



## Seasonal Physiological Responses of *Phillyrea latifolia* to Drought Stress in the Tunisian Dorsal

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Received 14 Dec 2024,

Revised 07 Jan 2025,

Accepted 08 Jan 2025

### Keywords:

- ✓ *Phillyrea latifolia*;
- ✓ Drought;
- ✓ Gas exchanges;
- ✓ Water status;
- ✓ Variability;

**Citation:** Nefzi K., Fkiri S., Baraket M., Ghazghazi H., Nasr Z. (2025) Seasonal Physiological Responses of *Phillyrea latifolia* to Drought Stress in the Tunisian Dorsal, *J. Mater. Environ. Sci.*, 16(1), 46-55

**Abstract:** The aim of this study was to investigate the physiological responses of *Phillyrea latifolia* to seasonal drought stress. Measurements were conducted between March and December 2018. The parameters studied included leaf water potential, net photosynthesis (Pn), stomatal conductance (gs), leaf transpiration (Tr), maximum efficiency of PSII photochemistry (Fv/Fm), and hydraulic conductivity. The results showed that all measured parameters varied significantly with the season ( $P < 0.0001$ ). The highest average  $\psi_{\text{leaf}}$  was observed in summer ( $-2.99 \pm 0.08$  MPa). Similarly, the highest values of Fv/Fm were also recorded in summer ( $0.83 \pm 0.06$ ). However, the highest values of Pn ( $3.62 \pm 0.41 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and Tr ( $0.3 \pm 0.028 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) were noted in autumn. The initial hydraulic conductivity (Kin) was highest in spring ( $1.34 \times 10^{-4} \pm 1 \times 10^{-5} \text{mmol s}^{-1} \text{m}^{-2} \text{MPa}^{-1}$ ) and autumn ( $1.18 \times 10^{-4} \pm 2.3 \times 10^{-6} \text{mmol s}^{-1} \text{m}^{-2} \text{MPa}^{-1}$ ). The maximal hydraulic conductivity (Kmax) reached its peak during the spring season ( $3.45 \times 10^{-4} \pm 2.7 \times 10^{-11} \text{mmol s}^{-1} \text{m}^{-2} \text{MPa}^{-1}$ ). The lowest values of stomatal conductance (gs) were recorded in summer ( $0.19 \pm 0.04$  MPa), and the percentage of loss in conductivity (PLC) reached 66%. During the spring season, soil moisture decreased with depth, ranging from  $15.23 \pm 5.48\%$  at 20 cm to  $6.26 \pm 2.46\%$  at 80 cm. The best physiological performances of *Phillyrea latifolia* were reported in spring and autumn, which may be attributed to favorable environmental conditions. The plant's responses depend not only on the species but also on the climatic conditions in which they grow.

## 1. Introduction

Climate change is one of the main determinants of the types and distribution of global vegetation. According to [Schwinning and Ehleringer \(2001\)](#), plant species segregate along natural gradients of water availability based on their capacity to withstand drought. Annual precipitation patterns play a crucial role in shaping plant adaptations in water-use strategies and in determining the composition of plant communities in arid environments. However, species from different biogeographic origins and with contrasting ecological requirements coexist in transition zones. The Mediterranean region has historically served as such a transition zone over geological timescales, and

many species of the Mediterranean flora are Tertiary relicts or remnants from vegetation shifts during glaciations (Palamarev, 1989; Martín-Forés, 2017; Carrión *et al.*, 2024).

Mediterranean regions are particularly vulnerable to water deficits due to the unprecedented rate of warming and the increasing frequency of extreme weather events (Dai, 2013; Alaoui *et al.*, 2013). One key feature of Mediterranean ecosystems is the dry summer period, but the extent to which Mediterranean plants are fully adapted to this seasonal drought remains unclear. Species coexisting in Mediterranean habitats exhibit remarkable differences in their ecophysiological traits, as well as in their responses and tolerances to water restrictions (Cabrera, 2002; Gulías *et al.*, 2002; Ogaya and Peñuelas, 2003; Laita *et al.*, 2024a; Laita *et al.*, 2024b). There are different alternative strategies for coping with drought. Mediterranean species have been classified as drought-tolerant when they can maintain photosynthesis under severe water stress, as seen in some evergreen oaks, and as drought-avoiders when they either shed leaves or close stomata during dry periods, as observed in certain pine species (Martínez-Ferri *et al.*, 2000; Ferrio *et al.*, 2003; Valladares *et al.*, 2005).

