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Higher transpiration in plant invasive species impacts soil water

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ABSTRACT

Studies on plant invasives are largely focused on their impacts on plant community structure, native biodiversity, ecosystem services, and economy, but their ecosystem effects as high water-spenders are underestimated. Here, we report contrasting results in transpiration volumes in *Prosopis juliflora* (Sw.) DC (*Prosopis juliflora*), a widespread invasive alien, its native non-invasive congener, *Prosopis cineraria* (L.) Druce (*P. cineraria*), and an unrelated co-occurring native, *Azadirachta indica* A. Juss. (*Azadirachta indica*) at 3 sites spread across North and South between 200 and 550 m elevations in India. Our results demonstrate that *P. juliflora* shows higher transpiration than the native *P. cineraria* and *A. indica* at all the three investigated sites. The transpiration volumes of *P. juliflora* were 2.9–8 times higher than *P. cineraria* and *A. indica* at Jodhpur, and 6–11 times higher than *A. indica* at New Delhi and Hyderabad, respectively. The soil moisture content in the rhizosphere of *P. juliflora* dominated sites was 2–5 times lower than that of *P. cineraria* and *A. indica* dominated sites during summer. The results clearly demonstrate that invasive species transpire more water than the natives that consequently leads to decrease in soil moisture availability. Our investigations provide a strong rationale for managing the alien invasive *P. juliflora* and restoring native vegetation. Controlling the invasive species is particularly important for the regions with prolonged hot summers and freshwater shortages, such as tropical Asia, Middle East and tropical Africa, where *P. juliflora* has invaded vast areas.

1. Introduction

Non-native invasive plant species have characteristics such as superior resource acquisition traits, higher photosynthetic rates and efficiency, higher nitrogen-use efficiency, higher leaf nitrogen content, greater phenotypic plasticity, functional trait differences, greater water-use efficiency, etc. (Pyšek and Richardson, 2008; Funk et al., 2016). These characteristics make non-native species competitively superior and with better adaptability over native species cause widespread negative impacts on ecosystem structure, function, resilience, services and ecological balance (Simberloff, 2013). Studying impacts of non-native in comparison to native species is, therefore, essential for informed decision-making regarding the management of invasive species. Recent reports have shown that invasive alien species cost USD 423 billion annually to the world economy, threatening nature, economies, food security and human health (Roy et al., 2023). These staggering figures may well echo only a fraction of actual economic losses due to biological invasions. Ecological literature on plant invasives, so far, is largely focused on invasives' effects on plant community structure, native biodiversity, ecosystem services, economy and human health, but their effects on ecosystems as high water-spenders remain less understood (McNeely, 2001; Charles and Dukes, 2008; Cavaleri and Sack, 2010; Powell et al., 2011; Bernard-Verdier and Hulme, 2015; Vilà and Hulme, 2017; Mazza and Tricarico, 2018; Zenni et al., 2021; Roy et al., 2023). Isotopic studies have shown that transpiration constitutes the largest water flux globally, comprising 80–90 % of evapotranspiration on the Earth (Jasechko et al., 2013). Understanding this relationship between transpiration and water flux is crucial, in particular for arid and semi-arid environments, where water is a scarce resource (Ivanov et al., 2008). Sap flow rate studies, as surrogate indicators of transpiration, have reported higher water use by invasive plants with landscape level impacts on watershed hydrology (Cavaleri and Sack, 2010; Kumar et al., 2022). Some studies indicate that invasive plants are less water-use efficient than non-invasives (Matzek, 2011), while others have shown the opposite trend (Valliere, 2019). We believe that the majority of these studies are based on estimates that may not truly reflect actual water loss from the leaf surface or canopy. Despite its importance, transpiration related water loss by invasives across geographies and plant phylogenies

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is not well-represented in ecological literature.

Notwithstanding the reported differences in water-use between invasive and non-invasive plant species (Cavaleri and Sack, 2010; Kumar et al., 2022), direct measurement of water loss via transpiration in invasive species is lacking. Here, we address this knowledge gap by specifically examining the following: (i) Do invasive species transpire more water than the native species? (ii) Does infestation of invasive species lead to drier soils (low soil moisture content) compared to ecosystems harbouring native species? (iii) Do the transpiration rates of the invasive and native species vary across seasons? We found that a globally widespread non-native invasive species, *Prosopis juliflora* (Sw.) DC (*Prosopis juliflora*) transpires more water than its native congener, *Prosopis cineraria* (L.) Druce (*P. cineraria*) and a phylogenetically unrelated but co-occurring species, *Azadirachta indica* A. Juss. (*Azadirachta indica*). We also observed that higher transpiration (2.9–11 times) by invasive species than the native species is positively correlated with drier soils. Moreover, transpiration in the invasive species was significantly higher during summer than in winter. These findings establish a positive association between temperature and transpiration and a negative correlation between transpiration and rhizosphere soil moisture in vegetation communities infested with invasive species. From these results, we infer that the on-going global warming will likely exacerbate the impacts of plant invasives due to higher transpiration. Global warming can potentially lead to higher transpiration rates and consequently drier soils. Low water availability in areas ridden with invasive species will seriously impact native ecosystems and their biodiversity. We conjecture that underestimating the significance of plant invasion-related water loss could be potentially perilous, for its consequences may overshadow the well-recognized impacts of plant invasion in ecological literature. The protocols and the empirical design used in the present study provide

