

Ecophysiological responses of *Stipa tenacissima* L. under grassland degradation in a Mediterranean arid bioclimate (Postprint)

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Abstract

Under arid and semi-arid bioclimates, steppes are increasingly threatened by anthropogenic disturbance and climatic variability, which strongly affects ecosystem functioning and subsequently leads to desertification. We investigated the morphological and physiological responses of *Stipa tenacissima* L. across three disturbance levels (undisturbed, slightly disturbed, and highly disturbed) in three Tunisian steppe areas (Kasserine, Sidi Bouzid, and Sfax). Morphological and physiological traits were monitored over one year, together with microclimatic variables. Result showed that disturbance was a strong driver of plant functional dynamics, with significant effects on all traits and strong interactions with site and season. Disturbance reduced photosynthetic activity and water use efficiency, particularly in Sfax, where plants adopted conservative strategies (i.e., higher leaf dry matter content and reduced leaf area). In contrast, undisturbed populations maintained a stronger coordination between physiological and morphological traits. Seasonal analyses revealed that disturbance amplified physiological stress with limited recovery. Heatmap analyses further showed that disturbance weakened trait coordination and reshaped trade-offs between acquisitive and conservative traits. Partial least squares-path modeling showed that morphology strongly drove physiological performance (path coefficient=0.48). Disturbance (path coefficient=0.41) and tussock cover (path coefficient=0.47) influenced morphology both directly and indirectly through their effects on physiology. In conclusion, *S. tenacissima* adjusts physiological and morphological traits under disturbance, favoring stress tolerance, while undisturbed sites maintain high physiological efficiency and coordinated trait integration, reflecting a trade-off between survival and performance while overriding local site differences. Disturbance strongly restructures trait networks, drives site-specific adjustments, and modulates the seasonal balance between morphological stability and physiological flexibility.

Full Text

Preamble

J Arid Land (2026) 18(4): 657-675 Ecophysiological responses of *Stipa tenacissima* under grassland degradation in a Mediterranean arid bioclimate Khouloud KRICHEN , Mohamed CHAIEB Laboratory of Biodiversity and Ecosystems in Arid Environments (LEBIOMAT), Faculty of Sciences, University of Sfax, Sfax 3000, Tunisia

Abstract

Under arid and semi-arid bioclimates, steppes are increasingly threatened by anthropogenic disturbance and climatic variability, which strongly affects ecosystem functioning and subsequently leads to desertification. We investigated the morphological and physiological responses of *Stipa tenacissima* across three disturbance levels (undisturbed, slightly disturbed, and highly disturbed) in three Tunisian steppe areas (Kasserine, Sidi Bouzid, and Sfax). Morphological and physiological traits were monitored over one year, together with microclimatic variables. Result showed that disturbance was a strong driver of plant functional dynamics, with significant effects on all traits and strong interactions with site and season.

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Heatmap analyses further showed that disturbance weakened trait coordination and reshaped trade-offs between acquisitive and conservative traits. Partial least squares-path modeling showed that morphology strongly drove physiological performance (path coefficient=0.48). Disturbance (path coefficient=0.

41) and tussock cover (path coefficient=0.

42) influenced morphology both directly and indirectly through their effects on physiology. In conclusion,

S. tenacissima adjusts physiological and morphological traits under disturbance, favoring stress tolerance, while undisturbed sites maintain high physiological efficiency and coordinated trait integration, reflecting a trade-off between survival and performance while overriding local site differences. Disturbance strongly restructures trait networks, drives site-specific adjustments, and modulates the seasonal balance between morphological stability and physiological flexibility.

Keywords

disturbance; physiological traits; morphological traits; arid and semi-arid steppes; plant adaptation Citation:

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1 Introduction

Disturbances are abrupt and unexpected changes that modify the physical and biological conditions of ecosystems (Kumar et al., 2023). Increasing anthropogenic pressure, particularly under ongoing climate change, disrupts natural dynamics and can reduce species richness (Spicer © 2026 Xinjiang Institute of Ecology and Geography, Chinese Academy of Sciences, and Science Press. Publishing services by Elsevier B.

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et al., 2023). Both anthropogenic and natural disturbances may significantly alter ecosystem structure and functioning (Kumar et al., 2023). When disturbances exceed the grassland's self-regulating capacity, they can cause grassland degradation, a process driven by biotic and abiotic factors, which reduces resilience, slows recovery, and leads to retrogressive succession, ultimately affecting ecosystem functioning and biodiversity (Li et al., 2021). Such disturbances influence key physiological processes in plant species such as gas exchange (e.g., photosynthesis, stomatal conductance, etc.), and alter growth patterns, leading to biodiversity loss and diminished ecosystem services (Afuye et al., 2021).

