Bot. Bull. Acad. Sin. (2003) **44:** 291-296

Effect of soil water status on the physioecological traits and the ecological replacement of two endangered species, *Changium smyrnioides* and *Chuanminshen violaceum*

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(Received April 21, 2003; Accepted June 9, 2003)

Abstract. Both *Changium smyrnioides* Wolff and *Chuanminshen violaceum* Shen et Shan are monotypic species of the family Umbellaceae. They have narrow distribution areas and can only be found in the Yangtze River basin in China. *Changium* is distributed from the east to middle subtropical zone of China, and *Chuanminshen* from the middle to the west; they almost meet in the middle of the Yangtze basin. Because the climate varies from humid to semi-humid, an experiment was carried out to find out the two species' demand for soil water and analyze their niche separation by determining changes in their physio-ecological and structural traits in response to different soil water statuses. Results showed that the two species have similar structural characters and functional intensity. Diurnal variations, daily mean values, and relationships of irradiation and temperature to P_N, E and WUE among the three treatments indicate that *Chuanminshen* has more tolerance to drought than *Changium*. Changes in morphological traits also suggest that *Changium* adapts to medium to wet soil conditions while *Chuanminshen* adapts to drought soil conditions. The differences in the adaptation of physiological and morphological traits to the water environment should be part of the reason these two species have become geographically vicarious species. The results indicate that, at least, the mechanism and the approach to conservation for the two species are similar.

Keywords: Ecological replacement; Endangered species; Growth; Morphology; Photosynthesis; Subtropical zone; Transpiration; Water use efficiency.

Introduction

Both *Changium smyrnioides* Wolff and *Chuanminshen violaceum* Shen et Shan are monotypic species of the family Umbellaceae. There are some interesting viewpoints on the relationship between *Changium* and *Chuanminshen*, for they were classified as the same species before 1980. Shen et al. (1980) indicated that *Chuanminshen violaceum* should belong to different genera with a distant relation in systematic development with *Changium smyrnioides*.

Because their fleshy roots are prized in Chinese medicine, and because of land use, the natural populations of the two species have been seriously disturbed by human activity and have decreased in recent years to the point that they are now endangered species (Qiu et al., 2000). *Chuanminshen* has been cultivated as a medicinal material on a large scale, but *Changium* has not yet been cultivated.

The two species have narrow distribution areas and can be found only in the drainage basin of the Yangtze River in China. *Changium* is distributed in the area from the east to the middle subtropical zone of China while *Chuanminshen* is from the middle to the west. The distribution areas of the two species meet in the middle of the Yangtze basin, but barely overlap (Figure 1). Thus, the distribution of the two species shows ecological replacement. They should be geographically vicarious from an ecological viewpoint. Because the climate from east to west of the subtropical zone of China varies from humid to semi-humid (Wu, 1983), we suppose each species should fit into different water environments with different morphological adaptations and physio-ecological requirements, especially different demands for water; i.e. there would be niche partitioning between the two species.

To test the hypothesis, we designed an experiment on the appearance and plasticity of the physioecological and structural traits of the two species in response to different soil water statuses (Rajendrudu et al., 1997), to find out their demands for soil water and analyze their niche separation.

Although there are studies of geographically vicarious species, much of the work is on their systematics, morphology, anatomy, molecular biology, genetics (Liu et al., 2002), or paleobiology (Prado and Gribs, 1993). Some work has been done on the distribution patterns and their relationship to climate and water conditions (Prado and

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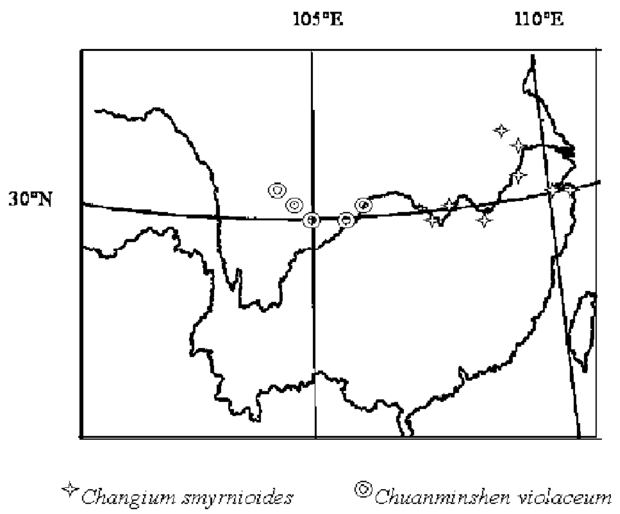

Figure 1. Distribution of *Changium smyrnioides* and *Chuanminshen violaceum.*

Gribs, 1993); however, little has been known about the physio-ecological reasons for the ecological replacement of the vicarious species. Our work can increase the understanding of the ecological mechanisms of vicarious distributions of the plant species and assist in the development of approaches to conserve the two endangered species.

