Bot. Bull. Acad. Sin. (2004) **45:** 229-236

Phenotypic plasticity of *Mosla chinensis* and *M. scabra* (Labiatae) response to soil water status

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(Received October 8, 2003; Accepted April 1, 2004)

Abstract. The growth and architectural plasticity of *Mosla chinensis* Maxim. in response to soil water status were compared with the congeneric plant, *Mosla scabra* (Thunb.) C. Y. Wu et H. W. Li. Two-week-old seedlings were exposed to five levels of soil water for a 6-week period. The results indicated that: an individual's total mass, root mass, apical height, basal diameter, accumulative branch length and branch fresh weight / dry weight ratio (FW_B / DW_B) of both species had high plasticity in response to soil water content ($P < 0.05$), and the plasticity of these traits in *M. scabra* is mostly higher than in *M. chinensis*. The leaf mass ratio (LMR), specific leaf area (SLA), root mass ratio (RMR), and root / shoot ratio (R / S) of both species had low plasticity. Furthermore, leaf mass, branch mass, branch mass ratio (BMR), and branch length ratio (BLR) had high plasticity ($P < 0.05$) in *M. chinensis* but not in *M. scabra* ($P > 0.05$) while branch number exhibited contrary trends. In response to soil water, *M. scabra* adjusted the traits of total mass and size, in terms of a bigger PI, more than *M. chinensis* while *M. chinensis* only adjusted partial branch and root traits, such as BMR, BLR, FW_B / DW_B, RMR and R / S, more than *M. scabra*. The optimum water niches (OWN) of both *M. chinensis* and *M. scabra* are from 40% soil water holding capacity (WHC) to constant saturation, but *M. chinensis* is only found in relatively dry environments while *M. scabra* is distributed from dry to wet environments in the field, so the actual water niche (AWN) was separated from the OWN in *M. chinensis*, but not in *M. scabra*. *Mosla chinensis* grew slower and remained smaller than *M. scabra* and other neighbor species in the field, and it therefore had no competitive superiority in the community. *Mosla scabra* was very competitive because of its higher yield and taller growth.

Keywords: Interspecific difference; *Mosla chinensis*; *Mosla scabra*; Phenotypic plasticity; Relative soil water content; Water niche.

Introduction

Plants of the same genotype can produce different phenotypes in different environments, a property called phenotypic plasticity (Sultan, 2001). Adaptive phenotypic plasticity is the predicted evolutionary response to environmental factors, such as soil moisture in plant habitats (Sultan and Bazzaz, 1993). Differences among species in plasticity patterns may contribute to their differences in ecological breadth with respect to soil factors and climatic conditions (Cook et al., 1980). Bell and Sultan (1999) investigated how two *Polygonum* species altered their root growth and deployment over time in response to different soil moisture conditions, and they found that species differences in plastic response to specific moisture conditions would correspond to differences in their field distribution. Ryser and Eek (2000) reported two congeneric grass species with contrasting shade tolerance responded to low resource availability, and they indicated that interspecific differences in phenotypic plasticity were crucial factors for survival and distribution.

It is well known that the distribution and abundance of most plant species greatly depend on water supply (Schulze et al., 1987). The influence of water availability on plant performance in natural and managed ecosystems has been of great concern in plant physiological ecology and related disciplines (Schulze et al., 1987). Plant growth may decrease in dry soils due to tissue dehydration as well as reduced mineral availability (Fitter and Hay, 1993). Conversely, flooding also reduces plant growth by decreasing the availability of oxygen to roots (Etherington, 1984; Ernst, 1990). There have been a number of studies on the phenotypic plasticity of plants in response to the water supply (Stevens et al., 1997; Šrùtek, 1997; Bell and Sultan, 1999; Clifton-Brown and Lewandowski, 2000; Kotowski et al., 2001), including a lot of studies elaborating the effect of plasticity on local traits for individuals, e. g., leaf and root traits (Bell and Sultan, 1999; Clifton-Brown and Lewandowski, 2000; Ryser and Eek, 2000).