Arid steppes, which form transitional zones between grasslands and deserts, are highly sensitive to natural and anthropogenic disturbances. In water-limited environments, severe droughts can push systems beyond recovery thresholds (Meng et al., 2025), and disturbances strongly influence plant community dynamics and ecosystem multifunctionality (Maestre et al., 2012). Because of their low resilience, arid steppes are particularly vulnerable to degradation and biodiversity loss, especially when human pressures intensify existing stresses and accelerate desertification processes (Kumar et al., 2023; Spicer et al., 2023; Meng et al., 2025). Within this context, the arid and semi-arid Mediterranean steppes dominated by *Stipa tenacissima*

L. are of major ecological importance in North Africa and the Iberian Peninsula, where they cover 60%–80% (Le Houérou, 1986). These ecosystems experience prolonged drought, irregular precipitation, high temperature, and strong evaporative demand (Le Houérou, 2001), conditions that are amplified by climate change and human disturbance. As a keystone species, *tenacissima*

contributes substantially to soil stability and biodiversity (Floc'h and Aronson, 1995; Derbel and Chaieb, 2007; Cortina et al., 2009), but its persistence is increasingly threatened. The species survives under extreme aridity through conservative functional traits, including dense tussocks, high root-to-shoot ratios, sclerophyllous leaves, and leaf folding that reduces gas exchange (Pugnaire et al., 1996; Pugnaire and Haase, 1996; Krichen et al., 2019; Zagoub et al., 2022). The species also develops smaller and thicker leaves under drought, minimizing surface exposure and water loss (Balaguer et al., 2002; Hamdani et al., 2019; Ojija, 2024). Together, these adaptations support a stress-tolerant strategy, enabling the species to persist in resource-poor and degraded environments where more demanding plants may fail (Huanca-Nunez et al., 2024).

Functional traits, such as specific leaf area, leaf dry matter content, and plant height, along with physiological traits like photosynthetic rate, stomatal conductance, and transpiration, provide key insights into how plants interact with their environments and respond to disturbance. These traits reveal potential trade-offs and adaptive strategies that allow

S. tenacissima to survive under degraded land conditions.

Despite its ecological significance, the effects of disturbance on

S. tenacissima remain poorly understood. Previous studies have primarily examined ecosystem-level outcomes such as vegetation structure or productivity, rather than the physiological and morphological strategies that enable individual plants to cope with stress (Maestre et al., 2005; Cortina et al., 2009, 2010; Maestre et al., 2012). Research on population-level responses has focused on water limitation, seasonality, and xeric versus mesic conditions, highlighting the species' plasticity (Pugnaire et al., 1996; Balaguer et al., 2002; Krichen et al., 2019; 2022; 2024a). However, no study has examined how different disturbance intensities affect both physiological and morphological traits of *tenacissima* across different populations over a year, covering the complete seasonal cycle of the plant, including both growth and dormancy phases (You et al., 2022).

To address this knowledge gap, we investigated whether disturbance intensity alters physiological (e.g., photosynthesis, stomatal conductance, and water use efficiency (WUE)) and morphological traits (e.g., leaf area, plant height, and leaf number) in

S. tenacissima and whether populations from different sites exhibit distinct adaptive responses. Specifically, we hypothesized that disturbance would reduce tussock architecture traits and physiological efficiency and favor stress-tolerant traits. We further expected that populations from more arid or xeric sites would show stronger survival strategies, reflecting local adaptation. Finally, we predicted that both physiological and morphological traits would be severely affected under disturbance, threatening

steppe functioning and ecosystem vulnerability. Given that steppes represent

the last successional stage before desert, such impacts could accelerate land degradation and contribute to desertification. 2 Materials and methods

2.1 Study area and experimental design

The study was conducted to evaluate the effects of disturbance levels on plant gas exchange parameters and functional traits in three

S. tenacissima steppes located in North Africa: Kasserine, Sidi Bouzid, and Sfax of Tunisia (Fig. 1 [Figure 1: see original paper]). Kasserine hosts the largest continuous steppes in Tunisia, Sidi Bouzid includes areas within Bouhedma National Park and adjacent steppes, and Sfax comprises semi-arid steppes in the Gonna Natural Reserve. The three sites had a semi-arid Mediterranean climate, characterized by hot, dry summers and mild, wet winters. Mean annual precipitation ranges from 250 to 450 mm, with Kasserine receiving 350 mm, Sidi Bouzid 300 mm, and Sfax 280 mm. Annual mean temperatures vary between 15°C and 20°C. Soils are generally shallow, calcareous, and low in organic matter. The bioclimatic zones differ among the sites:

Kasserine corresponds to an upper semi-arid zone, Sidi Bouzid to a semi-arid zone, and Sfax to a lower semi-arid zone. The sites experience varying levels of human pressure, including harvesting *Stipa* for artisanal and handmade uses, as well as climatic drought. The experimental design included three disturbance levels—disturbed, slightly disturbed, and undisturbed—defined based on varying degrees of human vegetation management or environmental pressure. Within each disturbance level, three plots were established, resulting in a total of nine plots per site (3 disturbance levels \times 3 plots). The plots, each measuring 30 m \times 30 m, were separated by at least 0.5 km to ensure spatial independence (Maestre et al., 2012). Eight individual

