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SEASONAL VARIABILITY OF GAS EXCHANGE RESPONSES AND HYDRAULIC TRAITS OF THREE PROVENANCES OF *PINUS HALEPENSIS* MILL.

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Abstract: *The now regenerating forests will have to adapt to overcome novels climatic conditions in order to sustain for several decades, even more than a century. These terrestrial ecosystems play an important role against the increase of greenhouses gas emissions in the atmosphere and so in the prevention from climate change that significantly modify ecophysiological responses of trees and deeply affects ecosystems. The aim of this study was to compare the water status of three Aleppo pine sites from different bioclimatic stages: Djebel Zaghouan (DZ), Djebel Mansour (DM) and Djebel Sarj (DS), based on soil-plant-atmosphere continuity. The experimental approach was based on monitoring soil water behavior, gas exchange and hydraulic conductivity with climatic variability. Our results showed that DZ was both tolerable water status and physiology compared to the others sources DM and DS. It also showed the best performance in terms of adaptation with a low average of* ET_0 *(3.2 mm/d); while DM and DS recorded 5.3 and 5.5 mm/d, respectively. In addition, DZ showed a significant relative humidity in the soil reaching 26% and a xylemic conductivity with 16.3% of embolism compared to DM and DS, which have the highest percentages related to the increase in drying up. In conclusion, our data showed a significant difference in physiological behavior between the three provenances.*

Key words: *Aleppo pine, climate change, gas exchange, conductivity, water status.*

1. Introduction

The forest sector is a vital natural resource in the world. It is closely related to the water sector, being capable of modifying its quality and availability. The forest, through its biological functions, plays an indispensable role by reducing surface runoff and improves water storage. It is as an essential filter of pollutants for the conservation of biodiversity. In Tunisia, forests, maquis and garrigue trees reach 686.459 ha and almost half of the surface is occupied by

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Aleppo pine, which remains an important plant in terms of productivity at national level [6]. One third of Aleppo pine plantations (115045 ha) are located in northeast Tunisia in the regions of Zaghouan and Siliana. These regions were affected by the adverse effects of climate change which had been caused the destruction of quite 6158 ha in the last decade [6]. These effects are mainly explained by the increase of greenhouse gas (GHG) emissions due to the anthropogenic activity.

The manifestations of climate change such as the arising temperatures, the decrease in rainfall, the appearance of extreme events, fires were affected our country more deeply from south to north, which is proven by an increase in aridity from which the forestry sector, like other sectors, is actually increasingly threatened.

Climatic disturbances are also causing the decrease of summer soil humidity [4, 6], the increase of evaporation in all Mediterranean regions and the accentuation of extreme events such as droughts ; they become more intense and more severe, leading to water deficits and decreasing availability of water resources.

Tunisia was therefore facing a situation of water scarcity, which could be intensified further with the potential different scenarios of the future climate changes; bearing in mind that the volume of available water would be only around 360 m^3/year/inhabitant by 2030 [13]. Furthermore, ground water resources at the ground water level will decrease by 28% in 2030, while, the decrease in surface water will be around 5% at the same horizon [12].

The forests service in providing water was the objective of several studies that have a key role hence the reforestation projects around the world are increasing [9]. In Tunisia forestry studies, about adaptation and their productivity in relation to present and future climatic disturbances remain unsatisfactory. The aim of the present study was to create a model of hydrological, climatic and physiological study of the Aleppo pine trees to improve the knowledge of their general status and their spatiotemporal variability in three different geographical zones from Tunisia namely Jebel Zaghouan (DZ), Jebel Mansour (DM) and Jebel el Sarj (DS).

2. Materials and Methods

2.1. Plant Material

The experimental Sites were located in Northeast of Tunisia (Figure 1). Geographical characteristics of sites are illustrated in Table 1.