Mosla chinensis Maxim., distributed in east, south, middle and southwest China (Fang et al., 1986), is a medicinal herb which contains many volatile oils and has a long history of use in China for rheum and heliosis (Zhang, 1989; Fang et al., 1986). Many studies about the medicinal components and physiology of *M. chinensis* have appeared (Zhang and Xu, 1988; Zheng et al., 1996; Zhou et al., 1996, 1998; Pan et al., 1997), but ecological studies of it are rare (Ge et al., 1999; Ge and Chang, 2001; Guan et al., 2003). Though its distribution in the field is wide, *M. chinensis* has only a few individuals in each population,

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*Corresponding author. Tel & Fax: +86 571 8797 2193; E-mail: jchang@mail.hz.zj.cn so it could only be a concomitant, not a dominant species, in the community. Guan et al. (2003) found that *M. chinensis* normally lives in droughty environments with thin soil and more detritus such as at roadsides or around the rocks with plenty sunlight.

Mosla scabra (Thunb.) C. Y. Wu et H. W. Li occurs as a common weed, distributed widely in China, Japan and Vietnam (Fang et al., 1986). It is also a medicinal herb (Fang et al., 1986). In the field, *M. scabra* is distributed in dry to moist habitats. Few studies on *M. scabra* have been done either (Zhang and Xu, 1988).

Both *Mosla* species suffer from similar water stress in slightly dry environments, where *M. scabra* can become weedy and dominant (outnumbering any other species in the community) (Guan et al., 2003) while *M. chinensis* is a concomitant species. What factors result in the different abundance between these two *Mosla* species? Here we present a comparative study to probe the adaptive mechanisms of these two *Mosla* species using the phenotypic plasticity patterns in response to different soil water conditions, aiming to understand the relationship between the adaptive mechanism and field abundance.

Materials and Methods

Plants

Research was conducted at the plantation of Zhejiang University, Hangzhou (120°10'E, 30°15'N), eastern China. *Mosla scabra* and *M. chinensis* germinated at the end of April and early May, respectively. After seedlings had grown for two or three weeks, we transplanted 120 seedlings of each species into pots at May 2000. The two hundred and forty plants were transplanted into pots 17 cm in height and 15 cm in diameter. Pots with the same soil were placed in a greenhouse, which had only a roof of colorless plastic but no wall, in an attempt to replicate the temperature and irradiation conditions of the outside. The soil was a mixture of 30% sand soil, taken from a field in which *Mosla* grows and 70% loamy, fine garden soil, which included 10% humus. Each species used forty pots, with three plants in each pot. All treatments began from saturated soil water content on May 31, 2000.

Experimental Design

There were five treatments, each of which had twenty-four plants for repetition, interpreted in terms of relative soil water content (RWC) and measured in terms of soil water holding capacity (WHC) (Gituru et al., 2002; Misra and Tyler, 1999). The testing in dry soil base was 50.39%. For the 1st treatment, soil water was maintained as constant saturation, occasionally dropped to 90% WHC. For the 2nd treatment, plants were not watered unless the RWC dropped to 80% WHC. Similarly, distilled water was added to saturation whenever WHC dropped to 60%, 40%, and 20% in the 3rd, 4th and 5th treatments, respectively. The five treatments were defined as constant saturation (CS), W_{80}, W_{60}, W_{40} and W_{20}, respectively (Table 1). Our goal in the above treatments was to simulate field soil water conditions in which rainy and fine days alternate. To prevent water leakage from the bottom of the pots, plants were watered slowly so that water would be fully absorbed by the soil. Watering was performed around 6:00 p.m. everyday.

Individuals were harvested after 6 weeks of growth under the treatments. Apical height, basal diameter, branch number, and accumulative branch length of the individuals were measured before harvest. Plant samples were categorized into roots, branches, and leaves. Fresh weights and leaf area were measured immediately after harvest. Leaf areas of samples were determined using a leaf area meter (Li-cor-3000, Lincoln, NE, USA). The mass of every component was determined after oven-drying at 80°C for at least 72 h.

