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Root architecture adaptation of *Pistacia atlantica* subsp. *atlantica* according to an increasing climatic and edaphic gradient: case of a north–south transect in Algeria

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Abstract: Despite xeric conditions, *Pistacia atlantica* Desf. subsp. *atlantica* (Atlas pistachio) succeeds in developing impressive dendrometric dimensions (25-m high, 2-m trunk diameter). It is among the rare spontaneous phanerophytes of the North African steppe. With access to water being the primary condition for survival, we focused on its root system. According to a gradient of increasing climatic and edaphic aridity in Algeria, we recorded different root architectures set up by this tree. We sampled its underlying soil and determined its main physico-chemical characteristics. Root architecture is mainly of the superficial type with more than 60% of roots located in the top 50 cm of soil along the north–south transect. With the decrease in precipitation and the rising of temperatures, length of the dry season, and the content of sand in soil, the number of superficial roots and their ramifications decrease, while their average circumferences, and the length and average circumference of the deep roots increase. These deep and thick roots allow access and storage of moisture present in the deep levels and protected there from evaporation, and, on the other hand, provide an important anchor in these soft soils. The Atlas pistachio adapts to increasing climatic and edaphic aridity by adopting a phreatophytic strategy.

Key words: *Pistacia*, Atlas pistachio, roots adaptation, African steppe, arid soils, drought

1. Introduction

Understanding how xerophytes adapt to arid environments will allow their use in the global effort to fight/prevent desertification. *Pistacia atlantica* Desf. subsp. *atlantica* (Atlas pistachio) (Figure 1) is one such species with a significant adaptive potential.

Despite the conditions of xericity, the Atlas pistachio develops impressive dendrometric dimensions (up to 25-m tall and 2 m in trunk diameter) (Nègre, 1962). While the flora (and fauna) of these arid areas adopts strategies of avoidance during the dry period, the Atlas pistachio opts for endurance. Indeed, its bud burst, flowering, and fruiting coincide with the warmer periods of the year (between March and September). In addition, the rate of elongation of its roots, which is estimated as 1.5 m per season (Ozenda, 2004), gives it a major advantage in the success of its installation.

The Atlas pistachio is a valuable autogenous engineer in these indigent areas. Due to the lapse of its leaves and its extensive root system, it is a valuable source of organic matter (OM) for soils and stands that live there. Indigenous populations use its wood as fuel and its leafy branches for tanning leather (Ozenda, 2004). The seeds are edible and are very rich in fatty acids. It is also an excellent rootstock for *Pistacia vera* L.

In Algeria, although many studies have been conducted on the Atlas pistachio, they have primarily targeted its more accessible aerian part. We can cite nonexhaustively the work by Belhadj et al. (2008) on the analysis of morphological variability of its leaves and fruit and on its leaf micromorphology (Belhadj et al., 2007), and the work by Ait Said et al. (2011) on its leaf morpho-anatomy and phytochemistry. However, with regards to its underground part (its root system), few studies have been conducted. Indeed, many authors (Habib et al., 1991; Malamy, 2005; Watt and Weston, 2009) think that this body is generally left in "shadow", whereas it is vital in the acquisition of hydromineral resources, and the recipient of large proportions of the plant's resources (Fitter, 1987), up to 40% of its carbon resources (Morot-Gaudry et al., 2009).

Roots are hidden by soil, making their excavation and measurement of their size very laborious (Gregory, 2006) and difficult to analyze (Rood et al., 2011). However, the study of their spatial distributions allows the discovery of their main sources of water and minerals (Lynch, 1995). Given the quantitative and qualitative heterogeneity in

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Figure 1. Atlas pistachio in Béni Ounif (hyperarid) (Photo *A.Limane* 2010).

the distribution of these resources in space and time, the plasticity of root architecture plays a decisive role in successful resource acquisition (Spanos et al., 2008; Tsakaldimi et al., 2009). Through this work, which is original to the best of our knowledge, we aimed to approach the different root architectures established by this species along a gradient of increasing climatic and edaphic aridity. Thus the main abiotic variables (climatic and edaphic) that best explain the recorded variances were determined.

2. Materials and methods

2.1. Selection of populations and individuals

Following a north–south transect in Algeria, we selected 4 populations of the Atlas pistachio. They are the populations of: Sidi Naamane (wilaya of Médéa) (35°11′354″N/3°1′248″E/alt. 765 m), the daya[1] of el Mergueb (wilaya of M'sila) (35°33′177″N/03°56′214″E/alt. 584 m), daya of Lekhneg (wilaya of Laghouat) (33°41′400″N/2°39′761″E/alt. 837 m), and Béni Ounif (wilaya of Béchar) (31°48′728″N/1°44′871″E/alt. 760 m) (Figure 2).

We examined a sample of 27 individuals (Table 1) situated along the chosen north–south transect.

2.2. Climatic data

They were provided by the National Office of Meteorology (ONM, Algeria). With the station at Laghouat being unavailable, we extrapolated data from the nearest station, in this case, that at Hassi R'mel. ONM has placed at our disposal 10 years of data (1995–2004) for all stations, except for Hassi R'mel, whose 2002 data were missing. The data contain monthly averages of precipitation (P in mm) and temperatures (T in °C), which enabled us to realize the ombrothermic diagram of Bagnouls and Gaussen (1953) for each station and so to deduce the length of the dry season (LDS in months) for each of them. According to this diagram, one month is said to be dry when its total rainfall is less than or equal to twice its average temperatures ($P \leq 2T$). Other data (maximal temperatures, minimal temperatures, air moisture (%), wind velocity (m/s), and duration of insolation (h)) allowed us to calculate the mean monthly evapotranspiration (PET (mm/month)) for each station by the Penman–Monteith method using the software CROPWAT 8.0 (FAO, 2009).

In order to establish the respective ecoclimatic zonation (UNEP, 1992), we calculated the aridity index (AI) of each station according to the formula:

$$AI = P/PET$$

(Knowing that more AI is low, more aridity is high.)

