

SOIL CHARACTERISTICS AND PLANT FUNCTIONAL TRAITS UNDER LONG-TERM CONSERVATION IN ARID DESERT ECOSYSTEMS

MARWA MOUMNI, ABDERAZAK TLILI, JAMILA MSADEK, MOHAMED NEJI
AND MOHAMED TARHOUNI*

*Laboratory of Pastoral Ecosystems, Spontaneous Plants and Associated Microorganisms,
Arid Regions Institute - Médenine 4100. University of Gabes, Tunisia*

**Corresponding author's email: medhtarhouni@yahoo.fr*

Abstract

This research was done during the spring 2020 in Dghoumes national park, southwest desert region of Tunisia with extreme weather conditions that accelerate the natural resources degradation processes. Aims are to assess the soil properties (organic matter, pH, electrical conductivity, total nitrogen, texture, and total limestone) and their relationship with the existing plant communities. Soil samples were collected from two depths (0-20 cm, 60-80 cm) under the canopy of the dominant plant species as well as in the adjacent open areas (inter-patches, bare soil). The functional traits (leaf area, bio-volume, leaf dry matter content, canopy cover, leaf water content, and specific leaf area) of the six dominant plant species within the park (*Halocnemum strobilaceum* (Pall.) M. Bieb., *Helianthemum kahiricum* Delile, *Retama raetam* Forssk., *Anarrhinum brevifolium* Cosson & Kralik, *Haloxylon schmittianum* Pomel and *Limoniastrum guyonianum* Boiss.) are compared with those of outside. Main results show that the soil texture of the park ranges between sandy, sandy-loam and loamy-sand with very low nitrogen (< 0.1%) and organic matter contents. The total limestone is variable inside the park and reaches the highest value in salty soils. For the majority of studied species, the bio-volume and leaf water content are higher inside the park than outside and *vice-versa* for leaf dry matter content. There is a slight difference concerning the leaf area between inside and outside park. Despite the desert climate and dry soil conditions, the plant species are able to regenerate and to produce sufficient biomass in absence of human disturbances.

Key words: Soil properties, Functional traits, Grazing, Fencing, National Park, Desert ecosystems.

Introduction

Desert habitats can be considered as resistant to climate change and consequently important for preserving biodiversity (Liu *et al.*, 2022). Their particular climatic environments, geographical locations, and resource distribution patterns make them unique in terms of biodiversity and ecosystem multi-functionality (Whitford, 2002). Many human activities, such as overgrazing, continue to damage the biodiversity of desert and semi-arid ecosystems (Bainbridge, 2007). In Tunisia, the grazing activity covers large arid and desertic landscapes (Gamoun *et al.*, 2018). It destroyed both the scarce plant community and soils (Jeddi, 2010). In fact, the soils conditions are affected both by the trampling and the accumulation of some nutrients coming from dung and urine (Schrama *et al.*, 2013). As results, the soil properties changed and, therefore, modified the functional traits of the existing plants (Jager *et al.*, 2015; Deng *et al.*, 2017). Grazing can directly affect plants by damaging and loosening tissue with defoliation and trampling. It can also indirectly disturb plants by modifying their abiotic (quantity of light, soil fertility) and biotic (interactions between plants) environments (Nash suding & Goldberg, 2001; Rossignol, 2006). The various grazing effects constitute a kind of obstacles for the vegetation development and the ability of plants to cross them is determined through their functional traits (Violle *et al.*, 2007; Marion, 2010). According to Violle *et al.*, (2007), these traits can influence all the plant development phases. The functional trait-based approaches constitute a very promising area of research to understand the ecological strategies of the desert plants and their behavior under grazing (Zheng *et al.*, 2015; Akram *et al.*, 2020). In fact, the leaf area and specific leaf area decreased but the leaf dry matter content increased under heavy

grazing (Wang *et al.*, 2020). For this reason, leaf characteristics are regarded as one important sign of the grazing effects (Török *et al.*, 2018). Several authors noted also that specific leaf area (SLA) and plant tallness are recognized as important traits to study the plant response to animal activities (Díaz *et al.*, 2001; Cingolani *et al.*, 2005).

Conservation of natural ecosystem becomes a world-necessity mainly after the current biodiversity loss. The use of fencing technique is usually regarded as a simple and successful way to restore natural vegetation and soil in desert areas (Gamoun, 2014; Tarhouni *et al.*, 2014). Dghoumes national park depict one of Tunisian saharan protected areas. It was created since 2010 in order to protect desert plant communities, conserve biodiversity and restore ecological balance in the zone. In this context, the present research aims to better understand the long-term protection effects on vegetation and soil characteristics and their relationships. The main questions were: i) how the dominant species can tolerate stressful conditions using plant functional traits and ii) what roles can play to improve soil structure and fertility under desert climatic conditions?

Materials and Methods

Study site: The research is carried out inside and outside Dghoumes National Park (southwest Tunisia; 34°03'00.1"N 8°33'37.3"E; Fig. 1). Covering approximately 8000 ha, this park was created in 2010 and situated between a Salt Lake, on the southern side, and a mountain chain, on the north. The eastern and western limits of the park are flatty areas. The park contains three main landscapes: mountainous (3000 ha), piedmont (3800 ha) and salt depression (1200 ha). The investigated open to grazing area was located in the eastern outside of the park. This area suffered from

habitat degradation, mainly due to overgrazing by domestic livestock (goats and sheep). The climate of the park is desert-arid, with hot dry summers ($T_{max} = 50^{\circ}\text{C}$) and cool moist winters ($T_{min} = -3^{\circ}\text{C}$). The 10-years averages precipitation and temperature (2010-2020) are 65.98 mm and 22.91°C , respectively, with very notable variation between years. The biggest amount of rain is recorded in the 2014-2015 growing season (103.8 mm) but the lowest (20.2 mm) in 2012-2013.

Data collection: The park contains six plant groups called G1-6 (G1: *Halocnemum strobilaceum* and *Arthrocnemum indicum* (Wild.) Moq; G2: *Haloxylon schmittianum* (Pomel) and *Helianthemum Kahiricum*; G3: *Retama raetam* and *Traganum nudatum* Delile; G4: *T. nudatum* and *Anarrhinum brevifolium*; G5: *T. nudatum* and *H. schmittianum*; G6: *T. nudatum*, *Limoniastrum guyonianum* and *H. strobilaceum*). Six dominant plant species within the park (*H. strobilaceum*, *H. kahiricum*, *R. raetam*, *A. brevifolium*, *H. schmittianum* and *L. guyonianum*) were selected to study their functional traits. These species were compared with their homologues outside the park. Three tufts from each species with different sizes (large, medium and small) were sampled. The field measurements were conducted during the spring 2020.

