

Seasonal ecophysiological responses and behavior of phillyrea latifolia species to climate change in Tunisia

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Research

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Abstract

Background As part of global climate change, variation in precipitation in arid ecosystems is leading to plant adaptation in water-use strategies; significant interspecific differences in ecophysiological response will change the plant behavior. The main aim of this study was to investigate the ecophysiological responses of *Phillyrea latifolia* species to seasonal drought stress. Measurements were conducted between March and December 2018. The parameters studied were the Leaf Water Potential (ψ_{leaf}), Net photosynthesis (P_n), stomatal conductance (g_s) and leaf transpiration (T_r), maximum efficiency of PSII photochemistry (F_v/F_m), and Hydraulic conductivity. **Main results** The results showed that all measured parameters varied significantly with the season ($P < 0.0001$). The results of ψ_{leaf} showed the highest average in summer (-2.99 ± 0.08 MPa). Likewise, the highest values of the maximal photochemical efficiency of PSII (F_v/F_m) were observed in summer (0.83 ± 0.06). However, the highest values of P_n ($3.62 \pm 0.41 \mu\text{mol m}^{-2} \text{s}^{-1}$) and T_r ($0.3 \pm 0.028 \mu\text{mol m}^{-2} \text{s}^{-1}$) were noted in autumn. The Initial Hydraulic Conductivity (K_{in}) value was in spring ($1.34 \cdot 10^{-4} \pm 1.10 \cdot 10^{-5} \text{ mmol s}^{-1} \text{ m}^{-2} \text{ MPa}^{-1}$) and autumn ($1.18 \cdot 10^{-4} \pm 2.30 \cdot 10^{-6} \text{ mmol s}^{-1} \text{ m}^{-2} \text{ MPa}^{-1}$) and the Maximal Hydraulic Conductivity (K_{max}) was the highest during the spring season ($3.45 \cdot 10^{-4} \pm 2.70 \cdot 10^{-11} \text{ mmol s}^{-1} \text{ m}^{-2} \text{ MPa}^{-1}$). The results of the Stomatal Conductance (g_s) showed that the lowest values were recorded in summer (0.19 ± 0.04 MPa). The percentage of loss conductivity (PLC) reached 66%. During the spring season, the soil had a decreasing moisture profile as it moved to the depths and varied from $15.23 \pm 5.48\%$ at 20 cm to $6.26 \pm 2.46\%$ at 80 cm. **Conclusions** The best physiological performances of *Phillyrea latifolia* reported in spring and autumn may be attributed to favorable environmental conditions. The answers depend not only on the species but also on the climates in which they grow.

Background

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 regarding their capacity to withstand drought. Annual precipitation patterns play a crucial role in shaping plant adaptation in water use strategies, and in determining the compositions of plant communities in arid environments. However, species from different biogeographic origins and with contrasting ecological requirements coexist at transition zones. The Mediterranean region has played this role of transition zone over geological time scales and many species of the Mediterranean flora are tertiary relicts or remnants from vegetation shifts during glaciations (Palamarev, 1989). Mediterranean regions are particularly suffering water deficits due to the unprecedented rate of warming and more frequent extreme events (Dai, 2013). But one key characteristic of Mediterranean ecosystems is a dry period over the summer and to what extent Mediterranean plants are fully adapted to this drought remains unclear. Species coexisting in Mediterranean habitats differ remarkably in their ecophysiological traits and their responses and tolerances to water restrictions (Cabrera, 2002; Gulías *et al.*, 2002; Ogaya and Peñuelas, 2003). There are different alternative strategies for dealing with drought, and Mediterranean species have been classified as drought-tolerant when they can maintain photosynthesis

under severe water stress such as some evergreen plantsoaks, and drought avoiders, when they either shed leaves or close stomata during the dry periods, as certain pines do. (Martinez-Ferri et al., 2000; Ferrio et al., 2003; Valladares et al., 2005). Drought tolerance is generally associated with efficient use of water (Ferrio et al., 2003), but mixed results have been demonstrated for the efficiency of water use in the water stress in Mediterranean ecosystems (Reichstein et al., 2002). Comparisons of the survival, under similar environmental conditions, of species with different strategies are rare and, despite the frequent occurrence of drought in Mediterranean areas, our understanding of the ecology and evolution of Mediterranean species under restricted waters is still fragmentary. As a result, plants can respond to water stress with contrasting xylem attributes that can, however, coexist within communities under similar water stress (Martínez-Vilalta *et al.*, 2002). For this reason, it is important to study the impact of climate change on *phillyrea latifolia* by evaluating of their responses ecophysiological in sites of Sarej (DS) and to compare their behavior in the three seasons (spring, summer, and autumn)

Materials And Methods

Sites and species description

The study was carried out in mount of Sarej in northeastern Tunisia for 3 seasons (spring, summer, autumn 2018). The mount of Serj is the third summit of the Tunisian Dorsal positioned at a longitude of 009° 33.0' E and latitude of 35° 57.0' N in the UTM coordinate system with heights of 793 m above sea level. It belongs to the upper semi-arid with variations in cool and temperate winter. Dominant tree species are the Aleppo pine, green oak, cork oak, maple, evergreen cypress, and carob tree (UNDP, 2015). The climate is typically the Mediterranean, characterized by spring and autumn rains, with hot, dry winters and summers. The soil is almost entirely composed of Cretaceous limestone dating from the Secondary Era, who's raised, sometimes folded but exposed strata are the titanic steps of a giant staircase. *Phillyrea latifolia* are plants with narrow, slightly toothed, opposing leaves. It belongs to the family of Oléacées.

Measured parameters

Leaf Water Potential

The Leaf Water Potential (ψ_{leaf}) was measured using the pressure chamber technique. Small twigs were cut and placed in a pressure chamber (Arimad 2®, A.R.I, KfarCharuv, Israel) connected and fed by a nitrogen gas bottle and equipped with a magnifying glass holder.