S. tenacissima plants were selected within each plot for trait and gas exchange analyses.

Study area including Kasserine, Sidi Bouzid, and Sfax sites in Tunisia, and classification of disturbance level Daily relative humidity, precipitation, and temperature variation data during the experiment period were collected with monitoring sensors located in the study sites. Daily solar radiation data were obtained from the European Centre for Medium-Range Weather Forecasts (ECMWF) Reanalysis v.5 (ERA5)-Land reanalysis dataset via the Google Earth Engine platform. The photosynthetically active radiation (PAR) was estimated using the standard empirical relationship:

$PAR = 0.45 \times G$ where G is the global solar radiation (MJ/m

We conducted physiological and morphological measurements across a continuous 12-month period (Fig. 2 [Figure 2: see original paper]), thereby capturing the complete seasonal (annual) cycle of the species, including both growth and dormancy phases, as recommended in similar long-term ecophysiological studies (e.g., You et al., 2022).

Daily estimated photosynthetically active radiation (PAR; a), precipitation (b), relative humidity (RH; c), and air temperature (d) from January to December 2024 across Kasserine, Sidi Bouzid, and Sfax sites in Tunisia

2.2 Disturbance assessment

Disturbance levels were quantified using two complementary vegetation-based metrics: (1) tussock cover of

S. tenacissima measured in situ as a field-based indicator of degradation; and (2) normalized difference vegetation index (NDVI) obtained from Sentinel-2 imagery, reflecting large-scale vegetation condition.

Tussock cover Tussock cover of

S. tenacissima was used as an in-situ disturbance metric. Disturbance levels were quantified in three 30 m \times 30 m plots per site. Each plot contained three transects, and along

each transect four 2 m \times 2 m quadrats were placed at regular intervals, giving a total of 12 quadrats per plot. In each quadrat, we visually estimated the percentage cover of

S. tenacissima tussocks, defined as the horizontal projection of live tussock crowns. Declines in

S. tenacissima cover are widely recognized as indicators of grazing intensity, trampling pressure, and overall degradation status in arid and semi-arid rangelands (Rey et al., 2011; Ghiloufi et al., 2016; Lang et al., 2021).

Difference in NDVI (DNDVI) We used NDVI as a disturbance indicator because it is one of the most widely employed remote-sensing indices for quantifying vegetation degradation. Numerous studies have demonstrated its sensitivity to changes in plant cover, biomass reduction, and land use impacts, particularly in arid and semi-arid ecosystems (Meneses-Tovar, 2012; Pettorelli, 2013; Yengoh et al., 2015; Chen et al., 2023; Marques et al., 2024). NDVI was derived from Sentinel-2 satellite images using Google Earth Engine. This index reflects vegetation density and physiological condition, with values ranging from -1 to 1, where higher values indicate greater vegetation cover. NDVI was calculated using the standard equation (Rouse et al., 1974):

Red / NIR where NIR is the value of near infrared, which corresponds to band B8; and Red corresponds to band B4 of Sentinel-2. Monthly composites were generated for the selected time frame to reduce cloud contamination.

To assess vegetation disturbance, we calculated DNDVI, which quantifies how current vegetation deviates from its historical maximum. The formula used was as follows: $\text{point NDVI} / \text{maximum NDVI}$ where NDVI is the maximum NDVI recorded at each location over the reference period (1 January 2020–31 December 2023);

and NDVI point is the NDVI at that location during the analysis period (April 2024).

Higher DNDVI values indicate that current vegetation condition is close to its historical maximum, reflecting stable and less disturbed vegetation. Conversely, lower DNDVI values suggest a reduction in vegetation cover or quality, indicating disturbed or degraded conditions.

We used these DNDVI values to classify the points into three disturbance levels: disturbed, slightly disturbed, and undisturbed (Table 1). The analysis and classification were done using Google Earth Engine, a cloud-based platform for processing satellite data.

Classification of disturbance Based on the distribution of tussock cover and DNDVI in our dataset, we classified the points into three disturbance levels as follows: disturbed: TC (tussock cover) $\leq 30\%$ and very low DNDVI; slightly disturbed: TC = $31\% - 45\%$ and intermediate DNDVI; undisturbed: TC $> 45\%$ and high DNDVI. This classification follows the observed data distribution and aligns with previous studies on steppe and grassland degradation (Kan et al., 2025; Yan et al., 2025; Zhang et al., 2025), providing a consistent framework to assess disturbance using both field-based tussock cover and remote-sensing indices (Table 1). The analysis and classification were performed in Google Earth Engine (Gorelick et al., 2017).

