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Plant Growth and Water Use Efficiency of Four Chinese Conifer Tree Species under Different Air Humidity

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Summary

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Air humidity is an important controlling factor for the establishment of tree seedlings. It is predicted that the annual amount of rainfall will decline in some parts of China due to the global climate change in the foreseeable future. There is limited information on the potential responses of this region's forest to the global climate change. Our study investigated the responses of four major Chinese conifer tree species to air humidity variations. Seedlings of *Pinus massoniana* Lamb. var. *massoniana*, *Pinus tabulaeformis* Carr. var. *tabulaeformis*, *Platycladus orientalis* (Linn.) Franco cv. Sieboldii and *Cunninghamia lanceolata* (Lamb.) Hook were grown in controlled environment chambers under four different air humidity (RH: 40, 50, 60 and 70 % or VPD: 2.4, 2.0, 1.6 and 1.2 kPa). Results showed that the growth of these four species responded to air humidity differently. *P. massoniana* was the most sensitive species, *P. tabulaeformis* and *P. orientalis* were less sensitive and *C. lanceolata* was the least sensitive species. However, the biomass increment (Δbiomass) and the relative growth rate (RGR) over the experimental period were higher under the RH 70 % treatment than that under the 40 % treatment for all the four species. Δbiomass and RGR were reduced by 54 % and 47 %, respectively, under the RH 40 % treatment compared with those under the RH 70 % treatment for *P. massoniana*, 24 % and 12 % for *P. tabulaeformis*, 22 % and 16 % for *P. orientalis*, 9 % and 5 % for *C. lanceolata*. The decreased growth under drier air conditions was partially due to the closure of leaf stomata and subsequently the depression of photosynthesis. Plants under higher humidity conditions had higher water use efficiency (WUE). There was a positive linear relationship between WUE and RH in all the four species. Our results may suggest that if air humidity becomes lower in some regions of China in the future, the area of distribution for the hu-

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midity sensitive species *P. Massoniana* may become smaller or this species may move to higher humidity region while the other three species will be less affected by this change.

Introduction

It is predicted that the annual amount of rainfall will likely decline in the northern, western and southern parts of China, and slightly increase in the southwest part of China by the end of the 21st century (IPCC 1995). How will trees in China respond to this global environmental change? There is hardly any study conducted in controlled environment to answer this question.

Air humidity is an important factor controlling the successful establishment of tree seedlings (MARSDEN & al. 1996). Controlled environment study of the responses of tree seedlings to air humidity is not only important for predicting forest species distribution changes in the future, but also important for the silviculture of these tree species. Although plant soil water stress has long been extensively studied, very few researches has been conducted to study the effects of air humidity on the growth and water use efficiency (WUE) of tree seedlings under adequate soil water condition. It is well-known that in water limiting environment (insufficient soil water or with a dry air), WUE is always important for the adaptation of plant to the environment.

Pinus massoniana, *Cunninghamia lanceolata* are the two major evergreen conifer forest types in the East China subtropical area and account for 13.2 % and 8.4 %, respectively, of the total forest area in China; *Pinus tabulaeformis* is the representative conifer forest type in North China, which accounts for 2.5 % of the total forest area in China (LI & LI 1996). *Platycladus orientalis* is a common tree species widely distributed in China (DELECTIS FLORAE REIPULICAE POPULARIS SINICAE AGENDAE ACADEMIAE SINICAE EDITA 1978).

The objectives of the present study were (1) to investigate the responses of the growth and WUE of the aforementioned four tree species to air humidity; (2) to provide base-line data for the prediction of the responses of forests in China to the global climate change, and for silviculture of these tree species.

Material and Methods

Four Chinese conifer tree species (*Pinus massoniana* Lamb. var. *massoniana*, *Pinus tabulaeformis* Carr. var. *tabulaeformis*, *Platycladus orientalis* (Linn.) Franco cv. Sieboldii and *Cunninghamia lanceolata* (Lamb.) Hook) were studied for their responses to air humidity in controlled environment chambers at the National Institute for Environmental Studies, Japan. Seeds were collected in Sichuan Province, China. Details of location and collecting methods, see SHIMIZU & al. 1999. Seeds, after receiving cold treatment under 4 °C, were sown in trays containing vermiculite in a greenhouse with an air temperature of 25/20 °C (day/night) and relative air humidity (RH) of 70 % under natural light conditions. Seedlings, with a height of *c.* 5-10 cm, were transplanted into pots (0.505 litre) containing vermiculite. Potted plants were grown in the same greenhouse and watered as needed with 0.1 % Hyponex solution with Hoagland's No. 2 microelements plus 142 μM Fe (III) EDTA.