Materials and Methods

Both species are winter species in the subtropical zone of the Yangtze basin of China, where the climate and soil environmental conditions are not too cool for plants. The main growth periods of the two species are winter and spring, and the seasonal climate should be the main factor limiting the physiological processes and growth of the species, and finally determining the distribution. In the period from late autumn to spring, the mean temperatures in the east and the west are similar while the west is significantly dryer with less precipitation (Figure 2).

Research was conducted at the plantation of Zhejiang University in the city of Hangzhou, eastern China (120º10´E, 30º15´N). Both species were cultivated in pots (height 14.5 cm and diameter of upper surface 17.5 cm) in January 2001, after the seeds germinated and the seedlings had reached 5 cm. Experiencing a growth season, *Chuanminshen* began dormancy in early June while *Changium* did so in mid-June. *Chuanminshen* began frondescing in late-September, and the treatments began in October 2001; *Changium* frondescence in mid-February 2002, and the treatments begin in early March 2002. The aim of the experiment was to provide the two species with the same treatments at the same life history stages. All treatments were carried out in a glass house with an open wall.

There were ten repetitions of three treatments, expressed by the relative soil water contents (RWC), which is the percentage of the soil water holding capacity (WHC) as follows: (1) Constant saturation (SS), replenished until 100% WHC whenever the RWC of samples dropped to 90% WHC due to evapotranspiration; (2) Alterative water (middle moist, AW_{50}), plants were not watered until the RWC dropped to 50% WHC; and (3) Alterative water (drought, AW_{20}), distilled water was added to saturation whenever RWC dropped to 20%. These treatments simulated field soil water conditions in which rainy and dry weather alternate: SS simulated waterside habitat, and AW_{50} and AW_{20} simulated soil moisture conditions with more or less intermittent precipitation, respectively.

Measurements of net photosynthetic rate (P_N) and transpiration (E) were carried out from 06:30 to 18:30 on clear days at the beginning of April, every hour in triplicate. P_N was measured using a CO_2 analyzer (GHX305A, Beijing,

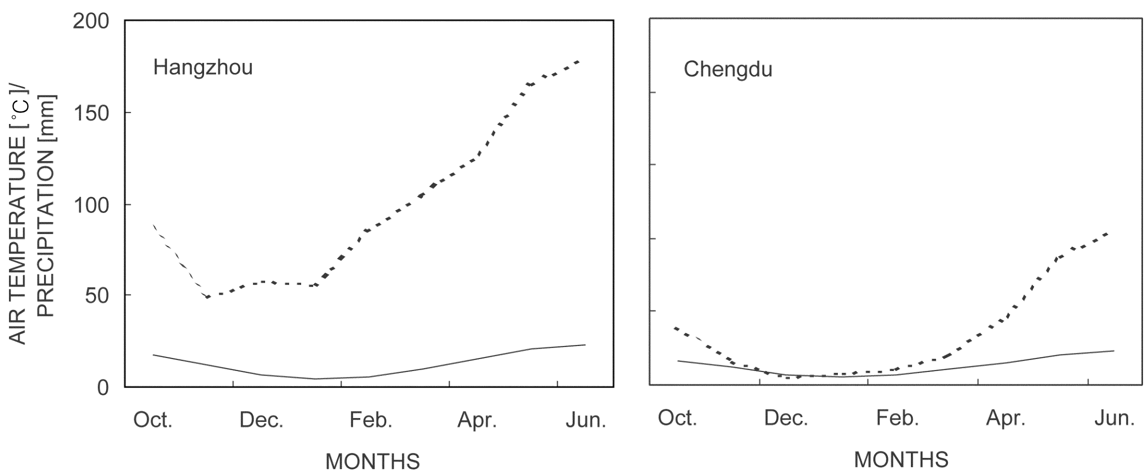

Figure 2. Combination of temperature (solid line) and precipitation (dot line) in east (e.g. Hangzhou) and west (e.g. Chengdu) subtropical zones of China, the distribution region of *Changium smyrnioides* and *Chuanminshen violaceum*. The drought period occurs when precipitation line falls below temperature line.