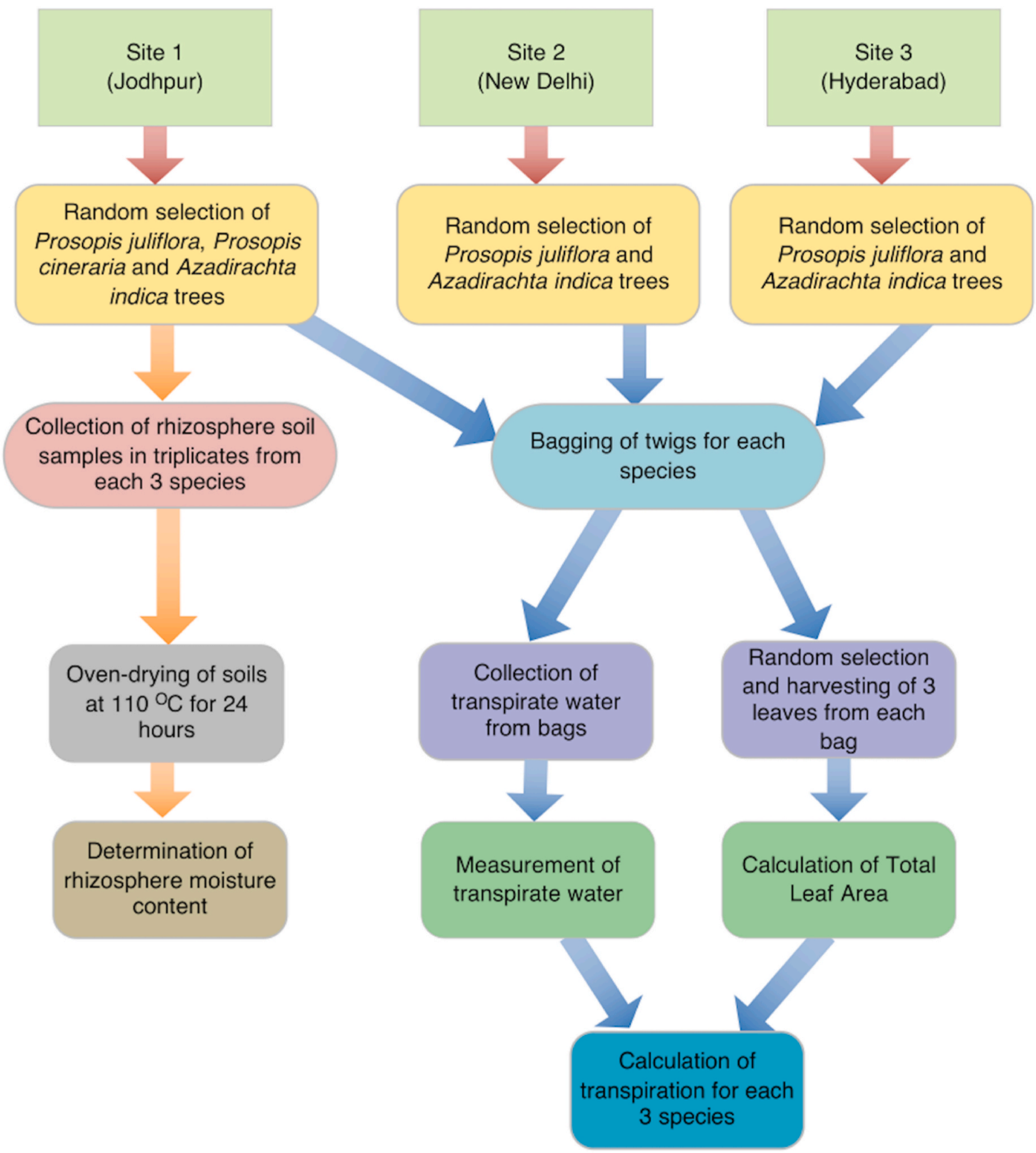

Fig. 1. Flowchart depicting the broad protocol of estimation of transpiration and rhizosphere moisture content of the 3 species (*Prosopis juliflora*, *P. cineraria* and *Azadirachta indica*) in the current study at 3 sites (Jodhpur, New Delhi and Hyderabad).

a simple, effective and novel way to directly estimate water loss as a result of transpiration in plant species and suggest ways how future studies can benefit from direct estimation of water losses instead of relying on indirect measures.