The samples of soil were obtained from 2 layers: i) 0-20 cm (containing debris of aerial parts of plants) and ii) 60-80 cm (carbon storage horizon) both under the canopy of the dominant species (patches) as well as in bare soil (inter-patches). For G2 and G5, only the 0-20 cm layer was sampled because the soil is rocky and it is not possible to

reach the 60-80 cm depth. A total of 60 soil samples were spontaneously desiccated and then-after sieved to 2 mm. The saturated paw was used to determine pH and electrical conductivity (EC) according to the AFNOR's (1987) method. Soil particles analysis was performed using a laser granulometer (Malvern Panalytical Mastersizer 2000) depending on size category. The organic matter in soil (OM) was calculated using Walkley & Black's (1934) method as: $\text{OM} (\%) = 1.724 \times \text{Total Organic Carbon}$. The micro-Kjeldhal method (Anon., 1984) was used for the total nitrogen (N) and the Bernard volumetric one for total limestone (Total CaCO_3).

In field, healthy leaves from the medium of each tuft were collected in wet-papers and placed in the refrigerator to prevent dehydration. In laboratory, these leaves were weighed, flattened, fixed and photographed. The obtained photos were analysed using 'Image J' software to calculate the leaf area (LA). After measuring their fresh matter (FM), leaves were desiccated in oven during 48 hours at 60°C to obtain their dry matter (DM) and calculate their water content (LWC) as: $\text{LWC} = ((\text{FM} - \text{DM}) / \text{FM}) \times 100$. SLA was determined as: $\text{SLA} (\text{cm}^2 \text{g}^{-1} \text{DM}) = \text{LA} / \text{DM}$ when the leaf dry matter content (LDMC) is: $\text{LDMC} (\text{mg g}^{-1} \text{FM}) = \text{DM} / \text{FM}$ (Garnier *et al.*, 2001). The bio-volume (BV) was calculated as: $\text{BV} (\text{m}^3) = ((4/3) \pi r^3) / 2$, where r is the average radius of the tuft obtained as $r = ((D / 2) + (d / 2) + h) / 3$, with D is the largest diameter, d is the smallest diameter and h is the height of tuft. The Canopy Cover (CC), the area covered by the aerial organs of the plant, is calculated as: $\text{CC} (\text{m}^2) = \pi r^2$.

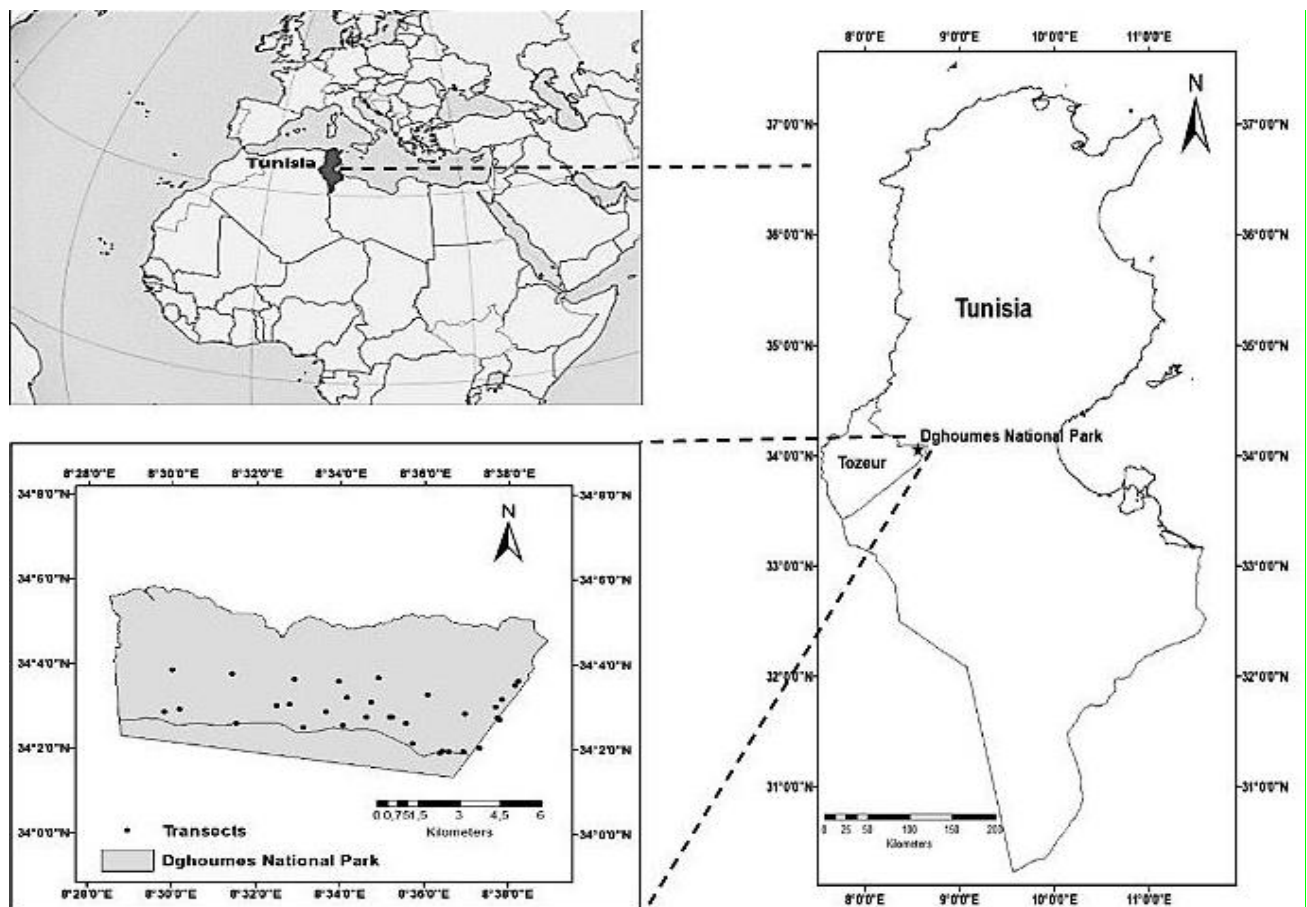


Fig. 1. Geographical location of Dghoumes national park.

