Interactive effects of water, nitrogen and phosphorus on the growth, biomass partitioning and water-use efficiency of *Bauhinia faberi* seedlings

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ABSTRACT

The scarcity of research on the interactive effects of multi-limiting resources has hampered the success in ecological restoration. The effects of water (W), nitrogen (N) and phosphorous (P) on the performance of a perennial shrub, *Bauhinia faberi* seedlings were studied through a full factorial experimental design. Eighteen treatments was involved including three water (W1: 10, W2: 20 and W3: 40% field capacity), two N (N1: 100 and N2: 280 mg N kg⁻¹ soil) and three P (P1: 12, P2: 24 and P3: 48 mg P kg⁻¹ soil) for 19 weeks in a greenhouse experiment. P strongly regulated the biomass allocation under severe drought stress. Elevated W and P with N1 or N2 level increased root surface area and length, root and shoot mass, water-use efficiency and tissue P concentration, but did not significantly decrease tissue N concentration. The interaction of N and P was significant. Compared to N1, N2 significantly decreased growth parameters at P1 and P2, slightly reduced them at P3, suggesting that P3 alleviated the negative effects of N2. Therefore, the interactive effects of soil N and P should be examined thoroughly in seedlings plantation sites in arid regions to avoid excess level of nitrogen.

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1. Introduction

Seedling planting is an often-adopted measure in the ecological restoration of arid lands, while resource limitation is recognized as a critical problem on plant growth, development, and reproduction in terrestrial ecosystems (Smith et al., 1997; Hooper and Johnson, 1999; Drenovsky and Richards, 2004; White and Beadle, 2004). It is critical to find out the level of resource limitations in vegetation restoration under stressed environments. However, little research has been carried out on the interactive effects of multiple resource limitations on restoration processes (Gleeson and Good, 2003; James et al., 2005). To ensure a successful restoration effort, it is important to understand the confounding resource limitations in the targeted study areas.

Nitrogen (N) and phosphorous (P) are normally important nutrients for ecosystem structure, process and function through limiting the production of plant biomass (Vitousek and Howarth, 1991; Hu and Schmidhalter, 2005). Thus, N and P have been the key elements in the study of nutrient limitations. There are currently two ways to detect nutrient limitations. 1) Critical foliar N/P ratio can

be used to predict N and/or P limitations at species and community levels (Koerselman and Meuleman, 1996). However, it does not give an indication of proper soil conditions for plant growth, and few studies have been conducted at species level (Drenovsky and Richards, 2004). 2) Nutrient limitations can also be determined from soil and/or plant nutrient levels or from fertilizer experiments (Güsewell et al., 2003; Drenovsky and Richards, 2004). However, the critical nutrient ranges in foliar analysis are usually determined in terms of crop plants (Marschner, 1995), which may have higher nutrient requirements than low-nutrient-adapted wild species (Drenovsky and Richards, 2004). Although fertilizer experiments are often laborious and lengthy, it is still accepted as a straight forward and effective way to evaluate the response of plant to resource limitation (Rubio et al., 2003; Niinemets and Kull, 2005).

Currently most fertilizer experiments are conducted by varying N supply while maintaining the other nutrients constant or non-limiting (e.g. Green et al., 1994; Qu et al., 2003); or by manipulating with simple combinations of N and P, such as high and low levels of fertilization and comparing to a control (Fernandez et al., 2000; Bennett and Adams, 2001; Güsewell et al., 2002; Grünzweig and Körner, 2003). However, the experiments seldom consider plant growth in relation to P supply or to the combinations of N and P, since P is thought less important to plant growth (Güsewell and Koerselman, 2002; Güsewell et al., 2003). This may be wrong in practice in that simple N and P experiments could

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not represent the complex interactive effects of these factors in natural ecosystems. Meanwhile, due to recent global environmental change, N input to ecosystems has been enhanced through atmospheric deposition, fertilizers, and spread of N-fixing plants (Bobbink et al., 1998; Balmford et al., 2002). The increased level of N may have impacts on plant growth if P is limited, although this has not been proved directly (but see Carroll et al., 2003; Perring et al., 2008). Given the key role of N and P in the ecosystems, a profound understanding of plant response to the combination of N and P gradients would be invaluable.

Water not only constrains plant growth and survival directly, but also influences plant responses to nutrients under drought stress indirectly (Otsus and Zobel, 2004). There is abundant evidence that drought stress reduces nutrient uptake and their availability for growth (Misra and Tyler, 2000; Engelbrecht et al., 2007). Thus the effects of nutrient supply and water regimes on plant growth may interact significantly (Hu and Schmidhalter, 2005). It is hence necessary to understand the interactive effects of soil water and nutrients on plant growth in the arid environments (Hooper and Johnson, 1999; Drenovsky and Richards, 2004).