Furthermore, we found it interesting to add an estimate proposed by Schenk and Jackson (2005). It is the long-term, mean seasonal surplus of water that is potentially available for deep storage (Wsur) and the long-term mean seasonal deficit of water, representing the potential transpirational demand for water stored deeply in the soil (Wdef).

The calculation of these 2 variables is done according to the following equations:

$$Wsur = \sum_{\text{months}} (Pm - PETm), \text{ for all months with } Pm - PETm > 0$$

$$Wdef = \sum_{\text{months}} (PETm - Pm), \text{ for all months with } PETm - Pm > 0$$

Figure 2. Geographic localization of the 4 populations.

[1] Alluvial depression

Table 1. Morphological characteristics of the individuals.

Stations	Individuals' code	High (m)	Trunk circumference (cm)	Crown diameter (m)
Sidi Naamane	SN1	7	254	12
	SN2	7	127	7.2
	SN3	5	104	6.8
	SN4	7	118	7.6
	SN5	6	106	6
	SN6	8	149	7.5
	SN7	8	242	7.5
	SN8	7	234	7
el Mergueb	ME1	3	85	4.35
	ME2	7	130	9.3
	ME3	7	178.52	7.86
	ME4	7	107	5.7
	ME5	2.5	38	1.75
	ME6	0.5	2.55	0.25
	ME7	3	75	4.5
Lekhneg	LE1	8.5	197	14
	LE2	8	188	9
	LE3	2	17.5	1.5
	LE4	1.8	24	1.5
	LE5	6	83	4.9
	LE6	7.5	140	9.9
Béni Ounif	BO1	7	278	12
	BO2	20	374	11.44
	BO3[2]	-	182	-
	BO4	11	229	12
	BO5	11	229	12.54
	BO6	10.5	280	12.27

SN*n*: individuals of Sidi Naamane; ME*n*: individuals of el Mergueb; LE*n*: individuals of Lekhneg; BO*n*: individuals of Béni Ounif.

2.3. Root profiles

In Algeria, the Atlas pistachio is an officially protected species. It is therefore forbidden to sacrifice individuals. In each population of the Atlas pistachio, to preserve the integrity of the trees, we made unilateral root profiles under each individual (a total of 27 root profiles). At the end of each operation, we reburied systematically excavated root systems. Using trowels, picks, hoes, and shovels, we dug vertically from the collar to an average depth of 0.80 m, a pit that allowed us to discover only one side of the root system (Figure 3), thus preserving the life of sampled trees. The width of each pit varied according to the length of discovered roots within each unilateral profile. This method corresponds to that of Rood et al. (2011); it was

[2] We have not found the aerial part of this individual. We found a trunk of 1.5 m high with a leaved green sprout from its collar.

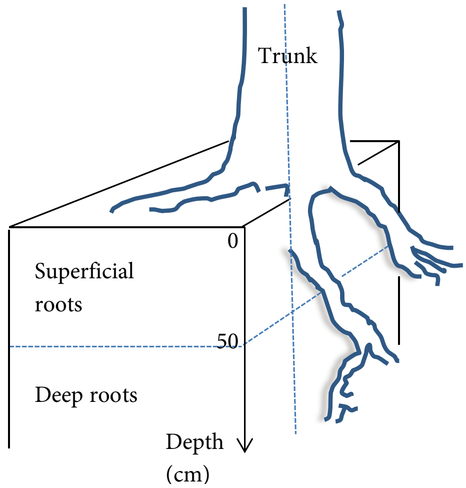

Figure 3. Unilateral root profile (discovering only one side of root system).

far less laborious, and benefited from the erosion of rivers banks through seasonal torrents, to study unilateral root profiles thereby naturally excavated.

The limit of 0.8 m depth was mostly imposed on us by limestone slab, which is ubiquitous in these arid regions of Algeria and inherited from the Quaternary (Pouget, 1980). Its depth being variable, we had to limit ourselves for less additional variance to the station where it was relatively shallow, therefore M'sila, in our study.

Furthermore, in the literature we found that 60% to 90% of roots of shrubs and trees are located in the first 0.50 m of soil (Dobson and Moffat, 1995; Jackson et al., 1996); in the majority of ecosystems, root biomass colonizes the first meter of the soil (Jackson et al., 1996). These same authors require as a precondition for the admissibility of the information on roots studies a minimum of 0.50-m depth. Schenk and Jackson (2002a) worked with root profiles with the median depth of 0.88 m.

The difficulty of the task in the field must also be considered. Indeed, the excavation of the root systems of adult trees in situ is very laborious and tedious (Ganatsas and Tsakaldimi, 2003; Gregory, 2006).

For each root profile, we identified the number of superficial main roots (SR), colonizing the top 50 cm of the soil, and the number of deep main roots (DR), which plunge more than 50 cm in depth. This subdivision into 2 levels is inspired by the 2-layers hypothesis proposed by Walter (1971). He subdivided soils into 2 levels: the deep one, whose water is reached only by trees, and the superficial one, where the herbaceous plants would be their main competitors.

As for determining the limit between the superficial and deep levels, we find in the literature a varied spectrum. The degree of evolution of soils (therefore their depths) is not the same in different terrestrial biomes; any subdivision becomes therefore relative.

Thus, several models exist, proposed by their authors in the context of their issues. We quote the MAPSS of Neilson (1995), the CASA of Potter et al. (1993), the TEM of Raich et al. (1991) and Melillo et al. (1993), and even the model CENTURY of Parton et al. (1988), which is an exception with its 5 levels of subdivision.

