Physiological and biochemical regulation mechanisms for drought adaption in typical desert shrubs


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ABSTRACT

The physiological and biochemical mechanisms for different photosynthetic pathways desert shrubs was not completely understood and raises the question if C₄ plants are better adapted for severe drought than C₃ plants. We selected two C₄ plants Calligonum mongolicum and Haloxylon ammodendron, and three C₃ plants Caragana korshinskii, Nitraria sphaerocarpa and Tamarix ramosissima in their natural environments, and to systematically study the water status, antioxidant enzyme activity, osmotic adjustment substances content and photosynthetic physiological characteristics. Our results suggested that two C₄ species showed higher leaf water potential and superoxide dismutase activity compared to the other three C₃ species. Higher light saturation point and apparent quantum yield were also found in C. mongolicum and H. ammodendron suggested they had more efficient solar energy utilization. C. korshinskii had higher catalase and peroxidase activities to auxiliary antioxidant activity, N. sphaerocarpa showed a greater capability for free amino acid and proline accumulation. T. ramosissima, as a non-belt plant, was accumulates soluble sugars to maintain internal osmotic balance. It was concluded that two C₄ species would be more competitive than the C₃ species in desert areas as for the higher antioxidant defenses capacity and light use efficiency.

Keywords: Desert plants, Antioxidant enzyme, Osmotic adjustment, Photochemical activity, Chlorophyll fluorescence

INTRODUCTION

The desert of central Hexi Corridor is a typical arid desert climate region, rare rainfall, high temperatures and high evaporative demand, as desert shrubs are generally the dominant vegetation types and have a unique growth advantage of its adaptability. Desert plants have evolved special physiological and morphology traits in the process of adapting to the environmental stresses, and exhibit a much higher drought tolerance [1]. The activities of desert plants are tightly coupled to water availability and can induce the physiological and biochemical responses. These responses of plants to environmental stresses have been well documented, and ranging from photosynthesis to antioxidant defenses and solute accumulation as components of drought tolerance [2, 3].

It is well known that photosynthetic systems in higher plants are extremely sensitive to drought stress and increased photooxidation was observed at extreme temperature [4]. High temperatures inhibit photosynthetic CO₂ fixation and damage photosynthetic electron transport, particularly at the site of PSII [5]. Chlorophyll fluorescence is closely related to photosynthesis, it reflects the photosynthetic efficiency and utilization of light energy. The parameters of chlorophyll fluorescence analysis can give insights into the ability of a plant to tolerate environmental stresses and...
the extent to which stresses damage the photosynthetic apparatus [6].

It has also been suggested that increase in photosynthetic electron flux to O$_2$ will result in the increased production of superoxide radicals and H$_2$O$_2$ [7]. Tolerant plants generally have a better capacity to protect themselves against drought-induced oxidative stress, which can also be achieved via the enhancement of the activities of antioxidant enzymes. Antioxidant enzymes, such as superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD), are known to increase in response to drought and high temperature. SOD converts O$_2^-$ into H$_2$O$_2$ and O$_2$, and CAT and POD scavenge H$_2$O$_2$ into H$_2$O [8]. On the other hand, the other potentially important mechanism of drought tolerance is osmotic adjustment, which can be achieved from the accumulation of compatible solutes in protoplasm [9]. Osmotic adjustment has been considered as an important physiological adaptation character associated with drought tolerance, which facilitate extracting water from dry soils and maintaining cell turgor, gas exchange and growth in very dry environments [4]. Meanwhile, there are a closely relationship between PSII light energy conversion and osmotic adjustment under drought stress. Accumulation of osmotic adjustment substances and antioxidant capacity enhancements are two important mechanisms through which plants can survive under adversity. In a physiological context, plants have developed three types of photosynthetic pathways: C$_3$, C$_4$ and CAM. C$_3$ pathway is considered to be an advantage survival pathway of plant under high temperature, strong light and drought conditions, and have superior water use efficiency (WUE) than C$_4$ plant [10]. In the desert regions of China, C$_4$ plants, especially C$_4$ woody plants, have an important position and role in the desert ecosystem. Wentworth [11] predicted that with the climate change, it is likely to have a large effect on the abundance and distribution of plant species in desert areas, and C$_4$ species should be proportionally more successful in desert areas. While, the photosynthetic physiological and biochemical mechanisms for different photosynthetic pathways is not completely understood and raises the question if C$_4$ plants are better adapted for severe drought than C$_3$ plants. Thus, the main objective of this study was to compare the photosynthetic characteristics and protective mechanisms in desert plants with different photosynthetic pathway. Understanding the ecological strategies of drought tolerance in desert plants would be better know the drought adaption mechanisms and predict plants response to climate change.

