

CLIMATIC FACTORS INFLUENCING GEOGRAPHICAL REPLACEMENT IN THE DESERT GENUS *CALLIGONUM* SECT. *MEDUSA* (POLYGONACEAE) IN XINJIANG, CHINA

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Abstract

Calligonum Sect. *Medusa* is most diverse and widespread taxon in the Xinjiang region. The species are morphologically similar with close phylogenetic ties and occupy narrow geographic ranges, thus becoming geographical replacement species. Eleven *Calligonum* species fall into three geographical displacement distribution series: *Calligonum jimunaicum*, *C. trifarium*, *C. ebinuricum* and *C. gobicum* occur in northern Xinjiang; *C. ruoqiangense* and *C. pumilum* occur in the east; and *C. kuerlese*, *C. roborowskii*, *C. yingisarium* have a southern distribution. Their distribution follows a pattern of geographical displacement from north to east to south, where they overlap and replace each other in space. We used ANOVA and PCA to identify the climatic factors that influence geographical partitioning in Sect. *Medusa* and found the most important factors to be annual precipitation and annual temperature. The geographical partitioning observed in Sect. *Medusa* may be the result of adaptation to long-term aridity in the region. Selective pressures from rainfall and temperature may have prompted adaptation to increasingly arid conditions in *Calligonum*.

Key words: Geographical replacement, *Calligonum* Sect. *Medusa*, Distribution, Climate contact zones.

Introduction

Geographical replacement theory is concerned with the phenomenon whereby adjacent populations, when presented with the necessary selective pressures, will diverge along a climatic gradient to form a cline (Wang, 2005). This phenomenon is usually observed in closely related species. The formation of geographical clines is the natural result of plants adapting to their environments (Crawley, 1986; Harriet *et al.*, 1999), and the vegetation types are often a reflection of the associated climatic features of the region. Previous studies have demonstrated geographical replacement in other plant species in China. For example, Zhang (1998) reported that *Caragana* exhibited a geographical replacement series in Inner Mongolia, while Wang (2005) analyzed the factors driving geographical substitution in *Artemisia* in Northern China. Similarly, Luo & Zhou (2001) investigated this phenomenon in *Cyclobalanopsis*. Several other studies have investigated the ecological factors responsible for the distributional patterns observed in plants (Xu & Chang 1999; Bacic & Jogan, 2001; Zhao 2005; Fang *et al.*, 2006).

Calligonum L. (Polygonaceae) is a dominant component of sandy desert vegetation where they act as important windbreaks and sand stabilizers, and are also used as a source of fodder, fuel, honey and traditional medicine. Due to these ecological and economic benefits, a lot of research has been done on *Calligonum* (Mao 1996; Mao & Pan 1986). Studies on morphology and DNA (Song *et al.*, 2020) have demonstrated the monophyly of the genus and *Calligonum* has been divided into four sections based on fruit shape: *Pterococcus* (Pall.) Borszcz., *Medusa* Sosk. et. Alexandr., *Calligonum* and *Calliphysa* (Fisch. et. Mey.). We have observed the geographic distribution of *Calligonum* and have found that many of the species appear to exhibit a signature of geographical replacement. Furthermore,

