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Effects of some properties of cedar forest soils on secondary roots of *Cedrus atlantica* Manetti

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Abstract

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The effect of textural and physicochemical characteristics of five cedar forest soils on 4- and 8-month-old seedlings of *Cedrus atlantica* Manetti was studied in a controlled growth chamber. During their growth, cedar seedlings show a change in the root architecture by the levels of C_{org}, N, P, and by the soil granulometry. The Tioumlilin soil conditions stimulate mainly the cumulative length and the number of secondary roots. However, the cedar forest soil of Tazekka predominates over most soils in its effect on growth by the balance of chemical elements and the high percentage of coarse particles. The analysis of the densities of secondary and tertiary roots and the cumulative length of secondary roots show four different root architectural development strategies of *C. atlantica* seedlings which may justify the low level of mycorrhization on young seedlings in the natural cedar forest soil. The variations of the root architectural parameters of *C. atlantica* seedlings are discussed in relation to the characteristics of cedar forest soils.

Keywords: architecture; growth; plasticity; seedling; underground

Conifers which have long generation times and very large genome size occupy a large surface area in the terrestrial globe (Ralph et al. 2008). In the family Pinaceae, the species *Cedrus atlantica* Manetti is an endemic forest tree in the morth of Africa with important bioecological and socio-economic values (M'hirit 1994). Its evolution confers this species a place of choice in the projects of creation and revalorization of the Mediterranean populations (M'hirit 1994). Despite this, it has long been recognized that cedar is subject to many obstacles, the most important of which is weak natural regeneration causing great difficulties in the conservation of the forest capital and the rejuvenation of the cedar forest (Zine El Abidine et al. 2014). The difficulty of seed germination and seedling maintenance to cross the period of summer heat and late cold is the crux of the problem, around which all the factors of the environment gravitate. Moreover, Moroccan cedar forests are waning more and rejuvenated less today, which may also be due to the impossibility to be mycorrhiza-colonized naturally or artificially when the optimal conditions are absent (Nezzar-Hocine et al. 1998; Boukcim et al. 2001; Gaba-Chahboub et al. 2017).

The forested ecosystem soil is heterogeneous both in time and space, even on a small scale (Šmilauerová, Šmilauer 2002). Organic carbon of soil has a major effect on plant and root growth by affecting microbial activity and soil properties (Li et al. 2018) and constitutes an important N source in coniferous forests (Zhang et al. 2018). It regulates the levels of primary and secondary nitrogen organic compounds, root growth and branching (Walch-Liu et al. 2006) depending on the growth stage and type of roots involved (Forde, Lorenzo 2002). Phosphorus fertilizer is a finite and slowly depleting resource (Cordell et al. 2009); its availability to plants is mainly related to its association with Ca and Fe, Al in alkaline and acidic soils, respectively (Richardson et al. 2009). In many species, scientists have also shown that the root growth and morphology are correlated with phosphorus availability in soil (Zhang et al. 2012).

The plasticity of root architecture was predicted to play an important role in the root response to soil properties (Fan, Yang 2007). It is well known that soil texture affects water circulation, ion exchange capacity, pore size distribution and thus water availability and root growth (Dexter 2004) and architecture (Lipiec et al. 2012). Moreover, root architecture plays an important role in the maintenance of young seedlings to assume the species regeneration (Šmilauerová, Šmilauer 2002).

The aim of this paper is to understand how soil texture and nutrient changes affect the root architecture of *C. atlantica* which may control its mycorrhization at a seedling level. This work describes the characterization of the *C. atlantica* seedling responses to changes in five natural cedar forest soils by analysing the architectural parameters of 4- and 8-old seedlings grown on these soils.

MATERIAL AND METHODS

Soil characteristics. The studied soils were sampled from five localities (Table 1). With five replications, total organic carbon of soil (C_{org}) was determined according to the titrimetric method of Walkley, Black (1934). The soil contents of total nitrogen and total phosphorus were estimated by the colorimetric method according to Berthelot (1859) and Murphy and Riley (1962), respectively, after mineralization of 100 mg of soil by the mixture of sulphuric acid and hydrogen peroxide according to the method of Kjeldahl (1883). After drying and sieving 100 g of soil, granulometric characteristics of the cedar forest soils were determined according to Bouyoucos (1927).