We finally opted for the limit of 50 cm between the superficial level and the deep one. We were inspired by the work by Floret and Pontanier (1982), pioneers in studying arid environments in North Africa, who consider that the roots that do not exceed 50-cm depth are shallow. The targeted roots are those considered main, emerging directly from the pivot (when it occurs) or from the collar. They have a diameter of 5 mm or more (Tufekcioglu et al., 1999). For each main root (superficial or deep), we:

- counted the number of branches in the centrifugal direction (developmental) (Berntson, 1997); therefore, we distinguish between the number of branches of superficial roots (BSR), that of deep roots (BDR), and that of total root branches (TRB);
- measured root length, which corresponds to the sum of the lengths of the constituent segments of roots; therefore, we distinguish between the total length of the superficial roots (TLSR), that of deep roots (TLDR), and total length of roots (TLR);
- measured root average circumference, which corresponds to the average of circumferences of constituent segments of each superficial or deep root; therefore, we distinguish between the average circumference of the superficial roots (ACSR), that of deep roots (ACDR), and that of total roots (ACR).

Finally, we transformed in percentages the results of different root measurements to weight differences in the strength of our 4 stations.

2.4. Soil sampling

The pits of 0.80 m made previously for root profiles were also used like pedologic pits. Soils of those arid areas (except those of Sidi Naamane, the northernmost part of the north–south transect) are, in general, little differentiated profiles (Demangeot and Bernus, 2001), especially in hyperarid areas where pedogenesis is extremely reduced (Pouget, 1980). Thus, in order to avoid the maximum of additional variance, we chose to equally divide each of the soil profiles in 4 levels of 20 cm each. Thus, we sampled 4 levels of soil under each studied Atlas pistachio.[3]

[3] However, 2 individuals in each station grow in the same soil (the cases of the 6th and 7th individuals in Sidi Naamane, the 5th and 6th ones in el Mergueb, the 1st and 2nd ones in el Khneg, and the 3rd and 4th ones in Béni Ounif); thus we considered in each case the same soil samples for both individuals, which explains the lack of 4 samples in each station.

In the laboratory, soil samples underwent standard soil analyses (Baize, 2000), which enabled us to determine their:

- Water-holding capacity (WHC);
- Soil texture using Robinson's pipette method;
- Content of total limestone ($CaCO_3$) by acidimetry.
- Content of carbon (OM) by Anne's method (Jackson, 1965 in Aubert, 1978).

2.5. Statistical analyses

We performed one-way ANOVA using Excel 2010 software, in order to verify the significance of the differences between the averages of the root characteristics of sampled populations. The same software enabled us to realize curves of trends of the different variables using the method of least squares and calculate their respective coefficients of correlation (R^2). When necessary, we proceeded to a log-transformation for better readability of our results.

Furthermore, we used SatBox 6.40 software to carry out principal component analysis (PCA), to visualize the interactions between soil variables and root architectures of along the north–south transect.

3. Results

3.1. Climatic characteristics and quantity of water potentially available for deep storage

The main climatic data (P and T), as well as calculated climatic indicators (PET, AI, and LDS) (Table 2; Figure 4) show a net decrease in precipitation and a net increase in temperature and aridity according to the north–south transect. Indeed, the latter begins with a semiarid climate in Médéa and ends with a hyperarid climate in Béchar passing through arid climates in M'sila and Laghouat. The curve of trends as well as their respective coefficients of correlation (Figure 5) shows the high significance of this evolution.

The application of Schenk and Jackson's (2005) formulas (Figure 6) shows that Médéa is the only station that offers potentially storable water at depth. This excess water (Wsur) is recorded during January/February and November/December (the rainier and coldest months at this station). The remaining months are characterized by a water deficit (Wdef) due to high evapotranspirational demand. With the increase in climatic aridity along the north–south transect, Wsur becomes zero throughout the year, unlike Wdef, which continues to increase at the 3 remaining stations.

3.2. Physico-chemical characteristics of soils

The results of the Atlas pistachio underlying soil analysis (Table 3) show that according to the north–south transect they gradually pass from a relatively fine texture (silty-clay) rich in OM (case of Sidi Naamane) to a coarse one (sandy-silt) (case of Béni Ounif), passing through intermediate textures (silty-sandy) (case of M'sila, Laghouat) increasingly poor in OM (case of M'sila, Laghouat, and Béni Ounif).

The trend curves and their respective coefficients of correlation (Figure 7) indicate that these different evolutions are very significant. Indeed, contents of clay (C), fine silts (FS), and coarse silts (CS) tend to decrease significantly along the north–south transect, while the content of fine sand (FSd) and coarse sand (CSd) increases clearly. The water-holding capacity (WHC) of these soils tends to decrease significantly along the north–south transect, while their content of limestone ($CaCO_3$) increases.

3.3. Root architectures

The total number of counted roots amounted to 288. We found that in all sampled stations SR is always higher than DR and constitutes in each individual more than 60% of its total roots (Tables 4 and 5).

The ANOVA results (Table 6) showed significant differences between the 4 populations for their ACR, TRB, SR, ACSR, BSR, TLDR, and ACDR. On the other hand, the other root variables, namely total number of roots (TR), TLR, TLSR, DR, and BDR, did not show this significance.

Considering the significant variables, we find that SR and their BSR tend to decrease along the north–south transect and their ACSR to increase. As for the deep roots,

Table 2. Climatic data of the 4 stations along the north–south transect.

Stations	P mm/year	T (°C) (average annual)	PET mm/year	AI	Ecoclimatic zonation (UNEP, 1992)	LDS (Bagnouls and Gaussen, 1953) (months/year)
Médéa	627.6	15.43	1597.38	0.39	Semiarid	4.5
M'sila	216.42	19.47	1573.86	0.14	Arid	10
Hassi R'mel	110.29	19.8	2168.03	0.05	Arid	11
Béchar	75.92	21.62	2365.57	0.03	Hyperarid	12

P: precipitation (mm/year); T: average annual temperature (°C); AI: aridity index; LDS: length of dry season (months/year).