EXPERIMENTAL SECTION

Study site and plants material
The experiment was carried out in the middle reaches of Heihe river in northern Linze country, Gansu province (39°19′-39°21′ N, 100°02′-100°21′ E), at an altitude of 1370 m. It is a typical drought desert climate with an average annual precipitation of 117 mm. This area is one of the most seriously desertified areas of China [12].

Five desert shrubs Caragana korshinskii Kom., Nitraria sphaerocarpa Maxim., Calligenum mongolicum Turcz., Haloxylon ammodendron (C.A.Mey.) Bge. and Tamarix ramosissima Ledeb. were selected to study their photochemical and biochemical activities in natural environments. All of these species are widely distributed in desert areas, the leaves of H. ammodendron and C. mongolicum were all degradation, by the assimilating shoots for photosynthesis. C. korshinskii has a very strong ecological adaptability, N. sphaerocarpa displays tenacious growth in soils with extremely low moisture content and T. ramosissima is a non-zonal plant with a large distribution across desert-oasis ecotone. All plant specimens were collected at growing and developing stages in late July, 2011. Samples of plant photosynthetic organs (leaves or assimilating shoots) were immediately frozen in liquid nitrogen and stored at -70 °C until required.

Measurement of the δ$^{13}$C values
Take plant leaves or assimilating shoots back to the laboratory and the stable carbon isotope ratio was analyzed by MAT-252 mass spectrometer using the formula:

$$\delta^{13}C (\%) = [(R_{sample} - R_{standard})/ R_{standard}] \times 10^3 \quad (1)$$

Where: $R_{sample}$ and $R_{standard}$ were the abundance ratios, $^{13}$C/$^{12}$C, of the sample and the standard, Pee Dee belemnite (PDB), respectively.

Determination of the relative water content (RWC) and leaf water potential (LWP)
The RWC of leaves and assimilating shoots were measured in early August, 2011 and calculated with the following formula:

$$\text{RWC} (%) = [(\text{FW}−\text{DW})/ (\text{SW}−\text{DW})] \times 100 \quad (2)$$

LWP was measured using a WP4-T Dew point water meter (Decagon, American).
Photosynthesis response to light intensity
Light response curves were made by using LI-6400 gas exchange system (LI-COR, Lincoln, USA). Afterwards, all the leaves were collected, and their areas were measured using the LI-3100 Area Meter (LI-COR), then recomputes the date through the LI-6400.

Measurement of chlorophyll fluorescence and chlorophyll content
Chlorophyll fluorescence was measured with a PAM-2100 portable modulated chlorophyll fluorometer (WALZ, Germany). Leaves were dark-adapted before measurement and from 8:00 to 18:00 with 1-h intervals in the same plant.

Chlorophyll (Chl) and carotenoids (Car) were extracted by 95% ethanol and the calculation of pigment content was performed according to the method by Lichtenthaler [13].

Antioxidant enzymes activity and membrane lipid peroxidation determination
SOD activity was assayed according to Giannopolitis and Ries [14]. CAT activity was assayed according to the method of Aebi [15]. POD activity was assayed according to Rao [16]. Lipid peroxidation was estimated by measuring the MDA content [17].

Measurement of osmotic adjustment solute content
Soluble sugar was extracted and determined following the phenol method. Soluble protein content was assayed by using the Coomassie Brilliant Blue G-250 chromogenic method. Total free amino acids were determined following the ninhydrin coloration method by Lee et al. [18]. Proline was determined following the method of Bates et al. [19]. All absorbance measurements for enzyme activity and content determination were conducted using a GeneQuant 1300 spectrophotometer (Britain) and all the measurements were repeated at least three times.

Statistical analysis
Values presented are means ± one standard error (SE) of three replicates. The significance of the same index for different plants was determined using Duncan’s new multiple range test. All the statistical analyses were carried out on SPSS 16.0 statistical package (SPSS Inc., Chicago, IL, USA).