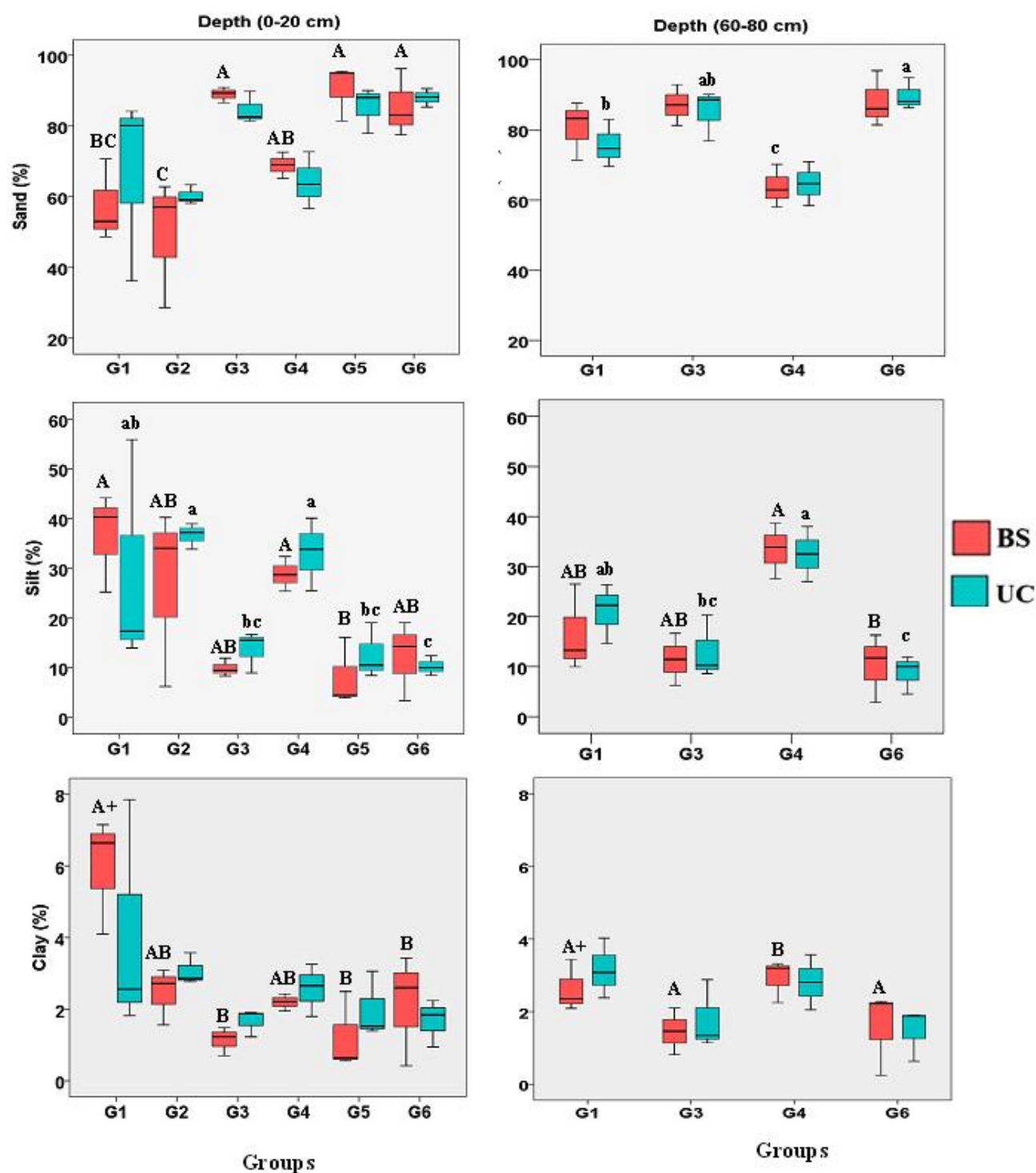


Fig. 2. Box-plot of the soil physical properties under canopy (UC) and bare soil (BS) inside Dghoumes national park during the spring 2020. G1: *Halocnemum strobilaceum* (Pall.) M. Bieb.; G2: *Helianthemum kahircicum* Delile; G3: *Retama raetam* Forssk.; G4: *Anarrhinum brevifolium* Cosson & Kralik; G5: *Haloxylon schmittianum*; G6: *Limoniastrum guyonianum* (L.). A/B reflect significant difference between groups in BS at same depth; a/b designed the significant difference between groups UC at same depth according to the test of Duncan; (*) indicates the significant difference between UC and BS at the same group and depth; (+) indicates the significant difference between depths in the same group and same location.

Data analysis: The normality and homogeneity of variance of the collected data was verified using the method of Kolmogorov-Smirnov (Ferignac, 1962). In case of non-normal distribution, the log conversion of data was considered. To compare differences in leaf and soil characteristics between plant-groups, the analysis of variance (ANOVA) was performed. The Duncan posthoc

test was used to find differences in soil properties. Then, the 'aov' of 'Lme4' in R platform (Bates *et al.*, 2014) was applied in order to explore the differences in leaf traits. The association between plant-groups, functional features, and soil parameters was further elaborated using the redundancy analysis (RDA). SPSS 20 (Anon., 2011) and R 3.4.4 statistical programs were used.