Table 1

Geographical characteristics of study areas

Forest	Location	Latitude	Longitude	Altitude [m]
Djebel Zaghouan	Zaghouan	36° 22.0' N	010° 07.0' E	320 - 330
Djebel Mansour	El Fahs	36° 15.0' N	009° 47.0'E	397 - 405
Djebel el Sarj	Siliana	35° 57.0' N	009° 33.0' E	793-798

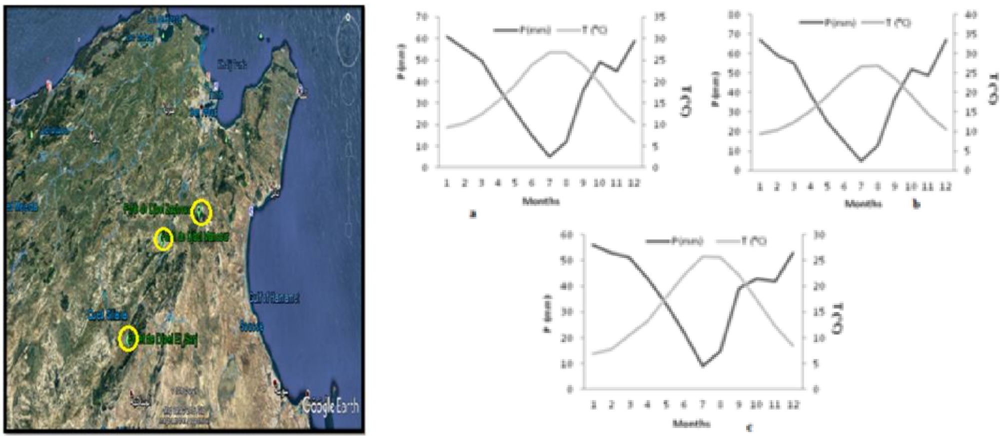

Fig. 1. Location of sites and climatic diagrams of studied sites
for the period 1982 – 2012 [23]

2.2. Relative Sol Humidity

Soil water content was monitored weekly by time domain refractometry (TDR, Trase system I, Soil moisture Equipment Corp., USA).

2.3. Leaf Water Potential

Leaf water potential (LWP) was determined using the pressure chamber technique. Small twigs were cut and put in a pressure chamber (Arimad 2®, A.R.I, Kfar Charuv, Israel) fed by a Nitrogen gas cylinder and equipped with a lamp-carrying magnifying glass.

2.4. Evapotranspiration

Evapotranspiration was determined using The 'MABIA-ET0' software according to the FAO-PENMAN-MONTHEITH method [1]:

$$ET_0 = \frac{0{,}408 \cdot \Delta \cdot (R_n - G) + \gamma \cdot \frac{900}{T+273} \cdot u_2 \cdot (e_s - e_a)}{\Delta + \gamma \cdot (1 + 0{,}34 \cdot u_2)} \quad (1)$$

where:

- ET_o is reference evapotranspiration [mm/day];
- R_n - net radiation on the culture surface [MJ/m^2/day];
- G - soil heat flux density [MJ/m^2/day] negligible (G = 0);
- $T_{moyenne}$ - average air temperature [°C];
- u_2 - wind speed measured at 2 m height [m/s];
- e_s - saturation vapour pressure [kPa];
- e_a - actual vapour pressure [kPa];
- e_s - e_a - saturation vapour pressure deficit [kPa];
- D - slope vapour pressure curve [kPa/°C];
- g - psychrometric constant [kPa/°C].

2.5. Climatic Parameters of Studied Sites

The climatic parameters characteristics of the studied sites are summarized in Tables 2, 3 and 4.

