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Community diversity, functional traits and adaptation of *Stipa tenacissima* L. under different grazing regimes in a North African arid montane rangeland

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The mountain rangeland chain of Matmata (southern Tunisia) is characterised by an arid Mediterranean climate with severe droughts and high temperatures, combined with substantial human disturbance. In order to withstand these harsh conditions, plants have developed adaptive strategies and functional traits to survive. This study aims to evaluate the impact of three grazing regimes (grazing exclusion, seasonal and continuous grazing) on *Stipa tenacissima* L. functional traits, a dominant native and multi-use plant species, and its community. The findings suggest that the diversity of plant communities and traits of *S. tenacissima* are strongly affected by the management regime. Diversity is higher under seasonal grazing. Traits, such as leaf water content, specific leaf area and bio-volume are higher under seasonal grazing, compared with continuous grazing and/or sites fenced off to prevent grazing. Hence, seasonal grazing is recommended to maintain diversity of the plant community and to enhance the adaptation strategies of the local species under montane dryland conditions.

Keywords: aspect, elevation, management, mountainous drylands, vegetation

Supplementary material: available at <https://doi.org/10.2989/10220119.2020.1845796>

Introduction

Rangelands represent about one-third of terrestrial ecosystems around the world (Ellis and Ramankutty 2008). They provide many ecosystem services, such as forage resources, water infiltration and storage, erosion control, wildlife habitat, biodiversity and carbon sequestration (Vecchio et al. 2019). Tunisia, along with other countries in northern Africa, is currently facing degradation and desertification of its most fragile ecosystems, including the arid rangelands. The natural vegetal cover in these ecosystems is subject to several constraints related to edapho-climatic conditions and human activities, which affect the biophysical environment. Human pressure causes various disturbances that considerably modify the structure and the functioning of these ecosystems. For example, overgrazing is leading to the rarefaction or disappearance of the most palatable plant species and the spread of unpalatable ones (Tarhouni et al. 2010; Ouled Belgacem and Louhaichi 2013; Louhaichi et al. 2019). These degraded rangelands could be remediated by the application of appropriate management techniques, such as restoration and rehabilitation that provide sufficient capacity to these disturbed ecosystems to allow them to regenerate (Ouled Belgacem et al. 2008).

The dominant perennial Poaceae in southern Tunisia, and specifically in the montane rangeland chain of Matmata, is *Stipa tenacissima* L. This key plant species is used as fodder for local herds, particularly in seasons of low productivity or during dry years (Aloui 2006). In addition, the local population

use leaves of this species for traditional practices, such as some artefacts (baskets, strings and shoes). Such uses are the main biotic cause of degradation that threatens the natural vegetation cover in this area. In addition to human pressures, *S. tenacissima* is subject to many abiotic climate or soil stresses. Over the next 50 years, Ben Mariem and Chaieb (2017) forecast a negative impact of climate on *S. tenacissima* ecosystems, due to severe loss of suitable habitats. To promote sustainability in these unique ecosystems, it is important to apply effective management regimes and to assess the adaptability of functional traits of the dominant plant species. The most common regime is to fence off areas to prevent grazing, but this can negatively affect plants and their communities (Tarhouni et al. 2017a, 2017b). Studies have shown that seasonal grazing, including strategic rest periods, is generally better for rangelands than long-term exclusion (Ouled Belgacem et al. 2019). In order to evaluate the vegetation behaviour and highlight adaptations to intense grazing, it is important to understand and predict plant responses through their functional traits that are easy to measure. In fact, some traits associated with resource acquisition, such as SLA (specific leaf area), LDMC (leaf dry matter content) and LA (leaf area), can provide important insights to the adaptation of plants to grazing (Diaz et al. 2001). This study aims to predict and evaluate the effect of three grazing systems (exclusion, seasonal and continuous grazing) on the selected functional traits of *S. tenacissima*, and on the diversity of species in montane arid rangelands.

Material and methods

Study sites

Three sites located in the region of Toujane (south-east Tunisia) and belonging to the Matmata Mountain Chain were studied (Figure 1). The annual rainfall recorded in the region during the three vegetative growth periods of 2016–2017, 2017–2018 and 2018–2019 was 250 mm, 459 mm and 190 mm, respectively (Table 1). The mean annual precipitation in the region is approximately 150 mm. The physical environments of the three sites are similar (same soil substratum, topography and geology), but differ in altitudinal range and grazing regime. The first site (Zmertén, 33°26'07.20" N, 10°07'29.02" E, 3 000 ha) is located in the middle of the mountain chain and has been strictly protected from grazing for 42 years. Its natural vegetation is dominated by *Juniperus phoenicea* L., *S. tenacissima* and *Rosmarinus officinalis* L. Site 1 is approximately 9 km from site 2 and 8.5 km from site 3. The second site (Brighith, 33°29'23.40" N, 10°12'02.88" E, 100 ha) is located on the north-eastern border of the chain. This site is dominated by *S. tenacissima* and is

devoted to seasonal grazing (protected in spring and summer and grazed in autumn and winter) with controlled animal charge (100 animals in the whole site during three months). The third site (Control, 33°29'14.95" N, 10°11'58.24" E) is close to site 2 (0.5 km), dominated by *S. tenacissima* and continuously open to grazing with uncontrolled animal charge.

