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Early growth, dry matter allocation and water use efficiency of two sympatric *Populus* species as affected by water stress

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Abstract

We exposed cuttings of two sympatric species of *Sect. Tacamahaca* Spach, *Populus cathayana* Rehder and *Populus przewalskii* Maximowicz, to two watering regimes in a greenhouse. In the semi-controlled environmental study, two watering treatments which were watered to 100 and 25% of field capacity were used, respectively. The effects of water deficit on early growth, biomass allocation and water use efficiency (WUE) were investigated. We found that there were significant interspecific differences in early growth, dry matter allocation and water use efficiency between two sympatric *Populus* species. Compared with *P. cathayana*, *P. przewalskii* showed higher shoot height, dry matter accumulation, number of leaves, total leaf area, fine root mass, fine root/total root ratio and water use efficiency under both well-watered and water-stressed treatments. On the other hand, *P. przewalskii* also showed higher root mass/foliage area ratio, root/shoot ratio and carbon isotope composition than *P. cathayana* under water-stressed treatment. The results suggested that there were different water-use strategies between two sympatric *Populus* species, *P. przewalskii* with higher drought tolerance may employ a conservative water-use strategy, whereas *P. cathayana* with lower drought tolerance may employ a prodigal water-use strategy. The findings confirm the existence of interspecific genetic differences in early growth, dry matter allocation and water use efficiency as affected by water stress, these variations in drought responses may be used as criteria for species selection and tree improvement.

Keywords: Carbon isotope composition; Dry matter allocation; Early growth; *Populus cathayana*; *Populus przewalskii*; Water-use efficiency

1. Introduction

In arid and semi-arid regions, drought is a major constraint imposed on tree survival and growth (William, 1981; Gower et al., 1992; Becker et al., 1994). When soil water is gradually depleted, a number of tree functions are inhibited. During evolution, many tree species have developed various mechanisms to enhance their drought adaptation, including well-developed root systems, growth rate adjustment, plant structure modification and water use efficiency (WUE) increase. Although much is known about physiological and morphological responses to water deficits in woody plant studies (reviewed by Levitt, 1980; Kramer, 1983; Jones, 1992; Larcher, 1995;

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Blum, 1997; Kozlowski and Pallardy, 2002), particularly in poplar (Tschaplinski et al., 1998; Brignolas et al., 2000; Johnson et al., 2002; Amlin and Rood, 2003; Siemens and Zwiazek, 2003), interspecific differences in these responses between the sympatric species have been studied relatively little.

There has been a considerable effort to elucidate the degree and nature of the genetic control over WUE in plant. WUE is traditionally defined as the ratio of dry matter accumulation to water consumption over a season. Increasing WUE could theoretically affect plant growth. When water is limited, plants that use a finite water supply more efficient would grow more rapidly, in this case, high WUE would positively affect plant productivity (Wright et al., 1993). Another way to increase WUE is to close stomata partially, thus restricting photosynthesis relative to plants whose stomata are fully open, this strategy would result in a negative correlation between WUE and plant productivity (Richards and Condon, 1993). Recently, effects of water deficits on plant productivity and WUE have been extensively reviewed, and measurement of WUE has been simplified by the discovery of a strong correlation between WUE and stable isotope composition (δ^{13}C)(Farquhar and Richards, 1984; Farquhar et al., 1989; Hubick and Gibson, 1993; Li, 1999). The carbon isotope ratio of plant tissue provides an integrated measurement of internal plant physiological and external environmental properties influencing photosynthetic gas exchange over the time when the carbon was fixed (Anderson et al., 1996; Brodribb and Hill, 1998).

Poplars (*Populus* spp.) are important components of ecosystems and, due to their fast growth, represent optimal species for the production of biomass suitable as a source of fuel, fiber, lumber and plywood. *Populus* spp. showed a wide variability in WUE and drought-tolerance (Schulte et al., 1987; Ceulemans et al., 1990; Tschaplinski et al., 1994; Tschaplinski and Tuskan, 1994). In the five sections of *populus* genus, the species of Sect. *Tacamahaca* are the most and mostly originated from China. In this study, we used two sympatric species of *Sect. Tacamahaca* Spach, *Populus cathayana* Rehder and *Populus przewalskii* Maximowicz, as materials to: (1) determine effects of water deficit on growth and morphology; (2) measure interspecific differences in WUE and δ^{13}C between two sympatric species; (3) analyze the relationships between early growth, biomass allocation and WUE under two watering regimes. Such knowledge is essential for species selection and tree improvement.

