



Water regime and gas exchange dynamics in Tunisia's native *Pinus halepensis* forests

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Abstract: This study aimed to assess the seasonal impacts on crop water requirements and actual evapotranspiration within Aleppo pine forests under two Tunisian bioclimates. Also, the research sought to examine the influence of environmental conditions on water balance and gas exchange. The results revealed an estimated annual potential evapotranspiration for Aleppo pine of approximately 714 mm at Djebel Sarj (DS) and 561 mm at Djebel Zaghouan (DZ). A distinct seasonal transition was observed, indicating a shift in water uptake by Aleppo pine during the summer and early autumn. The model predicted the possibility of zero water uptakes when the root soil layers approach desiccation, indicating extreme forest water stress after the rainy season and very low physiological activity during the summer and autumn. Moreover, the deeper water depletion by Aleppo pine in DS compared to DZ was found to be highly dependent on the soil type. Djebel Sarj's soil exhibited higher water holding capacity (50 mm/m) compared to Djebel Zaghouan (40 mm/m). Water balance and availability were identified as major factors influencing growth, with a recorded significant difference between populations ($p < 0.05$). Aleppo pine in Djebel Zaghouan exhibited better growth than those in DS. Stomatal conductance in Djebel Zaghouan was lower than in Djebel Sarj DS, with water deficit in Djebel Zaghouan DZ leading to stomatal closure, thereby reducing transpiration and inhibiting photosynthesis. In conclusion, our study underscores the critical impact of changing environmental conditions such as drought on Aleppo pine forests, shedding light on the complex interplay between water availability, soil characteristics, and forest growth.

1. Introduction

As we address the complexities of climate change impacts on Aleppo pine (*Pinus halepensis*) and related pine species, it is essential to consider the broader ecological implications. Recent studies highlight the interconnectedness of tree responses to climatic stressors, emphasizing the role of ecological dynamics in shaping adaptation strategies (Smith *et al.*, 2019; Williams *et al.*, 2020). Furthermore, the increasing prevalence of extreme weather events in the Mediterranean region introduces new challenges for forest ecosystems (Seidl *et al.*, 2017), requiring a nuanced understanding

of how these events interact with the physiological mechanisms of drought-tolerant species such as *Pinus halepensis*.

In view of these climate changes, it is becoming essential to understand the complex relationships between trees and climate, in particular the interactions between climate, growth and tree physiology. Numerous studies (e.g. [Birami et al., 2020](#); [Manrique-Alba et al., 2020](#); [De Cáceres et al., 2021](#)) underline the centrality of these aspects in the context of water management in forests and trees. Among pine species, Aleppo pine (*Pinus halepensis* Mill.) stands out as one of the most drought-tolerant, a crucial attribute given its distribution in various drought-prone Mediterranean countries, including large areas in Tunisia ([Alexou, 2013](#)).

Indeed, the native range of *Pinus halepensis* spans across the Mediterranean region, covering countries such as Spain, Italy, Greece, Turkey, Lebanon, and Tunisia ([Barbero et al., 1998](#)). In Tunisia specifically, Aleppo pine forests are integral components of the landscape, playing a vital role in biodiversity conservation and providing essential ecosystem services. However, these natural pine ecosystems face ongoing challenges due to various anthropogenic and environmental factors. Human activities, such as urbanization and agriculture expansion, contribute to habitat fragmentation, disrupting the continuity of Aleppo pine forests ([Ganatsas, 2018](#)). Additionally, the changing climate further compounds these challenges, affecting the suitable habitats for Aleppo pine and altering the composition of plant communities within these forests ([Ruiz-Labourdette et al., 2013](#)).

Indeed, pine forests are under the dual pressure of global climate change and deforestation, which could rapidly alter local climatic conditions ([Menzel et al., 2006](#)). The scientific community has long been interested in how forests adapt to stressors, recognizing the central role of plant adaptations in shaping ecosystem functionality ([Wright et al., 2004](#)).

Scopus provides more than 2200 articles on "Aleppo pine" OR "*Pinus halepensis*" from 1907 to 2024; and > 2030 articles from 1995 to 2024 where the evolution of articles towards the time is shown in [Figure 1](#). The pic (122 articles) is observed in 2021 to fall down in 2024 (86 articles). The majority of papers (70.8%) concerned the agriculture (40.0%), the environmental science (24.8%), the earth & planet (6.0%) ([Figure 2](#)).