Gas exchange measurement

Net photosynthesis (Pn), stomatal conductance (gs) and leaf transpiration (Tr) were measured by the portable photosynthesis system Li-Cor Li-6400XT (Li-Cor, Li-6400XT Lincoln, NE, USA) based on the IRGA (Infra Red Gas Analysis) principle. One plant from each season was chosen for the A/Ci curves. For each curve, the leaf reached an equilibrium corresponding to a CO₂ concentration of 400 mmol.mol⁻¹, for 30 min to acclimate the plants to the conditions of temperature, PAR, ventilation rate and CO₂

concentration corresponding to the first point of the curve. The temperature is adjusted to 25 °C. Relative humidity was maintained at 60%.

Chlorophyll fluorescence

Measurements of the maximum efficiency of PSII photochemistry (F_v/F_m) were conducted in situ on attached leaves with a portable pulse-modulated fluorimeter PAM-2000 (Walz, Effeltrich, Germany). Leaves were dark-adapted with leaf clips for 1 h, which was determined to be sufficient to allow complete relaxation of energy-dependent quenching. The F_v/F_m ratio was calculated as $(F_m - F_o)/F_m$, where F_m and F_o are the maximum and basal fluorescence yields, respectively, of dark-adapted leaves (Genty et al., 1989).

Hydraulic conductivity

We have determined the hydraulic conductivity of the xylem using the high-pressure flowmeter method (Sack et al., 2002; Tyree et al., 2005). This method includes infusing degassed water at positive pressure P (2 MPa) into the segment and quantifying the flow rate at the inlet. Measuring the maximum hydraulic capacity was deduced by cavitation as follows:

$$PLC = 100 * \left(1 - \left(\frac{K_{in}}{K_{max}}\right)\right)$$

Where: PLC is the percentage of conductivity loss, K_{in} is the initial conductivity and K_{max} is the maximum conductivity measured after removing the gas trapped in the pipes (Sperry et al., 1988; Tyree and Yang, 1992; Hietz et al., 2008).

Gravimetric soil moisture

This method is considered as a reference method, it consists of 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 back weighing. Soil samples are taken with a helical auger up to 80 cm, given the heterogeneity of the soil and the rocks which sometimes prevent samples from being taken.

Statistics analysis

The data were subject to two ways ANOVA analysis with the GLM procedure of the statistical software package SAS version 9.1 (SAS Institute Inc., Cary, NC). The statistical assumption of residual normality was evaluated using the Shapiro-Wilk, while Levene's test was used for homogeneity of variances. Means difference was determined using the Student-Newman-Keuls test. Significance was considered at $P < 0.05$. The data were expressed as a mean $\pm$ standard error. The statistical model was:

$$Y_{ijk} = \mu + \alpha_i + e_{ij}$$

Where: Y_{ijk} = response variable of the plant (k) in the season i . μ = overall mean value for Y . α_i = fixed effect of the seasons ($j = 1-3$), and e_{ij} = error term.

Results

Rainfall seasonal variations

Precipitation and temperature differed between 2017 and 2019 in the areas being studied (Fig. 1). In 2017, in the period from January to September, the mean accumulated precipitation was low when compared with the same period of 2018 (21 mm and 38 mm, respectively). This was caused by a 44% decrease in rainfall from June onwards when compared with the same period of 2018. This decrease gave rise to lower water availability for plants over a long period.

This decrease in precipitation in Summer decline in rainfall affected gas exchange and water relations differently in the species studied. The differences in meteorological conditions mentioned above throughout the study is reflected in the results of the gas study exchanges and relationships in the field of water (Figs. 2, 3, 4 and 5). This being indicative of severe water stress since g_s is an integrative indicator of the degree of water stress (Flexas *et al.* 2002, Galmés *et al.*, 2007).

Leaf Water Potential (ψ_{leaf})

The results of Leaf Water Potential (ψ_{leaf}) are presented in Fig. 2. We observed significant differences among seasons ($P < .0001$) under seasonal variations conditions. During spring, ψ_{leaf} remained higher (-1.61 ± 0.075 MPa). However, during summer, ψ_{leaf} was increased with an increase in water stress. The measurements were around -2.99 ± 0.08 MPa. In autumn, *Phillyrea latifolia* reached lower levels of the ψ_{leaf} (1.20 ± 0.04 MPa).

Gas exchange

Net Photosynthesis (Pn) and transpiration (Tr)

The results of the photosynthesis (Pn) and Transpiration (Tr) are shown in Fig. 3. We observed significant differences in seasons ($P < .0001$). We noticed that during the study, the rainfall was concentrated in spring and autumn seasons, whereas the summers were the driest periods coinciding with higher air temperatures. 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 recorded in autumn, however, we have reported the lowest Pn and Tr average values of 0.39 ± 0.046 and $0.073 \pm 0.015 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively in summer.

Stomatal Conductance (g_s)

The results of the Stomatal Conductance (g_s) were shown in Fig. 4. We observed significant differences among seasons ($P < .0001$). The lowest values of the g_s were measured in summer (0.19 ± 0.04 MPa), under the higher temperature and water unavailability. The highest values of stomatal conductance were reached in autumn (1.12 ± 0.02 MPa) when temperatures were the lowest ones, and intermediate values were measured in spring (0.21 ± 0.05 MPa), either because of low water availability or low temperature, respectively.

