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BRIEF COMMUNICATION

Plasticity in physiology and growth of *Salix matsudana* in response to simulated atmospheric temperature rise in the Mu Us Sandland

W.-M. HE and M. DONG*

Laboratory of Quantitative Vegetation Ecology, Institute of Botany, the Chinese Academy of Sciences, Beijing, 100093, P.R. China

Abstract

In a controlled experiment, *Salix matsudana* cuttings were subjected to three atmospheric temperatures (*i.e.* control, 0.5 and 1.0 °C above the control, respectively) to explore their short-term plastic responses to simulated atmospheric temperature rise. Warming affected significantly net photosynthetic and transpiration rates, but had no significant impacts on water use efficiency, ratio of sub-stomatal to atmospheric CO_2 concentration, maximum quantum yield, water saturation deficit, tissue density, and water loss. Leaf natality and leaf mortality were affected significantly by increasing atmospheric temperature. Total plant biomass, leaf mass ratio, root mass ratio, and canopy productivity index exhibited significant responses to the warming treatments, but obvious differences in the changing details did appear among the four traits. Hence: (*1*) *S. matsudana* cuttings were sensitive to small-range atmospheric temperature increases such as 0.5-1.0 °C, which can alter growth and allocation through modifying photosynthetic rate and leaf turnover. (*2*) Short-term physiological acclimation did not occur in young individuals of *S. matsudana.* (*3*) The warming depressed growth of young individuals of *S. matsudana* to various extents.

Additional key words: canopy productivity index; growth and allocation; leaf turnover; maximum quantum yield; net photosynthetic rate; physiological acclimation; sub-stomatal and atmospheric CO_2 concentration; transpiration rate; water use efficiency.

Recently, much attention has been given to the effects of global or regional warming on plants (*e.g.* Arft *et al.* 1999, Day *et al.* 1999, Morison and Lawlor 1999). It is impossible for these studies to distinguish the influence on phenotypic variance of warming from genetic difference because the used materials (*e.g.* seedlings or adult plants) have different genotypes. Moreover, many studies concern two temperature regimes (*i.e.* present and elevated temperatures), but some important details about changing processes are obscured. Over the past 40 years, the mean annual atmospheric temperature increased by 0.5-1.8 °C, exerting profound impacts on the structure and function of ecosystems in the semi-arid and arid regions in China (Zhao 1996). During this period, in the semi-arid Mu Us Sandland atmospheric temperature gradually increased whereas precipitation gradually decreased (Zhang 1994). Up to now the Mu Us Sandland has become very vulnerable due to frequent extreme climate and intentional exploitations, and its landscapes have become highly fragmented (Li 1990, Zhang 1994, Chen and Zhang 1996, Jiang and Zhu 2001). *Salix matsudana* forests are commonly found in the Mu Us sandland, where forest stands play a vital role to combat desertification in the semi-arid and arid regions in China (Li 1990, Zhang 1994, He and Dong 2003).

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*Corresponding author; Institute of Botany, the Chinese Academy of Sciences, No. 20 Nanxincun, Fragrant Hills, Haidian District, Beijing 100093, P.R. China; fax: 086-010-82596265; e-mail: dongming@95777.com

Abbreviations: C_i/C_a – ratio of substomatal to atmospheric CO_2 concentration; CPI – canopy productivity index; E – transpiration rate; k – coefficient of water loss; LM – leaf mortality; LN – leaf natality; LMR – leaf mass ratio; MQY – maximum quantum yield; P_N – net photosynthetic rate; RMR – root mass ratio; TD – tissue density; TPB – total plant biomass; WSD – water saturation deficit; WUE – water use efficiency.

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The aim of this research was to examine the short-term effects of atmospheric temperature rise on plasticity in physiology and growth of *S. matsudana* that still dominates after experiencing strong climate change in the Mu Us Sandland. We hypothesised that (*1*) the young individuals of *S. matsudana* can stand small-range warming such as 0.5-1.0 °C, simulating the atmospheric temperature rise over the last 40 years in the semi-arid regions in China, and (*2*) this warming does not depress significantly the growth of the young individuals. To test the hypotheses, a short-term controlled experiment subjected *S. matsudana* to three contrasting temperatures (*i.e.* control, 0.5 and 1.0 °C above the control, respectively).

S. matsudana Koidz. (Salicaceae) is a cold- and drought-tolerant tree species; its buds and catkin are usually initiated in the previous year and fully developed in winter, and break in spring; and its defoliation ends in October (EBFC 1984). This species can occupy wider habitats through asexual propagation. The experiment was conducted at the Ordos Sandland Ecological Station (110°15'E, 39°34'N, 1 247 m a.s.l.), Institute of Botany, the Chinese Academy of Sciences, where the mean annual precipitation is 388 mm, *ca*. 70 % of which falls in July to September. The mean annual temperature is 6 °C, and the potential evapotranspiration rate may be up to 2.0 (Zhang 1994).