2. Materials and methods

2.1. Experimental sites

Studies were carried out at three sites in India. The three sites were selected to represent a gradient of arid to semi-arid environments, where ecological impacts of *P. juliflora* are pronounced, and water scarcity is a critical concern. Site 1 (Jodhpur; 26°14′42″N, 73°01′08″E) is located in the arid region of Western India. Investigations on leaf canopy transpiration and rhizosphere soil moisture content were carried out between 2017 and 2019 during the summer (May–June) and winter (December–January) seasons. Site 2 (New Delhi; 28°36′15″N, 77°10′14″E), is located in a semi-arid region in North India. Investigations on transpiration were carried out between 2018 and 2019 during the summer (May–June) and winter (December–January) seasons. Site 3 (Hyderabad; 17°27′03″N, 78°18′47″E) is located in a semi-arid region in South India. Investigations on transpiration were carried out over one year in 2020 during the summer (May–June) and winter (December–January) seasons (Fig. 1). All 3 sampling sites have witnessed cyclic fluctuations in climate (temperature and precipitation during the past 4 decades (Fig. S1). During 1981–2022, the annual average temperature of Jodhpur has varied between 25.3 and 27.84 °C, while that of Delhi has varied between 24.34 and 27.25 °C, and that of Hyderabad between 26.16 and 27.54 °C (Fig. S1a). Similarly, the annual precipitation between 1981 and 2022 has varied between 52.73 and 506.62 mm in Jodhpur, 295.31–1117.97 in Delhi and 358.59–1186.52 in Hyderabad (Fig. S1b). The soil types of the 3 sites (as per the World Reference Base for Soil Resources) range from Haplic Xerosols (Jodhpur) to Calcic Xerosols (New Delhi) and Chromic Luvisols (Hyderabad).

2.2. Species investigated

Experiments were carried out on alien invasive *P. juliflora*, its native congener, *P. cineraria* and a phylogenetically unrelated co-occurring non-invasive species, *A. indica* (Fig. 1). All the 3 species are common and dominant species across the arid and semi-arid regions of India. Investigations on transpiration and rhizosphere soil moisture were carried out in *P. juliflora*, *P. cineraria* and *A. indica* at Jodhpur site. Investigations on transpiration in *P. juliflora* and *A. indica* sites were carried out at New Delhi and Hyderabad. *P. juliflora* is a native of Central and South America and has invaded major parts of Africa, the Middle East, large parts of tropical Asia, Australia, America and Atlantic islands (Fig. S2a). The species is a widespread alien invasive throughout tropical areas of the Indian subcontinent. It has been reported to cause widespread disruption in ecosystem structure and function globally (Walter and Armstrong, 2014; Singh et al., 2021). In Africa, *P. juliflora* has been reported to reduce native biodiversity (Abdulahi et al., 2017), exhibit higher water-use, and decreased water-runoff and groundwater recharge (Shiferaw et al., 2023). In the Middle East, *P. juliflora* is reported to exert allelopathic effects and decrease native biodiversity, primarily invading areas with shallow water tables (El-Keblawy and Al-Rawai, 2007; El-Keblawy and Abdelfatah, 2014). The hydrological impacts of *P. juliflora* are more prevalent in the arid and semi-arid regions of the world where water is the limiting resource (Shiferaw et al., 2023). *P. juliflora* invasion in arid regions of USA and Mexico results in approximately 10 % losses in the annual water yield of the watersheds (Nie et al., 2012). Similar observations of depleting water table due to the *P. juliflora* invasion have been reported from South Africa (Dzikiti et al., 2017). Because of these reasons, we selected *P. juliflora* to test our hypotheses whether invasive species transpire more water than the natives and if it consequently leads to lower soil moisture availability.

P. juliflora was introduced in India between 1857 and 1878 by British to control desertification. The species has occupied vast spaces throughout the Indian subcontinent since its introduction in mid 19th century. *P. juliflora* is a small tree or shrub (3–5 m high) with wide ecological amplitude and can survive in exceptionally dry climates and diverse soil types (Walter, 2011). *P. juliflora* is also known to produce allelochemicals, uptake nutrients from the soil at higher rates than the natives and possess better reproductive strategies (Walter, 2011). *P. juliflora* is a polyploid across its invaded ranges (2n = 4x, 8x = 56, 112), while its native congener, *P. cineraria* is a diploid (2n = 28), and polyploids are known to outperform their diploid native congeners in growth performance resulting in their faster geographic spread across invaded habitats (Pandit et al., 2011; Kaushik et al., 2023).

P. cineraria is a tree of moderate height, native to the Indian subcontinent, and plays many important ecological and social roles including soil nitrogen fixation, soil erosion control and stabilization, water mobilization, and is used as nutritious fodder for livestock (Fig. S2b; Baibout et al., 2021).

A. indica is a medium to large evergreen tree with a wide environmental tolerance. The species grows well across desert, semi-arid, and sub-humid climates and plays diverse ecological roles, including checking soil erosion and desertification, and soil amelioration. (Siddiqui, 1995). *A. indica* was chosen as a control due to its naturalization, common distribution, ecological significance and widespread use in afforestation programs across India (Fig. S2c).