2.6. Gas Exchange Measurement

Gas exchanges were measured with a Li-Cor Li-6400XT Portable Photosynthesis

System (Li-Cor, Li-6400XT Lincoln, NE, USA) based on the IRGA principle (Infra RedGas Analysis). The leaf stomata conductance (g, in mol H_2O $m^{-2}s^{-1}$), net carbon assimilation (A, in µmol CO_2 $m^{-2}s^{-1}$), and transpiration (T, in mmol H_2O $m^{-2}s^{-1}$), were measured on the *Pinus halepensis* needles of each studied sites. Twelve branches were used from each site. They were cut and placed in tubes with their bases under water. The experiments were carried at a leaf temperature of 25°C and humidity of 50-60%. The needles of each branch were placed under the clamp of the chamber assimilation (6 cm^2) and they were acclimatized for 35 minutes. A program was then set to make a variation of the CO_2 concentration. These measurements were used for the calculation of intrinsic water-use efficiency (WUE, in mmol CO_2 $mol^{-1}H_2O$) according to: WUE = A / g.

Table 1

Climatic characteristics (November 2016 – October 2017) for DZ

Months	T_{max} [°C]	T_{min} [°C]	HR_{max} [%]	HR_{min} [%]	N [h]	U_z [m/s]	ET_o [mm/j]	Precipitation [mm/j]
1	13.8	5.8	72.5	72.5	8.7	5.3	1.7	1.6
2	17.8	8.4	71.5	71.5	12.1	4.8	1.9	1.4
3	20.5	9.6	65.9	65.9	17.7	5.0	2.4	0.3
4	22.4	11.4	61.7	61.7	20.5	4.7	2.9	0.5
5	27.7	15.4	56.9	56.9	25.0	4.4	3.6	0.0
6	32.5	20.1	50.8	50.8	26.6	4.0	4.3	0.6
7	35.1	22.7	45.3	45.3	27.6	5.4	6.1	0.0
8	36.0	23.8	45.0	45.0	25.0	3.8	4.9	0.1
9	30.4	19.7	56.8	56.8	19.0	4.4	3.9	0.2
10	24.8	15.7	68.2	68.2	13.8	4.3	2.5	1.5
11	21.8	13.3	68.0	68.0	9.0	4.2	2.3	0.7
12	17.0	10.5	77.9	77.9	7.0	4.3	1.4	4.5

Table 3

Climatic characteristics (November 2016 – October 2017) for DM

Months	T_{max} [°C]	T_{min} [°C]	HR_{max} [%]	HR_{min} [%]	N [h]	U_z [m/s]	ET_o [mm/j]	Precipitation [mm/j]
1	11.6	2.0	6.3	6.3	8.2	4.8	4.3	1.1
2	17.0	5.3	10.2	10.2	11.5	4.7	4.9	1.0
3	20.0	6.7	12.5	12.5	17.1	4.6	5.3	0.8
4	22.1	8.4	14.7	14.7	19.9	4.2	5.5	0.8
5	28.9	12.7	20.3	20.3	24.3	4.0	6.1	0.0
6	33.6	17.6	25.2	25.2	26.0	3.4	5.9	0.7
7	36.5	20.3	28.1	28.1	26.6	4.8	7.5	0.0
8	37.4	21.5	29.0	29.0	24.7	3.7	6.4	0.0
9	30.1	16.2	22.6	22.6	18.3	3.7	5.9	0.3
10	23.7	12.0	17.0	17.0	13.7	3.8	5.3	1.3
11	20.2	9.2	13.7	13.7	9.7	3.8	5.0	0.5
12	15.0	6.9	10.3	10.3	7.0	3.7	4.3	2.5

Table 4

Climatic characteristics (November 2016 – October 2017) for DS

Months	T_{max} [°C]	T_{min} [°C]	HR_{max} [%]	HR_{min} [%]	N [h]	U_z [m/s]	ET_o [mm/j]	Precipitation [mm/j]
1	12.1	1.2	5.9	5.9	10.2	4.5	4.2	1.0
2	17.6	5.2	10.5	10.5	13.5	4.3	4.8	0.6
3	20.9	7.2	13.2	13.2	18.5	4.7	5.4	0.7
4	22.8	8.7	15.3	15.3	20.4	4.2	5.4	0.7
5	28.9	13.8	21.0	21.0	25.1	3.6	5.7	0.1
6	34.0	18.5	26.0	26.0	27.1	3.4	5.8	0.7
7	36.9	20.7	28.5	28.5	27.6	4.0	6.6	0.0
8	37.2	22.0	29.2	29.2	25.2	3.1	5.6	0.0
9	30.5	16.9	23.1	23.1	20.2	3.7	5.8	0.2
10	24.1	12.1	17.4	17.4	15.2	3.6	5.1	0.4
11	20.5	9.5	14.1	14.1	10.6	3.7	4.9	0.5
12	14.9	6.4	10.0	10.0	8.2	3.7	4.2	2.0