Bauhinia faberi is a perennial and dominant shrub that native to the arid valleys of the Hengduan Mountains and other arid regions of China (Li et al., 2008). It is thus considered a key species for ecological restoration. However, the soil in this area, which is classified as Calcic cambisols (FAO-UNESCO, 1988) is poor in water supply and nutrients. Consequently, the growth and regeneration of *B. faberi* is limited. To date, existing research in the area is mainly focused on the spatial distribution of soil moisture and its controlling factors (Ma et al., 2004; Xu et al., 2008), the adaptability of dominant plants to soil water and water limitation on *B. faberi* growth (Li et al., 2008). Field investigations also show that soil N and P together with soil moisture are limiting factors to vegetation distribution in the area (unpublished data), however, only a few relevant soil nutrient experiments exist (Wu et al., 2008). In fact, none of these experiments has examined the interactive effects of soil water and nutrients on the plant growth. Such experiments designed to study the interactive effects of soil factor on plant growth would be very meaningful to clarify the ranks and interactions of the main factors for selecting sites for planting of seedlings. At the mean time, ecological restoration is urgent in this area in that the Hengduan Mountains have the largest arid valley area to be restored to ensure the ecological security of southern China. Moreover, a recent geological disaster (Wenchuan Earthquake) struck the mountain ecosystems and led to further ecological degradation.

This experiment cultivates *B. faberi* through the combinations of two N, three P and three water treatments to decouple the integrated effects of soil N and P under drought stresses. Specifically, this study is designed to (i) determine the different impacts of soil water, N and P on *B. faberi* growth, (ii) evaluate the interactions of resources on the performances of *B. faberi*, and finally (iii) provide some recommendations for restoration of the species in the region.

2. Materials and methods

2.1. Experiment design

The dry valley of the upper Minjiang River, is a first-order branch of the Yangze River and located at the eastern edge of the Tibetan plateau. The mountainous topography has a large degree of vertical

variation in precipitation and air temperature. Mean annual precipitation is about 500 mm, mean annual potential evapotranspiration is about 1332 mm, and mean annual temperature is about 11.2 °C. Vegetation is dominated by arid shrubs, such as *B. faberi*, *Sophora viciifolia*, and *Indigofera bungeana*.

Seeds of *B. faberi* were collected from the dry valleys of Minjiang River in Maoxian County, Sichuan Province (103°54'–103°56' E, 31°37'–31°44' N) in the fall of 2005. Healthy seeds were selected, air-dried, and stored at ambient laboratory temperature (20–25 °C) until the experimental pre-treatment in March 2006. Soil samples (below 30 cm) were taken from the central dry valleys of Minjiang River and sieved to 10 mm (Table 1). Each cylindrical pot (30 cm high with a diameter of 10 cm, polyvinyl chloride) was filled with 5.5 kg soil. Seeds were surface-sterilized with 2.5% of sodium hypochlorite (NaOCl) for 2 h, sowed (seven seeds per pot) and germinated on moist container soil for 15 days. One high quality seedling was picked up in terms of seedling height, leaf number and total leaf area after emergence. All the pots were arranged in a sunlit, open sided, plastic covered greenhouse (103°51'59" E, 31°41'52" N, 1650 m a.s.l.), at ambient temperature ranging from 11 to 22.4 °C, relative humidity ranging from 43.2 to 94.6% and photoperiod of 12 h.

The soil water, N and P were manipulated using a factorial experimental design. Specifically, the experiment was consisted of three water treatments (W1, W2 and W3 with 10, 20 and 40% of field capacity) crossed with two N (N1 and N2 with 100 and 280 mg N kg⁻¹ soil) and three P (P1, P2, and P3 with 12, 24 and 48 mg P kg⁻¹ soil) treatments. N and P were applied with ammonium nitrate (NH₄NO₃) and monopotassium phosphate (KH₂PO₄). Additionally, four control pots with no additional fertilizers and water were included. Each treatment had four replicates. Fertilizer was mixed with the soil substrates before filling up the pots to homogenize N and P distribution throughout the soil. Seedlings were randomly assigned to the treatments and the pots were regularly rotated throughout the experiment period to reduce edge effects. Soil water-withholding treatment was initiated at 30 days after sowing. Soil water levels were maintained with manual irrigation by weighing individual pots at 5:00 a.m. every other day. Each target soil moisture level was achieved by reducing water supply progressively over the course of about 20 days subsequent to the date withholding of water started.

In order to simulating the drought and nutrient levels in field, we referred to the soil properties measured in the field during the growing seasons of 2001, 2003 and 2006 (unpublished data). Based on those available water, N and P ranges, P1, P2 and P3 levels represented the lower, moderate and upper values of soil available P. N1 and N2 represented the moderate and upper levels of soil available N. W1 represented the extreme lower (severe drought) soil water availability, W2 reflected an intermediate soil water availability and W3 reflected the upper value of soil water in the field during the growing seasons.