China-German cooperation) in the closed system. Diurnal mean photosynthetic rate (P_{Nmean}) was calculated by average the P_N of every hour from morning to afternoon. E of whole shoots were measured by weighting the whole pots, the upper surfaces of which were covered with plastic film to prevent evaporation from the soil,

$$E = (W_t - W_{t+1})/A$$

where W_t is the weight of pots the previous time, W_{t+1} is the weight the current time, and A is the total area of the leaves in pots. Diurnal mean transpiration rate (E_{mean}) was calculated by the average of the E of every hour. Water use efficiency (WUE) was calculated as P_N/E. Photosynthetically active radiation (PAR) above the leaf, air temperature (T_a), leaf temperature (T_l), and relative humidity (RH) were measured simultaneously with P_N. An admixture of acetones and ethanol (2:1) was used to distill chlorophyll, and then the absorbency of chlorophyll-a and chlorophyll-b were measured at 663 nm and 645 nm, respectively, with a 751 spectrophotometer (HP, Shanghai). Three individuals of every species were harvested from the three-replication pots. Before drying the samples in an oven at 80°C for at least 72 h, leaf area was determined with a portable area meter. Leaf area per unit leaf mass (specific leaf area; SLA), leaf area per unit of total mass (leaf area ratio; LAR), and leaf mass per unit of total mass (leaf mass ratio; LMR) were determined (Hunt, 1978). The differences between the traits were statistically analyzed with ANOVA in SPSS (8.0).

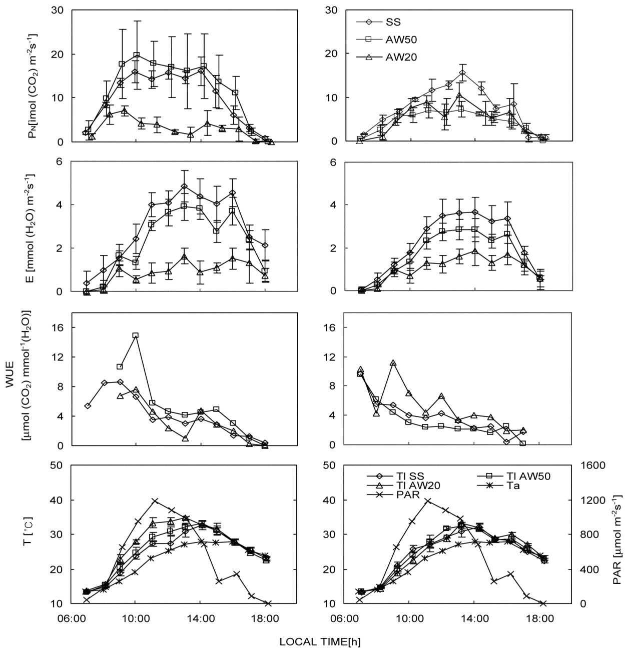

Figure 3. Diurnal variations of the net photosynthetic rate (P_N), transpiration (E), water use efficiency (WUE), photosynthetic photon flux density (PAR), leaf temperature (T_l) and air temperature (T_a) for *Changium smyrnioides* and *Chuanminshen violaceum* in different soil water statuses (SS, soil water near saturation constantly; AW_{50}, soil water content altered from saturation to 50% soil water holding capacity; AW_{20}, soil water content altered from saturation to 20% soil water holding capacity).

Results and Discussion

Diurnal Pattern of Photosynthesis, Transpiration and Water Use Efficiency in Response to Soil Water Status

Daily changes of photosynthesis differed between the species in the same soil water status (Figure 3). In SS, the P_N of *Changium* increased in the morning in response to PAR, peaked at 10:00, then did not respond to the increase of PAR and held steady until 14:00. In *Chuanminshen* the P_N increased more slowly than *Changium* and peaked at 13:00, showing a single peak curve. In dry soil (AW_{20}), the P_N of *Changium* showed double peaks (at 9:00 and 14:00) while the P_N of *Chuanminshen* fluctuated at midday (the peak was at 13:00). The diurnal curves of P_N of *Changium* in AW_{50} were close to those of SS while that of *Chuanminshen* in AW_{50} approached AW_{20}.

The diurnal variations of E of both species were similar. The values for *Chuanminshen* were lower than *Changium* in SS and AW_{50} and slightly higher than *Changium* in AW_{20}.