Data collection

The functional and biometric traits of *S. tenacissima* were measured during the spring of 2019, taking into account three elevation levels (low, medium and high) and two aspects to sunlight (south (high), north (low)) of the mountain hill. To characterise the whole plant community of the sites, three 20 m line-transects, 100 m apart, were installed at each level and aspect (in total, 18 lines per site). The methodological approach is a pseudo replicated-nested design, with the three grazing treatments confounded with site, within each of which is nested aspect (north aspect *versus* south), within which again is nested altitude (low, medium, high). The three transects at each elevation/aspect combination have been used as replicates. Data were collected using the quadrat point method (Daget and Poissonnet 1971; Floret 1988). A metal fine pin was entered into the vegetation every 20 cm along the transect (100 hits per line). The plant species touching each pin was recorded. The total vegetation cover (TVC in %) was calculated as: $TVC = (n/N) \times 100$ where n is number of points where the vegetation is present and N is the total number of the measured points along the line. The specific contribution (Sc in %) reflects the proportion of the species in the vegetation cover and was calculated as $Sc_i = FS_i / \sum FS \times 100$, where FS_i is the specific cover of the species and $\sum FS$ the sum of the cover of all species. Alpha diversity was obtained using the H' index (Shannon and Weaver 1949): $H' = -\sum FS_i \log_2 FS_i$. The H' index can be converted to the effective number of species, or true diversity, by taking its exponential (Jost 2006). In this study, H' is calculated with the binary logarithm; hence, the true diversity is $2^{H'}$.

To characterise *S. tenacissima*, nine tufts of different sizes (three big, three medium and three small) were measured for each level and aspect. In total, 54 measurements were made for each site (two aspects $\times$ three levels $\times$ three sizes $\times$ three replications). Five leaves were collected from each tuft to measure the leaf traits. The collected leaves were placed in moistened paper, and put in a refrigerator to prevent dehydration. In the laboratory, the leaves were weighed (to obtain their fresh matter (FM)), flattened, fixed and photographed. The photos were then analysed using 'Image J' software to calculate the leaf area

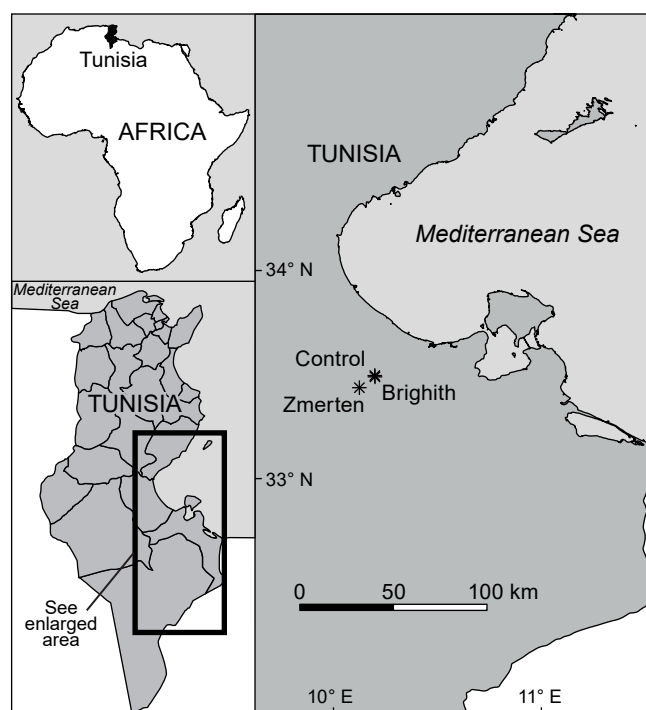


Figure 1: Geographical location of the study region in southern Tunisia

Table 1: Rainfall (mm) recorded in Toujane weather station during the three vegetative growth seasons of 2016–2017, 2017–2018 and 2018–2019

Period	Autumn				Winter		Spring			Summer			Total
	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	
2016–2017	7.7	45.0	20.7	69.6	6.4	10.0	28.5	56.3	6.5	0.0	0.0	0.0	250.7
2017–2018	0.0	87.0	227.0	55.0	0.0	37.0	5.5	18.5	0.0	0.0	0.0	29.0	459.0
2018–2019	60.0	51.0	26.5	2.2	6.0	8.5	16.2	12.5	7.4	0.0	0.0	0.0	190.3

(LA). The sampled leaves were oven dried for 48 hours at 60°C to obtain their dry matter content (DM). The leaf water content (LWC), as a percentage of FM, was calculated as $LWC = ((FM - DM)/FM) \times 100$. The leaf dry matter content (LDMC), in $mg\ g^{-1}$ FM, is DM/FM (Garnier et al. 2001). Specific leaf area (SLA), in $cm^2\ g^{-1}$ DM, is LA/DM . The biovolume (in m^3) is calculated as $BV = ((4/3) \pi r^3)/2$, where r is the average radius of the tuft and it is 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 in m^2) is the area covered by the aerial organs of *S. tenacissima* and it is calculated as $CC = \pi r^2$.

Data analysis

A number of separate one-way ANOVAs were undertaken to compare parameters within and among sites. The combined effect of elevation and aspect in the same site was analysed using two-way ANOVA. A three-way ANOVA was used to study the combined effect of sites, elevations and aspects. When an ANOVA was significant, the Least Significant Difference test (LSD) was used for classification. Pearson indices were used to study the correlation between *Stipa* functional traits. When perfectly related to one another, only one trait was included for the principal component analysis (PCA). Hence, the six retained variables for the analysis are LWC, LA, SLA, BV, Sc and TVc. The study sites were clustered based on these variables to identify groups in factorial planes. SPSS 20 software was used for all statistical analysis.

Results

S. tenacissima plant community – variations within sites

At the exclusion site (Zmerten), the total vegetation covers were 51.7, 54.7 and 47.3%, respectively, for low, medium and high elevations for the northern aspect, and 33.0, 41.7 and 51.7% for the southern aspect (Table 2). Vegetation cover did not differ ($p > 0.05$) between the north (51.2%) and south (42.1%) aspects nor between elevations on the same aspect. Total richness ($p < 0.001$), richness of annuals ($p = 0.011$), richness of perennials ($p = 0.002$), annual and perennial forbs ($p = 0.002$ and $p = 0.001$, respectively), and shrubs ($p = 0.016$) varied significantly, at medium elevation, according to aspect (Table 3). However, the only effect of elevation was for annual forbs on the south-facing slope ($p = 0.047$). The interaction effect between aspect and elevation was not significant for all parameters.