Drought tolerance is generally associated with efficient water use (Ferrio *et al.*, 2003), but mixed results have been reported regarding water-use efficiency under water stress in Mediterranean ecosystems (Reichstein *et al.*, 2002). Comparisons of survival rates between species employing different strategies under similar environmental conditions are rare, and despite the frequent occurrence of droughts in Mediterranean regions, our understanding of the ecology and evolution of Mediterranean species under water-limited conditions remains incomplete. As a result, plants can exhibit contrasting xylem attributes in response to water stress, yet these traits can coexist within communities experiencing similar levels of water stress (Martínez-Vilalta *et al.*, 2002).

In this context, it is important to study the impact of drought on *Phillyrea latifolia*, in a natural environment, notably at Djebel Sarej (DS) in Tunisia, by assessing their ecophysiological responses across the three seasons (spring, summer and autumn).

## 2. Methodology

### 2.1 Study sites

The study was conducted on Djebel Sarej in Northeastern Tunisia over three seasons (spring, summer, and autumn of 2018). Mount Serj is the third-highest peak in the Tunisian Dorsal, located at a longitude of 009° 33.0' E and latitude of 35° 57.0' N, according to the UTM coordinate system, with an elevation of 793 m above sea level. The area falls within the upper semi-arid zone, experiencing variations between cool and temperate winters. The dominant tree species include Aleppo pine, holm oak, cork oak, maple, evergreen cypress, and carob tree (UNDP, 2015). The climate is typically Mediterranean, characterized by spring and autumn rains, along with hot, dry summers and mild winters. The soil is predominantly composed of Cretaceous limestone dating back to the Secondary Era, with its uplifted, sometimes folded strata forming the massive steps of a giant staircase. *Phillyrea latifolia* is a plant with narrow, slightly toothed, opposite leaves and belongs to the Oleaceae family.

### 2.2 Leaf Water Potential

The Leaf Water Potential ( $\psi_{\text{leaf}}$ ) was measured using the pressure chamber technique. Small twigs were cut and placed in a pressure chamber (Arimad2®, A.R.I, Kfar Charuv, Israel), which was connected to a nitrogen gas cylinder and equipped with a magnifying glass holder for precise observation.

### 2.3 Gas exchange parameters

Net photosynthesis (Pn), stomatal conductivity (gs) and leaf transpiration (Tr) were measured by the Li-CorLi-6400XT portable photosynthesis system (Li-Cor, Li-6400XT Lincoln, NE, USA) based on the IRGA (InfraRedGasAnalysis) principle. One plant per season was chosen for the A/C curves. For each curve, the leaf reached an equilibrium corresponding to a CO<sub>2</sub> concentration of 400 mmol.mol<sup>-1</sup> for 30 minutes, in order to acclimatize the leaf to the conditions of temperature, PAR, ventilation rate and CO<sub>2</sub> concentration corresponding to the first point. Temperature is adjusted to 25°C. Relative humidity maintained at 60%.

### 2.4 Chlorophyll fluorescence

Measurements of the maximum efficiency of PSII photochemistry (Fv/Fm) were carried out in situ on attached leaves using a portable pulse-modulated fluorometer, the PAM 2000 (Walz, Effeltrich, Germany). Leaves were dark-adapted with leaf clamps for 1 hour, which was deemed sufficient to allow complete relaxation of energy-dependent quenching. The Fv/Fm ratio was calculated as (Fm-Fo)/Fm, where Fm and Fo are the maximum and baseline fluorescence yield, respectively, of dark-adapted leaves (Genty *et al.*, 1986).

