Effects of water stress on growth, phenology, photosynthesis, and leaf water potential in *Stipagrostis ciliata* (Desf.) De Winter in North Africa (Postprint)

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Abstract

Stipagrostis ciliata (Desf.) De Winter is a pastoral C4 grass grown in arid regions. This research work focused on assessing the growth of S. ciliata accessions derived from two different climate regions (a wet arid region in the Bou Hedma National Park in the central and southern part of Tunisia (coded as WA), and a dry arid region from the Matmata Mountain in the south of Tunisia (coded as DA)) under water stress conditions. Specifically, the study aimed to investigate the phenological and physiological responses of potted S. ciliata seedlings under different water treatments: T1 (200 mm/a), T2 (150 mm/a), T3 (100 mm/a) and T4 (50 mm/a). Growth phenology, net photosynthesis (Pn), stomatal conductance (gs), midday leaf water potential (Ψmd), predawn leaf water potential (Ψpd), soil water content (SWC) and soil water potential (Ψs) were observed during the water stress cycle (from December 2016 to November 2017). The obtained results showed that the highest growth potential of the two accessions (WA and DA) was recorded under treatment T1. The two accessions responded differently and significantly to water stress. Photosynthetic parameters, such as Pn and gs, decreased sharply under treatments T2, T3 and T4 compared to treatment T1. The higher water stress increased the R/S ratio (the ratio of root dry biomass to shoot dry biomass), with values of 1.29 and 2.74 under treatment T4 for accessions WA and DA, respectively. Principal component analysis (PCA) was applied, and the separation of S. ciliata accessions on the first two axes of PCA (PC1 and PC2) suggested that accession DA was detected in the negative extremity of PC1 and PC2 under treatments T1 and T2. This accession was characterized by a high number of spikes. For treatments T3 and T4, both accessions were detected in the negative extremity of PC1 and PC2. They were characterized by a high root dry biomass. Therefore, S. ciliata accessions responded to water stress by displaying significant changes in their behaviours. Accession WA from the Bou Hedma National Park (wet arid region) showed higher drought tolerance than accession DA from the Matmata Mountain (dry arid region). S. ciliata exhibits a significant adaptation capacity for water limitation and may be an important species for ecosystem restoration.

Full Text

Preamble

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Effects of water stress on growth phenology, photosynthesis and leaf water potential in *Stipagrostis ciliata* (Desf.) De Winter in North Africa

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Abstract: *Stipagrostis ciliata* (Desf.) De Winter is a pastoral C4 grass grown in arid regions. This research focused on assessing the growth of S. ciliata accessions derived from two different climate regions (a wet arid region in the Bou Hedma National Park in central and southern Tunisia (coded as WA), and a dry arid region from the Matmata Mountain in southern Tunisia (coded as DA)) under water stress conditions. Specifically, the study investigated the phenological and physiological responses of potted S. ciliata seedlings under different water treatments: T1 (200 mm/a), T2 (150 mm/a), T3 (100 mm/a) and T4 (50 mm/a). Growth phenology, net photosynthesis (Pn), stomatal conductance (gs), midday leaf water potential (Ψmd), predawn leaf water potential (Ψpd), soil water content (SWC) and soil water potential (Ψs) were observed during the water stress cycle (from December 2016 to November 2017). The results showed that the highest growth potential of the two accessions (WA and DA) was recorded under treatment T1. The two accessions responded differently and significantly to water stress. Photosynthetic parameters, such as Pn and gs, decreased sharply under treatments T2, T3 and T4 compared to treatment T1. Higher water stress increased the R/S ratio (the ratio of root dry biomass to shoot dry biomass), with values of 1.29 and 2.74 under treatment T4 for accessions WA and DA, respectively. Principal component analysis (PCA) was applied, and the separation of S. ciliata accessions on the first two axes of PCA (PC1 and PC2) suggested that accession DA was detected at the negative extremity of PC1 and PC2 under treatments T1 and T2. This accession was characterized by a high number of spikes. For treatments T3 and T4, both accessions were detected at the negative extremity of PC1 and PC2. They were characterized by high root dry biomass. Therefore, S. ciliata accessions responded to water stress by displaying significant changes in their behaviours. Accession WA from the Bou Hedma National Park (wet arid region) showed higher drought tolerance than accession DA from the Matmata Mountain (dry arid region). S. ciliata exhibits significant adaptation capacity for water limitation and may be an important species for ecosystem restoration.