2.3. Estimation of transpiration volume

Transpiration in *P. juliflora*, *P. cineraria* and *A. indica* was measured using a conventional technique outlined in a previous study on *Pinus taeda* (Luvall and Murphy Jr, 1982). A summarised protocol for the experiments has been provided in Fig. 1. A live branch of each investigated species full of healthy leaves was enclosed in a transparent, dry plastic bag, and tied after closing using a cotton thread. The technique is hereafter referred to as 'bagging'. Each bag enclosed a branch with sufficient number of leaves so that a measurable volume of transpirate could be collected at the termination of the experiment. The number of leaves per bag was not predetermined but selected randomly. However, it was ensured that only twigs with many healthy, undamaged leaves (free from cuts or discolouration) were included in the experiment. Before bagging, surface moisture, if any, on the leaves was removed by vigorous shaking of the branch. Bagging began between 6 and 7 a.m. on clear sunny days and the transpirate was collected around 6–7 PM comprising a 12-h day period. The sampling size ranged between 10 and 20 trees. At the end of each experiment, bags were removed, and their sides were gently tapped so that the transpirate sticking to the sides was collected at the bottom of each bag. The volume of water collected in each bag was measured with the help of a graduated 20 ml syringe. As compared to the isotope tracer and sap flow sensor methods, the bagging method followed in this study for estimating transpiration has certain advantages, such as it being a non-destructive, cost-effective and on-field technique. However, we are conscious of some limitations of the bagging method which include poor effectiveness in estimating transpiration rates of small sized plant species or the species with low transpiration rates (Kulmatiski and Forero, 2021).

After collection of the transpirate, respective branches were harvested and brought to the lab for calculation of total leaf area (TLA). TLA for each branch was determined by measuring individual leaf areas using a previously described conventional graph paper method (Pandey and Singh, 2011). TLA (cm^2) was calculated as x/y, where x is the weight (g) of the portion of graph paper covered by the leaf outline, and y is the weight (g) of one cm^2 area of the graph paper. Three such leaf measurements within each bag were used to calculate the average leaf area. The average leaf area was then multiplied by the total number of leaves to obtain the TLA of that branch which yielded the respective transpirate. The precision of measuring leaf area using this method compared to costly leaf area meters has shown that the estimates obtained by the two methods are significantly and linearly related (Pandey and Singh, 2011). We double-checked our TLA measurements using a combination of photography and Adobe Photoshop software. There was negligible or little difference in the results of leaf area measurements of the two methods. The leaf transpiration for each investigated species was finally collated and expressed in terms of L m^{-2} d^{-1}.

To avoid confounding results due to likely higher temperatures inside the closed polythene bags compared to open air, we placed thermometers inside these bags; another thermometer was tied to a branch of the same tree and left hanging in the open air and used as a control. We did not find any significant difference between the ambient air temperature and that inside the bags in all the three investigated species. Therefore, the effect of temperature as a result of bagging was discounted.

2.4. Estimation of soil moisture content

In order to estimate whether invasive species had drier soils as a result of higher transpiration than the native species, we analyzed the soil moisture content in the rhizosphere of all three species. Rhizosphere soil samples in triplicate of 50 g each of *P. juliflora*, *P. cineraria* and *A. indica* were collected from the same individual trees as in experiment 1 at the Jodhpur site (Fig. 1). All the samples were brought to the lab and oven-dried at 110 °C for 24 h and weighed again after oven-drying. The difference between the initial weight (50 g) and the final weight after drying was taken as the moisture content of various soil samples of the respective species and expressed as a percentage. Triplicate sampling was employed to minimize variability and ensure reliable estimates of soil moisture content.

2.5. Statistical analysis

All datasets were checked for normality using the D'Agostino & Pearson and Shapiro-Wilk normality test. All our datasets (except the transpiration datasets from the Hyderabad site) passed the normality test and hypothesis testing was performed using parametric tests such as one-way ANOVA and *t*-Test. Non-parametric Mann-Whitney test was used to test the significance of null and alternate hypotheses for datasets from the Hyderabad site. We also analyzed if the transpiration levels were specific to each of the 3 species (*P. juliflora*, *P. cineraria* and *A. indica*) during summer and winter seasons. For this purpose, we pooled the transpiration value datasets of the 3 species across the sites for the two seasons and performed Detrended Correspondence Analysis (DCA). We used GraphPad Prism 10 software (GraphPad Inc., San Diego, CA) for performing normality tests, parametric and non-parametric tests, and PAST 4.02 software (Hammer et al., 2001) for performing DCA.

3. Results

Our results are demonstrated by two simple experiments in which we measured: (i) leaf canopy transpiration which corresponds to actual water loss, and (ii) soil moisture content (%) of rhizosphere soils of invasive alien and native plant species. In the first experiment, we observed that transpiration by the invasive alien, *P. juliflora* at site 1 (Jodhpur) was significantly higher, both in the summer and winter seasons (0.178 ± 0.004 L m^{-2} d^{-1} and 0.094 ± 0.005 L m^{-2} d^{-1}) compared to native non-invasives, *P. cineraria* (0.061 ± 0.002 L $m^{-2}d^{-1}$ and 0.037 ± 0.002 L m^{-2} d^{-1}) and *A. indica* (0.022 ± 0.003 L $m^{-2}d^{-1}$ and 0.013 ± 0.001 L $m^{-2}d^{-1}$), respectively (Table 1; Fig. 2a). The transpiration in *P. juliflora* at site 1 during summer corresponds to 3- and 8-times higher than that of natives *P. cineraria* and *A. indica*, respectively, and 2.5- and 7-times higher than *P. cineraria* and *A. indica* in winter, respectively. The transpiration in *P. juliflora* and *A. indica* at site 2 (New Delhi) was 0.260 ± 0.027 L $m^{-2}d^{-1}$ and 0.041 ± 0.005 L $m^{-2}d^{-1}$, respectively which corresponds to 6-times higher transpiration in the invasive alien species compared to the non-invasive *A. indica,* in summer (Table 1; Fig. 2b). Likewise, the transpiration in *P. juliflora* and *A. indica* at site 3 (Hyderabad) was 0.261 ± 0.014 L $m^{-2}d^{-1}$ and 0.023 ± 0.003 L $m^{-2}d^{-1}$, respectively which corresponds to 11-times higher transpiration in the invasive *P. juliflora* compared to non-invasive *A. indica,* during summer (Table 1; Fig. 2c).