### 2.5 Hydraulic conductivity

The hydraulic conductivity was determined using the high-pressure flow measurement method (Sack *et al.*, 2002; Tyree *et al.*, 2005). This method involves introducing degassed water at positive pressure (2MPa) into the segment and quantifying the flow rate at the inlet. Measurement of maximum hydraulic capacity was deduced from cavitation as follow:

$$PLC = 100 * (1 - (kin/kmax)) \text{ Eqn. 1}$$

### 2.6 Gravimetric Soil moisture

This method is considered a reference method; it involves drying a soil sample in an oven at 105°C for two days and then determining the weight of water contained in the sample by final weighing. Soil samples are taken using a helical gauge down to 80 cm, given the heterogeneity of the soil and the stones that sometimes prevent samples from being taken.

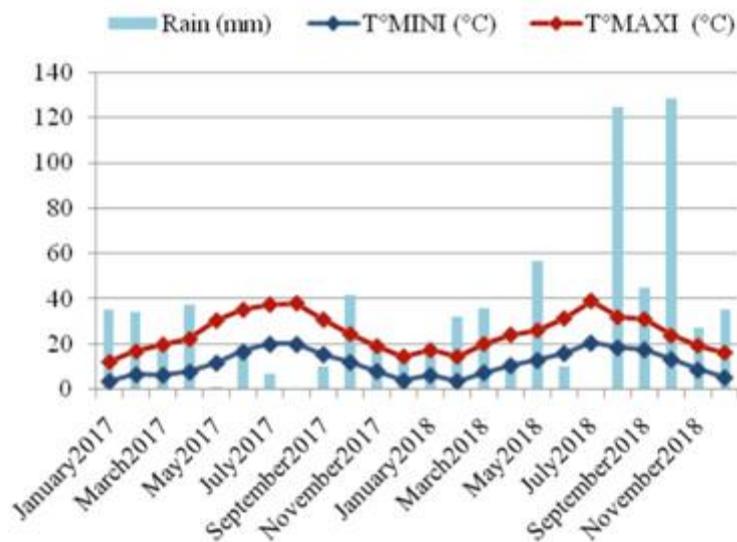
### 2.7 Statistical Analysis

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 Seasonal Variations in Rainfall and Temperature

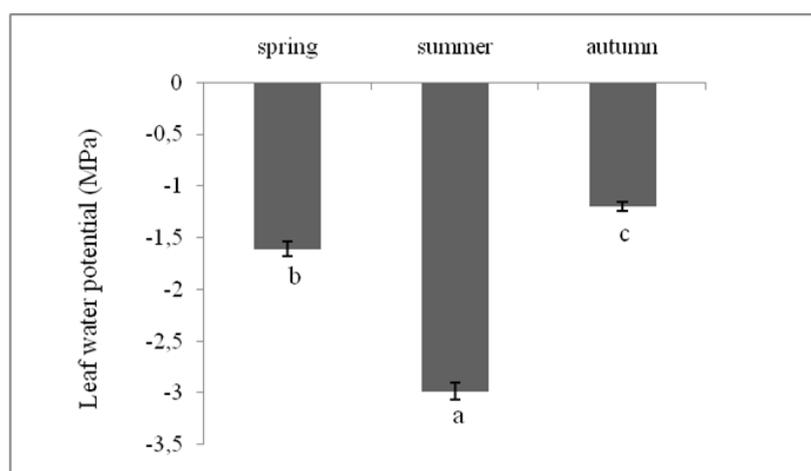
Precipitation and temperature exhibited notable differences between 2017 and 2019 in the study areas (Figure 1). In 2017, the mean accumulated precipitation from January to September was significantly lower compared to 2018 (21 mm versus 38 mm, respectively), with a 44% decrease in rainfall from June onward. This decline in rainfall reduced water availability for plants over an extended period, particularly during summer. The impact of reduced summer precipitation on gas exchange and water relations varied among the studied species (Miranda *et al.*, 2009; Mas *et al.*, 2024). Such meteorological conditions reflected severe water stress, as evidenced by the stomatal conductance (gs), an integrative indicator of water stress (Flexas *et al.*, 2002; Galmés *et al.*, 2007).