The E of *Changium* increased much more slowly than P_N in the morning in SS and AW_{50}, causing an increase in WUE of *Changium* in the early morning, and the P_N of *Changium* was not correlated with E ($P>0.05$). While the E increased simultaneously with P_N for *Chuanminshen* ($P<0.05$), that made WUE of *Changium* higher than *Chuanminshen* in the morning.

WUE of the two species had higher values and larger fluctuations in the morning than in the afternoon. The differences were more significant in the morning than in the afternoon among the treatments, especially for *Changium*.

The diurnal variation of P_N, E and WUE in response to soil water status indicates that the physiological traits of *Changium* change little when soil water is kept at a wet or medium wet level, but change significantly when water levels varied from medium wet to drought level conditions. In contrast, the physiological traits of *Chuanminshen* change little when soil water varied from medium wet to drought level conditions; i.e., *Chuanminshen* can keep a high physiological vigor at drought level conditions.

The differences between P_N and E among the three treatments in *Changium* outstrip those in *Chuanminshen*, indicating that *Changium* is more sensitive in response to soil water than *Chuanminshen* in photosynthesis and transpiration, while the two species did not show differences in WUE.

Daily Mean Photosynthesis, Transpiration, and Water Use Efficiency Responds to Soil Water Status

The P_{Nmean} of *Changium* showed a significant decrease when conditions changed from medium wet to drought level; in contrast, that of *Chuanminshen* showed an increase with a change from medium wet to drought level

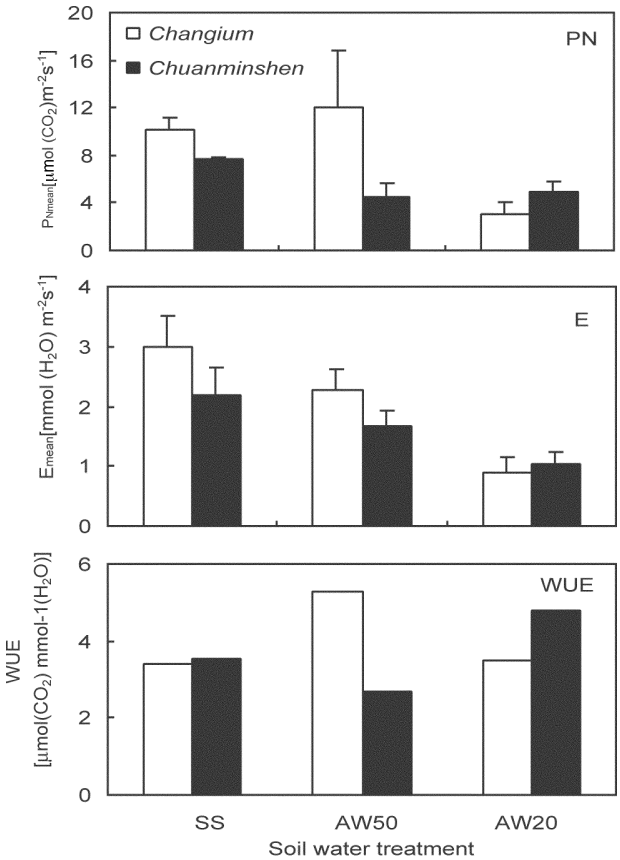

Figure 4. Daily mean net photosynthetic rate (P_{Nmean}), daily mean transpiration (E_{mean}) and water use efficiency (WUE) of *Changium smyrnioides* and *Chuanminshen violaceum* in different soil water statuses (legends as in Figure 3).

conditions. P_{Nmean} of *Changium* was similar in SS and AW_{50}, but that of *Chuanminshen* was similar in AW_{50} and AW_{20} (Figure 4). The P_{Nmean} of *Changium* was higher than that of *Chuanminshen* in SS and AW_{50}, but lower in AW_{20}.

The E_{mean} of two species was SS>AW_{50}>AW_{20}, entirely in response to soil water content. Like P_{Nmean}, the E_{mean} of *Changium* was higher than that of *Chuanminshen* in wet to medium wet soil, but lower than *Chuanminshen* in drought.

The highest daily mean WUE of *Changium* was in AW_{50} while the highest in *Chuanminshen* was in AW_{20}, with the smallest in AW_{50}. The WUE of *Changium* was nearly two times that of *Chuanminshen* in medium wetness, but was lower than *Chuanminshen* in drought. This indicates that a medium soil water status suits *Changium* best and that it has a lower tolerance than *Chuanminshen* for drought.