The following parameters of the two *Mosla* species were determined according to Hunt (1978), Bell and Sultan (1999), and Ryser and Eek (2000): leaf mass ratio (LMR, leaf mass / total mass), specific leaf area (SLA, leaf area / leaf mass), branch mass ratio (BMR, branch mass / total mass), branch length ratio (BLR, branch length / total mass), branch fresh weight to dry weight ratio (FW_B/DW_B), root mass ratio (RMR, root mass / total mass), and root: shoot ratio (R/S, root mass / shoot mass). Biomass allocated parameters such as (LMR, BMR, RMR and R / S) can reflect the functional plasticity for plant response to soil water (Sultan, 2001). Generally, a bigger SLA means more water rising per leaf area per leaf mass, and BLR can reflect the extension of branch competition for light in response to soil water (Ryser and Eek, 2000). FW_B / DW_B is an index of water deposition in the plant branch (Schulze et al., 1987). A plasticity index (PI) of phenotypic ranging from zero to one was calculated for each variable and species as the difference between the minimum and the maximum mean values among the five water treatments divided by the maximum mean value (Valladares et al., 2000). Mean phenotypic plasticity was calculated for each species by averaging the indices of plasticity obtained for each of the variables.

Table 1. The five soil water treatments for *Mosla chinensis* and *M. scabra*.

Soil water	Treatments				
	W_{20}	W_{40}	W_{60}	W_{80}	CS
RWC (%)	20-100	40-100	60-100	80-100	90-100
AWC (%)	7.48-50.39	18.21-50.39	29.43-50.39	33.87-50.39	39.33-50.39

RWC: relative soil water content (percentage of soil water holding capacity); AWC: actual soil water content (dry soil base).

Statistical Analysis

Statistical analysis was conducted using Microsoft Excel 2000 and SPSS 8.0 for Windows. The means and standard errors (SE) of every trait were calculated. Interspecific differences and influence of treatments were tested with a nested ANOVA using the General Linear Model (GLM) with species or (and) treatments. In order to clearly show the differences among treatments, we used histograms instead of lines to present data in Figures 1 and 2.

Results

Overall Patterns of Plasticity

Both *M. chinensis* and *M. scabra* had the highest biomass at W_{60} and the lowest at W_{20} (Figure 1), and significant growth limitation was observed in both species at W_{20} ($P < 0.05$; Table 2). However, the mass of *M. chinensis* at W_{20} was 30% of the mass at W_{60}, while the mass of *M. scabra* at W_{20} was only 21% of W_{60}. Even so, *M. scabra* always had higher biomass than *M. chinensis* at all water

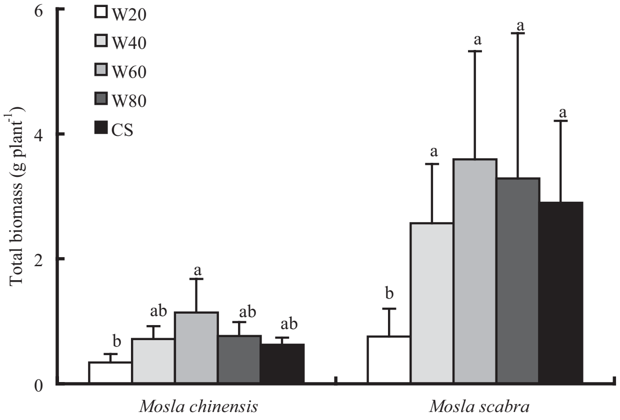

Figure 1. Individual total mass of *Mosla chinensis* and *M. scabra* (Mean ± SE) at five soil water statuses. W_{20}: 20% water holding capacity (WHC); W_{40}: 40% WHC; W_{60}: 60% WHC; W_{80}: 80% WHC; CS: constant saturation.