**Figure 1.** Mean and accumulated precipitation and temperature per month from 2017 to 2019 of the study site

### 3.2 Leaf Water Potential ( $\psi_{leaf}$ )

The leaf water potential ( $\psi_{leaf}$ ) results are presented in Figure 2, showing significant seasonal differences ( $P < 0.0001$ ). During spring,  $\psi_{leaf}$  remained relatively high at  $-1.61 \pm 0.075$  MPa, indicating adequate water availability. However, summer conditions intensified water stress, with  $\psi_{leaf}$  dropping to  $-2.99 \pm 0.08$  MPa. In autumn,  $\psi_{leaf}$  improved, reaching  $-1.20 \pm 0.04$  MPa. These variations highlight the influence of seasonal rainfall on plant water status, where summer droughts impose significant stress on Mediterranean species. These findings align with previous studies demonstrating that Mediterranean species exhibit substantial seasonal variability in leaf water potential, which is closely tied to the availability of soil water and atmospheric demand (Flexas *et al.*, 2006; Helman *et al.*, 2017; Fishman *et al.*, 2024). Such adaptations are critical for coping with the prolonged summer droughts characteristic of Mediterranean climates, as noted by Ogaya & Peñuelas (2003), who highlighted similar patterns in other drought-tolerant forest species.

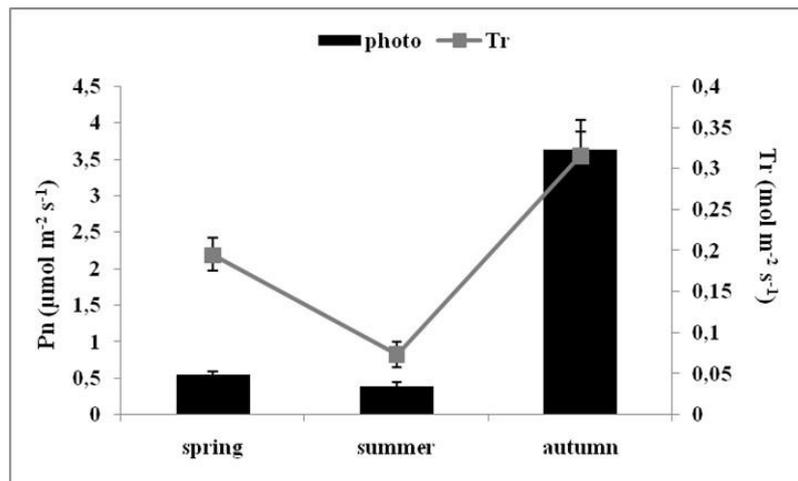


**Figure 2.** Seasonal variability of leaf water potential ( $\psi_{leaf}$ ) of *Phillyrea latifolia*

### 3.3 Gas Exchanges

#### 3.3.1 Photosynthesis and Transpiration

Seasonal variations in photosynthesis (Pn) and transpiration (Tr) are shown in Figure 3. Significant differences were observed ( $P < 0.0001$ ). Pn and Tr peaked during autumn ( $3.62 \pm 0.41 \mu\text{mol m}^{-2} \text{s}^{-1}$  and  $0.3 \pm 0.028 \mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively) due to favorable temperatures and increased soil moisture. Conversely, the lowest values were recorded in summer (Pn:  $0.39 \pm 0.046 \mu\text{mol m}^{-2} \text{s}^{-1}$ ; Tr:  $0.073 \pm 0.015 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), correlating with high temperatures and low soil moisture. These findings align with studies highlighting similar reductions in Pn and Tr under drought stress (Oechel *et al.*, 1981; Tenhunen *et al.*, 1987; Peñuelas *et al.*, 1998; Abouatallah *et al.*, 2011 & 2012).