Seedling growth conditions. After an imbibition in water for 48 h, seeds of the Atlas cedar (*C. atlantica*) harvested from a tree felled in the Saheb forest (21.09.2013), were transferred onto wet paper until the appearance of a radicle of about 1.5 cm. The germinated seeds were transplanted into one-litre pots containing cedar soils from five provenances (Table 1) to 4 and 8 months. The culture was carried out at a temperature ranging from 24 to 32°C, photoperiod of 16/8 h and relative humidity of the order of 50 to 70% in the growth chamber from November to July. Seedlings on all soils were irrigated with running water twice a week with daily humidification during dry periods. The growth was estimated by measuring the length and number of roots using the ImageJ software (Version 1.50i, 2016) and weighing the dry mass of needles, stem, main root (R_1), secondary roots (R_2) and tertiary roots (R_3) obtained after drying at 70°C for 48 h.

Statistical analysis. With four replications of each organ, the obtained data have been subjected to the analysis of variance (ANOVA) and the means were compared by Fisher's least significant difference (LSD) post hoc test at $P < 0.05$. The Pearson bilateral correlation coefficients were calculated to estimate the relationship between soils and the parameters of root seedlings at 5% risk of error. All these statistics have been done by IBM SPSS Statistics (Version 20.0, 2011).

RESULTS

Textural characteristics of cedar forest soils

The texture of soils tested in this study is shown in Table 2. Tazekka soil is the most aerated with only 0.36% of silt-clay and 19.64% of fine sand compared to 80% of gravel and coarse sand. The soil of the Saheb forest is the most sandy with more than 90% of sand. Those of Zerouka and Tioumlilin have almost the same tendencies with more than 50% of fine particles (fine sand, silt-clay) and low gravel content. On the other hand, the soil of Moudemame is characterized by a preponderance of silt-clay and coarse sand, containing a proportion of gravel similar to that of fine sand (Table 2).

Table 1. Geographical and climatic coordinates of the soil provenances

Locality	Latitude	Longitude	Altitude (m a.s.l.)	Annual average	
				temperature (°C)	precipitation (mm)
Zerouka	33°32'22.56''N	5°06'00.88''W	1,675	11.3	843
Moudemame	33°24'49''N	5°11'48''W	1,746	14.2	779
Tioumlilin	33°24'46''N	5°12'31''W	1,654	14.2	779
Saheb	33°22'4''N	5°13'23''W	1,824	14.2	779
Tazekka	34°05'03''N	4°10'36''W	1,782	12.1	456

Table 2. Percentages of granulometric characteristics of the cedar forest soils

Particle diameter (mm)	Saheb	Zerouka	Tazekka	Moudemame	Tioumlilin
Gravel (> 2)	7.66	3.08	19.28	16.02	0
Coarse sand (0.2–2)	60.62	41.4	60.72	34.8	49.54
Fine sand (0.05–0.2)	30.8	35.32	19.64	13.64	25.6
Silt-clay (< 0.05)	0.92	20.2	0.36	35.54	24.86

Table 3. Chemical characteristics of the cedar forest soils

Locality	C_{org} (%)	N ($mmol \cdot g^{-1}$)	P ($mg \cdot g^{-1}$)	Salinity (ppt)
Saheb	9.788 ± 0.002	4.20 ± 0.193	52.87 ± 0.41	0.1
Zerouka	14.215 ± 0.233	5.50 ± 0.520	52.16 ± 0.88	0.1
Tazekka	14.914 ± 0.02	4.90 ± 0.606	39.4 ± 3.85	0.3
Moudemame	7.937 ± 0.452	5.55 ± 0.530	49.21 ± 0.89	0.6
Tioumlilin	0.934 ± 0.001	0.31 ± 0.035	10.3 ± 0.3	0