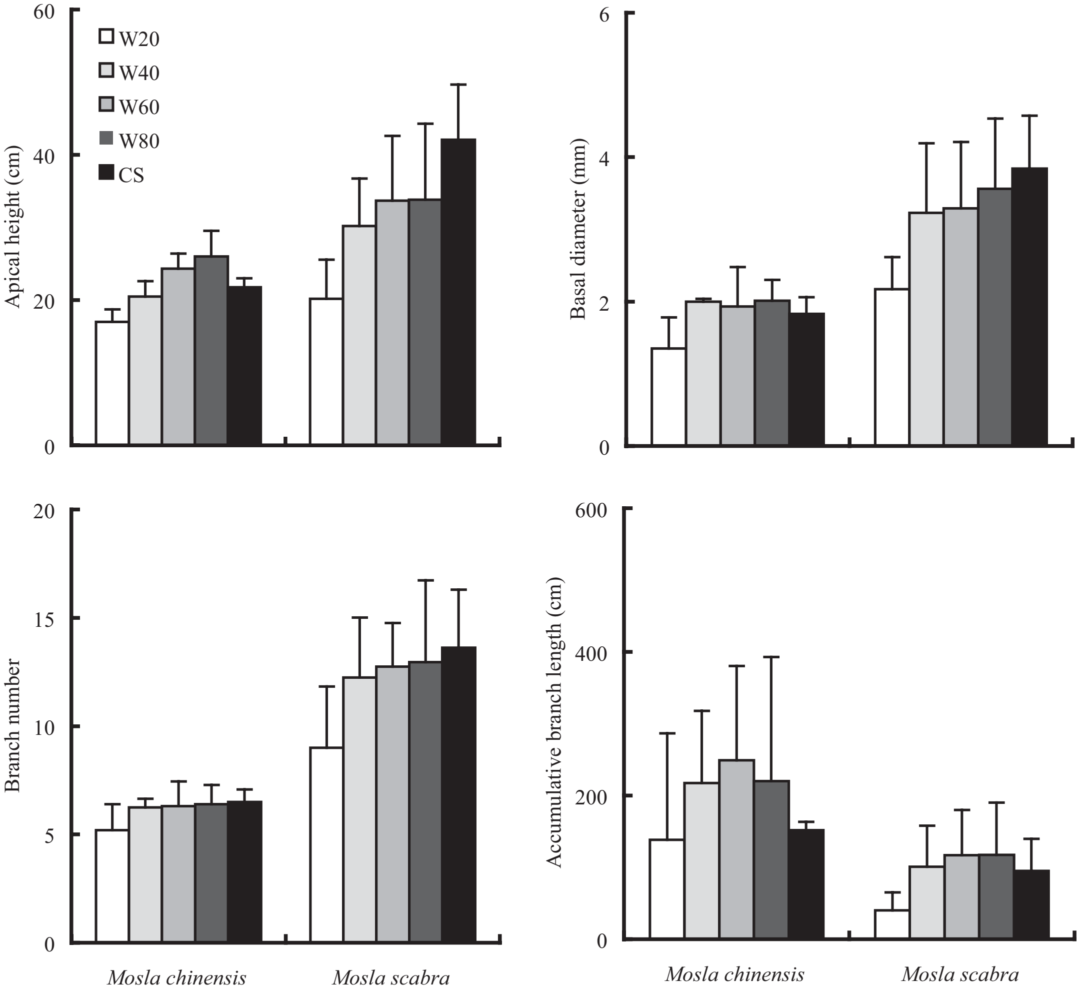

Figure 2. Morphological traits of *Mosla chinensis* and *M. scabra* (Mean ± SE) at five soil water statuses. W_{20}: 20% water holding capacity (WHC); W_{40}: 40% WHC; W_{60}: 60% WHC; W_{80}: 80% WHC; CS: constant saturation.

statuses. There were no significant differences ($P > 0.05$) in mass among the W_{40}, W_{60}, W_{80} or CS in either species. The PI of total biomass of *M. chinensis* was lower than that of *M. scabra* (Table 2).