2.7. Hydraulic Conductivity

Measurements of xylem hydraulic conductivity were performed using the HPFM method (high pressure flow meter) as described by Sack et al (2002) and Tyree et al. (2005). The technique consists in perfusing degassed water under positive pressure +P (MPa) in the segment and to measure the flow at the entry. The measured flow values (F, mmol s^{-1}) are automatically recorded in a computer connected to the machine HPFM. The relevant parameter is the extent to which the maximum hydraulic capacity has been reduced by cavitations: Per cent loss conductivity:

$$PLC = \frac{K_{S\,max} - K_S}{K_{S\,max}} \cdot 100 \quad (2)$$

where: K_{min} is the initial conductivity and K_{max} is the maximum conductivity measured after gas trapped within the conduits has been removed, using a high-pressure flush with partially degassed water or holding the measured segment in solution under a partial vacuum [10, 15, 19].

2.8. Statistical Analyses

Data were the object of an analysis of the variance to two factors (Provenance and water stress), significance levels were established at P<0.05. It was completed by a multiple comparison of the averages by the test of Newman-Keuls test (P<0.05) accordingly. The differences between populations for the investigated variables were tested with a Principal Component Analysis (PCA) using R software.

3. Results

3.1. Leaf Water Potential

We observed that in DZ, water potential values (Figure 2a) varied between 4.5 and 5.9 Bar. This variability is highly significant between seasons one can note that there was low variability between measurements on the same trees in different seasons. This variability reflects, as a first approximation, differences in water consumption, due to the low inputs they receive, especially during the summer.

While, it was observed for DM (Figure 2b), water potential were higher than those obtained in the DZ site. They were between 7 and 5.5 Bar in both spring and summer but increase more for the DS site (Figure 2c) but no significant differences were recorded between sites.

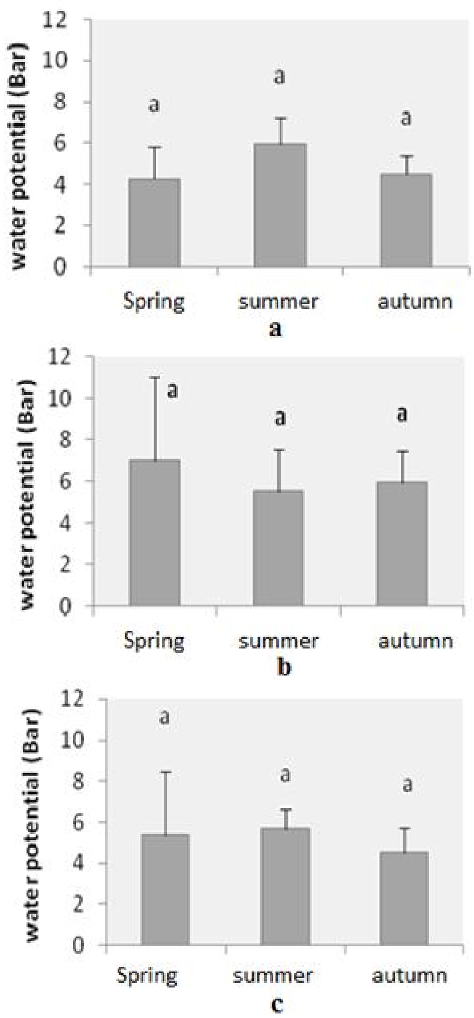

Fig. 2. Leaf water potential in: a. Djbel Zaghouan: b. Djbel Mansour; c. Djbel Sarj

3.2. Seasonal Variation of Net Photosynthesis

For DZ site, the Transpiration (Tr) and Photosynthesis (An) decreased from spring to autumn (Figure 3a) Photosynthesis varies from 8 µmol m^2s^{-1} in spring to 1.5 8 µmol m^2s^{-1} in autumn. The measured values were positively correlated with trees conductivity variation of the trees (Figure 3a).