RESULTS

Stable carbon isotope ratio (δ13C) and water status with desert shrubs
There was a positive correlation between δ13C and WUE, so the δ13C value can indicate plants WUE. From table 1 we can see that H. ammodendron and C. mongolicum had a higher δ13C values than other three species. It also indicated that H. ammodendron and C. mongolicum had higher WUE in arid environment.

There were obvious differences between RWC in the five desert shrubs (Table 1). The average of RWC in two C4 plants C. mongolicum and H. ammodendron (71.7%) were lower than in other C3 plants (75.2%). N. sphaerocarpa had the highest RWC than other species, and had significantly differences (F=18.394, P<0.05) among of them.

LWP reflects the ability of plants to absorb and hold water and contributes to drought tolerance. Among the five desert shrubs, the C4 plants had higher LWP than the C3 plants (F=8.598, P<0.05), and C. mongolicum had the highest LWP of -1.5 MPa. C3 plants C. korshinskii had the lowest value of LWP with -4.7 MPa.

The response of PN to different photosynthetic photon flux density (PPFD)
There were significant differences in the responses of PN to PPFD in the five plants. Of the five shrubs, two C4 plants had higher light saturation point (LSP), apparent quantum yield (AQY) and lower light compensation point (LCP) compared to three C3 shrubs. C. mongolicum had the highest LSP and AQY values, which were 2040 µmol·m⁻²·s⁻¹ and 0.059 mol·mol⁻¹, respectively (Table 2), while N. sphaerocarpa had the lowest LSP and AQY values.
Table 2. Photosynthetic physiological parameters with five desert shrubs

<table>
<thead>
<tr>
<th>Parameters</th>
<th>C. korshinskii</th>
<th>N. sphaerocarpa</th>
<th>T. ramosissima</th>
<th>C. mongolicum</th>
<th>H. ammodendron</th>
</tr>
</thead>
<tbody>
<tr>
<td>LCP (µmol·m⁻²·s⁻¹)</td>
<td>100.2±3.1 a</td>
<td>106.1±3.0 a</td>
<td>90.2±6.9 b</td>
<td>53.6±2.9 b</td>
<td>44.4±1.1 b</td>
</tr>
<tr>
<td>LSP (µmol·m⁻²·s⁻¹)</td>
<td>1690±85 b</td>
<td>1580±92 d</td>
<td>1500±44 d</td>
<td>2040±131 d</td>
<td>1825±51 b</td>
</tr>
<tr>
<td>AQY (µmol·mol⁻¹)</td>
<td>0.04±0.003 c</td>
<td>0.036±0.001 c</td>
<td>0.037±0.002 c</td>
<td>0.059±0.006 c</td>
<td>0.05±0.002 b</td>
</tr>
</tbody>
</table>

Chlorophyll fluorescence characteristics

It can be seen from table 3 that lower maximum photochemical efficiencies of PSII (Fv/Fm), apparent electron transport rate (ETR) and effective photochemical efficiency (Yield) were observed in two C₄ plants H. ammodendron and C. mongolicum, and had significantly differences than C₃ plants. N. sphaerocarpa, on the other hand, had the highest values of the three parameters. Although two C₄ plants C. mongolicum and H. ammodendron showed the lower daily average (8:00-18:00) of Fv/Fm, but the difference between the maximum and minimum values were smaller than three C₃ plants (data not shown).

Non-photochemical quenching (qN) is a good indicator to reflect plants against photoinhibition (Demmig-Adams et al. 1996), and photochemical quenching (qP) reflect the light adaptation state of the photochemical reaction of PS II capacity. In our study, N. sphaerocarpa had higher qP values but lower qN value, while H. ammodendron had the highest qN in the five plants, and the differences was significantly (F=7.647, P<0.05).

