

# Growth responses of two *Mosla* species to soil nitrogen and water supply

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**ABSTRACT.** The different responses to growth condition changes due to nitrogen deposition and rainfall variability among congeneric species may alter their differentiation pattern. We grew two *Mosla* species (Lamiaceae) under different nitrogen and water conditions. Under waterlogging, the two species showed similar positive growth responses to high nitrogen supply, implying potential chances to extend their populations in very wet habitats. However, under the wet and relatively dry conditions, *M. dianthera* was less tolerant to high nitrogen (biomass of *M. dianthera* was suppressed by high nitrogen more remarkably than that of *M. cavaleriei*) but more tolerant to nitrogen limitation than *M. cavaleriei* (with the decrease in water supply, root mass ratio of *M. dianthera* was increased by nitrogen limitation more noticeably than that of *M. cavaleriei*). Therefore, in relatively dry habitats, soil nitrogen addition might be unfavorable for *M. dianthera*.

**Keywords:** Differentiation; Habitat; Morphology; *Mosla cavaleriei*; *Mosla dianthera*; N deposition.

## INTRODUCTION

Plant species are experiencing global environmental changes including increasing nitrogen (N) input into soils due to deposition (Moore et al., 2004) and altered precipitation regimes (Geßler et al., 2007). Each species has its unique niche and environmental optimum. Thus, the responses to changes in growth conditions possibly differ among species. For instance, rare species are more susceptible to N fertilization than abundant species (Suding et al., 2005). The different responses among species co-occurring in one ecosystem bring changes in ecosystem composition (Suding et al., 2005), which is studied extensively. However, less attention is paid to species belonging to phylogenetic groups, though the different responses among closely-related taxa may change the differentiation pattern. Moreover, for a given species, the combination of current status of existence with its special response may determine its fate in the context of global environment changes.

The genus *Mosla* Buch.-Ham. ex Maxim. (Lamiaceae) is very suitable for studying the responses of closely-related species to changing growth conditions. Most

species in the genus are mainly distributed in South and East China, the most likely origin of the genus (Zhou, 1995). All species are annual herbs and reproduce through seed dispersal. In the main distribution areas, plants of the genus are experiencing environmental changes. The maximum of N deposition rates in South and East China reaches 64 kg N ha<sup>-1</sup> yr<sup>-1</sup> (Lu and Tian, 2007). Simultaneously, the frequencies of intense rainfalls and the annual precipitation are increasing, but the annual rainy days are decreasing in these areas (Qian et al., 2007). *Mosla cavaleriei* Lévl. and *M. dianthera* (Buch.-Ham. ex Roxb.) Maxim. are included in this study. These two species have the greatest morphological and genetic similarities in the genus (Zhou, 1995), but they differ in their current status of existence. *M. cavaleriei* is limited to wet and fertile habitats, where it is subordinate in its communities; *M. dianthera* is found in habitats with relatively low N concentration and diverse soil water status and is frequently dominant in its communities. The questions asked in this study are (1) whether the two congeneric species with similar morphology and genetics but different current status of existence respond differently to changes in growth conditions and (2) whether the differences in responses to soil N between species are related to the N status in their natural habitats. This may aid us to predict the effects of global environmental changes on closely-related taxa.

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## MATERIALS AND METHODS

### Plant materials and cultural conditions

Major habitats of the two *Mosla* species are hilly roadsides, forest edges, and brims of streamlets, where the soils are usually less than 10 cm thick. Therefore, we used pots (12 cm diameter, 9 cm height) to cultivate the plants in this study. The pots should not limit the root growth of the two species substantially compared with fields. In natural habitats of *M. cavaleriei* and *M. dianthera*, the alkali-hydrolyzable N concentration in soils is in the range of 150-350 mg kg<sup>-1</sup> and 50-270 mg kg<sup>-1</sup>, respectively. Thus, we designed four levels of N concentration to simulate the different N status in habitats of the two species. Besides, constant waterlogging and discontinuous watering were used to respectively simulate the constant stream at brims of streamlets and intense rainfalls followed by many non-rainfall days in nature.