Under seasonal grazing (Brighith), total vegetation cover of the northern aspect was 76.3, 75.7 and 63.0%, respectively, at low, medium and high elevation. The respective covers on the southern aspect were 57.7, 45.3 and 50.0%. Richness of annual grasses ($p = 0.004$) and shrubs ($p = 0.049$) on the northern aspect, and, on the southern aspect, total richness ($p = 0.045$), and the richness of perennials ($p = 0.045$) and shrubs ($p = 0.03$) varied according to elevation. However, vegetation cover, perennial forbs and perennial grasses at medium elevation ($p = 0.013$, $p = 0.006$ and $p = 0.024$, respectively) were different between the north and the south aspects, as were perennial forbs ($p = 0.021$) and annual grasses ($p = 0.016$) at high elevation (Table 3). There was a significant

interaction effect between aspect and elevation for annual richness ($p = 0.047$) and annual grasses ($p < 0.001$) (Table 3). There were no significant variations in true diversity ($p > 0.05$) with elevation for either aspect.

At the control site, total vegetation cover on the north aspect was 48.4% compared with 37.6% on the south aspect. Total vegetation covers were 60.0, 39.0 and 46.3%, respectively, at low, medium and high elevations on the north aspect (Table 2). The respective covers on the south aspect were 29.0, 38.7 and 45.0%. Elevation influenced cover ($p = 0.026$) on the north aspect. Only vegetation cover ($p = 0.012$) and annual forbs ($p = 0.002$) at low and medium elevations, respectively, showed a significant effect of aspect (Table 3). The interaction effect between aspect and elevation was significant for vegetation cover ($p = 0.022$).

S. tenacissima plant community – variations among sites

The highest vegetation cover and most of the highest true diversity indices were obtained under seasonal grazing for both aspects and all elevations (Table 2). Regardless of site, the richness of perennials was higher than that of annuals and indicates the strong resilience of these ecosystems. The main shrubs in the seasonal grazing and the control sites were *Rosmarinus officinalis*, *Gymnocarpus decander* Forssk. and *Atractylis serratuloides* Cass. The protected site was dominated by perennial forbs, such as *Herniaria fontanesii* J. Gay. *Teucrium polium* L. and *Kickxia aegyptiaca* L. Perennial grasses were mainly represented by *S. tenacissima* in all sites. The difference in true diversity between sites was not significant ($p > 0.05$), despite the slightly higher index of the seasonally grazed site. Seasonal grazing appeared to increase vegetation cover through inducing large, vigorous tufts, and did not affect true diversity compared with grazing exclusion and continuous grazing. On the northern aspect, annual grasses ($p = 0.027$) at low elevation, and total richness ($p = 0.001$), richness of annuals ($p = 0.001$), richness of perennials ($p = 0.015$), annual forbs ($p < 0.001$), annual grasses ($p = 0.027$) and shrubs ($p = 0.007$) at medium elevation, differed between sites. On the southern aspect, most variables varied significantly between sites. Here, the interaction effect between site and elevation was significant only for annual forbs ($p = 0.046$). The significant interaction effect between site, elevation and aspect was noted for total richness ($p = 0.01$), richness of annuals ($p = 0.02$) and shrubs ($p = 0.021$).

S. tenacissima traits

The first three components (PC 1, 2 and 3) of a successful PCA together explained 90% of the variance. PC1 (37.4% of the variance) showed a high positive loading of LWC and LA and a negative loading with Sc. PC2 (32.4% of the variance) was highly positively correlated with BV and TVc and negatively associated with SLA. The third PC (20.2% of the variance) displayed a high positive loading of SLA and LA, and a negative loading of LWC.

The studied transects were bi-plotted, on the PC1-PC2/ PC1-PC3 planes, together with the six analysed functional traits (Figure 2). Four groups were identified according to the hierarchical cluster (Supplementary Figure 1). The

Table 2: Floral richness, vegetation cover (%) and true diversity indices in the three study sites of the montane rangeland chain of Matmata during spring 2019. N: northern aspect, S: southern aspect. L1: low elevation, L2: medium elevation, L3: high elevation. ^{A/B/C} indicate the differences between sites in the same elevation and same aspect; ^{a/b/c} indicate the differences between elevations in the same site and same aspect. * indicates the significant difference between Northern and Southern aspect in the same site and same elevation. Multiple comparisons are according to the LSD test when the ANOVA is significant. Values are means $\pm$ SD ($n = 3$)