C_{org} – organic carbon

Chemical characteristics of cedar forest soil

The physicochemical characterization of soils studied in this paper is shown in Table 3. The soils of Zerouka and Tazekka have the highest content of organic carbon (> 14%). In return, Tioumlilin soil has the lowest percentage with only 0.934%. The two soils Saheb and Moudemame have 7.937 to 9.788% of organic carbon. For total nitrogen, only the soil of Tioumlilin has a very low quantity of the order of 0.31 $mmol \cdot g^{-1}$ of soil against 4.2 to 5.55 $mmol \cdot g^{-1}$ in the other soils. The phosphorus content shows the same trend as that of total nitrogen with a low quantity of the order of 10.3 $mg \cdot g^{-1}$ of soil at Tioumlilin and high content of 39.4 to 52.87 $mg \cdot g^{-1}$ in the other soils. Moudemame soil has the highest salinity of 0.6 ppt and Tioumlilin soil the very lowest with 0 ppt (Table 3).

Growth of young cedar on different soils

Among the five soils, the average length of R_1 shows no significant difference in the 4^{th} month but it increases on Tioumlilin soil (43.8 cm) and decreases on Saheb and Zerouka soils in the 8^{th} month (Fig. 1a). The cumulative length of R_2 in the 4^{th} month is low in Tazekka soil and high in Moudemame soil, whereas in the 8^{th} month, it becomes similar on Tazekka and Moudemame soils with a maximum of 232.10 cm on Tioumlilin soil (Fig. 1a) which also stimulates the number of R_2 at both growth stages (53.8 to 79.3, Fig. 1b). The average number and cumulative length of R_3 decrease on Tioumlilin, Tazekka and Saheb soils at the 4-month stage (Figs 1a, b). In return, the R_3 cumulative length of Tazekka soil (235.5 cm) significantly exceeds those of the other soils at the 8-month stage, whereas the number of these roots remains unchanged at this stage of growth (Figs 1a, b).

Fig. 2 shows that the type of soil affects the root architecture at the 4-month stage. At the 8-month stage the length of R_1 significantly distinguishes

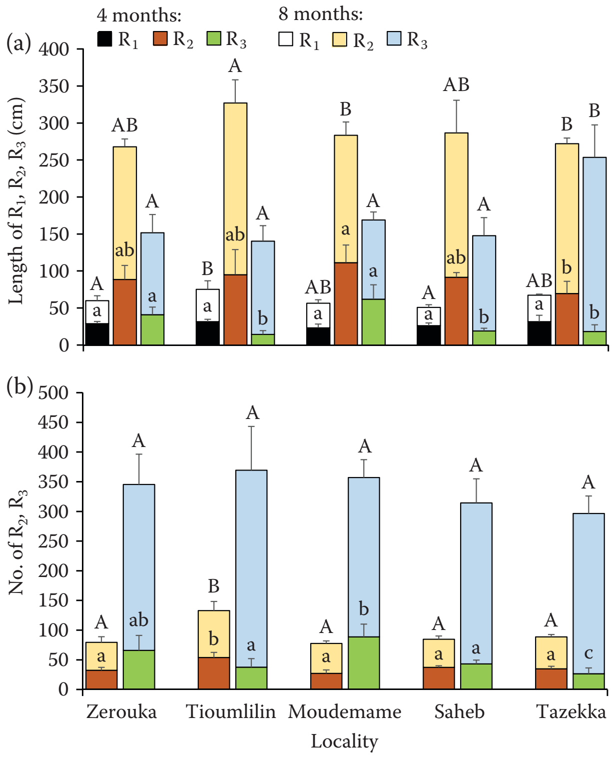

Fig. 1. Average of cumulative length (a) of main root (R_1), secondary roots (R_2) and tertiary roots (R_3) and number (b) of R_2 and R_3 grown on cedar forest soils for 4 and 8 months

Lowercase and uppercase letters indicate significant differences (P < 0.05 least significant difference test) in the 4^{th} and 8^{th} month, respectively