**Figure 3.** Seasonal variability of net photosynthesis (Pn) and Transpiration (Tr) of *Phillyrea latifolia*

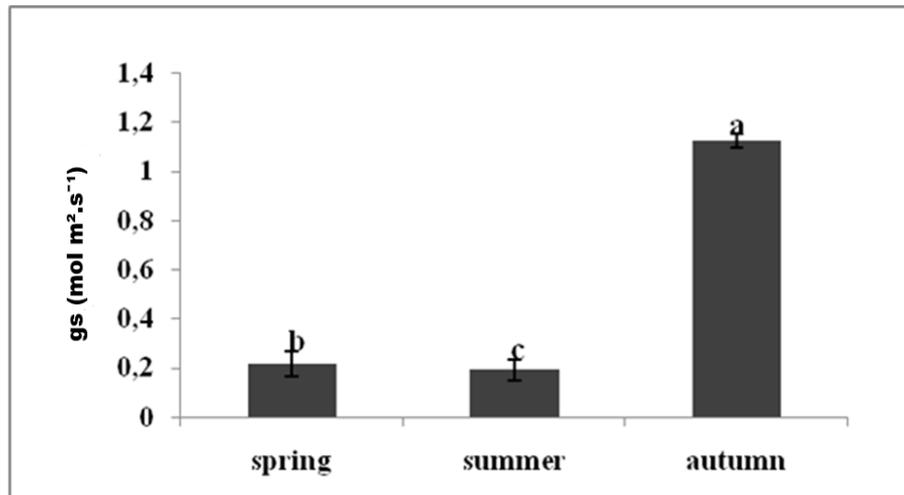
#### 3.3.2 Stomatal conductance

The results for  $g_s$  (Figure 4) also revealed significant seasonal variations ( $P < 0.0001$ ). The lowest  $g_s$  values were recorded in summer ( $0.19 \pm 0.04 \text{ MPa}$ ), consistent with high temperatures and limited water availability. In autumn,  $g_s$  reached its highest values ( $1.12 \pm 0.02 \text{ MPa}$ ), with intermediate levels observed in spring ( $0.21 \pm 0.05 \text{ MPa}$ ). These seasonal trends underline the physiological adaptations of Mediterranean plants to optimize gas exchange under varying water conditions. Such seasonal trends in  $g_s$  have been extensively documented, emphasizing that stomatal regulation plays a key role in balancing water loss and carbon assimilation under fluctuating environmental conditions (Chaves *et al.*, 2002; Flexas *et al.*, 2006; Medrano *et al.*, 2002). This mechanism is particularly critical for Mediterranean species, which face prolonged drought stress during the summer months.

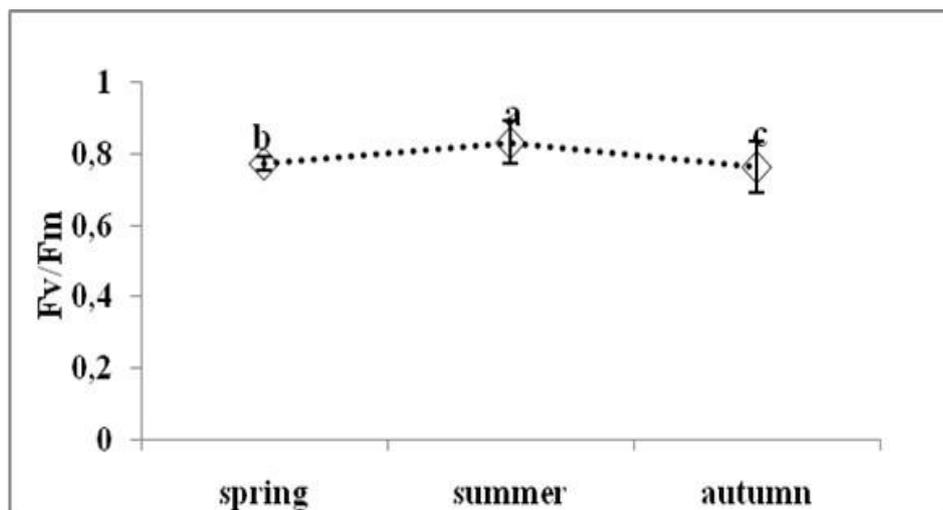
#### 3.4 Potential Photochemical Efficiency of PSII ( $F_v/F_m$ )