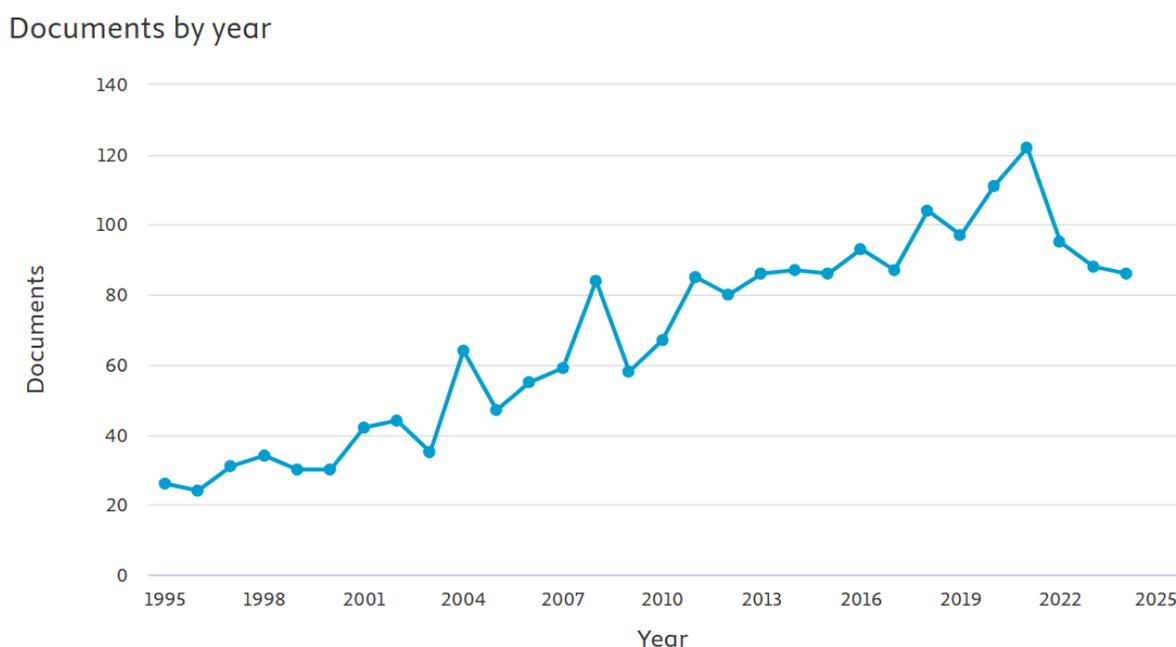


Figure 1. variation of articles from 1995 to 2024 (Scopus data May, 31th, 2025)

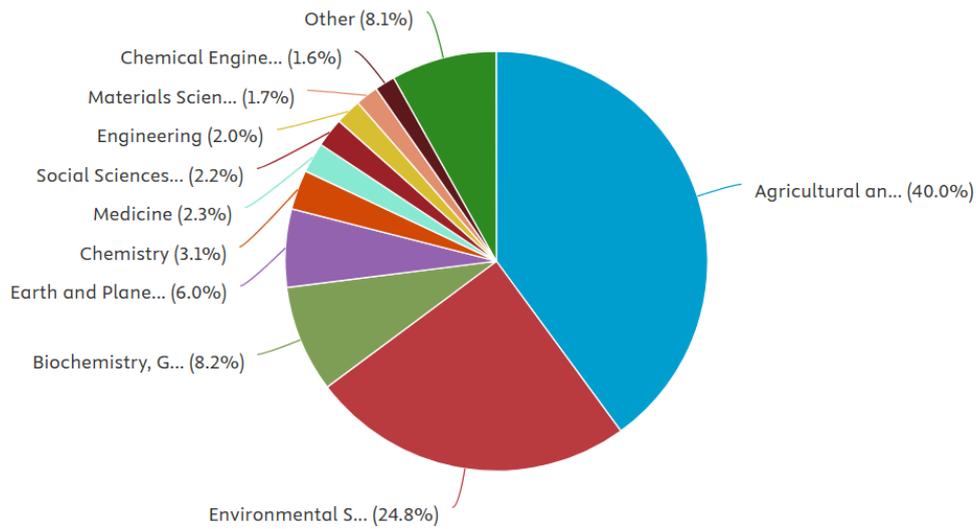


Figure 2. Percentages of articles by subject area from 1995 to 2024 (Scopus data May, 31th, 2025)

Data show that the Spanish Camarero is the most profiler author (44 papers), followed by the French Fernandez (42 papers), Moya (Spain) in the third position and the others in **Figure 3**. The authors can be visualized by VOS viewer mapping as indicated in **Figure 4**, by colored nodes. The size of each node related to a given author is function of the number of publications (Orduña-Malea & Costas, 2021; Ech-chihbi *et al.*, 2022; Laita *et al.*, 2024; Kachbou *et al.*, 2025). The top author, Camarero, shown by light mustard node, Fernandez (dark green), Moya (medium green), Yakir with light green. The nodes are connected by lines to show the cooperation between researchers and countries (Chuang & Chen, 2022; Salim *et al.*, 2022; Baquero *et al.*, 2025). Spain, France, Grece, Italy etc are the most countries concerned by *Pinus halepensis*. Spain is the top published one, with more than 870 articles possesses the largest node in light green (**Figure 5**).

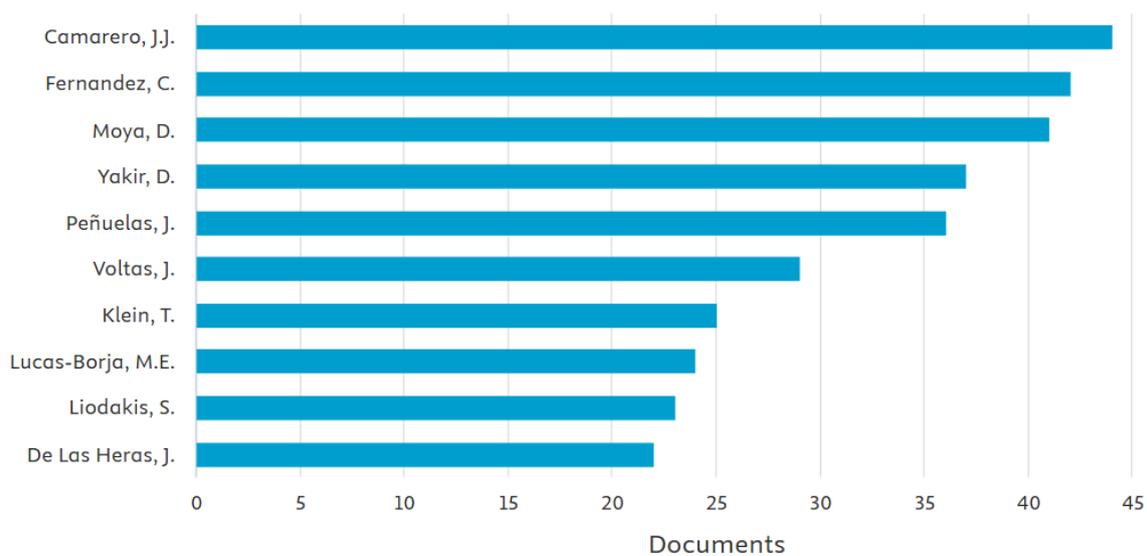


Figure 3. Top Ten ranked authors from 1995 to 2024 (Scopus data May, 31th, 2025)