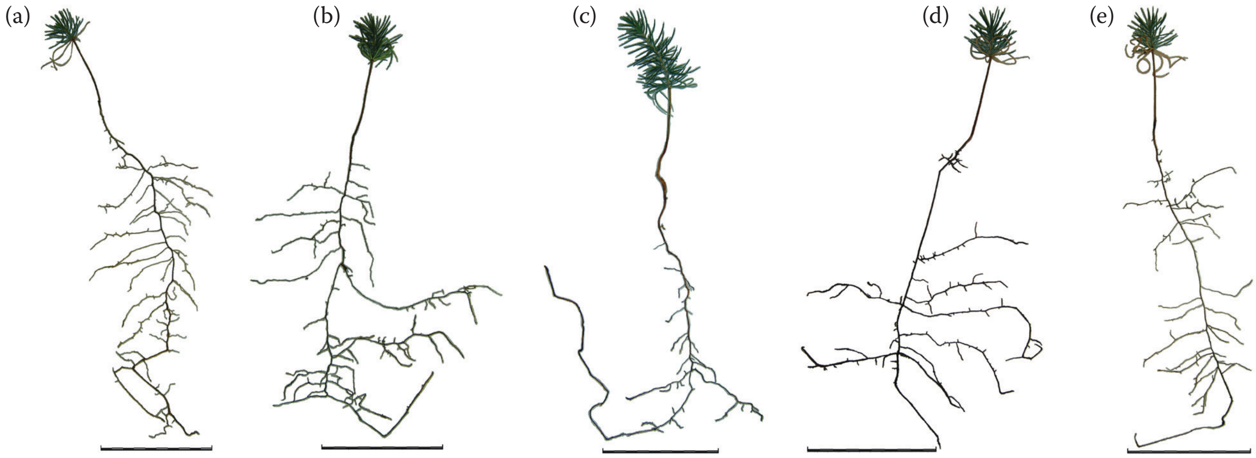

Fig. 2. Root system architecture of cedar seedlings grown on five cedar forest soils for 4 months (the scale bar corresponds to 10 cm): Tioumlilin (a), Moudemame (b), Tazekka (c), Zerouka (d), Saheb (e)

the architecture of cedar roots on Tioumlilin soil from those of Zerouka and Saheb but not of Tazekka and Moudemame (Fig. 1a), while the length of the R_2 of Tioumlilin soil is distinct from those of Tazekka and Moudemame but not Zerouka and Saheb (Fig. 1a). The density of R_2 (number of R_2/length of R_1) is stimulated by Tioumlilin whereas the density of tertiary roots (number of R_3/length of R_2) by the group of Zerouka and Moudemame soils (Fig. 3a). The density of secondary roots and R_3 always follows the group with low values in Tazekka or is intermediary in Saheb (Fig. 3a). The type of soil affects the density of R_2 at the 8-month stage in the same way as in the 4th month (Fig. 3b). On the other hand, no effect of the soil on the density of R_3 in the 8th month was observed.

DISCUSSION

Effect of textural characteristics on root architecture

The texture corresponds to the size distribution of the primary mineral particles in the soil. Different textures give rise to differentiation of pore

