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Water abstraction of invasive *Prosopis juliflora* and native *Senegalia senegal* trees: A comparative study in the Great Rift Valley Area, Ethiopia



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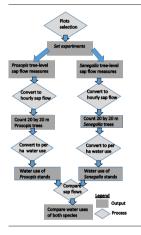
HIGHLIGHTS

- At the stand scale, *P. juliflora* consumes approximately 6,636 L/day/ha (transpiration: 242 mm per year) and *S. senegal* stands consume 2,723 L/day/ha (transpiration: 87 mm per year).
- P. juliflora stands are multi-stemmed and denser than S. senegal stands, and which foster P. juliflora to consume more water than S. senegal.
- P. juliflora invasion resulted in severe impacts on water resources of the dry lowland areas of Ethiopia, with direct and indirect consequences to rural livelihoods.

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ABSTRACT

Besides direct water abstraction, natural water scarcity in semi-arid and arid regions may be further exacerbated by human-assisted changes in vegetation composition, including the invasion by non-native plant species. Water abstraction by the invasive tree *Prosopis juliflora* and by the native *Senegalia senegal* was compared in the dry Great Rift Valley, Ethiopia. Transpiration rates were quantified using the heat ratio method on six trees each of *P. julifora* and *S. senegal*, growing adjacent to each other in the same environment. Water use for *P. juliflora* trees ranges from 1 to 26 L/day (an average of 4.74 ± 1.97), and that of *S. senegal* trees from 1 to 38 L/day (an average of 5.48 ± 5.29 during two study years). For both species, soil heat, latent heat, and soil moisture status influenced the rates of sap flow of trees; in addition, water use by *P. juliflora* trees was related to vapor pressure deficit; the higher the vapor pressure deficit, the higher the water abstraction by *P. juliflora*. Stand densities of pure *P. juliflora* and *S. senegal* treas and 400–600 trees per ha, respectively. At the stand scale, *P. juliflora* consumed approximately 6636 L/day/ha (transpiration: 242 mm per year) and *S. senegal* stands consumed 2723 L/day/ha (transpiration: 87 mm per year). That is, *P. juliflora* stands consumed three times more water than *S. senegal* stands, and (2) *P. juliflora* stands evergreen and uses water all year-round, while *S. senegal* sheds its leaves during the peak dry seasons. Our findings

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GRAPHICAL ABSTRACT

suggest that, compared to *S. senegal*, *P. juliflora* invasion results in severe impacts on groundwater resources of the drylands of Ethiopia, with direct and indirect consequences to ecosystem services and rural livelihoods.

1. Introduction

The increasing anthropogenic impacts, which demand more resource utilization and associated environmental pressures to satisfy the economic development of an ever-increasing human population, result in climate change and the scarcity of natural resources (Zhang et al., 2018; Eisenmenger et al., 2020). Water resource is one of the scarce resources at scale (Vörösmarty and Sahagian, 2000). Freshwater scarcity is considered to be the main threat to the sustainable development of human societies, particularly in arid and semi-arid areas, which are by definition water-limited ecosystems (Mekonnen and Hoekstra, 2016; Greve et al., 2018). Meeting the everrising demands for freshwater and restoring ecosystem services so that ecosystems can sustainably replenish water stocks is considered as one of the most critical challenges of this century. Invasive alien plant species (IAPS) are key drivers of anthropogenic global environmental change as they threaten native species (Abbas et al., 2019), communities, and ecosystems (Vilà et al., 2011), with significant consequences to the people living in the invaded range (Pejchar and Mooney, 2009; Pimentel et al., 2005; Le Maitre et al., 2015).

In addition to human interventions that extract water resources, water is lost naturally through interception, evaporation, and transpiration. Evapotranspiration rates depend on the climatic factors of a given area including air temperature, air humidity, solar radiation, soil moisture, and wind speed (Gebler et al., 2015; Farley et al., 2005; Allen et al., 2005; Allen, 1998), as well as the vegetation structure of the dominant plant species (Sun et al., 2008; Farley et al., 2005). Plant physiology, stem diameter size and leaf structure, stomatal, and root architecture affect water abstraction both at the individual plant and the community level (Farley et al., 2005; Jackson et al., 2005; Le Maitre et al., 2015).