Keywords: *Stipagrostis ciliata*; drought stress; water deficit; gas exchange; arid regions; Tunisia

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1 Introduction

Water stress is among the most important and devastating phenomena in the world [?] and its frequency is likely to increase because of climate change [?, ?, ?]. In fact, in agreement with IPCC [?], climate change in arid regions will decrease water resources and consequently affect the productivity of biological ecosystems. From this perspective, the decrease in soil water is becoming an important field of research aiming to explore plant responses to water deficit to improve agricultural management practices and predict the fate of natural vegetation [?]. On the other side, it has been reported that the increase of CO2 rate is driving the climate in the Mediterranean and tropical areas towards important changes, mainly represented by high temperatures and low annual precipitation [?]. Plant growth and productivity are adversely affected by water stress, though morphological, metabolic and physiological modifications have appeared in all plant organs [?]. Drought also decreased leaf areas, owing to the loss of turgor and reduction of leaf numbers [?]. Shao et al. [?] proved that drought also suppresses leaf expansion and tillering as well as leaf area reduction due to early senescence.

Wellstein et al. [?] highlighted that drought can generate a series of reductions in morphological and physiological traits, such as plant height, specific leaf area, leaf water potential, leaf tissue density and root length. These variations of plant traits may lead to a decline in yield and nutritive value. Within this framework, Seleiman et al. [?] emphasized that water stress is a major environmental and multidimensional stress factor leading to reduced crop yield and biomass productivity worldwide. Water stress severely affects plant growth and generates a strong relapse in reproduction.

The restoration of degraded ecosystems (rangelands and grasslands) under these environmental conditions becomes a necessity to maintain biological productivity. The choice of a plant candidate species for restoration is a crucial issue [?, ?]. For instance, to choose plant species adapted to the Mediterranean climate conditions, it is necessary to investigate the relationship of soil water status with phenological and physiological parameters of plants [?] to improve vegetation adaptation and production against water stress. However, Jones [?] asserted that the measurement of plant and soil water status is crucial in any experiment concerned with exploring the effects of water stress on plant growth. Overall, soil water potential (Ψs) is an ecological parameter that affects seed germination, seedling establishment, plant nutrition and plant growth [?]. West et al. [?] clarified how plants use water resources in the soil and how this affects their growth and ability to resist the greatest droughts. Indeed, to accurately predict species dynamics and ecosystem water balances, investigating how climate change will alter plant water acquisition, belowground interactions for water resources and their subsequent impact on plant functions is highly significant. Hence, knowledge of Ψs is fundamental to understanding plant water stress tolerance in arid regions. Soil moisture storage stands for the main water source for plants between precipitation events, affecting plant growth phenology [?].

Water stress corresponds to one of the most limiting environmental parameters to plant productivity and can be triggered by both atmospheric and soil water deficits [?]. In arid regions of North Africa and South Sahara, the response of C4 plant photosynthesis pathways to water deficit has been scarcely addressed. Furthermore, C4 grasses dominate in hot Saharan arid regions [?, ?]. In this regard, Christin and Colin [?] proved that the physiological advantages conferred by C4 plants are important for the ecological dominance of C4 plants in arid environments. Understanding the mechanism underlying the resistance of perennial species, especially grasses to drought stress, is of extreme importance for improving the productivity of perennial species in arid regions. However, for ecological restoration programmes, some species such as those in the perennial genus *Stipagrostis* (e.g., *Stipagrostis ciliata* (Desf.) De Winter, *S. obtusa* (Delile) Nees and *S. plumosa* (L.)) can be regarded as good candidate species for effective pastoral improvement under arid Saharan and tropical arid bioclimate conditions.

S. ciliata is a native arid species characterized by important pastoral value in arid regions. It is a pastoral C4 plant species belonging to the Poaceae family. *S. ciliata* has a widespread distribution in the hotter and drier parts of arid regions [?]. This perennial densely tufted grass species is up to 1 m high, with basally concentrated leaves. It forms a rounded hummock with the flowers emerging in clumps. *S. ciliata* exhibits high ecological abilities to tolerate Saharan and arid bioclimate conditions, gypsy soil and mobile sandy soil [?]. Therefore, it is a useful grass species to fix sand in arid regions. This species plays an important role in protecting the soil from erosion and reducing water loss. In addition, *S. ciliata*, a Mediterranean arid species, can grow under precipitation greater than 250 mm/a [?].