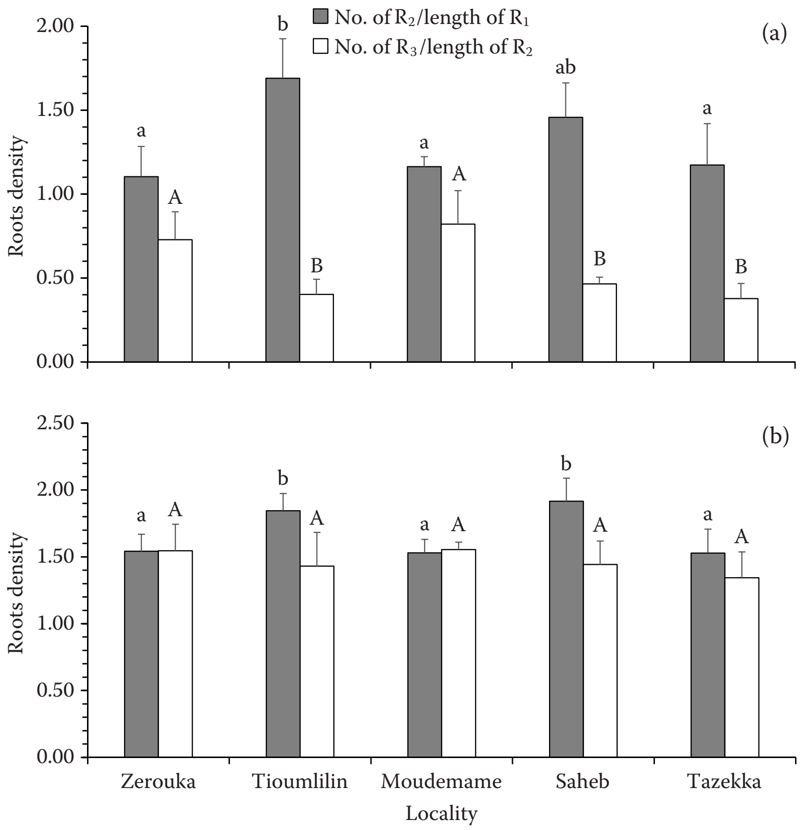

Fig. 3. Secondary (R_2) and tertiary (R_3) roots density of *Cedrus atlantica* Manetti grown on cedar forest soils for 4 (a) and 8 (b) months

R_1 – main root; lowercase and uppercase letters indicate significant differences ($P < 0.05$ least significant difference test) in secondary and tertiary root density, respectively

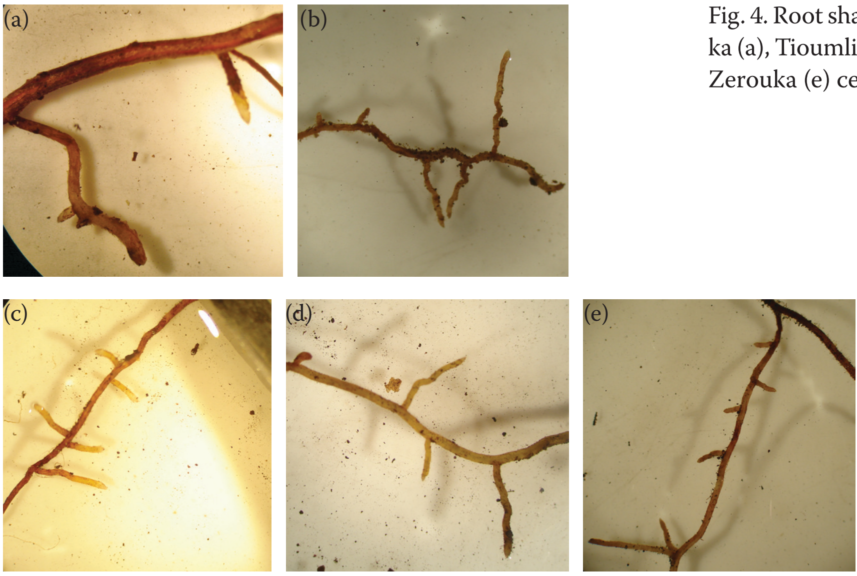

Fig. 4. Root shape of cedar seedlings grown on Tazekka (a), Tioumlilin (b), Moudemame (c), Saheb (d) and Zerouka (e) cedar forest soils for 4 months

sizes, mechanical impedance and water retention of soil. The balance between these parameters controls the growth of the root system and the whole plant afterward (Lipiec et al. 2012). As it has been shown in Table 2, the soil of Tioumlilin may provoke compressive strength since it contains 50% of fine particles (clay, silt and fine sand) with less organic matter (Table 3). In this soil, the elongation and the number of R_2 were increased (Figs 1a, b) compared to the Tazekka soil which contains only 20% of fine particles, 19.28% of gravel and 60.72% of coarse sand (Table 2) with 14.91% of organic matter (Table 3). On a soil with characteristics similar to those of Tazekka soil, Dexter (2004) found to provide a light and airy state with low water retention in the soil system.