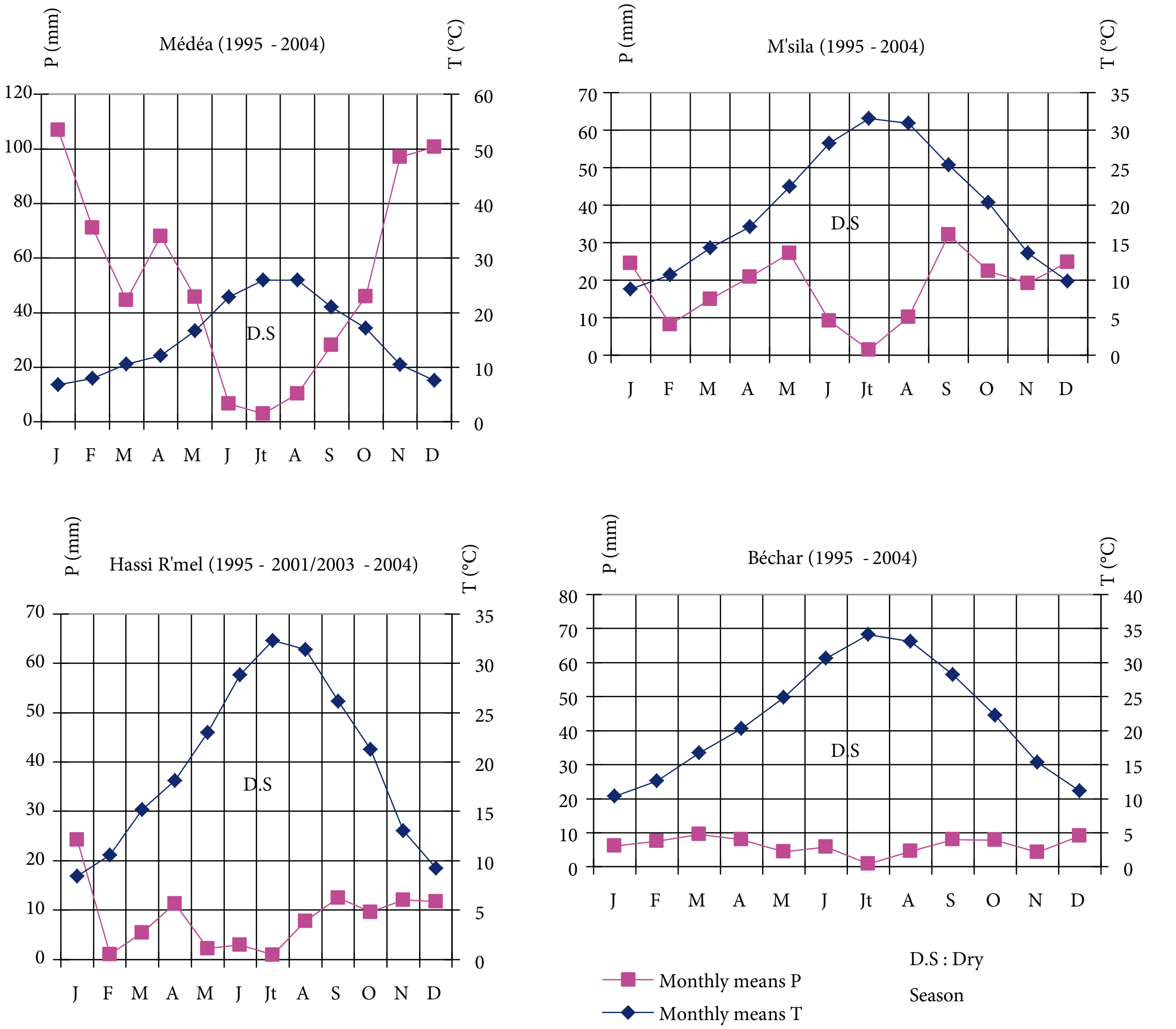

Figure 4. Ombrothermic diagrams of Bagnouls and Gaussen (1953) for the 4 stations.

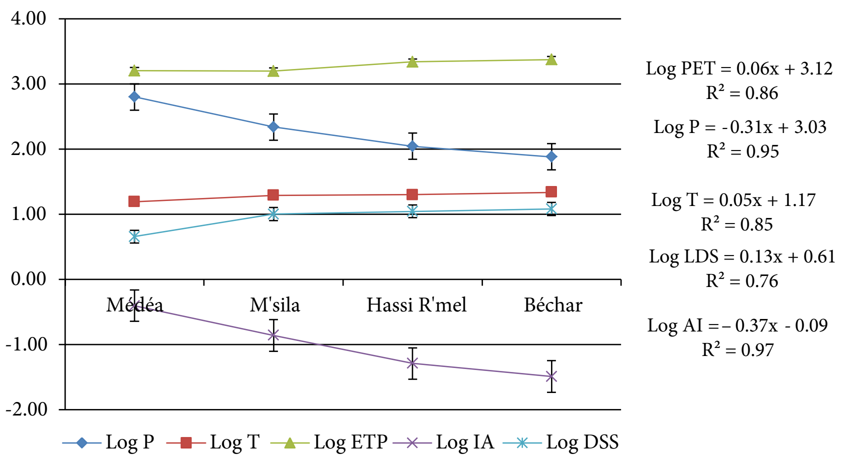

Figure 5. Curves of trends and coefficient of variations (R^2) of the main climatic variables according to the north–south transect. ETP: evapotranspirational potential (mm/year); P: precipitation (mm/year); T: average annual temperature (°C); LDS: length of dry season (months/year); AI: aridity index.

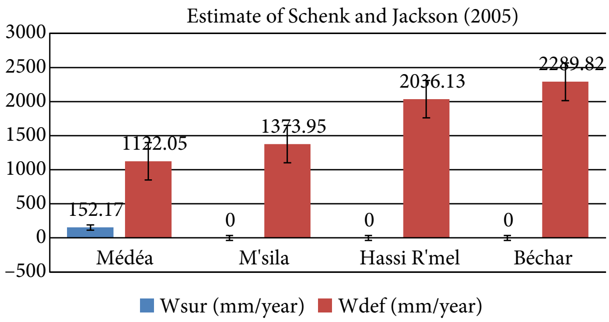

Figure 6. Quantities of water potentially storable in depth (Wsur) and water deficit (Wdef) according to the north–south transect.
Wsur: surplus of water that is potentially available for deep storage.
Wdef: potential transpirational demand for water stored deeply in the soil.