Table 1
Descriptive statistics of transpiration and rhizosphere soil moisture content for the 3 investigated species (*Prosopis juliflora*, *P. cineraria* and *Azadirachta indica*) across the 3 sites (Jodhpur, Delhi and Hyderabad) during summer and winter seasons.

Transpiration (L m^{-2} d^{-1})	*Prosopis juliflora*		*Prosopis cineraria*		*Azadirachta indica*	
	Summer	Winter	Summer	Winter	Summer	Winter
Minimum	0.141	0.015	0.047	0.018	0.005	0.009
Maximum	0.449	0.345	0.082	0.050	0.068	0.047
Sum	13.974	7.934	1.216	0.741	0.850	0.471
Mean	0.233	0.132	0.061	0.037	0.028	0.016
Standard error	0.010	0.008	0.002	0.002	0.003	0.001
Variance	0.006	0.004	0.000	0.000	0.000	0.000
Standard deviation	0.076	0.062	0.010	0.009	0.016	0.008
Median	0.202	0.119	0.058	0.037	0.027	0.014
25 percentile	0.174	0.089	0.055	0.031	0.016	0.010
75 percentile	0.278	0.172	0.069	0.044	0.037	0.017
Skewness	0.998	1.129	0.747	−0.341	0.758	2.381
Kurtosis	0.181	1.955	−0.185	−0.061	0.050	7.397
Geometric mean	0.222	0.118	0.060	0.036	0.024	0.014
Coefficient of variation	32.542	46.738	16.048	23.028	55.692	50.632

Rhizosphere soil moisture content (%)	*Prosopis juliflora*		*Prosopis cineraria*		*Azadirachta indica*	
	Summer	Winter	Summer	Winter	Summer	Winter
Minimum	0.480	0.170	1.090	0.830	2.600	0.260
Maximum	1.110	3.450	2.260	3.630	5.920	3.360
Sum	16.200	33.330	32.620	37.580	75.482	45.840
Mean	0.810	1.667	1.631	1.879	3.774	2.292
Standard error	0.037	0.220	0.069	0.179	0.206	0.157
Variance	0.027	0.965	0.094	0.644	0.852	0.492
Standard deviation	0.166	0.982	0.307	0.803	0.923	0.701
Median	0.815	1.315	1.615	1.770	3.516	2.150
25 percentile	0.723	0.905	1.478	1.250	3.123	1.988
75 percentile	0.923	2.648	1.738	2.318	4.060	2.840
Skewness	−0.307	0.502	0.495	0.945	1.161	−0.928
Kurtosis	−0.206	−0.958	0.463	0.421	0.802	2.563
Geometric mean	0.792	1.355	1.604	1.731	3.679	2.102
Coefficient of variation	20.467	58.953	18.795	42.712	24.452	30.596

Though transpiration in absolute terms was lower across the species during winter, the trend of higher transpiration in invasive *P. juliflora* compared to the native, non-invasive species remained unchanged ($P < 0.0001$; Fig. 2a–c). The results of DCA ordination analysis revealed that all the 3 species showed marked differences in the transpiration during summer and winter seasons after the datasets were pooled across all the sites (Fig. 3). All the 3 species showed clear separation in the DCA plot with respect to the transpiration during summer and winter seasons (Fig. 3).

In the second experiment carried out at site 1, we observed that the rhizosphere soil moisture contents of *P. juliflora* during the summer and winter seasons were 0.81 ± 0.037 % and 1.667 ± 0.219 %, respectively (Table 1; Fig. 2d). Contrastingly, the soil moisture contents of native *P. cineraria* and *A. indica* during the two seasons were 1.631 ± 0.068 %,