each section occupies a more-or-less discrete distribution with seemingly little overlap. For example, Sect. *Calliphysa* (monotypic) and Sect. *Pterococcus* are centrally distributed with smaller disjunct populations in the Irano-Turanian region, Central Asia and west of China, while Sect. *Calligonum* occupies the western end of distribution area, and is continuously distributed across northern Africa, southern Europe and Asia. Conversely, Sect. *Medusa* occupies the eastern part of the distribution area, and is continuously distributed across South and Central Asia. Within China, *Calligonum* species occur mainly in the regions of Xinjiang, Gansu, Ningxia and Inner Mongolia. With 22 species present in the region, *Calligonum* is one of the dominant genera of the Xinjiang desert flora (Mao, 1998), and Sect. *Medusa* is the most diverse and widespread within Xinjiang, where about 11 species are represented, five of which are endemic (Feng, 2003). These eleven species include: *C. mongolicum*, *C. gobicum*, *C. ebinuricum*, *C. kuerlese*, *C. pumilum*, *C. roborowskii*, *C. ruoqiangense*, *C. yingisarium*, *C. jimunaicum*, *C. trifarium* and *C. taklamakanensis*. Not only are these species all morphologically quite similar with close phylogenetic ties; they also appear to occupy relatively narrow geographic ranges. Distributed across the desert region of Xinjiang, species diversity within Sect. *Medusa* declines as precipitation and altitude increase. Their distributions appear to correlate with particular regional climatic characteristics where they replace one another in space; thus becoming geographical replacement species. Several reports on the phytogeography of the Xinjiang region have been published (Tan *et al.*, 2008; Sabirhazi *et al.*, 2012; Liu *et al.*, 2017), but little attention has been paid to the possible mechanisms influencing the observed patterns, and experimental evidence is lacking. There are no previous studies that have investigated the ecological foundation of the geographical partitioning in *Calligonum* Sect. *Medusa*.

Here we investigated the distribution pattern of the species along with the possible climatic factors responsible for the geographical replacement observed in Sect. *Medusa*. Possible environmental factors driving the geographical partitioning in Sect. *Medusa* are identified and discussed. The results of this study elucidate the possible ecological factors responsible for the natural ecological law of *Calligonum*. This research should have great practical significance in guiding the protection of the desert ecosystem and informing regional sustainable development.

Materials and Methods

Sampling and study area: *Calligonum* is adapted to grow in very harsh, arid desert conditions and generally in an altitude range of 400–1500 m. Low rainfall and strong evaporation rates are inherent to its temperate continental arid habitat, along with abundant heat and sunshine as well as high wind speeds. The topography of the region is flat, and the fine, sandy soils are topped with gravel and a calcareous crust. The organic matter layer is about 0.99–1.73 g/kg and the groundwater at a depth of over 10 m. The vegetation of the region is low in diversity, sparsely distributed (less than 30% coverage) with low ground coverage and is dominated by xerophytic, salt-tolerant and alkaline communities, including the species *Sympegma regelii*, *Sarcozygium xanthoxylon*, *Haloxylon ammodendron*, *Hexinia polydichotoma*, *Reaumuria soongoric*, *Nitraria tangutorum*.

During the 2013–2014, we investigated the spatial distribution of the 11 species of Sect. *Medusa* in the arid and semi-arid Xinjiang regions. Species points were

collected from field observations, specimen records and relevant documents, and plotted using the Google Earth (Fig. 1), resulting in a total of 50 × 12 points. We observed that the distributions of *C. jimunaicum*, *C. trifarium*, *C. ebi-nuricum* and *C. gobicum* represent a substitution pattern from the west to the east in northern Xinjiang, replaced by *C. pumilum*, *C. mongolicum* and *C. ruoqiangense* in the east, while in the southern region *C. roborowskii*, *C. taklamakanensis*, *C. kuerlese* and *C. yingisarium* also present a substitution pattern from the east to the west.

Climate data collection and statistical analyses: We obtained our climatic data from the China Meteorological Agency, the Xinjiang Province Aerograph Bureau and the National Climatic Center. Data was mostly available for the period 1970–2000. Precipitation, temperature, sunlight and wind speed were extracted for the growing season in Xinjiang. The temperature and precipitation at the upper and lower elevation limits of species were estimated for each locality using a mean lapse rate of 0.5°C and 15 mm per 100 m conversion (Barry, 1992), in combination with data from the nearest climatic station. Eight biologically significant indices were identified and calculated using long-term climatic observations. Climatic data for the 50 species points were derived from spatial interpolation algorithms. One-way analysis of variance (ANOVA) and Principal Component Analysis (PCA) were used to identify which climatic factors that influence the distributions of the species of *Calligonum* Sect. *Medusa*. The SPSS V. 19.0 was used to assess the variation in the relationships between geographic distribution and climatic space.

