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RELATIONSHIP BETWEEN PHYSIOLOGICAL VARIATION AND DROUGHT TOLERANCE OF CALLIGONUM SPECIES IN CENTRAL ASIA

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Abstract

Calligonum L. are typical desert plant species in the arid region of Central Asia, which has great significance to the ecological restoration and reconstruction in the desert area, and widely used for wind prevention and sand fixation, soil and water conservation, soil improvement, drought resistance. In this study, the physiological differences assimilation branches related to drought resistance of 16 Calligonum species were investigated under the same growth conditions growing in the desert botanical garden. Factor correlation analysis and principal component analysis were used to compare the relationship between physiological differences and drought tolerance among Calligonum species. The results are as follows: ① This study confirms that the genus Calligonum exhibits typical C4 photosynthetic pathway characteristics. Under arid conditions, Calligonum plants with higher δ13C values optimize water use efficiency through stomatal regulation. ② in order to adapt to the extreme environment, Calligonum plants maintain the internal water balance by accumulating osmotic substances such as soluble protein, soluble sugar and proline, so as to ensure the normal physiological metabolism, growth and development of cells. ③ the Calligonum species enhance drought resistance by increasing and maintaining high activities of antioxidant enzymes (MDA, SOD, POD, H_2O_2) to reduce and eliminate oxygen stress and reduce plasma membrane damage. ④ the factors that have the greatest influence on drought resistance of 16 species of Calligonum are Soluble protein > Soluble sugar > Chlorophyll > Biomass > Transpiration intensity > Biomass > δ ^{13}C. ⑤ the ranking of Calligonum Species by drought resistance is as follows: *C.roborowskii* > *C.junceum* > *C.cordatum* > *C. densum* > *C.gobicum* > *C.rubicundum* > *C.mongolicum* > *C.arborescens* > *C.aphyllum* > *C.ebinuricum* > *C. klementzii* > *C. leucocladum* > *C.colubrinum* > *C.caput-medusae* > *C.squarrosum* > *C. pumilum*. Therefore, when Calligonum plants are under drought stress, they will increase the content of soluble protein and soluble sugar to provide energy and matter for plants, and help plants reduce water transpiration and maintain high water potential and photosynthetic capacity. The results revealed that Calligonum plants exhibit physiological resistance-type adaptations to arid environments. The remarkable drought adaptability of Calligonum species, enabling their widespread distribution and growth in arid regions, can be attributed to their distinctive physio-ecological characteristics.

Key words: *Calligonum* L.; Interspecific; Physiological variation; Drought tolerance

Introduction

Drought is a long-standing global problem. The world's land area is 1.62 × 108 km^2, representing 30.3% of the Earth's total area, of which about 1/3 is arid and semi-arid desert, and 43% of the land is at risk of desertification. With the intensification of biotic and abiotic stresses in nature (Miguel *et al*., 2020). However, because some desert plants grow in the harsh environment of drought and heat for a long time, in terms of, it has formed a series of survival mechanisms to resist various adverse environmental factors and natural disasters" to "they have evolved a series of mechanisms, such as morphological structure and physiological function, to resist various adverse environmental factors and natural disasters. There are about 45 species of *Calligonum* L. the world, widely distributed in the arid regions of western Asia, southern Europe and northern Africa. The arid region of Central Asia is the center of its origin and is the dominant species of long-term natural selection in arid desert regions (Song *et al*., 2020). Calligonum has a developed root system and dense branches. To adapt to extreme drought conditions, its leaves are extremely degraded and photosynthesis is replaced by green branches. It has characteristics of drought resistance, saline-alkali tolerance, sand burial tolerance and barren tolerance.

The impact of drought on plants is considerable and pervasive. Calligonum plants exhibit a wide range of geographical distributions and display a variety of biological characteristics and ecological adaptability, which is closely related to the genetic variation of Calligonum plants. Such differences may also manifest in the stress resistance of different species. This phenomenon is observed throughout the life cycle of the plant, including seed germination, vegetative growth, reproductive growth, flowering and fruiting. Additionally, it affects various physiological and metabolic processes, including photosynthesis, respiratory metabolism, water and nutrient element absorption and transport, enzyme activity and transformation, organic matter transport and accumulation. Consequently, numerous scholars have conducted research on the biological characteristics of Calligonum, including its biological characteristics (Feng *et al*., 2008), pot experiments under drought stress (Liu *et al*., 2011), photosynthesis physiology (Su *et al*., 2003), plant functional characteristics (Song *et al*., 2012) and adaptability to the environment (Xu *et al*., 2016). However, to date, there have been few reports on the physiological differences and

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adaptability among *Calligonum* L. plants. Consequently, it is not possible to analyze the characteristic differences and interrelationships among different species of *Calligonum* L. This may be due to the wide distribution and scattered population of Calligonum in arid environments, which makes it difficult to carry out large-scale experimental studies at the same time. We carried out a comparative experimental study on the physiological and water physiological characteristics, osmotic regulation ability and antioxidant capacity of 16 species of Calligonum. The aim of the study was to comprehensively analyze the drought resistance of Calligonum and evaluate its potential application in drought-resistant plant breeding. This study not only reveals the resource utilization strategies of desert plants but also provides a reference for the study of plant resource utilization and ecological adaptation in other ecosystems. These mechanisms and differences can elucidate the adaptation strategies of different plants and provide a theoretical basis for the research and utilization of plant drought tolerance.

