. When the first 75 ml has nearly infiltrated, a new volume is poured, and the procedure is repeated until the time intervals between infiltrations are similar—indicating that a near steady-state has been reached. For each test we poured a minimum of 8 and a maximum of 20 volumes (Lassabatere et al 2006). Some of our Beerkan infiltration experiments carried out next to juniper shrubs showed inverted (convex) infiltration curves, with infiltration rates gradually increasing throughout the experiment until reaching a stable state. This was attributed to hydrophobicity—a transient phenomenon that mainly affects initial infiltration rates (Di Prima et al 2016, Alagna et al 2019). With that in mind, we chose to estimate Kfs following the SSBI method, a simplified version of the Beerkan procedure proposed by Bagarello et al (2017). This method uses only the final points of the infiltration curve when a near-steady-state infiltration rate has been achieved and is the least sensitive to hydrophobicity (Bagarello et al 2017, Di Prima et al 2019). We adopted the value of 0.12 cm $^{-1}$ for the alpha parameter, as recommended by the authors for structured clayey soils.

Beerkan tests are practical, fast, and replicable, allowing for large sample sizes and making them ideal for contrasting differences in infiltrability between different sites and land covers. However, like other infiltrometer methods, Beerkan tests often overestimate infiltrability because they do not replicate raindrop impact and its effect on soil compaction and mechanical aggregate breakdown (Di Prima et al 2017). Thus, one must be careful when incorporating such Kfs results into models or using them to estimate runoff potential. Besides, Kfs does not represent infiltration under unsaturated conditions, which are often present in semiarid regions. Aware of these limitations, we still opted to use Kfs as our metric because, being unaffected by initial water content, it is more suitable for contrasting differences between shrub and non-shrub soils under various moisture conditions.

Our experimental layout for the Kfs tests was as follows: To evaluate the effect of shrub size on infiltrability, we randomly picked 17 Redberry juniper shrubs within five size classes ranging from small seedlings to shrubs greater than 3 m tall. The size classes, based on shrub height, were (1) 20–30 cm; (2) 50–80 cm; (3) 120–150 cm; (4) 210–250 cm; and (5) 330–380 cm (figure 1). The age ranges for these classes, estimated employing an allometric equation for the species (McPherson 1987), were (1) 2–3 years; (2) 7–10 years; (3) 17–23 years; (4) 35–42 years; and (5) more than 75 years. To avoid possible confounding influences of other shrubs, we selected only isolated plants (whose canopy edge was at least 6 m distant from that of other shrubs).

To avoid directional bias, infiltration tests were carried out along two transects with randomly determined orientations (north–south, west–east, southwest–northeast, or southeast–northwest) and each originating at a shrub trunk. Before each test, lateral branches were removed and grasses were carefully clipped. Beginning at 10 cm from the shrub trunk (40 cm for size class 5 shrubs), the infiltration test points were located every 30 cm along the transect to just past the canopy drip line (the points falling immediately before and after the drip line serving to define the canopy edge). If a center point measurement fell where there was an obstacle, such as a rock or a large bunch of tall grass, a test point adjacent to it was selected (at the same distance from the shrub trunk).

**Figure 1.** Pictures of Redberry juniper shrubs of the five size classes selected for this study. The reference PVC pipe is 3 m tall with markings at 0.5 m intervals.

| Size class 1 | Size class 2 | Size class 3 | Size class 4 | Size class 5 |
|--------------|--------------|--------------|--------------|--------------|
| Height: 0.2–0.3 m | Height: 0.5–0.8 m | Height: 1.2–1.5 m | Height: 2.1–2.5 m | Height: 3.3–3.8 m |
| Age: 2–3 years | Age: 7–10 years | Age: 17–23 years | Age: 35–42 years | Age: 75+ years |
For each shrub we also performed infiltration tests in the intercanopy zone, at three 30 cm intervals 300 cm away from the drip line and at least 300 cm away from any other shrub. Before clipping grasses or removing leaf litter, we visually determined the dominant surface cover at each test point and classified it as either litter, grass, or bare soil.