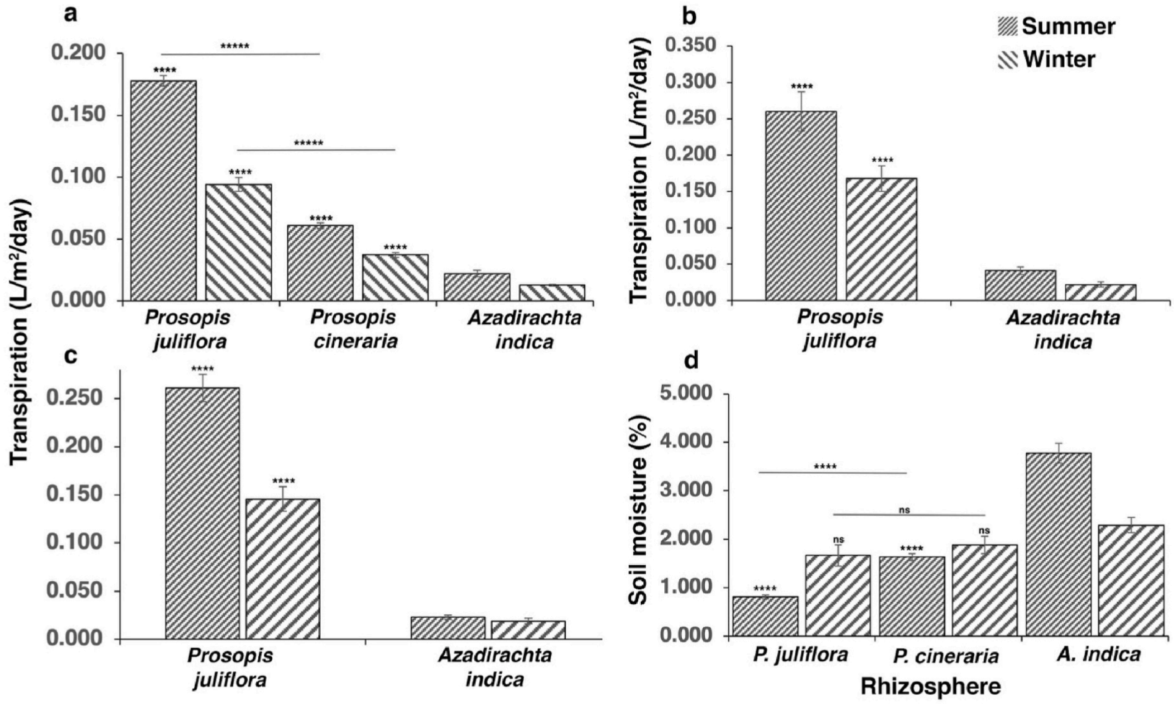

Fig. 2. Comparative transpiration in alien invasive *Prosopis juliflora* and native, non-invasive tree species *P. cineraria* and *Azadirachta indica*. (**a**) Transpiration related water-loss in invasive *P. juliflora* and the two non-invasives, *P. cineraria* and *A. indica* during summer and winter seasons at site 1 (Jodhpur). *P. juliflora* exhibited significantly higher transpiration during summer (2.9- and 8-times) and winter (2.5- and 7-times) compared to the two non-invasives, *P. cineraria* and *A. indica*, respectively. (**b**) Transpiration by alien invasive *P. juliflora* and the native species, *A. indica* during summer and winter seasons at site 2 (New Delhi). The invasive *P. juliflora,* showed significantly higher transpiration compared to the non-invasive *A. indica* during summer (6 times) and winter (7.7 times). (**c**) Transpiration by invasive *P. juliflora* and the non-invasive species, *A. indica* during summer (11 times) and winter (7.6 times seasons at site 3 (Hyderabad). Test of significance was carried out using one-way ANOVA followed by Tukey's multiple comparison test (site 1) and *t*-Test (site 2), while Mann-Whitney test was used for the site 3. ****$P < 0.0001$. **(d)** Rhizosphere soil moisture content (%) of the alien invasive *P. juliflora* and the two native, non-invasive species, *P. cineraria* and *A. indica* during summer and winter. The alien invasive, *P. juliflora*, had lower rhizosphere soil moisture content (0.811 ± 0.037 %) in the rhizosphere soil as compared to the two non-invasive species, *P. cineraria* and *A. indica* during summer, which is consistent with the higher transpiration by the invasive species, as reported in experiment 1. However, due to lower transpiration in the winter months, the differences between invasive and non-invasive native species were not significant. Test of significance was carried out using One-Way ANOVA followed by Tukey's multiple comparison test, ****$P < 0.0001$, ns (non-significant). All p-values indicated on the individual graphs are relative to the positive control, *A. indica*. The p-values displayed over dashed lines represent differences specific to groups.