Potential photochemical efficiencies of PSII (Fv/Fm)

The results of the quantum yield of primary photochemistry of PSII (Fv/Fm) were shown in Fig. 5. We observed significant differences among seasons ($P < .0001$). The highest values of the maximal photochemical efficiency of PSII (Fv/Fm) were observed in summer (0.83 ± 0.06), under the higher temperature and water unavailability. Though the lowest Fv/Fm values were reached in autumn (0.76 ± 0.07) when temperatures were the lowest ones, and intermediate values (0.77 ± 0.02) were measured in spring, either because of low water availability or low temperature, respectively.

Hydraulic Conductivity (K_{in} and K_{max})

Hydraulic Conductivity was presented in Fig. 6. Initial Hydraulic Conductivity (K_{in}) and Maximal Hydraulic Conductivity (K_{max}) were significantly different ($P < 0.001$) among seasons. The highest K_{in} value was reported during the spring season ($1.34 \cdot 10^{-4} \pm 1.10 \cdot 10^{-5} \text{ mmol s}^{-1} \text{ m}^{-2} \text{ MPa}^{-1}$), and in autumn ($1.18 \cdot 10^{-4} \pm 2.30 \cdot 10^{-6} \text{ mmol s}^{-1} \text{ m}^{-2} \text{ MPa}^{-1}$), followed by summer ($1.75 \cdot 10^{-5} \pm 3.61 \cdot 10^{-6} \text{ mmol s}^{-1} \text{ m}^{-2} \text{ MPa}^{-1}$). Whereas, the highest K_{max} value was reported during the spring season ($3.45 \cdot 10^{-4} \pm 2.70 \cdot 10^{-11} \text{ mmol s}^{-1} \text{ m}^{-2} \text{ MPa}^{-1}$). The lowest value was recorded in summer ($5.23 \cdot 10^{-5} \pm 6.73 \cdot 10^{-11} \text{ mmol s}^{-1} \text{ m}^{-2} \text{ MPa}^{-1}$).

Percentage of loss conductivity (PLC)

The results of the Percentage of loss conductivity (PLC) are presented in Table 1. We have reported a significant difference ($P < 0.001$) in PLC among seasons. In fact, during the spring season, the PLC values reached 61% for *Phillyrea latifolia*. In the dry season, the PLC peaked and reached 66%. For the autumn season, the PLC has been fully restored by decreasing their percentage to reach 41%.

Gravimetric soil moisture

Analysis of the water profile (Fig. 7) showed significant variations ($P < .0001$) in soil moisture content at different soil depths and as a function of seasons. During the spring season, the soil had a decreasing moisture profile as it moved to the depths and varied from $15.23 \pm 5.48\%$ at 20 cm to $6.26 \pm 2.46\%$ at 80 cm. In summer, the measurements exhibited that the volume of humidity is lower than in the spring, which can be explained by the absence of rainfall in this month 0 mm. These moisture levels ranged from $6.03 \pm 2.60\%$ during the spring season in the 20 cm depth to $2.24 \pm 1.63\%$ in the 80 cm depth. In autumn, *Phillyrea latifolia* reached higher levels of the soil moisture content. These levels ranged from $19.08 \pm 2.70\%$ in the 20 cm depth to $11.70 \pm 1.07\%$ in the 80 cm depth.

Discussion

In the Mediterranean area, water shortage represents the main limiting factor for plant growth (Zavala et al., 2000). Especially in shallow soils, where the vegetation does not completely cover the whole surface, water losses through evaporation in the dry season can deeply reduce the soil water content to values as low as 5% (Kemp et al., 1997; Pariente, 2002; Villegas et al., 2010). This results in a decreasing trend of

soil water content from the wet to the dry season. In this study, lower soil water contents were observed under the serval of climate change due to precipitation removal. Variability in water status shows that surface horizons 20 to 80 cm are very sensitive to summer drought in the DS site, which has very dry soils. Aussenacet *et al.* (1979), have proven these results by showing that the drying has spread to greater depths and is practically nil after 130 to 140 cm depth. The distinction of this water profile allows a comparison of the ecophysiological parameters of plants between seasons so that they can be classified with their adaptations to temporal variation in precipitation and temperature.

whereas after temperature increased and no precipitation events occurred, similar soil water content values were measured under both control and drought treatments. The reduced plant water availability under the drought treatment was also reflected in the lower leaf water potential measured in the summer compared to spring. In summer, the difference in soil water content was founded, and leaf water potential decreased to the minimum values in correspondence with the minimum soil water content measured at the end of summer. Different studies on leaf gas exchange in Mediterranean plants have highlighted similar leaf responses to those mentioned here. Net rates of photosynthesis, transpiration, and stomatal conductances decline with increasing drought (Oechel *et al.*, 1981; Tenhunen *et al.*, 1987; Damesin and Rambal, 1995; Penuelas *et al.*, 1998), but the response and the sensitivity rate depended on the species (Acherar and Rambal, 1992). Stomatal closure is one of the first responses of plants to protect it from exposure to severe water stress.

Phillyrea latifolia sprouts from underground organs; this is a common response to plants in Mediterranean-type ecosystems that have been affected by disturbances (Canadell *et al.*, 1991). This species has shown physiological performances that enable it to withstand climate change (Vitale *et al.*, 2007). We investigated whether the resilience of this species, from a functional point of view, is affected by climate change.