Dye tracing
For half of the tests done in under-canopy and canopy-edge locations for size classes 1 to 3, and for tests done in six intercanopy locations, we added 20 g of Brilliant Blue dye per liter of water and used a consistent application of 10 volumes. One hour after the water had infiltrated, a pit was excavated parallel to the transect to the depth of the Bk horizon; the maximum penetration depth (MPD) of the dye tracer was then measured on two parallel vertical soil sections 5 cm apart—one at the edge of the ring and the other at the center—and the two results were averaged. Dye tracing was not performed for shrub classes 4 and 5 because manually excavating through the thick roots of those shrubs was not practical.

Unlike infiltration from natural precipitation, infiltration from Beerkan tests is strongly influenced by lateral capillary forces. For this reason, our MDP data is not intended to mirror percolation depth during rainfall but is simply a quantitative metric suitable for contrasting the potential for deeper percolation of different soil covers (Devitt and Smith 2002, Bachmair et al 2009, Zwartendijk et al 2017).

Additional soil data
Also, we collected accessory soil data that could shed light on variations in Kfs. Litter depth was averaged from measurements made with a ruler at three random points around each infiltration test point. Bulk density (g/cm$^3$) and volumetric soil moisture (cm$^3$/cm$^3$) were estimated from cores obtained from the surface (0–7.5 cm) soils adjacent to each infiltration test point and oven-dried for 24 h at 105°C.

Statistical analysis
Using the Shapiro-Wilk test and Levene’s test, we determined that our Kfs data distribution was non-Gaussian and variances were heterogeneous. To ensure conformance with parametric assumptions, the data was log-transformed. We used one-way ANOVA followed by Tukey’s HSD to test for significant differences. Additionally, we tested for correlations between response variables (Kfs and MPD) and explanatory variables (distance from the trunk, litter depth, antecedent soil moisture, and bulk density) using simple linear regressions. For Kfs, the regressions were performed separately for each shrub class—with two exceptions in the case of shrub class 1: distance from trunk (because infiltration tests were performed at only two distances from the trunk, one under-canopy and one canopy-edge) and litter thickness (because there was no litter accumulation). Since we had fewer data points for MPD, the size classes were analyzed together (except size class 1 was excluded from correlation analyses for distance from trunk and litter depth, as explained above).

Results
Mean Kfs under shrub canopies was 493 mm h$^{-1}$—approximately 3.5 times higher than at canopy edges (138 mm h$^{-1}$; p < 0.0001) and 5 times higher than in intercanopy zones (98.3 mm h$^{-1}$; p < 0.0001). There was also a significant difference between the latter two locations (p = 0.009) (table S1 is available online at stacks.iop.org/ERC/2/115005/mmedia).

Surprisingly, Kfs in under-canopy locations was not significantly different among the size classes. Only canopy-edge locations showed a difference, with size class 1 shrubs having a lower Kfs than size class 5 shrubs (p = 0.039) (figure 2).

The number of infiltration points that landed on litter, grass, and bare soil patches were 46, 96, and 21, respectively. There were significant differences (p < 0.0001) in mean Kfs among these three types of soil cover, with litter showing 528 mm h$^{-1}$, grass 179 mm h$^{-1}$, and bare soil 72.4 mm h$^{-1}$ (figure 3).

Average MPD at the under-canopy, canopy-edge, and intercanopy locations exhibited significant differences (p < 0.0002) at 29 cm, 19.6 cm, and 12.8 cm, respectively (figure 4).