Material and Methods

Studying area: This study was carried out in the Turpan Desert Botanical Garden of the Chinese Academy of Sciences. The botanical garden is located in the central and eastern part of the Turpan Basin, Xinjiang, China, with longitude 89.184, latitude 42.940, altitude-105m. It belongs to a typical inland arid desert climate, with an average annual temperature of 13.9℃, an average annual precipitation of 16.4mm and an annual evaporation of 2837.8mm. Calligonum has been successfully introduced and cultivated for more than 40 years in this Garden. 16 Calligonum species were selected for our research, including *C. junceum, C. leucocladum, C. rubicundum, C. aphyllum, C. gobicum, C. mongolicum, C. pumilum, C. arborescens, C. caput-medusae, C. roborowskii, C. squarrosum, C. colubrinum, C. densum, C. klementzii* and *C. cordatum*. The healthy branches were sampled at fruiting period to test physiochemical indexes.

Experimental method: $\delta^{13}C$ content was determined by isotope ratio mass spectrometer, chlorophyll content was determined by acetone extraction, carotenoid content was determined by spectrophotometer, plant total nitrogen content was determined by micro Kjeldahl method. The content of total phosphorus was determined by molybdenum-antimony resistance colorimetric, the content of total potassium was determined by flame photometer, the relative water content of leaves was determined by drying weighing method, the leaf water potential was measured by WP4-T dew point water potential meter, and the transpiration rate was measured by in vitro rapid weighing method. Proline content was determined by ninhydrin colorimetric method, soluble sugar content was determined by phenol colorimetric method, soluble protein content was determined by Coomassie brilliant blue staining method, and plant biomass was estimated according to plant height, crown width, basal diameter and density. The activities of POD and SOD were determined by Solar bio enzyme kit. The content of MDA was determined by TBA method and the activity of superoxide dismutase was determined by nitrogen blue tetrazolium photoreduction method.

Statistical analysis: SPSS26.0 was used for model fitting, correlation analysis, principal component analysis, and the data illustration was implement in Origin 9.0.

Results and Discussion

Six indexes including $\delta^{13}C$, chlorophyll, carotenoid, nitrogen, phosphorus and potassium were selected for testing photosynthetic physiology. As illustrated (Fig. 1) the $\delta^{13}C$ value of the 16 species of Calligonum ranged from -12.76% to -14.57%, indicating a C_4 photosynthetic type. The maximum $\delta^{13}C$ was observed in *C. mongolicum*, while the minimum was observed in *C. pumilum*. C_4 plants are more suited to environments with low latitudes and strong seasonal dry and wet changes, which may explain the emergence of C_4 plants in areas prone to drought. The stable carbon isotope composition of plants can provide insight into a multitude of physiological and ecological processes, particularly those related to photosynthesis and water metabolism. A higher $\delta^{13}C$ value is indicative of a higher plant water use efficiency (Sage, 2004). The $\delta^{13}C$ value can be employed as an indicator of alterations in plant populations in relation to diverse physiological mechanisms and environmental conditions.

The most effective and important pigments in photosynthesis are chlorophyll and carotene. The higher the chlorophyll content, the stronger the photosynthesis, which can promote plant growth. The (Fig. 2) showed that most of the chlorophyll and carotene contents was *C. rubicundum* and the lowest was *C. pumilum*.

The maximum Nitrogen content was found in *C. arborescens*, while the minimal value observein in *C. rubicundum*. *C. densum* had the highest phosphorus content, and *C. pumilum* had the lowest phosphorus content. For the potassium content, the highest value was observed in *C. roborowskii*, while the lowest in *C. junceum*. The increase in total nitrogen, total phosphorus, and total potassium content leads to higher nutrient levels in plants, thereby accelerating the photosynthetic rate. Nitrogen deficiency is the primary cause of reduced photosynthesis and leaf senescence. Additionally, the phosphorus and potassium content in leaves also decreases accordingly (Reich *et al*., 2014).

In arid-semi-arid areas, water is the most important factor restricting plant growth. Relative water content, water potential, transpiration intensity was selected to test the plant water physiological index. As demonstrated (Fig. 3) *C. roborowskii* exhibits the highest Relative water content, while *C. pumilum* demonstrates the lowest. It is evident that under identical conditions, an increase in Relative water content is accompanied by a decrease in water deficit, thereby enhancing the water absorption and retention capacity of plants. Consequently, plants exhibiting robust drought resistance are capable of maintaining a higher Relative water content in their leaves.

Under drought conditions, the leaves of plants increase the absorption of soil water by reducing their own water potential. The lower the water potential of plants is, the stronger the passive water absorption capacity is (Arend *et al*., 2021). The experimental data demonstrated that *C. rubicundum* exhibited the highest levels of growth, while *C. roborowskii* demonstrated the lowest levels. The prevailing conditions were characterized by elevated temperatures, intense light, high air velocity, and substantial transpiration. The test data demonstrate that *C. mongolicum* exhibits the highest transpiration intensity, while *C. pumilum* displays the lowest, thereby reflecting the divergent water loss regulation and drought adaptation mechanisms observed among Calligonum.