Almost all architectural traits—including apical height, basal diameter and branch number of *M. scabra*—increased with increasing RWC, the only exception being accumulative branch length, which increased from W_{20} to W_{80} and then decreased at CS (Figure 3). All architectural traits of *M. chinensis* were the lowest at W_{20}, and the apical height, basal diameter, and branch number had the highest values at W_{80}, but the accumulative branch length was highest at W_{60}. *Mosla scabra* always had higher apical height, more branch number, and less accumulative branch length than *M. chinensis*, and the branch length of *M. scabra* degressed from nether to top to form a compact crown like a tower while *M. chinensis* formed an incompact crown like a sphere.

The PI of all architectural parameters of *M. scabra* was higher than that of *M. chinensis* (Table 2), indicating that

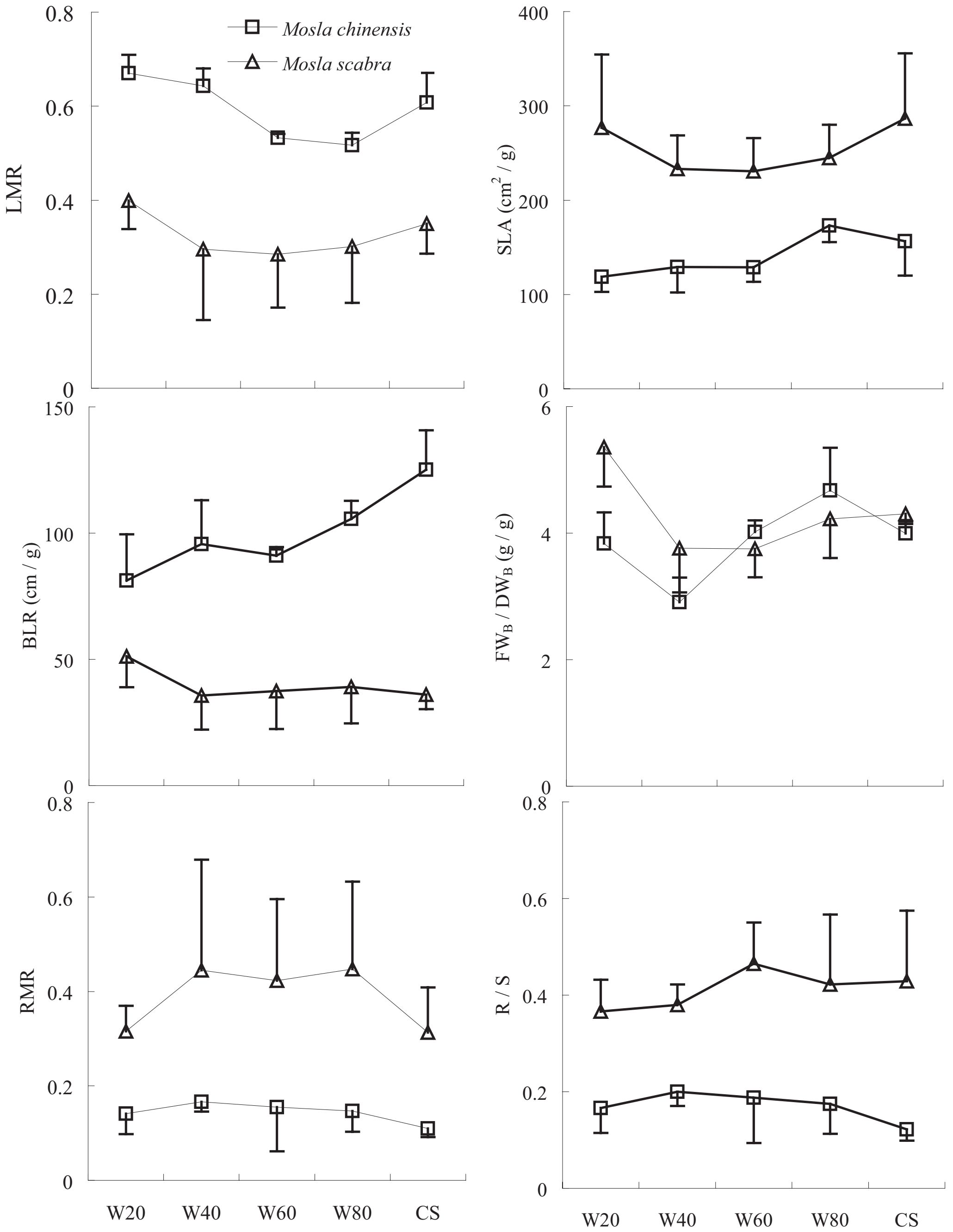

Figure 3. Growth parameters of *Mosla chinensis* and *M. scabra* (Mean ± SE) at five soil water statuses. LMR: leaf mass ratio; SLA: specific leaf area; BLR: branch length ratio; FW_B/DW_B: branch fresh weight / branch dry weight; RMR: root mass ratio; R / S: root shoot ratio.

Table 2. One-way ANOVA by rank for the effect of water on all dependent variables of *Mosla chinensis* (Mc) and *M. scabra* (Ms).

Variable source	PI (Mc)	Post-hoc					PI (Ms)	Post-hoc				
		1	2	3	4	5		1	2	3	4	5
TM	0.70	b	ab	a	ab	ab	0.79	b	a	a	a	a
LM	0.79	b	a	a	b	b	0.68	b	ab	a	ab	ab
BM	0.73	b	ab	a	a	ab	0.75	b	ab	a	a	a
RM	0.65	c	ab	a	b	bc	0.82	b	a	a	a	a
AH	0.35	b	ab	ab	a	ab	0.52	c	b	b	b	a
BD	0.33	b	a	a	a	a	0.44	b	a	a	a	a
BN	0.20	b	ab	ab	ab	a	0.34	b	a	a	a	a
ABL	0.44	b	ab	a	a	ab	0.66	b	a	a	a	a
LMR	0.23	a	a	ab	b	ab	0.29	a	a	a	a	a
SLA	0.11	b	b	b	a	ab	0.31	b	ab	ab	ab	a
BMR	0.44	b	ab	ab	a	a	0.32	b	ab	ab	b	a
BLR	0.35	b	b	b	ab	a	0.30	a	b	b	b	b