The Kfs values were best explained by two variables: distance from the trunk (a negative correlation) and litter depth (a positive correlation) (table 1). The two variables were highly correlated with each other. A negative correlation was found between Kfs and antecedent soil moisture for classes 3, 4, and 5. The MPD values had strong positive correlations with Kfs ($R^2 = 0.7; p < 0.0001$) as well as with the explanatory variables distance from trunk ($R^2 = 0.66, p < 0.0001$) and litter depth ($R^2 = 0.57, p = 0.002$), and a weak negative correlation with antecedent soil moisture. Neither Kfs nor MPD was correlated with bulk density.
Our results clearly show that encroaching Redberry juniper shrubs dramatically increase soil infiltrability in the Edwards Plateau. The most surprising and important result of this study is that significant changes to soil infiltrability occur within a few years of shrub germination. We had expected to see only small differences in infiltrability between soils underlying seedlings and those in intercanopy areas. Instead, we found almost a fivefold difference. Further, infiltrability did not appreciably increase with increasing shrub size. While studies comparing infiltration rates of soils underlying shrubs of multiple size classes are rare, a close parallel would be studies comparing secondary forests of different successional stages. Those studies have consistently shown that infiltrability gradually increases with forest age (Zimmermann et al 2006, Hassler et al 2011, Archer et al 2016, Leite et al 2018). For this reason, it was contrary to our initial expectations to find that $K_f$s under juniper shrubs is not significantly influenced by shrub size. Since a key objective of this study was to determine at which stages of development shrubs start to influence infiltrability, we focused on isolated shrubs to avoid confounding influences of multiple shrubs. While relatively isolated shrubs were the most common at our site, in other areas...
of the Edwards Plateau (and of other woody-plant-encroached regions) shrubs are commonly found in clusters containing multiple individuals of different sizes, ages, and species (mainly *J. ashei* and *Q. virginiana* at our site). Because infiltration did not differ significantly by shrub size, it would be reasonable to assume that infiltration under clusters is also on the order of 5 times higher than that of intercanopy soils. Future studies could test this assumption and also evaluate the spatial variability of infiltration inside shrub clusters.

Another key point is that we were able to document a clear spatial pattern of infiltration, with *Kfs* values gradually decreasing as distances from trunks increased. The highest *Kfs* values were mostly restricted to the under-canopy zone, whereas the canopy-edge zone showed only modestly higher *Kfs* than intercanopy soils (and mainly for larger shrubs). These results are somewhat consistent with those of Dunkerley (2000), who also found that infiltration gradually decreased with distance from trunks of the Australian dryland shrub *Maireana spp.* But contrary to the Redberry junipers at our site, the zone of influence of *Maireana spp.* extends well beyond the canopy edge, measuring up to 3.3 times the size of the canopy zone. In stark contrast to our findings, Madsen et al (2008) found that unsaturated hydraulic conductivity was lower under shrub canopy and gradually increased with distance from the trunks of *Juniperus osteosperma* and *Pinus edulis*. Madsen et al estimated unsaturated hydraulic conductivity by means of a mini-disc infiltrometer, which has a small sampling area and operates under tension, not allowing macropore flow to take place and overcome the hydrophobicity (Buczko et al 2006). Such differences would render the results not directly comparable with those of our study or of others for which ponding infiltrometers were used to estimate *Kfs*.

Key questions raised by our findings that need resolution are (1) What are the mechanisms by which infiltration is increased? (2) How generalizable are these results? and (3) What are the larger-scale implications of enhanced soil infiltration?

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**Table 1.** Adjusted R² values obtained by simple linear regression for (i) correlations between the explanatory variables and soil *Kfs* values for shrubs in the five size classes (including values in the under-canopy and canopy-edge zones); and (ii) correlations between the explanatory variables and maximum dye penetration depth (size classes 2 and 3).

| Variable                  | Class 1 | Class 2 | Class 3 | Class 4 | Class 5 | MDP  
|---------------------------|---------|---------|---------|---------|---------|-------
| Distance from trunk       | —       | 0.58*** | 0.56*** | 0.42*** | 0.45*** | 0.66***
| Litter depth              | —       | 0.41*** | 0.43*** | 0.3***  | 0.55*** | 0.57***
| Antecedent soil moisture  | n.s.    | n.s.    | 0.31**  | 0.23**  | 0.21**  | 0.29*
| Bulk density              | n.s.    | n.s.    | n.s.    | n.s.    | n.s.    | n.s.  

Significance levels: n.s. = not significant, * = P < 0.05, ** = P < 0.01, *** = P < 0.001.
By what mechanisms is infiltrability increased?