Besides natural succession and human-mediated land degradation, land-use change, and invasive alien plant species (IAPS) are reported as among the most important drivers of changes in vegetation composition and ecosystem services and functions (Masters and Norgrove, 2010; Vilà et al., 2011). Due to the invasive characteristics of IAPS, they have become the dominant plant species at different geographic scales, for example, in Ethiopia (Shiferaw et al., 2019a, 2019b; Shiferaw et al., 2019c; Linders et al., 2019), in Australia (Robinson et al., 2008), and in South Africa (Le Maitre et al., 2015). In reviews of water abstraction by invasive and native plant species, reports indicated that individual invasive and native trees tend to have similar sap flow rates (Dzikiti et al., 2013a, 2013b; Cavaleri et al., 2015), but native-dominated ecosystems show less amount of sap flow rates per unit area than invasive-dominated ecosystems (Shiferaw et al., 2021; Dzikiti et al., 2013a, 2013b) because native species like Senegalia senegal (L.) Britton (formerly Acacia senegal (L.) Willd.) thend to grow in less dense stands than invasive species, like Prosopis juliflora (Swartz D.C) (Dzikiti et al., 2013a, 2013b; Shiferaw et al., 2019c).

The *Prosopis* species and their hybrids are reported as among the most aggressive IAPS, particularly in semi-arid and arid areas (Shackleton et al., 2014; Castillo et al., 2020). *Prosopis* species were introduced to different regions including Africa, India, and Australia, to provide shelter, shade, fuelwood, timber, fodder, and protect soil and ecosystem degradations (Pasiecznik et al., 2001; Boy and Witt, 2013). However, many of the *Prosopis* species, like *P. juliflora*, have become invasive, impacting the natural ecosystems by suppressing native vegetation, negatively affecting biodiversity, and reducing the supply of ecosystem services that rural livelihoods depend on (Engda et al., 2009; Wakie et al., 2012; Shackleton et al., 2014; Linders et al., 2020; Mehari, 2015; Edmund, 2019).

Moreover, *Prosopis* species have been reported as some of the most water-consuming plant species (Dzikiti et al., 2013a, 2013b; Shiferaw et al., 2021). *Prosopis* invasion is considered as one of the burning issues

in dryland rural communities due to its noxious behavior that has allowed it to invade 1.2 million ha within 31 years in the study area alone (Shiferaw et al., 2019a, 2019b, 2019c). Different studies were conducted in South Africa indicating that invasive *Prosopis* species affects groundwater tables (van Wilgen and Wannenburgh, 2016; Le Maitre et al., 2015; Dzikiti et al., 2013a, 2013b). Eco-physiological studies of *Prosopis* species have been conducted in different regions, e.g. in the native range in Southern Arizona (McShane et al., 2015; Webb and Leake, 2006) and in the introduced range in South Africa (Dzikiti et al., 2013b; Dzikiti et al., 2013a, 2013b), where *Prosopis* trees shed their leaves particularly during the cold season. Only one study has been conducted so far on water use of *Prosopis* species in arid and semi-arid areas of Eastern Africa (Shiferaw et al., 2021).

Accurate monitoring of the impact of P. juliflora on the water resources in the invaded areas in Eastern Africa requires comparative information on the water use of P. juliflora and that of common native species, which have been displaced by the invasive species. Senegalia senegal is found in dryland parts of West and East Africa. Senegalia senegal is likely to also consume groundwater resources and affect other ecosystem services as it is mainly found in water-scarce areas. However, water use rates of S. senegal or closely related Senegalia species in the tropical region of Africa have not been assessed so far. Our hypothesis was that both the native and invasive alien species consume the same amount of water as both are tree species, may have similar stem diameters and sapwood areas and are found in the same environmental setting. In this study, water use was quantified as the diurnal and seasonal water abstractions of P. juliflora species and cooccurring native S. senegal in the dry lowland areas of Ethiopia. Specifically, water use of the two species was estimated at the individual tree and the stand levels, also to assess whether water use of these plant species was related to environmental factors.

2. Materials and methods

2.1. Study species

Invasive *Prosopis* species are deep-rooted leguminous trees or shrubs (Orwa et al., 2009). Numerous species of this genus are native to Central and South America, from where they were introduced to different parts of the world (Pasiecznik et al., 2001; Boy and Witt, 2013). *Prosopis juliflora* (hereafter *Prosopis*) was introduced to Ethiopia in the late 1970s and early 1980s for the purpose of soil and water conservation (Keller et al., 2009; Ayanu et al., 2014; Shiferaw et al., 2021). Within 35 years, this species had invaded approximately 1.2 million ha in the Afar Region (Shiferaw et al., 2019a).

Senegalia senegal (hereafter Senegalia) is a leguminous tree found in dry parts of Africa and Asia. Senegalia is commonly found in the dry moist, and semi-arid agro-climatic zones of Ethiopia, particularly in the Afar plain, Harerge, western Wello, Gamo Gofa, Shoa, Sidamo, Arsi, and Bale areas (Bekele, 2007). Senegalia tolerates longer dry season and high daily temperatures but it prefers well-drained and moist soils and it is widely grown in dry scrub, woodland and grassland, with an altitudinal range of 300–1700 m in Ethiopia (Bekele, 2007). Senegalia is a multi-purpose tree and is used for hand-tools, charcoal, firewood, food (from the seed), medicine (from bark and roots), fodder (from pods and leaves), high-quality gum, dye (from the seeds), and fishnets (from root fibers, Bekele, 2007).