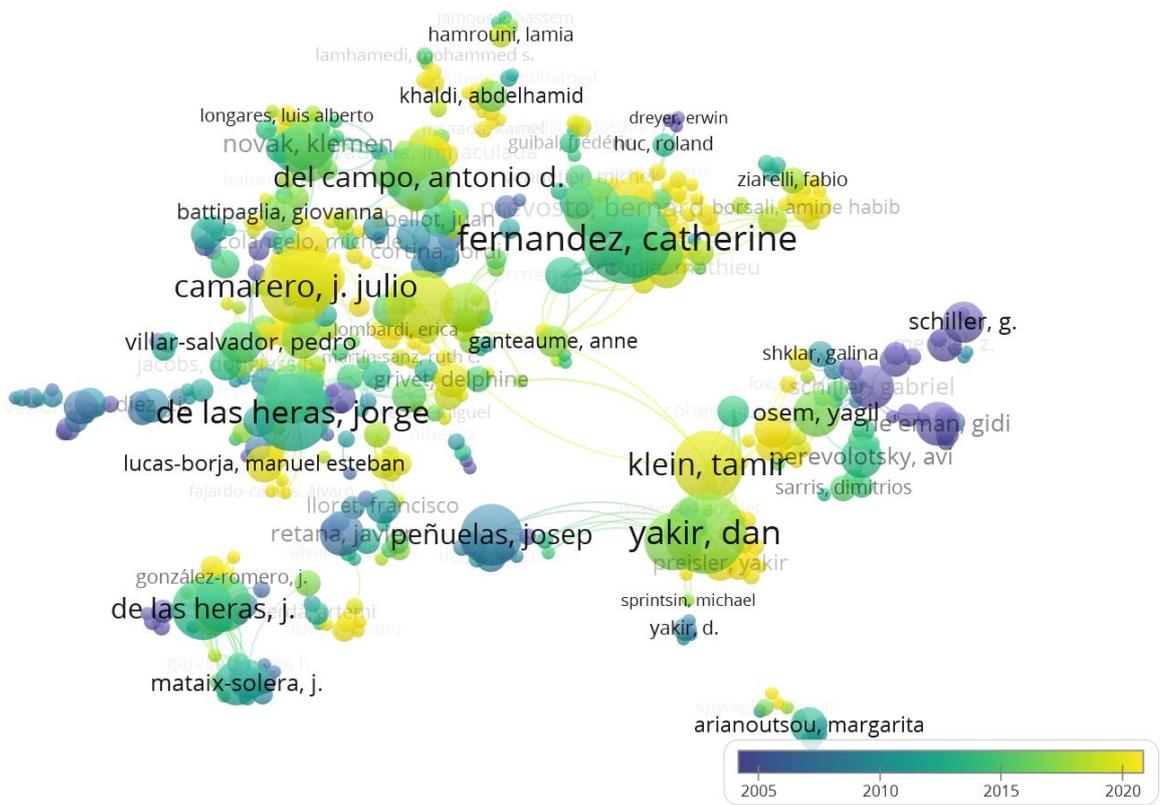


Figure 4. Overlay network of the most productive authors (≥ 3 articles) from 1995 to 2024

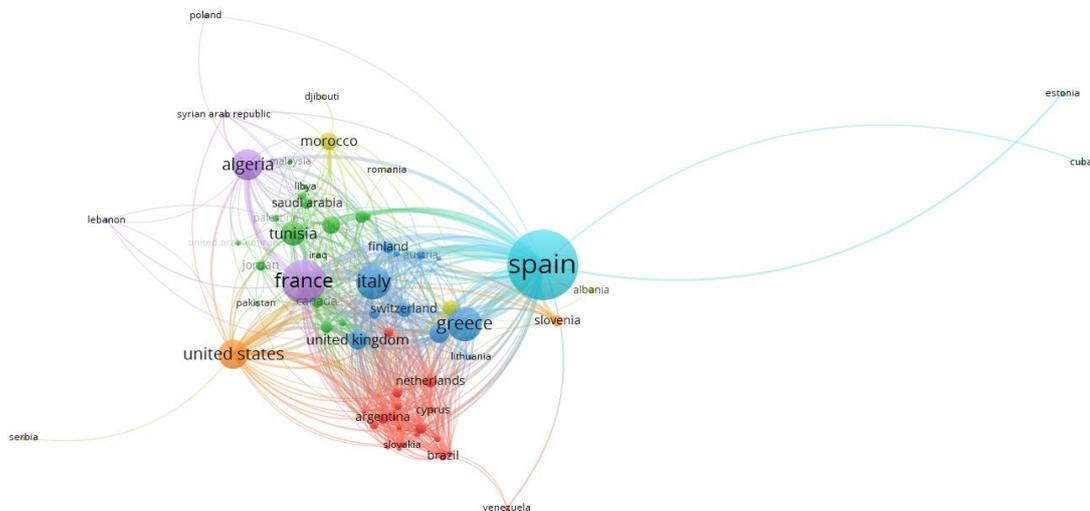


Figure 5. Most productive countries (≥ 2 articles) from 1995 to 2024

Climate change and increasing drought frequency pose significant threats to Mediterranean forest ecosystems, yet the seasonal dynamics of water use and physiological responses in these ecosystems remain poorly understood. This study addresses the critical gap in knowledge concerning how seasonal environmental variability affects crop water requirements and actual evapotranspiration in *Pinus halepensis* (Aleppo pine) forests under two contrasting Tunisian bioclimates. Specifically, we examined the influence of environmental conditions on forest water balance and gas exchange processes.