2.3 Physiological trait analysis

Leaf gas exchange rates were measured every month in each site over a full 12-month period. In the three study sites and each plot, eight individuals' tussocks per plot were selected.

Measurements were made early in the morning on sunny days using a portable open-flow gas exchange system (LC Pro, ADC BioScientific Ltd., Hertfordshire, UK). Temperature was set at levels approximating air temperature. PAR was delivered as photosynthetic photon flux density (PPFD) fixed at $1500 \mu\text{mol photons}/(\text{m}^2 \text{ s})$. Eight tussocks in each plot were selected for measurements. Then, we measured 24 tussocks per site. Net CO assimilation rate per unit leaf area (A), transpiration rate (E), stomatal conductance (g), and intercellular CO concentration (C) were recorded. WUE was calculated by A and g (von Caemmerer and Farquhar, 1981).

Classification of disturbance levels based on normalized difference vegetation index (NDVI), difference in NDVI (DNDVI), and field-measured tussock cover (TC) of *Stipa tenacissima*

L. across Kasserine, Sidi Bouzid, and Sfax sites in Tunisia Kasserine Sidi Bouzid $34^{\circ}42'11.0'' \text{N}$ $10^{\circ}31'18.0'' \text{E}$ Slightly disturbed $34^{\circ}42'24.0'' \text{N}$ $10^{\circ}32'39.0'' \text{E}$ $34^{\circ}42'40.0'' \text{N}$ $10^{\circ}32'23.0'' \text{E}$ $34^{\circ}41'59.0'' \text{N}$ $10^{\circ}31'40.0'' \text{E}$ Undisturbed $34^{\circ}42'00.0'' \text{N}$ $10^{\circ}31'26.0'' \text{E}$ $34^{\circ}42'09.0'' \text{N}$ $10^{\circ}31'25.0'' \text{E}$ Note: Band B4 and Band B8 are the values of red and near infrared, respectively.

2.4 Morphological trait analysis

In the three study sites and in each plot, eight individuals' tussocks per plot were selected. Leaf functional traits, including specific leaf area (SLA), leaf dry matter content (LDMC), and leaf thickness (LTh) were measured to evaluate the ecological strategies of plant species across disturbance levels (Tables 1 and 2). Five leaves per tiller were scanned and leaf area was measured using the ImageJ analysis software. SLA was defined as the one-sided area of a fresh leaf divided by its dry mass. LDMC was also calculated as the oven dry mass of a leaf divided by its saturated fresh mass. Leaf thickness (LTh), an important structural trait that contributes to SLA, was not measured directly but calculated following Pérez-Harguindeguy et al. (2013) as SLA and LDMC, reflecting the relationship between leaf mass, area, and density (Pérez-Harguindeguy et al., 2013). We conducted the leaf sampling and preservation in refrigerated conditions according to the protocols of Pérez-Harguindeguy et al. (2013). Three tillers per tussock were randomly selected from different sides to measure the number of green

leaves (GL), brown leaves (BL), and leaf length (LL).

2.5 Statistical analysis

All analyses were conducted in R v.4.5.1 software. Generalized linear models (GLMs) with a Gamma distribution and log link were used, with analysis of variation (ANOVA) to test the significance of main effects and interactions. Relationships between traits were explored using Spearman's rank correlation, and results were visualized as heatmaps that show correlation values and significance levels. These analyses were performed separately for each disturbance level (disturbed, slightly disturbed, and undisturbed).

Morphological and physiological traits were summarized into two composite indices using principal component analysis (PCA), retaining the first principal component. Seasonal patterns and disturbance effects were tested with generalized additive models (GAMs), using disturbance as a factor and month as a smooth term. Predictions with 95% confidence intervals were plotted with "mgcv" and "ggplot2" packages. Finally, partial least squares-path modeling (PLS-PM) was conducted using "plsplm" package to evaluate direct and indirect relationships between disturbance, physiological traits, and morphological traits.

3 Results

3.1 Site- and disturbance-driven trait variation Gas exchange traits (A_g , E , and C_i) and WUE showed significant differences both within and among sites along the disturbance gradient (Table 2). In Sidi Bouzid, the undisturbed site maintained the highest A_g and E , whereas the disturbed and slightly disturbed sites had lower values. In contrast, Kasserine displayed a clear increase in A_g , E ,

C, and WUE from disturbed to undisturbed sites. Sfax showed a mixed pattern: A and g were the highest under undisturbed conditions, but E increased under slightly disturbed conditions. Across sites, Kasserine consistently recorded the highest A under undisturbed conditions, while Sidi Bouzid tended to have higher WUE in less disturbed sites. Disturbed sites in Sfax generally retained higher C than that of Sidi Bouzid, but lower than that of Kasserine, indicating site-specific physiological adjustments to disturbance.