2.2. Plant harvesting, measurements and statistical analysis

After 9 weeks of treatments, the photosynthetic rate and stomatal conductance of all seedlings were measured between 8:00 a.m. and noon using a Li-6400 portable gas exchange system

Table 1
Key physical and chemical properties of substrate soil (below 30 cm).

pH	Bulk density (g cm ⁻³)	Field capacity (%)	Gravel content (%)	Soil organic matter (g kg ⁻¹)	Electronic conductivity (μS cm ⁻¹)	Available N (mg kg ⁻¹)	Available P (mg kg ⁻¹)	CaCO ₃ (g kg ⁻¹)
8.69	1.31	18.24	22.51	9.76	81.23	10.53	8.07	8.80

(Li-Cor, Lincoln, Nebraska, USA). The photosynthetic flux density was about $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$. The seedlings were harvested after 15-weeks of treatments. After harvesting, the roots of seedlings were washed free from growing media and separated into leaves, stems and roots for morphological measurement and chemical analysis. Root nodules were not found. Roots were scanned for making a photocopy. Total root length and main root length were measured by a metal tape measure. Root surface area was analyzed with Area Meas (Honggu, Akinori MYKA. Lab. 1.01 Ver, 1995). All seedling samples were oven-dried to constant mass at 65°C for 72 h and weighed. Tissue N was measured by micro-kjeldahl, and tissue P was measured according to the methods of Nicholson (1984). Total fine root length ($<2 \text{ mm}$) was estimated from regressing the relationship between total root length (Y , cm) and dry root mass (X , g): $Y = 272.89 + 134.60X$, $R^2 = 0.95$, $P < 0.0001$ (unpublished data). Root shoot ratio was calculated as the root dry mass divided by stem and leaf dry mass. Water-use efficiency at a single leaf level (WUE_{leaf}) was defined as the ratio between the rate of light-saturated photosynthesis (A_{max}) and the rate of stomatal conductance (g_s) for water vapor.

A full factorial approach was used to investigate the influence of the resources interaction to seedling growth and function. Variables were analyzed with three-way factorial ANOVA with water, N and P as factors for growth and functional responses. Firstly, the soil treatments effects on all the 15 plant variables were evaluated using multivariate analysis of variance (MANOVA). And then a univariate ANOVA model on each of the 15 plant variables was run, and the normality of residuals was evaluated using Shapiro Wilk tests (see James et al., 2005 for details). All the variance analyses of the univariate model were visually checked and log transformed when necessary to meet assumptions of homogeneity. Multiple comparisons were performed with the Tukey–Kramer honestly significant difference (HSD) *post hoc* tests at 0.05 level among means. All analyses were conducted using the SPSS program (SPSS Institute Inc., 2002) and considered significant at 0.05 level.

3. Results

3.1. Effects of resource interactions on overall seedling and individual variables

Multivariate comparisons showed that soil water, N and P produced significant main effects and interactions on the overall performance of seedlings (Table 2), while univariate analyses further indicated that the individual variable responses to the main and interactive effects differed greatly. Parameters, such as root dry mass, were significantly impacted by all the main effects and interactions; while the others, such as main root length, were weakly responded to single resources and their interactions (Table 3). Specifically, in the 18 combinations of resources, $W \times N$ interactions did not significantly impact on any parameters except shoot mass, while $W \times P$ interactions were significant for only 6 parameters (leaf dry mass, root dry mass, total root length, WUE_{leaf} , $\text{WUE}_{\text{plant}}$, and root N concentration), $N \times P$ interactions significantly influenced most parameters (except main root length, WUE_{leaf} , $\text{WUE}_{\text{plant}}$, and P concentrations of leaf and root), and $W \times N \times P$ terms were notable for 8 variables (root mass, total dry biomass, total root length, WUE_{leaf} , $\text{WUE}_{\text{plant}}$, N concentration of leaf and root, and P concentration of leaf) (Table 3).

3.2. Effects of single resource on root growth

The main effects of the resources on total root length and root surface area were remarkable, but did not significantly affect the

Table 2

MANOVA contrasts of morphological and physiological variables of *B. faberi* seedlings between treatments.^a

Effect	Wilks' lambda	Hypothesis df	Error df	F-Values	Sig.
Intercept	0.000	18.00	34.00	8352.23	0.000***
W	0.026	36.00	68.00	0.03	0.000***
N	0.177	18.00	34.00	8.81	0.000***
P	0.107	36.00	68.00	3.90	0.000***
$W \times N$	0.190	36.00	68.00	2.44	0.001**
$W \times P$	0.047	72.00	136.00	2.22	0.000***
$N \times P$	0.114	36.00	68.00	3.72	0.000***
$W \times N \times P$	0.032	72.00	136.00	2.64	0.000***

^a Data with either *, ** or *** annotated $p < 0.05$, 0.01 or 0.001, respectively. W: water; N: nitrogen; P: phosphorus.

main root length. Compared with control seedlings or seedlings with lowest water or P supply, the main root length was not markedly increased with the increase of W or P supply, but the total root length and root surface area were significantly increased with the increase of water or P supply (Table 4). N1 level did not significantly increase the main root length and root surface area, but the total root length was markedly increased at N1 supply (Table 4). For example, the total root surface area at W3 increased by 46% over that at W1, and the root surface area at P3 increased 40% than that at P1 (Table 4).