Considering the predictable climate changes in the Saharan region, particularly in Tunisia [?], and the predictable decrease of precipitation in arid and tropical regions [?], it would be promising to study the phenological and ecophysiological characteristics of *S. ciliata* and how this species reacts against conditions of water stress resulting from the possible precipitation decrease. Therefore, to answer this question, we subjected this species to artificial water stress. As far as our study is concerned, the response of this grass species to the applied experimental conditions under an arid climate will probably be the same as its response under a dry tropical climate.

From this perspective, the present study was conducted at an experimental site in the south of Tunisia. The main objectives of our investigation were (i) assessing the impact of water stress on the physiological and phenological characteristics of *S. ciliata* through analysing accessions from different soil origins and (ii) evaluating the relationship between soil water content (SWC) and plant ecophysiology behaviour. The elaborated hypothesis corresponds to the fact that water stress would give rise to significant changes in terms of the ecophysiological and growth responses of *S. ciliata* accessions. The results will be crucial for evaluating the variation in tolerance to water stress of this perennial grass, which may stand as a potential candidate for the restoration of degraded arid rangelands as well as dry tropical grasslands.

2.1 Plant growth and experimental design

S. ciliata seed accessions were collected in October 2015 in North Africa. Accessions were selected from opposing arid environments in Tunisia. The first accession was picked up from the protected Bou Hedma National Park (34°39 N, 09°48 E) located in the Governorate of Sidi Bouzid (the central and southern part of Tunisia). The climate of this region is wet arid, characterized by irregular annual precipitation (200–250 mm) and dry summer period. Soil in the protected Bou Hedma National Park belongs to the sandy soil type. The *S. ciliata* accession from this region was coded herein as WA. The second accession was collected from the Matmata Mountain in the south of Tunisia (33°53 N, 10°01 E). The climate of this region is dry arid, characterized by lower annual precipitation (50-150 mm) and high summer temperature. Soil in the Matmata Mountain belongs to the loam soil type. The *S. ciliata* accession from this region was coded herein as DA.

The mature seeds for each accession sown in 30 pots in November 2015 were processed under a sheltered greenhouse in the experimental field localized in Sfax City (34°43 N, 10°41 E) in the central and eastern part of Tunisia. The pots were 20 L in capacity, 30 cm in diameter and 30 cm in depth. The volume of the used pots was thus 0.021 m^3, which resembles the volume of the rhizosphere for the normal growth of Poaceae species. This was in good accordance with what Kharrat-Souissi et al. [**?**, **?**, **?**] reported when examining the behaviour of *Cenchrus ciliaris* species, which proved to be very comparable to that of *S. ciliata*. The chemical composition of the potting soil was 6.64 mmol/L of Na, 3.16 mmol/L of K and 0.44% of $CaSO_4 \cdot 2H_2O$. The total $CaCO_3$ content of the soil was about 13.00%, the organic matter percentage was 3.70% and the electric conductivity was 3.7 mS/cm. Each pot contained only one individual. Irrigation water used during the establishment year contained 1.00 g/L of NaCl. One year after sowing (i.e., November 2016), namely as soon as adult plants were obtained, they were cut above the soil surface. This procedure was conducted for each plant to simulate the zero level of growth during the experimental period (from December 2016 to November 2017). The water treatments (water stress levels) of plants were designed as follows: T1 (200 mm/a), T2 (150 mm/a), T3 (100 mm/a) and T4 (50 mm/a). The experimental design was made with 10 replications examining water regimes at four levels of water stress (T1, T2, T3, and T4) for the two investigated accessions (WA and DA). In fact, according to the IPCC report [?], arid Tunisia is subject to climate change over the next few decades. This change will be mainly marked by falling precipitation and rising temperatures, affecting the different types of climates in the country. We expected to predict the response of perennial grasses to this climate change by carrying out response tests of *S. ciliata* to the amounts of future precipitation that will mark the Tunisian arid regions.