2.2. Study area

This study was conducted in one of the heavily invaded areas known as Amibara District (Fig. 1) of the Afar Region, Ethiopia (geographical range from 9.16° to 9.21^{0} N and from 40.08° to 40.12° E at an altitude of

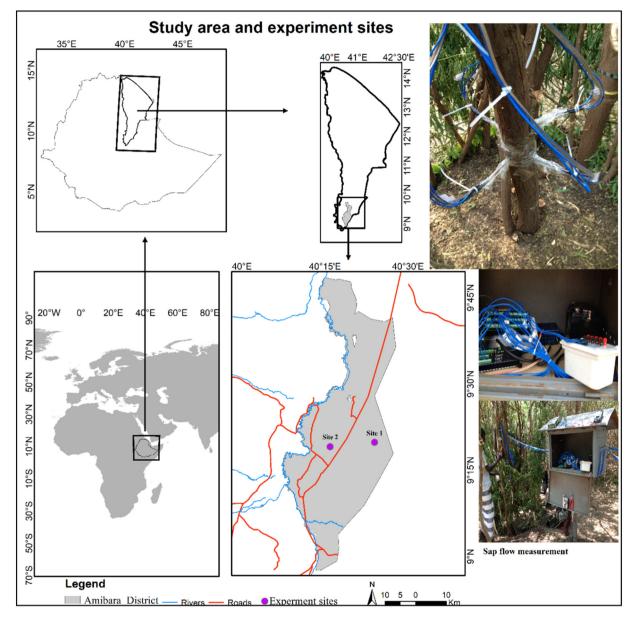


Fig. 1. Map of the study area (Amibara District) and experimental sites (site 1 & site 2 for *Prosopis*, and site 2 for *Senegalia*) (right side pictures are sap flow measurements installed in *P. juliflora* stem) in Afar Region, Ethiopia.

740 m). The study area is about 250 km northeast of Addis Ababa and. The area is found in the Awash River Basin, which is part of the Great Rift Valley. The Awash Basin is a highly exploited basin in Ethiopia (Kidanewold et al., 2014), although its water resources are scare both in terms of quality and quantity. The estimated human and livestock populations in the basin were 18.6 and 34.4 million, respectively, in 2016 (CSA, 2016). About 70 % of the large scale irrigation projects in Ethiopia are developed in this basin (Awash Basin Authority, 2017), but still a high volume of water is drained to downstream areas. For example, the mean annual river flow of the basin is estimated at 4.6 billion m^3 at the terminal Lake Abe (MoWE and FAO, 2012; Kidanewold et al., 2014). Nevertheless, water quality and availability in the downstream areas of the Awash Basin are the main limiting factors for large-scale irrigation development, particularly during the low- flow seasons of the year (Kidanewold et al., 2014).

The study area has a mean annual precipitation of about 475 mm per year (Shiferaw et al., 2021). With a mean annual temperature of 31 °C, a mean maximum temperature of up to 41 °C (June) and a mean minimum temperature of 21° C (November), it is one of the hottest areas of the

country (Shiferaw et al., 2019c). The biome is described as an arid and semi-arid agro-climatic zone. The natural vegetation cover is composed of bushland, grassland, scattered dry shrubs, woodland comprising different *Senegalia* species, and wooded grassland. The soil of the area consists of different soil types, ranging from alluvial fertile soil to sand and heavy clays, stony soils, rocky outcrops. The altitudinal range of the region is between 175 m below sea level and 2992 m a.s.l. The main sources of livelihood for the local people are mainly pastoralism, and some agro-pastoralism particularly around rural towns (Shiferaw et al., 2019b

2.3. Experimental sites and design

Experimental data were collected from four plots of 20 m by 20 m at two sites with the highest densities of *Prosopis* and *Senegalia* found in the study region. A total of six *Prosopis* trees from two plots (three *Prosopis* trees from each plot) were measured at Site 1 and Site 2, and a total of six *Senegalia* trees (three *Senegalia* trees from each plot) were measured in two different plots at Site 2. The two sites were about 5 to 7 km and the plots within the site at least 500 m apart.

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2.3.1. Site 1 (Prosopis only)

This site was in the drylands of the Hallaidaghe grassland area (Fig. 1), which is characterized by sandy and partly loam soil formation. There is no surface water resource except precipitation and seasonal flooding from the adjacent highlands of the eastern part of the area. The area is highly invaded by *Prosopis* with a closed canopy cover, and the average height of trees reaches about 5 m. About 100 ha of land is invaded at this site.