2. Materials and methods

2.1. Plant materials and experimental design

The plant materials of two sympatric species of *Sect. Tacamahaca* Spach, *P. cathayana* and *P. przewalskii*, were from cuttings which were collected in their natural habitats (32°33′–33°06′N, 101°27′–103°55′E, 1450–3100 m Altitude) in Northwest Sichuan, Southwest China. Mean annual rainfall, temperature, maximum temperature and minimum temperature were 635 mm, 9.1, 32.8 and –14.4 °C, respectively. Forty healthy cuttings of uniform height were chosen from each species and each cutting was transferred to a plastic pot with 5 l of volume filled with homogenized soil and grown in a naturally lit greenhouse under the semi-controlled environment with a day temperature range of 12–31 °C and a night temperature ranged of 9–15 °C, and the relative humidity range of 35–85% during 1 May to 30 September 2003, in Maoxian Field Ecological Station.

The experimental layout was completely randomized with two factors (species and watering regime). Two watering treatments which were watered to 100 and 25% of field capacity were used, respectively. Twenty cuttings from each species were exposed to each watering treatment. Five replications, each with four cuttings, were used in each species and each watering treatment. In the well-watered treatment, the pots were weighed every second day and re-watered to field capacity by replacing the amount of water transpired, in this case, the soil water content was always kept at 40.20% by two-daily watering. In the water-stressed treatment, the pots were watered to 25% of field capacity by watering every second day, in this case, the soil water content was always kept at 10.05% by two-daily watering. Evaporation from the soil surface was prevented by enclosing all pots in plastic bags sealed at the base of the stem of each cutting. A total of 12 g slow release fertilizer (13% N, 10% P and 14% K) was added to each pot during the experiment.

An empirical relationship between plant fresh weight (Y, g) and plant height (X, cm): $Y = 0.975 + 0.112X$, ($R^2 = 0.968$, $P < 0.001$) (Li et al., 2004) was used to correct pot water for changes in plant biomass. In addition, 10 pots without plants were used to monitor evaporative water loss from the soil surface throughout each watering regime. Dead branches were substituted for plants at the top of the pot to reduce direct isolation and air movement.

2.2. Growth measurements

All cuttings were harvested at the end of the experiment, and divided into leaves, stem and roots (including coarse roots and fine roots, fine roots were defined as those less than 2 mm in diameter). Biomass samples were dried (70 °C, 48 h) to constant and weighed. Leaf area was determined by Portable Laser Area Meter (CI-203, CID Inc., USA). Fine root/total root ratio, root mass/foliage area ratio and root/shoot ratio were then calculated.

2.3. Water use efficiency

WUE was calculated for each plant as the ratio of biomass production to water transpired during the experiment. Biomass at the beginning of the experiment was estimated using empirical relationships with diameter and height for each species and subtracted from biomass at the end of the experiment. While calculating the amount of water transpired during the experiment, evaporative loss from the pots was taken into account by subtracting the average amount of water loss from the control pots.

2.4. Carbon isotope composition

Leaf samples from all harvested cuttings were used for carbon isotope analysis. The oven dried leaves were homogenized by grinding in a ball mill and abundance of stable isotopes of carbon in combusted samples was measured with a mass spectrometer (Finnegan MAT DeltaE). The overall precision in δ-values was better than 0.1% determined by repetitive samples.

2.5. Statistical analysis

Analyses of variance (ANOVA) for variables from measurements were used for testing the species and treatment differences. Pearson's correlation coefficients were calculated to determine the relationships between variables using individual data. Statistical analysis was done with SPSS 11.0 for Windows statistical software package.