When plants are under stress, proline increases the ability of osmotic regulation, protects enzyme activities against drought stress, and increases the content of soluble sugars and soluble proteins to provide plants with the necessary energy substances to ensure the normal metabolism of plants. As demonstrated (Fig. 4) the maximum proline content was observed in *C. roborowskii*, while the lowest was recorded in *C. colubrinum*. Furthermore, the maximum content of soluble protein and soluble sugar is observed in *C. roborowskii*, while the lowest is found in *C. ebinuricum*. Finally, the maximum biomass was observed in *C. arborescens*, while the minimum was recorded in *C. colubrinum*.

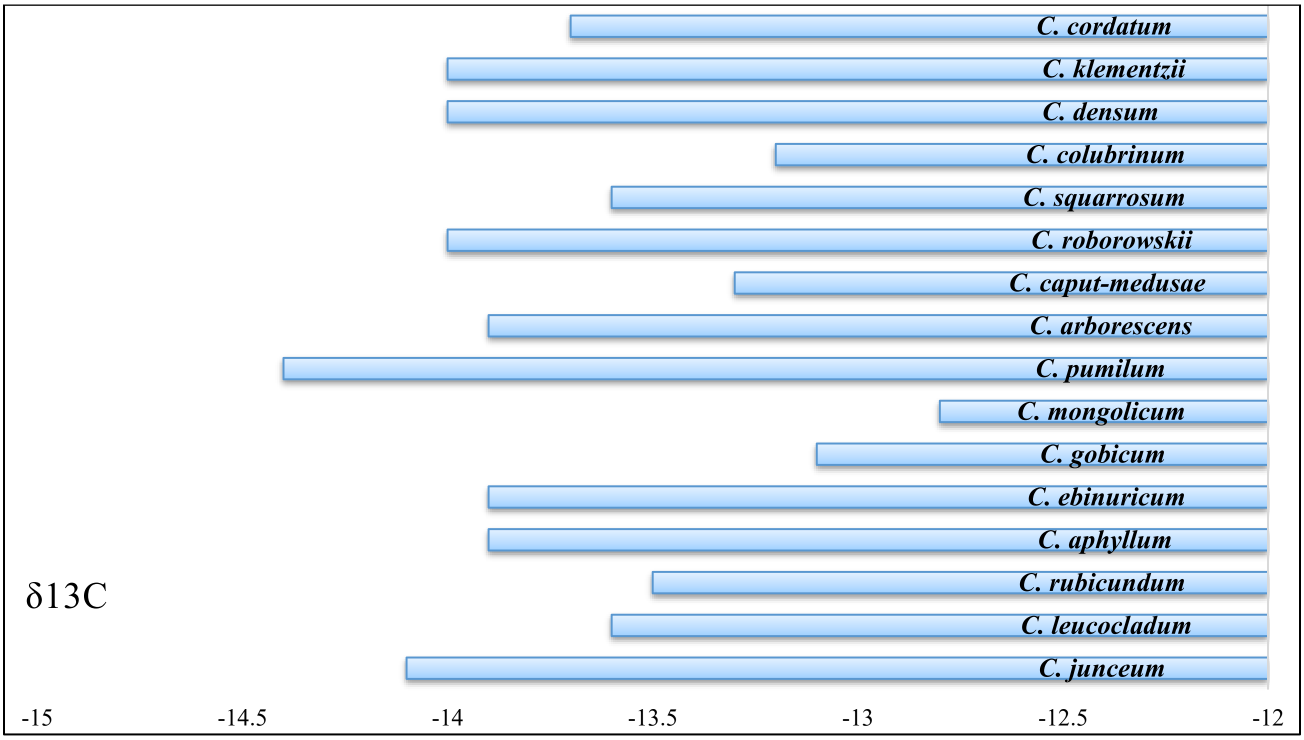

Fig. 1. Carbon isotope content of 16 species of Calligonum.