In October 2006, we collected seeds of *M. cavaleriei* and *M. dianthera* from natural populations in Yongjia County (120.78° E longitude, 28.48° N latitude), Zhejiang Province in East China. After the air-dried seeds were placed in a refrigerator (0-4°C) for one month to break dormancy, the seeds were germinated in trays with peat (Metro Mix 290) on 20 April 2007. The trays were placed in growth chambers with a 16 h photoperiod, day/night temperatures of 25/15°C, and 70-80% relative humidity at an irradiance of about 25 μmol photon m<sup>-2</sup> s<sup>-1</sup> (photosynthetically active radiation, λ= 400-700 nm). After emergence, the seedlings were watered with full strength Hoagland's nutrient solution (Hoagland and Arnon, 1950). When the seedlings reached about 5 cm (20 May 2007), they were transplanted to pots mentioned above (filled with 120 g of a peat, vermiculite, and perlite mixture (10:7:3 v:v:v)). The soil water holding capacity (WHC) was 79.2%. One week later, the N and water treatments were applied.

### Experimental design

The experiment was conducted in a greenhouse at Zhejiang University (120.08° E longitude, 30.30° N latitude), where we used a completely randomized factorial design. Factor one, N condition, had four levels: high N (HN, 167% N), medium N (MN, 100% N, as control), low N (LN, 40% N), and severely low N (SN, 10% N). The MN, LN, and SN treatments were 100%, 40%, and 10% N concentration (the amount of compounds including N was reduced in proportion) of the complete Hoagland's solution (Hoagland and Arnon, 1950) with addition of CaCl<sub>2</sub>, KH<sub>2</sub>PO<sub>4</sub>, and KCL to maintain equal Ca<sup>2+</sup>, K<sup>+</sup>, and H<sub>2</sub>PO<sub>4</sub><sup>-</sup> concentrations in solution. For these three treatments, 15 ml nutrient solution was sprayed equably in each pot every week. We designed the HN treatment in reference to studies on N deposition (Bowden et al., 2004). We simultaneously added 15 ml complete Hoagland's solution and 15 ml solution of 6.48 mmol L<sup>-1</sup> NH<sub>4</sub>NO<sub>3</sub> per pot per week for the HN treatment, equivalent to the addition of 15 g N m<sup>-2</sup>

yr<sup>-1</sup> on the base of sufficient N supply. Consequently, the N concentration in the HN treatment increased to 1.67-fold that of the MN treatment. Factor two, water condition, had three levels: waterlogging (WL, water surface was maintained at about 2 cm above soil surface), wet (water content ≥ 90% of WHC), and dry (water content ≥ 30% of WHC) condition. For the wet and dry treatments, plants were not watered with distilled water unless the soil water content dropped to 90% and 30% of WHC, respectively. 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 18:00 every day. In total, there were 12 treatment combinations for each of the two species. Each treatment combination had six replicates (six pots). Three individuals were grown in each pot. The extent of soil water depletion depended on the plant growth and weather conditions, so the pots were weighed every day to determine the watering time for wet and dry treatments. The day/night temperature during the experiment was about 35/20°C. The average daily amount of light the plants experienced was 29.3 mol m<sup>-2</sup> d<sup>-1</sup> on cloudless days.

### Measurements and calculations

Seven weeks after the treatments were applied (15 July 2007), when plants of the two species were at the vigorous vegetation growth stages, all individuals were measured for their height. Then, each individual plant was clipped at the soil surface. All green leaves from each plant were collected and scanned with a scanner (ScanMaker 4900, Microtek International Inc., USA) immediately after harvesting. The leaves with severe chlorosis or wilting were not measured. The WinFLORA Pro 2002a software (Regent Instruments INC, Quebec, Canada) was used to determine leaf area from the images scanned. However, because the roots of plants in each pot were so entangled that it was not feasible to separate them by individuals, the biomass of roots, stems, and leaves of all individuals in each pot were measured totally after being dried in an oven at 65°C for at least 48 h to constant weight. Leaf mass ratio (LMR, leaf mass/total mass), stem mass ratio (SMR, stem mass/total mass), root mass ratio (RMR, root mass/total mass), specific leaf area (SLA, leaf area/leaf mass), and leaf area ratio (LAR, leaf area/total mass) were calculated following Hunt (1978).