The high percentage of fine particles of Saheb, Tioumlilin, Moudemame and Zerouka soils (30 to 50%) may cause mechanical impedance in these soils inducing an increase of the number of secondary roots, flattening the root and modifying its shape as found in Tioumlilin soil (Figs 1b, 2 and 4). This response is consistent with the findings of Lipiec et al. (2012), who showed that the mechanical impedance of the substrate increases root thickness and promotes the ramification of the root system and flattens the root. Furthermore, it is well known that compaction also increases the water content in the soil but dehydrates the roots and always implies abscisic acid – ABA (Richard et al. 2001; Sreenivasulu et al. 2012).

The seedlings grown on Tazekka soil show high growth, compared to the others, although its average salinity (0.3 ppm) is located in the middle of the salinity variation range (Fig. 5 and Table 3). Furthermore, the excess salinity reduces the mechanical impedance of soil by contributing to the flocculation formation ('t Lam et al. 2016). These data show that the soils of Tioumlilin, Zerouka and Saheb which have low salinities and mechanical barrier caused by the high level of fine particles (30–50%) may be responsible for a decrease in the growth of the whole seedlings (Fig. 5). The fact that on Moudemame soil the growth is decreased de-

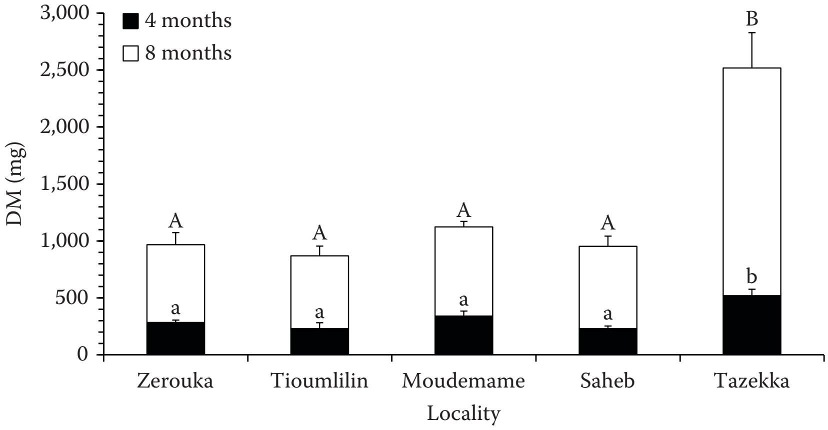

Fig. 5. Dry mass (DM) of whole seedlings grown on cedar forest soils for 4 and 8 months

Lowercase and uppercase letters indicate significant differences (P < 0.05 least significant difference test) in the 4th and 8th month, respectively spite having a salinity of 0.6 ppt suggests that other factors may reduce the seedling growth or 0.6 ppt is not sufficient to reduce its mechanical hindrances considerably.

Effect of soil physicochemical characteristics on root architecture

The low N, P and C_{org} contents of Tioumlilin soil stimulate the number of R_2 at both growth stages relative to other soils (Fig. 1) which is found to be highly negatively correlated with these three parameters (Table 4). Similarly, the length of R_1 and R_2 at the 8-month stage is found to be also stimulated and correlated with the low P and N content of Tioumlilin soil (Table 4). This observation was confirmed by Boukcim and Mousain (2001), who showed that the level of mineral fertility in growing media affects the growth of the root system of Atlas cedar seedlings which tends to adopt branching or intense elongation when the input of P or N is very low, respectively. It is well known that N deficiency induces changes in carbon and protein metabolisms in roots and leaves (Møller et al. 2011). Recently, Møller et al. (2011) have found that methylmalonate-semialdehyde dehydrogenase (MSD) and its role in root elongation increased by N starvation. On the other hand, many genes and proteins had been upregulated when plants suffered from P deficiency (Wu et al. 2003). Also, P deficiency caused plant oxidative stress which upregulated the phosphoprotein AP-K2A and elongation factor 1-beta proteins in roots (Yao et al. 2011).