Table 3. Chlorophyll fluorescence parameters of the five desert shrubs

<table>
<thead>
<tr>
<th>Parameters</th>
<th>C. korshinskii</th>
<th>N. sphaerocarpa</th>
<th>T. ramosissima</th>
<th>C. mongolicum</th>
<th>H. ammodendron</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fv/Fm</td>
<td>0.794±0.009 a</td>
<td>0.802±0.005 a</td>
<td>0.799±0.015 a</td>
<td>0.744±0.006 a</td>
<td>0.774±0.011 b</td>
</tr>
<tr>
<td>ETR</td>
<td>86.85±4.53 b</td>
<td>88.71±0.983 b</td>
<td>125.31±6.794 a</td>
<td>81.32±0.562 b</td>
<td>61.79±0.147 c</td>
</tr>
<tr>
<td>qP</td>
<td>0.95±0.025 a</td>
<td>0.97±0.033 a</td>
<td>0.96±0.022 a</td>
<td>0.93±0.028 a</td>
<td>0.95±0.029 a</td>
</tr>
<tr>
<td>qN</td>
<td>0.73±0.012 b</td>
<td>0.68±0.015 b</td>
<td>0.74±0.073 b</td>
<td>0.74±0.007 b</td>
<td>0.78±0.023 a</td>
</tr>
<tr>
<td>Yield</td>
<td>0.54±0.037 a</td>
<td>0.54±0.041 a</td>
<td>0.52±0.023 a</td>
<td>0.50±0.022 a</td>
<td>0.43±0.030 a</td>
</tr>
</tbody>
</table>

Chlorophyll content with desert shrubs

Chlorophyll a (Chl a), Chl b, total Chl (a + b) contents and Car in C. korshinskii was highest than other species (Table 4). H. ammodendron, on the other hand, had the lowest chlorophyll content among the five plants. In the five desert plants, H. ammodendron had the highest Chl a/b ratio, while in C. korshinskii had lowest value of 2.15, which is contrary to the chlorophyll content results, but the differences in the five plants were not significantly (F=2.626, P>0.05).

Table 4. The chlorophyll (Chl) content and Chl a/b ratio with desert plants

<table>
<thead>
<tr>
<th>Parameters</th>
<th>C. korshinskii</th>
<th>N. sphaerocarpa</th>
<th>T. ramosissima</th>
<th>C. mongolicum</th>
<th>H. ammodendron</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chl a (mg·g⁻¹·FW)</td>
<td>1.76±0.02 a</td>
<td>0.79±0.14 b</td>
<td>0.83±0.01 a</td>
<td>0.64±0.05 a</td>
<td>0.41±0.01 c</td>
</tr>
<tr>
<td>Chl b (mg·g⁻¹·FW)</td>
<td>0.82±0.02 a</td>
<td>0.36±0.07 b</td>
<td>0.38±0.02 b</td>
<td>0.29±0.07 b</td>
<td>0.15±0.03 c</td>
</tr>
<tr>
<td>Chl a+b (mg·g⁻¹·FW)</td>
<td>2.59±0.04 a</td>
<td>1.14±0.19 b</td>
<td>1.12±0.03 b</td>
<td>0.93±0.11 b</td>
<td>0.56±0.03 a</td>
</tr>
<tr>
<td>Car (mg·g⁻¹·FW)</td>
<td>0.35±0.01 a</td>
<td>0.17±0.04 b</td>
<td>0.20±0.01 b</td>
<td>0.12±0.01 c</td>
<td>0.09±0.01 c</td>
</tr>
<tr>
<td>Chl a/b</td>
<td>2.15±0.04 a</td>
<td>2.19±0.32 a</td>
<td>2.16±0.13 a</td>
<td>2.20±0.40 a</td>
<td>2.74±0.58 a</td>
</tr>
</tbody>
</table>

Antioxidant enzymatic activity and MDA content

The antioxidant enzymes activities in the five desert plants are show in Fig. 1. The average SOD activity was 144.71 U·g⁻¹·FW and 179.46 U·g⁻¹·FW in C₃ and C₄ plants, respectively. Among the five shrubs, C. mongolicum had the highest SOD activity (193.74 U·g⁻¹·FW) while N. sphaerocarpa had the lowest SOD activity. CAT is a high capacity enzyme with low oxygen affinity that destroys hydrogen peroxide. C. korshinskii is distinguished from the other four plants by its high CAT activity of 9.35 U·g⁻¹·min⁻¹ (Fig. 1b). The average POD activity for the C₃ plants was higher than for the two C₄ plants (Fig. 1c). Among the three C₃ plants, the highest POD activity was exhibited by C. korshinskii (257.53 U·g⁻¹·min⁻¹), while the POD activity of C. mongolicum was too small to be detected. MDA is the product of lipid peroxidation and its content can reflect the level of lipid peroxidation. The highest MDA content, which was measured in C. korshinskii, was 32.27 nmol·g⁻¹·FW, and significantly greater that the content of all other plants (Fig. 1d, P<0.05). The MDA content of the other four plants were similar to each other. Of the five desert plants, the lowest MDA content was observed in H. ammodendron (6.81 nmol·g⁻¹·FW).
Fig. 1. Antioxidative enzymatic activity and MDA content in five desert plants
Comparison among the different species, the different lowercase in the same index means significant differences (P<0.05). CK, C. korshinskii; NS, N. sphaerocarpa; CM, C. mongolicum; HA, H. ammodendron; TR, T. ramosissima