The highest  $F_v/F_m$  values were observed in summer ( $0.83 \pm 0.06$ ), despite severe drought, suggesting that PSII maintained its efficiency under stress (Figure 5). However, the lowest  $F_v/F_m$  values were recorded in autumn ( $0.76 \pm 0.07$ ), likely influenced by cooler temperatures. Intermediate values ( $0.77 \pm 0.02$ ) were measured in spring. These findings corroborate previous studies showing that  $F_v/F_m$  reflects the balance between photochemical and non-photochemical quenching under environmental stress. The stability of  $F_v/F_m$  during summer highlights the resilience of the photosynthetic apparatus in Mediterranean plants, which rely on efficient photoprotective strategies to avoid photoinhibition

under high light and drought stress (Demmig-Adams & Adams, 1996; Flexas *et al.*, 2004). The reduction observed in autumn could also be attributed to seasonal shifts in photoprotection efficiency and recovery dynamics influenced by decreasing photoperiod and temperatures, as previously reported by Verhoeven, (2014) and Öquist & Huner, (2003).



**Figure 4.** Seasonal variability of stomatal conductance (gs) of *Phillyrea latifolia*

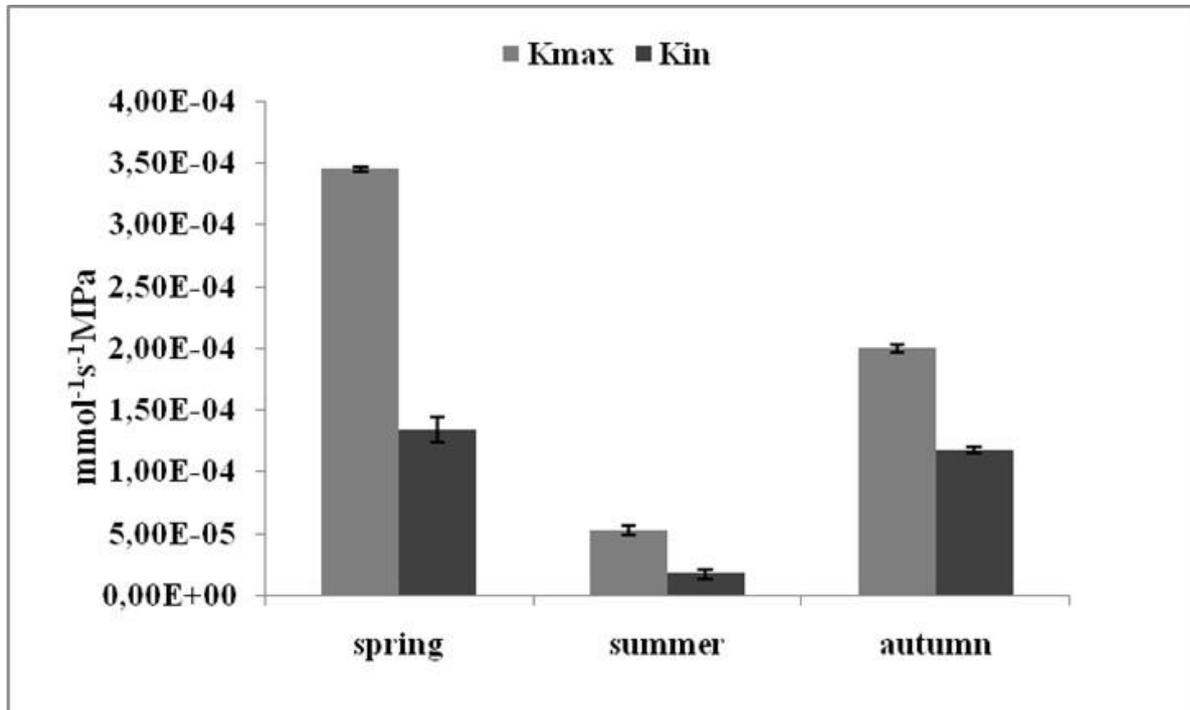


**Figure 5.** Seasonal variation of maximum quantum yield of PSII (Fv/Fm) of *Phillyrea latifolia*

### 3.5 Xylem Conductivity

The seasonal dynamics of initial (Kin) and maximal hydraulic conductivity (Kmax) are shown in Figure 6. Both Kin and Kmax differed significantly across seasons ( $P < 0.001$ ). The highest Kin values were observed in spring ( $1.34 \times 10^{-4} \pm 1 \times 10^{-5} \text{ mmol s}^{-1} \text{ m}^{-2} \text{ MPa}^{-1}$ ) and autumn ( $1.18 \times 10^{-4} \pm 2.3 \times 10^{-6} \text{ mmol s}^{-1} \text{ m}^{-2} \text{ MPa}^{-1}$ ), while the lowest occurred in summer ( $1.75 \times 10^{-5} \pm 3.6 \times 10^{-6} \text{ mmol s}^{-1} \text{ m}^{-2} \text{ MPa}^{-1}$ ). Similarly, Kmax