According to Llorens *et al.* (2003a) and Llusia *et al.* (2008), Pn, Tr, and gs are complex under unembellished climate change. Though, the imposed water accessibility has an impact on the leaf water potential, either in spring or in summer or autumn. During spring, it remained higher. However, during summer, ψ_{leaf} was increased with an increase in water stress. The best photosynthetic performance, Transpiration and stomatal conductance of *Phillyrea latifolia* were observed in spring and autumn and may be due to advantageous environmental conditions (non-limiting rainfall and air temperature). Nevertheless, during summer a general reduction of gs and photosynthesis was observed in the drought. The ecophysiological characteristics described in this study are in agreement with the different other species (Nogues *et al.*, 2012; Domenico de Dato *et al.*, 2013; Tattini *et al.*, 2002; Filella *et al.*, 1998). For example, in an earlier study on evergreen and broad-leaved oak (Ogaya and Peñuelas, 2003), it is clear that The carry-over effects of the summer drought were observed during the following cold season, decreasing the photosynthetic capacity of plants previously exposed to drought. Under conditions of extreme drought, *Phillyrea Latifolia* showed a decrease in photosynthesis performances, indicating a lower sensitivity to drought or high temperatures. Thus, to compare different adaptative strategies it is very important to conduct long term observations. It has been reported for *Phillyrea* plants,

the Fv/Fm ratio was slightly higher in summer than in spring and autumn. In our study, the maximum values of Fv/Fm were within the optimal range reported by Bjorkman and Demmig (1987) and they took place in the spring to fall. Conversely, summer Fv/Fm values were greater than 0.75 with a minimum of 0.83 ± 0.06 for phillyrea in summer, in agreement with previous studies on Mediterranean vegetation that also reported lower Fv/Fm values during these seasons. (García-Plazaola *et al.*, 1997, Karavatas and Manetas, 1999; Larcher, 2000; Oliveira and Penuelas, 2001).

Persistent reductions in PSII efficacy is mainly attributed to decreased photosynthesis, stomatal closure, and reduced stomatal conductance. Nevertheless, lasting reductions in Fv/Fm values can also result from the accumulation of nonfunctional PSII reactions and the partial photoinactivation of PSII (Niyogi, 1999).

There is increasing supporting evidence that xylem embolism limits gas exchange (Sperry *et al.*, 1998) and, in general, the ability of plants to cope with water stress (Pockman and Sperry, 2000; Sperry, 2000). In this study, it was found that the level of embolism in DS in the autumn is lower than in the other two seasons. This low rate may be an indication of the adaptation of this site to the drought phenomenon. These results are in agreement with Sperry *et al.* (2005) and Salleo *et al.* (2001) who showed that xylemic hydraulic conductance is controlled by physical processes such as vessel dimensions, wall structure that can be disturbed by the creation of embolism or air and water vapor bubbles that expel the liquid phase. The vessel is then said to be cavitared or embolized (Tyree *et al.*, 1989). Cavitation occurs particularly in cases of soil dryness (Vilagrosa *et al.*, 2003, Ennajeh *et al.*, 2008). It can also be seen that stomatal conductance follows the same aspect of variation of xylemic conductance presented in Fig. 33, these findings are proven by Cornic (2007). Previous studies have shown that plants differ widely in their vulnerability to drought-induced cavitation and that this variation is associated with the range of water potentials experienced in the field (Pockman and Sperry, 2000; Sperry, 2000). As a result, the difference between the critical leaf water potential causing catastrophic levels of xylem embolism and the minimum values under field conditions (Tyree and Sperry, 1988) tends to be small. This result suggests that there are disadvantages in having xylem that is overly resistant to cavitation. The main disadvantage that has been proposed is the existence of a trade-off between hydraulic potential and resistance to xylem embolism. Such a trade-off would have important evolutionary implications (Tyree *et al.*, 1994). Alternatively, it may also be that there are direct advantageous effects of cavitation. Xylem embolism can be viewed as a control mechanism which, in connection with the stomatal activity, regulates the amount of water extracted by the plant (Salleo *et al.*, 2001). Since differences in environmental conditions may introduce confounding effects in the relationships between hydraulic properties, we have focused on species coexisting in one single area.

Conclusion

In conclusion, seasonal variations in the physiological functioning of plants have occurred in both ambient and dry climates. Comparing the species's behavior requires a good knowledge of the soil-plant-atmosphere system during the study periods (March-January 2018).

The best photosynthetic performance, Transpiration and stomatal conductance of *Phillyrea latifolia* reported in spring and autumn may be attributed to favorable environmental conditions. Nevertheless, during summer a general reduction of g_s and photosynthesis was observed in the drought. the F_v/F_m ratio was slightly higher in summer than in spring and autumn. The vulnerability of xylem cavitation varies considerably according to season. The answers depend not only on the species but also on the climates in which they grow.

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Tables

Table 1: Percentage of loss conductivity (PLC)

	PLC (%)		
	Spring	Summer	Autumn
<i>Phillyrea latifolia</i>	61.15±1.2 ^b	66.58±1.62 ^a	41.15±1.7 ^c