2. Methodology

2.1 Study site

The study was conducted in two natural forest areas in Tunisia: Djebel Zaghouan (Northeast) and Djebel El Sarj (Northwest), selected for their contrasting bioclimatic conditions. Both sites belong to the national forest network managed by the Tunisian General Directorate of Forests. Djebel Zaghouan is located within the superior sub-humid bioclimatic zone, characterized by mild, temperate winters. It experiences an average annual temperature of 17.6 °C and a mean annual precipitation of 483 mm. In contrast, Djebel El Sarj lies in the superior semi-arid zone, with cooler winters and slightly lower rainfall, recording an average annual temperature of 15.8 °C and 459 mm of precipitation. These climatic parameters were obtained from the Tunisian National Institute of Meteorology, based on long-term averages (1990–2020) from the nearest weather stations (Zaghouan and Siliana, respectively). Fieldwork was conducted between March and September 2023, corresponding to the active growing season of most Mediterranean forest species. At each site, experimental plots were established in relatively homogeneous forest stands to minimize topographic and edaphic variability. Physiological measurements including reference evapotranspiration (ET_0), leaf water potential, gas exchange parameters, and xylem hydraulic conductivity were performed on three mature individuals per species per site, selected based on average diameter. Measurements followed standardized protocols as detailed in the subsequent methodological sections. The two study sites differ not only in climate but also in elevation and forest composition, providing a representative framework for evaluating how local water availability and altitude modulate the physiological performance of native woody species.

Table 1. Geographical and ecological characteristics of study sites

Natural Forest	Region	Latitude	Longitude	Altitude (m)	Mean	
					Temperature (°C)	Mean Precipitation (mm)
Djebel Zaghouan	Zaghouan	36° 22.0' N	010° 07.0' E	320-330	17.6	483
Djebel elSarj	Siliana	35° 57.0' N	009° 33.0' E	793-798	15.8	459

2.2 Estimation of evapotranspiration ET_0

The WEAP-MABIA approach, which applies the double coefficient culture (K_c) from the Drainage and FAO Irrigation method (Allen et al., 1998), was used to determine ET_0 .

$$ET_0 = \frac{0.408\Delta(R_n - G) + \gamma \frac{900}{T+273} u^2 (e_s - e_a)}{\Delta + \gamma(1 + 0.34u^2)}$$

ET_0 = Standard evapotranspiration [mm/day].

R_n = Net radiation at the surface of the crop [MJ / m² / day].

G = Soil heating flux density [MJ / m² / day] negligible ($G = 0$).

T average = Mean air temperature [° C].

U^2 = Wind speed at 2 m elevation [m / s].

e_s = Saturation vapor pressure [kPa].

e_a = Actual vapor pressure [kPa].

$e_s - e_a$ = Saturation vapor pressure drop [kPa].

Δ = Vapor pressure curveslope [kPa / ° C].

γ = Psychrometric constant [kPa / ° C].

2.3 Cultural coefficient (Kc)

The crop coefficient Kc of Aleppo pine is estimated at 0.2 (BRL-exploitation, 2010), it was a constant coefficient throughout the year as the Aleppo pine is an annual tree.

2.4. Soil water depletion

Tarissement (dry-down level) was measured using the Jabloun & Sahli (2008) method, which estimates water stress based on growing conditions and relative soil water content percentages.

$$\text{Soil water depletion (mm)} = 10 \times (\theta_{cc} - \theta_j) \times Z_{rac}$$

2.4. Leaf Water Potential

The leaf water potential (Ψ_{leaf}) of three Aleppo pine samples was measured using the chamber pressure method (Arimad 2®, A.R.I, KfarCharuv) as described by Scholander *et al.* (1965).

2.5. Gas exchange measurements

Gas exchange parameters, including net photosynthesis (A_n), stomatal conductance (g_s), and transpiration (Tr), were assessed using an infrared gas analyzer (IRGA, LI-6400) combined with a conifer chamber model LI-6400 (Li-Cor Inc., Lincoln, NE, USA) that featured a 2x3 cm light-source chamber. Ambient conditions were monitored, maintaining a temperature of 25°C, an incoming air humidity of 60%, and a fixed radiation level of 1500 ppm. The calculations for net photosynthesis (A_n), stomatal conductance (g_s), and transpiration (Tr) followed the methodology of Von Caemmerer and Farquhar (1981). Instead of traditional water-use efficiency, intrinsic water-use efficiency (iWUE) was computed as the ratio of A_n to Tr .

2.6. Xylem hydraulic conductivity

Leaf-specific hydraulic conductance (KL, $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$) was calculated as the flow-to-hydrostatic pressure gradient ratio. The determination of specific hydraulic conductivity (Ks) was conducted according to the protocol outlined by Sperry *et al.* (1988) using the XYLEM (Embolism Meter, Bronkhorst, Montigny-les-Cormeilles, France). Hydraulic conductivity (Kh) was computed by dividing the flow through each segment by the corresponding hydrostatic pressure gradient. Kh was then normalized by the xylem cross-sectional area and converted to specific hydraulic conductivity (Ks, $\text{kg m}^{-1} \text{MPa}^{-1} \text{s}^{-1}$) following the method described by Tyree *et al.* (2005).

To assess the percentage loss of conductivity (PLC) attributable to xylem cavitation, the following formula was employed:

$$PLC = 100 * (1 - (K_{in} / K_{max}))$$

Where K_{max} represents maximal conductivity and K_{in} denotes initial conductivity.

2.7 Statistical Analysis

Data were analyzed by ANOVA using the GLM procedure in SAS statistical software version 9.1 (SAS Institute Inc. Cary, NC).