FW_B / DW_B	0.38	a	b	a	a	a	0.30	a	b	b	b	b
RMR	0.38	a	a	a	a	a	0.30	a	a	a	a	a
R / S	0.39	a	a	a	a	a	0.32	a	a	a	a	a
Mean	0.43	-	-	-	-	-	-0.48	-	-	-	-	-

Post-hoc shows the results of Duncan's honestly differences. TM: total mass; LM: leaf mass; BM: branch mass; RM: root mass; AH: apical height; BD: basal diameter; BN: branch number; ABL: accumulative branch length; LMR: leaf mass ratio; SLA: specific leaf area; BMR: branch mass ratio; BLR: branch length ratio; FW_B / DW_B: branch fresh weight / branch dry weight; RMR: root mass ratio; R / S: root shoot ratio. PI: plasticity index. In post- hoc: relative water content, 1: 20% WHC; 2: 40% WHC; 3: 60% WHC; 4: 80% WHC; 5: constant saturation.

M. scabra can better regulate its architecture than *M. chinensis* in response to soil water status.

Mass Allocation

The LMR of the two species had the same trends with increasing RWC: it decreased firstly from W_{20} to W_{60}, then ascended from W_{60} to CS, the highest value appeared at W_{20}. However the SLA of the two species followed different trends: that of *M. scabra* decreased from W_{20} to W_{60}, and then increased from W_{60} to CS while that of *M. chinensis* increased from W_{20} to W_{80}, then decreased from W_{80} to CS. With increasing RWC, the BLR of *M. chinensis* increased, but *M. scabra* decreased, indicating that with increasing soil water availability and at the same level of biomass yield, *M. chinensis* produced longer branches than *M. scabra*. At the lower RWC (W_{20} and W_{40}), *M. scabra* had higher FM_B / DM_B than *M. chinensis*. *Mosla scabra* had low RMR at W_{20} and CS, and similar values in the other three treatments; *M. chinensis* had a similar RMR from W_{20} to W_{80}, the lowest at CS. With increasing RWC, the R/S of *M. chinensis* decreased, but *M. scabra* increased.