Figures

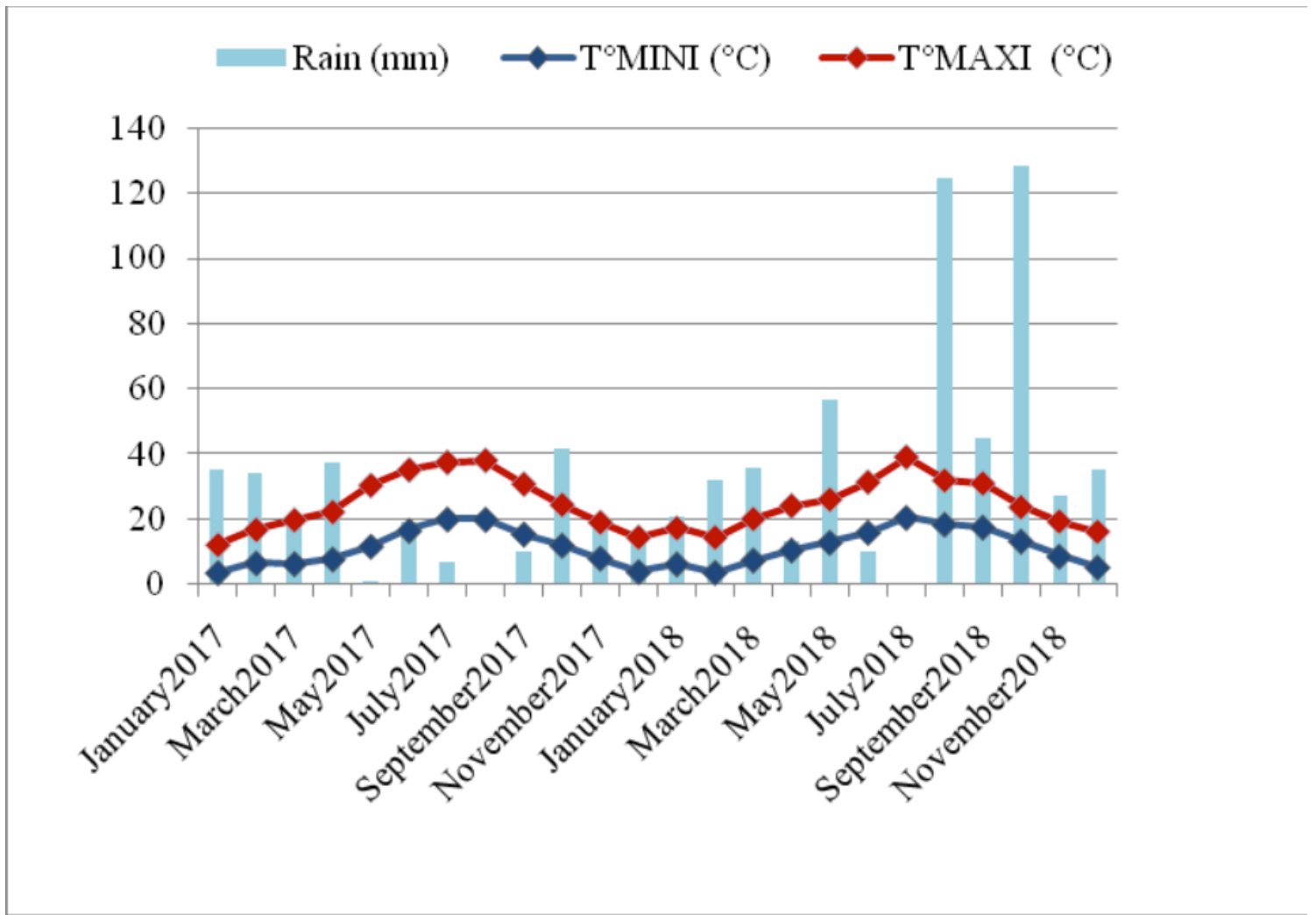


Figure 1

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

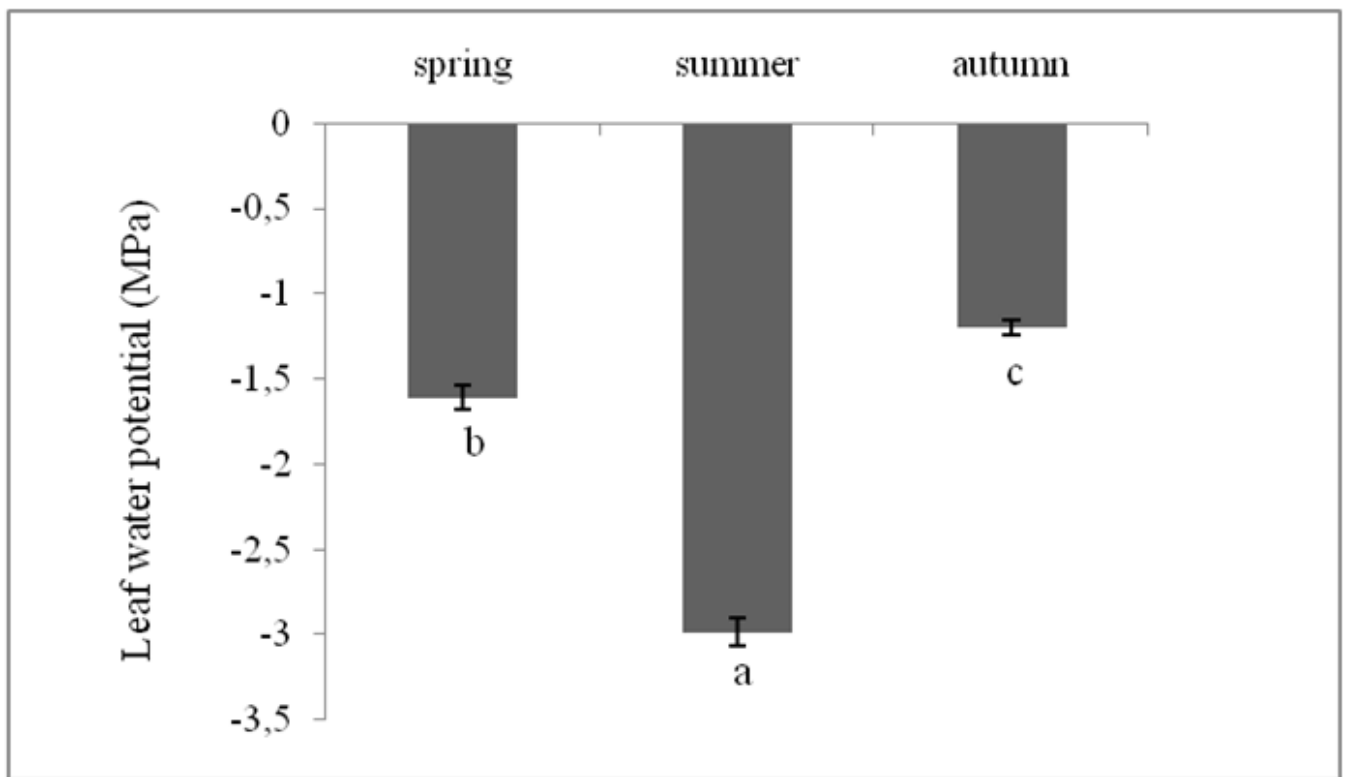


Figure 2

seasonal variability of ψ_{leaf} .