Morphological traits of

S. tenacissima varied along the disturbance gradient. BL generally decreased with disturbance, while GL increased in Sidi Bouzid and Kasserine but peaked at slightly disturbed sites in Sfax. LL, plant diameter (D), and height (H) consistently increased with disturbance, whereas SLA decreased. LDMC increased with disturbance in Sfax and Kasserine but was the highest in undisturbed Sidi Bouzid. LTh slightly increased in Sidi Bouzid and Kasserine but remained stable in Sfax. Structural traits including D and H, consistently increased from disturbed to undisturbed sites. Overall, Sidi Bouzid exhibited the largest morphological shifts between disturbed and undisturbed sites, while Sfax showed more gradual changes, and Kasserine displayed trait-specific, non-linear responses.

All morphological and physiological indicators showed significant impacts of site, disturbance, and month (<0.001 ; Table 3). Treatment was the main factor influencing morphological traits such as H, D, SLA, LDMC, and LTh. Seasonal variation and the interaction among site, disturbance, and month also had a significant impact. Significant effects of all parameters were also demonstrated by physiological parameters associated with gas exchange (A, E, g, and WUE). While site, disturbance, and season all had a significant impact on C and WUE, seasonal fluctuation (month) had the most impact, especially on A, E, and g. Disturbance strongly affected both physiological and morphological traits. A, g, E, and WUE were reduced in disturbed plots, while BL was higher. Conversely, GL, LL, SLA, LDMC, LTh, D, and H increased in less disturbed or undisturbed plots. These patterns were observed across all the three sites, with some variation in absolute values.

Morphological and physiological traits of

S. tenacissima across Sidi Bouzid, Kasserine, and Sfax sites under different disturbance levels

Trait	Parameter	Disturbance level	Disturbed	Slightly disturbed	Undisturbed
H (m)			0.623±0.017	0.891±0.013	1.017±0.014
BL (cm)			2.722±0.098	1.253±0.088	1.111±0.074
GL (cm)			1.870±0.092	3.083±0.050	1.050±0.050

Mean±SE; A, photosynthesis; g, stomatal conductance; E, transpiration; C, intercellular CO₂ concentration; WUE, water use efficiency.

Results of analysis of variation (ANOVA) for physiological and morphological variables among different sites, disturbance, and months

Variable	Effect	Chi-square	Significance
Physiological trait	Site×Disturbance	<0.001	<0.001
	Site×Month	<0.001	<0.001
Disturbance×Month	Disturbance×Month	<0.001	<0.001
	Site×Disturbance×Month	<0.001	<0.001
Disturbance	Disturbance	<0.001	<0.001
	Month	<0.001	<0.001
Site×Disturbance	Site×Disturbance	<0.001	<0.001
	Site×Month	<0.001	<0.001

Disturbance×Month <0.001 Site×Disturbance×Month <0.001 Morphological trait <0.001 Disturbance <0.001 Month <0.001 Site×Disturbance <0.001 Site×Month <0.001 Disturbance×Month <0.001 Site×Disturbance×Month <0.001 To be continued

Continued Variable Effect Chi-square <0.001 Disturbance <0.001 Month <0.001 Site×Disturbance <0.001 Site×Month <0.001 Disturbance×Month <0.001 Site×Disturbance×Month <0.001 <0.001 Disturbance <0.001 Month <0.001 Site×Disturbance <0.001 Site×Month <0.001 Disturbance×Month <0.001 Site×Disturbance×Month <0.001 <0.001 Disturbance <0.001 Month <0.001 Site×Disturbance <0.001 Site×Month <0.001 Disturbance×Month <0.001 Site×Disturbance×Month <0.001 <0.001 Disturbance <0.001 Month <0.001 Site×Disturbance <0.001 Site×Month <0.001 Disturbance×Month <0.001 Site×Disturbance×Month <0.001 <0.001 Disturbance <0.001 Month <0.001 Site×Disturbance <0.001 Site×Month <0.001 Disturbance×Month <0.001 Site×Disturbance×Month <0.001 <0.001 Disturbance <0.001 Month <0.001 Site×Disturbance <0.001 Site×Month <0.001 Disturbance×Month <0.001 Site×Disturbance×Month <0.001 <0.001 Disturbance <0.001 Month <0.001 Site×Disturbance <0.001 Site×Month <0.001 Disturbance×Month <0.001 Site×Disturbance×Month <0.001 <0.001 Disturbance <0.001 Month <0.001 Site×Disturbance <0.001 Site×Month <0.001 Disturbance×Month <0.001 Site×Disturbance×Month <0.001 <0.001

3.2 Trait-trait relationships across disturbance levels The analysis of heatmaps (Fig. 3 [Figure 3: see original paper]) showed the interaction between physiological, morphological, and environmental variables across the three disturbance levels. At disturbed sites, correlations were contrasted, with several moderate to strong positive or negative relationships. DNDVI showed weak to moderate associations with most traits, while TC was generally weakly correlated.