These results showed consistency with the response of cedar seedlings to the low N and P soil like Tioumlilin soil (Table 3) compared to the other soils. In Tioumlilin soil seedlings, the present study demonstrated for the first time how *C. atlantica* seedlings respond to concomitant N and P limitations by increasing both the elongation of primary and secondary roots (R_1 and R_2 length) and branching out of primary root (R_2 number) (Fig. 1). This elongation gain can be caused by MSD induced by low N whereas the increment of branching out by the upregulation of proteins related to the formation of lateral root, such as auxin-responsive family proteins in roots and sucrose phosphate synthase-like protein in roots and leaves and the downregulation of proteins related to leaf growth and root cellular organization under P starvation. These events are developed in Tioumlilin soil seedlings which have displayed the longest and branched root system at the expense of leaf biomass (not shown here) displaying the high *C. atlantica* capacity of adaptation to N and P deprivation.

In this part, we study the root architecture of *C. atlantica* to test if it is affected by the availability of N, P, C_{org} and soil texture as it has been checked for shoot height and photosynthetic capacity under transplantation and drought effect (Kaushal, Aussenac 1989). On the other hand, its tolerance to drought resides mainly in the flexibility of its root architecture (Courbet et al. 2012). Our results are in agreement with their findings and according to the root architecture criteria (Figs 1 and 3), we find that the type of soil affects the root architecture in both growth stages (Fig. 2) by the availability of N, P, C_{org} and soil texture, as has been reported in several studies (Boukcim, Mousain 2001; Boukcim, Plassard 2003; Dexter 2004). The criteria of the root architecture used in this paper show that the length of R_1 significantly influences the architecture of the roots on Tioumlilin soil compared to those of Zerouka and Saheb but not to those of Tazekka and Mou (Fig. 1a). In contrast, the length of R_2 significantly differentiates the architecture of the roots on Tioumlilin soil from those of Tazekka and Moudemame but not

Table 4. Pearson correlation coefficients between soil chemical characteristics and growth of 4- and 8-month-old cedar organs at 5% risk of error

		4 months			8 months		
		P	N	C_{org}	P	N	C_{org}
Length	R_1	–0.34	–0.26	0.02	–0.59**	–0.46*	–0.38
	R_2	0.01	–0.03	–0.27	–0.52*	–0.52*	–0.33
	R_3	0.43	0.51*	0.11	–0.09	0.07	0.38
Number	R_2	–0.72**	–0.79**	–0.57**	–0.77**	–0.72**	–0.62**
	R_3	0.36	0.38	–0.01	–0.36	–0.37	–0.31

R_1 – main root, R_2 – secondary roots, R_3 – tertiary roots; bilateral correlation is significant at the 0.01 (**) or 0.05 (*) level; C_{org} – organic carbon from those of Zerouka and Saheb (Fig. 1a). On the other hand, the density of secondary roots and R_3 significantly discriminates the Tioumlilin and Saheb group of soil from those of Zerouka and Mou (Fig. 3a) and the density of secondary and tertiary roots of Tazekka always follows the group with low values (Fig. 3a). The results show four different root architectural-development strategies of C. *atlantica* seedlings in response to the physical and chemical characteristics of soils and these strategies can explain the variations in the receptivity of cedar seedlings to mycorrhizal fungi. They also show a clear distinction between R_1 and (R_2 + R_3) in response to the physicochemical soil limits. These strategies are certainly controlled by auxin homeostasis induced by soil parameters considering that auxin positively regulates the size of the root apical meristem by promoting the cell division antagonistically to cytokinin. It is also involved in the regulation of cell elongation by ethylene (Muday et al. 2012) and is the main regulator of each lateral root (LR) formation step (Fukaki, Tasaka 2009). Likewise, it has been found that ABA is involved in the response of root architecture by its negative effect on root elongation and LR emergence in response to soil mechanical constraints (Tracy et al. 2015). The results demonstrated that hormonal mechanisms must be studied in Atlas cedar seedlings under soil limits to elucidate how texture, N, P and C_{org} caused the modification of cedar root architecture. Supplementary information on these molecular subjects may help to select efficient soil conditions which may contribute to obtain mycorrhiza-colonized Atlas cedar seedlings in the reforestation project.

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