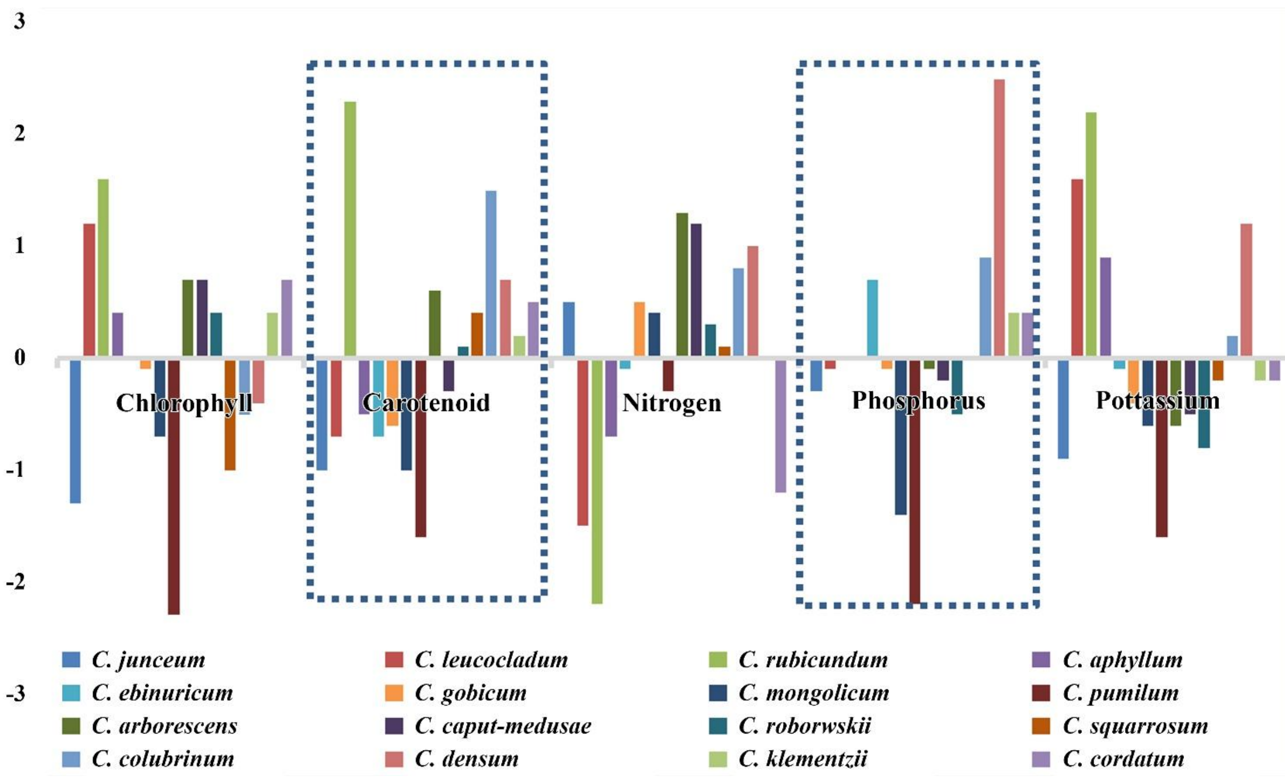

Fig. 2. Five physiological indexes between of 16 species of Calligonum.

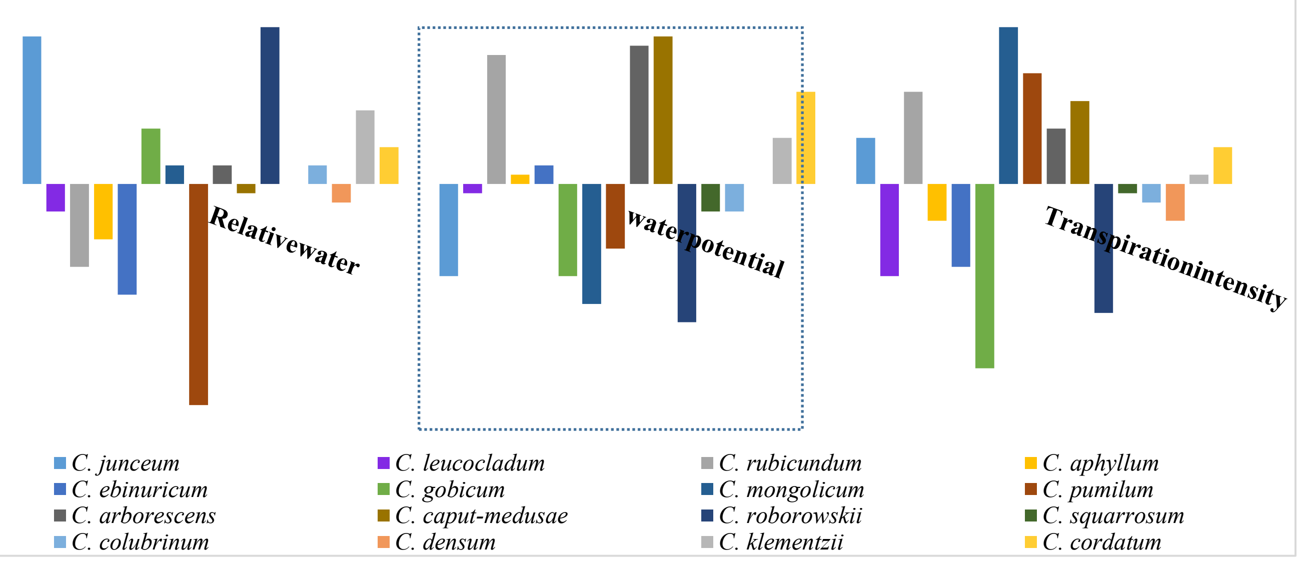

Fig. 3. Three water physiological indexes of 16 species of Calligonum.