Increased macroporosity

We believe that a primary factor contributing to higher soil infiltrability is that shrubs increase soil macroporosity. This assertion is supported by the dye tracing results, which demonstrate that the potential for deep percolation was much higher in the under-canopy and canopy-edge locations than in intercanopy soils. Other supporting evidence comes from the work of Sassen et al (2009), who performed ground penetration radar measurements after large-scale rainfall simulations in Ashe juniper stands. They found deeper water percolation under Ashe juniper trunks, which they attributed to a combination of high stemflow and enhancement via root channels of preferential percolation under Ashe juniper trunks, which they attributed to a combination of high stemflow and enhancement via root channels of preferential flow through fractures in the limestone. The agency of root-induced soil macropores as a key mechanism by which woody plants improve infiltrability and subsurface flows has been widely documented for other landscapes as well (Wilcox et al 1997, Newman et al 1998, Devitt and Smith 2002, Beven and Germann 2013, Tobella et al 2014, Niemeyer et al 2017). Greenhouse experiments using willow saplings planted on repacked fallow soils showed that in as little as eight weeks, saturated hydraulic conductivity increased by an order of magnitude (Leung et al 2018). This result was attributed to the fast growth of roots having thicknesses greater than 0.5 mm, which produces high soil macroporosity.

Litter accumulation

A secondary factor is the accumulation of litter under juniper shrubs. The protective effect of the canopy and leaf litter plays an important role in mitigating soil aggregate breakdown and soil surface crusting from raindrop impact (Geddes and Dunkerley 1999, Bochet et al 2000, Hoffman et al 2013). Besides, higher organic matter inputs contribute to aggregate stability (Cerda 1998). Because these mechanisms are directly related to litter thickness (Madsen et al 2008, Marin-Castro et al 2017), which decreases with distance from trunks, they could explain the positive correlation we found between distance from trunks and infiltrability. The presence of litter could also explain the unexpected negative correlation between antecedent soil moisture and Kfs. Since we ensured that all tests reached a nearly stable-state in infiltrate rate, we do not believe that antecedent soil moisture affected our Kfs results. During the 70-day period of data collection there were 11 precipitation events, of which only 4 were larger than 2 mm (the largest was 5 mm). Such small events are typically intercepted by the canopy and leaf litter of juniper shrubs (Owens et al 2006). This can explain why the soils with the highest infiltrability (under–canopy) were drier than those with lower infiltrability (intercanopy). Since larger shrubs have more litter accumulation under their canopies, interception by litter can also explain why such a correlation was found only for shrub classes 3 to 5 and not for classes 1 and 2 nor for intercanopy soils.

Soil mounding

Although many studies have found that shrubs tend to have mounds under their canopies, this phenomenon is mainly restricted to more arid climates. Where they occur, shrub mounds often have a coarser texture and higher porosity, giving rise to higher infiltratability (Ravi et al 2007). The genesis of such mounds has been attributed to processes such as differential interrill erosion (Rostagno and Delvalle 1988), accumulation of wind-blown (Ravi et al 2007) or raindrop-splashed sediment (Parsons et al 1992), bioturbation by burrowing animals (Eldridge et al 2009), or a combination of these processes (Bochet et al 2000, Parizek et al 2002, Buis et al 2010). We do not believe mounding is a factor in our study. At our site, there are no mounds under shrubs and no textural differences between canopy and intercanopy soils (Hester et al 1997).

How generalizable are these results?