The coefficient variation of P_{Nmean} and E_{mean} of *Changium* (56%, 52%) was larger than that of *Chuanminshen* (30%, 35%) in three treatments, showing that the P_N of *Changium* had a higher phenotypic plasticity in response to soil water content than *Chuanminshen*.

Diurnal Pattern of Photosynthesis, Transpiration and Water Use Efficiency in Response to Light and Temperature

An increase in PAR and T_l brought a linear increase in P_N of *Changium* in wet to medium wet soil (SS and AW_{50}), and the response was AW_{50}>SS (Table 1). However, the P_N of *Changium* did not respond to PAR or T_l in drought. Subsection analysis showed that the P_N only responds to PAR (R^2=0.725**, n=24) below light saturation (PAR<300

Table 1. Relation between net photosynthetic rate (P_N) and photosynthetically active radiation (PAR), leaf temperature (T_l) in different relative soil water contents of *Changium smyrnioides* and *Chuanminshen violaceum*. Where the dependent variation is P_N, the independent variations are the other factors above. Correlation coefficients are shown only for the relations which are significant (P<0.05). ns: no significant.

Independent variations	Species	RWC	Constant (a)	Slope (b)	r^2	n
PAR	*Changium*	SS	2.108	0.012	0.727	52
		AW_{50}	3.328	0.016	0.567	52
		AW_{20}			ns	52
	Chuanminshen	SS	2.641	0.010	0.661	39
		AW_{50}	1.913	0.005	0.519	39
		AW_{20}	1.457	0.007	0.544	39
T_l	*Changium*	SS	-3.108	0.466	0.208	52
		AW_{50}	-4.471	0.616	0.190	52
		AW_{20}			ns	52
	Chuanminshen	SS	-8.739	0.639	0.477	39
		AW_{50}	-3.029	0.297	0.417	39
		AW_{20}	-5.299	0.399	0.428	39
T_a	*Changium*	SS			ns	52
		AW_{50}			ns	52
		AW_{20}			ns	52
	Chuanminshen	SS	-5.426	0.495	0.416	39
		AW_{50}	-2.675	0.269	0.385	39
		AW_{20}	-5.029	0.380	0.474	39

Table 2. Relation between transpiration rate (*E*) and photosynthetically active radiation (PAR), leaf temperature (T_l), relative humidity (RH) in different relative soil water contents of *Changium smyrnioides* and *Chuanminshen violaceum*. Where the dependent variation is P_N, the independent variations are the other factors above. Correlation coefficients are shown only for the relations which are significant (P<0.05). ns: no significant.

Independent variations	Species	RWC	Constant (a)	Slope (b)	r^2	n
PAR	*Changium*	SS	1.62	0.0026	0.442	48
		AW_{50}	1.01	0.0024	0.459	48
		AW_{20}	0.63	0.0005	0.108	48
	Chuanminshen	SS	0.85	0.0025	0.522	36
		AW_{50}	0.59	0.0020	0.573	48
		AW_{20}	0.60	0.0008	0.249	48
T_l	*Changium*	SS	-3.57	0.2849	0.762	48
		AW_{50}	-3.58	0.2547	0.735	48
		AW_{20}	-0.98	0.0811	0.446	48
	Chuanminshen	SS	-3.34	0.2394	0.686	36
		AW_{50}	-2.68	0.1887	0.715	48
		AW_{20}	-1.40	0.1060	0.585	48
RH	*Changium*	SS	7.28	-0.0721	0.587	48
		AW_{50}	6.03	-0.0630	0.541	48
		AW_{20}	2.25	-0.0229	0.428	48
	Chuanminshen	SS	5.63	-0.0581	0.486	36
		AW_{50}	4.37	-0.0454	0.499	48
		AW_{20}	2.72	-0.0282	0.499	48

μmol $m^{-2}s^{-1}$) and only to T_l (negative correlation, R^2= 0.287**, n=28) above light saturation, meaning that temperature stress occurs at higher temperatures in drought conditions.

In contrast to *Changium*, P_N of *Chuanminshen* responds to PAR and T_l in all three soil water statuses, and the degree of response was $SS>AW_{20}>AW_{50}$. It means that P_N of *Chuanminshen* still functions normally in the dry soil in which the physiological process of *Changium* has changed.