The experiments were carried out under environmental conditions with natural sunlight and temperature. Mean temperature and relative humidity were measured during the experimental period (from December 2016 to November 2017) with a Combined Thermohygrograph 3.015 Wittich & Visser, UK. Mean monthly temperature varied between 11°C and 30°C, and mean relative humidity ranged between 52% and 85% (Fig. 1 [Figure 1: see original paper]).

2.2 Phenological and physiological parameters

Phenological observations on leaf and spike development growth were performed every second week of each month. The following parameters were determined: tiller, spike and leaf numbers. Net photosynthesis (Pn) and stomatal conductance (gs) were measured between 10:00 am (LST) and noon, biweekly on sunny days. For the new leaves of *S. ciliata*, a Scholander Pressure Chamber (PMS Instrument Company, Oregon, USA) [?] was used.

For each water treatment and each studied accession, twenty plants were randomly chosen. Leaf water potential was specified with a Scholander Pressure Chamber [?] following the precautions proposed by Turner [?]. For each water treatment, leaves were randomly selected from plants under both accessions for the determination of predawn leaf water potential (Ψpd) and midday leaf water potential (Ψmd). Ψpd and Ψmd were measured at 05:00 am and 14:00 pm every two weeks, respectively. According to Ritchie and Hinckley [?], the time between excision and determination was approximately 40–50 s.

SWC was determined by a Moisture meter, Model HH2 (Delta Device, Cambridge, UK) periodically at 09:00 am every two weeks during the experimental period. SWC was considered as an index of drought intensity. Ψs, which is defined as the potential energy of water in the soil, was measured with a New

Automated Psychrometer Scanner (Model PSYPRO, Type Vescor, Washington University, Washington, USA) placed at a 20-cm depth at 09:00 am every two weeks. The values of Ψs were quantified relative to a standard state where water has no solutes, free from external forces except gravity [**?**]. To determine root dry biomass and shoot dry biomass at the end of the experiment (in November 2017), we scraped the roots carefully and cleaned them with water. Shoots and roots were dissociated and dried at 75°C to obtain dry weight. Then, root dry biomass and shoot dry biomass were determined. The ratio of root dry biomass to shoot dry biomass was determined as the R/S ratio.

2.3 Statistical analyses

All statistical analyses were performed using SPSS 12.0. Design-Expert version 12 software was applied for the experimental design and statistical analyses in this research work. Differences in phenological and physiological parameters were tested using a two-way analysis of variance (ANOVA) according to Tukey' s test (significance level of P<0.05). Moreover, the data recorded in this study were submitted to a normalized principal component analysis (PCA) [**?**]. Soil characteristics as well as physiological and phenological parameters assessed throughout the study (from different water treatments) were considered. Discrimination between the effects of different levels of drought (T1, T2, T3 and T4) in both accessions (WA and DA) was evaluated by observing the projection of plots of the extracted factors on the factorial plane consisting of the statistically significant axis of the PCA. A simple log(x+1) transformation (where x is the value of variable) was applied to the PCA data to correctly stabilize variance [**?**].

3.1 Growth phenology and biomass of S. ciliata

The initiation of the growth cycle of *S. ciliata* occurred in late winter (temperature$ 15°$C)andappearedtobeassociatedwiththeincreaseoftemperatureintheexperimentalfield(Fig.1).Theres$
leaves/tiller under the same treatment.

The tiller production of *S. ciliata* during the growth year was the highest under treatment T1, with values of 15.00 ($±1.00$)and13.00(±1.00)tillers/stem, respectively, foraccessionsWAandD$
$0.06).AccessionWAdevelopedmoretillersperplantunderalltreatments, whileaccessionDAexhibitedlowernum$
$0.01).ThedataillustratedinTable1provedthatirrigationof * S.ciliata *$
$accessionswith200mm/aofwater(T1)presentedahighspikenumbercomparedtoplantsirrigatedwith150mm/a($
under treatment T1, respectively, for accessions WA and DA. The difference among the spike number was highly significant (P<0.001) at the treatment level.

The reproductive phase was earlier under treatment T1 for both accessions. Spike production was enhanced under treatment T1. Water stress was the most significant variable affecting the phenological parameters measured in this study, exhibiting significant differences in all phenological parameters. Both accessions (WA and DA) responded differently and significantly to water stress, displaying different values for leaf, tiller and spike numbers (Table 1).