2.3.2. Site 2 (both Prosopis and Senegalia)

This area was situated in the dry areas of the Berta locality and is characterized by sandy soils with a very high stone content (Fig. 1). *Senegalia* species, shrubs, and grasses are the dominant indigenous vegetation at this site. Besides the *Senegalia*-dominated vegetation, there are *Prosopis* stands with a closed canopy cover consisting of trees reaching a height of 4 m. A meteorological monitoring station was installed in an open area between the *Senegalia* and *Prosopis* plots.

2.4. Trees and stand (community) level water use monitoring

Water use of *Prosopis* and *Senegalia* was measured for two years from March 2018 –April 2020. The amount of water abstracted by individual *Prosopis* and *Senegalia* trees was monitored by heat pulse velocity technique and estimated using the heat ratio method (HRM, Shiferaw et al., 2021; Dzikiti et al., 2013b; Bayona-Rodríguez and Romero, 2016; Burgess et al., 2001). This technique was chosen because it is a modified and improved technique for measuring sap flows for desert-adapted species (Shiferaw et al., 2021; Dzikiti et al., 2013b; Scott et al., 2008; Hultine et al., 2006). The same procedure and technical specifications were followed in previous studies in South Africa (Dzikiti et al., 2013b) and in Ethiopia (Shiferaw et al., 2021). In total, four sap flow plots (two for *Prosopis* and two for *Senegalia*) were established at two sites and three trees instrumented per plot.

The measured trees had variable stem diameters to capture the variation in transpiration rates of stands consisting of different-sized trees. The stem diameters of the measured trees were taken at 60 cm aboveground just below the branching. Each of the sap flow stations consisted of a data logger (CR1000) and a multiplexer (AM16/32B) of the Campbell Scientific provider (Inc., Logan UT, USA). Each system was energized by a 70 Ah (12 V) with rechargeable battery of 50 W solar panels. From the power source, four sets of heaters supplied heat to each tree for 0.5 s every hour through a relay control module. A pair of equally spaced (0.6 cm) T-Type thermocouples were mounted on either side of the heater to measure the heat ratio before and after pulsing. Two 2.0 mm diameter holes were made with a precision drilling ring for the thermocouples to minimize errors due to probe misalignments. The holes for the heaters were about 1.8 mm in diameter, which was to ensure a tight fit and facilitate heat transfer through the sap wood during pulsing.

The heat ratio method of sap flow monitoring technique (McJannet and Fitch, 2004; Burgess et al., 2001) was based on the heat pulse velocity (Vh, cm/h), which is logarithmically related to the ratio of temperature increase upstream and downstream from a heater (v_1/v_2) as shown in the following equation (Burgess et al., 2001):

$$Vh = \left(\frac{k}{x}\right) (\ln\left(\frac{V1}{V2}\right) 3600$$

where "*k* is the thermal diffusivity, which was assigned a nominal value of 2.5×10^{-3} cm²/s for wood, *x* is the distance (cm) between the heater and either temperature probe, and v_1 and v_2 are temperatures before and after pulsing" (Dzikiti et al., 2013a, 2013b; Burgess et al., 2001).

The heat flow rates were measured at depth of *Prosopis* sapwood ranging between 0.3 and 0.96 cm, and *Senegalia* sapwood ranging from 0.3 to 2.1 cm excluding the bark to capture the radial changes of both plants. Trees were wounded while drilling and wounding corrections were applied according to Swanson and Whitfield (1981). The sapwood depth and sapwood area were determined visually from heartwood boundaries and thermocouples were installed across the sapwood area so that conversion of sap flux densities were calculated.

Moreover, the heat energy transferred through the ground was measured using soil heat flux plates (Model: HFP01SC-L, Delft, The Netherlands), and soil temperature was recorded using soil averaging thermocouples (Model: TCAV-L: Campbell Scientific, Inc., Logan UT, USA). The clusters of heat flux plates were installed at 50 cm depth and averaged the soil moisture content using the soil water content reflectometers (Model: CS616-L: Campbell Scientific, Inc., Logan UT, USA). Temperature and humidity probes were used to measure air temperature and humidity, respectively (Campbell Scientific, 2013). To monitor the content of soil water, four CS-616 probes were installed at all four plots placed horizontally in the root zone at 50 cm depth near the *Prosopis* and *Senegalia* plots. All these datasets were stored in the data loggers and transferred to personal computers for further computation.

At each plot, three trees were measured, resulting in a total of 12 trees (6 trees for *Prosopis* and 6 trees for *Senegalia*). Furthermore, the volume of sap flow for the individual tree in liters per hour per tree was converted into stand-level transpiration (mm per hour per hectare) by collecting the number of trees per plot in five randomly selected plots of 20 m by 20 m for each species, including experimental plots, and converted into number of trees per hectare (Dzikiti et al., 2013b). The number of other species in the study area was negligible (<50 stems per hectare) and they were therefore excluded from this analysis.