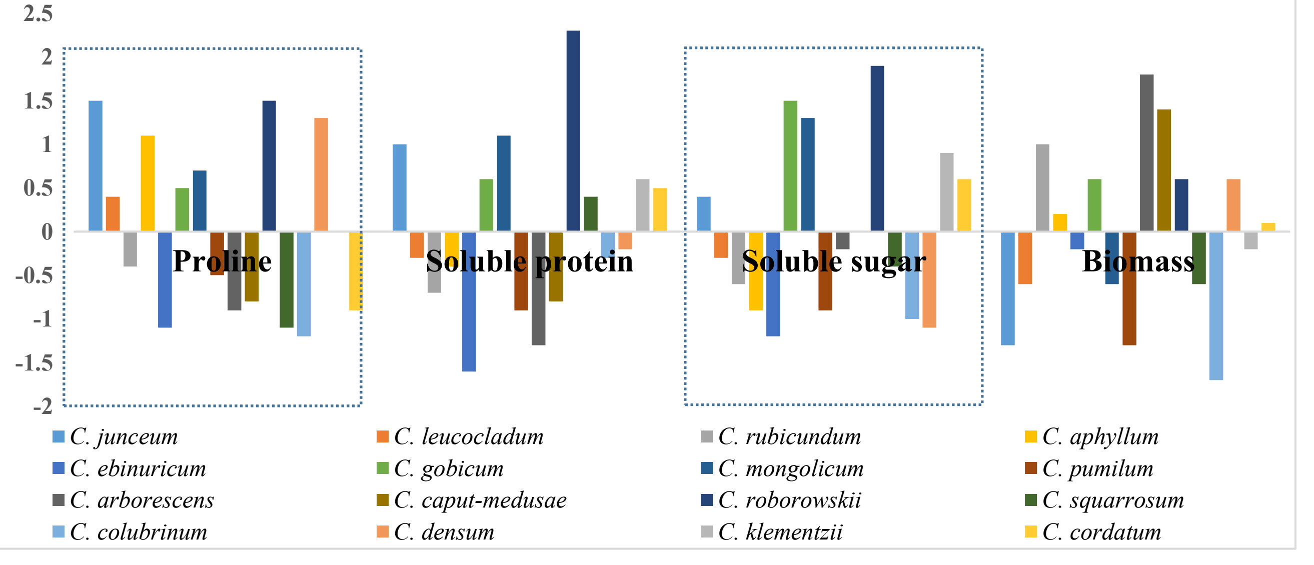

Fig. 4. Four antioxidant enzyme indexes of 16 species of Calligonum.

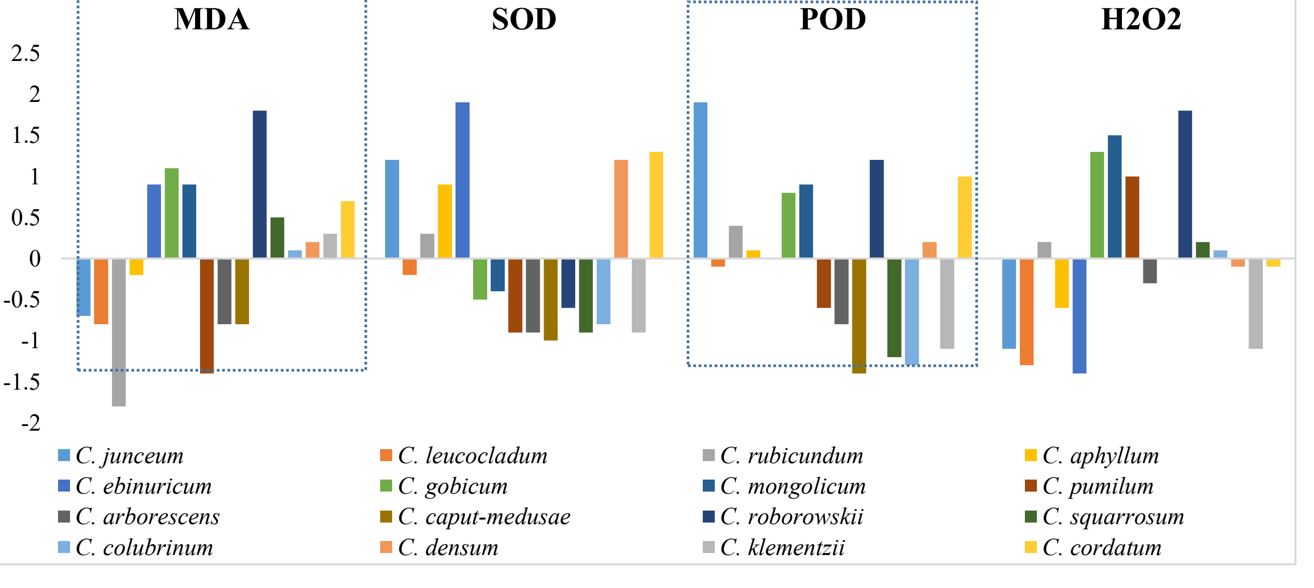

Fig. 5. Four energy indexes of 16 species of Calligonum.