Many, but not all, studies have demonstrated that infiltratability is greater under shrub canopies than in intercanopy zones (Eldridge et al 2015, Wilcox et al 2017), and the same conclusion has been reached by most studies of juniper specifically. Soil infiltratability under Ashe Juniper (Juniperus ashei), also common in the Edwards Plateau region of Texas, is appreciably higher than in intercanopy zones. Taucer et al (2008) and Wilcox et al (2008b) found that no overland flow was generated from the Ashe juniper stands even for high rainfall intensity, while overland flow was substantial from the adjacent intercanopy zones. In the Cross Timbers region of Oklahoma, Zou et al (2014) found that soil infiltratability was three times greater under Eastern Redcedar (Juniperus virginiana) than in adjacent grasslands. Similarly, soil infiltratability is generally greater under one-seed juniper (Juniperus monosperma) canopies than in the intercanopy zones (Reid et al 1999, Wilcox et al 2003). In contrast to these findings, Madsen et al (2008) found that unsaturated hydraulic conductivity was lower on the hydrophobic soils under juniper canopy (Juniperus osteosperma) than in the intercanopy areas having a high cover of biological soil crust. Such low unsaturated infiltration rates can be attributed to both the hydrophobicity and the method used in the study (mini-disk tension infiltrometer). At our site, many of the soils under Redberry juniper were also hydrophobic. However, because we measured infiltratability with a ponded method (Beerkan) and estimated Kfs based on terminal infiltration rates of nearly saturated soil, hydrophobicity was always
overcome and did not influence our results. While it might be argued that hydrophobicity under juniper shrubs could lead to runoff generation during high-intensity storms, there is no evidence that this is the case. On the contrary, some studies suggest that hydrophobicity under junipers can enhance infiltration rates and deep percolation by channeling water down through soil macropores (Robinson et al. 2010) or fractures in the bedrock (Sassen et al. 2009).

What are the larger-scale implications of enhanced soil infiltrability?

As noted above, the soils under shrub canopies often show high infiltration rates; however, the ways in which this translates to larger-scale effects on runoff and recharge can vary significantly and depend on a number of factors, such as (1) the influence of encroaching shrubs on intercanopy soils, (2) overall surface and subsurface infiltrability, (3) shrub cover, and (4) shrub transpiration.

Influence of encroaching shrubs on intercanopy soils

The influence of WPE on the intercanopy differs as a function of net rainfall, tending toward xerification at one extreme and thicketization at the other (Schreiner-McGrav et al. 2020). Xerification is the rule in arid climates, where WPE results in the concentration of water and nutrient resources in the canopy zones, leading to degradation of the intercanopy—commonly referred to as the ‘island of fertility’ phenomenon (Schlesinger et al. 1999, Schlesinger et al. 1999). The consequence is increased connectivity of bare patches, and thus higher runoff and erosion. Thicketization, on the other hand, occurs in regions where annual rainfall exceeds a threshold of around 400 mm. Under these conditions, intercanopy zones receive sufficient moisture and are not depleted by the establishment of woody plants and enhanced soil infiltrability in canopy zones. In other words, in more humid landscapes—and given the absence of external disturbances, such as heavy grazing—WPE does not cause degradation of intercanopy soils and vegetation and may even have a net positive influence on landscape infiltrability (Basant et al. 2020).

In terms of how these changes influence runoff, streamflow, and groundwater recharge, the response has been variable. In the desert southwest, where WPE leads to xerification increased overland flows may actually enhance groundwater recharge because of greater opportunity for recharge via transmission loss in ephemeral streams (Schreiner-McGrav et al. 2020). Conversely, in more humid landscapes where WPE leads to thicketization, increased soil infiltrability may lead to reduced overland flow and ultimately lower streamflows. This process would be important where overland flow is the predominant source of streamflow, such as the Rolling Plains of Texas (Wilcox et al. 2008a) or the South Texas shrublands. In more humid grasslands, such as the Tallgrass Prairie in Oklahoma, thicketization leads to lower recharge despite increased soil infiltrability because of the shrubs’ role in increasing transpiration (Zou et al. 2014).

For semi-arid karst landscapes, such as the Edwards Plateau, the landscape-scale response to increased soil infiltrability from thicketization differs from those in the non-karst regions discussed above. Previous work has demonstrated remarkably increased recharge and springflows in the region (Wilcox and Huang 2010). Our current work strongly suggests that enhanced soil infiltrability as a result of WPE is an important factor in higher groundwater recharge and subsequent increases in river baselows.