Table 3. Underlying Atlas pistachio soils' characteristics at the 4 stations.

Stations	n	Means (%) ± standards errors										Textures
		C	FS	CS	TS	FSd	CSd	TSd	$CaCO_3$	WHC	OM	
Sidi Naamane	28	38.18 ± 1.71	17.51 ± 2.00	12.8 ± 2.01	30.31 ± 2.29	14.43 ± 0.89	17.07 ± 2.28	31.50 ± 1.97	20.96 ± 2.83	37.87 ± 2.40	6.95 ± 2.11	Silty-clay
el Mergueb	24	9.89 ± 1.75	12.17 ± 2.26	9.08 ± 2.64	21.25 ± 3.30	39.24 ± 3.62	29.63 ± 2.65	68.87 ± 3.22	13.06 ± 1.97	25.4 ± 0.52	3.29 ± 0.26	Silty-sandy
Lekhneg	20	16.7 ± 1.69	7.85 ± 1.27	5.66 ± 1.90	13.51 ± 2.24	57.12 ± 2.80	12.71 ± 1.42	69.83 ± 3.14	9.16 ± 0.66	27.74 ± 0.77	3.12 ± 0.23	Silty-sandy
Béni Ounif	20	9.31 ± 0.87	3.49 ± 0.64	7.92 ± 1.67	11.41 ± 1.98	44.6 ± 5.09	34.67 ± 6.19	79.27 ± 2.15	17.75 ± 3.28	24.59 ± 0.79	1.45 ± 0.09	Sandy silt

C: clay; FS: fine silt; CS: coarse silt; TS: total silt; FSd: fine sand; CSd: coarse sand; TSd: total sand; $CaCO_3$: total limestone; WHC: water holding capacity; OM: organic matter.

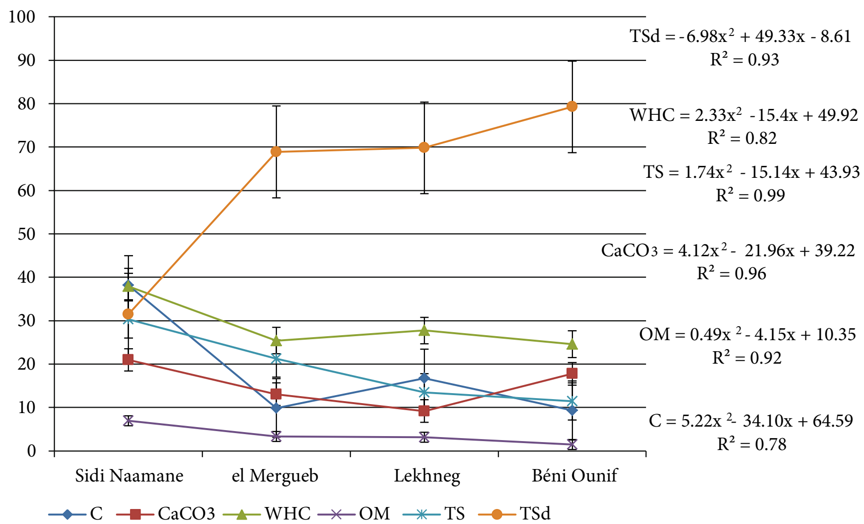

Figure 7. Evolution of physico-chemical variables of underlying soil of Atlas pistachio according to the north–south transect.
C: clay; TS: total silt; TSd: total sand; $CaCO_3$: total limestone; WHC: water holding capacity; OM: organic matter.

Table 4. Number of trees sampled by station (n), number of their superficial roots (SR), that of deep roots (DR), and their frequencies.

Stations/Roots	n	SR ± standard error	%	DR ± standard error	%	Total of roots ± standard error
Sidi Naamane	8	88 ± 1.27	89.76	10 ± 0.84	10.2	98 ± 2.06
el Mergueb	7	43 ± 0.88	72.88	16 ± 0.71	27.19	59 ± 1.08
Lekhneg	6	37 ± 1.56	61.66	23 ± 1.14	38.33	60 ± 1.39
Béni Ounif	6	47 ± 1.05	66.19	24 ± 1.00	33.8	71 ± 1.25
Total	27	215 ± 0.7	74.65	73 ± 0.49	25.35	288 ± 0.68

Table 5. Sampled roots' characteristics.

Stations	SR	TLSR (cm)	ACSR (cm)	BSR	DR	TLDR (cm)	ACDR (cm)	BDR
Sidi Naamane	88	12607.63	19.26	881	10	679	19.65	51
el Mergueb	43	1356.5	9.32	129	16	635.75	13.8	40
Lekhneg	37	2183	17.22	219	23	1329	11.37	118
Béni Ounif	47	18366	33.69	225	24	4580	23.19	131

SR: number of superficial roots; TLSR: total length of superficial roots; ACSR: average circumferences of superficial roots; BSR: number of branches of superficial roots; DR: number of deep roots; TLDR: total length of deep roots; ACDR: average circumferences of deep roots; BDR: number of branches of deep roots.

Table 6. Results of ANOVA applied to root characteristics of the 4 populations.

Variables	Results	Conclusion
TR	$F (3.23) = 1.94; P < 0.15$	Nonsignificant (n.s.)
TLR	$F (3.23) = 14.58; P < 1.56$	n.s.
ACR	$\mathbf{F (3.23) = 6.52; P < 0.002}$	**Significant (s)**
TRB	$\mathbf{F (3.23) = 3.45; P < 0.03}$	**s**
SR	$\mathbf{F (3.23) = 3.91; P < 0.02}$	**s**
TLSR	$F (3.23) = 11.58; P < 7.93$	n.s.
ACSR	$\mathbf{F (3.23) = 8.03; P < 0.0007}$	**s**
BSR	$\mathbf{F (3.23) = 4.03; P < 0.01}$	**s**
DR	$F (3.23) = 2.12; P < 0.12$	n.s
TLDR	$\mathbf{F (3.23) = 4.38; P < 0.01}$	**s**
ACDR	$\mathbf{F (3.23) = 3.27; P < 0.03}$	**s**
BDR	$F (3.23) = 1.43; P < 0.25$	n.s.