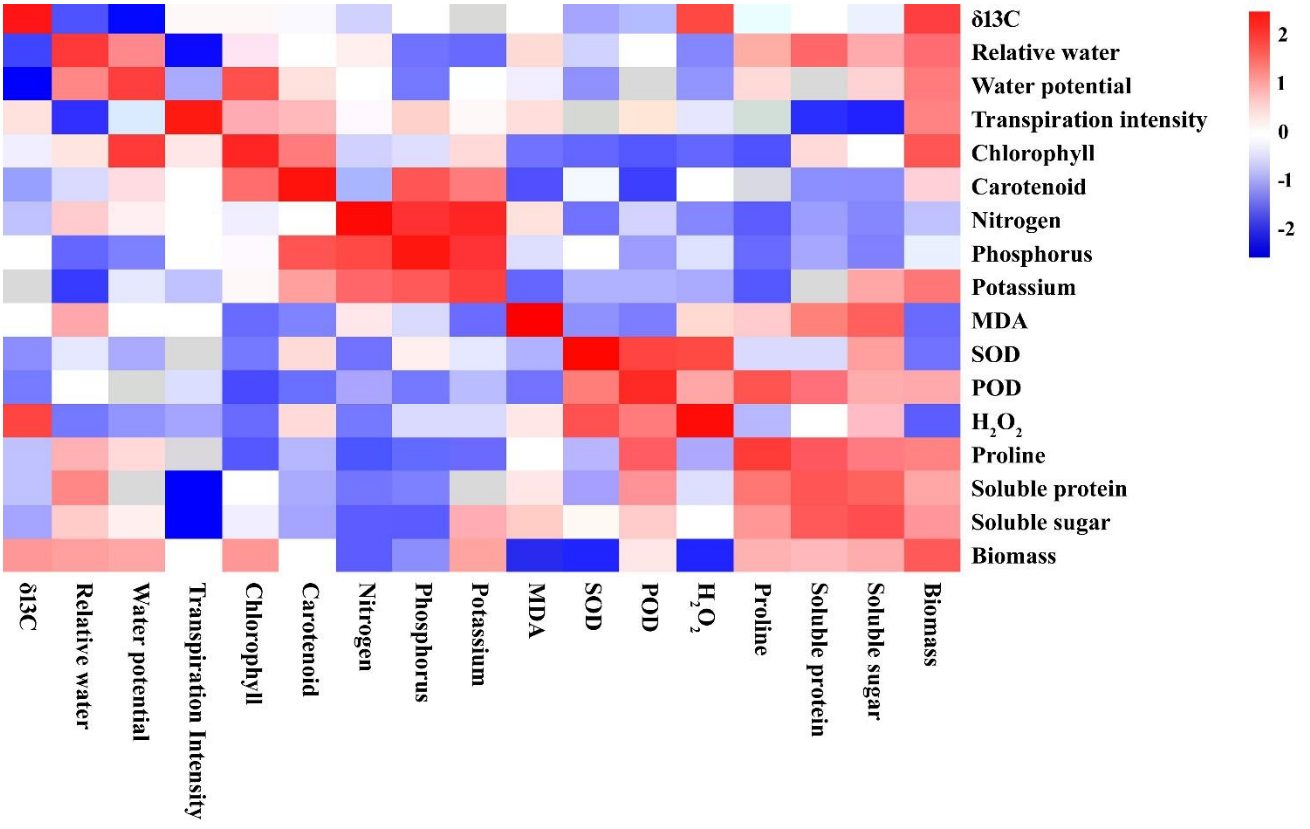

Fig. 6. The correlation analysis among 17 evaluation factors of Calligonum.

Plants have evolved a comprehensive defense system to combat reactive oxygen species. The enzymes malondialdehyde (MDA), superoxide dismutase (SOD), peroxidase (POD) and H_2O_2 are pivotal in this process, as they are capable of effectively scavenging reactive oxygen species and thereby reducing oxidative damage induced by water stress (Alvarez *et al*.,2021).

As shown (Fig. 5) there was a significant difference in the content of antioxidant enzymes among of Calligonum species in the same habitat, in which the largest content of MDA was *C. roborowskii*, the smallest content was *C. rubicundum*, the maximum content of SOD was *C. ebinuricum*, the lowest content was *C.caput-medusae*, the maximum content of POD was *C. junceum*, and the lowest content of H_2O_2 was *C. roborowskii*, the smallest content was *C. ebinuricum*.

Correlation Analysis

The correlation analysis among 17 evaluation factors was carried out to understand how 17 factors affect the physiological status of Calligonum plants in arid environment. The Pearson correlation coefficient among the measured indexes is given as shown (Fig. 6).

The main results were as follows: 1) when the light was enhanced, the δ ^{13}C value of C_4 plants was positively correlated with Biomass, the biomass of photosynthetic products increased, and δ ^{13}C was positively correlated with H_2O_2 (R = 0.74, p<0.05), indicating that the antioxidant capacity of Calligonum leaves became stronger under drought stress to resist the damage of reactive oxygen species. There was a negative correlation between δ ^{13}C and Relative water content and a significant negative correlation between δ ^{13} C and water potential, indicating that there is water deficit in assimilated branches of Calligonum in arid environment, reflecting the resistance and adaptability of plants to external drought stress (Reich *et al.*, 2014).However, there was no significant correlation between δ^{13}C, chlorophyll, Nitrogen, Phosphorus and Potassium, which may be due to the decrease of photosynthetic capacity of plants under drought stress, thus reducing the absorption and utilization of carbon dioxide.In addition, drought directly affects the structure and chlorophyll content of chloroplasts in photosynthetic apparatus, which in turn affects the efficiency of photosynthesis. Therefore, the results of this study are consistent with those of previous studies (Ma *et al.*, 2017), indicating that the effect of drought on Calligonum is stomatal.