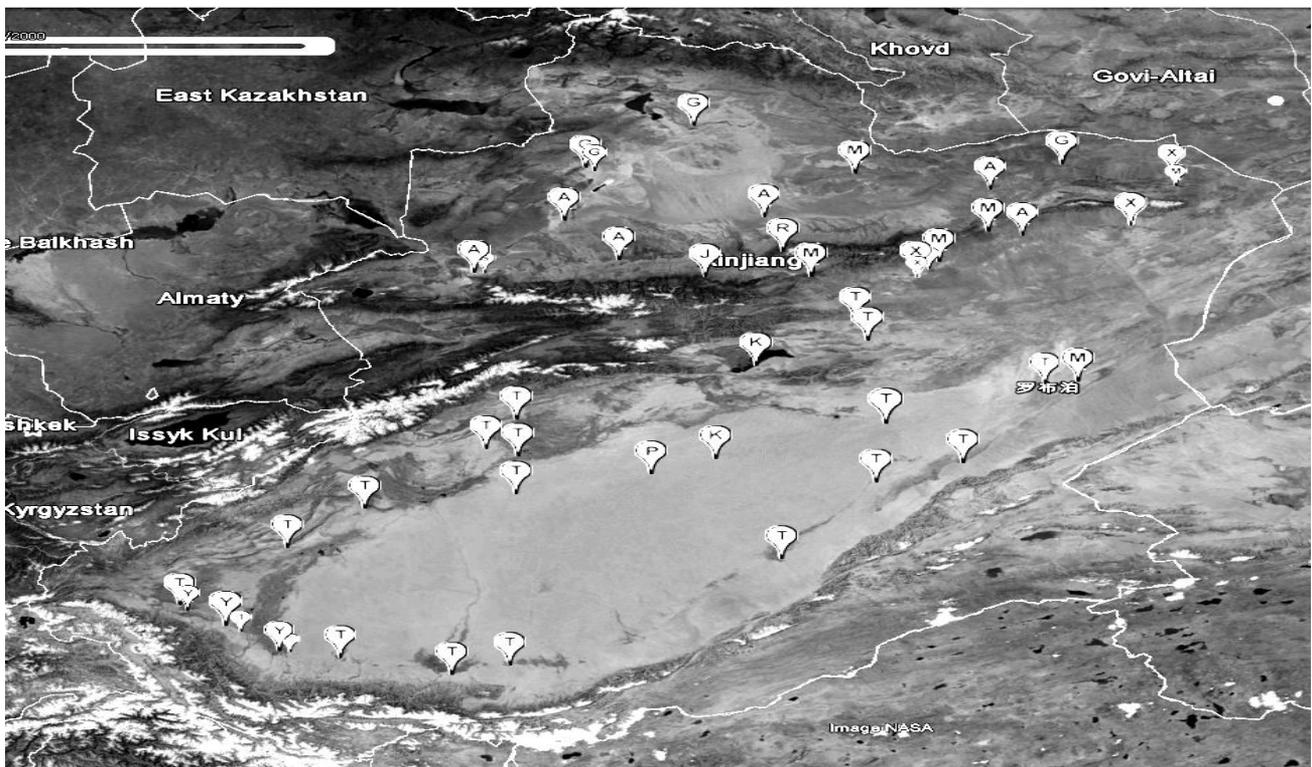


Fig. 1. The geographical distribution of the 11 *Calligonum* Sect. *Medusa* species in the Xinjiang region sampled. The symbols refer to species names: A, *C. ebi-nuricum*. G, *C. gobicum*. J, *C. jimunaicum*. K, *C. kuerlese*. L, *C. taklamakanensis*. M, *C. mongolicum*. R, *C. ruoqiangense*. S, *C. trifarium*. T, *C. roborowskii*. X, *C. pumilum*. Y, *C. yingisarium*.

Table 1. The quantity of climatic indexes of eleven species of *Calligonum*.