### Data analysis

To evaluate the differences in the growth traits between species and among N and water conditions, a three-way ANOVA was performed after data transformations (if necessary, Table 1). After ANOVA, coefficients of variance (CVs) for the growth traits of each species were calculated from standard deviations and means. The least significant difference (LSD) post-hoc comparisons were used to separate the results among N treatments under the same water conditions. In all of the above tests about significance levels, differences were considered

**Table 1.** The *P* values of three-way ANOVAs for testing the differences in the growth traits of two *Mosla* species (*M. cavaleriei* and *M. dianthera*) between species and among soil water conditions (wet and relatively dry conditions, and waterlogging), N supply (high, medium, low, and severely low).

Trait	Species (S) (d.f.=1)	Water (W) (d.f.=2)	N (d.f.=3)	S×W (d.f.=2)	S×N (d.f.=3)	W×N (d.f.=6)	S×W×N (d.f.=6)
Total mass <sup>log</sup> (g)	***	***	**	***	*	***	NS
Leaf mass <sup>log</sup> (g)	***	***	*	***	**	**	NS
Stem mass <sup>log</sup> (g)	***	***	***	***	NS	***	NS
Root mass <sup>log</sup> (g)	***	***	NS	***	NS	***	NS
LMR	NS	***	NS	NS	***	**	*
SMR	NS	*	***	NS	***	**	NS
RMR	NS	**	***	NS	NS	NS	*
Plant height <sup>log</sup> (cm)	***	***	**	***	NS	NS	NS
SLA (cm <sup>2</sup> g <sup>-1</sup> )	***	NS	NS	NS	NS	***	NS
LAR (cm <sup>2</sup> g <sup>-1</sup> )	***	**	**	NS	**	**	NS

\*, *P*<0.05; \*\*, *P*<0.01; \*\*\*, *P*<0.001; NS, *P*>0.05, not significant. The superscripts above parameters denote the functions of data transformation. LMR, leaf mass ratio; SMR, stem mass ratio; RMR, root mass ratio; SLA, specific leaf area; LAR, leaf area ratio.

statistically significant if *P*<0.05. All the statistical analyses were conducted using STATISTICA version 6.0 (StatSoft Inc., OK, USA).

## RESULTS

### Biomass production

Biomass production was significantly different between the two *Mosla* species (Table 1). For these species, water conditions significantly affected all four mass traits while root mass did not significantly differ among N treatments. The CVs of mass traits were greater in *M. cavaleriei* than in *M. dianthera* (Table 2). Under the wet and relatively dry conditions, total mass of *M. dianthera* was significantly lower in the SN and HN treatments than in the MN treatment. For *M. cavaleriei* the differences of total mass among N treatments were not so large as for *M. dianthera* (only under the wet conditions. The total mass of *M. cavaleriei* was significantly lower in the HN treatment than in the LN treatment) (Figure 1). Under the WL conditions, total mass of the two species was significantly greater in the HN treatment than in the other three N treatments.