On 6 April 1999, we collected 100 two-year-old twigs (*ca*. 15 cm length) from the same plant of *S. matsudana*, and then planted each twig into a growth container (about 9 000 cm^3) filled with top soil from local habitats. The *S. matsudana* cuttings shared the same genotype, so the plasticity in physiology and growth derived from the warming treatments. On 4 May 1999, plastic greenhouses were constructed in the form of 1.5 m high dome-shaped tents using PVC tubes as support for the transparent cover out of optically neutral, 0.05 mm thick polythene film. The film reduced photosynthetically active radiation by *ca*. 10 % on the basis of the results measured with a quantum sensor. The tents had a base area of 2.0×1.5 m. Greenhouses consisted of three kinds of tents. For the first type, as the control, only the top surface of the tents was kept and the other parts were removed; the second type had 10 vents (25×25 cm) in each side; the third type had five similar vents in each side. Maximum, minimum, and mean temperatures were recorded at 30-min intervals with data-loggers (model *CR10*, *Campbell Scientific*, Sutton Bonnington, England). The average atmospheric temperatures in the second and third types of tent were *ca*. 0.5 and 1.0 °C higher than that in the first type of tents (*i.e.* the control), respectively, and were denoted +0.5 and +1.0, respectively, while the first type of tent was control. On 16 May 1999, we selected similar cuttings and then put them randomly in the treatments of control, +0.5, and +1.0. Each treatment had 10 replicates. During the experiment, the plants were watered and provided with nutrient solution as necessary. The experiment ran from 16 May to 15 August 1999. The numbers of natal and dead leaves were recorded daily, leaf natality (LN) (*i.e.* the number of new leaves per day) and leaf mortality (LM) (*i.e.* the number of dead leaves per day) were calculated as described by He and Dong (2003).

We selected five similar leaves per treatment for physiological measurements. Net photosynthetic rate (P_N), transpiration rate (E), atmospheric CO_2 concentration (C_a), and sub-stomatal CO_2 concentration (C_i) were determined at one-hour intervals with an open flow gas exchange system (*LCA-4, ADC*, Hoddesdon, England) from 07:00 through 18:00. Water use efficiency (WUE) was calculated according to Gibson (1998). Chlorophyll *a* (Chl) fluorescence was measured from 21:00 through 22:00 on the leaves used for gas exchange measurement. After at least 20 min of dark adaptation, the minimal level of Chl fluorescence (F_0) was measured with a Plant Efficiency Analyzer (*PEA*) (*Hanatech*, UK), and the maximal Chl fluorescence (F_m) was induced by a 1 s saturating flash provided by the *PEA*. Variable Chl fluorescence (F_v) is $F_m - F_0$, and the maximum quantum yield (MQY) of photosystem 2 was calculated as F_v/F_m (Adams *et al.* 1990).

On 13 August 1999, we collected 20 fully developed leaves from each atmospheric temperature to determine water saturation deficit (WSD), tissue density (TD), and coefficient of water loss (k) (Beadle *et al.* 1993, Wright and Westoby 1999, He *et al.* 2003). At the end of experiment, all experimental plants were harvested and then separated into roots, stems, and leaves. Leaf area was measured with a *CI-203* area meter, the harvested materials were oven-dried at 85 °C for 48 h, and then weighted. Canopy productivity index (CPI) was calculated as described by Norby (1996). All the physiological and growth characteristics were statistically analysed by one-way analysis of variance according to the General Linear Model (SAS 1985).

During the experimental period, the average atmospheric temperature under the control condition was 24.4 °C, there were no significant differences in both relative atmospheric humidity (63±2 %) and atmospheric CO_2 concentration (346±4 $cm^3\ m^{-3}$) between the three treatments ($p > 0.05$). P_N and E were affected significantly by the warming treatments ($p < 0.05$), but WUE, C_i/C_a, and MQY were not affected ($p > 0.05$) (Table 1). Hence the warming treatments had different impacts on gas exchange and Chl fluorescence. WSD, TD, and k did not respond significantly to the warming treatments ($p > 0.05$), suggesting that structurally drought-tolerant capacity did not increase with increasing atmospheric temperature.

LN was significantly greater for the cuttings grown at the control and +0.5 than those grown at the +1.0 ($p < 0.05$). LM decreased gradually with increasing atmospheric temperature (Table 1). This indicated that leaf turnover decreased with increasing atmospheric temperature. TPB was significantly greater for the cuttings grown at the control and +0.5 than those grown at the

+1.0 ($p < 0.05$). LMR increased gradually with increasing atmospheric temperature. CPI showed an opposite pattern to LMR. RMR was significantly smaller for the cuttings grown at elevated temperatures than for the control ones ($p < 0.05$). These changes (Table 1) indicated that the growth and biomass allocation of the cuttings were highly sensitive to the warming treatments.