2) Relative water content was positively correlated with water potential (r =0.65, p<0.05) and negatively correlated with Transpiration intensity (r =-0.91, p<0.01), indicating that plant tissue could improve plant drought tolerance (Wang *et al.*, 2019) by increasing water storage capacity. At the same time, Water potential was positively correlated with Chlorophyll (r = 0.91, p<0.01) and Biomass (r = 0.73, p<0.05). Chlorophyll was positively correlated with Carotenoid (r = 0.64, p<0.05) and Biomass (r = 0.77, p0.05). It can be seen that the enhancement of plant water absorption capacity leads to the improvement of water potential, thus promoting photosynthesis and plant growth and development. Chlorophyll is one of the important components of photosynthesis. with the increase of water potential and light, the concentration of chlorophyll will increase accordingly, in order to improve the efficiency of photosynthesis and the production of biomass. therefore, the adaptation mechanism of plants in arid environment is

often realized by improving water use efficiency and photosynthesis efficiency. This chain reaction reflects the strategy of plants to make full use of water resources and light resources under arid conditions, so as to ensure the survival, growth and development of xerophytes.

3) Relative water content was positively correlated with proline (r = 0.54), Soluble protein (r = 0.78), soluble sugar (r = 0.51), biomass (r = 0.73), proline and soluble protein (r = 0.85), soluble sugar (r = 0.70) and biomass (r = 0.69).There was a significant negative correlation between transpiration and soluble protein (r =-0.90) and soluble sugar (r =-0.99).The results show that in the face of drought stress, plants will increase the concentration of cell sap by accumulating osmotic regulating substances, so that the cells can maintain normal swelling and pressure, so as to create conditions for the normal life activities of plants. Among them, osmotic regulatory substances such as soluble protein, soluble sugar and proline can effectively increase the osmotic pressure of cells, thus increasing the water retention capacity and drought resistance of cells. In addition, increasing the concentration of intracellular solute can reduce the cell water potential and keep the cell water absorption capacity in a relatively balanced state, thus ensuring that the metabolic activities of the cell can be carried out normally (Chaves *et al*., 2004). Therefore, osmotic regulators play an important role in plant drought resistance physiology and have an important impact on plant growth, development and adaptability in arid environment.

4) There was a positive correlation between Carotenoid and Phosphorus (r = 0.72) and Potassium (r = 0.61). The results showed that carotenoid content directly affected the accumulation of plant organic matter and played a role in accepting and converting energy into photosynthesis (Boomiraj *et al*., 2022). Among them, nitrogen and phosphorus (r = 0.76) and potassium (r = 0.82) were positively correlated. At the same time, potassium was positively correlated with soluble sugar (r = 0.60) and biomass (r = 0.76), indicating that potassium increased the osmotic potential of mesophyll cells and reduced stomatal resistance, thus promoting photosynthetic electron transport and photophosphorylation, directly affecting the accumulation of plant organic matter and improving plant biomass, which further proved that Calligonum is a photosynthetic cooperative plant with stomatal limitation.

5) POD was positively correlated with H_2O_2 (r = 0.54), proline (r = 0.81), soluble protein (r = 0.71), soluble sugar (r = 0.52) and biomass (r = 0.51). The results showed that under drought stress, plants with strong drought resistance could maintain higher activities of antioxidant enzymes to reduce and eliminate oxygen stress and reduce plasma membrane damage (Ajtahed *et al*., 2021). Some studies have pointed out that the stronger the drought resistance of plant species is, the higher the content of osmotic regulatory substances such as soluble sugar and free proline is, and the accumulation of osmotic regulatory substances is also one of the important ways for plants to respond to drought stress. (Smith *et al*., 2022).

Correlation analysis was performed on a set of 17 drought resistance physiological indicators. The analysis revealed that Calligonum plants exhibited a response to drought stress by regulating osmotic substances, accumulating organic matter and enhancing oxidoreductase activity.

Principal Component Analysis: The method of principal component analysis enables the explanation intensity and contribution rate of each principal component to be obtained, thus allowing the main factors related to drought resistance to be distinguished and the physiological characteristics and environmental adaptability of Calligonum to be fully reflected. Concurrently, the disparities in principal component scores and single indexes can be employed to ascertain the dissimilarities in drought resistance among the various species of Calligonum. This approach allows for a comprehensive evaluation and explanation of the physiological adaptation and drought resistance of Calligonum under drought stress.

Table 1. Principal component analysis of drought stress of 16 species of *Calligonum*.

Factors	Principal Component				
	1	2	3	4	5
Soluble protein	0.86	0.32	0.10	0.15	0.05
Water potential	-0.85	0.11	0.34	0.08	-0.22
Soluble sugar	0.78	0.24	0.37	0.23	-0.26
MDA	0.65	0.35	0.16	-0.34	0.29
H_2O_2	0.59	-0.22	0.43	0.34	0.25
Relative water	0.59	0.53	0.29	-0.17	-0.17
Potassium	-0.58	0.57	-0.13	0.28	0.28
Proline	0.57	0.43	-0.38	0.10	-0.25
POD	0.55	0.44	-0.44	0.38	-0.07
Chlorophyll	-0.44	0.69	0.34	0.28	-0.19
Phosphorus	-0.37	0. 56	0.00	-0.51	0.33
Transpiration intensity	-0.21	-0.55	0.10	0.45	-0.08
SOD	-0.15	0.47	-0.68	-0.01	0.15
Biomass	-0.27	0.42	0.54	0.10	-0.39
Carotenoid	-0.45	0.41	0.48	0.13	0.44
Nitrogen	0.30	-0.21	0.36	-0.71	-0.13

$\delta^{13}C$	0.35	-0.21	0.26	0.25	0.73
eigenvalue	5.01	3.18	2.22	1.71	1.49
contribution	0.29	0.19	0.13	0.10	0.88
cumulative contribution	0.29	0.48	0.61	0.71	0.80

The drought resistance of 16 species of Calligonum was evaluated by calculating F=F1 × 0.29+F2 × 0.19+F3 × 0.13+F4 × 0.10+F5 × 0.88. This enabled the drought resistance of each species of Calligonum to be evaluated

Table 2. Comprehensive evaluation of drought resistance of 16 species of *Calligonum*.