Twelve seedlings of each species, after grown in the greenhouse for *c.* 1 yr with a height

of 10-20 cm, were transferred to each of four artificially-lighted controlled environment growth chambers (KG-50 HLA-D, Koito Ind. Japan; width × length × height: 120 cm × 82 cm × 190 cm; for details see SHIMIZU & al. 1996). Each chamber was illuminated with 14 fluorescence lamps (Twin 1FPR96EX-N/A, Panasonic Co., Japan) and 4 incandescent lamps (100 W, Hitachi Co., Japan) to provide a 10 hr PPFD (photosynthetic photon flux density) at canopy levels of 600 μmol m^{-2} s^{-1}. Air temperatures were maintained at 29°C in the light period (14 hrs) and 22°C (10 hrs) in the dark period, respectively. RH in the four chambers were maintained at 40/50 %, 50/60 %, 60/70 % or 70/80 % to achieve a light/dark vapour pressure deficit (VPD) of 2.40/1.32, 2.00/1.06, 1.60/0.79 or 1.20/0.53 kPa, respectively. From 6:00 to 8:00, the above environment factors were gradually changed from dark period conditions to light period conditions and from 18:00 to 20:00 gradually changed back, simulating the natural environment by computer. CO_2 concentration was controlled at 400 μl l^{-1} for all the chambers by mixing fresh air with CO_2 gas induced from a liquid CO_2 cylinder and injected through a thermal mass-flow controller into the air stream. In each chamber, the concentration of CO_2 was monitored with an infrared gas analyser (ZRH1DZY1-0AZYY, Fuji Electric Co., Japan) and regulated using an automatic mass-flow controlling system.

Plants were watered once a day in a sub-irrigation system with the same nutrient solution used in the propagation stage. During the experiment, the differences of canopy light levels within the four chambers were controlled within 1 %. Previous to the start of the experiment, the overall environment conditions of the four growth chambers were balanced by adjusting the chamber air flow rates to ensure that the plant canopy level water evaporation rate differences among different chambers were less than 5 %. The evaporation rate was measured by placing two trays containing adequate water at canopy level in each chamber.

Transpiration rate of plants in each chamber was measured by placing 12 plants on a balance (KA15, Mettler Instrument AG, Switzerland). Balance was logged in a personal computer through which data were collected automatically every 30 min during the measurement. The measurement was started on the first day of the experiment and then once a week on the same day. Each measurement lasted for 24 hr, and in total, 5 measurements were made during the 4-week period. Plants were well watered and then the vermiculite was well drained before each measurement. During the transpiration measurement, pots were wrapped with plastic bags to prevent water loss from plant growth substrate. Blank transpiration rate was measured following the same method with pots containing the same vermiculite and with wood sticks in the pots instead of plants. WUE (g dry weight kg^{-1} water) was calculated as:

$$WUE = \Delta biomass/total\ transpiration,$$

where Δbiomass is the total biomass (g, dry weight) increment of the 12 plants during the experiment, and total transpiration (kg, H_2O) was calculated by integrating the transpiration over the 4 wks growing period.

When plants were initially transferred to the growth chambers, 12 plants were harvested. Each plant was separated into leaf, stem and root, oven dried at 80°C for more than 3 days and weighed separately. At the final harvest, this process was repeated on 12 plants of each species for each treatment.

Relative growth rate (RGR), net assimilation rate (NAR), leaf weight ratio (LWR), stem weight ratio (SWR) and root weight ratio (RWR) were calculated according to EVANS 1972 as follows:

$$RGR=1/W\cdot dW/dt=(\ln W_2-\ln W_1)/(t_2-t_1)$$

$$NAR=1/F\cdot dW/dt=[(w_2-w_1)(\ln F_2-\ln F_1)]/[(t_2-t_1)(F_2-F_1)]$$

$$LWR=F/W=[(F_2-F_1)(\ln W_2-\ln W_1)]/[(\ln F_2-\ln F_1)(W_2-W_1)]$$

$$SWR=S/W=[(S_2-S_1)(\ln W_2-\ln W_1)]/[(\ln S_2-\ln S_1)(W_2-W_1)]$$

$$RWR=R/W=[(R_2-R_1)(\ln W_2-\ln W_1)]/[(\ln R_2-\ln R_1)(W_2-W_1)],$$

where W_i, F_i, S_i and R_i are the dry weights of whole plant, leaves, stem and root at time t_i (t_1: initial, t_2: final), respectively. The calculation was based on the mean of 10 plants of each species for each treatment.

Correlation, linear regression and analysis of variance (ANOVA) were performed using SPSS (SPSS Inc. Chicago, Illinois, USA 1997).