The content of osmotic adjustment solute
The soluble sugar content of the C₃ and C₄ plants did not differ significantly (Fig. 2a). T. ramosissima had the largest soluble sugar content (76.72 mg·g⁻¹) and H. ammodendron had the lowest content. The soluble protein content was higher in C. korshinskii than other desert plants (Fig. 2b), and T. ramosissima had the lowest soluble protein content among the five shrubs. The total free amino acid varied significantly among the five desert shrubs (Fig. 2c). N. sphaerocarpa had the highest free amino acid contents with value of 208.57 mg·g⁻¹. Proline is the main osmotic adjustment substance in plants. Generally, plants with higher proline content are more adapted to drought. The highest proline content was found in N. sphaerocarpa, which was significant difference from other four plants (Fig. 2d, P<0.05). The lowest values were observed in T. ramosissima, with a value of 25.26 ug·g⁻¹.

DISCUSSION
Desert plants in harsh environments, with different photosynthetic pathways respond differently to environmental factors, and therefore have dissimilar environmental adaptation strategies. Water deficit caused by drought and high temperature changes in morphology, water status, gas exchange and chlorophyll content which are connected with the onset of protective mechanisms in the plant [20]. RWC are physiological processes very susceptible to drought stress, and can reflect the water-holding capacity of leaves. The leaf of N. sphaerocarpa is fleshy leaf, with higher RWC to resist drought. High RWC may be an adaptive feature for N. sphaerocarpa to overcome the effect of drought and water deficit environments. LWP is an important physiological indicator predicting plant water stress and drought tolerance, and higher LWP value were observed in the two C₄ plants C. mongolicum and H.
ammodendron. While, C. korshinskii had the lowest value of LWP. Lower LWP in C. korshinskii and *N. sphaerocarpa* was beneficial to absorb soil water, which is a physiological response of plants to withstand drought.

Photosynthesis is a biochemical process and acts as an index to determine plant growth and resistance to adverse conditions. Extensive reviews of leaf-level research suggests that C₄ species should outperform C₃ individuals at higher temperatures given inherent properties associated with their photosynthetic pathways [21]. In the present studies, highly significant differences in photosynthetic capacity were found among C₃ and C₄ plants. Two C₃ plant *H. ammodendron* and *C. mongolicum* with lower LCP, higher LSP and AQY (Table 2), thus had more efficient solar energy utilization than other three C₃ plants, and suggested that they have a stronger adaptation tolerance for high temperature and dry environments. Ehleringer et al. [22] proposed that C₄ plants are typically found in warmer and drier habitats and with climate warming, is therefore likely to favour C₃ species at the expense of C₄ species. Comparatively speaking, the two C₃ plants were adaptable to a wider range of light than the C₄ plants.

Two C₄ plants *C. mongolicum* and *H. ammodendron* had lower Fv/Fm, ETR, and Yield values, while *N. sphaerocarpa* had the highest Fv/Fm, qP and Yield values. Fv/Fm represents the photosynthetic institutions absorbed light to chemical reaction for maximum efficiency. In drought environmental, the Fv/Fm values of dark-adapted plants are above 0.83. Results from this research showed that the daily average of Fv/Fm in five plants were all below 0.83, suggesting all plants investigated may suffer severe photoinhibition of PS II.

Earlier study proved that chlorophyll contents usually decreased under drought stress due to their slow synthesis or fast breakdown. In this study, the chlorophyll content of three C₃ plants was higher than that of two C₄ plant, while the Chl a/Chl b ratios of the two C₄ shrubs were higher. Li and Cao [23] found that under drought environment, the chlorophyll content in *Termitina paniculata* seedlings was reduced and Chl a/Chl b ratio tended to increase. The reduction in chlorophyll contents may be a strategy of photo-protection reducing light absorption and thus decreasing energetic pressure at the PSII level. Studies have shown that Chl a/Chl b increases with adversity [24]. The higher Chl a/Chl b ratios in the two C₄ plants suggested that they are better adapted to drought than C₃ shrubs, and also considered as a decreased emphasis on light collection in relation to the rates of PSII photochemistry.