Elevation level	Altitude (m)		Livestock exclusion			Seasonal grazing						Control		
			L1	L2	L3	L1	L2	L3	L1	L2	L3	L1	L2	L3
Richness	Perennial forbs	N	3.7 $\pm$ 0.58	2.7 $\pm$ 0.58*	4.7 $\pm$ 1.15	4.3 $\pm$ 1.53	4.3 $\pm$ 1.15*	4.0 $\pm$ 1.00*	4.0 $\pm$ 1.73	3.3 $\pm$ 0.58	4.7 $\pm$ 1.53			
		S	4.0 $\pm$ 3.00	0.0 ^{B*}	3.7 $\pm$ 2.52	1.7 $\pm$ 1.53	0.3 $\pm$ 0.58 ^{B*}	1.0 $\pm$ 1.00*	4.0 $\pm$ 1.00	3.0 $\pm$ 1.00 ^A	2.7 $\pm$ 0.58			
	Perennial grasses	N	1.0	1.0	1.3 $\pm$ 0.58	1.0	1.7 $\pm$ 0.58*	1.3 $\pm$ 0.58	1.7 $\pm$ 0.58	2.0 $\pm$ 1.00	1.7 $\pm$ 0.58			
		S	1.0 ^B	1.0 ^B	1.0	3.0 ^A	3.3 $\pm$ 0.58 ^{A*}	2.3 $\pm$ 1.15	2.0 $\pm$ 1.00 ^{AB}	3.0 $\pm$ 1.00 ^A	2.0 $\pm$ 1.00			
	Annual forbs	N	3.0 $\pm$ 1.73	3.7 $\pm$ 0.58 ^{A*}	2.7 $\pm$ 1.53	0.0	0.0 ^B	0.7 $\pm$ 1.15	1.7 $\pm$ 2.08	3.3 $\pm$ 0.58 ^{A*}	2.3 $\pm$ 1.53			
		S	0.3 $\pm$ 0.58 ^{Bb}	0.3 $\pm$ 0.58 ^{Bb*}	1.7 $\pm$ 0.58 ^{Aa}	0.0 ^B	0.0 ^B	0.0 ^B	2.0 $\pm$ 1.00 ^A	1.0 ^{A*}	1.7 $\pm$ 0.58 ^A			
Richness	Annual grasses	N	1.0 ^A	2.0 $\pm$ 1.00 ^A	2.3 $\pm$ 1.15	0.0 ^{Bb}	0.0 ^{Bb}	1.3 $\pm$ 0.58 ^{a*}	0.7 $\pm$ 0.58 ^A	0.7 $\pm$ 0.58 ^B	1.0 $\pm$ 1.00			
		S	0.7 $\pm$ 0.58 ^A	0.3 $\pm$ 0.58	0.7 $\pm$ 0.58	0.0 ^B	0.0	0.0 [*]	1.0 ^A	0.0	1.0 $\pm$ 1.00			
	Shrubs	N	4.7 $\pm$ 1.15	4.0 $\pm$ 1.00 ^{B*}	5.7 $\pm$ 1.53	5.3 $\pm$ 1.53 ^a	3.0 $\pm$ 1.00 ^{Bb}	5.7 $\pm$ 0.58 ^a	7.0 $\pm$ 1.73	7.0 $\pm$ 1.00 ^A	5.7 $\pm$ 1.53			
		S	2.3 $\pm$ 1.15 ^B	1.3 $\pm$ 0.58 ^{B*}	4.0 $\pm$ 2.00	6.7 $\pm$ 1.15 ^{Aa}	3.0 $\pm$ 1.00 ^{Bb}	4.3 $\pm$ 1.53 ^{ab}	6.7 $\pm$ 0.58 ^A	6.7 $\pm$ 2.31 ^A	5.7 $\pm$ 1.15			
	All perennials	N	9.3 $\pm$ 0.58	7.7 $\pm$ 1.54 ^{B*}	11.7 $\pm$ 3.06	10.7 $\pm$ 2.88	9.0 $\pm$ 1.73 ^B	11.0 $\pm$ 2.0	12.7 $\pm$ 1.53	12.3 $\pm$ 1.15 ^A	12.0 $\pm$ 2.64			
		S	7.3 $\pm$ 4.04	2.3 $\pm$ 0.58 ^{C*}	8.7 $\pm$ 4.04	11.3 $\pm$ 2.52 ^a	6.7 $\pm$ 1.53 ^{Bb}	7.7 $\pm$ 1.15 ^b	12.7 $\pm$ 2.08	12.7 $\pm$ 3.21 ^A	10.3 $\pm$ 2.31			
Richness	All annuals	N	4.0 $\pm$ 1.73	5.7 $\pm$ 1.53 ^{A*}	5.0 $\pm$ 2.64	0.0	0.0 ^C	2.0 $\pm$ 1.73	2.3 $\pm$ 2.31	4.0 ^B	3.3 $\pm$ 0.58			
		S	1.0 $\pm$ 1.00 ^B	0.7 $\pm$ 1.15*	2.3 $\pm$ 0.58 ^A	0.0 ^B	0.0	0.0 ^B	3.0 $\pm$ 1.00 ^A	1.0	2.7 $\pm$ 1.53 ^A			
	Total richness	N	13.0 $\pm$ 1.00	13.3 $\pm$ 0.58 ^{B*}	17.0 $\pm$ 4.58	10.7 $\pm$ 2.89	9.0 $\pm$ 1.73 ^C	11.0 $\pm$ 2.00	15.0 $\pm$ 3.00	16.3 $\pm$ 1.15 ^A	15.7 $\pm$ 2.52			
		S	7.7 $\pm$ 4.16 ^B	3.0 $\pm$ 1.00 ^{B*}	11.0 $\pm$ 4.36	11.3 $\pm$ 2.52 ^{ABa}	6.7 $\pm$ 1.53 ^{Bb}	7.7 $\pm$ 1.15 ^b	15.7 $\pm$ 1.15 ^A	13.7 $\pm$ 3.21 ^A	13.0 $\pm$ 1.00			
	Vegetation cover (%)	N	51.7 $\pm$ 14.5	54.7 $\pm$ 32.35	47.3 $\pm$ 6.11	76.3 $\pm$ 2.52	75.7 $\pm$ 6.76*	63.0 $\pm$ 15.72	60.0 $\pm$ 9.17 ^{a*}	39.0 $\pm$ 7.21 ^b	46.3 $\pm$ 2.51 ^{ab}			
		S	33.0 $\pm$ 10.8 ^B	41.7 $\pm$ 13.58	51.7 $\pm$ 14.81	57.7 $\pm$ 13.20 ^A	45.3 $\pm$ 10.26*	50.0 $\pm$ 3.46	29.0 $\pm$ 8.19 ^{B*}	38.7 $\pm$ 11.02	45.0 $\pm$ 13.45			
True diversity		N	3.1 $\pm$ 1.02	2.7 $\pm$ 1.16	2.9 $\pm$ 0.48	2.4 $\pm$ 1.29	2.6 $\pm$ 1.18	3.6 $\pm$ 0.55	3.6 $\pm$ 1.26	2.8 $\pm$ 0.55	3.0 $\pm$ 0.58			
		S	1.7 $\pm$ 0.22	1.7 $\pm$ 0.35 ^B	2.7 $\pm$ 0.87	2.4 $\pm$ 0.76	3.9 $\pm$ 0.58 ^A	3.8 $\pm$ 1.33	2.3 $\pm$ 0.37	2.8 $\pm$ 1.02 ^{AB}	3.0 $\pm$ 0.87			