The two sites DM and DS showed the same trend of variation as recorded in DZ site, but with lower averages (Figures 3b and 3c). This parameter does not have a significant difference between seasons.

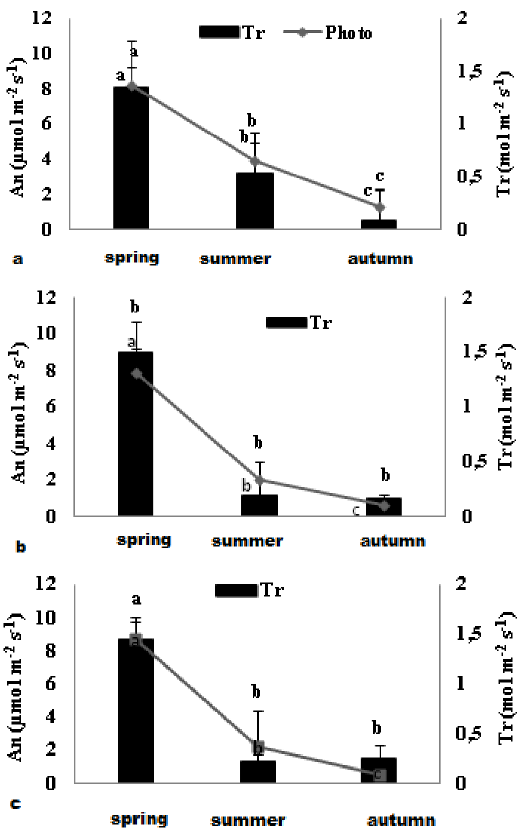

Fig. 3. Seasonal variability net photosynthesis and transpiration of three provenances

For Tr, a significant variability was observed especially in summer and autumn (Figures 3a, 3b and 3c) when the climatic factors are severe. It was recorded between July and August 0 mm office plurality of rain with an increase in temperature about 16 C compared to spring (Figure 4).

The variability of gas exchange was strongly correlated positively with the change in relation to the humidity of the air.

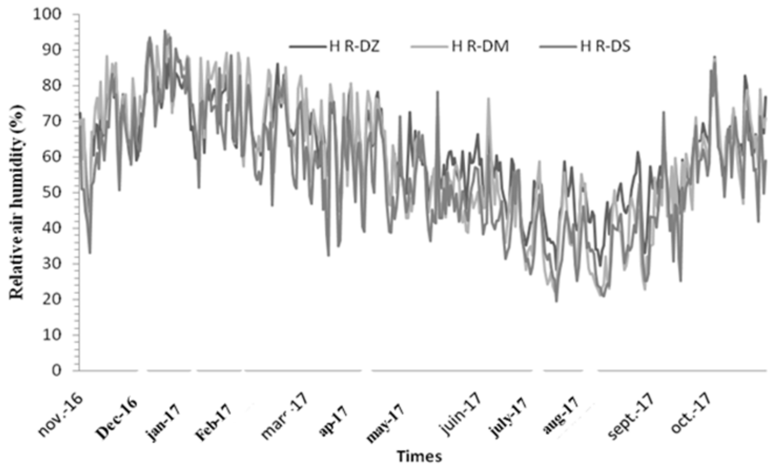

Fig. 4. Evolution of the percentage of relative air humidity in three sites

3.3. Hydraulic Conductivity and Stomata Conductance

In the DZ site, the results obtained from statistical analysis showed that K_{min} had significant inter-seasonal differences.