3. Results and Discussion

3.1 Climatic variables in two sites

Given the atmospheric water demand of these regions, the estimated annual Aleppo pine potential evapotranspiration (ETc) was 714, and 561 mm at Djebel Sarj, and Djebel Zaghouan respectively

(Table 2). For both sites, the water balance indicates that during periods of high moisture and low evaporative demand, the actual evapotranspiration (ET_a) of Aleppo pine can match the potential evapotranspiration (ET_c). Regarding ET_a the daily average values ranged from 0.0 mm to 1.61 mm respectively during May and January for the DZ site and from 0.0 mm to 2.35 mm during July and December for the DS site. The same ranges of daily values were found by Ungar *et al.* (2013). The monthly pattern of actual evapotranspiration in the two Aleppo pine forests revealed a steady decrease during the dry season, ultimately reaching near-zero values (Table 2). On an annual basis, ET_a was respectively 304 mm in the DZ site and 330 mm in the DJ site and was almost equal compared to the rainfall. These results were also found by Ungar *et al.* (2013) and Qubaja *et al.* (2020). These results were confirmed by field measurements of photosynthetic rate and transpiration rate (Figure 11). Early in the season in 2016, between November and December, Djebel Sarj's Aleppo pine depleted water at a faster rate than at Djebel Zaghounan. The maintenance of favorable water conditions at Djebel Zaghounan during winter by rainfall events gives an advantage of soil water status in this site. Later in the season, during spring, insufficient seasonal rainfall (R) and increasing evaporative demand of the atmosphere (ET_o), clearly affect the soil moisture status with higher water depletion rate in the two sites. At the two sites, monthly ET_o had an increasing trend from January to July (Table 2). The maximum monthly ET_o for the two sites were registered during July and were 300, and 289 mm at Djebel Sarj, and Djebel Zaghounan respectively. Minimum monthly ET_o were 48 mm at Djebel Zaghounan, and 121 mm at Djebel Sarj and were obtained during December. Annual reference evapotranspiration was lower at Djebel Zaghounan with 1732 mm compared to the value at Djebel Sarj where it achieved 2370 mm. Inversely, rainfall had an overall decreasing trend from December to July (Table 2). Annual rainfall for the two sites was 271 mm and 342 mm, at Djebel Sarj, and Djebel Zaghounan respectively, with a dry rainless period from March to September (Figure 6). Also, data show that monthly rainfall was generally below monthly reference evapotranspiration except in December at Djebel Zaghounan (Table 2).

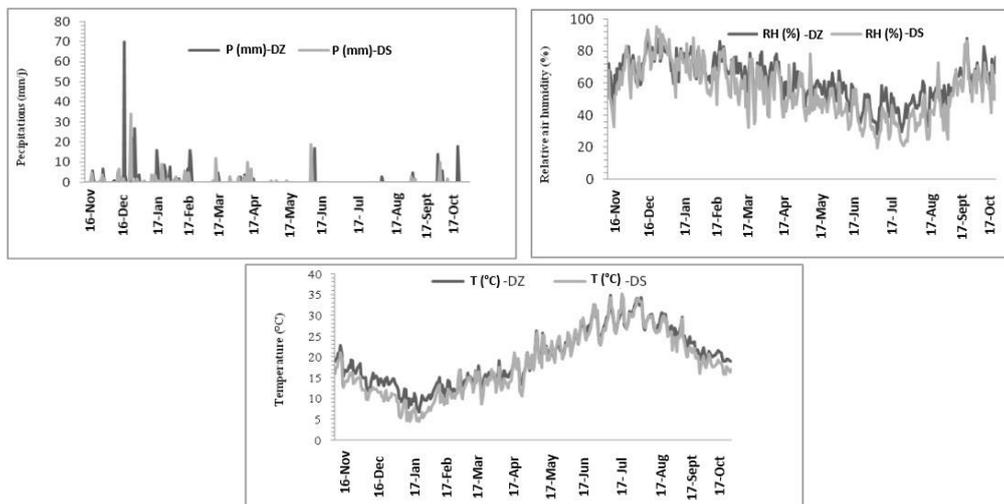


Figure 6. Daily Precipitations (mm), Temperature (°C), and Relative air Humidity (%) in the two Aleppo pine forests (Djebel Zaghounan (DZ) and Djebel Serj (DS)) monitoring over a year.

Results show that under semiarid and arid conditions, Aleppo pine potential evapotranspiration (ET_c) can vary from 561 mm to 714 mm. Results depict also the effect of atmospheric water demand and rainfall regime on actual evapotranspiration (ET_a) and soil moisture dynamic. As reported by the IPCC (2013) and Allani *et al.* (2020), a rise in reference evapotranspiration (ET_o) of approximately 6%

is projected for the future, alongside a potential reduction in rainfall of up to 8% under the RCP 4.5 and RCP 8.5 emission scenarios. Such alterations could have detrimental effects on both the water supply and the water demand within forest ecosystems.

Table 2. Monthly Rainfall (R), Reference evapotranspiration (ET_o), Aleppo pine water requirement (ET_c) and actual evapotranspiration (ET_a) during the growing season 2016-2017 at the two sites.

Month	DjbelZaghouan (DZ)				DjbelSarj (DS)			
	R	ET _o	ET _c	ET _a	R	ET _o	ET _c	ET _a
11	21	78	43	43	16	141	52	52
12	138	48	42	42	77	121	73	73
1	50	56	50	50	32	126	57	54
2	39	68	41	41	28	139	55	33
3	9	109	30	30	24	189	61	25
4	15	134	42	25	25	201	65	25
5	0	189	38	0	1	243	50	1
6	17	225	61	18	20	263	71	20
7	0	289	58	0	0	300	60	0
8	3	248	53	4	0	262	52	0
9	5	174	39	4	8	215	51	8
10	45	106	63	46	40	171	66	39
Sum	342	1723	561	304	271	2370	714	330

3.2 Soil water depletion

Figure 7 illustrates a distinct seasonal shift in which Aleppo pine alters its water uptake during the summer and early autumn. The model suggests that water absorption could drop to zero as the root-soil layers near desiccation. This severe water stress in the forest after the rainy season, coupled with the notably reduced physiological activity of the pine forest during the summer and autumn, has been reported by Baraket *et al.* (2019) in Tunisia and Schiller and Cohen (1995) in other Mediterranean areas. Additionally, the greater depletion of water by Aleppo pine in Djebel Sarj compared to Djebel Zaghouan (Figure 7) is largely influenced by soil type, with Djebel Sarj's soil exhibiting a higher water-holding capacity (50 mm/m) compared to that of Djebel Zaghouan (40 mm/m).