Root dry biomass and shoot dry biomass data as well as the R/S ratio are illustrated in Table 1. A significant effect of water treatment on the plant biomass production of *S. ciliata* was recorded. Accession DA also tended to have a low root dry biomass under treatment T1, with 19.67 ($±2.08)*g/plant.However,ifwaterstressincreased,shootdrybiomassdecreasedslowlywhilerootdrybiomassinc* respectively.

3.2 Physiological parameters of S. ciliata

Significant effects of water stress on the gs and Pn of both accessions are highlighted in Table 3 . The highest values of Pn were observed for accessions WA and DA under treatment T1 (62.4 ($±2.62)*and*33.17(±0.76)*mol*/(*m*{2}·*s*), *respectively*).*Themaximumphotosyntheticact* (Table 2).

Throughout the experimental period, SWC was significantly lower under severe stress treatment (T4) than under other treatments (T1, T2 and T3). SWC differed significantly depending on the treatment (Fig. 2 [Figure 2: see original paper]). The decrease of SWC generated a rapid reduction in Ψpd and Ψmd under all treatments. Such significant differences among treatments are highlighted in Figure 2. In both accessions, Ψpd was significantly lower for very drought-treated *S. ciliata* plants than for drought-treated plants. Additionally, Ψs decreased significantly with the increase in water stress ($P<0.01$; Fig. 3 [Figure 3: see original paper]). The values of Ψmd were very low under treatment T4, at -3.54 and -3.48 MPa, respectively, for accessions WA and DA. The correlations among Ψpd, Ψmd and Ψs under all treatments are illustrated in Table 2. The strongest correlation was found between Ψmd and Ψpd, with R^2=0.966.

The decreases of Pn and gs were closely correlated to the severity of water stress, exhibiting a high correlation with leaf water potential and SWC. Pn exhibited negative correlations with Ψpd and Ψmd (Table 2).

3.3 Principal component analysis (PCA) biplot of phenological and physiological parameters

In the first axis of PCA (PC1) (79.24% of the total variance), a positive correlation was proved in total dry biomass, shoot dry biomass, Pn, gs, and tiller and leaf numbers (Fig. 4 [Figure 4: see original paper]). In the second axis of PCA (PC2), which explained 14.66% of the total variance, root dry biomass, Ψmd, Ψpd, R/S ratio and Ψs associated positively, while these and other variables (spike number and SWC) associated negatively. The spike number was not associated with any variable. Dispersion of *S. ciliata* accessions on the principal components of PC1 and PC2 proved the different responses of both accessions to different water treatments. However, accession WA was detected at the positive extremity of PC1 and PC2. It was characterized by a large number of leaves and tillers and high shoot biomass production under treatments T1 and T2. Accession DA was located at the negative extremity of PC1 and PC2 under treatments T1 and T2. This accession was characterized by a high number of spikes. Under treatments T3 and T4, both accessions were detected at the negative extremity of the two axes (PC1 and PC2). They were characterized by high root dry biomass. In this case, *S. ciliata* plants responded to water stress by producing more root biomass, closing their stomata and decreasing Pn and gs. These results were confirmed by the highly negative correlations of physiological parameters (Pn and gs) with root dry biomass and SWC (Table 2).

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4 Discussion

Perennial grass phenological responses to water deficit have been extensively studied, with special attention on the growth and biomass accumulation of plants [**?**, **?**, **?**]. The choice of highly tolerant grass species plays a crucial role in the restoration of degraded ecosystems. The selected plant species should have high drought tolerance to maintain ecosystem biodiversity. *S. ciliata*, as well as many other Mediterranean and perennial grasses, exhibits a conservative strategy in the use of water, based mainly on avoiding water stress [**?**]. Understanding the phenological and physiological responses of plants to water deficit is an important basis for selecting tolerant plant species. In this study, the results demonstrated that there were significant differences in the drought responses of two *S. ciliata* accessions coming from different arid regions of Tunisia. However, water stress had different effects on plant growth according to accession type.