The obtained averages ranged from 1.4 x 10^{-5} during the autumn to 4.87 x 10^{-4} mmol s^{-1} m^{-2} MPa^{-1} in the spring (Figure 5a) with an intermediate of 1.2 x 10^{-5} mmol s^{-1} m^{-2} MPa^{-1}during the summer season.

We also observed that K_{max}, values were positively correlated with K_{min}. The measurement of embolism showed only 16.3%, which can prove that the drought does not necessarily affect the conductivity in this site (Figure 6).

For the DM site, a significant difference in initial hydraulic conductivity values between the three seasons were recorded. They were almost non-existent during the summer and autumn, compared to spring time (Figure 5b).

Furthermore, low spring temperatures may explain this inter-seasonal variability.

The averages of changes in conductivity at this site ranged from a low level of $5.92.10^{-6}$ in the fall to a higher level of $2.17.10^{-4}$ mmol s^{-1} m^{-2} MPa^{-1}in the spring, which had significant differences with K_{max} values following 63.20% increase in embolism.

Similarly at DS site (Figure 5c) the conductivity increased during the spring compared to the two other seasons but it remains very low and has a significant difference between K_{min} and K_{max}.

We observed that K_{in} and K_{max} xylem conductivity in this site were lower than the two other sites, DZ and DM showing a 70.6% increase in PLC percentage (Figure 6).

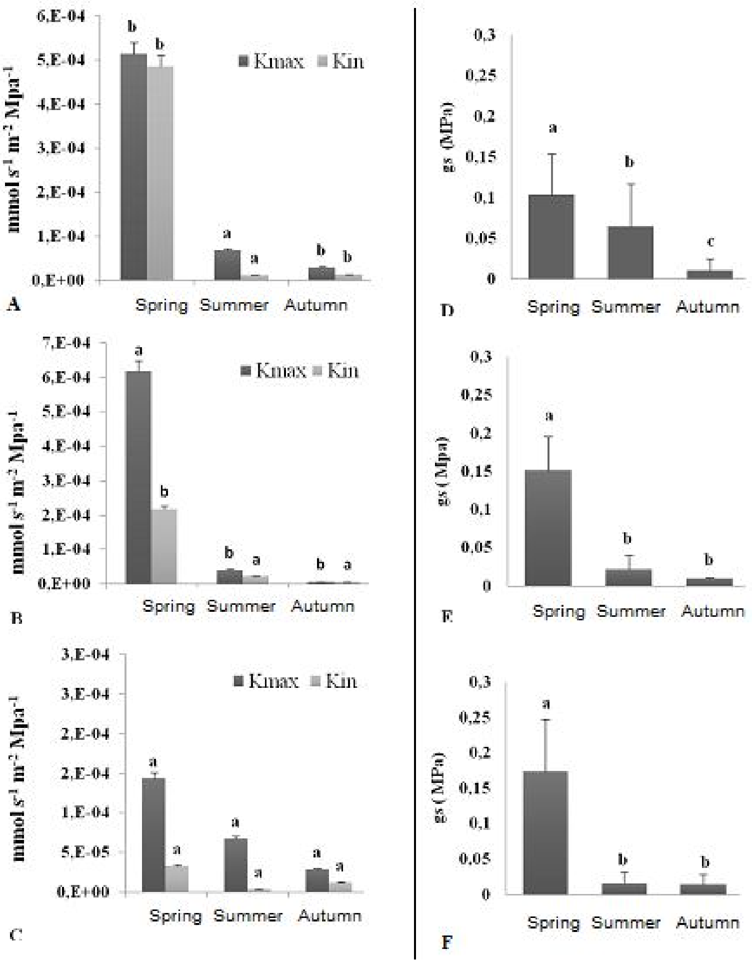

Fig. 5. Seasonal variability of xylem conductivity (Kin and K_{max}) and stomatal conductance (gs) of three provenances