In slightly disturbed sites, DNDVI was positively correlated with LL, LTh, D, and H, while TC showed similar patterns except for

H. A and g were negatively correlated with BL and positively with

LL. Undisturbed sites exhibited the strongest correlations: DNDVI, WUE, C, and E were positively associated with morphological traits (BL, GL, D, and H), with TC showing similar trends. Overall, the results indicate a gradient of functional integration, from contrasted correlations under disturbance to coherent trait coordination in undisturbed conditions.

3.3 Seasonal patterns of

S. tenacissima traits Morphological and physiological indices, predicted by GAMs (Fig. 4 [Figure 4: see original paper]), exhibited clear seasonal fluctuations, with distinct responses to disturbance treatments. Morphological indices remained relatively stable across the year, showing only moderate seasonal variations. Undisturbed sites consistently maintained the highest morphological values, while disturbed sites displayed the lowest values, particularly from spring to autumn. Slightly disturbed sites showed intermediate values,

following a similar seasonal pattern to undisturbed sites.

In contrast, physiological indices displayed a stronger seasonal variability. All treatments showed a decline during spring and summer, with the most pronounced reduction observed in disturbed sites, where physiological values dropped markedly between April and August.

Undisturbed sites maintained comparatively higher physiological values throughout the year, whereas disturbed sites showed substantial reductions, especially during mid-summer. Slightly disturbed sites again exhibited intermediate values, though closer to undisturbed conditions in autumn and winter. Disturbance intensity strongly influenced both morphological and physiological performances, with greater disturbance associated with lower index values and higher seasonal variability.

3.4 Structural relationships among

S. tenacissima traits The PLS-PM analysis revealed significant relationships among disturbance indicators, morphological traits, and physiological traits (Fig. 5 [Figure 5: see original paper]). Disturbance had a strong effect on plant structure: TC was strongly and positively associated with morphological traits (path coefficient=0.41). DNDVI additionally had a moderately direct and positive effect on physiological responses (path coefficient=0.35), whereas TC had a negligible direct effect (path performance (path coefficient=0.48), indicating that plant structure mediates much of the physiological variation observed. Hence, disturbance influenced physiology both directly through DNDVI and indirectly through its strong effect on morphology.

4 Discussion

Arid ecosystems are strongly affected by disturbances, particularly those resulting from human activities and climate change (Jeddi and Chaieb, 2010; Haq et al., 2025). Arid steppes with *tenacissima* are threatened by desertification, which represents the next stage in ecological succession, due to their proximity to desert ecosystems as well as the long-term human activities (Cortina et al., 2010; Maestre et al., 2012). Along disturbance gradients, adaptive strategies of *tenacissima* significantly changed in relation to resource availability and disturbance level. Both TC and NDVI are vegetation-based indices of disturbance, which implies that the observed relationships with plant traits may be partly confounded, since both predictor and response variables reflect vegetation characteristics (Meneses-Tovar, 2012; Pettorelli, 2013). Despite this

Correlation heatmaps showing pairwise Spearman's correlation coefficients among physiological, morphological, and environmental variables in disturbed (a), undisturbed (b), and slightly disturbed (c) sites. T, temperature; PAR, photosynthetically active radiation; P, precipitation; RH, relative humidity. , <0.050 level; <0.010 level; **, <0.001 level.

Seasonal variation of morphological (a) and physiological (b) indices across disturbed, slightly disturbed, and undisturbed sites, as predicted by generalized additive models (GAMs). Shaded areas represent 95% confidence intervals.

Partial least squares-path modeling (PLS-PM) linking disturbance indicators (DNDVI and TC (tussock cover)) to Physio (physiological) and Morpho (morphological) traits. Standardized path coefficients are shown on the arrows. Disturbance indicators affected morphology through two pathways: a moderate effect of DNDVI and a stronger effect of TC. limitation, these indices are widely used and recognized as reliable indicators of ecosystem degradation in arid and semi-arid rangelands (Rey et al., 2011; Ghiloufi et al., 2016; Chen et al., 2023). The combined use of field-based (TC) and remote-sensing metrics (NDVI and DNDVI) allowed us to capture both local and landscape-scale patterns of disturbance, providing robust evidence of the links between vegetation condition and plant morphological and physiological responses.

The strong site effect observed across both morphological and physiological parameters indicates that local environmental conditions play a central role in shaping the performance of *tenacissima*. Marked differences were observed among the three study sites, indicating that local climatic conditions strongly affect the functional strategies of

S. tenacissima. Plants from the

driest sites displayed lower A_g , and E, coupled with higher WUE. This pattern reflects a conservative strategy, where stomatal regulation is prioritized to minimize water loss under severe water shortage. Such responses have been reported in semi-arid ecosystems, where

S. tenacissima shows high plasticity in regulating stomatal activity and carbon assimilation depending on soil moisture availability (Ramírez et al., 2008a).