TR: total number of roots; TLR: total length of roots; ACR: average circumferences of roots; TRB: total number of root branching; SR: number of superficial roots; TLSR: total length of superficial roots; ACSR: average circumferences of superficial roots; BSR: number of branches of superficial roots; DR: number of deep roots; TLDR: total length of deep roots; ACDR: average circumferences of deep roots; BDR: number of branches of deep roots.

they elongate (TLDR) and thicken (ACDR) increasingly along the considered transect (Figure 8).

3.4. Correlations between climatic variables and root variables

Pearson's correlation test for climatic variables and root variables (Table 7) shows a high positive correlation between both P and AI with SR and BSR. These same climatic variables affect negatively DR and BDR.

LDS shows at the same time a high negative influence on SR and BSR, and also a high but positive influence on DR and BDR.

BDR, unlike BSR, is highly and positively correlated with temperature.

3.5. Correlations between soil's physicochemical variables and root variables

Analysis of the considered variables (Table 8) shows a very strong positive correlation between total content of silt (TS) and both SR and BSR, unlike DR and BDR, with which the correlation is significantly negative. The total content of sand (TSd) shows a very negative influence on BSR, whereas it correlates very strongly with BDR.

The TLSR shows a strong affinity to $CaCO_3$ soil content, which is not the case for TLDR.

As for the OM contained in these soils, it correlates positively with BSR but negatively with BDR.

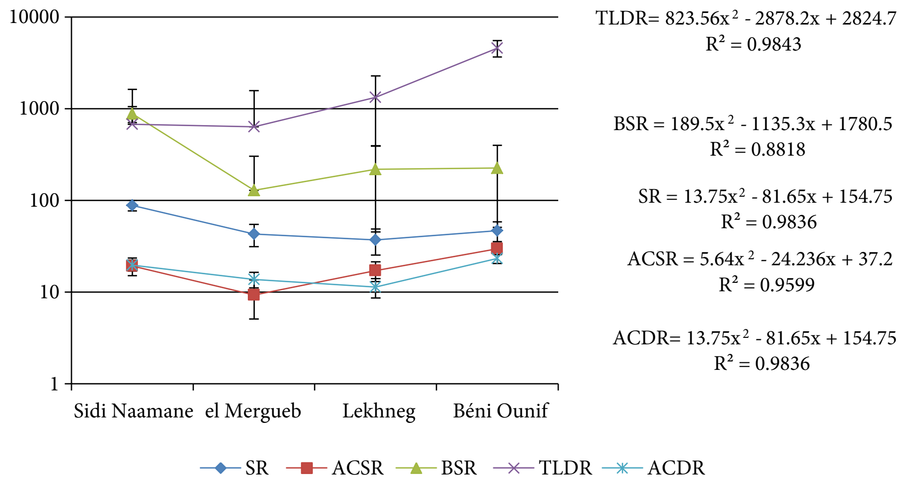

Figure 8. Curves of trends and coefficients of correlation (R^2) of roots variables according to the north–south transect.
TLDR: total length of deep roots; BSR: number of branches of superficial roots; SR: number of superficial roots; ACSR: average circumferences of superficial roots; ACDR: average circumferences of deep roots.

Table 7. Pearson correlation test for climatic and root variables.

	P	T	PET	AI	LDS
SR	**0.97**	−0.90	−0.75	**0.98**	**−0.95**
TLSR	0.78	−0.63	−0.29	0.77	−0.75
ACSR	0.48	−0.40	0.25	0.44	−0.48
BSR	**0.98**	**−0.96**	−0.84	**0.99**	**−0.98**
DR	**−0.97**	0.90	0.75	**−0.98**	**0.95**
TLDR	−0.79	0.66	0.26	−0.78	0.77
ACDR	−0.71	0.65	0.04	−0.68	0.71
BDR	**−0.98**	**0.96**	0.84	**−0.99**	**0.98**

In bold, significant values (off-diagonal) at alpha = 0.05 (2-tailed test)

SR: number of superficial roots; TLSR: total length of superficial roots; ACSR: average circumferences of superficial roots; BSR: number of branches of superficial roots; DR: number of deep roots; TLDR: total length of deep roots; ACDR: average circumferences of deep roots; BDR: number of branches of deep roots. P: precipitation (mm/year); T: average annual temperature (°C); AI: aridity index; LDS: length of dry season (months/year).

Table 8. Pearson correlation test for pedologic and root variables.

	C	TS	TSd	$CaCO_3$	WHC	MO
SR	0.83	**0.96**	–0.92	0.77	0.85	0.89
TLSR	0.73	0.65	–0.73	**0.98**	0.74	0.63
ACSR	0.68	0.22	–0.52	0.67	0.65	0.42
BSR	0.85	**0.99**	**–0.95**	0.62	0.88	**0.95**
DR	–0.83	**–0.96**	0.92	–0.77	–0.85	–0.89
TLDR	–0.77	–0.64	0.76	**–0.96**	–0.77	–0.66
ACDR	–0.85	–0.50	0.75	–0.75	–0.83	–0.66
BDR	–0.85	**–0.99**	**0.95**	–0.63	–0.88	**–0.95**

In bold, significant values (off-diagonal) at alpha = 0.05 (2-tailed test)

SR: number of superficial roots; TLSR: total length of superficial roots; ACSR: average circumferences of superficial roots; BSR: number of branches of superficial roots; DR: number of deep roots; TLDR: total length of deep roots; ACDR: average circumferences of deep roots; BDR: number of branches of deep roots. C: clay; TS: total silt; TSd: total sand; $CaCO_3$: total limestone; WHC: water holding capacity; OM: organic matter.