Species	Evaporation capacity (EC) Mean \pm SD		Wind speed (m/s) (WS) Mean \pm SD		Annual precipitation (mm) (AP) Mean \pm SD	
<i>C. ebinuricum</i>	1882.8 \pm 265.45	A, B	2.18 \pm 0.47	A	140 \pm 16.60	C, D
<i>C. trifarium</i>	1625 \pm 594	A	2 \pm 1.06	A	101 \pm 37.11	B, C
<i>C. gobicum</i>	2751.38 \pm 297	B, C	3.48 \pm 0.53	A, B	102.35 \pm 18.56	B, C
<i>C. jimunaicum</i>	2169.9 \pm 594	A, B, C	5.5 \pm 1.06	A, B	175 \pm 37.11	D
<i>C. mongolicum</i>	2978 \pm 242	B, C	3.68 \pm 0.43	A, B	66.25 \pm 15.15	A, B
<i>C. pumilum</i>	3253.6 \pm 265	C	4.52 \pm 0.47	A, B	37.80 \pm 16.60	A, B
<i>C. ruoqiangense</i>	2920 \pm 594	B, C	2.7 \pm 1.06	A	28.5 \pm 37.11	A
<i>C. taklamakanensis</i>	3100 \pm 594	C	2.6 \pm 1.06	A	40 \pm 37.11	A, B
<i>C. kuerlese</i>	2430 \pm 419.729	A, B, C	2.05 \pm 0.75	A	65 \pm 26.24	A, B
<i>C. roborowskii</i>	2597 \pm 130	A, B, C	2.34 \pm 0.23	A	54.22 \pm 8.10	A, B
<i>C. yingisarium</i>	2327 \pm 343	A, B, C	1.9 \pm 0.61	A	64.47 \pm 21.43	A, B

The letters represent sets of groups whose means do not differ significantly from each other. Means with the same letters are not significantly different from one another ($p > 0.05$), while means that do not share letters represent statistically significant comparisons ($p < 0.05$)

Table 2. Contribution of various principal components to climate factory.

Climatic index	Principal component	
	1st	2nd
Annual precipitation (mm)	0.881	0.615
The wind speed (m/S)	0.580	0.514
Evaporation capacity (mm)	-0.759	0.422
Sunshine duration (h)	0.596	0.249
The frost-free period (day)	0.385	-0.439
The mean temperature in July ($^{\circ}$ C)	0.652	0.379
The mean temperature in January ($^{\circ}$ C)	0.698	-0.147
Annual temperature ($^{\circ}$ C)	0.611	0.714
Eigen value	3.478	1.996
Contribution rate (%)	43.479	68.431

Results and Discussion

One-way ANOVA: Eight climatic variables were investigated for the 11 species and analyzed using one-way ANOVA separately. The results are shown in Table 1. Several of the eight variables tested were found to be significant (Table 1). For the variable evaporation capacity, the results showed that there were significant differences between *C. trifarium* and *C. gobicum*, *C. mongolicum*, *C. pumilum*, *C. ruoqiangense* and *C. taklamakanensis*. *Calligonum ebinuricum* was also found to be significantly different from *C. pumilum* and *C. taklamakanensis*. We noticed that *C. trifarium*, *C. ruoqiangense*, and *C. taklamakanensis* occupies limited, narrow ranges, thus perhaps this variable greatly influenced their niche.

Annual precipitation was found to be significantly different between *C. ebinuricum*, *C. trifarium*, *C. gobicum*, *C. jimunaicum* and the remaining species (p at the most 0-05). Interestingly, we observed that AB, SL, GB, JM are distributed in northern Xinjiang, while MG, CP, RQ, TG, CK, TL, YJ are distributed in southern Xinjiang, suggesting that annual precipitation has divided these two groups quite sharply and appears to be one of the most important climatic factors limiting species' distributions between the north and south.

For sunlight duration, a significant difference was found between SL and GB, MG, CP, RQ. It appears that SL is sensitive to sunlight duration; only growing at 2434-2967 hrs.

For mean temperature in July (summer), a significant difference was found between CP, RQ and CK, TL, YJ.

Among these, CP and RQ in eastern Xinjiang occur in a warmer ecological niche than the southern Xinjiang species (CK, TL, YJ). Obviously, CK, YJ and TL are instead of CP, RQ distribution in southern Xinjiang.