Considering the interactive effects, the root surface area and the total root length of seedlings were significantly increased by 12 combinations of water and fertilization, while the main root length was increased only by 5 combinations compared with the control seedlings. The largest root surface area occurred at N1P3 combination under W1 and W3 conditions, followed by N2P3 under W2 level (Fig. 1a). The longest total root length was caused by the N2P3 combination under W1 and W2 condition, and the N1P2 combination under W2 level (Fig. 1b). The longest main root length was produced by the N1P3 combination under W1 condition, and the N1P2 combination under W2 and W3 level (Fig. 1c). N2P1 supply produced generally negative effects on root characters across all the water regimes (Fig. 1a–c). The W2N1P3 treatment combination led to the highest root surface area and total root length among the 18 treatments (Fig. 1a and b).

3.3. Biomass production, partitioning and water-use efficiency

Considering the main resource effects, the high levels of both W and P significantly increased the leaf mass, stem mass, shoot mass, root mass and total mass compared with respective low resource level (Fig. 2a and b). However, N2 decreased these five parameters compared with N1 level (Fig. 2c). The shoot and root mass of the seedlings under W3 treatment were 61% and 39% larger than those under W1 level, respectively; while under P3 condition, they were 12% and 31% larger than those under P1 level, respectively (Fig. 2a and b). These two parameters were 43% and 36% smaller, respectively, under the highest N supply compared to the low N treatment (Fig. 2c), although N2 did not significantly decrease the five parameters compared with those at N1 level (Fig. 2c).

Furthermore, increasing water significantly decreased the root shoot ratio, as the lowest ratio was found under P2 level or N1 level; while P3 and N2 did not significantly elevate the root shoot ratio compared with the lowest value (Fig. 2d–f). When considering combined effects, the shoot and root mass of seedlings were obviously increased by combination of water and fertilization compared with control seedlings (Fig. 3). The largest root, shoot and total biomass were caused by the N1P2 combination under W1 and W3 condition, but high biomass was also found with the N2P3 treatment combination under the intermediate water level, the

Table 3
F-values and probability levels from univariate ANOVA models for morphological and physiological variables of *B. faberi* seedlings at the different water and fertilization regimes.^a

Variable	W (d.f. = 24)	N (d.f. = 24)	P (d.f. = 24)	W × N (d.f. = 24)	W × P (d.f. = 24)	N × P (d.f. = 24)	W × N × P (d.f. = 24)
Leaf dry mass	17.67***	45.60***	4.10*	0.74	2.16*	10.63***	0.58
Stem dry mass	23.19***	48.40***	4.04*	0.58	0.95	4.13**	1.22
Above ground mass	29.19***	47.66***	2.68*	4.39**	1.42	6.89**	0.57
Root dry mass	18.35***	40.59***	19.07***	0.39	2.62*	9.30***	4.14***
Total dry mass	22.80***	60.05***	15.33***	0.27	1.91	9.54***	2.78**
Total root length	16.26***	28.00***	17.10***	0.73	3.99**	7.58**	3.26**
Root shoot ratio	19.96***	22.29***	3.03*	0.54	0.97	4.76**	1.42
Main root length	6.79***	1.72	0.21	0.16	0.38	1.35	1.57
Root surface area	9.31***	44.95***	12.75***	0.65	1.61	3.61*	1.02
WUE _{leaf}	7.01***	77.69***	5.19*	0.17	7.32***	0.58	5.09***
WUE _{plant}	6.86***	67.70***	2.04	0.20	7.14***	0.40	9.25***
Leaf N concentration	4.74**	3.50*	2.60	1.72	2.06	17.97***	3.95**
Leaf P concentration	3.65*	6.5**	4.95**	0.43	0.85	0.38	2.31*
Root N concentration	0.80	2.23	4.97**	1.68	5.14***	4.99**	6.39***
Root P concentration	4.93**	7.71**	6.46**	0.62	0.52	1.23	0.60

^a Data with either *, ** or *** annotated $p < 0.05$, 0.01 or 0.001 , respectively. W: water; N: nitrogen; P: phosphorus; WUE_{leaf}: Water-use efficiency at a single leaf level; WUE_{plant}: Water-use efficiency at whole plant level.

smallest increases in root mass and total mass found with the combination of N2P1 across the three water regimes, while the N2P2 combination caused the smallest increase in shoot biomass (Fig. 3). The P elevation insignificantly increased total biomass under N1 level across three water regimes, and significantly increased total biomass under N2 level across three water regimes (Fig. 3). However, no further positive effects were found with the P2 with N1 supply, and reached the highest value under P3 level with N2 supply.