3. Results

3.1. Variation in early growth and dry matter allocation

Water stress was a very important limiting factor at the initial phase of plant growth and establishment. Changes in early growth and dry matter allocation in response to water stress exhibited the primary signals for drought tolerance. There were significant differences in shoot height, total biomass, total number of leaves, total leaf area, coarse root mass, fine root mass, fine root/total root ratio, root mass/foliage area ratio and root/shoot ratio between two sympatric *Populus* species (Tables 1–4). Compared with *P. cathayana*, *P. przewalskii* showed higher shoot height, total biomass, total number of leaves, total leaf area, fine root mass and fine root/total root ratio, and lower coarse root mass under well-watered and water-stressed treatments. On the other hand, *P. cathayana* showed higher root mass/foliage area ratio and root/shoot ratio than *P. przewalskii* under well-watered treatment, but opposite results were found under water-stressed treatment. In addition, the watering regimes significantly affected all these morphological properties, and the watering × species interaction effect was also significant except for fine root mass.

3.2. Variation in WUE and δ^{13}C

Water stress not only changed plant growth and structure, but also affected plant physiological properties, such as WUE and δ^{13}C. Significant difference in WUE between two sympatric *Populus* species was detected under well-watered and water-stressed treatments (Table 4). However, significant difference in δ^{13}C was only found under water-stressed treatment. Compared with *P. cathayana*, *P. przewalskii* had higher WUE under two watering regimes. On the other hand, *P. przewalskii* also exhibited higher δ^{13}C as affected by water stress than *P. cathayana*. In addition, the watering effect was highly significant

Table 1
Early growth of two sympatric *Populus* species as affected by two watering regimes

Watering regime (%)	Species	Height (cm)	Dry mass (g)			
			Root	Stem	Leaves	Total
100	JZ	160.50 ± 3.68	42.90 ± 1.15	39.68 ± 2.63	23.34 ± 1.51	105.92 ± 2.94
	AB	198.88 ± 2.60	42.44 ± 2.14	65.15 ± 2.64	36.33 ± 0.22	143.92 ± 2.45
	P > Fs	<0.001	0.845	0.001	0.001	<0.001
25	JZ	27.47 ± 0.72	2.20 ± 0.50	0.71 ± 0.04	1.38 ± 0.11	4.28 ± 0.65
	AB	31.95 ± 0.29	9.90 ± 0.61	1.64 ± 0.02	2.47 ± 0.23	14.01 ± 0.52
	P > Fs	<0.001	0.001	<0.001	0.012	<0.001
	P > Fw	<0.001	<0.001	<0.001	<0.001	<0.001
	P > Fs	<0.001	0.020	<0.001	<0.001	<0.001
	P > Fw × s	<0.001	0.011	<0.001	<0.001	<0.001

JZ, *P. cathayana*; AB, *P. przewalskii*. Fw, watering effect; Fs, species effect; Fw × s, watering × species interaction effect. The data presented were means ± standard error.

Table 2
Leaf morphological characteristics of two sympatric *Populus* species as affected by two watering regimes

Watering regime (%)	Species	Leaves			
		No. of leaves	Total area (dm^2)	Length (cm)	Width (cm)
100	JZ	41.00 ± 1.16	28.40 ± 0.87	12.93 ± 0.25	8.03 ± 0.21
	AB	55.33 ± 3.76	51.89 ± 1.21	13.56 ± 0.30	9.84 ± 0.19
	P > Fs	0.022	<0.001	0.182	0.003
25	JZ	15.00 ± 0.00	1.67 ± 0.03	5.27 ± 0.11	2.94 ± 0.17
	AB	18.67 ± 1.20	3.41 ± 0.42	6.65 ± 0.51	4.06 ± 0.29
	P > Fs	0.038	0.014	0.058	0.029
	P > Fw	<0.001	<0.001	<0.001	<0.001
	P > Fs	0.002	<0.001	0.075	<0.001
	P > Fw × s	0.032	<0.001	0.282	0.157

JZ, *P. cathayana*; AB, *P. przewalskii*. Fw, watering effect; Fs, species effect; Fw × s, watering × species interaction effect. The data were means ± standard error.