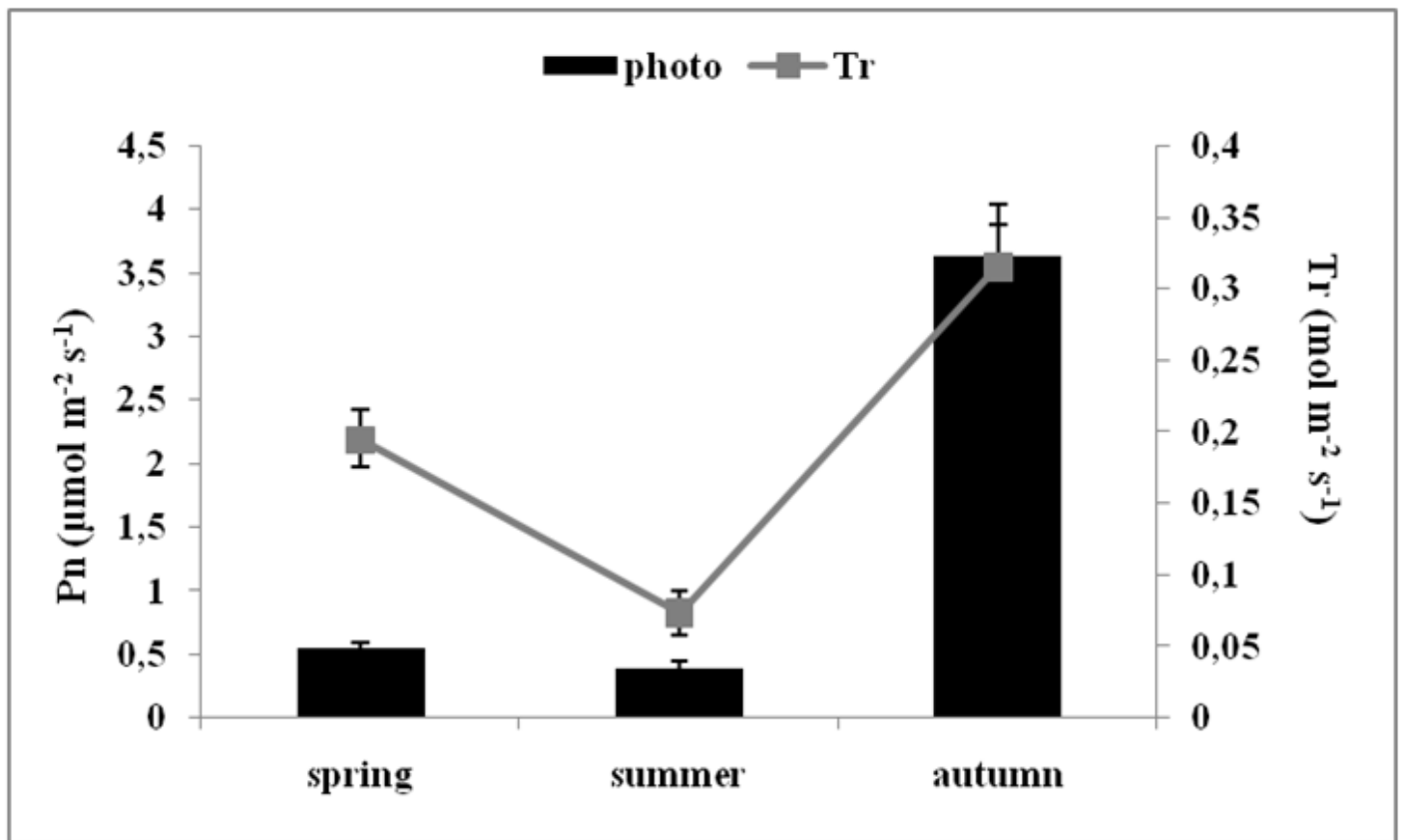


Figure 3

Seasonal variability of net photosynthesis (Pn) and Transpiration (Tr).