Surface and sub-surface infiltrability

Surface infiltrability is the main control for infiltration-excess overland flow, the dominant runoff process in semi-arid regions (Kidron 2020). At our site, where Kf is much higher than the maximum rainfall intensities, very little to no runoff is expected from under-canopy areas. For the intercanopy zones, Kf was still fairly high at 100 mm h⁻¹, an indication of the good condition of these rangelands. With such high overall infiltrability and the consequent expectation of little runoff from the site, it is surprising that overland flow is a significant part of the water budget (Richardson et al. 1979, Wilcox et al. 1990) and is generated exclusively from intercanopy patches (Wilcox et al. 2008b). We believe that a reason for these apparently contradictory observations is that the Beerkan method (and other point infiltration methods) tends to overestimate soil infiltrability by failing to replicate the effects of soil crusting and sealing by raindrop impact. This was shown by Di Prima et al. (2017), who found that infiltrability obtained with simulated rainfall was an order of magnitude lower than infiltrability obtained with both the Beerkan and the mini-disk tension infiltrometer methods. Therefore, we recommend discretion when applying to hydrologic models Kf obtained with point infiltration methods such as the Beerkan, which might lead to underestimations of runoff. For realistic estimates of runoff under different vegetation covers in these landscapes, future studies could rely instead on direct measurements of natural runoff events in small plots (Reid et al. 1999).

Saturation-excess overland flow can also occur in semi-arid landscapes, but mainly on shallow hillslope soils underlain by impermeable layers (Schreiner-McGrav and Vivoni 2018). In the Edwards Plateau, where most soils are underlain by highly fractured and permeable limestone, saturation-excess overland flow is probably not
important. However, subsurface lateral flow through the weathered limestone can account for a significant proportion of the water budget and is much higher under shrub patches than intercanopy patches (Taucer et al 2008, Wilcox et al 2008b). This suggests that woody plants either are establishing in locations with more fractured and water-conductive limestone or are accelerating limestone weathering and improving its water conductivity. This topic has received little attention and deserves further investigation, as it might improve our understanding of the drivers and consequences of WPE in karst regions.

Shrub cover
The influence of WPE on the overall infiltrability of the landscapes will also depend on the total amount of woody plant cover. Since shrubs quintuple infiltrability under their canopies, weighting the calculation by the percentage of shrub cover at our site (around 40%) could lead to the conclusion that shrubs are doubling the overall infiltrability of these landscapes. However, this could translate into disproportionally lower runoff because, in addition to not generating runoff, under-canopy zones can act as sinks and capture some of the overland flow generated from the intercanopy zones (Bochet et al 1999, Reid et al 1999, Ludwig et al 2005, Rossi et al 2018). While large shrubs will have larger runoff sink areas, smaller individuals likely also play an important role—especially if they are more abundant. Additionally, small juniper shrubs have been shown to transpire considerably less than larger ones per unit of canopy area (Starks et al 2014), and thus could have a disproportionally greater effect on groundwater recharge than larger, more water-demanding trees. Another factor may be stemflow—juniper species funnel a large amount of water down their trunks (Thurow and Hester 1997, Owens et al 2006) and into deep soil and rock layers through preferential flow.

Shrub transpiration
It could be argued that higher infiltration and deeper percolation could be counterbalanced by an increase in transpiration rates, as seen by Zou et al (2014) in Oklahoma. But this does not seem to be the case in the Edwards Plateau, as shown by Heilman et al (2009), who used eddy covariance fluxes to estimate evapotranspiration in an oak–juniper woodland over a two-year period and concluded that water use by woody plants was limited to the top 20 cm of soil. Since soils in the region are mostly shallow and underlain by highly fractured and permeable limestone and the root zone of Junipers is mainly restricted to the soil (Heilman et al 2009, Cardella Dammeyer et al 2016), a significant proportion of the infiltrated water will likely move past the root zone and become groundwater recharge and baseflow. A schematic illustration of these processes is shown in figure 5.

Conclusion
We have demonstrated here that in semiarid karst landscapes, WPE dramatically enhances soil infiltrability; and further, that changes in soil infiltrability occur within two to three years after germination. The primary mechanisms by which this takes place are enhanced macropore flow and the addition of soil organic matter through litter accumulation. Enhanced soil infiltrability is a key driver of increased groundwater recharge in karst savanna landscapes, which has large-scale consequences for runoff and streamflow.
Acknowledgments

This work was supported by the Texas A&M Sid Kyle Endowment and the USDA-NIFA Grant 12726253. We are grateful for the collaboration and support from the research staff at the Texas A&M Sonora Research Station. We are also thankful to Simone Di Prima for his helpful advice on the SSBI method.

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