Mean temperature in January (winter) was found to be significantly different between SL, GB and RQ, TG. Interestingly, SL, GB grow in the cold northern Xinjiang, and RQ, TG grow in the warmer southern Xinjiang. Low temperature is an abiotic stress affecting plant growth, and possibly limiting distribution.

The annual average temperature results indicated significant differences between SL, GB, JM and RQ, TG, CK, YJ. It appears that this variable sharply divides the southern (SL, GB, JM) and northern (RQ, TG, CK, YJ) groups. Temperature appears to have a strong influence on *Calligonum* species distributions; species substitute each other geographically between the north and south.

Conversely, wind speed and frost-free period were not found to be significantly different across all species tested.

These results suggest that evaporation capacity, wind speed and sunlight duration have little influence on geographical replacement in *Calligonum*, while precipitation and temperature are more influential constraints controlling the distribution of *Calligonum* species.

Principal component analysis (PCA): Our ANOVA results indicate that precipitation and temperature are important factors dictating geographical replacement in Sect. *Medusa*. In order to further test which factors play the most significant role in dictating species' ranges, we performed a PCA.

Table 2 indicates the contributions of the variables for the principal components where the Eigen values are greater than 1.00. The first principal component accounts for 43.5% of the total variance in the data, while 68.4% of the variance is accounted for by the first two principal components. The first principal component is most strongly correlated with five of the variables (annual precipitation, evaporation capacity, mean temperature in July, mean temperature in January and annual temperature), which all scored a correlation above 0.6 or below -0.6 . These five variables vary together; an increase in one variable is associated with an increase in the remaining variables. For instance, an increase in precipitation is correlated with a decrease in evaporation

capacity. The strongest correlation is with annual precipitation (0.881), suggesting that the first principal component is primarily a measure of precipitation. In the second principal component, only annual precipitation and annual temperature receive a value above 0.6, and temperature has the strongest correlation with 0.714. The results indicate that the most important factors for determining plant distribution are annual precipitation and annual temperature.

The results from the ANOVA and PCA provide a hypothesis for geographical replacement in *Calligonum* Sect. *Medusa*. These results suggest the existence of such an ecological transition.

Conclusions

The research indicates that the 11 species of *Calligonum* Sect. *Medusa* are divided into three geographical displacement distribution series. *Calligonum jimunaicum*, *C. trifarium*, *C. ebinuricum* and *C. gobicum* occur in northern Xinjiang; *C. ruoqiangense* and *C. pumilum* are in the east; and *C. kuerlese*, *C. roborowskii* and *C. yingisarium* occur in the south. The most influential climatic factors determining their distributions were found to be annual precipitation and annual temperature. They present a geographical displacement series from north to east to south, at the same time overlap and replace each other. This pattern is largely correlated with drought resistance in the plants.

The influence of climate on plant distribution is mainly manifested in two aspects: Heat is a primary source of energy and water is essential for the maintenance of normal physiological activity. While climate restricts the geographical distribution of vegetation, vegetation types often reflect the characteristics of the climate. Heat mainly influences the distribution of vegetation in latitudinal change, while water influences vegetation change from the coast to inland in latitudinal change. The geographical transitioning of *Calligonum* species could be the result of long-term adaptation to extremely arid weather. Variation in the ranges of deserts caused by climate changes might have forced plants to exist in habitats experiencing greater drought and mobile dunes can easily bury seeds or plants. Thus, physiological adaptation to different desert habitats is implied in the divergence of *Calligonum* (Wen *et al.*, 2017).

The analysis of spatial and temporal variations of temperature, precipitation and sunlight will help to predict how changes in climate might influence species distributions, and aid decision-making. Managing regional desertification and protecting existing habitats will be an effective means of maintaining regional plant growth and development.

Acknowledgments

This research was supported by the Uzbekistan Desert Plant Diversity and Specimen Digitization Study (No: RCEECA-2018-003), the National Science Foundation of China (NSF-31770227), Science and Technology Basic Resources Survey special (2018FY100704), and the Youth Innovation Promotion Association Foundation of the Chinese Academy of Sciences (No.2019429). We would

like to thank the curators of XJBI, LZD, XJA and PE for lending us the specimens and for the permission to examine the specimens.

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