Table 1. Differences in net photosynthetic rate (P_N) [µmol m^{-2} s^{-1}], transpiration rate (E) [mol m^{-2} s^{-1}], water use efficiency (WUE) [mmol mol^{-1}], ratio of sub-stomatal to atmospheric CO_2 concentration (C_i/C_a), maximum quantum yield (MQY), water saturation deficit (WSD) [kg kg^{-1}], tissue density (TD) [kg kg^{-1}], coefficient of water loss (k), leaf natality (LN) [number per day], leaf mortality (LM) [number per day], total plant biomass (TPB) [g], leaf mass ratio (LMR) [kg kg^{-1}], root mass ratio (RMR) [kg kg^{-1}], and canopy productivity index (CPI) [kg m^{-2}] induced by atmospheric temperature. +0.5 and +1.0 indicates that the average atmospheric temperature during the whole experiment was about +0.5 and +1.0 °C higher than in the control. Means ± SE, $n = 5$ (P_N, E, WUE, C_i/C_a, MQY), 20 (WSD, TD, k), or 10 (LN, LM, TPB, LMR, RMR, CPI).

	Control	+0.5	+1.0
P_N	12.02±0.03	9.11±0.18	8.34±0.17
E	9.52±0.21	8.11±0.22	6.73±0.19
WUE	1.30±0.04	1.12±0.06	1.34±0.07
C_i/C_a	0.81±0.04	0.77±0.05	0.71±0.05
MQY	0.855±0.015	0.851±0.016	0.853±0.012
WSD	0.095±0.006	0.085±0.004	0.099±0.004
TD	0.318±0.011	0.316±0.009	0.318±0.008
k	0.968±0.032	0.966±0.028	0.963±0.027
LN	0.823±0.025	0.824±0.024	0.754±0.036
LM	0.17±0.01	0.14±0.01	0.12±0.01
TPB	17.73±1.03	17.24±0.99	12.23±0.97
LMR	0.30±0.01	0.326±0.01	0.35±0.01
RMR	0.27±0.02	0.21±0.02	0.22±0.02
CPI	0.52±0.03	0.43±0.03	0.39±0.03

Gas exchange is sensitive to changing environment (Long *et al.* 1993, Gibson 1998, Morison and Lawlor 1999). This is supported partly by our results. For example, P_N and E decreased significantly with increasing atmospheric temperature. MQY is a good estimation of the maximum photochemical efficiency of photosystem 2 (Adams *et al.* 1990). The difference in gas exchange and Chl fluorescence suggests that both may differ in the sensitivity to warming (for similar results see Gordon *et al.* 1999, Morison and Lawlor 1999). C_i/C_a, which is usually used to assess the physiological adaptation of stomata to stress, tends to decrease with increasing water stress (He and Dong 2003). Variation in WSD, TD, and k can reflects the difference in structurally drought-resistant capacity (cf. He and Dong 2003). These values indicate the leaf capability to resist drought and to conserve water: high values of WSD, TD, and k correspond to low drought-tolerant and water-holding capability (Beadle *et al.* 1993, He and Dong 2003). The changes in WUE, C_i/C_a, WSD, TD, and k with atmospheric temperature indicated that the plasticity in drought-resistant and water-holding capacity might be relatively conservative, and this capacity was not enhanced significantly for the plants grown at the elevated temperatures compared with the control plants.

Both LN and LM restricted leaf turnover. High leaf turnover corresponds to high carbon cost (Carlton and Bazzaz 1998). LN and LM were depressed by atmospheric temperature rise to some extent (Table 1), which may be beneficial to reduce the expense of leaf production and help plants accumulate more biomass (He and Dong 2003). Based on the TPB data, the growth of the young individuals of *S. matsudana* might not be depressed when atmospheric temperature increased only by 0-0.5 °C, but the growth of young individuals of *S. matsudana* might be depressed obviously at atmospheric temperature increase by 0.5-1.0 °C. CPI simultaneously concerns biomass accumulation and leaf area, so it is a good indicator of matter production efficiency per unit leaf area (Norby 1996). Based on the CPI values, the cuttings grown at elevated atmospheric temperatures were inhibited compared with those grown at control condition, regardless of 0-0.5 and 0.5-1.0 °C. This plasticity in growth is likely associated with the above-mentioned variation in physiology because the latter's variation might influence growth and carbon balance (Palmroth *et al.* 1997). LMR increased with increasing atmospheric temperature. This may be an adaptive strategy because increased LMR is useful to reduce leaf surface temperature of the plants grown under higher temperature.

Atmospheric temperature rise has diverse influence on photosynthesis, dark respiration, and transpiration; one effect may be offset or masked by the others (Arft *et al.* 1999, Gordon *et al.* 1999). However, there are still no general patterns regarding warming effects because the results of experiments depend on the species, experimental treatment, and duration of the experiment (Arft *et al.* 1999, Morison and Lawlor 1999). Regional warming will continue in northern China (Zhao 1996). The present work revealed considerable plasticity in physiology and growth of the *S. matsudana* cuttings during one growing season. It is inferred that: (*1*) The young individuals of *S. matsudana* may tolerate temperature stress in the period from May to August because they can stand small-range atmospheric temperature rise (0.5-1.0 °C) through modifying their physiology. But we do not know how they can stand elevated temperatures for a longer period, in winter in particular, because elevated temperature may perturb rhythm of normal plant dormancy and change plant tolerance of low temperatures in wintertime. (*2*) This small-range atmospheric temperature rise may be harmful to the growth and maintenance of *S. matsudana* seedlings during the growing season.

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