Accessions WA and DA highlighted different phenological adaptations by reducing leaf number, tiller number and shoot dry biomass. The growth reduction of *S. ciliata* accessions under different water stress conditions is similar to the responses of other perennial grasses like *Cenchrus ciliaris* (L.) and *Stipa tenacissima* (L.). For grasses, the tillering stage is an important parameter commonly used in the determination of the stress tolerance of plants [**?**]. Notably, during the observations of the phenological parameters of *S. ciliata*, we found that leaf and tiller numbers decreased significantly with increasing water stress. In this study, tiller and leaf numbers varied significantly with water treatment and accession. Du et al. [**?**] emphasized that the reduction of leaf growth is generally the primary response to water stress. These results were proved by the positive correlation between leaf and tiller numbers and SWC (Table 2). In addition, leaf phenological plasticity is very crucial in terms of coping with water stress, because the first response of plant to water stress is the reduction of leaf growth.

Guo et al. [?] reported that the growth of grasses is greatly inhibited under drought conditions. Zhao et al. [?] highlighted that *S. ciliata* persists well in desert habitats owing to the species' ability to respond with important growth to precipitation and its tolerance to drought and grazing.

In our study, severe drought stress treatments (T3 and T4) led to an increase in root dry biomass. However, Xiong et al. [?] proved that under water stress conditions, the decrease of plant growth results in a reduction of shoot biomass and an increase of root biomass. The significant negative correlation between shoot dry biomass and root dry biomass mentioned in Table 2 showed that plants search for more water in the soil. However, the perennial grass (*S. ciliata*) increased the R/S ratio to overcome the water deficit, which increased water absorption and reduced water consumption. This response showed that under the severe water treatments T3 and T4, both *S. ciliata* accessions (WA and DA) increased the belowground fraction and decreased the aboveground fraction. The significant increase in the R/S ratio (>1.29) under severe water deficit treatment (T4) was the result of a significant decrease in shoot dry biomass and a significant increase in root dry biomass.

In this study, the shoot dry biomass and root dry biomass of *S. ciliata* varied considerably and significantly with the quantity of soil water. However, the shoot dry biomass of this perennial grass declined and root dry biomass concurrently increased with the increase in drought level, thus leading to a high R/S ratio. Henschel et al. [?] asserted that the biomass production of *S. ciliata* varies considerably with changes in precipitation. Indeed, roots are the first part exposed to water stress. Even though plant growth rates are decreased when soil water supply is limited, shoot growth tends to be slower than root growth. Chaieb et al. [?] emphasized that the root system of *S. ciliata* has a high concentration of roots in the upper soil layer (0–30 cm depth). The increase in *S. ciliata* root biomass (between 20 and 100 cm) is in good conformity with those of certain studies carried out in arid regions [?]. We can therefore conclude that the roots of plants in arid regions are a satisfactory solution to better utilize the soil water reserves. The root system can assure the production of plant species, although locally deep roots (30–80 cm layer) need to maintain not only production but also species survival under water stress conditions, because at these depths, the soil is not completely dry. A reduction in water can reduce the number of spikes in both *S. ciliata* accessions (WA and DA). However, other studies have also proven the reduction of this parameter (spike number) describing the reproductive growth phase [?, ?]. The essential variations inferred for phenological parameters exhibited a wide phenological variability among *S. ciliata* accessions in response to different water treatments, reinforcing their adaptation to water stress resistance.

Soil water stress is a major environmental factor forbidding the productivity and photosynthesis of plants in arid regions. *S. ciliata* is renowned for its drought resistance [?]. Nevertheless, there were no differences in drought resistance among both accessions (WA and DA) deriving from different bioclimate environments.

Therefore, the loss of water resulted in the poor adaptation of plants to the water deficit. It has been shown that osmotic adjustment can be an intrinsic mechanism of drought resistance, operating by lowering the water potential at which stomatal closure appears when the stomatal control of transpiration is not adequate for regulating water supply to leaf cells [?]. This may sometimes be accounted for in terms of interpreted conferring the inherent resistance to the water stress of C4 plants [?]. This goes in good accordance with the results obtained for both studied accessions of *S. ciliata* in the current study. The photosynthetic pathway of C4 plants has developed as an adaptation to elevated photo-respiratory pressures resulting from combinations of stress, which include low CO2 concentration, high temperature, aridity and salinity [?]. Yu et al. [?] proved that C4 plants present various adaptation strategies to drought to minimize damage from environmental stress. Indeed, leaf gas exchange measurements confirmed the significant differences in CO2 assimilation and gs characteristics among seedlings under water deficit conditions. Moreover, plants can adapt to water deficit through the modification of phenological and physiological characteristics [?]. From this perspective, in this study, the phenological and physiological variations of *S. ciliata* plants were remarkable under water stress conditions (Fig. 4).