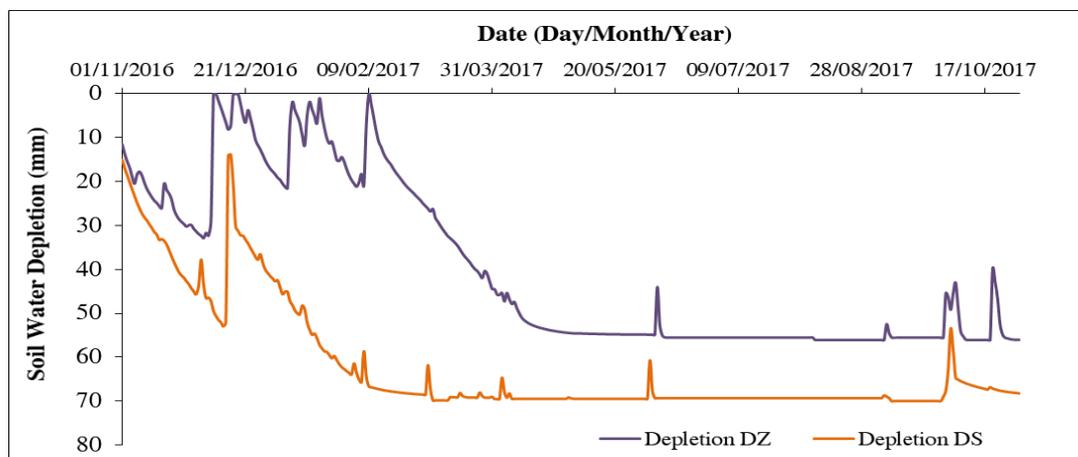


Figure 7. Soil water depletion rates of *Pinus halepensis* Mill. During the growing season 2016-2017 at Djebel Zaghouan and Djebel Sarj estimated by the WEAP-MABIA module.

3.3 Seasonal variability of leaf water potential (Ψ_{leaf})

There is no significant difference between the seasons for the DZ population ($P > 0.05$), while a significant difference is noted for the DS population ($P < 0.05$). For both populations, leaf water potential (Ψ) is higher in the summer (Figure 8). An increase in Ψ_{leaf} is seen as an indicator of water deficit, as higher water potential suggests that water is leaving this compartment when soil moisture is low (Lucot *et al.*, 1994). This rise is more noticeable in DS than in DZ and is more significant during the dry season than in the wet season. Furthermore, the increase in water potential is correlated with increased stomatal closure (Cruziat *et al.*, 2001).

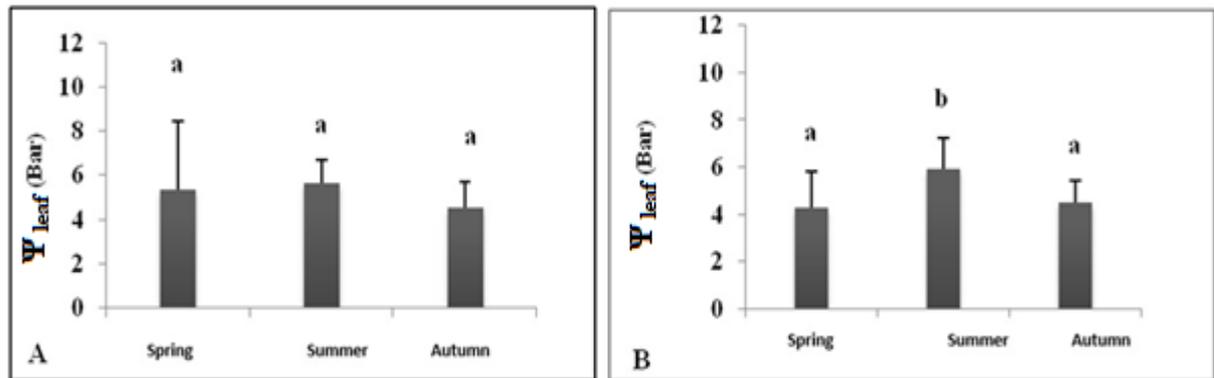


Figure 8. Seasonal fluctuations in leaf water potential (Ψ_{leaf} in Bar) in two Aleppo pine forests (A: Djebel Zaghouan and B: Djebel Serj) under three seasons (spring, summer, and autumn).

3.4 Growth patterns of two populations

A significant difference was observed between populations ($P < 0.05$), with Aleppo pine in Djebel Zaghouan exhibiting better growth than those in Djebel Serj (Figure 9). The species shows a positive correlation with variations in soil water storage, which, in turn, is influenced by climatic data, particularly rainfall.