Table 3: Statistical analysis showing the effects of sites, elevation and aspects and their interactions on the retained parameters. N: northern aspect, S: southern aspect. L1: low elevation, L2: medium elevation, L3: high elevation, B: Brighith (seasonally grazed), C: control (continuously grazed) and Z: Zmerten (Livestock exclusion)

Parameters	Location	Main effects	Sum of squares	DF	Mean of squares	F	p
Specific contribution	L1N	Among Sites	4 301.615	2	2 150.807	14.122	0.005
	ZL1	Among Aspect	3 361.140	1	3 361.140	22.909	0.009
	CL3	Among Aspect	1 419.882	1	1 419.882	10.291	0.033
	L1	Interaction Site × Aspect	4 312.609	2	2 156.305	5.337	0.022
Total vegetation cover	CN	Among Elevation	681.556	2	340.778	7.183	0.026
	L1S	Among Sites	1 446.222	2	723.111	5.211	0.049
	BL2	Among Aspect	1 380.167	1	1 380.167	18.443	0.013
	CL1	Among Aspect	1 441.500	1	1 441.500	19.093	0.012
	C	Interaction Elevation × Aspect	910.778	2	455.389	5.340	0.022
True Diversity	L2S	Among Sites	7.086	2	3.543	6.733	0.029
Total richness	BS	Among Elevation	36.222	2	18.111	5.433	0.045
	L2N	Among Sites	81.556	2	40.778	26.214	0.001
	L1S	Among Sites	96.222	2	48.111	5.773	0.040
	L2S	Among Sites	176.222	2	88.111	19.341	0.002
	ZL2	Among Aspect	160.167	1	160.167	240.25	0.000
	L2	Interaction Site × Aspect	61.444	2	30.722	10.055	0.003
		Interaction Site × Aspect × Level	222.778	12	18.565	2.709	0.010
Annuals richness	L2N	Among Sites	50.889	2	25.444	32.714	0.001
	L1S	Among Sites	14.000	2	7.000	10.500	0.011
	L3S	Among Sites	12.667	2	6.333	7.125	0.026
	ZL2	Among Aspect	37.500	1	37.500	20.455	0.011
	B	Interaction Elevation × Aspect	4.000	2	2.000	4.000	0.047
	L2	Interaction Site × Aspect	19.000	2	9.500	15.545	0.000
		Interaction Site × Aspect × Level	43.481	12	3.623	2.416	0.020
Perennials richness	BS	Among Elevation	36.222	2	18.111	5.433	0.045
	L2N	Among Sites	34.667	2	17.333	9.176	0.015
	L2S	Among Sites	161.556	2	80.778	18.641	0.003
	ZL2	Among Aspect	42.667	1	42.667	51.200	0.002
	L2	Interaction Site × Aspect	24.111	2	12.056	3.875	0.050
<i>Stipa</i> cover	L1N	Among Sites	4 108.222	2	2 054.111	23.701	0.001
	L3S	Among Sites	1 372.222	2	686.111	5.291	0.047
	BL2	Among Aspect	2 646.000	1	2 646.000	19.456	0.012
	CL3	Among Aspect	384.000	1	384.000	9.404	0.037
		Interaction Site × Aspect × Level	4 834.185	12	402.849	2.202	0.034
Perennial forbs	L2S	Among Sites	16.222	2	8.111	18.250	0.003
	ZL2	Among Aspect	10.667	1	10.667	64.000	0.001
	BL2	Among Aspect	24.000	1	24.000	28.800	0.006
	BL3	Among Aspect	13.500	1	13.500	13.500	0.021
	L2	Interaction Site × Aspect	10.333	2	5.167	9.300	0.004
Perennial grasses	L1S	Among Sites	6.000	2	3.000	9.000	0.016
	L2S	Among Sites	9.556	2	4.778	10.750	0.010
	BL2	Among Aspect	4.167	1	4.167	12.500	0.024
	L1	Interaction Site × Aspect	3.444	2	1.722	7.750	0.007
Annual forbs	ZS	Among Elevation	3.556	2	1.778	5.333	0.047
	L2N	Among Sites	24.667	2	12.333	55.500	0.000
	L1S	Among Sites	6.889	2	3.444	7.750	0.022
	L2S	Among Sites	1.556	2	0.778	7.000	0.027
	L3S	Among Sites	5.556	2	2.778	12.500	0.007
	ZL2	Among Aspect	16.667	1	16.667	50.000	0.002
	CL2	Among Aspect	8.167	1	8.167	49.000	0.002
	L2	Interaction Site × Aspect	8.778	2	4.389	26.333	0.000
Annual grasses	BN	Among Elevation	3.556	2	1.778	16.000	0.004
	L1N	Among Sites	1.556	2	0.778	7.000	0.027
	L2N	Among Sites	6.222	2	3.111	7.000	0.027
	L1S	Among Sites	1.556	2	0.778	7.000	0.027
	BL3	Among Aspect	2.667	1	2.667	16.000	0.016
	B	Interaction Elevation × Aspect	1.778	2	0.889	16.000	0.000
Shrubs	BN	Among Elevation	12.667	2	6.333	5.182	0.049
	BS	Among Elevation	20.667	2	10.333	6.643	0.030
	L2N	Among Sites	26.000	2	13.000	13.000	0.007
	L1S	Among Sites	37.556	2	18.778	18.778	0.003
	L2S	Among Sites	44.667	2	22.333	10.050	0.012
	ZL2	Among Aspect	10.667	1	10.667	16.000	0.016
		Interaction Site × Aspect × Level	51.222	12	4.269	2.401	0.021

codes of transects are based on the initial of the site names (Z: Zmerten, B: Brighith, C: Control), aspects (N: North, S: South) and elevations (1: low, 2: Medium, 3: High). The first group contains a mixture of exclusion, seasonal grazing and control transects (BS3, CN2, CN3, BS2, CS2, ZN1, CN1, BN3, BS1 and ZN3) where the *S. tenacissima* showed intermediate values of Sc, LWC, LA, TVc, BV and SLA. The second group includes only two control transects (CS1 and CS3) with low values of TVc, Sc and BV whereas group three, which includes two seasonally grazed transects (BN1 and BN2), had high values of these same three traits. The last group includes the four grazing exclusion transects (ZN2, ZS1, ZS2 and ZS3). Exclusion of grazing appeared to decrease the majority of *S. tenacissima* functional traits (low values of LWC, LA, BV and TVc). These effects were more pronounced than those of continuous grazing (Supplementary Table 1).