The PCA (Figure 9) shows, according to the F1 axis, a distribution of individuals conforming mainly to the gradient of increasing aridity. Indeed, we can distinguish 3 main sets: group A, comprising mainly individuals of the southernmost station (BO: Béni Ounif); group C, comprising mainly individuals of the northernmost station (SN: Sidi Naamane) passing through group B, which includes individuals of the 2 intermediate stations (ME: Mergueb and LE: Lekhneg).

We see along the same axis that SR and BSR follow the fine components of soils (C and TS) and also their OM, which are the most positively influential soil variables on WHC. On the other hand, DR and their characteristics (TLDR, ACDR, and BDR) follow the coarse fraction (TSd) in abundance in soils of these increasingly arid stations.

4. Discussion

The results obtained confirm that the chosen north–south transect is undoubtedly following a gradient of increasing pluviothermic and pedologic aridity. The station at Sidi Naamane, the northernmost of the north–south transect, is the wettest one. It shows the shortest LDS. The climatic conditions are therefore favorable for the evolution of these soils to fine textures and rich OM. Their WHC are therefore the most important in this north–south transect.

To the south, precipitation decreases drastically while temperatures and the PET increase and the LDS is getting longer. The development of soils slows and presents more coarse textures, rich in sands and poor in OM, decreasing the WHC of these soils. This textural variation influences root development (Korkmaz, 2013).

All along the north–south transect, the root systems of the sampled individuals invest more than 60% of their roots in the top soil levels (0–50 cm). Indeed, according to Canadell et al. (1996), many studies conclude that the major part of root biomass is located in the top 50 cm of soil. Dobson and Moffat (1995) estimated it as 60%–90%. Gwenzi et al. (2011) found that in ecosystems with limited water resources 90% of the density of root biomass is located in the top 40 cm of soil.

Furthermore, according to Ganatsas and Tsakaldimi (2003), the root system is highly affected by the stress factors of soil (absence of sufficient soil depth, mechanical resistance of underground bedrock); thus, the highest root density of fine, medium, and coarse roots was observed in the upper soil layers (0–30 cm).

The shallow root system is generally favored over the deep root system (Schenk and Jackson, 2002b) because (i) energy costs for construction, maintenance, and resource uptake are lower for shallow roots (Adiku et al., 2000); (ii) shallow soil layers are usually less likely to be oxygen-deficient (Hillel, 1998; Schenk and Jackson, 2002a); and (iii) nutrient concentrations are often higher in the upper soil layers (Jobbagy and Jackson, 2001). However, these levels are too hot and dry in summer.

High temperatures can cause a decrease in root abundance in shallow levels (Jackson et al., 1996), which would explain the significant decrease in the SR of the Atlas pistachio along the north–south transect. In these particular soils, SR becomes positively influenced by silt content, which is in these arid soils the main fine fraction instead of clays, which are struggling to develop under these conditions of xericity.

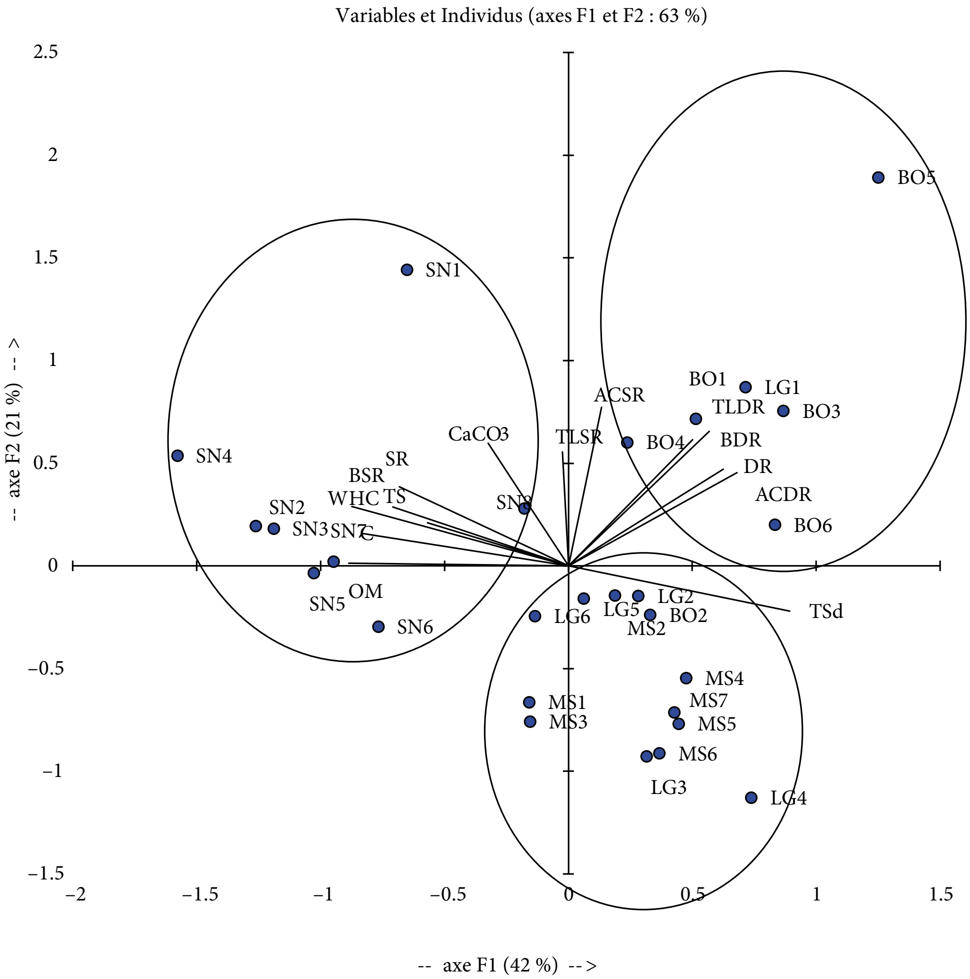

Figure 9. PCA showing the contribution of pedologic and roots variables.
TLDR: total length of deep roots; TLSR: that of superficial roots; BSR: number of branches of superficial roots; BDR: that of deep roots; SR: number of superficial roots; DR: that of deep roots; ACSR: average circumferences of superficial roots; ACDR: that of deep roots; C: clay; TS: total silt; TSd: total sand; $CaCO_3$: total limestone; WHC: water holding capacity; OM: organic matter.
(SN*n*: Individuals of Sidi Naamane; ME*n*: Individuals of el Mergueb; LE*n*: Individuals of Lekhneg; BO*n*: Individuals of Béni Ounif.)