Generally, it has been proven that dry soil has a hydraulic effect on plant water status and leaf gas exchange. The basic theory is that a decrease in Ψs requires a reduction in plant water potential, inducing reduced cell expansion and stomatal closure. This is confirmed in this study by the strong correlation between Pn and Ψpd of both *S. ciliata* accessions (Table 2). Stomatal closure as well as leaf expansion is controlled by mechanisms additional to changes in the pressure potential of leaf cells [?]. Reductions in gs of plants in dry soil are related more strongly to changes in soil water status rather than leaf water status. It has been noted that plants can 'sense' that the soil in the root zone is drying and can communicate this information to the leaves by another means than through a decrease in leaf water status [?]. This is consistent with our results, which yielded a significant difference in gs for all water treatments. The effect of water stress on Pn has been little explored, and the decreases in Pn and gs were observed with increasing water stress. However, this reduction has been attributed to both non-stomatal and stomatal limitations. Kadioglu and Terzi [?] reported that gs was proved to be a reliable physiological indicator of drought tolerance. As far as our research is concerned, it was found that both accessions WA and DA presented gradual decreases in Pn and gs with decreasing Ψpd and Ψs, confirming this important relationship between Ψpd and Pn under severe drought condition (treatment T4). Furthermore, Yu et al. [?] pointed out that stomatal closure is the first line of defence against desiccation for plants. Sayed [?] revealed that water stress-induced stomatal closure depletes intercellular CO_2, leading to photoinhibition. Stomatal control is crucial for adjusting leaf gas exchange, especially for plants in arid regions [?]. Stomatal closure and leaf growth inhibition are among the primary plant responses to drought, preserving the plants from intense water loss.

Both phenological and physiological changes exist when plants are subjected to water deficit [?, ?]. Indeed, water stress may reduce Pn by stomatal closure and metabolic processes. Liu et al. [?] proved that physiological parameters are more responsive than phenological parameters under different drought conditions. The data of this study corroborated that for this C4 species (*S. ciliata*), SWC affected the leaf water potential. Thus, in case of water stress, this grass species with fasciculate and superficial root systems tends to adjust their water transfer by stopping their leaf transpiration. This observation was similar with other C4 grasses (*C. ciliaris*, *Stipa lagascae* R. & Sch. and *Digitaria nodosa* Parl.) of the same region [?]. Under arid and semi-arid bioclimate conditions, soil drought was reported to impact plants from several aspects [?]. Roots are the first part of the plants suffering from water stress. Plants grow slowly with limited SWC due to the decrease in photosynthesis, resulting in reduced biomass [?]. Leaf water potential also decreases during periods of drought. Plants take up water from the soil and transpire it through the leaves. Leaf water potential decreases with the reduction in SWC as the rate of leaf water loss exceeds the rate of root water uptake.

5 Conclusions

Knowledge of plant growth under water deficit is crucial in terms of assessing the productivity of rangelands and grasslands. In this regard, the hypothesis postulating that *S. ciliata* accessions present a high capacity to tolerate drought imposed by water stress was confirmed. Accession WA (coming from the Bou Hedma National Park) was more resistant than accession DA (coming from the Matmata Mountain). The ability of *S. ciliata* to keep photosynthetic active tissue has proved that the species has a higher rooting rate, with a tendency to extract the soil water. These strategies ensure that plants are well regulated in gas exchanges under arid conditions. Water stress seems to be a crucial factor limiting the Pn process of *S. ciliata* accessions. These results are indicative that this perennial grass adopts the strategy of avoidance (stomatal closure) as a drought resistance mechanism that may probably prevent physiological and biochemical damages to plants during drought periods. It is noteworthy that a close relationship between SWC and plant growth and physiological processes was recorded for both accessions of *S. ciliata*. At this stage of analysis, this behaviour therefore stands for an endogenous characteristic of this pastoral species, which is a potential candidate for the ecological restoration of degraded rangelands and grasslands in North Africa.

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Note: Figure translations are in progress. See original paper for figures.