peaked in spring ( $3.45 \times 10^{-4} \pm 2.7 \times 10^{-11} \text{ mmol s}^{-1} \text{ m}^{-2} \text{ MPa}^{-1}$ ) and was lowest in summer ( $5.23 \times 10^{-5} \pm 6.7 \times 10^{-11} \text{ mmol s}^{-1} \text{ m}^{-2} \text{ MPa}^{-1}$ ). These variations highlight the impact of seasonal water availability on hydraulic function and emphasize the vulnerability of xylem under drought stress.

The marked decline in hydraulic conductivity during summer underscores the vulnerability of xylem to cavitation under severe drought conditions, a phenomenon well-documented in Mediterranean tree species (Sperry *et al.*, 1996; Brodribb *et al.*, 2003). The recovery of  $K_{in}$  and  $K_{max}$  in autumn reflects seasonal plasticity in xylem function, likely facilitated by embolism repair or the formation of new xylem tissues, as suggested by Johnson *et al.* (2012) and Cochard & Delzon, (2013).



**Figure 6.** Seasonal variability of xylem conductivity ( $K_{in}$  and  $K_{max}$ ) of *Phillyrea latifolia*

### 3.6 Percentage of Loss of Conductivity (PLC)

PLC results are summarized in Table 1. Significant seasonal differences ( $P < 0.001$ ) were observed, with PLC peaking in summer (66%) due to severe drought. In spring, PLC was 61%, while autumn exhibited a full recovery, with PLC decreasing to 41%. These findings indicate seasonal recovery mechanisms in xylem functionality, consistent with studies on Mediterranean woody species. The high PLC observed in summer reflects the impact of drought-induced embolism, a common response in Mediterranean woody species facing water stress (Sperry *et al.*, 1993; Brodribb *et al.*, 2010). The autumn recovery suggests active mechanisms such as embolism refilling or the production of new functional xylem, as highlighted in studies by Hacke & Sperry, (2003) and Nardini *et al.* (2011), which emphasize the resilience of these species to seasonal hydraulic stress.