2.5. Weather and soil water dynamics

At Site 2, microclimate data were collected using an automatic weather station (data logger and other accessories) equipped to measure solar radiation, temperature, rainfall, relative humidity, and air pressure. The radiation sensor was mounted on a horizontal leveling fixture at 90° on a south-facing crossbar to exclude self-shading errors. Rainfall was measured using a tipping bucket rain gauge (Model TE525-L of Campbell Scientific, at Logan UT, USA). The weather station was accompanied with an Em50 (a specialized 5-channel data-logger) and ECH₂O utility application (from Decagon, USA). The other weather station was installed at the height of 2.0 m at Worer Agricultural Research Center, within 7 km distance from the experimental sites; this station also measured wind speed and direction (Model CS500, Vaisala, Finland). All of these tools were connected to a data-logger programmed at a scanning interval of 90 s and recoded data were stored at 30 min intervals. The data were downloaded from dataloggers every 21 days. All datasets were collected in 24/7 for two years. For security reasons, besides the hired security personnel, safety-boxes were also used to protect sensors, data-loggers, multiplexer, and power sources (battery, solar panel, and power controllers) from bad weather and vandalism. Moreover, the experimental sites were fenced to prevent animal and human interventions.

2.6. Drivers of water consumption

To assess the major drivers or factors affecting water abstraction of *Prosopis* and *Senegalia*, environmental variables were collected during sap flow measurements with the same data loggers and additional stations. The approach was used to evaluate the effects of wind speed, solar radiation, surface and latent heat, soil moisture, relative humidity, and vapor-pressure-deficit (VPD) on hourly, daily, and yearly water use of individual trees.

2.7. Data conversion and statistical analyses

In this study, different statistical analyses were carried out to manage the big datasets, which were collected in half-hour and hourly intervals for two years from those experimental plots. LoggerNet 4.1 was used to download sap flow data from data loggers. It was also used to convert the big xxx.dat and yyy.flux files to 30 min interval values of zzz.xlxs files. ECH₂O utility software was used to download and process 30 min of weather data (solar radiation, relative humidity, precipitation, and temperature) into hourly data and usable zzz.xlxs format. Multiple linear regressions were run using sap flow as response variable and explanatory variables such as wind speed, solar radiation, soil and latent heat, soil moisture, relative humidity, and vapor-pressure-deficit (VPD). An opensource R software version 3.3.3 (R Core Team, 2019) and an open-source Quantum GIS (QGIS3.8.3) software were used to analyze and map the data, respectively.

3. Results

3.1. Stand characteristics and allometric relations of instrumented trees

Diameters of instrumented trees ranged between 3.5 and 7.3 cm for *Prosopis* trees and from 3.1 to 6.3 cm for *Senegalia* trees. There were positive relationships between tree diameters and sapwood areas of the sampled trees (Fig. 2). The sapwood areas and stem diameters of instrumented trees were highly correlated (R^2 of 0.93 for *Prosopis*, and R^2 of 0.75 for *Senegalia*).

3.2. Sap flow of Prosopis and Senegalia trees

Prosopis trees consumed on average 4.74 \pm 1.97 L/day, whereas *Senegalia* trees consumed 6.46 \pm 3.7 L/day (Annex 1). Stem diameters explained about 42 % and 13.5 % of the variation in sap flow for *Prosopis* and *Senegalia*, respectively (Fig. 3). When analyzing the two species separately, sap flow was positively related to stem diameter for *Prosopis* (*P* < 0.013), but not for *Senegalia* (*P* < 0.86).

3.3. Stand-level sap flows of Prosopis and Senegalia

Tree densities of *Prosopis* and *Senegalia* were found to be 1200–1600 trees and 400–600 trees per ha, respectively, indicating that *Prosopis* stands were denser than *Senegalia* stands. Thus, on average, *Prosopis* stands consumed

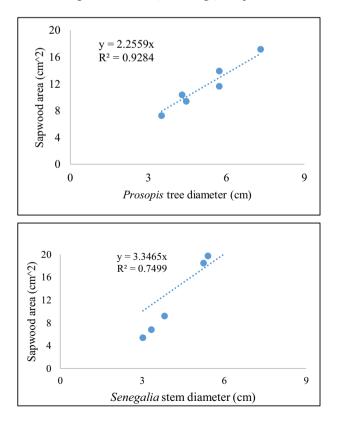


Fig. 2. Allometric relationships between stem diameters and sapwood areas of sampled *Prosopis* and *Senegalia* trees.