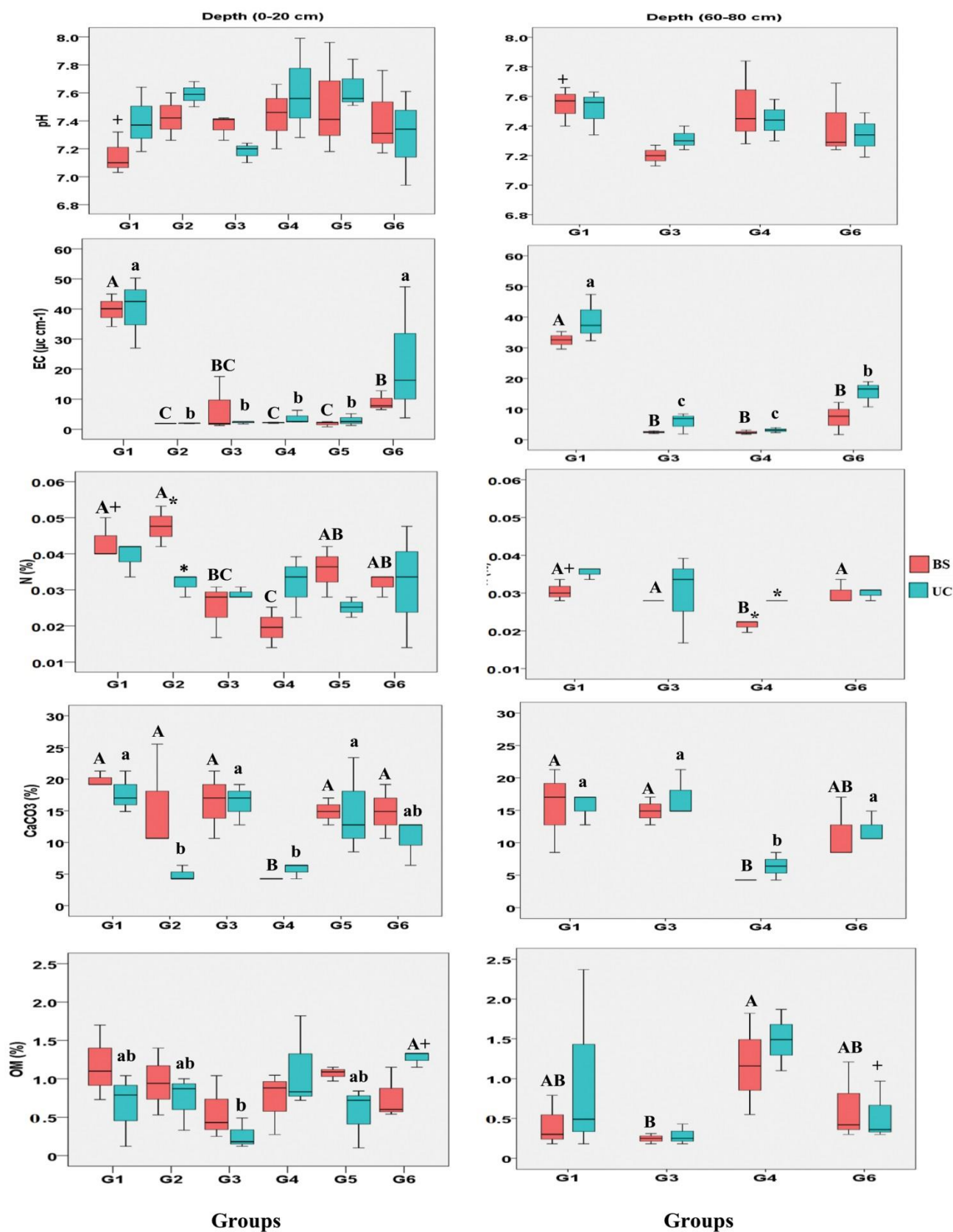


Fig. 3. Box-plot of the soil chemical properties under canopy (UC) and bare soil (BS) inside Dghoumes national park during the spring 2020. G1: *Halocnemum strobilaceum* (Pall.) M. Bieb.; G2: *Helianthemum Kahiricum* Delile; G3: *Retama raetam* Forssk.; G4: *Anarrhinum brevifolium* Cosson & Kralik; G5: *Haloxylon schmittianum*; G6: *Limoniastrum guyonianum* (L.). EC: electrical conductivity; OM: organic matter; N: total nitrogen. A/B indicated the significant difference between groups in BS at same depth; a/b indicated the significant difference between groups UC at the same depth according to the test of Duncan; (*) indicates the significant difference between UC and BS at the same group and depth; (+) indicates the significant difference between depths in the same group and same location.