Discussion

The total vegetation cover of the site under seasonal grazing was higher than that of the fenced and control sites. Similar results were obtained by Gamoun et al. (2011) and Vecchio et al. (2019), who showed an increase in total vegetation cover in response to seasonal grazing. These results can relate, in part, to improvements in soil characteristics. In fact, seasonal grazing and grazing exclusion modified the soil habitat by increasing its organic matter content and improving physical and chemical conditions (Vecchio et al. 2018). The vegetation cover in the protected site was lower than the cover under seasonal grazing. The latter, including short grazing periods, alternated with fencing during the growing season, is generally better than strict protection; slight grazing activity can temporarily decrease the aerial organs of the existing

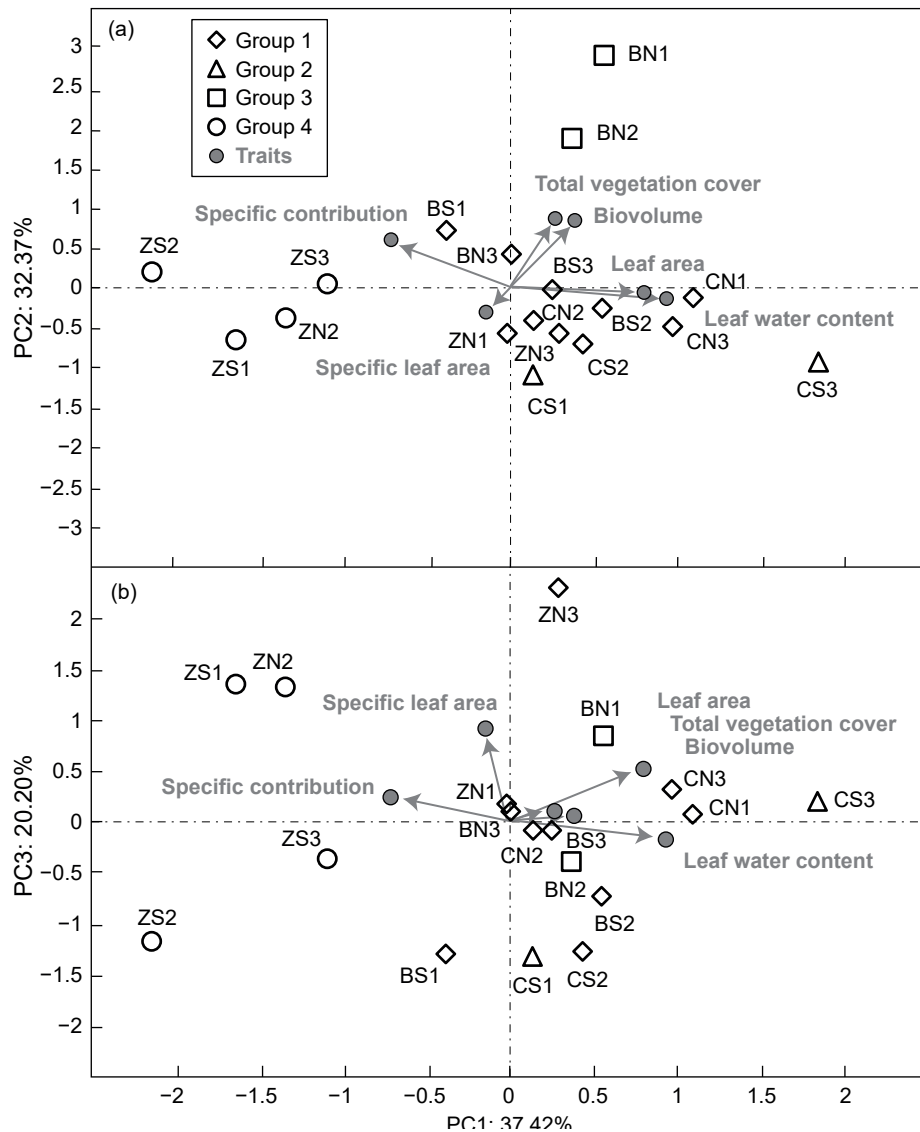


Figure 2: Two-dimensional PCA bi-plots showing the relationship among six variables in 27 locations in the PC1-PC2 (A) and PC1-PC3 planes (B). B: Brighith (seasonally grazed), C: control (continuously grazed) and Z: Zmerten (Livestock exclusion). N: northern aspect, S: southern aspect, 1: low elevation, 2: medium elevation, and 3: high elevation. For example: BN1 is Brighith North, low elevation

species and consequently increase their growth rate by allowing the root systems to revitalise the rest of the plant materials. As a result, the individual plants become more vigorous and the vegetation cover increases. The low total cover at the continuous grazing site could result from livestock selectivity and high disturbance of vegetation (Witten et al. 2005; Abdallah et al. 2011; Louhaichi et al. 2012). In the same context, overgrazing decreases plant cover and is the main cause of qualitative and quantitative change in vegetation communities (Tarhouni 2008).