Table 3
Root morphological characteristics of two sympatric *Populus* species as affected by two watering regimes

Watering regime (%)	Species	Root dry mass (g)		
		Coarse root (>2 mm)	Fine root (≤2 mm)	Fine root/total root ratio
100	JZ	17.61 ± 1.22	11.28 ± 0.85	0.37 ± 0.00
	AB	10.30 ± 0.92	15.76 ± 0.79	0.61 ± 0.02
	P > Fs	0.007	0.013	<0.001
25	JZ	0.39 ± 0.08	0.78 ± 0.07	0.70 ± 0.01
	AB	0.00 ± 0.00	3.05 ± 0.46	1.00 ± 0.00
	P > Fs	0.009	0.008	<0.001
	P > Fw	<0.001	<0.001	<0.001
	P > Fs	0.002	0.001	<0.001
	P > Fw × s	0.004	0.142	0.006

JZ, *P. cathayana*; AB, *P. przewalskii*. Fw, watering effect; Fs, species effect; Fw × s, watering × species interaction effect. The data were means ± standard error.

Table 4

Root mass/foliage area ratio (R_f), root/shoot ratio (R_s), water-use efficiency (WUE) and carbon isotope composition (δ^{13}C) of two sympatric *Populus* species as affected by two watering regimes

Watering regime (%)	Species	R_f (g dm^{-2})	R_s	WUE (g kg^{-1})	δ^{13}C (%)
100	JZ	1.13 ± 0.07	0.55 ± 0.04	4.13 ± 0.05	−33.12 ± 0.23
	AB	0.73 ± 0.06	0.41 ± 0.02	4.59 ± 0.07	−32.20 ± 0.38
	P > Fs	0.016	0.012	0.005	0.081
25	JZ	2.31 ± 0.41	1.85 ± 0.37	7.93 ± 0.62	−30.22 ± 0.51
	AB	3.99 ± 0.36	3.01 ± 0.16	13.00 ± 2.12	−28.51 ± 0.13
	P > Fs	0.037	0.045	<0.001	0.031
	P > Fw	<0.001	<0.001	<0.001	<0.001
	P > Fs	0.049	0.015	0.015	0.030
	P > Fw × s	0.006	0.004	0.034	0.267

JZ, *P. cathayana*; AB, *P. przewalskii*. Fw, watering effect; Fs, species effect; Fw × s, watering × species interaction effect. The data were means ± standard error.

Table 5

Correlation coefficients among some morphological and physiological properties of two sympatric *Populus* species as affected by well-watered treatment (upper triangle) and water-stressed treatment (lower triangle)

Properties	H_t	T_b	L_a	F_t	R_f	R_s	WUE	δ^{13}C
H_t		0.853**	0.950***	0.922***	−0.795**	−0.850**	0.879**	0.770**
T_b	0.799**		0.860**	0.932***	−0.418	−0.525	0.935***	0.873**
L_a	0.639*	0.788**		0.919***	−0.762*	−0.760*	0.810**	0.674*
F_t	0.373	0.832**	0.679*		−0.654*	−0.740*	0.880**	0.836**
R_f	0.520	0.773**	0.249	0.781**		0.965***	−0.746*	−0.527
R_s	0.554	0.869**	0.464	0.900***	0.938***		−0.720*	−0.600
WUE	0.897***	0.928***	0.748*	0.593	0.642*	0.679*		0.944***
δ^{13}C	0.847**	0.682*	0.645*	0.526	0.595	0.647*	0.857**	

H_t: shoot height; T_b: total biomass; L_a: total leaf area; F_t: fine root/total root ratio; R_f: root mass/foliage area ratio; R_s: root/shoot ratio; WUE: water use efficiency; δ^{13}C, carbon isotope composition.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

for both physiological properties, and the watering × species interaction effect was also significant except for δ^{13}C.

3.3. Early growth correlated with dry matter allocation, WUE and δ^{13}C

Biomass production, including shoot height, total biomass and total leaf area showed a significant positive correlation with WUE and δ^{13}C under two watering regimes (Table 5). Under well-watered treatment, root mass/foliage area ratio and root/shoot ratio were negatively correlated with shoot height, total leaf area and fine root/total root ratio. However, under water-stressed treatment, root mass/foliage area ratio and root/shoot ratio were positively correlated with total biomass and fine root/total root ratio. In addition, the correlation between WUE and δ^{13}C was also highly significant under both watering regimes.