Kasserine region, which constitutes the main Alfa (

S. tenacissima) steppes in Tunisia, showed the highest morphological development (greater height and leaf area) and enhanced physiological activity (A_g , and E), reflecting the relatively higher elevation, and more mesic conditions of this site.

S. tenacissima follows an acquisitive strategy, optimizing carbon gain and growth when water stress is less severe (Ramírez et al., 2007; Fajardo-Cantos et al., 2023; Krichen et al., 2024b, 2025). This finding is consistent with previous works (Puigdefábregas and Mendizabal, 1998; Krichen et al., 2019, 2024a), highlighting the improved vigor and biomass production of *tenacissima* in more favorable environments. Sidi Bouzid represented an intermediate pattern in comparison with the other study sites.

S. tenacissima displayed moderate photosynthetic rates, SLA, and WUE, suggesting a heterogeneity of response (i.e., growth or water conservation) that depends on resource availability. This balance highlights the plasticity of

S. tenacissima, enabling persistence under fluctuating resource conditions that are typical in central Tunisian steppes (Msadek et al., 2021). In Sfax, the most xeric site, the species exhibited strongly conservative patterns with minimizing photosynthetic activity, g , and E , but maintained the highest WUE. This pattern suggests that plants from Sfax adapt stomatal regulation to persistent water limitation (Ramírez et al., 2008a). Hence, populations from xeric sites (Sfax) emphasize drought tolerance, while those from relatively favorable sites (Kasserine) prioritize productivity, with Sidi Bouzid populations showing intermediate response. The ability of

S. tenacissima to modify its functional characteristics across environmental gradients may be a key component in preserving its dominance and resilience in Mediterranean arid environments (Le Houérou, 2001). Species response can vary differently in different disturbance levels and varying resource acquisition strategies in different sites, which may be explained by the higher intraspecific variation (Noualhaguet et al., 2024).

Under disturbed conditions, plants allocate more resources to structural reinforcement manifested as increased leaf density and thickness. This structural investment slows growth but favors stability, longer leaf lifespan and carbon retention (Khan et al., 2025). According to Khan et al. (2025), leaves with high LDMC values are denser and have a higher percentage of structural materials like cellulose and lignin, which improve resilience and reduce physical damage. Such structural investment supports conservative above-ground carbon strategies by retaining carbon in plant biomass over extended periods (Hamdani et al., 2019; Krichen et al., 2019; Chieppa et al., 2022). Here, long-term carbon refers to the portion stored in plant tissues that contributes to ecosystem carbon storage, stability, and resilience, especially in arid or disturbed systems (Chieppa et al., 2022). The decline in photosynthetic performance and WUE further supports this conservative and stress-tolerant strategy. The decrease in photosynthesis is usually caused by stomatal limitations under arid conditions, where plants restrict growth and reduce investment in above-ground biomass (Krichen et al., 2019, 2022, 2024a). Conversely, in undisturbed environments, individuals exhibit maximal A , WUE, and greater structural growth (e.g., height and leaf area), suggesting an acquisitive, growth-oriented strategy. Krichen et al. (2019) found

S. tenacissima allocate resources to aboveground when the condition is suitable. In mesic sites, the species showed a higher productivity and an important aboveground architecture (Krichen et al., 2024a). In our study, the species in non-disturbed sites are protected from anthropic activity like uprooting and overgrazing.

S. tenacissima has developed adaptive strategies that allow it to better withstand harsh climatic conditions compared with other tussock species exposed to destruction in degraded ecosystems. Populations in slightly disturbed sites often exhibit intermediate traits, such as elevated SLA and regulated stomatal conductance,

reflecting a balanced and opportunistic growth strategy.

S. tenacissima develops this approach as a survival mechanism in response to climatic variability and unstable environments (Pugnaire and Haase, 1996; Slimani et al., 2010). Moreover, under moderate grazing regimes,

S. tenacissima showed a flexible response to environmental stress by increasing SLA and leaf water content (Msadek et al., 2021).