As climatic and edaphic gradients increase, the texture of soils becomes coarser; thus their WHC decreases, causing a deep infiltration of water (Schenk and Jackson, 2005). The root system of the Atlas pistachio reorganizes by increasing significantly the TLDR and their ACDR to reach these deep levels. Although the number of deep roots constitutes a smaller part of the total number of roots, they play a crucial role in supplying the plant with water during dry seasons (Gregory et al., 1978; Stone and Kalisz, 1991). In some shrubs and trees of Western Australia with a Mediterranean-type climate, the hydraulic conductivity of deep roots is substantially greater than that of superficial roots, mainly due to the very large xylem vessels (1.5–2 mm for the first) (Pate et al., 1995). They often show portions of a high density of vessels per unit area, indicating that their major function is the transportation of water (Higgins et al., 1987; Pate et al., 1995). This water supply is sufficient to keep the stomata open and overcome the dry season (Canadell et al., 1996).

The ecological significance of these deep roots for water flow in ecosystems subject to intense conditions of evapotranspiration has been demonstrated by the mechanism of "hydraulic lift" found in many species (Richards and Caldwell, 1987; Caldwell and Richards, 1989; Dawson, 1993). During the night, these roots absorb water from deep levels, which is then released into the superficial levels. Water is reabsorbed the next day by the same plants (through their shallow roots) and the superficial roots of nearby plants that do not have access to the waters of those deep levels. This mechanism is of significant ecological importance, because it allows the plants to maintain intense evapotranspiration during dry periods (Canadell et al., 1996). The superficial and deep roots of the Atlas pistachio thicken significantly along the north–south transect. According to Hodge et al. (2009), thickening of the roots would increase by 100 to 1000 times their axial conductivity compared to the tissues without secondary formations.

According to Schenk and Jackson's (2005) formulas (Figure 6), the station at Sidi Naamane is theoretically the only one that provides potentially storable water in depth that the Atlas pistachio could reach with its deep roots. Otherwise, the north–south transect is predominantly in water deficit throughout the year. Despite this, and all along the north–south transect, the Atlas pistachio significantly increases the length and thickness of its deep roots and the thickness of its superficial roots, and flourishes in the warmest and driest periods of the year. This necessarily means that it has found a source of sufficient moisture.

In fact, its "foraging strategy" for water is essentially based on the choice of the most advantageous biotopes for its water supply in these arid environments. It settled in dayas, which are closed alluvial depressions from metric to kilometric order that accumulate runoff water (Pouget, 1980). Waters remains a few days or a few weeks; a portion evaporates and another percolates very slowly through a medium- to very fine-textured soil (Pouget, 1980). This is the case in the daya of el Mergueb (M'sila) and daya of Lekhneg (Laghouat) (Figure 10). The vigorous roots of the Atlas pistachio allow it to penetrate between cracks of limestone slabs and generate interlamellar spaces, and thus to reach the deepest wet levels. These stress soil factors affect strongly root system architecture, causing its restriction and deformation (Ganatsas and Tsakaldimi, 2003).

The topography of the station at Béni Ounif describes a Ouedi bed with a seasonal flow regime (Figure 11). During the realization of our pedologic pits, the deep soils levels of this station, although that mostly coarse, were very wet. A groundwater flow is not ruled out even during

Figure 10. Daya of Laghouat temporarily flooded (Photo *A.Limane* 2011).

Figure 11. Ouedi bed in Béni Ounif with an Atlas pistachio partially uprooted by the seasonal flood (Photo *A.Limane* 2011).

the drier seasons. The curve of variation in temperature of soil is amortized rapidly with depth because of the low thermal conductivity of the soil (Pouget, 1980); thus the water of deep levels of the Ouedi was kept protected from evaporation and was reached by the deep roots of the Atlas pistachio.

This deep rooting at the same time allows this phanerophyte to increase its anchor in these rather soft soils subject to very strong winds.

Soil–plant water relations are crucial for understanding the mechanisms by which plants adapt to their environments (Zheng, 2014). The roots grow only as deeply as needed to fulfill plant resource requirements (Schenk and Jackson, 2002b). This assumption is true for the Atlas Pistachio. In accordance with the global foraging theory, this species invests its root biomass sparingly to optimize the acquisition of hydromineral resources, unevenly distributed in space and time.

In the case of our north–south transect, precipitation, the length of the dry season, and soil silt content seem to be the abiotic variables that best explain the variability in root architecture in *Pistacia atlantica* species.

The root system of the Atlas pistachio is opportunistic. Under semiarid climates, the Atlas pistachio develops a mainly superficial root system, sufficient for its consistent hydromineral needs. With the increase in climatic and edaphic aridity along the gradient, it adopts a phreatophytic strategy, by increasing the length and thickness of its deep roots in contact with wet deep levels, protected from evaporation during the long dry seasons, and is sustained by an associated biocoenosis in these fragile ecosystems.

It succeeds in occupying inaccessible ecological niches for potential competitors, thus increasing both its own selective value and the resilience of biotopes that it colonizes.

We can anticipate by saying that in the context of global warming the Atlas pistachio is one of the best adapted plants to survive due to the phenotypic plasticity of its root system. A better known and preserved Atlas pistachio will be a valuable ally for an uncertain future.

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