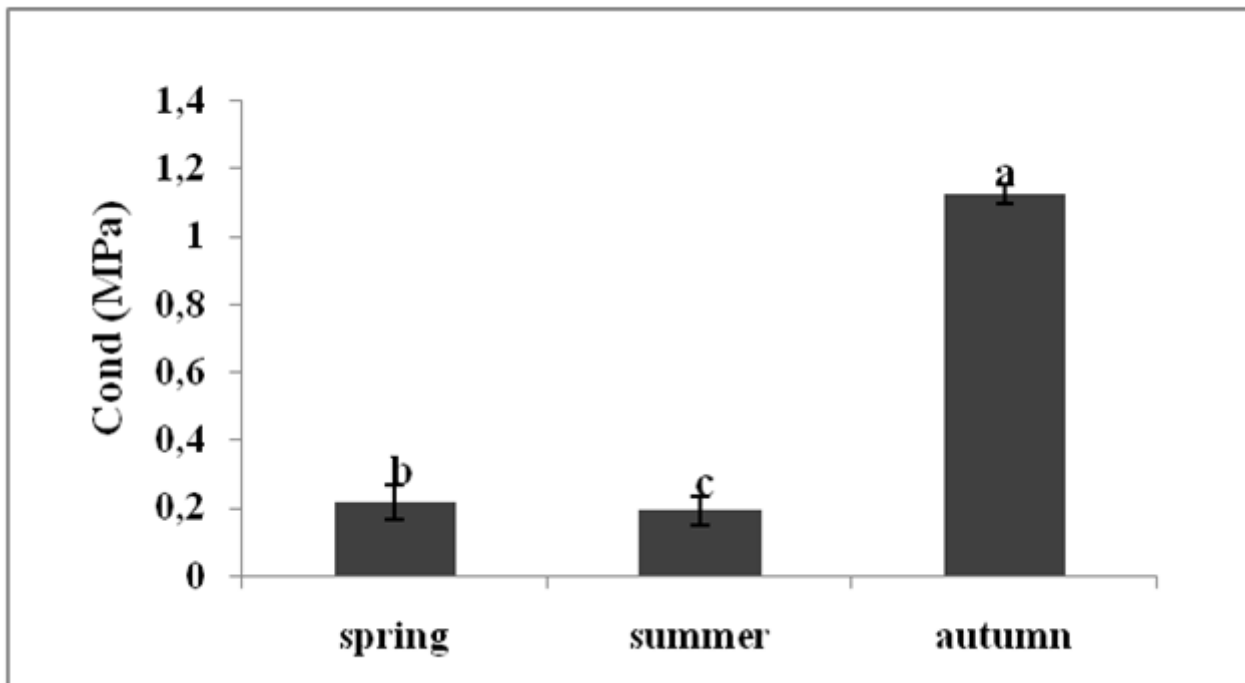


Figure 4

Seasonal variability Stomatal Conductance

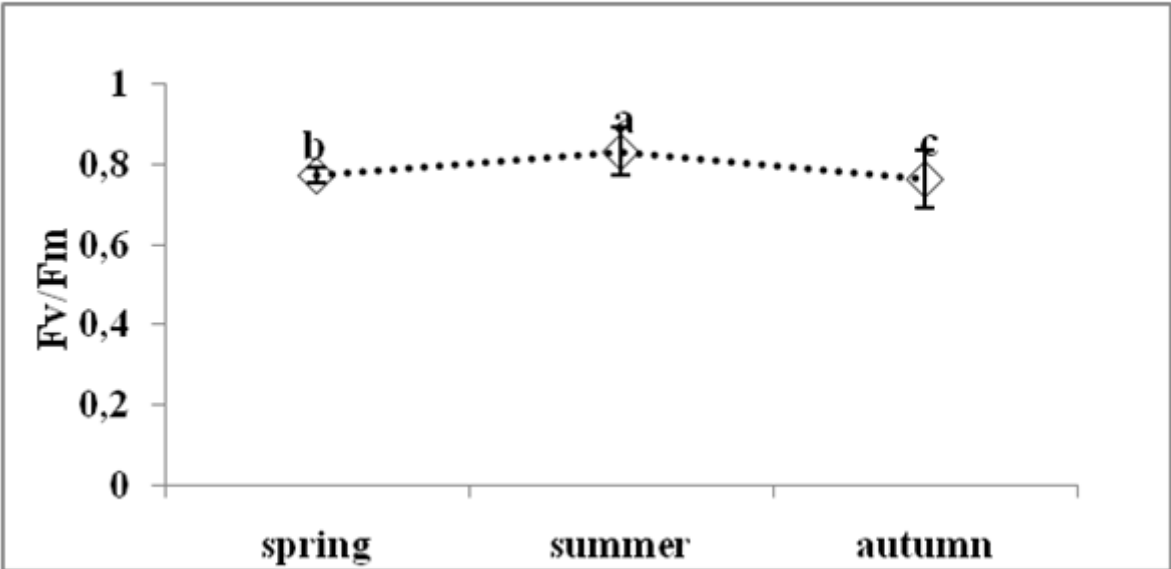


Figure 5

Seasonal variation of maximum quantum yield of primary photochemistry.