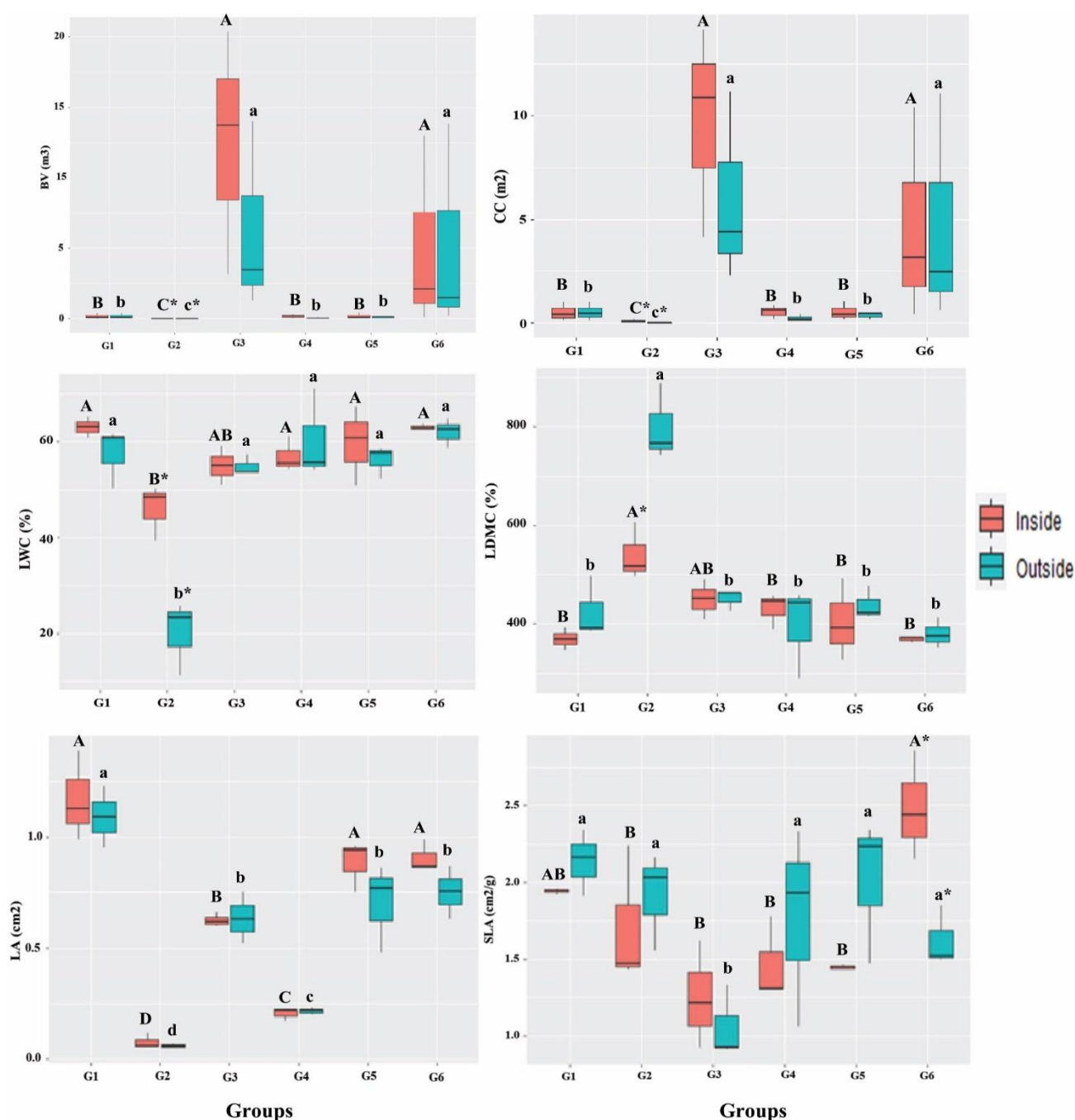


Fig. 4. Box-plot of the dominant plant functional traits inside and outside Dghoumes national park during the spring 2020. G1: *Halocnemum strobilaceum* (Pall.) M. Bieb.; G2: *Helianthemum Kahiricum* Delile; G3: *Retama raetam* Forssk.; G4: *Anarrhinum brevifolium* Cosson & Kralik; G5: *Haloxylon schmittianum*; G6: *Limoniastrum guyonianum* (L.). LDMC: leaf dry matter content; LWC: leaf water content; SLA: specific leaf area; LA: leaf area; BV: Bio-volume; CC: canopy cover. A/B/C/D/E/F and a/b/c/d/e/f/ revealed the significant difference between the groups inside and outside the park, respectively, according to the LSD test; (*) indicates the significant difference between inside and outside the park at the same group.

Results

Soil properties: Physico-chemical soil properties under canopy (UC) and bare soil (BS) in each plant group are done in (Figs. 2 and 3). The main results revealed that particle sizes distribution indicates the dominance of the sand fraction, varying from 49.53% to 90.65% with low amounts of silt and clay in all groups. When comparing locations and depth, the analysis of variance revealed no notable changes between the soil samples, except in group 1 between depths in bare soil ($p < 0.05$). The soil texture varied

softly in G1, G5 and G6. In fact, soils in G1 are loamy-sand in the first layer (0-20 cm) and sandy-loam at 60-80 cm. For G5 and G6, soil textures varied from sandy-loam UC to sandy in BS at 0-20 cm layer. The soil in G3 was sandy and sandy-loam in both G2 and G4, in both locations (UC and BS). The comparison between groups showed significant difference of sand proportions in both locations at 60-80 cm layer and only in BS at 0-20 cm depth. Concerning silt, remarkable dissimilarities between plant-groups ($p < 0.05$) were obtained in both layers. For clay, only the 0-20 cm layer in BS was different between groups.

The soils of the six plant-groups were weakly alkaline (pH ranging from 7.15 to 7.64) with a slight increase among groups ($p > 0.05$) and soil depths except between (0-20) and (60-80) layers in BS of group 1. The highest pH was measured UC in G4 and G5 (7.64 and 7.61, respectively). Total nitrogen (N) recorded both at UC and BS are very low ($< 0.1\%$) and it was almost the same in the six groups. The highest value was recorded in BS of G2 at the 0-20 cm depth (0.05%). Duncan's test was significant between depths in BS of G1 ($p < 0.01$), between BS and UC at 0-20 depth of G2, between BS and UC at 60-80 depth of G4 and between groups in BS at both depths.

The highest EC was recorded in G1 (39.93 mS/cm) while the lowest one at G5 (1.84 mS/cm). A significant difference between groups was founded in both locations and depths. The averages OM for all groups were less than 2%. At 0-20 UC and 60-80 BS, the OM vary between groups ($p < 0.05$). Also in group 6, a difference between depths is noted UC. In most groups, OM contents decrease with depth in BS and increase UC. The highest OM was recorded under the *A. brevifolium* canopy (G4) at 0-20 soil depth (1.72 %). Like the OM, the total limestone (CaCO_3) decreases with depth in BS and increases with depth UC. The highest levels of limestone were obtained at 0-20 depth in BS and UC of *H. strobilaceum* group (G1). CaCO_3 vary among plant-groups ($p < 0.05$) at 0-20 and 60-80 layers in both BS and UC.

Leaf traits: The average values of the retained plant traits are showed in (Fig. 4). All traits varied significantly between species inside and outside the park ($p < 0.05$). The highest biometric traits (BV and CC) are noted in *R. raetam* and *L. guyonianum* while the lowest ones are in *H. kahiricum*. This last species has the highest LDMC and the lowest LWC. The highest LA were found in *H. strobilaceum* and *L. guyonianum* but the lowest values are in *H. kahiricum* both in the interior and the exterior of park. The highest SLA are founded in *H. strobilaceum* and *L. guyonianum* while the lowest are in *R. raetam*. For *H. kahiricum*, *A. brevifolium* and *H. schmittianum* the lowest SLA are noted inside the park.

The comparison between inside and outside the park showed no significant effect on all measured traits ($p > 0.05$) in group 1, 3, 4 and 5. In group 2, *H. kahiricum* increased significantly the BV, CC and LWC ($p < 0.01$) and decreased the LDMC ($p < 0.01$) when compared with those outsides. Likely *L. guyonianum* (G6) increased the SLA ($p < 0.05$) inside the park.

The first two RDA axes were statistically significant and accounted 86.1% and 9.52% of variance, respectively (Fig. 5). CC, CaCO_3 , LA and EC were founded in the positive side of the first RDA axis but LDMC, pH, and SLA were in the negative one. The second axis showed high positive loading of LDMC and negative loading with SLA, EC, LA and CaCO_3 . The first and the fifth groups, dominated respectively by *H. strobilaceum* and *H. schmittianum*, showed high SLA and pH, while group three, dominated by *R. raetam*, had low values of these same two parameters. Group 6 presented high EC, CaCO_3 , CC and LA and low LDMC. Group 4 showed strong LDMC, pH, and SLA. The last group (G2) presented high LDMC.

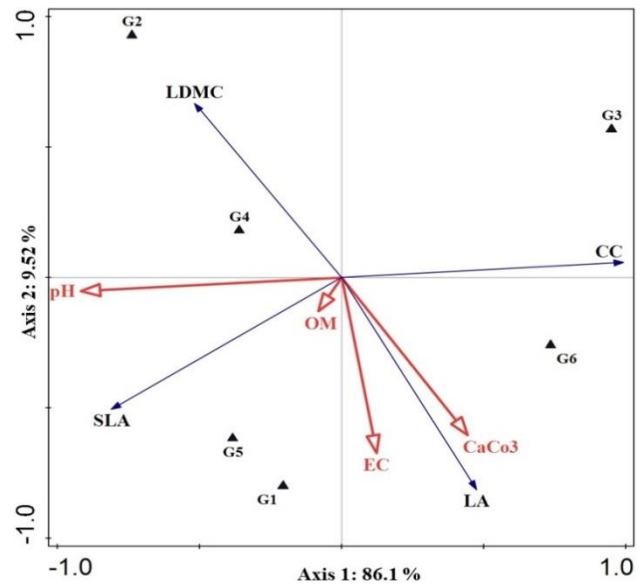


Fig. 5. Bi-plots diagram of the redundancy analysis (RDA) of soil properties and plant functional traits in different groups. G1: *Halocnemum strobilaceum* (Pall.) M. Bieb.; G2: *Helianthemum Kahiricum* Delile; G3: *Retama raetam* Forssk.; G4: *Anarrhinum brevifolium* Cosson & Kralik; G5: *Haloxylon schmittianum*; G6: *Limoniastrum guyonianum* (L.). LA: leaf area; LDMC: leaf dry matter content; SLA: specific leaf area; CC: canopy cover; EC: Soil electrical conductivity; OM: organic matter.