4. Discussion

There were many studies focusing on the morphological and physiological adaptation of *Populus* to drought stress (Souch and Stephens, 1998; Brignolas et al., 2000; Johnson et al., 2002; Marron et al., 2003; Siemens and Zwiazek, 2003; Li et al., 2004). WUE increase, plant structural modifications and growth pattern adjustments are useful indices of the consequences of water deficit (Nativ et al., 1999; Li et al., 2000; Tsialtas et al., 2001; Ponton et al., 2002; Li and Wang, 2003). In our study, differences in drought adaptations between two sympatric species of *Sect. Tacamahaca* Spach, *P. cathayana* and *P. przewalskii*, were demonstrated and attributed to interspecific differences in these morphological and physiological responses to water availability.

Significant interspecific differences between two sympatric *Populus* species were found in shoot height, total biomass, total number of leaves, total leaf area, fine root/total root ratio, root mass/foliage area ratio, root/shoot ratio and WUE under well-watered and water-stressed treatments. The effect of watering and interaction between watering and species were also significant in these morphological properties and WUE. Under water stress, biomass production, such as shoot height, total biomass, total number of leaves, total leaf area, were significantly decreased, while fine root/total root ratio, root mass/foliage area ratio, root/shoot ratio and WUE were significantly increased. Similar results also reported in many previous studies (Tschaplinski et al., 1998; Li et al., 2000; Amdt et al., 2001; Marron et al., 2002; Siemens and Zwiazek, 2003; Zhang et al., 2004). Compared with *P. cathayana*, *P. przewalskii* showed higher biomass production, fine root/total root ratio and WUE under both well-watered and water-stressed treatments.

On the other hand, *P. cathayana* showed higher root mass/foliage area ratio and root/shoot ratio than *P. przewalskii* under well-watered treatment, but opposite changes were found under water-stressed treatment. It implied that *P. przewalskii* was more responsive to water deficit and well-developed root systems than *P. cathayana*. Root systems are complex and dynamic structures, water uptake may be limited by the amount of roots in a particular soil layer and enhancing root growth can increase drought-tolerance (Klepper and Rickman, 1990). Plant productivity under drought stress is strongly related to the processes of dry matter partitioning and the spatial and temporal root distribution (Kage et al., 2004). Biomass allocation to root, and the quantity and length of functional roots increased under water stress (reviewed by Larcher, 1995; Kozlowski and Pallardy, 2002). Accordingly, water deficit mostly reduced leaf growth and increased at least relatively dry matter allocation into the root fraction, leading to a significant raise of root mass/foliage area ratio, root/shoot ratio and fine root/total root ratio under drought stress. Similarly, comparing the drought-tolerant clones with drought-sensitive ones, the former had greater carbon allocation to roots during the early stages of drought, but the latter had no plasticity of biomass allocation under water deficit (Timothy et al., 1998).

Significant difference in δ^{13}C between two sympatric *Populus* species was only found under drought stress. *P. przewalskii* exhibited a distinctly higher δ^{13}C as affected by drought than *P. cathayana*. Variation in δ^{13}C was less in well-watered treatment than in water-stressed treatment, suggesting that relationships between physiological responses and drought adaptations were complicated by internal drought tolerance mechanisms and external environmental factors, such as water availability, or their interaction. Similar results were also reported in many previous studies (Farquhar et al., 1989; Zhang et al., 1993; Anderson et al., 1996; Li, 2000; Ponton et al., 2002). Although δ^{13}C was increased significantly by water stress, no interaction between genotype and watering was detected, which is consistent with most previous studies (Johnson and Bassett, 1991; Read et al., 1992; Zhang et al., 1994; Li, 1999; Ponton et al., 2002).

In conclusion, we found that there were significant interspecific differences in early growth, dry matter allocation, and WUE between two sympatric *Populus* species under well-watered and water-stressed treatments. Compared with *P. cathayana*, *P. przewalskii* showed higher biomass production and WUE under two watering regimes. On the other hand, *P. przewalskii* also showed higher plasticity of biomass allocation and greater carbon allocation to roots than *P. cathayana* under water-stressed treatment. Moreover, *P. przewalskii* also exhibited a distinctly higher δ^{13}C as affected by drought than *P. cathayana*. These results suggested that there were different water-use strategies between two sympatric *Populus* species, *P. przewalskii* with higher drought tolerance may employ a conservative water-use strategy, whereas *P. cathayana* with lower drought tolerance may employ a prodigal water-use strategy.

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