### Biomass allocation

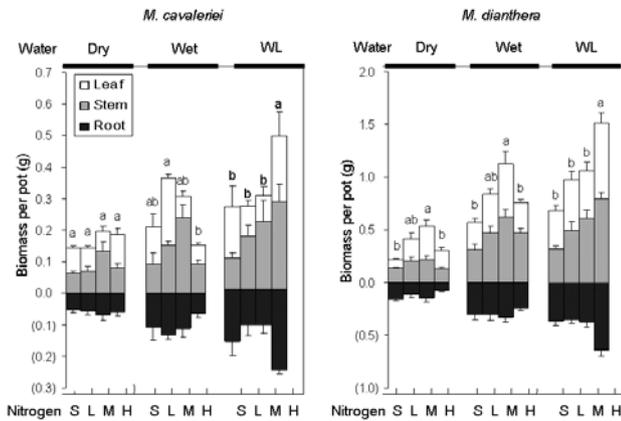
Although the two species considerably responded to N and water conditions in terms of biomass allocations (Table 1), the allocation traits were not significantly different between these species. The CVs of allocation traits were greater in *M. cavaleriei* than in *M. dianthera* (Table 2). Under the three water conditions, the RMR of the two species rose when N supply turned limited. With the decrease in water supply, the differences in RMR between the MN and SN treatments increased for *M. dianthera* while they decreased for *M. cavaleriei* (Figure 2). The LMR of *M. cavaleriei* was much greater in the

**Table 2.** Coefficients of variance (CVs) of growth traits of two *Mosla* species supplied with four levels of N (H, high; M, medium; L, low; S, severely low) under three water conditions (wet and relatively dry conditions, and waterlogging).

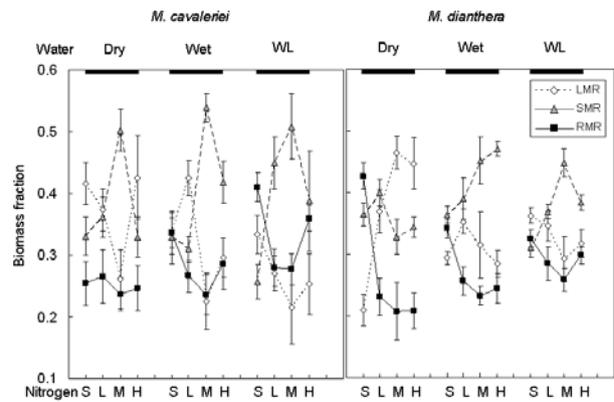
Trait	CV (%)	
	<i>M. cavaleriei</i>	<i>M. dianthera</i>
Total mass <sup>log</sup> (g)	18.1	9.4
Leaf mass <sup>log</sup> (g)	18.1	13.9
Stem mass <sup>log</sup> (g)	14.1	11.7
Root mass <sup>log</sup> (g)	18.0	13.1
LMR	40.5	29.6
SMR	31.9	18.8
RMR	31.7	31.4
Plant height <sup>log</sup> (cm)	25.2	12.7
SLA (cm <sup>2</sup> g <sup>-1</sup> )	35.2	32.4
LAR (cm <sup>2</sup> g <sup>-1</sup> )	52.6	38.8

The superscripts above parameters denote the functions of data transformation and the corresponding CVs of these traits were calculated from the data transformed. LMR, leaf mass ratio; SMR, stem mass ratio; RMR, root mass ratio; SLA, specific leaf area; LAR, leaf area ratio.

low and high N treatments than in the MN treatment under the three water conditions. In contrast, *M. dianthera* stressed by drought significantly decreased its LMR when N supply was limited. For *M. cavaleriei* grown under the WL and wet conditions and *M. dianthera* grown under WL conditions, the SMR decreased while the LMR and RMR increased in the HN treatment compared with the MN treatment.



**Figure 1.** Biomass (means  $\pm$  SE) of two *Mosla* species supplied with four levels of N (H, high; M, medium; L, low; S, severely low) under three water conditions (dry and wet conditions and waterlogging (WL)). The different letters above the bars denote significant differences in total mass among N treatments. Note the different scales in the two histograms.



**Figure 2.** Biomass allocation (means  $\pm$  SE) to leaves (LMR), stems (SMR), and roots (RMR) of two *Mosla* species supplied with four levels of N (H, high; M, medium; L, low; S, severely low) under three water conditions (dry and wet conditions and waterlogging (WL)).