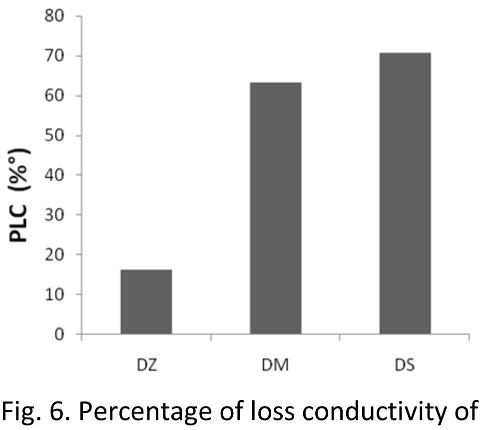

Fig. 6. Percentage of loss conductivity of three provenances

In spring, it was shown an increases in K_{in} and K_{max} values while they also appear to be non-existent during the fall and summer.

These variations are positively correlated with climatic factors such as the rainfall decrease in summer and the increase of the daylight period.

We showed a significant correlation between net photosynthesis, stomatal conductance, and transpiration. While, not significant correlation was observed with K_{in} an K_{max} (Table 5).

Table 5

Correlation matrix of the different parameters measured

	WP	K_{max}	K_{in}	g_s	Photo	WUE	Tr
WP	1						
K_{max}	-0,178	1					
K_{in}	-0,389	0,453	1				
Cond	0,312	-0,446	-0,390	1			
Photo	0,191	-0,497	-0,375	**0,959**	1		
WUE	-0,175	0,020	-0,413	-0,298	-0,400	1	
Tr	0,228	-0,449	-0,449	**0,969**	**0,977**	-0,241	1

In bold, significant values (off diagonal) at the alpha threshold = 0.050 (two-sided test).

Principal components analysis showed that the interactions between the sites and the parameters studied are close. Depending on these parameters, two distinct groups can be distinguished (Figure 7):

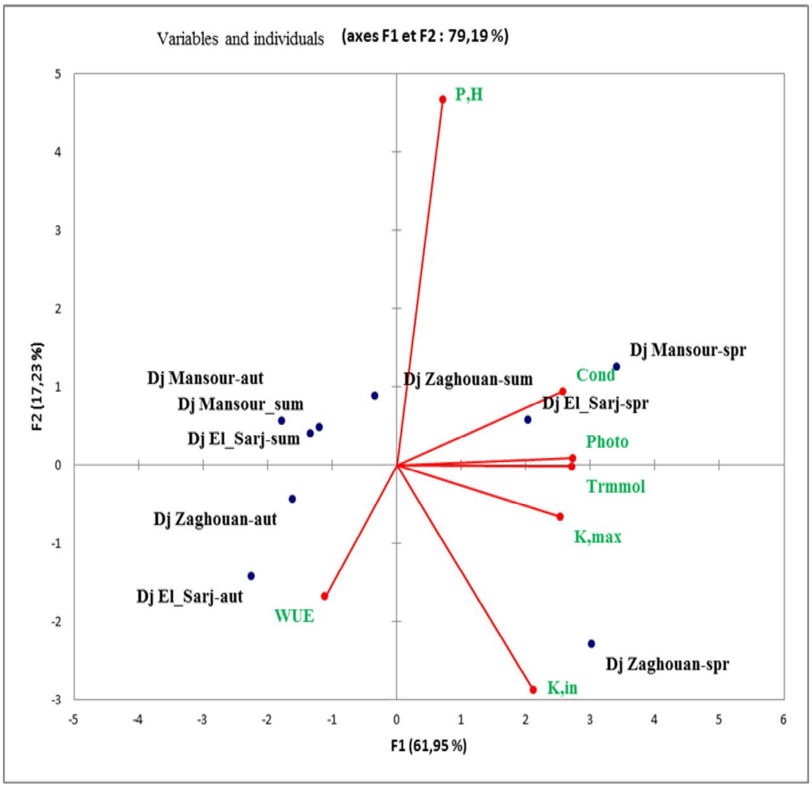

Fig. 7. Distribution of physiological parameters according to provenances and seasons

Zone A: includes the two sites Jebel Zaghouan and Jebel Mansour where most of the studied parameters have positive correlations, which can probably confirm that the physiological state of the Aleppo pine trees in these two provenances, which are probably more resilient towards the climatic disturbances and that they are then more resistant.