The PIs of BMR, BLR, FM_B/DM_B, RMR, and R/S of *M. chinensis* were all larger than that of *M. scabra* (Table 2), indicating that *M. chinensis* could better adjust branch and root traits than *M. scabra* in response to soil water status.

Interspecies Differences

In all treatments, the total biomass, apical height, basal diameter, and branch number of *M. chinensis* were lower than that of *M. scabra*, indicating that the adaptation of *M. scabra* is better than *M. chinensis*. *M. chinensis* always had higher accumulative branch length, LMR and BLR, lower RMR, SLA, and R/S than *M. scabra* in all treatments (Table 3). Furthermore, leaf mass, apical height, basal diameter, LMR, SLA, and RMR showed significant differences between two species ($P<0.05$).

Leaf mass, branch mass, BMR, and BLR had high plasticity ($P<0.05$; Table 2) in *M. chinensis* but not in *M. scabra* ($P>0.05$) in response to soil water while branch number showed contrary trends.

Discussion

General Phenotypic Plasticity

Water is an important factor restricting plant growth (Schulze et al., 1987). Analyzing plant growth and architecture traits is an approach to understand how plants adapt to soil water content changes (Stevens et al., 1997). In the present study, *M. chinensis* and *M. scabra* each displayed traits of considerable phenotypic plasticity in response to soil water variety, such as total biomass accumulation, root mass, branch fresh weight / branch dry weight (FW_B / DW_B) and architectural traits. Plants can adapt to various water environments with these adjustments (Bell and Sultan, 1999).

The phenotypic plasticity index of *M. chinensis* was lower than that of *M. scabra*. *Mosla chinensis* mainly adjusts plasticity of branch and root traits in response to soil water while *M. scabra* mainly adjusts plasticity of total biomass and architectural traits, such as apical height, basal diameter, branch number, and accumulative branch length.

Table 3. *F* and *P* values of General Linear Model (Multivariate) for the morphological parameters measured with the factors of species and treatments.

Parameter	Species (df = 1)		Treatments (df = 4)		S × T (df = 4)	
	F	P	F	P	F	P
LM	5.081	0.033*	0.21	0.931ns	0.734	0.577ns
BM	1.323	0.26ns	0.247	0.909ns	0.312	0.867ns
RM	2.185	0.151ns	0.294	0.879ns	0.456	0.767ns
A	17.495	<0.001***	3.577	0.018*	1.562	0.213ns
BD	24.806	<0.001***	2.39	0.076ns	0.299	0.876ns
BN	1.935	0.176ns	3.823	0.014*	1.244	0.316ns
ABL	3.434	0.075ns	1.528	0.222ns	0.238	0.914ns
LMR	21.726	<0.001***	0.503	0.736ns	0.528	0.716ns
SLA	28.059	<0.001***	1.021	0.414ns	0.692	0.604ns
BMR	0.702	0.409ns	2.225	0.093ns	0.726	0.582ns
BLR	86.063	<0.001***	7.996	0.001**	13.807	0.001**
FW_B / DW_B	1.918	0.177	4.264	0.008**	4.186	0.009**
RMR	21.173	<0.001***	1.834	0.151ns	0.423	0.791ns
R / S	0.408	0.671ns	2.711	0.059	0.038	0.848ns

In order to avoid the difference between the sizes of the individuals of two species, plant total dry mass was used as covariate. LM: leaf mass; BM: branch mass; RM: root mass; AH: Apical height; BD: basal diameter; BN: branch number; ABL: accumulative branch length; LMR: leaf mass ratio; SLA: specific leaf area; BMR: branch mass ratio; BLR: branch length ratio; FW_B / DW_B: branch fresh weight / branch dry weight; RMR: root mass ratio; R / S: root shoot ratio. Significance values: *: P<0.05, **: P<0.01, ***: P < 0.001, ns: not significant.