Across all the water regimes, the root, shoot and total mass of seedlings under N2 level were notably reduced compared with those under N1, irrespective of P level, but the differences between N1 and N2 regime were smaller under P3 level at W1 and W3 regimes, and N2 even caused a larger biomass than N1 with P3 level under W2 condition (Fig. 3). The decrease in total biomass between N1P1 and N2P1, N1P2 and N2P2, N1P3 and N2P3, were 55%, 56% and zero under W1 treatment, 50%, 60% and 27% under W2 treatment, and 61%, 40% and 24% under W3 treatment (Fig. 3). All the combinations of elevated water and fertilization yielded total biomass more than would the sum of the separate responses to each factor. This was obvious for the combination of W3N1P2, which resulted in the highest (298%) increase in total biomass over the combination of W1N2P1 (Fig. 3). The responses to individual factors summed up to a significant increase of 228% (+141% from W3 vs. W1, +53% from N1 vs. N2, and +34% from P2 vs. P1). The eighteen treatments caused a significantly smaller root shoot ratio than the control seedlings (Fig. 3). Across the three water regimes,

at N1 level, P supply produced the largest, moderate and smallest range of root shoot ratio, but the root shoot ratio remained stable at N2 level (Fig. 3).

The WUE_{leaf} of *B. faberi* seedling was significantly increased with the increase of water and P supply, excluding W1, W2 and P1 level (Fig. 4a). The WUE_{leaf} increased up to 22% and 13% following the highest water and P additions compared to that of control seedlings when only considering their main effects (Fig. 4a). With N1 and N2 supplies, they resulted in 5% increase and 4% reduction in the WUE_{leaf} compared to the control seedlings, respectively (Fig. 4a). On the other hand, the WUE_{leaf} increased with water addition under the N1 condition irrespective of P level, but it had a decreasing tendency under N2 excluding P2 level (Fig. 4b). Compared with the control seedlings, combination of N1 with P2 and P3 levels produced obviously higher WUE_{leaf}, while the combination of N2 with P1 and P2 levels caused obviously a lower WUE_{leaf} than the control, but the combination of N2P3 produced a similar WUE_{leaf} to the control (Fig. 4b). The largest increases were generated by the treatment W3N1P3 among the 18 combinations (Fig. 4b). These results indicated that the interaction of water, N and P was complex on the WUE_{leaf}.

3.4. Nutrient concentrations of leaf and root

Only considering the main resource effects, the N concentrations of root and leaf were the largest under W1 level, P1 level and N1 level, and insignificantly decreased by W2, W3, P2, P3 and N2

Table 4
Mean ($\pm$ SE, $n = 4$) root surface areas, total root length, main root length of *B. faberi* seedlings grown for 19 weeks at various fertilizer regimes and water regimes during the growing seasons.^a

	Control	W1	W2	W3
Main root length (cm)	27.50 $\pm$ 2.78ab	24.30 $\pm$ 0.79a	25.65 $\pm$ 1.15ab	30.78 $\pm$ 1.35b
Total root length (cm)	165.62 $\pm$ 10.49a	198.85 $\pm$ 10.33ab	239.06 $\pm$ 15.40b	225.89 $\pm$ 11.00ab
Root surface area (cm ²)	28.55 $\pm$ 3.63ab	27.65 $\pm$ 2.26a	33.38 $\pm$ 2.85ab	40.22 $\pm$ 3.11b
	Control	P1	P2	P3
Main root length (cm)	27.50 $\pm$ 2.78a	26.96 $\pm$ 0.98a	27.14 $\pm$ 1.30a	27.67 $\pm$ 1.46a
Total root length (cm)	165.62 $\pm$ 10.49a	187.86 $\pm$ 10.14a	223.87 $\pm$ 11.58ab	252.40 $\pm$ 13.01b
Root surface area (cm ²)	28.55 $\pm$ 3.63ab	27.09 $\pm$ 2.29a	32.59 $\pm$ 1.91ab	37.86 $\pm$ 2.32b
	Control	N1	N2	
Main root length (cm)	27.50 $\pm$ 2.78a	27.61 $\pm$ 0.99a	26.15 $\pm$ 6.24a	
Total root length (cm)	165.62 $\pm$ 10.49a	243.46 $\pm$ 7.29b	197.06 $\pm$ 11.81ab	
Root surface area (cm ²)	28.55 $\pm$ 3.63ab	40.28 $\pm$ 1.91b	27.21 $\pm$ 2.34a	

^a Different letters indicate a significant difference (HSD; $p < 0.05$). W: water, N: nitrogen, P: phosphorus.

Fig. 1. Interactions of water, N and P addition on *B. faberi* seedlings root surface area, total root length, main root length at the end of the growing season. Within each mound type, different letters indicate a significant difference (HSD; $p < 0.05$). Bars indicate standard error of the mean. W: water; N: nitrogen; P: phosphorus.