Zone B: concerns Djebel El Sarj where the existence of the increase of water potential was observed which is a factor describing the state of stress with climatic factors not very suitable to the growth of this species.

4. Discussions

Drought tolerance is a known characteristic of Aleppo pine trees compared to other species, and is probably due to efficacy stomatal control. The closure and opening of stomata are strongly related mainly to water availability [2]. In the studied sites, DZ presented the site with the lowest stomatal conductance when compared to the other two sites. It gathers then the character of the most tolerant source of climate variability. The increase in pH was considered as a drought alert state of the studied species because the more it increases the more water tends to leave this compartment the lower the humidity on the ground [11]. This increase was more observed in DS than DM and DZ in relation to the increase in stomata conductance in the same site.

It was found that the level of embolism in DZ is lower than the other two sites studied. This low rate can be an index of the adaptation of this site to the drought, which increased more and more when considering the other two sites. These results are in agreement with those of Sperry et al. (2005) and Salleo et al. (2001) who showed that xylemian hydraulic conductance was controlled by physical processes such as vessel dimensions, wall structure that can be disturbed by the creation of embolism or bubbles of air and water vapour that chase the liquid phase. The vessel is then called cavity or embolized [20]. It was also reported that cavitation occurs particularly in case of soil drought [8, 22].

It can also be seen that the stomatal conductance followed the same aspect of variation in the xylem conductance [3]. These results are in agreement with those described by Cruiziat et al. (2001) who found that the variation of the stomatal conductance was positively correlated with the opening and closing of the stomata.

The variation of photosynthesis is dependent on temperature. By causing stomata closure, the water deficit prevents gas exchange and thus a reduction in photosynthesis [14] as the case studied in the three sites during the summer season.

Leaf transpiration is a parameter of the water status of the plant. Its variation is related to that of photosynthesis, at the same stages. The reduction of transpiration was observed mainly in the DS site with increasing temperatures.

The analysis of these parameters shows that the water status of DZ despite increasing temperatures and lowering precipitation is the most resilient site in terms of adaptation to climate change.

5. Conclusion

The adaptability of the Aleppo pine species to climatic factors, such as the variability of temperatures and the reduction of cumulative rainfall, which consider themselves as inhibiting factors of its resilience, does not prevent it from to be more productive and tolerant in more sites than others.

The comparison of the three provenances DZ, DM and DS requires a good knowledge of the soil-plant-atmosphere system during the same periods of study (March-October, 2017).

Principal component analyzes (PCA) after experimental analyzes at the three provenances indicated positive correlations between tree gas exchange, conductivity, and water profile during seasonal variability with maximum spring averages.

Modeling of ET0 using the Penman-Montheith method (FAO-56) by MABIA-ET0 revealed that the DZ site is the most tolerant, with the lowest average (3.2 mm/d).

Using the statistical study of physiological data (stomatal, xylemian conductance) of Aleppo pine trees, a positive correlation was confirmed. These are related to the seasonal variability that affects stomatal status in all sites.

DZ has a lower conductivity than DM and DS which gives it the character of the source having more stomatal control.

In the same context, the decrease in the values of the physiological parameters due to the summer drought is accompanied by an increase in the water potential in the three provenances.

According to all this results, Jebel Zaghouan has the most favourable characteristics for the development of Aleppo pine and the lowest vulnerability to the climatic disturbances that Jebel Mansour and Djebel El Sarj.

No other conflict of interest between my work and that of the authors.

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