Optimum and Actual Water Niche

Both *M. chinensis* and *M. scabra* grew well from 40% water holding capacity to constant saturation, for they appeared to have higher biomass and bigger plant sizes at these water statuses. In the field, *M. chinensis* is mainly found in quite arid environments with the relative soil water content around 20% of water holding capacity (Guan et al., 2003), meaning that the optimum and actual water niches are separated in *M. chinensis*. Meanwhile, *M. scabra* is distributed from arid environments (like those of *M. chinensis*) to moist environments (beside water) in the field (Fang et al., 1986), suggesting that the actual water niche can meet the optimum one in *M. scabra*.

Inter-Specific Phenotypic Plasticity Differences and Ecological Consequences

Root mass ratio (RMR) and root shoot ratio (R/S) are crucial indices of drought tolerance (Schulze et al., 1987). Higher RMR and R / S means more mass transforming into root to absorb water from the soil, which can contribute to better drought tolerance. *Mosla chinensis* had a higher RMR and R / S than *M. scabra* at low water status, and *M. chinensis* can evidently tolerate more drought.

Though *M. chinensis* can tolerate drought in many traits, it was observed to have lower biomass and smaller size than *M. scabra* and other neighbor species (Guan et al, 2003), making it less competitive in capturing sunlight. The only advantage *M. chinensis* has in competing for sunlight is that the branch length ratio (branch length per total biomass, BLR) is higher than in *M. scabra*. That might make it extend the branches to get more sunlight at the lower layer and to maintain survival. However, little sunlight is available at the lower layer when all the neighbors grow higher than it after late spring. Evasive strategies like this may be the main reason *M. chinensis* becomes rare and is a concomitant species.

At a low water status, *M. scabra* can transform its water supply into biomass more efficiently than *M. chinensis*. It produced more biomass, higher apical height, bigger basal diameter, much higher branch number, less accumulative branch length, and less branch length per branch mass (BLR), forming a much more compact tower crown than *M. chinensis* most neighbor species in the community. That is a superior adaptation feature and allows a plant growing higher than its neighbors in a dry environment to acquire more sunlight (Ryser and Eek, 2000; Sultan, 2001), but it cannot grow higher than some grasses in a wet environment, and may be a reason *M. scabra* can be the dominant species in a dry but not in a wet environment.

Acknowledgement. We thank the NSFC for its financial support (No. 39970058).

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華薺苧（*Mosla chinensis*）和石薺苧（*Mosla scabra*）回應不同水分狀態的表型可塑性

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本文比較研究了華薺苧（*Mosla chinensis* Maxim.）和同屬植物石薺苧（*Mosla scabra*（Thunb.）C. Y. Wu et H. W. Li）的生長和形態特徵回應水分條件的表型可塑性。萌發兩周後的幼苗在 5種水分條件下處理 6周左右。處理條件是類比野外自然降水，分別為：持續飽和、100%-80% 田間持水量（water holding capacity, WHC）、100%-60% WHC、100%-40% WHC 以及 100%-20% WHC（分別類比不同的降雨間隔期）。結果表明：兩個物種的總生物量、根生物量、株高、基莖粗、累加分枝長和枝鮮／幹重比在回應不同的相對土壤含水量時都表現出高的表型可塑性，而且石薺寧的這些特徵的表型可塑性大部分大於華薺寧；但是兩個物種的葉生物量比（leaf mass ratio, LMR）、比葉面積（specific leaf area, SLA）、根生物量比（root mass ratio, RMR）和根冠比（root / shoot, R / S）則表現出低的可塑性。此外，葉生物量，枝生物量，枝生物量比（branch mass ratio, BMR）在華薺寧中表現出高可塑性，但在石薺寧中則表現出低可塑性，分枝數正相反。石薺寧更多地通過生物量和植株大小的可塑性來回應水分，而華薺寧則通過枝和根特徵的少量可塑性來回應水分。兩個物種的最適水分生態位為 40% WHC 到飽和水分。華薺苧在乾旱條件下生長緩慢，植株矮小，使它在野外群落中不具有競爭優勢；而石薺苧則以相對較高的生物量和高大的植株，在群落中具有競爭優勢。

關鍵詞：種間差異；華薺苧；石薺苧；表型可塑性；土壤相對含水量；水分生態位。