Floral richness, which describes both the structure and functioning of a plant community is used for the qualitative characterization of an ecosystem, since any increase in richness may facilitate self-restoration of a degraded ecosystem (Bonet 2004; Zhang et al. 2005). Differences in species richness were significant between the seasonally and the continuously grazed sites. Indeed, an increase in pastoral pressure leads to a decline of species richness (Gamoun et al. 2011). In addition, an increase in grazing pressure is responsible for changes in the composition of vegetation (Metzger et al. 2005; Westbrooke et al. 2005). The high perennial richness shows a good phyto-ecological balance at the three studied sites, and supports the results of Ben Salem et al. (2009) concerning the same montane region. This may indicate a higher capacity of mountain ecosystems to withstand drought and disturbance. The early grazing effects can explain the low presence of annuals in the grazed sites (continuous and/or seasonal), since livestock prefer to graze the fresh annual species before perennials (Ouled Belgacem et al. 2019). The functioning of an ecosystem is closely linked with its biodiversity. True diversity shows the same trends in the three study sites. Biodiversity does not necessarily lead to an increase in the grazing services provided by an ecosystem (Tarhouni et al. 2017a). For example, the presence of unpalatable invasive plants in an open grazing area increases its biodiversity and species richness, but not its grazing value.

The contribution of *S. tenacissima* varied strongly among the tested management regimes. It was higher in the fenced site, due to its high ability to compete for water and nutrients, consistent with protection favouring more competitive and stress-tolerant species, regardless of their palatability (Louhaichi et al. 2012; Tarhouni et al. 2017b). The contribution of *Stipa* key species under seasonal grazing is greater than that in the control. Hence, heavy and continuous grazing leads to the loss of *S. tenacissima* and its replacement by undesirable shrub species, such as *Astragalus armatus* Willd. that are characterised by their resistance to animal activities. Seasonal grazing results in a higher contribution of preferred species, compared with continuous grazing (Vecchio et al. 2019), where the BV and CC of *S. tenacissima* under seasonal grazing are greater than in fenced and grazed areas. Fencing periods (provided by seasonal grazing) can allow fast-growing, competitive species to develop and enhance full flowering, pollination and seed dispersal of highly preferred plant species (Vecchio et al. 2019). Hence, seasonal grazing with controlled animal charge seems to be better for the natural vegetation than long-term protection or continuous grazing.

The LWC is an important factor and indicates the plant water status. A physiological imbalance marked by high

LDMC and low LWC was found in the studied sites. These results can be explained, in part, by the local climate conditions causing water deficits for the plants, which respond by increasing their LDMC. According to Wilson et al. (1999) 'Leaf dry matter content is a compromise between rapid assimilation and growth leading to an extreme and effective conservation of resources in the well-protected tissues'. It is probable that LA plays a fundamental role in competition for light (Schneider and Huyghe 2015). It is linked to strategies for the acquisition and use of resources by the plant. The sites studied showed small differences in LA. This indicates that *S. tenacissima* is well adapted to the edapho-climatic conditions of the region. The low values of SLA in the three sites give an idea about the adaptive capacity of *Stipa* in the mountainous arid rangelands. *Stipa tenacissima* in seasonal grazing, showed the lowest value of SLA and seems to be better adapted than plants in fenced and grazed sites. In addition, SLA is involved in the trade-off between rapid biomass production (high SLA) and efficient nutrient conservation (low SLA) (Poorter and de Jong 1999).

Conclusion

Continuous grazing in the studied arid montane rangeland, with its harsh climatic conditions, decreased the vegetation cover and caused the disappearance of some species. Management techniques, such as fencing and controlled grazing can reduce these effects and enhance the development of vegetation. Key pastoral plants, such as *S. tenacissima*, are promoted by these management regimes. Our overall aims were to highlight management techniques that contribute to better animal performance, provide more income for animal breeders, maintain the pastoral activities under harsh dryland conditions and exploit the montane ecosystems. The results suggest that seasonal grazing, with controlled animal charge, is more beneficial to plant species and communities than strict fencing or continuous grazing. These findings can be used to inform the sustainable development of rangelands to provide economic and environmental benefits, such as reducing animal feeding costs, reducing the grazing pressure on natural rangelands and rehabilitation of degraded rangelands using locally adapted plant material.

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References

- Abdallah F, Ouled Belgacem A, Chaieb M. 2011. Effects of ten years enclosure on vegetation characteristics of a national park in South Tunisia. *Acta Botanica Gallica* 158: 161–168. <https://doi.org/10.1080/12538078.2011.10516263>.
- Aloui K. 2006. Etude des techniques de régénération de l'alfa (*Stipa tenacissima* L.). MSc thesis, Institut National Agronomique de Tunisie, Tunisia.