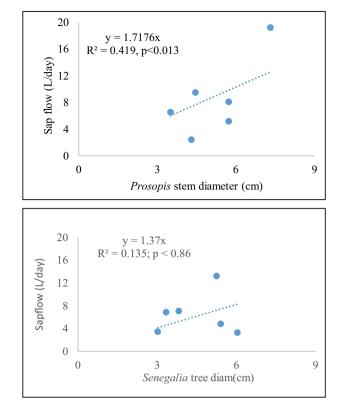


Fig. 3. Average sap flow (L/day/tree) and relationships between stem diameters and sap flows of sampled *Prosopis* and *Senegalia* trees.

about 5688–7584 L/day/ha, while *Senegalia* stands consumed about 2584–3876 L/day/ha. *Prosopis* stands transpired about 208–277 mm per year, while *Senegalia* stands transpired about 70–105 mm per year, indicating that *Prosopis* stands consumed two to three times as much water as *Senegalia* stands (Annex 2).

3.4. Drivers of water consumption

Water use of the two tree species was significantly influenced by several environmental variables. Solar radiation was very high between 10:00 and 14:00 h, with a peak at noon when relative humidity was very low, which made the site with a high vapor pressure deficit, driving high water use by trees. Thus, transpiration was also high during the high solar radiation part of the day.

From these analyses, latent heat, pressure, relative humidity, vapor pressure deficit, and soil moisture were highly significantly correlated with water use by *Prosopis trees* (P < 0.001; Table 1a). However, only three explanatory variables had a significant contribution to the water use of *Senegalia*, i.e. surface heat, latent heat, and soil moisture (Table 1b, annex 5).

4. Discussion

Our study provides evidence that at the level of individual trees, the daily water abstraction of invasive *Prosopis* and native *Senegalia* trees was comparable. However, at the stand (community) level, *Prosopis* consumed three times more water than *Senegalia* trees, largely because the evergreen *P. juliflora* can build up much higher densities than *Senegalia* and it consumed water throughout the year (annexes 3 and 4).

4.1. Sap flows in individual trees

Water abstraction of *Prosopis* trees was significantly related to stem diameter (P<0.013) while no significant relationship was found for

Table 1

Linear regression of dependent variable (sap flow in mm/day) from:

Model inputs	Unstandardized coefficients		Standardized coefficients	<i>t</i> -Test	Significant level
	В	Std. Error	Beta		
a) Sap fl	ow of Prosopis dominated	areas with explanatory va	riables (2 years hourly and daily datasets,	P<0.05 is significant leve	1)
(Constant)	-0.024	0.015		-1.675	0.095
Surface heat [W/m ²]	0.001	0.001	0.010	2.090	0.037
Latent heat [W/m ²]	0.002	0.001	0.017	3.668	< 0.001
Estimated pressure [Pa]	0.001	0.001	-0.038	-3.865	< 0.001
Relative humidity [%]	-0.004	0.001	-0.022	-2.833	< 0.005
Wind speed [m/s]	-0.003	0.001	-0.001	-0.208	0.836
Soil moisture (%)	0.993	0.005	0.991	205.893	< 0.001
Vapor pressure deficit [Pa]	0.001	0.001	-0.135	- 4.695	<0.001
b) Sap flow of Senegalia dominated	areas with explanatory va	riables (2 years hourly and	d daily datasets)		
(Constant)	64.750	15.431	-	4.196	< 0.001
Surface heat [W/m2]	-0.217	0.062	-0.257	-3.472	< 0.001
Latent heat [W/m2]	1.385	0.437	0.238	3.172	< 0.002
Estimated pressure [Pa]	-0.098	0.062	-0.545	-1.563	0.119
Relative humidity [%]	-0.048	0.024	-0.408	-1.979	0.049
Wind speed [m/s]	-0.237	0.161	-0.101	-1.474	0.141
Soil moisture (%)	-16.874	5.111	-0.251	-3.301	< 0.001
Vapor pressure deficit [Pa]	-0.011	0.080	-0.065	-0.139	0.889

Senegalia trees. Trees with higher stem diameters have higher sapwood areas. This in turn supports higher sap flow rate up to a certain point, but in older trees sapwood area changes to heartwood and thus decreases the amount of sap flow (Alsheimer et al., 1998). These findings are in line with studies conducted in South Africa (Dzikiti et al., 2013b; Le Maitre et al., 2020), indicating that there is considerable variation among plant species in terms of the relationship between stem diameter and sapwood area, as well as between stem diameter and sap flow rate at the tree level.