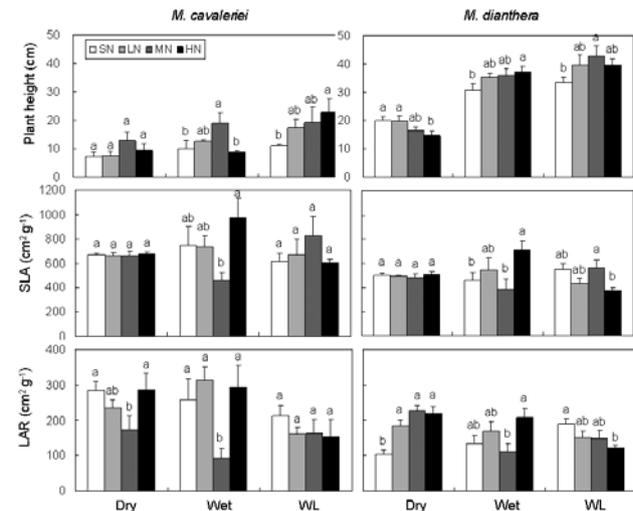
## Morphological traits

Both plant height and LAR of the *Mosla* species were significantly different between species and among N and water conditions while SLA showed no significant response to N or water treatments (Table 1). The CVs of the three traits were greater in *M. cavaleriei* than in *M. dianthera* (Table 2). Under the three water conditions, high and low N supply considerably decreased the plant height of *M. cavaleriei* (except high N under the WL conditions), but the impacts on *M. dianthera* were minor (Figure 3). Compared with the MN treatment, high and low N supply tended to increase SLA and LAR of the two species under the wet conditions, but the tendency was more remarkable in *M. cavaleriei* than in *M. dianthera* (Figure 3). Under the relatively dry conditions, SLA did not respond to N supply for the two species while LAR showed considerable responses.

## DISCUSSION

### Similarly positive responses of the two species to high N under waterlogging conditions

The enhanced growth under the WL conditions suggests that the two *Mosla* species exhibited positive responses to high N supply when the roots were waterlogged. Waterlogging favors the availability and effective diffusion of some nutrients (Teo et al., 1994) and root uptake of plants (Rubio and Lavado, 1999), which might ameliorate relative nutrient limitation in the HN treatment, thus maintaining vigorous growth of the species under supra-optimal N conditions. Moreover, the waterlogged plants of the two species favorably adjusted their biomass allocation and morphological traits (increasing plant height, RMR, and LMR, and decreasing SMR) to contribute to the improved growth.



**Figure 3.** Plant height, specific leaf area (SLA) and leaf area ratio (LAR) (means  $\pm$  SE) of two *Mosla* species supplied with four levels of N (HN, high; MN, medium; LN, low; SN, severely low) under three water conditions (dry and wet conditions and waterlogging (WL)). The different letters above the bars denote significant differences among N treatments.

### Stronger tolerance of *M. cavaleriei* to high N under non-waterlogging conditions

The depressed growth under the wet and dry conditions indicates that the two *Mosla* species responded negatively to high N supply under non-waterlogging conditions. This may be related to relative (rather than absolute) limitation of other nutrients (such as P) due to supra-optimal N, like other terrestrial plants (grassland species, Johnson et al., 1999; moorland species, Kirkham, 2001). Nevertheless, the suppressive effects on *M. dianthera* were more remarkable than those on *M. cavaleriei*, which suggests that the former may be less tolerant to high N

supply than the latter under non-waterlogging conditions. This is supported by the adjustments of biomass allocation and morphological traits. For *M. cavaleriei* the increase of RMR, LMR, SLA and LAR, and the decrease of SMR and plant height in the HN treatment should promote the efficiency of light capture and the absorption ability of roots when nutrient resources other than N are relatively limited. No similar adjustments were observed in *M. dianthera*.