**Table 1.** Seasonal variability of Percentage of loss conductivity (PLC %) of *Phillyria latifolia*

<i>Phillyria latifolia</i>	Spring	Summer	Autumn
	61.15±1.2 <sup>b</sup>	66.58±1.62 <sup>a</sup>	41.15±1.7 <sup>c</sup>

### 3.7 Gravimetric Soil Moisture

Highly significant differences were observed across soil depths and seasons ( $P < 0.0001$ ). In spring, soil moisture decreased with depth, ranging from  $15.23 \pm 5.48\%$  at 20 cm to  $6.26 \pm 2.46\%$  at 80 cm (Figure 7). In summer, soil moisture levels were drastically lower due to the absence of rainfall (0 mm), with values ranging from  $6.03 \pm 2.60\%$  at 20 cm to  $2.24 \pm 1.63\%$  at 80 cm. By autumn, soil moisture improved significantly, reaching  $19.08 \pm 2.70\%$  at 20 cm and  $11.70 \pm 1.07\%$  at 80 cm. These findings align with previous studies showing that Mediterranean soils are highly sensitive to seasonal drought, with water availability closely tied to vegetation performance (Kemp *et al.*, 1997; Pariente, 2002).

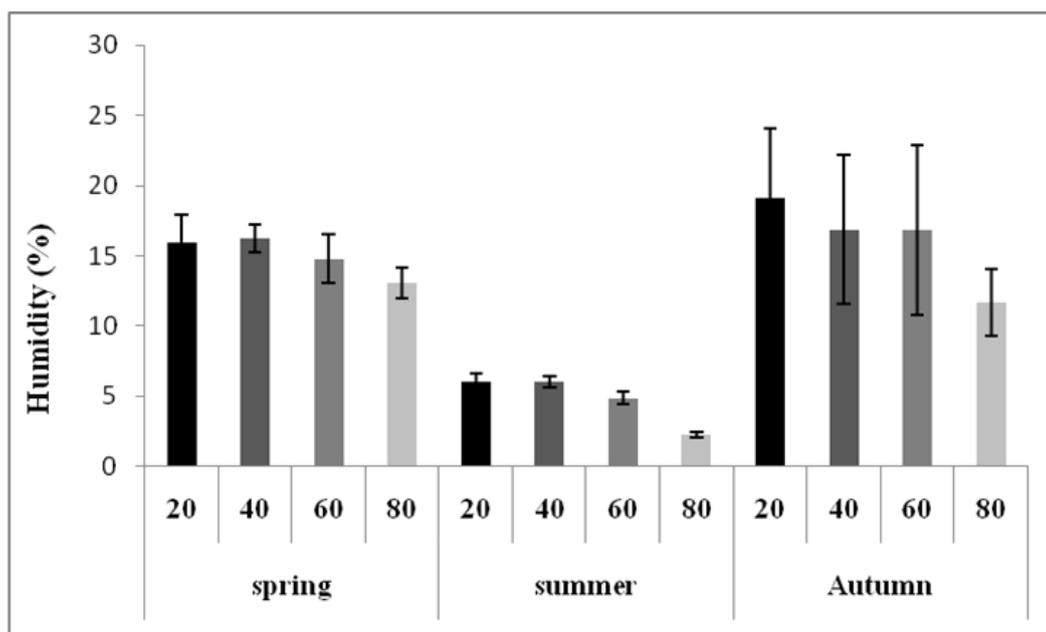


Figure 7. Evolution of in soil moisture content from 20 to 80 cm depth during the three seasons.

### Conclusion

Seasonal variations in the physiological functioning of plants have been observed in both ambient and dry climates. Effectively comparing the behavior of species requires a thorough understanding of the soil-plant-atmosphere system during the study period (March to January 2018). The best photosynthetic performance, transpiration, and stomatal conductance in *Phillyrea latifolia* were observed in spring and autumn, attributed to favorable environmental conditions. However, during the summer, a general reduction in stomatal conductance and photosynthesis was noted due to drought stress. Interestingly, the Fv/Fm ratio was slightly higher in summer than in spring and autumn, indicating the photosynthetic system's resilience under dry conditions. The vulnerability to xylem cavitation varies significantly across seasons, reflecting the hydraulic adjustments of plants to fluctuating water availability. These physiological responses depend not only on the species but also on the climatic conditions in which they grow.

**Acknowledgement,** The National Institute of Rural Engineering, Water is acknowledged.

**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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