The *E* of both species responds to PAR and T_l (positive) and RH (negative) significantly and the slope of correlation was $SS>AW_{50}>AW_{20}$. In wet to medium wet conditions, *Changium* responds to the above three factors more sensitively than *Chuanminshen* but does just the opposite in drought conditions (Table 2).

The diurnal pattern of the main physiological traits suggests that the P_N of *Chuanminshen* has a higher tolerance to drought than that of *Changium*.

Morphology and Growth Traits of the Two Species

Our investigation concluded both species to be nearly identical in morphology from the first to the third euphylis of the seedling, and then the leaves become different from the fourth euphylis on, i.e. they are almost the same in the early stages of individual development and differ later. We suggest that the systematic development of both *Changium* and *Chuanminshen* is very close.

Changium resides under the forest gap caused by defoliated trees in winter. Individuals finish vegetative growth after re-foliation of deciduous trees, so as to avoid shading and competition with other plants (Busso et al., 2001). Such a pattern of *Changium* could be seen as a competition-avoidance strategy through temporal niche partition. With higher SLA, LAR, and chloral content (Table 3), *Changium* uses irradiation fully in carbon accumulation in a short time in compensation for its short growth period. In humid environments, the plant often has a larger SLA and LAR than in drought (Fownes, 1999; Gurnier et al., 2001). The humid climate in *Changium'*s distribution area, the east to middle subtropical zone of China, ensure it a larger SLA and LAR. *Chuanminshen* has a lower SLA and LAR, adapts to the dryer environment in the west, and has a longer growth period to meet the requirement of carbon accumulation.

Conclusions

The two species, *Changium smyrnioides* and *Chuanminshen violaceum* have similar structural charac-

Table 3. Specific leaf area (SLA, dm^2 g^{-1}), leaf area ratio (LAR, dm^2 g^{-1}) and leaf mass ratio (LMR, g g^{-1}), chlorophyll content in fresh leaf weight (Chl, mg g^{-1}) and the ratio of Chl-a and Chl-b (a/b) of *Changium smyrnioides* and *Chuanminshen violaceum*. Mean ± SE, n=9-30. Differences of the traits between the two species are all significant (p<0.01).

Species	SLA	LAR	LMR	Chl	a/b
C. smyrnioides	2.10±0.57	0.68±0.17	0.35±0.08	1.73±0.23	1.37±0.28
C. violaceum	1.82±0.39	0.24±0.07	0.16±0.05	1.28±0.07	2.01±0.07

ters and functional intensity, such as the net photosynthetic rate (P_N), transpiration (E), water use efficiency (WUE), and the fact that each is endangered. Meanwhile, these two species showed different plasticity for the main physiological process and their morphological traits respond differently to different soil water statuses. *Changium smyrnioides* demands medium to wet soil conditions while *Chuanminshen violaceum* adapts readily to droughty soil. The differences in the adaptation of physiology and morphology to the water environment cause niche partitioning, part of the reason these two species are geographical replacements in distribution. The results indicate that, at least, the mechanism and the approach of conservation for the two species should be similar.

Acknowledgements. We are grateful for the funding provided by the National State Key Basic Research and Development Plan (973) (No. G2000046805).

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土壤水分狀況對兩瀕危種明黨參和川明參生理生態的影響及其生態替代

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傘型科的明黨參（*Changium smyrnioides* Wolff）和川明參（*Chuanminshen violaceum* Shen et Shan）都只限於分佈在中國的長江流域，分佈範圍很窄。明黨參分佈在亞熱帶東部到中部，川明參則只分佈在中部至西部，在中部幾乎重疊。由於兩植物分佈區的氣候從濕潤到半濕潤過渡，我們設計實驗查明其對土壤水分的要求，並通過其生理生態特徵和結構特徵對土壤水分的回應分析其生態位分離。實驗結果表明，兩種植物有相似的結構特徵和功能強度；但兩個種光合、蒸騰和水分利用效率在 3種土壤水分條件下的日變化、日平均及其與光強和溫度的關係表明川明參比明黨參更耐乾旱。形態學特徵也顯示明黨參適於中等到濕潤的土壤環境，而川明參適應於較乾旱的土壤環境。生理和形態特徵對土壤水分環境適應性的差異應是兩植物成為地理替代種的部分原因。實驗結果表明，這兩種植物在保護的機理和途徑上應該是相似的。

關鍵詞：生態替代；瀕危種；生長；形態；光合；亞熱帶；蒸騰；水分利用效率。