(Fig. 5a). Under N1 condition, the leaf N concentration obtained the largest/smallest with P2 and P3 levels across the three water regimes, respectively, and the root N concentration reached the maximum with P3 level under W1 and W3 condition (Fig. 5b). Under N2 condition, the leaf N concentration peaked with P3 level under W1 and W3 levels across three water regimes, the root N concentration peaked with P1 level across three water regimes (Fig. 5b).

When considering the main effect only, the P concentrations of leaf and root were unmarkedly elevated with increased water compared with W1 treatment (Fig. 6a). The P concentrations of leaf and root were markedly elevated with increased P compared with P1 treatment (Fig. 6a). The P concentrations of root and leaf were 20% and 24% larger under W3 condition, and 34% and 24% larger under P3 condition, respectively, compared with W1 and P1 treated seedlings (Fig. 6a).

Fig. 2. The main effects of water, N and P on biomass production and partitioning of *B. faberi* seedlings. Within each mound type, different letters indicate a significant difference (HSD; $p < 0.05$). Bars indicate standard error of the mean. W: water; N: nitrogen; P: phosphorus.

Fig. 3. Interactions of water, N and P addition on above-ground (upper part of chart) and belowground (lower part of chart) biomass of *B. faberi* seedlings raised for 15 weeks under different water regimes and fertilization treatments. Bars indicate standard error of the mean. ns: non-significant; *, ** or *** annotated $p < 0.05$, 0.01 or 0.001 , respectively (HSD). W: water, N: nitrogen, P: phosphorus.

The P concentrations of leaf and root strongly responded to N1 with an average 39% and 213% increase over control seedlings, but they decreased 16% and 15% at N2 treatment compared with N1 treatment (Fig. 6a).

Under N1 condition, the leaf P concentration insignificantly increased with water addition, and it reached the highest level with the W2 level with P1 supply, at W3 level with P2 and P3 supply, it was also insignificantly increased with P addition, reaching the highest level at the P3 level across the water regimes; Under N2 condition, the leaf P concentration was unobviously increased with water addition, and it reached the highest level at the W3 level with P1 supply, at W1 level with P2 and P3 supply, it was also

insignificantly increased with P addition, reaching the highest level at the P2 level across water regimes (Fig. 6b).

Under N1 condition, the root P concentration insignificantly increased with water addition, and it reached the highest level at the W2 level with P1 and P2 supply, at W3 level with P3 supply, it was also insignificantly increased with P addition, reaching the highest level with the intermediate P level under W1 and W3 regimes and peaking at P3 level under W1 condition; Under N2 condition, the root P concentration was obviously increased with water addition, and it reached the highest level with W2 level with P1 and P2 supply, at W3 level with P3 supply, it was also significantly increased with P addition, reaching the highest level at the P2 level across water regimes (Fig. 6b).

Fig. 4. Water-use efficiency at a single leaf level of *B. faberi* seedlings at different water and fertilization supply regimes. Bars indicate standard error of the mean. ns: non-significant; *, ** or *** annotated $p < 0.05$, 0.01 or 0.001 , respectively (HSD). W: water, N: nitrogen, P: phosphorus.

Fig. 5. The relationship of N concentration between root and leaf of *B. faberi* seedlings under various fertilization and water conditions. Bars indicate standard error of the mean. ns: non-significant; *, ** or *** annotated $p < 0.05$, 0.01 or 0.001 , respectively (HSD). W: water, N: nitrogen, P: phosphorus.

4. Discussion

4.1. Hierarchical resource limitation structure

Non-forming root nodules indicated that the *B. faberi* would probably one non-nodulating legume shrub in the study area. So it was negligible of the influence of nitrogen-fixing process on the interaction among soil water, N and P. Control seedlings produced the smallest root traits, biomass production, nutrient status and WUE_{leaf} indicating that the growth of *B. faberi* was strongly limited by drought and nutrient-deficiency (N and P) under ambient conditions.

Seedlings grown at the high water regime produced higher survival, more branches, leaf numbers, longer shoot height and thicker basal radius than those of grown on low water supply (unpublished data). The growth parameters were also enhanced by

high P levels across the water supply gradient, irrespective of N supply. High P level alone could not alter the decline in production which was caused by drought. These findings imply that drought played a primary limitation role and P was only secondary.

N1 supply significantly increased the root growth, biomass production, nutrient status and WUE_{leaf} more so than the N2 level. Since N1 level was the lower soil N concentration in our study area, we conclude that N was only a weak limiting factor to the growth of *B. faberi* seedlings.

P concentrations of leaf and root had a positive increment in response to water and P supply, yet N concentrations of leaf and root produced a negative increment; this indicated that *B. faberi* was limited by P and weakly influenced by N in our experiment.