- Ben Mariem H, Chaieb M. 2017. Climate change impacts on the distribution of *Stipa tenacissima* L. ecosystems in North African arid zone – a case study in Tunisia. *Applied Ecology and Environmental Research* 15: 67–82. https://doi.org/10.15666/aeer/1503_067082.
- Ben Salem F, Tarhouni M, Ouled Belgacem A, Neffati M. 2009. Variations saisonnières de quelques attributs structuraux des écosystèmes des Monts de Matmata en Tunisie méridionale sous l'effet de la sécheresse et de l'action anthropozoïque. *Sécheresse* 20: 204–209. <https://doi.org/10.1684/sec.2009.0184>.
- Bonet A. 2004. Secondary succession of semi-arid Mediterranean old-fields in southeastern Spain: insights for conservation and restoration of degraded lands. *Journal of Arid Environments* 56: 213–233. [https://doi.org/10.1016/S0140-1963\(03\)00048-X](https://doi.org/10.1016/S0140-1963(03)00048-X).
- Daget P, Poissonet J. 1971. Une méthode d'analyse phytologique des prairies. Critères d'application. *Annales Agronomiques* 22: 5–41.
- Diaz S, Noy-Meir I, Cabido M. 2001. Can grazing response of herbaceous plants be predicted from simple vegetative traits? *Journal of Applied Ecology* 38: 497–508. <https://doi.org/10.1046/j.1365-2664.2001.00635.x>.
- Ellis E, Ramankutty N. 2008. Putting people in the map: anthropogenic biomes of the world. *Frontiers in Ecology and the Environment* 6: 439–447.
- Floret Ch. 1988. Méthodes de mesure de la végétation pastorale. Pastoralisme et développement. Montpellier: CIHEAM.
- Gamoun M, Ouled Belgacem A, Hanchi B, Neffati M. 2011. Floristic diversity variations according to management types in dry rangelands of Southern Tunisia. *Ecologia Mediterranea* 37: 33–44. <https://doi.org/10.3406/ecmed.2011.1336>.
- Garnier E, Shipley B, Roumet C, Laurent G. 2001. A standardized protocol for the determination of specific leaf area and leaf dry matter content. *Functional Ecology* 15: 688–695. <https://doi.org/10.1046/j.0269-8463.2001.00563.x>.
- Jost L. 2006. Entropy and diversity. *Oikos* 113: 363–375. <https://doi.org/10.1111/j.2006.0030-1299.14714.x>.
- Louhaichi M, Ghassali F, Salkini A K, Petersen SL. 2012. Effect of sheep grazing on rangeland plant communities: Case study of landscape depressions within Syrian arid steppes. *Journal of Arid Environments* 79: 101–106. <https://doi.org/10.1016/j.jaridenv.2011.11.024>.
- Louhaichi M, Ouled Belgacem A, Petersen LS, Hassan S. 2019. Effects of Climate change and grazing practices on shrub communities of West Asian rangelands. *International Journal of Climate Change Strategies and Management* 11: 660–671. <https://doi.org/10.1108/IJCCSM-02-2018-0017>.
- Metzger KL, Coughenour MB, Reich RM, Boone RB. 2005. Effects of seasonal grazing on plant species diversity and vegetation structure in a semi-arid ecosystem. *The Journal of Arid Environments* 61: 147–160. <https://doi.org/10.1016/j.jaridenv.2004.07.019>.
- Ouled Belgacem A, Ben Salem H, Bouaicha A, El Mourid M. 2008. Communal rangeland rest in arid area, a tool for facing animal feed costs and drought mitigation: the case of Chenini community, Southern Tunisia. *Journal of Biological Sciences* 8: 822–825. <https://doi.org/10.3923/jbs.2008.822.825>.
- Ouled Belgacem A, Louhaichi M. 2013. The vulnerability of native rangeland plant species to global climate change in the West Asia and North African regions. *Climatic Change* 119: 451–463. <https://doi.org/10.1007/s10584-013-0701-z>.
- Ouled Belgacem A, Ben Salem F, Gamoun M, Chibani R, Louhaichi M. 2019. Revival of traditional best practices for rangeland restoration under climate change in the dry areas: A case study from Southern Tunisia. *International Journal of Climate Change Strategies and Management* 11: 643–659. <https://doi.org/10.1108/IJCCSM-02-2018-0019>.
- Poorter H, de Jong R. 1999. A comparison of specific leaf area, chemical composition and leaf construction costs of field plants from 15 habitats differing in productivity. *The New Phytologist* 143: 163–176. <https://doi.org/10.1046/j.1469-8137.1999.00428.x>.
- Schneider A, Huyghe C. 2015. *Les légumineuses pour des systèmes agricoles et alimentaires*. Editions Quae. <https://doi.org/10.35690/978-2-7592-2335-0>.
- Shannon CE, Weaver W. 1949. *The mathematical theory of communication*. Chicago, IL: University of Illinois Press.
- Tarhouni M. 2008. *Indicateurs de biodiversité et dynamique du couvert végétal naturel aux voisinages de trois points d'eau en zone aride tunisienne: cas des parcours collectifs d'El-Ouara*. PhD thesis, University of Tunis El-Manar. FS. Tunis.
- Tarhouni M, Salem FB, Ouled Belgacem A, Neffati M. 2010. Acceptability of plant species along grazing gradients around watering points in Tunisian arid zone. *Flora* 205: 454–461. <https://doi.org/10.1016/j.flora.2009.12.020>.
- Tarhouni M, Ben Hmida W, Ouled Belgacem A, Louhaichi M, Neffati M. 2017a. Is long-term protection useful for the regeneration of disturbed plant communities in dry areas? *African Journal of Ecology* 55: 509–517. <https://doi.org/10.1111/aje.12381>.
- Tarhouni M, Ben Hmida W, Neffati M. 2017b. Long-term changes in plant life forms as a consequence of grazing exclusion under arid climatic conditions. *Land Degradation & Development* 28: 1199–1211. <https://doi.org/10.1002/ldr.2407>.
- Vecchio MC, Golluscio R A, Rodríguez AM, Taboada MA. 2018. Improvement of saline-sodic grassland soils properties by rotational grazing in Argentina. *Rangeland Ecology and Management* 71: 807–814. <https://doi.org/10.1016/j.rama.2018.04.010>.
- Vecchio M C, Bolaños VA, Golluscio RA, Rodríguez AM. 2019. Rotational grazing and exclosure improves grassland condition of the halophytic steppe in Flooding Pampa (Argentina) compared with continuous grazing. *The Rangeland Journal* 41: 1–12. <https://doi.org/10.1071/RJ18016>.
- Westbrooke ME, Florentine SK, Milberg P. 2005. Arid land vegetation dynamics after a rare flooding event: influence of fire and grazing. *Journal of Arid Environments* 61: 249–260. <https://doi.org/10.1016/j.jaridenv.2004.09.004>.
- Wilson WA, Mahrenholz AM, Roach PJ. 1999. Substrate targeting of the yeast cyclin-dependent kinase Pho85p by the cyclin Pc110p. *Molecular and Cellular Biology* 19: 7020–7030. <https://doi.org/10.1128/MCB.19.10.7020>.
- Witten GQ, Richardson FD, Shenker N. 2005. Aspatial-temporal analysis on pattern formation around water points in a semi-arid rangeland system. *Biological Systems* 13: 59–81. <https://doi.org/10.1142/S0218339005001355>.
- Zhang J, Zhao H, Zhang T, Zhao X, Drake S. 2005. Community succession along a chronosequence of vegetation restoration on sand dunes in Horqin Sandy Land. *Journal of Arid Environments* 62: 555–566. <https://doi.org/10.1016/j.jaridenv.2005.01.016>.