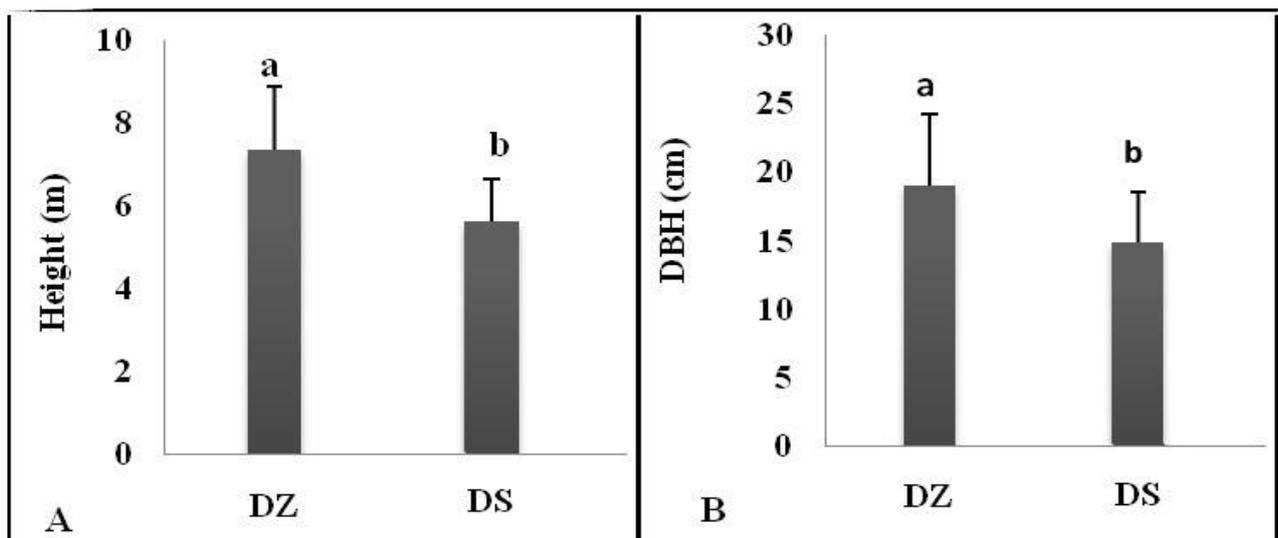


Figure 9. Difference between growth parameters at the two sites (mean tree heights for the three sites (A); mean tree diameters for the three sites (DBH) (B)).

Numerous studies have demonstrated that rainfall and altitude are closely associated with its growth (Vila *et al.*, 2008; Guit *et al.*, 2015). Consequently, water balance and availability are crucial factors

influencing the growth of this species (Vennetier *et al.*, 2010). In Tunisia, El Korchani *et al.* (2006) found that Aleppo pine productivity is impacted by climate change, especially drought. They indicated that the decline in productivity of natural stands was linked to increased water deficit due to reduced rainfall and elevated temperatures, supporting our findings. Furthermore, research by Papadopoulou *et al.* (2001) demonstrated that the radial growth of Aleppo pine in Greece is influenced by water storage during winter dormancy and evapotranspiration processes during the early growth phase in spring. The observed differences are also correlated with the geographical origins of the populations.

3.5 Net photosynthesis and transpiration patterns

Analysis of variations in transpiration (Tr) and net photosynthesis (An) revealed a decline in values from spring to autumn at both sites (Figure 10). At DZ, photosynthesis decreased from $8 \mu\text{mol m}^{-2} \text{s}^{-1}$ in spring to $1.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ in autumn, mirroring the trend observed in transpiration. Climatic factors affect various tree functional traits, such as stomatal conductance (Yagoubi, 1993; Prytz *et al.*, 2003; Flexas *et al.*, 2014; Wu *et al.*, 2020) and photosynthesis (Moran *et al.*, 1994; Urban *et al.*, 2017; Miner *et al.*, 2017). Several studies have reported a linear correlation between these variables (Yuan *et al.*, 2004). The patterns observed in photosynthesis align with temperature trends (Hikosaka, 2006; Yamori, 2014). Water deficit leads to stomatal closure, which restricts gas exchange and consequently reduces transpiration and photosynthesis (Prytz *et al.*, 2003; Li *et al.*, 2017), as seen in both sites during the summer. Despite rising temperatures and declining precipitation throughout the seasons, the water status of DZ and its physiological behavior indicate that this population exhibits resilience and adaptability to climate change.

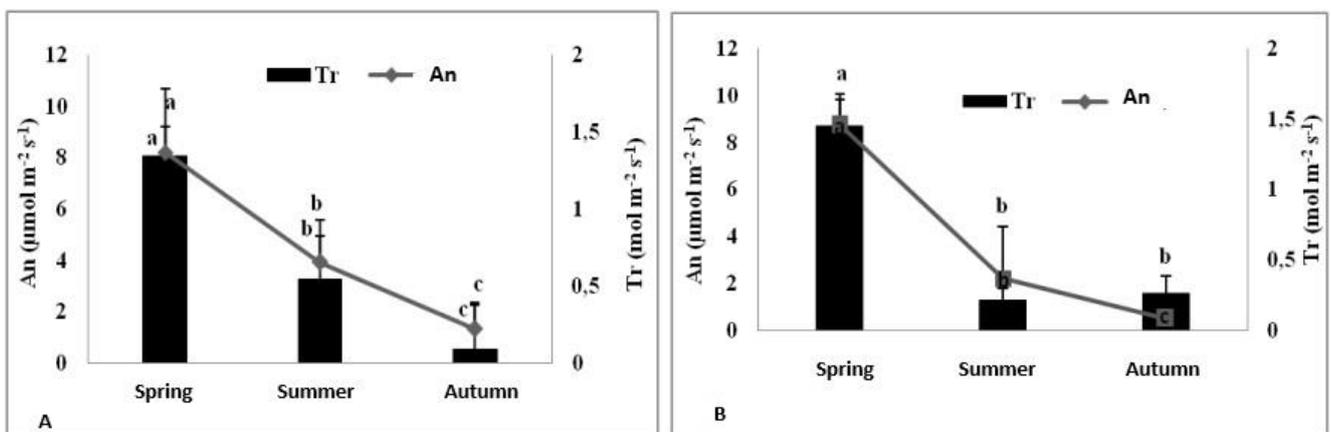


Figure 10. Net photosynthetic (An) and transpiration (Tr) during three seasons at (A) Djebel Zaghouan and (B) Djebel Serj under three seasons (spring, summer, and autumn).