There are many processes affecting *Pₛ* performance in plants, including increased photorespiration, damage to the CO₂ fixed reaction mechanism, as well as an occurrence of reactive oxygen species (ROS). Under drought environments, generation of excessive ROS in the chloroplasts can result in photoinhibition and photooxidation damages. Schwanz and Polle [25] suggested that increase the drought tolerance of plants is related to increase biochemical protection at the tissue level. Our findings revealed that both the plant species had varying ability to deal with oxidative stress that might govern their differential sensitivity to drought environments (Fig. 1). The higher levels of SOD activities in *C. mongolicum* and *H. ammodendron* reflect their greater involvement in C₄ plants to counter oxidative stress as compared to C₃ plants like *C. korshinskii*, which had relatively more activity of CAT and POD. Streb et al. [26], who investigated the antioxidant protection mechanism of two desert plants (*Atriplex halimus* and *Retama raetam*), suggested that desert plants employ different strategies to protect themselves against high light intensity and temperature. Similar to our findings, Caravaca et al. [27] pointed that SOD activity was also increased by drought stress in shoots of Mediterranean plants such as *Myrtus communis* and *Phillyrea angustifolia*. Relative to C₃ shrubs, the higher SOD activity in C₄ plants lends a defense against free radical formation and photo-inhibition triggered by high temperature environment. Significantly, In this research, the activities of CAT (9.35U·g⁻¹·min⁻¹) and POD (257.53 U·g⁻¹·min⁻¹) were higher in *C. korshinskii* compared to the other four desert plants, and increase in CAT and POD activity helps to overcome the damage of tissue metabolism by reducing the toxic level of H₂O₂.

The increasing of osmotic adjustment substances content could be lowering the cell osmotic potential and maintenance of leaf turgor under water-limited conditions. Plants with strong drought tolerance have higher accumulation of osmotic adjustment substances. Soluble sugars might play a central role in photochemical apparatus protection and ROS scavenging in stressed plants. In the present study, soluble sugar content had greater difference in the five species (Fig. 2a). *T. ramosissima* as a non-belt plant, had the highest soluble sugar content differ from other four desert plants. Higher soluble sugars content would be involved in dehydration tolerance by protecting the macro-molecules through preferential hydration during water loss. Higher accumulates soluble sugars of *T. ramosissima* accumulates is closely related to their tolerant of high salinities, and could be maintain internal osmotic balance and compensates for loss of other osmotic adjustment substances, which was also demonstrated in Cui et al. [28]. Studies by Rajendrakumar et al. [29] indicated that proline may protect protein structures by maintaining their structural stability. *N. sphaerocarpa* had the highest content of free amino acids and proline contents among the five species (Fig. 2d). Higher accumulation of proline is a result of long-term adaptation to a drought environment. Tobe et al. [30] reported that the xerophytes accumulated very high levels of proline, and proline serves as an alternative compatible solute for osmotic adjustment.
Numerous papers showed that global change will affect the relative distribution of C₃ and C₄ plants by affecting the key physiological and biochemical parameters. Physiologically, C₃ and C₄ species do not inherently differ in the degree to which they withstand severe drought, and the main difference in performance in response to aridity is greater water use efficiency, higher solar energy utilization and carbon fixation capacity in C₄ plants. Meanwhile, C₃ plants C. mongolicum and H. ammodendron, with higher LWP and SOD activity, is drought tolerant by postponement of dehydration with high tissue water potential. Whereas, C. korshinskii triggered an efficient enzymatic auxiliary antioxidant system (higher in CAT and POD activity) and an effective protection against photochemical damages. N. sphaerocarpa was succulent xerophytes, higher accumulation of total free amino acid and proline could increase the water-holding capacity and tolerate drought environments. Higher soluble sugar content in T. ramosissima would improve its osmotic regulation ability, and that’s maybe the reason why T. ramosissima would widely surviving in adverse environments such as salinity and drought areas. Finally, the results of this study suggest that different species developed different photosynthetic characteristics and protective mechanisms for drought adaption. The advantages of the C₃ plants could lead to higher drought resistance due to higher SOD activity and higher light use efficiency, and would be more abundant in desert areas with higher temperatures, higher irradiance and lower moisture.

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