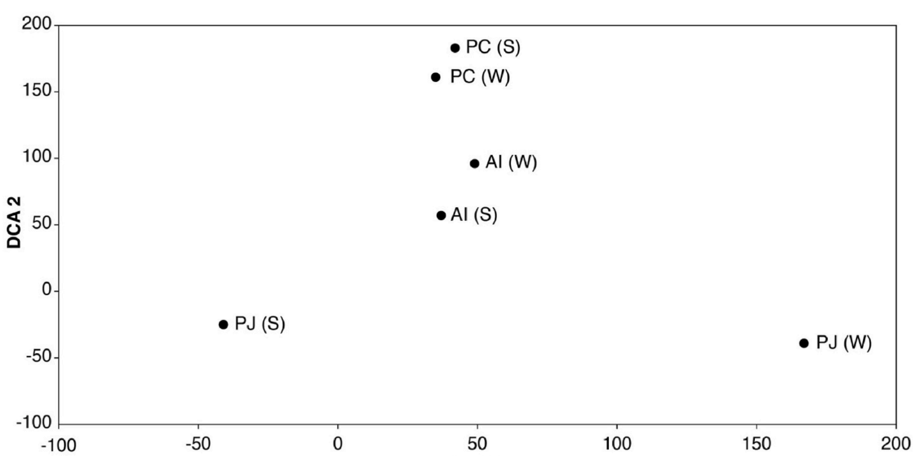

Fig. 3. Results of Detrended Correspondence Analysis (DCA) based on transpiration data for the 3 investigated species (*Prosopis juliflora*, *P. cineraria* and *Azadirachta indica*) across all the sites for the summer and winter seasons. The figure illustrates the clear separation of the 3 species from each other with respect to their transpiration values and indicates that all the 3 species transpires differently in the summer and winter seasons. The notations in the figure represents the following: PJ (S) – Transpiration of *P. juliflora* in the summer season; PJ (W) – Transpiration of *P. juliflora* in the winter season; PC (S) – Transpiration of *Prosopis cineraria* in the summer season; PC (W) – Transpiration of *P. juliflora* in the summer season; AI (S) – Transpiration of *A. indica* in the summer season; AI (W) – Transpiration of *A. indica* in the winter season.

1.88 ± 0.179 %, and 3.774 ± 0.206 % and 2.293 ± 0.156 %, respectively (Table 1; Fig. 2d). The rhizosphere soil moisture content of the natives, *P. cineraria* and *A. indica* were 2 and ~5 times higher than that of the invasive, *P. juliflora* during summer and these differences were statistically highly significant ($P < 0.0001$; Fig. 2d). The higher rhizosphere soil moisture contents of the two native species compared to alien *P. juliflora* suggest that the invasive species pumped more water from soil into the leaves for transpiration during summer when temperatures were higher. The extent of soil moisture or relative dryness of soils was taken as a surrogate indicator for water availability in the respective soils. Drier rhizosphere soil indicates higher water-use by invasive plant species during summer.

4. Discussion

Our study reveals a clear positive relationship between invasive species and higher transpiration-related water loss, in particular, under warmer conditions of summer. This suggests that the ecological impacts of invasive species may be more severe under the influence of global warming. *P. juliflora*, a widespread global invasive of tropics, is well distributed across arid and semi-arid regions of the Indian subcontinent. The invasive species recorded significantly higher transpiration than non-invasive natives, *P. cineraria* and *A. indica*, during summer and winter seasons. Rhizosphere soil moisture of *P. juliflora* was significantly lower than *P. cineraria* and *A. indica* during summer indicating a positive correlation between higher temperature and higher transpiration on one hand and higher transpiration and drier soils on the other.

Soil moisture depletion significantly impacts local plant communities, influencing plant species composition, growth and ecosystem sustainability (Deng et al., 2016). In arid and semi-arid regions deep soil moisture is crucial for vegetation restoration (Li et al., 2021). Dry soils are known to impact native plant community structure mediated by changes in the soil rhizosphere microbiome (Schimel, 2018; Kaushik et al., 2021; Ettinger and LaForgia, 2024). Water stress and soil microbiota dynamics are understood to determine the growth responses of plant species (O'Brien et al., 2018). Soil moisture is also known to be crucial for the survival and maintenance of indigenous microbial species, which in turn are central to pathogen resistance in native species through the production of antibiotics (Bhattacharyya et al., 2021), and their better fitness. Thus, soil moisture content plays the most important role in shaping native biodiversity through the soil microbiome, and in turn, native plants help conserve sub-surface water by expending significantly less water than invasives (Fig. 2a–c).

Our experimental results suggest that the ability of *P. juliflora* to extract more sub-soil water to its advantage leads to the loss of native biodiversity as indicated by lower species richness in its invaded habitats (Kaur et al., 2012). *P. juliflora* possesses various physiological traits such as a deep taproot system, evergreen leaf habit, and genetic traits such as polyploidy that allow it to withdraw water at much higher rates than the native species (Shiferaw et al., 2021). The high transpiration rates of *P. juliflora* can also be attributed to the different leaf physiological traits such as high stomatal conductance, high gas exchange rates and effective water management in response to varying vapor pressure deficit (VPD) (Shirke and Pathre, 2004; Elfadl and Luukkanen, 2006). As such, alien invasive polyploid species have higher and faster reproductive rates resulting in range expansion and ground cover rapidly (Carleton, 2017; Kaushik et al., 2023). As a result, invasive species' impact on groundwater could be much greater than is perhaps being realized at present. Our results of significantly higher transpiration rates in the non-native invasive species (*P. juliflora*) than the native species (*P. cineraria* and *A. indica*) suggest that invasives have competitive edge over natives in water utilization. Previous studies have shown that an alien invasive of Mediterranean sand dunes, *Acacia longifolia*, had detrimental effects on the ecosystem with native *Pinus pinaster* via reduced water flow to the native pine community (Rascher et al., 2011). In areas with limited water resources, such as the Datça Peninsula and the arid regions of the southwestern United States, *Tamarix* has been reported to switch between exploiting groundwater and vadose-zone water. This strategy allows the invasive *Tamarix* to survive and continue consuming water even during droughts, further stressing groundwater resources (Nippert et al., 2010). The watershed-scale estimates in South Africa show that the catchment areas cleared of invasive species recorded 15.1–29.5 % recovery in the surface water flow (Rebelo et al., 2022). Thus, invasive species often outcompete native species in the uptake of water and other resources, which can lead to a decline in native biodiversity. Such competition is particularly pronounced in ecosystems where water is a limiting factor, such as semiarid regions (Barros et al., 2020).