Trait–trait correlations revealed how disturbance alters functional integration across *tenacissima* populations. In disturbed sites, the weak to moderate associations between disturbance indices (DNDVI and TC) and functional traits indicate heterogeneous and less coordinated response that is typical in stress-driven structural degradation in perennial tussock grasses (Díaz et al., 2004). A and g were negatively correlated with BL and positively with LL, reflecting a key adaptive mechanism of

S. tenacissima, the maintenance of a dense layer of dead leaves that protects the tiller base while prioritizing functional photosynthetic leaves for resource acquisition (Mehdadi et al., 2008; Ramírez et al., 2008b; Moulay and Benabdeli, 2012). The positive relationships of SLA and LTh with E highlight physiological adjustments associated with rapid evaporative cooling and gas exchange, which is typical strategy for this species to avoid drought (Flexas and Medrano, 2002). In slightly disturbed sites, the positive correlations of DNDVI with LL, LTh, D, and H, mirrored by TC except for H, indicate structural plasticity of the tussock, a known adaptation of

S. tenacissima that allows it to rebuild leaf biomass and expand tiller bases as disturbance pressure decreases (Poorter et al., 2012; Krichen and Chaieb, 2025). In undisturbed sites, strong coordination between DNDVI, WUE, C, E, and morphological traits (BL, GL, D, and

H) reflects integrated functional networks, where the species has deep root system, tight tussock architecture, and high WUE act synergistically to optimize performance under stable steppe conditions (Reich, 2014; Krichen et al., 2019). These results show that *tenacissima* relies on a combination of tussock structural resilience, protective brown leaf layers, and physiological plasticity, with functional integration strengthening as disturbance intensity declines. The seasonal dynamics modeled by GAM further highlight how disturbance modifies trait responses.

Morphological indices were relatively stable across the year, especially in undisturbed sites, reflecting a resilience of structural investment. Plants adjust structural traits in response to seasonal stresses such as drought, allowing them to optimize water use while maintaining resilience and photosynthetic function (Yavas et al., 2024). Physiological indices showed strong seasonal fluctuations, with pronounced declines in disturbed sites during spring and late summer.

Photosynthetic activity decreases or even ceases in

S. tenacissima due to the extreme rolling of leaves induced by bulliform cells (Yavas et al., 2024). This mechanism reduces water loss and protects tissues from desiccation and involves a trade-off since it limits carbon assimilation (Yavas et al., 2024). Leaf rolling thus reflects a key drought survival strategy, where water conservation is prioritized over photosynthetic efficiency in arid steppes (Pugnaire and Haase, 1996). Disturbance primarily destabilizes physiological processes, which are more plastic and sensitive to environmental variability than morphological traits (Reich, 2014). Alterations in photosynthetic traits related to carbon assimilation may therefore result in significant losses in plant growth and productivity (Yavas et al., 2024). Undisturbed ecosystems cope better with seasonal stresses because coordinated growth and functional traits enhance stability and resilience, while in disturbed sites, disruption weakens this coordination and reduces resilience (Yan et al., 2024). Undisturbed and slightly disturbed sites demonstrated partial physiological recovery during autumn months. Disturbed sites remained physiologically impaired during the whole season, with a reduced functioning even during periods normally associated with resource accumulation and recovery (Herben et al., 2018).

The PLS-PM analysis highlights a hierarchical organization of plant responses to disturbance, in which morphological traits play a central role in shaping physiological functioning.

Disturbance effects associated with TC were primarily expressed through changes in plant

structure, suggesting that long-term disturbance constrains morphology before influencing physiological processes. In contrast, DNDVI reflected more immediate disturbance effects, influencing both structural traits and physiological performance through complementary pathways. This result suggests that plants adjust structurally and physiologically in response to disturbance, reflecting stress-induced plasticity and compensatory growth (Adler et al., 2014).

Morphology mediates most of the plant's physiological response to disturbance, while disturbance acts both as a direct stressor and as a modifier of structural traits, which in turn influence function.

These patterns align with trait-based ecological theory, where structural traits mediate functional responses to environmental variation (Funk et al., 2017). Functional traits track environmental changes and determine how ecosystems respond to perturbations, connecting species-level adjustments with overall ecosystem functioning (Sparks and Menzel, 2013; Adler et al., 2014).

5 Conclusions

Disturbance emerges as the dominant driver of variation in

S. tenacissima functional traits across Tunisian steppes, exerting stronger impacts on physiological processes than on morphological structures. Physiological

traits act as the primary mediators of morphological response *tenacissima* adjusts its functional traits along the disturbance gradient through a combination of structural plasticity and physiological flexibility. Under high disturbance, it relies on physiological adjustments and trade-offs between leaf number and length. Moderate disturbance promotes tussock structural plasticity, and undisturbed conditions show tightly coordinated traits forming integrated functional networks that optimize efficiency and resilience.

Along the disturbance gradient,

S. tenacissima populations shift from acquisitive strategies with high efficiency and coordinated growth in undisturbed sites, to intermediate strategies balancing growth and tolerance in slightly disturbed sites, and ultimately to conservative, stress-tolerant strategies in highly disturbed sites. Overall, the species adopts a “morphological stability-physiological flexibility” strategy that mitigates disturbance impacts, ensuring persistence under stress while highlighting the limits of recovery under severe or prolonged disturbance. However, severe or prolonged disturbance reduces plant functional performance, decreasing steppe ecosystem functioning and resilience, which may accelerate land degradation and contribute to desertification in these vulnerable arid and semi-arid ecosystems.

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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