Discussion

The present study examines the plant and soil characteristics in protected desert ecosystems. Soils are crucial for increasing vegetative production and nutrient control. Since its creation, the park was not benefited from any pedological study. The transposition of the granulometric results on the texture classification shows that the main soil textures of the park ranges between sandy, sandy-loam and loamy-sand. The pH locates the different groups among weakly alkaline soils. UC, pH values were bigger than those of BS. Likely, Abule *et al.*, (2005) noticed higher pH in the covered sub-habitats than bare soils. According to Hagos & Smit (2005), a large number of interchangeable cations in vegetation patches is generally associated with higher pH. Our results showed that the EC was variable from one group to another. The higher salinity levels in groups 1 and 6 are mainly due to their position, which extends along the northern proximity of a salt depression. In arid areas, Nitrogen, resulting from the litter decomposition, is considered as essential element for plant production and soil fertilisation (Schlesinger *et al.*, 2006). For all the analyzed samples, N contents are very low ($< 0.1\%$) and cannot meet the plants needs from this essential element for their growth. According to Schlesinger *et al.*, (1990) the mixed effects of anthropogenic disturbances and global climate variations led to drier situation with less biological control of the nitrogen cycle. The total limestone is present in variable proportions reaching a high value in halophyte group (G1). This can be explained by the sedimentation process in this group which is characterized by the lowest elevation in the park. In fact, erosion material from all the park is transported by water and deposited in this group.

Among soil properties, organic matter content is regarded as very important element of quality. Schjonning *et al.*, (2004) reported that the OM content of soils is globally influenced by several factors such as climate, landscape, texture, inputs and disturbances. In our results, all soils of the studied groups have a very low OM contents. Some of them (i.e., G2 and G3) are very poor (< 1%). Generally, this can be clarified according to the dry climate influence. Thus, the role of vegetation is reduced in arid zones due to the low cover and the limited development of the plant aerial parts. In desert regions, a slight increase in OM contents can be observed (1% < OM < 2%). It can be explained both by the big amount of litter and the reduced compaction of soil especially in absence of the animal trampling. Similar results are obtained by Xie & Wittig (2004).

Vegetation characteristics as well as plant traits were usually employed to clarify the functional trade-offs and how they affect both the community composition and the ecosystem dynamics (McGill *et al.*, 2006). Studying the variation in leaf traits of plants in desert habitats helps to understand their adaptation to regional environmental changes and serves as an important basis for revealing the classification and structure of plant communities (Li *et al.*, 2021). *H. kahiricum*, *R. raetam* and *A. brevifolium* seem to be the most sensible plants to grazing due to their higher palatability indices (4, 3, and 4, respectively). Hence, these species show a decrease in their BV and their CC outside the park. Same findings are reported by Tarhouni *et al.*, (2007) who showed that the BV is affected by animal pressure (trampling and grazing). In contrast, the BV and CC of *H. strobilaceum* and *L. guyonianum* are almost the same inside and outside the park. This can be explained either by their resistance to grazing or that they are not preferred by animals since these two species are characterized by low palatability indices (2 and 1 respectively). In fact, *H. strobilaceum* is a halophyte species and cannot represent a real pastoral resource, probably because it is very loaded with salt.

For all the studied species, the leaf water contents (LWC) inside the park were higher than those outside and *vice-versa* for the dry matter content (LDMC). The park climate characteristics, causing water deficits for plants, can clarify these observations. Hence the plant species react by increasing their LDMC. The *H. kahiricum* xerophytic species has the lowest LWC and the highest LDMC. This high LDMC can be related to the leaf longevity and persistence (Withington *et al.*, 2006). Also, the location of the species on high position (mountain) in the park increased the impact of water stress (more LDMC). Besides, the stability of these two parameters for *R. raetam* in the interior and the exterior of the park is due to the location of species in wadis, where edaphic and hydraulic conditions are more favourable for growth. Moreover, this species is characterized by a strong adaptation to the extreme conditions and it develops a molecular mechanism that allows it to resist to lack of nutrients and water stress (Mittler *et al.*, 2001). The LA is crucial for the vegetation's light competition (Schneider & Huyghe, 2015) and their resource acquisition/use strategies. The situation within and out of the park, concerning LA, is very comparable for the

majority of species indicating that they adopted an avoidance strategy to reduce the animal impacts (Klimesova *et al.*, 2008; Rusch *et al.*, 2009). The low SLA inside and outside the park indicates a strong ability of the studied species to retain nutrients for a long time under harsh conditions. Poorter & de Jong (2002) showed that SLA plays a role in the trade-off between rapid biomass production (high SLA) and efficient nutrient conservation (low SLA). Diaz *et al.*, (2004) suggest that in poor and water-limiting environments, the dominant species tend to develop resource conservation strategies with low SLA and high LDMC. The obtained results showed the strong capacity of plants to conserve nutrients for a long time in low-productive and resource-poor environments. Garnier *et al.*, (2007) founded comparable results showing that declining SLA and growing LDMC are linked to the strategy of conservation which is a main characteristic of plants with very reduced growth speed. The plant characteristics can affect the soil properties and should be considered as main regulation key-element of ecosystem processes and services (Faucon *et al.*, 2017). Properties of soil were founded to be positively associated with CC and LA and negatively related to LDMC and SLA (axis 1). This suggests that soil characteristics are one of the most important elements for vegetation functioning and diversification (Zuo *et al.*, 2016). Such remarks can re-inforce those of Miatto *et al.*, (2016) showing that soil properties can influence all the plant community responses.

Conclusion

The plant functional traits can easily reflect how protection technique affects desert ecosystem dynamics and, therefore, permit to assess modifications in vegetation under grazing. Our results confirmed the positive influence of plant communities to enhance the soil structure and fertility even under desert conditions. This is particularly true with regard to soil organic matter, total limestone and pH which are all upper under canopy than bare soils. High LDMC with low SLA are informing about the strong capacity of plants to retain nutrients for a long time (conservative species) in low productive and resource-poor environments. All these results could be useful for understanding the plant functional traits under desert conditions and how they respond to protection in order to improve their conservation and management.