Studies comparing water use of invasive and co-occurring native species at the tree levels provided mixed results (Le Maitre et al., 2020). Scott-Shaw and Everson (2019) compared the water use of invasive trees with that of native trees in the same watershed in KwaZulu-Natal, South Africa, and found that individual trees of *Acacia mearnsii* De Wild and *Eucalyptus grandis* W.Hill used more than twice as much water as individual trees of the native species. On the other hand, Dzikiti et al. (2017) found no significantly different results in the sap flux density of individual trees of the invasive *Prosopis* and of the native *Vachellia karroo* (Hayne) Banfi & Galasso, although V. karroo had thicker sapwood than *Prosopis*.

Water abstraction of the evergreen P. juliflora trees throughout the year is possible because deep-rooting trees can tap groundwater, particularly during the dry seasons. Dzikiti et al., 2013b estimated that approximately 70 % of the water used by invasive, leaf-shedding Prosopis species in South Africa was extracted from the groundwater. It is likely that in the dryland areas like the Afar Region, the evergreen P. juliflora abstracts water almost entirely from the groundwater resources, particularly during the dry seasons. Tanaka et al. (2003) reported that water uses of trees in evergreen forests in Thailand were higher just after the dry season. Hence, these findings indicate that the evergreen feature of Prosopis species does not only lead to the abstraction of water from the groundwater but also contributes to the continued impacts on groundwater scarcity in the Afar Regions (Shiferaw et al., 2021). Prosopis invasions increased the decline of biodiversity, particularly native trees in South Africa (Shackleton et al., 2015). It has been reported to have allelopathic effects (El-Keblawy and Al-Rawai, 2007) beside to competition for water with its dense thickets over native vegetation (Schachtschneider and February 2013).

4.2. Sap flow at the stand level

Prosopis stands use larger amounts of water than *Senegalia* stands as the density of the *Prosopis* trees was higher than *Senegalia* trees. Our findings corroborate similar patterns found in other studies (Cavaleri et al., 2014; Dzikiti et al., 2013b; Le Maitre et al., 2020). In particular, Dzikiti et al., 2013b reported that, although the daily water use did not differ between

invasive *Prosopis* and the native *V. karroo* (see above), at the stand level *Prosopis trees* transpired five times (approx. 544 mm per year) more water than *V. karroo* (approx. 91 mm per year), since the density of *Prosopis* trees was six times higher than that of the native species. Also, Dzikiti et al., 2013b showed that removing *Prosopis* from an invaded area can reduce the rate of declining groundwater levels during the dry season.

In Ethiopia, Prosopis stands use about 208-277 mm of water per year, which is three times more than what Senegalia stands use. There may be other factors affecting the higher transpiration rates of Prosopis trees as revealed in this study. Not only are Prosopis stands denser (Wakie et al., 2016), but they are also evergreen and thus take up water year-round, while Senegalia sheds its leaves during the peak dry seasons, and thereby reduce water use to almost zero. That is, there are two major reasons why Prosopis stands use more water than Senegalia species in the study area. Firstly, the invasive Prosopis species in Ethiopia and tropical parts of Eastern Africa is an evergreen plant that uses water throughout the year for its active photosynthesis, whereas the Senegalia sheds its leaves during the peak dry season and, thus, has very low evapotranspiration and transpiration rates. Secondly, Prosopis trees build very dense thickets (or dense stands) and multi-stemmed trees in the study area that use more water than single-stemmed Senegalia trees. Moreover, when comparing Prosopis species in Ethiopia with those of South Africa, Prosopis in Ethiopia uses water throughout the year while in South Africa it sheds its leaves during the cold season (Shiferaw et al., 2021) and has slack periods for its photosynthetic activities. Thus, the current study revealed that Senegalia species consumed less amount of water per hectare than Prosopis species in the dry lowlands of Ethiopia.

The current findings based on two years of experimental measurement indicate that *Prosopis* stands at the community scale consumed more water than *Senegalia* stands per day and per hectare. Even though both species have the same tree structure and are found in the same environmental setting they have different water uptake capacities both at individual and population levels, which rejects our initial hypothesis that both species might abstract the same amount of water. Hence, this fast-growing invasive species impacts the ecosystem's water budget (Shiferaw et al., 2021) and aggravates the impacts of climate variability by compromising the resilience of indigenous trees and provisioning ecosystem services. According to Le Maitre et al. (2020), there were no studies assessing the monetary impacts of IAPS on the productivities of other native species, which may lead to an under consideration of the economic benefits the society while managing IAPS (Mudavanhu et al., 2017) except one estimation of economic loss due to water abstraction by *Prosopis* in Afar region (Shiferaw et al., 2021).

Water use by invasive species is of great concern for decision-makers and practitioners because it hinders the implementation of ecosystem

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restoration/rehabilitation programs in dry lowland areas. Native species adapt to climatic change and droughts by reducing competition for natural resources, particularly scarce water resources (Le Maitre et al., 2015; Dzikiti et al., 2013b), by shedding leaves during peak dry seasons. The extensive abstraction of groundwater by invasive species in the Awash Basin has created serious consequences on water availability in downstream (Shiferaw et al., 2021).