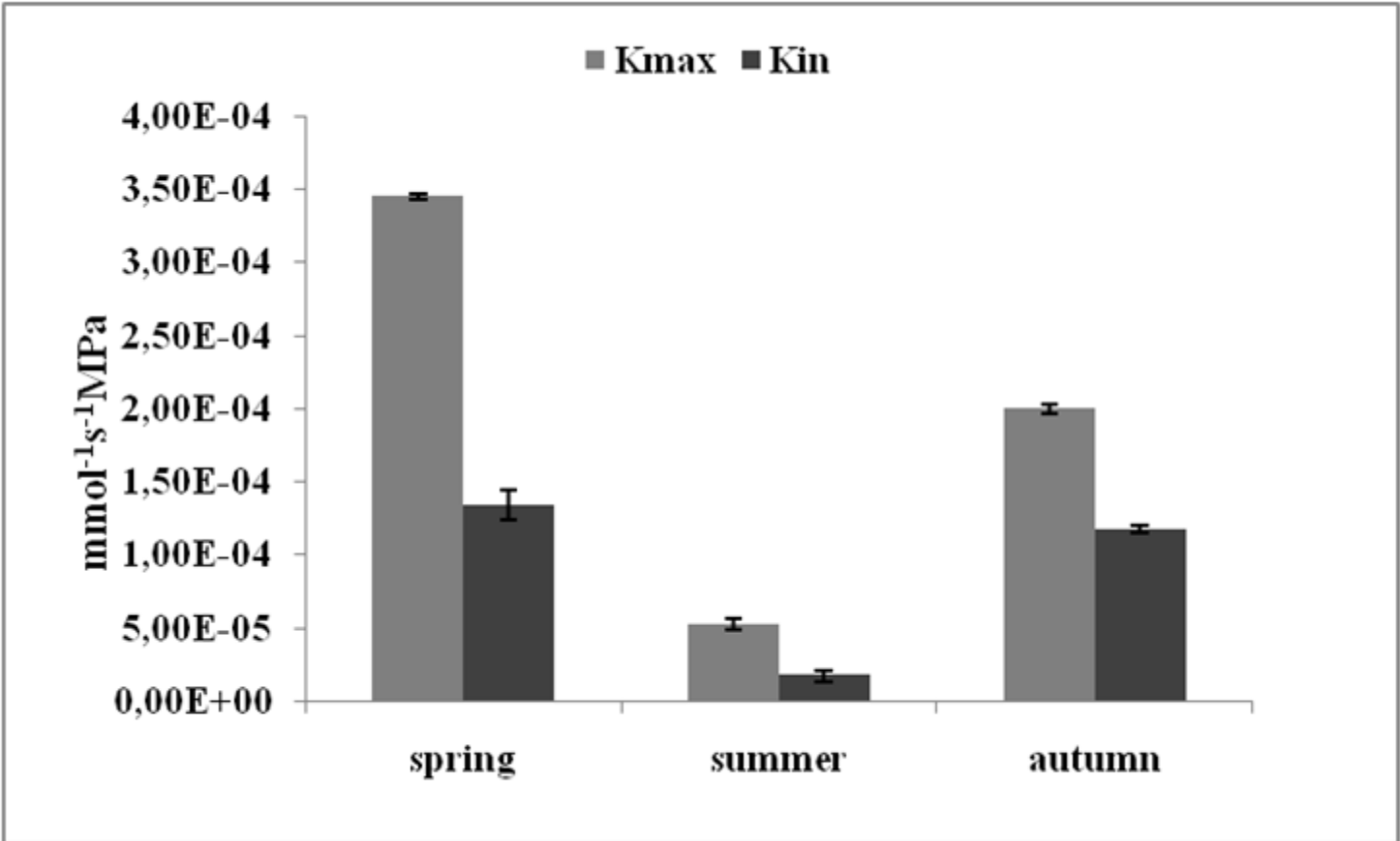


Figure 6

Seasonal variability of xylem conductivity (Kin and Kmax).

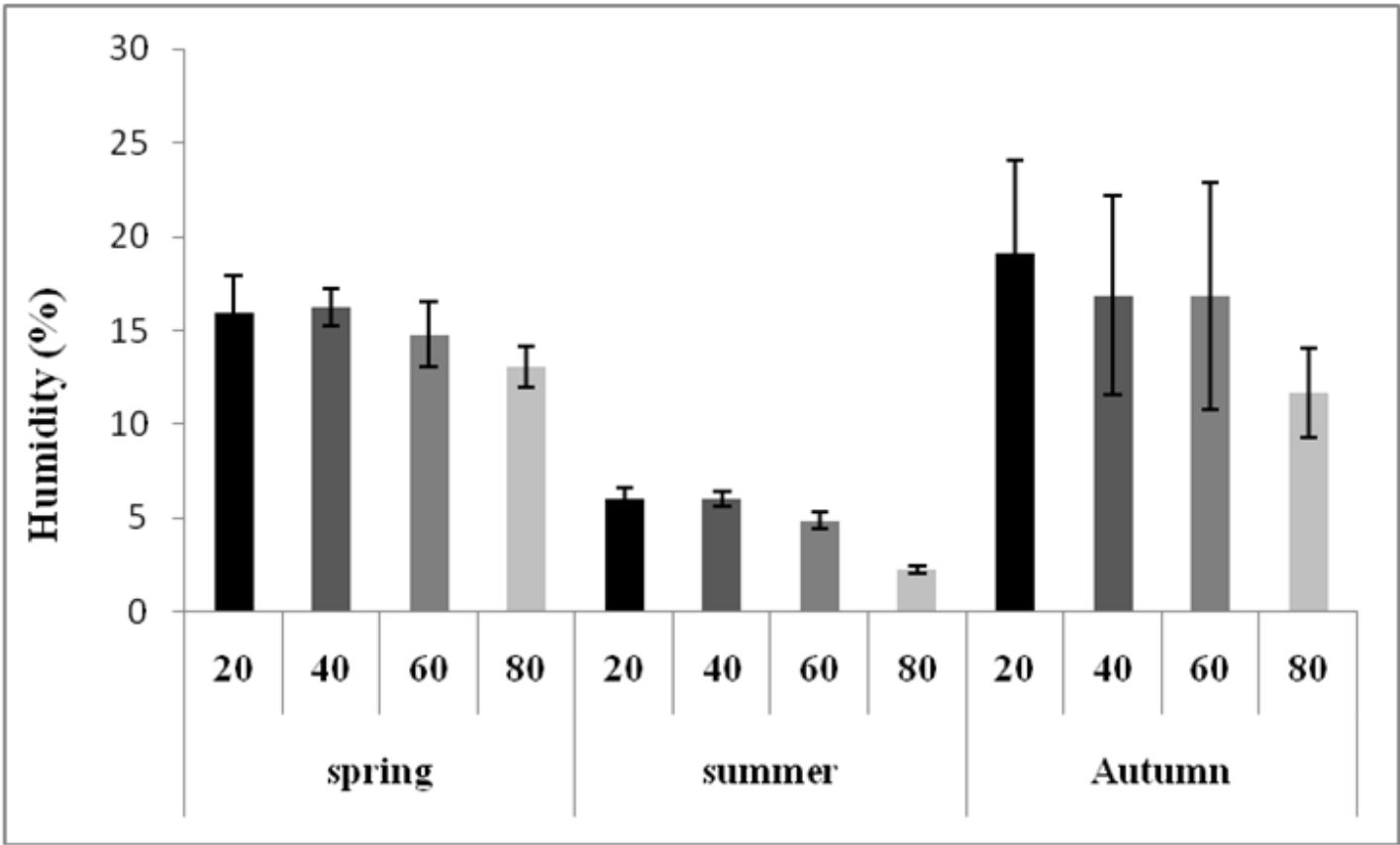


Figure 7

Evolution of the water profile from 20 to 80 cm depth during the three seasons.