Species	F1	F2	F3	F4	F5	Score	Ranking
Calligonum junceum	-1.28	-0.53	-0.54	1.29	1.65	1.28	2
Calligonum leucocladum	0.06	0.25	1.05	-0.14	-1.4	-0.44	12
Calligonum rubicundum	2.37	0.42	-0.61	0.16	0.3	0.87	6
Calligonum aphyllum	-0.04	-0.15	1.05	0.13	-0.72	0.07	9
Calligonum ebinuricum	-0.99	-0.84	0.44	1.26	-0.77	-0.15	10
Calligonum gobicum	1.17	-0.09	-0.55	0.48	0.83	0.97	5
Calligonum mongolicum	0.95	-0.81	0.06	-1.18	1.55	0.32	7
Calligonum pumilum	-1.12	-1.92	-0.23	-2.17	-0.12	-3.02	16
Calligonum arborescens	-0.68	-0.4	-0.71	0.37	0.95	0.2	8
Calligonum caput-medusae	-0.66	1.15	-1.43	-0.75	-0.5	-1.45	14
Calligonum roborowskii	-0.64	1.81	2.2	-0.95	1.04	2.19	1
Calligonum squarrosum	-0.59	1.44	-1.57	-0.52	-1.1	-1.69	15
Calligonum colubrinum	1.17	-1.38	0.4	-0.11	-1.47	-1.33	13
Calligonum densum	-0.23	-0.09	0.37	1.86	-0.32	1.18	4
Calligonum klementzii	0.16	0.58	-0.79	0.21	-0.33	-0.27	11
Calligonum cordatum	0.34	0.55	0.89	0.07	0.41	1.27	3

The order of drought resistance is illustrated in Table 2 as follows: *C. robrowskii* > *C. junceum* > *C. cordatum* > *C. densum* > *C. gobicum* > *C. rubicundum* > *C. mongolicum* > *C. arborescens* > *C. aphyllum* > *C. ebinuricum* > *C. klementzii* > *C. leucocladum* > *C. colubrinum* > *C. caput-medusae* > *C. squarrosum* > *C. pumilum*

Table 1 presents the principal component analysis of 17 physiological indexes of 16 species of Calligonum. Principal component analysis yielded five principal components with eigenvalues greater than 1, collectively accounting for 80% of the cumulative contribution rate. The first principal component, F1, is primarily comprised of soluble protein and soluble sugar, with a contribution rate of 29%. The second principal component, F2, is largely constituted by chlorophyll, with a contribution rate of 19%. The third principal component, F3, is primarily composed of biomass, with a contribution rate of 13%. The fourth principal component, F4, is predominantly represented by transpiration intensity, with a contribution rate of 10%. The fifth principal component, F5, is primarily characterized by $\delta^{13}C$, with a contribution rate of 8.8%.

Conclusions

The factors that exert the greatest influence on the drought resistance of 16 species of Calligonum are soluble protein, soluble sugar, chlorophyll, biomass, transpiration intensity, biomass, and δ13C. In response to drought stress, Calligonum plants increase the content of soluble protein and soluble sugar, providing energy and substances essential for plant growth. This process also helps plants reduce water transpiration and maintain high water potential and photosynthetic capacity (Pandey *et al*., 2023). These result demonstrate a physiological resistance to drought for the Calligonum species.

In the same growing environment, the species *C. roborowskii* exhibited the strongest drought resistance, while *C. pumilum* exhibited the weakest. The results of the drought resistance ranking of Calligonum are also consistent with the ecological distribution of Calligonum plant origin. For example, *C. roborowskii* has the strongest drought resistance, which is widely distributed in the extremely arid Karakum Desert, Kizilkum Desert and Taklimakan Desert. *C. junceum* is widely distributed in the southwestern basin of West Siberia, the Tulan lowland, and the gravel Gobi of southwestern Mongolia extending to the Junggar Basin. However, *C. pumilum* has weak viability in the field and is rarely distributed in the Kumtag Desert. Consequently, the study discussed the driving factors of floristic differentiation of Calligonum from the perspective of plant physiology and elucidated the historical causes of Calligonum growing in disparate distribution areas (Oliveira *et al*., 2020). It demonstrates that a series of physiological and biochemical alterations will occur in plants to respond to or adapt to a drought environment under drought stress.

Calligonum plants possess unique stress-resistant genetic resources (Feng *et al*., 2025). Through whole-genome sequencing and bioinformatics analysis, Gao *et al*. (2022) identified 12 functional gene clusters significantly associated with stress resistance in the germplasm resources of this genus. This study provides novel candidate gene resources for the genetic improvement of plant stress resistance and offers important guidance for future research in this field (Gasmi *et al*., 2022.

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