The response of seedlings to water, P and N regimes confirmed that water and P limit the growth of *B. faberi* seedlings in the first year of growth, yet limitation of N was not apparent. Extremely

Fig. 6. The relationship of P concentration between root and leaf of *B. faberi* seedlings under various fertilization and water conditions. Bars indicate standard error of the mean. ns: non-significant; *, ** or *** annotated $p < 0.05$, 0.01 or 0.001 , respectively (HSD). W: water, N: nitrogen, P: phosphorus.

low available phosphorus (8.30–21.2 mg kg⁻¹, Olson's method) and high available nitrogen (123.56–244.46 mg kg⁻¹, Cornfield's method) (Wang et al., 2003) in surface soil at site strengthened the argument that P was limiting to the growth of *B. faberi* seedling.

Studies in several other arid systems have shown that nutrients can limit growth once water limitations are removed (Drenovsky and Richards, 2004; James et al., 2005; Perring et al., 2008). P limitation of growth in this arid valley contradicts the widely held view that N limiting is widely occurring in arid lands (Hooper and Johnson, 1999; Bennett and Adams, 2001; James et al., 2005). However, several other studies reported that P was a limiting factor to the shrub *Larrea tridentata* in Chihuahuan Desert in both lab and field experiments (Lajtha and Schlesinger, 1988; Schlesinger et al., 1990).

There is a significant evidence that similar co-limitation of water and P may be important for other shrubs' growth in some arid systems (Gleeson and Good, 2003; James et al., 2005; Perring et al., 2008). High N level in our study area seems to be driven by the high levels of organic matter (32.55–72.78 g kg⁻¹ soil) and the high mineralisation rate of this soil that provide a good N supply (Wang et al., 2003; Lu et al., 2006). Atmospheric N deposition from the nearby Sichuan Basin (Liu et al., 2008) may also contribute to enriching the ecosystem with available N.

4.2. Interactive effects of water, N and P to seedling growth

Our results indicated that water and P produced positive effects on seedlings performance, and high N (N2) level had negative effects. The degree and direction were markedly different so that resources interactions could produce various interactive effects. Effects of W × N and W × P interaction for most parameters were not significant and indicated that the water and nutrients availability (especially N and P) had been controlled by independent factors under drought stress on calcareous soil.

Xu et al. (2008) found that the soil water was mainly depended on soil clay content, while N and P availability were determined by soil pH (unpublished data). Increasing alkalinity can reduce N availability through volatilization of mineralized NH₄⁺ and decrease P solubility (Lajtha and Schlesinger, 1988; Chapin, 1991; Marschner, 1995). In calcareous soil, the high soil pH (8.0–9.0) and the presence of free carbonate (49.44–102.75 g kg⁻¹) further decrease P mobility and diffusion, reducing available P to plants; this also concurs with garden research results in the Mediterranean Basin (Sardans et al., 2004) and fertilization experiment in Chihuahuan Desert (Schlesinger et al., 1990). This showed that decreasing soil pH could effectively weaken P limitation through releasing P under drought stress.

On the other hand, N availability was increased by decreasing soil pH and atmosphere N deposition. However, the effect of N on seedling growth depended on N level. High N fertilization has been shown to sharply decrease yield, growth and survival under drought stress (Linder et al., 1987; Güsewell et al., 2003). Therefore high N depressed root growth, biomass production, N and P concentration of tissue and WUE_{leaf}. The main reason could be that fine root growth was severely diminished by excess N supply and the absorption of N and P was restrained. The decline of leaf N and P concentration diminished the carbon fixation, hence declined the production of seedling biomass.

The depressed effects were strengthened with decreasing the P level. The depression effect of high N supply appeared to suggest that an increased N may aggravate P deficiency because high N supply decreased P concentration of leaf and root. Excess N supply might severely diminish root growth or even be toxic to plants (Salih et al., 2005). So, high N should be avoided when selecting sites and cultivating seedlings for vegetation restoration.

However the negative effects can be partially, sometimes, even completely overcome by high P level (P3). So there are significant interactive effects of N and P on plant growth. Graciano et al. (2006) found that P addition increased soil N absorption in young *Eucalyptus grandis*. Similar synergistic interactions of N and P have been widely documented in arid systems (Warren et al., 1996; James et al., 2005; Graciano et al., 2006).

Therefore, it is necessary to consider the interactive effects of water, N and P. For example, P2 and P3 level were optimum for biomass production under N1 and N2 level under drought stress. The water supply appeared to be a primary driver of N and P interaction due to its promoting positive effects of P and reducing depressing effects of high N.

4.3. Interactive effects of water, N and P to seedlings function

Biomass allocation may be a key sensitive predictor of plant functional response to stress (Gleeson and Good, 2003; James et al., 2005). Partitioning more biomass to roots and maintaining higher root shoot ratio are advantageous to drought-adapted plants as drought and nutrient stress occur, because greater water absorptive component (fine root) can sustain more water and nutrient uptake for transpiration and respiration (Singh et al., 2000; Gleeson and Good, 2003; Qu et al., 2003).