Significantly higher transpiration of *P. juliflora* resulting in drier soils during summer, demonstrated in the two experiments here, shows that invasive plants could negatively impact sub-surface water levels. Invasive species also demonstrate high water use efficiency than the native species especially in hot climates because of high sap flow rates per unit ground area (Cavaleri and Sack, 2010). Fluctuating diurnal water table in a comparable arid region of south-eastern Arizona, USA has been correlated with higher evapotranspiration rates in *P. juliflora* infested watersheds (Tromble, 1977). Combined with poor monsoon precipitation, higher transpiration in invasive plants such as *P. juliflora* with high abundance could negatively impact water bodies resulting in likely drying up of lakes and irrigation wells (Sakthivadivel, 2016). An observational study from India reported that *P. juliflora* was linked to the drying of lakes and irrigation wells and that the lands infested by the species may be associated with sharp annual fall in irrigation tube wells ranging from 40 to 90 feet with some wells having completely dried up (Sakthivadivel, 2016). The correlation between higher transpiration in invasive *P. juliflora* and its serious impacts on water bodies could have detrimental consequences for agricultural sustainability. A sap-flow rate study investigating water-use by invasive *P. juliflora* in the Afar Region of Ethiopia concluded that the catchment scale water loss due to transpiration by the invasive would be sufficient to irrigate about 460,000 ha of cotton or 330,000 ha of sugarcane fields (Shiferaw et al., 2021). Our study lends empirical support to these previous observations. The effects such as drying of wells and the attendant agriculture losses may eclipse the well-known invasion-driven impacts.

More importantly, climate change induced water shortages for irrigation have been associated with farmer suicides in India (Carleton, 2017). Considering that *P. juliflora* has infested large swathes of land in India, and from Africa to Asia (Fig. S2a), it is reasonable to project that a rapidly spreading invasive could be seriously detrimental to local hydrology and biodiversity with landscape level consequences in tropical regions globally. Our results assume greater significance in view of the positive correlation between summer temperature and higher transpiration. These findings indicate that plant invasives could turn out to be the leading drivers of global change with potential to impact surface and underground water availability and trigger a water crisis under the impact of impending warming. Going ahead, it is reasonable to suggest that the regional and global water woes may worsen due to the prodigious spread of plant invasives and progressive warming. This important facet of invasive species needs more attention of ecological researchers. Our results also lend support to the finding that the areas infested with *P. juliflora* need to be cleared of the invasive species and restored with planting native species such as *P. cineraria* and *A. indica* to reverse water losses, prevent land degradation and loss of ecosystem services. Management strategies, such as targeted removal, afforestation with native drought-resistant species, and sustainable land-use planning, should consider the hydrological impacts of invasive species. Controlling the spread of invasive species leads to enhanced regional hydrological supply and improved ecosystem services and human well-being (Pejchar and Mooney, 2009).

An important outcome of the study is to direct the attention of ecological researchers to a lesser-known impact of invasive species. That said, we acknowledge various limitations of the present study, including that of scale and exclusion of other soil physico-chemical properties except soil moisture. Future studies could focus on investigating these aspects while considering the transpiration and soil moisture content reported in this pilot study as a baseline. In light of our study, more detailed investigations may evaluate relative impact of other climate, physiological, genetic and physico-chemical variables on the transpiration levels in native and non-native species (for example, under controlled greenhouse conditions).

5. Conclusions

Notwithstanding the limitations, our study indicates a clear positive relationship between invasive species and significantly higher transpiration-related water losses which are amplified by higher temperatures. Based on these results, we anticipate that the spread of invasive alien species such as *P. juliflora* and ensuing high transpiration-related water losses under the influence of climate change may turn out more crucial for ecological research than is presently recognized. Future studies can focus on the potential association of the global spread of *P. juliflora* and its ensuing social consequences causing exacerbated water shortages and on-going climate change. Arid regions of Africa and the Middle East where *P. juliflora* covers vast areas of land may need to redouble their efforts to manage the rapid spread of *P. juliflora*. We surmise that combined with increasing temperatures globally, rapid geographic spread of invasive species, such as *P. juliflora*, may represent a double whammy that deserves more serious attention.

CRediT authorship contribution statement

Rishabh Kaushik: Methodology, Investigation, Formal analysis. **Maharaj K. Pandit:** Writing – original draft, Validation, Supervision, Resources, Conceptualization. **Kumar Manish:** Writing – review & editing, Formal analysis.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.indic.2025.100665.

Data availability

Data will be made available on request.

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