A comparison of annual rainfall and *Prosopis* water use in Afar region indicated that almost half of the rainfall was used by the invasive species (Shiferaw et al., 2021), which reduces the available water budget for the provisioning of other ecosystem services and rural livelihoods such as the production of crops or fodder for livestock. Groundwater table declined under *Prosopis* stands, which can be supposed to be the active water uptake by the trees to meet photosynthetic demand (Dzikiti et al., 2013a, 2013b). *Prosopis* affects not only water availability for other native species but also contributes to the degradation of ecosystem functions and services (Keller et al., 2009). For example, indigenous palatable grass species and multipurpose trees are threatened by the *Prosopis* invasion (Engda, 2009; Shackleton et al., 2015). Thus, there is a need for proper management of the *Prosopis* invasion so as to secure benefits from groundwater resources and other services offered by the ecosystems in these semi-arid and arid areas (Shiferaw et al., 2021).

We acknowledge that the current study is carried out using a limited number of experimental sites and some assumptions may entail certain level of uncertainties. Further investigations on the variation of water abstraction by *Prosopis* across the invaded landscapes in the Afar Region as well as in neighboring countries are needed to further improve our understanding on the impact of *Prosopis* to the water budget of semi-arid and arid ecosystems of the tropical regions in Eastern Africa.

4.3. Drivers of water consumption

In this study, the variation in sap flow among *Prosopis* trees in the dryland areas was affected by differences in stem diameter and sapwood area. In addition, water use was affected by environmental and/or climatic factors such as vapor pressure deficit, solar radiation, soil moisture, and latent heat of the soil. This indicates that *Prosopis* water use is affected by many external variables. Unlike *Prosopis, Senegalia* water use is sensitive to only a few external factors. One may speculate that this is because it is a native plant which has adapted to the environmental conditions in the study area. In a similar study assessing drivers of water use of the exotic *Eucalyptus globulus* Labill in Southern Ethiopia, Fritzsche et al. (2006) found that water use was largely independent of water content of topsoil, as this tree used the groundwater when necessary by its taproot systems.

The amount of water use at the stand level is mainly determined by vegetation density and environmental factors (Shiferaw et al., 2021). Also, the degree of ground cover can have a considerable influence on soil moisture and evaporation (Merta et al., 2006). In this study, however, soil evaporation contributed very little to water abstraction, as the soil was very dry and understory transpiration low because of the absence of undergrowth. However, the degree of soil moisture and its evaporation, in turn, is governed by climatic and environmental factors (Gardiol et al., 2003; Lund and Soegaard, 2003; Loranty et al., 2008).

In a previous study on the water use of *Prosopis* in the same study area in Afar Region (Shiferaw et al., 2021), both transpiration and evapotranspiration were influenced by microclimate, particularly precipitation and solar radiation and their effects on soil moisture, wind speed, and vaporpressure-deficit. The current study indicates that water uses of both *Prosopis* and *Senegalia* were significantly affected by soil heat, latent heat, and soil moisture status of the area. The other factors influencing higher water consumption of *Prosopis* trees in drylands than in wetlands were higher vapor-pressure-deficit and low relative humidity in the dry areas (Shiferaw et al., 2021). In general, vapor-pressure-deficit, soil heat, latent heat, and soil moisture (Bayona-Rodríguez and Romero, 2016) directly influence the rate of sap flow. In this study, soil moisture, soil heat, and vapor-pressuredeficit (for *Prosopis*) were found to be the major drivers of the water consumption of plants, similar to the previous study (Shiferaw et al., 2021).

5. Conclusions

The exotic *Prosopis juliflora* was introduced to the study area in the late 1970s and early 1980s for the purposes of soil and water conservation without understanding its future challenge to the environment, biodiversity, and rural livelihoods (Shiferaw et al., 2004; Keller et al., 2009; Ayanu et al., 2014; Shiferaw et al., 2021). The findings of this study provide evidence that the stands of the evergreen invasive *P. juliflora* consume three times more water than stands of native *S. senegal* in the Afar Region. Therefore, the invasion of *P. juliflora* should be contained and its stand density in the highly affected areas reduced as an initial measure so as to mitigate its negative effects on local water availability. If it is to be left uncontrolled, it has the potential to devastate biodiversity and water-dependent ecosystem services, and thus jeopardize the regional economy at large, which is largely constituted of pastoralism and agro-pastoralism.

CRediT authorship contribution statement

TA, US, and GZ conceived the idea. HS and DS designed the study. HS collected the field data, and developed and ran the model. HS, TA, and US wrote the draft. WB, TA and DT edited the draft manuscript. And all authors edited the paper.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare no competing interest.

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