Our results were in accordance with this opinion. The fact that the controls had the largest root shoot ratio indicated more biomass allocation to roots and suggested the strongest limitation of water and P. The significant range of root shoot ratio at N1 level indicated that severe water limitation (W1) could be weakened by improving plant plasticity, and the ratio was decreased with increasing water. Meanwhile, a smaller range of root shoot ratios among three P levels across drought regimes at N2 level also indicated that P could improve the drought adaptability by improving seedling plasticity. Root shoot ratio of seedlings was decreased 1–3 folds compared with control seedlings. The larger allocation range pattern means seedlings had strong adaptability to arid environments. Similar root shoot ratio changes (1.5–2.6-folds) were also observed for another shrub seedling (over 90 days) in the same site (Wu et al., 2008).

On the other hand, decreasing root allocation indicated the alleviation of resource limitation (Gleeson and Good, 2003). For example, treatment of W3N1P2 produced largest shoot biomass (6-fold) and smallest root biomass (2-fold) production of *B. faberi* seedlings compared to control. Increasing biomass allocation to roots by N2 supply indicated high N depression effect on *B. faberi* seedling growth compared with N1 supply. Primary limitation by water is indicated by significant responses of biomass allocation of seedling. The relatively small but positive response to P in allocation suggests a lesser limiting effect of P compared to that of soil water.

P increased the WUE_{leaf} irrespective of N level means increasing WUE_{leaf} of *B. faberi* seedlings may be the second way to improve the adaptability. WUE is a functional indicator strongly related to plant growth and health under water deficit conditions. At single leaf level, WUE_{leaf} can be defined as the ratio between the rate of light-saturated photosynthesis (A_{max}) and the rate of stomatal conductance (g_s) for water vapor (Marschner, 1995). In general, there is a good correlation between the WUE_{leaf} and WUE at whole plant level (WUE_{plant}) (Liu et al., 2005).

Our result, the decrease in WUE_{leaf} of *B. faberi* seedlings under water stress, agrees with the response of WUE_{plant} to soil drying (Li et al., 2008), which confirmed that *B. faberi* seedlings employed a luxury water-use strategy. Under N1 condition, P2 and P3 produced highest WUE_{leaf}, and they are higher than that of control; while only P3 level produced the higher WUE_{leaf} than that of control seedling across drought gradient under N2 condition.

P increased drought tolerance of seedling by elevating WUE in two ways. P fertilization increases root growth, which exhibited higher total root length and root surface area, this elevated water uptake efficiency. Furthermore, when soil was treated with P, high P concentrations of roots and leaves led to relatively high rates of water uptake and low transpiration rate, which resulted in more abscisic acid of leaf or xylem which could decline the stomatal conductance and transpiration rate of seedling (Singh et al., 2000; Liu et al., 2005), and then resulted in increase in both WUEs.

The reason for WUE_{leaf} decreased by N₂ in our study may be photosynthetic rate decreased more than transpiration rate when soil N supply was increased (Shangguan et al., 2000). Nakaji and Izuta (2001) explained that excess soil N could reduce the net photosynthetic rate mainly due to the decrease of rubisco quantity in the chloroplasts. Decrease in N and P concentrations of leaf with increase N supply in this study also supported the conclusion.

Our results also suggested that appropriate combination of resources (water, N and P) can obviously enhance the adaptability of *B. faberi* seedling to drought condition by getting better growth characters, increasing biomass production and WUE (Singh et al., 2000; Wu et al., 2008). Moreover, the decline of drought stress from W1 level to W3 level would increase the availability of N and P, which could contributed to seedling growth and nutrient status. WUE also increased dramatically with the addition of AP and AN, yet the high N level depressed the seedling growth and WUE. This result is consistent with Wu et al. (2008).

Above all, it is necessary to know the spatial and temporal patterns of soil water and nutrients, which would be the precondition to appropriate site selection for seedling plantation in the field. Conceiving that the performance and survival of seedlings are affected by the interactive effects of water and nutrients in soil.

5. Conclusion

Our greenhouse experiment showed that the performance of *B. faberi* seedlings was determined by the interactive effects of water and nutrients in the arid valley of Mingjiang River, SW China. Drought stress, P deficiency and high N level dramatically decreased the growth and biomass production of *B. faberi* seedling, allocated more biomass to root, and decreased nutrient status and WUE. The interactive effects of N and P were significant, and higher P significantly reduced the inhibitive effects of N₂ probably through enhancing P nutrient status and WUE_{leaf}. P addition enhanced the growth and adaptability of *B. faberi* seedlings under drought stress, and the optimum P level depended on soil N concentration. We recommend that appropriate resources combination (W3N1P2) would be the optimal condition to *B. faberi* seedling growth, but higher N and the combination of higher N and lower P should be avoided in restoration. Further studies should be conducted in field to test the above results and to detect the roles of soil pH and moisture on the nutrients availability.

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