3.6 Correlation between stomatal conductance and Xylem conductivity

With the resorption of emboli caused by the elevated hydrostatic pressure on the conductive segments, there is an increase in hydraulic conductivity (K_{max}). Then, the initial hydraulic conductivity (K_{in}) increases with the intensity of climatic conditions between seasons, including fluctuations in temperature and a decline in relative humidity. The lower embolism rate observed in DZ may be attributed to more favorable water conditions at this site, in contrast to the harsher edaphoclimatic conditions in DS (Table 3). Vilagrosa *et al.* (2003) demonstrated that cavitation primarily occurs in instances of soil drought. The pattern of hydraulic conductivity corresponds with that of stomatal conductance (Liu *et al.*, 2019). Drought resistance is a well-established trait of Aleppo pine, distinguishing it from other species (Alexou, 2013). This trait is likely linked to its low stomatal

conductance (Figure 11). stomatal opening and closing regulations are closely tied to water-related factors (Comstock, 2002; Kaiser & Paoletti, 2014). DZ exhibits the lowest stomatal conductance among the examined sites compared to DS, indicating its higher tolerance to climate variability, notably to drought.

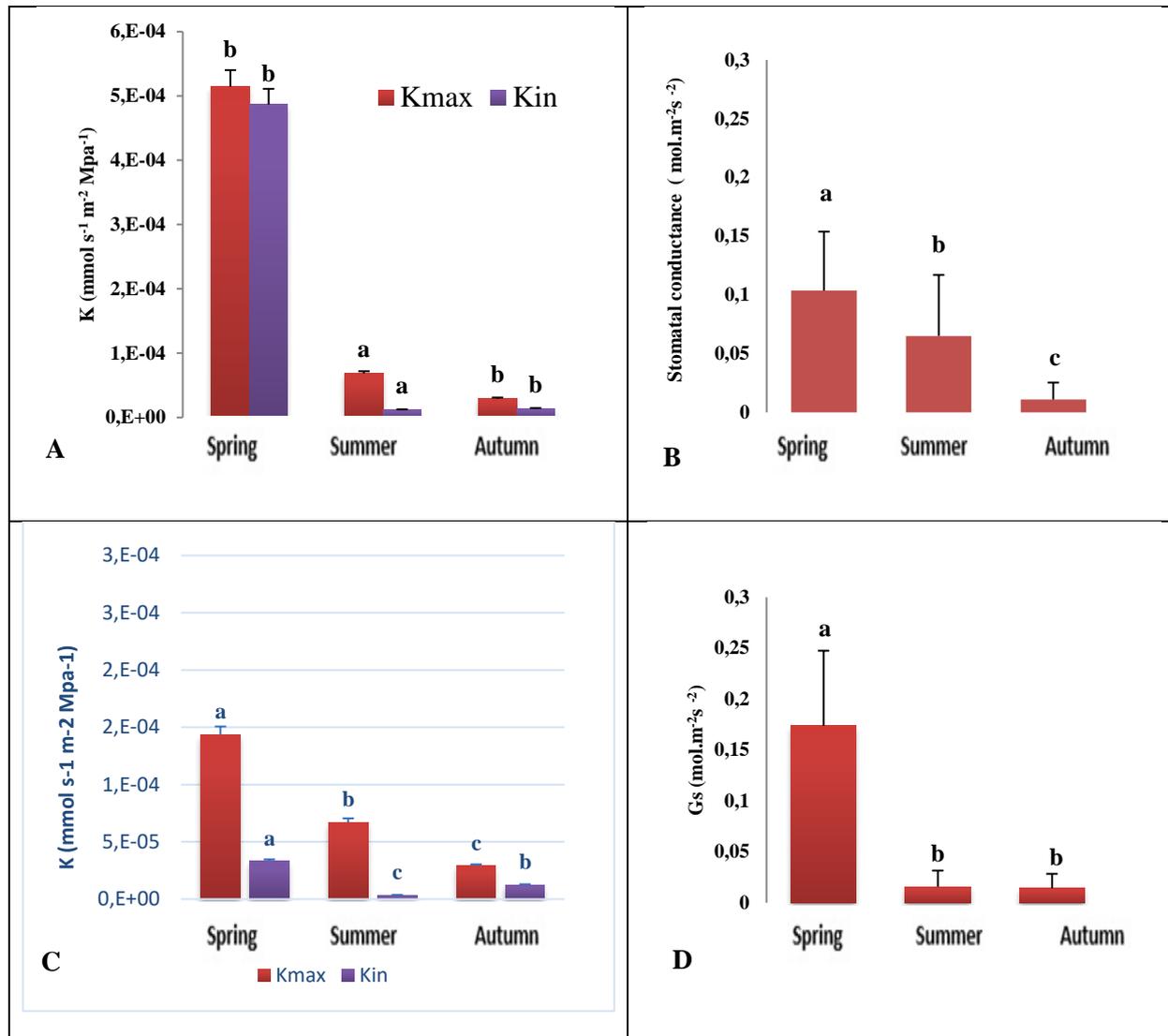


Figure 11. Seasonal variability of xylem conductance (K_{in} and K_{max}) in DZ(A) and DS(C) and stomatal conductance (G_s) in DZ(D) and DS(F) under three seasons (spring, summer, and autumn).

Table 3. Percent loss conductivity (PLC %) of two populations

Sites	DZ	DS
PLC(%)	16,29	70,60

Conclusion

In summary, our study emphasizes the significant influence of changing environmental conditions on Aleppo pine forests in Tunisia. Seasonal variations in water requirements showed distinct transitions, highlighting a shift in water uptake by Aleppo pines during the summer and early autumn. The models

indicated a potential for zero water uptake after the rainy season, signaling extreme water stress and reduced physiological activity throughout the summer and autumn months. Additionally, physiological analyses revealed lower stomatal conductance in Djebel Zaghouan, which resulted in stomatal closure, reduced transpiration, and inhibited photosynthesis. These findings offer important insights into the physiological reactions of Aleppo pine to environmental stress, enhancing our understanding of how Mediterranean forest ecosystems adjust to climate change.

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Disclosure statement: *Conflict of Interest:* The authors declare that there are no conflicts of interest.

Compliance with Ethical Standards: This article does not contain any studies involving human or animal subjects.

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