### More favorable adjustments of *M. dianthera* to N limitation than *M. cavaleriei*

Under the three water conditions, both of the two *Mosla* species were negatively responsive to limited N supply in terms of biomass production, though the amplitude of responses were different between species and among water conditions. Responsive to N limitation, the two species grown under the three water conditions increased RMR to a different extent, which is consistent with the “functional equilibrium” theory (Poorter and Nagel, 2000). In response to the decrease in water supply, nevertheless, the difference of RMR between N treatments increased in *M. dianthera* and decreased in *M. cavaleriei*. This shows that the influence of N limitation on plant growth depends on soil water status, and *M. dianthera* can favorably adjust biomass allocation to tolerate N limitation despite soil water limitation while *M. cavaleriei* can do so only under conditions that supply enough soil water. This shows that N and water in soils influence plants in an interactive way, which has been observed in a study on two *Picea* species (Patterson et al., 1997).

### Differentiation between species

The difference in responses to soil N variations between the two species may be explained by the long-term adaptation to different habitats. The strong tolerance of *M. cavaleriei* to high N independent of soil water supply may benefit from the adaptation to habitats with high N levels. For *M. dianthera*, however, the intolerance to high N under non-waterlogging conditions and the favorable adjustments to N limitation may be related to its preference for habitats with relatively low N levels. The differences in growth responses and adaptation to habitats indicate a differentiation of optimal and realized N niches between the two species, and their realized N niches are consistent with the optimal. This favors the survival and population extension of the two species. However, the differences in current status of existence between the species may be related to the strong tolerance of *M. dianthera* to limitations of other environmental factors (e.g., light and soil water, Liao et al., 2006) and its relatively high ability to produce seeds (Jie Chang, unpubl.). Similarly, Patterson et al. (1997) found that two *Picea* species differentiating in soil N niches exhibit different sensitivities to N limitation. (The species preferring nutrient-poor habitats is less sensitive). To N augmentation, four ecotypes of *Cochlearia officinalis* occupying habitats with different

N levels responded differently, and the differences in ecotype response were correlated to the N content of the soil in their natural habitats (Eriksen and Nordal, 1989). Therefore, for many plants the responses to soil N variations are closely related to adaptations to N concentrations in the natural habitats.

In the main distribution areas of the two *Mosla* species, they are experiencing similar environmental changes, including N addition and water status variation in soils. For both species, the negative responses to high N supply under non-waterlogging conditions and the positive responses under waterlogging conditions imply that the influences of N addition are dependent on soil water status. In the context of high rates of N input into ecosystems, therefore, the two species may have more potential chances to extend their populations in very wet habitats such as brims of streamlets and wetlands rather than relatively dry habitats. Under drought conditions, the two species responded differently to either high or low N: *M. dianthera* was less tolerant to high N but more tolerant to N limitation than *M. cavaleriei*. At present, the relatively dry habitats such as open lands on the top of hills are inhabited only by *M. dianthera* and not *M. cavaleriei*. Thus, N addition in soil environments might be unfavorable for the growth of *M. dianthera* in relatively dry habitats.

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## 石薺屬的兩個物種對土壤氮和水的回應

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由於氮沉降和降水的變異，同屬物種對生長條件改變的不同回應可能改變物種間的分化格局。我們將石薺屬的兩個物種培養在不同的氮和水條件下。兩物種在淹水條件下對高氮供應表現出相似的正面回應，預示著它們有潛在的機會在非常濕潤的生境拓展居群。但是，在中度濕潤和相對乾旱條件下，與小花薺相比，小魚仙草不耐受高氮供應（小魚仙草的生物量被高氮抑制的程度比小花薺的更大）卻更耐受限制氮（隨著水分供應的減少，小魚仙草的根生物量比被氮限制增加的程度比小花薺的更大）。因此，在相對乾旱生境，土壤氮增加可能不利於小魚仙草的生長。

**關鍵詞：**生境；形態；小花薺；小魚仙草；氮沉降；分化。