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References

- Abule, E., G.N. Smit and H.A. Snyman. 2005. The influence of woody plants and livestock grazing on grass species composition, yield and soil nutrients in the middle awash valley of Ethiopia. *J. Arid Environ.*, 60: 343-358. <https://doi.org/10.1016/j.jaridenv.2004.04.006>.
- AFNOR. 1987. Recueil de normes françaises, qualité des sols, méthodes d'analyses. 1. éd. Association française de normalisation (Afnor), pp. 19-30.

- Akram, M.A., X. Wang, W. Hu, J. Xiong, Y. Zhang, Y. Deng, J. Ran and J. Deng. 2020. Convergent variations in the leaf traits of desert plants. *Plants*, 9(8): 990. <https://doi.org/10.3390/plants9080990>.
- Anonymous. 1984. Official Method of Analysis, XIII edn. *Association of Official Analytical Chemist*, Washington, DC.
- Anonymous. 2011. "IBM SPSS statistics for Windows, version 20.0." New York: IBM Corp.
- Bainbridge, D.A. 2007. Guide for desert and dryland restoration: new hope for arid lands. Island Press, Washington, DC, USA, p. 416.
- Bates, D., M. Mächler, B. Bolker and S. Walker. 2014. Fitting linear mixed-effects models using lme4. *arXiv preprint arXiv:1406.5823*. <https://doi.org/10.18637/jss.v067.i01>.
- Cingolani, A.M., G. Posse and M.B. Collantes. 2005. Plant functional traits, herbivore selectivity and response to sheep grazing in Patagonian steppe grasslands. *J. Appl. Ecol.*, 42(1): 50-59. <https://doi.org/10.1111/j.1365-2664.2004.00978.x>.
- Deng, L., Z.P. Shangguan, G.L. Wu and X.F. Chang. 2017. Effects of grazing exclusion on carbon sequestration in China's grassland. *Earth-Sci. Rev.*, 173: 84-95.
- Díaz, S., I. Noy-Meir and M. Cabido. 2001. Can grazing response of herbaceous plants be predicted from simple vegetative traits? *J. Appl. Ecol.*, 38(3): 497-508. <https://doi.org/10.1046/j.1365-2664.2001.00635.x>.
- Díaz, S., J.G. Hodgson, K. Thompson, M. Cabido, J.H. Cornelissen, A. Jalili, G. Montserrat-Martí, J.P. Grime, F. Zarrinkamar, Y. Asri, S.R. Band, S. Basconcelo, P. Castro-Díez, G. Funes, B. Hamzehee, M. Khoshnevi, N. Pérez-Harguindeguy, M.C. Pérez-Rontomé, F.A. Shirvany, F. Vendramini, S. Yazdani, R. Abbas-Azimi, A. Bogaard, S. Boustani, M. Charles, M. Dehghan, L. de Torres-Espuny, V. Falczuk, J. Guerrero-Campo, A. Hynd, G. Jones, E. Kowsary, F. Kazemi-Saeed, M. Maestro-Martínez, A. Romo-Díez, S. Shaw, B. Siavash, P. Villar-Salvador and M.R. Zak. 2004. The plant traits that drive ecosystems: Evidence from three continents. *J. Veg. Sci.*, 15(3): 295-304. <https://doi.org/10.1111/j.1654-1103.2004.tb02266.x>.
- Faucon, M.P., D. Houben and H. Lambers. 2017. Plant functional traits: soil and ecosystem services. *Trends Plant Sci.*, 22(5): 385-394.
- Ferignac, P. 1962. Test de Kolmogorov-Smirnov sur la validité d'une fonction de distribution. *Revue de statistique appliquée.*, 10(4): 13-32.
- Gamoun, M. 2014. Grazing intensity effects on the vegetation in desert rangelands of Southern Tunisia. *J. Arid Land*, 6(3): 324-333. <https://doi.org/10.1007/s40333-013-0202-y>.
- Gamoun, M., A. Ouled Belgacem and M. Louhaichi. 2018. Diversity of desert rangelands of Tunisia. *Plant Divers*, 40: 217-225. <https://doi.org/10.1016/j.pld.2018.06.004>.
- Garnier, E., B. Shipley, C. Roumet and G. Laurent. 2001. A standardized protocol for the determination of specific leaf area and leaf dry matter content. *Funct. Ecol.*, 15(5): 688-695. <https://doi.org/https://doi.org/10.1046/j.0269-8463.2001.00563.x>.
- Garnier, E., S. Lavorel, P. Ansquer, H. Castro, P. Cruz, J. Dolezal, O. Eriksson, C. Fortunel, H. Freitas, C. Golodets, K. Grigulis, C. Jouany, H. Kazakou, J. Kigel, M. Kleyer, V. Lehsten, J. Leps, T. Meier, R. Pakeman, M. Papadimitriou, V. Papanastasis, H. Quested, F. Que'tier, M. Robson, C. Roumet, G. Rusch, C. Skarpe, M. Sternberg, J.P. Theau, A. The'ault, D. Vile and M. Zarovali. 2007. Assessing the effects of land-use change on plants traits, communities and ecosystems functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Ann Bot.*, 99: 967-985. <https://doi.org/10.1093/aob/mcl215>.
- Hagos, M.G. and G.N. Smit. 2005. Soil enrichment by *Acacia mellifera* subsp. *detinens* on nutrient poor sandy soil in a semi-arid southern Africa savanna. *J. Arid Environ.*, 61: 47-59. <https://doi.org/10.1016/j.jaridenv.2004.08.003>.
- Jager, M.M., S.J. Richardson, P.J. Bellingham, M.J. Clearwater and D.C. Laughlin. 2015. Soil fertility induces coordinated responses of multiple independent functional traits. *J. Ecol.*, 103(2): 374-385.
- Jeddi, K. and M. Chaieb. 2010. Changes in soil properties and vegetation following livestock grazing exclusion in degraded arid environments of South Tunisia. *Morphol. Distrib. Funct. Ecol. Plants.*, 205(3): 184-189.
- Klimesova, J., V. Latzel, F. de Bello and J.M. van Groenendael. 2008. Plant functional traits in studies of vegetation changes in response to grazing and mowing: Towards a use of more specific traits. *Preslia.*, 80(3): 245-253.
- Li, S., H. Wang, W. Gou, J.F. White, K.L. Kingsley, G. Wu and P. Su. 2021. Leaf functional traits of dominant desert plants in the Hexi Corridor, Northwestern China: Trade-off relationships and adversity strategies. *Glob. Ecol. Conserv.*, 28: e01666. <https://doi.org/10.1016/j.gecco.2021.e01666>.
- Liu, J., D. Hu, H. Wang, L. Jiang and G. Lv. 2022. Scale effects on the relationship between plant diversity and ecosystem multifunctionality in arid desert areas. *Forests*, 13(9): 1505. <https://doi.org/10.3390/f13091505>.
- Marion, B. 2010. Impact du pâturage sur la structure de la végétation: Interactions biotiques, traits et conséquences fonctionnelles. Thèse de doctorat. Université Rennes 1.
- McGill, B.J., B.J. Enquist, E. Weiher and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends Ecol. Evol.*, 21(4): 178-185.
- Miatto, R.C., I.J. Wright and M.A. Batalha. 2016. Relationships between soil nutrient status and nutrient-related leaf traits in Brazilian cerrado and seasonal forest communities. *Plant Soil*, 404(1): 13-33.
- Mittler, R., E. Merquiol, E. Hallak-Herr, S. Rachmilevitch, A. Kaplan and M. Cohen. 2001. Living under a 'dormant' canopy: a molecular acclimation mechanism of the desert plant *Retama raetam*. *Plant J.*, 25(4): 407-416. <https://doi.org/10.1046/j.1365-313x.2001.00975.x>.
- Nash Suding, K. and D. Goldberg. 2001. Do disturbances alter competitive hierarchies? Mechanisms of change following gap creation. *Ecology*, 82(8): 2133-2149. [https://doi.org/10.1890/0012-9658\(2001\)082\[2133:DDACHM\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[2133:DDACHM]2.0.CO;2).
- Poorter, H. and R. de Jong. 2002. A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from 15 habitats differing in productivity. *New Phytol.*, 143: 163-176. <https://doi.org/10.1046/j.1469-8137.1999.00428.x>.
- Rosignol, N. 2006. Hétérogénéité de la végétation et du pâturage : conséquences fonctionnelles en prairie naturelle. Thèse de 3ème cycle, Université de Rennes 1, France.
- Rusch, G.M., C. Skarpe and D.J. Halley. 2009. Plant traits link hypothesis about resource-use and response to herbivory. *Basic Appl. Ecol.*, 10(5): 466-474.
- Schjonning, P., S. Elmholt and B.T. Christensen (Eds.). 2004. Managing Soil Quality: Challenges in Modern Agriculture. CABI Publishing, Wallingford, UK, 368 pp. <https://doi.org/10.1079/9780851996714.0000>.
- Schlesinger, W.H., J.F. Reynolds, G.L. Cunningham, L.F. Huenneke, W.M. Jarrell, R.A. Virginia and W.G. Whitford. 1990. Biological feedbacks in global desertification. *Science*, 247(4946): 1043-1048. <https://doi.org/10.1126/science.247.4946.1043>.
- Schlesinger, W.H., K.H. Reckhow and E.S. Bernhardt. 2006. Global change: The nitrogen cycle and rivers. *Water Resour. Res.*, 42(3). <https://doi.org/10.1029/2005WR004300>.

- Schneider, A. and C. Huyghe. 2015. *Les légumineuses pour des systèmes agricoles et alimentaires*. Editions Quae.
- Schrama, M., P. Heijning, J.P. Bakker, H.J. van Wijnen, M.P. Berg and H. Olf. 2013. Herbivore trampling as an alternative pathway for explaining differences in nitrogen mineralization in moist grasslands. *Oecologia.*, 172(1): 231-243. <https://doi.org/10.1007/s00442-012-2484-8>.
- Tarhouni, M., F. Ben Salem, A. Ouled Belgacem, B. Henchi and M. Neffati. 2007. Mesure du biovolume de quelques espèces végétales autour de points d'eau en zone aride tunisienne. *Sécheresse*, 18: 240-245. <https://doi.org/10.1684/sec.2007.0108>.
- Tarhouni, M., W. Ben Hmida and M. Neffati. 2014. Caractérisation du couvert végétal naturel à l'extérieur et à l'intérieur du parc national de Sidi Toui, zone aride de la Tunisie. *Ecologia Mediterranea.*, 40(2): 41-52. <https://doi.org/10.3406/ecmed.2014.1257>.
- Török, P., K. Penksza, E. Tóth, A. Kelemen, J. Sonkoly and B. Tóthmérész. 2018. Vegetation type and grazing intensity jointly shape grazing effects on grassland biodiversity. *Ecol. Evol.*, 8(20): 10326-10335. <https://doi.org/10.1002/ece3.4508>.
- Violle, C., M.L. Navas, D. Vile, E. Kazakou, C. Fortunel, I. Hummel and E. Garnier. 2007. Let the concept of trait be functional! *Oikos*. 116(5): 882-892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>.
- Walkley, A. and I.A. Black. 1934. An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. *Soil Sci.*, 37(1): 29-38. <https://doi.org/10.1097/00010694-193401000-00003>.
- Wang, W., H. Liu, J. Zhang, Z. Li, L. Wang, Z. Wang, Y. Wu, Y. Wang and C. Liang. 2020. Effect of grazing types on community-weighted mean functional traits and ecosystem functions on inner mongolian steppe, China. *Sustainability*, 12(17): 7169. <https://doi.org/10.3390/su12177169>.
- Whitford, W.G. 2002. *Ecology of Desert Systems*; Academic Press: New York, USA.
- Withington, J.M., P.B. Reich, J. Oleksyn and D.M. Eissenstat. 2006. Comparisons of structure and life span in roots and leaves among temperate trees. *Ecol. Monog.*, 76: 381-397. [https://doi.org/10.1890/0012-9615\(2006\)076\[0381:COSALS\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2006)076[0381:COSALS]2.0.CO;2).
- Xie, Y. and R. Wittig. 2004. The impact of grazing intensity on soil characteristics of *Stipa grandis* and *Stipa bungeana* steppe in North China (autonomous region of Ningxia). *Acta Oecol.*, 25: 197-204. <https://doi.org/10.1016/j.actao.2004.01.004>.
- Zheng, S., W. Li, Z. Lan, H. Ren and K. Wang. 2015. Functional trait responses to grazing are mediated by soil moisture and plant functional group identity. *Scientific reports*. 5: 18163. <https://doi.org/10.1038/srep18163>.
- Zuo, X.A., S.K. Wang, P. Lv, X. Zhou, X.Y. Zhao, T.H. Zhang and J. Zhang. 2016. Plant functional diversity enhances associations of soil fungal diversity with vegetation and soil in the restoration of semiarid sandy grassland. *Ecol. Evol.*, 6(1): 318-328.

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