Results and Discussion

Seedlings of the four tree species responded to air humidity treatment differently (Figs. 1 & 2). Positive correlation between RH and biomass increment (Δbiomass) or RGR only existed in *P. massoniana* (between RH and Δbiomass, r = 0.99, $P = 0.0112$; between RH and RGR, r = 0.98, $P = 0.0198$), not in the other three species. Δbiomass and RGR were 54% and 47% depressed, respectively, under the RH 40 % treatment compared with those under the RH 70 % treatment for *P. massoniana*, 24 % and 12 % for *P. tabulaeformis*, 22 % and 16 % for *P. orientalis*, 9 % and 5 % for *C. lanceolata*. In other words, *P. massoniana* was particularly sensitive to air humidity and intended to grow faster under higher RH environment; *P. tabulaeformis* and *P. orientalis* were less sensitive and *C. lanceolata* was the least sensitive species under the RH range from 40 to 70 %. However, the biomass increment and relative growth rates were higher under the RH 70 % treatment than those under the 40 % treatment in all the four species. The results are in agreement with the present geographic distributions of three of the four species in China. *P. massoniana* is mainly distributed in southeast subtropical area, where the air humidity is high; and it is the main forest species in this part of China, too. *P. tabulaeformis* is distributed more broadly than *P. massoniana*. *P. tabulaeformis* can not only be seen across temperate to subtropical zones with high air humidity, but also can be found in dry areas (LI & LI 1996). *P. orientalis* is widely distributed in China, from south of Inner Mongolia in the North to north of Guangdong and Guangxi provinces in the South (DELECTIS FLORAE REIPULICAE POPULARIS SINICAE AGENDAE ACADEMIAE SINICAE EDITA 1978). One exception is *C. lanceolata*, which is geographically distributed in the same region as *P. massoniana*, but in the present experiment it was not as sensitive to air humidity as *P. massoniana*. *C. lanceolata* may be more sensitive to other environmental factors. The results suggested that if RH becomes lower accompanied by global climate change, the growing area of the RH sensitive species *P. massoniana* may become smaller or this species may move to higher RH area, while the other three species may become less affected by RH. Generally speaking, for breeding the seedlings of these tree species, air RH around 70 % is better than drier air.

NAR responded to RH treatment in the same pattern as RGR in the same species for all the four species (Fig. 2). LWR, SWR and RWR did not show any significant difference among the treatments for all four species. The effect of relative humidity on RGR might be due to its effect on NAR (Fig. 2). The higher RH might have made plants leaf stomata more open and have higher photosynthetic rates. This is supported by the evidence that the leaf intercellular CO_2 concentration (c_i) was higher under low VPD treatments for all the four species (see ZHENG & SHIMIZU 2005). Leaf photosynthetic capacity can be decreased by dry air and it is unlikely that there was a decrease of Rubisco activity under higher RH in the present study (FORSETH & EHLERINGER 1983, SCHULZE 1986). Similar results that the increase of RH increases stomatal conductance and photosynthetic rate has also been found in other tree species (LIVINGSTON & BLACK 1987, MARSDEN & al. 1996, LAUTERI & al. 1997, GROSSNICKLE & FAN 1998).

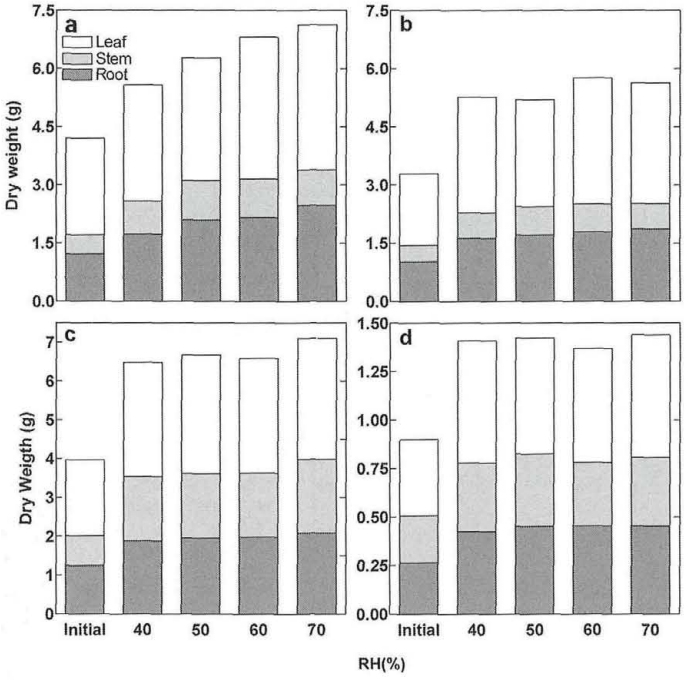

Fig. 1. Effect of relative air humidity (RH) on the growth of four Chinese conifer tree species (a, *P. massoniana*; b, *P. tabulaeformis*; c, *P. orientalis* and d, *C. lanceolata*). Initial means the plant dry weight at initial harvest. Data are means of 10 plants in each treatment for each species.

In our study, the partitioning of photosynthates was not affected by RH treatment in any of the species (Fig. 2). In contrast, SHARIF & RUNDEL 1993 showed that seedlings growing at a higher VPD allocated more carbon-to-root biomass than those growing at low VPD. The reason for the discrepancy is unknown. It is suspected that the difference may be due to the difference in treatments and plant species. In our study, the VPD ranged from 1.2 to 2.4 kPa, and in their experiment it ranged from 2.9 to 7.8 kPa (SHARIF & RUNDEL 1993).

There was a positive linear relationship between plant WUE and RH for each species, and for the four species as a whole (Fig. 3). When the slopes of the linear regression lines of different species were compared, it revealed that the sensitive order of WUE to RH was as *P. massoniana* (0.0634) > *P. orientalis* (0.0399) > *P. tabulaeformis* (0.0338) > *C. lanceolata* (0.0089).

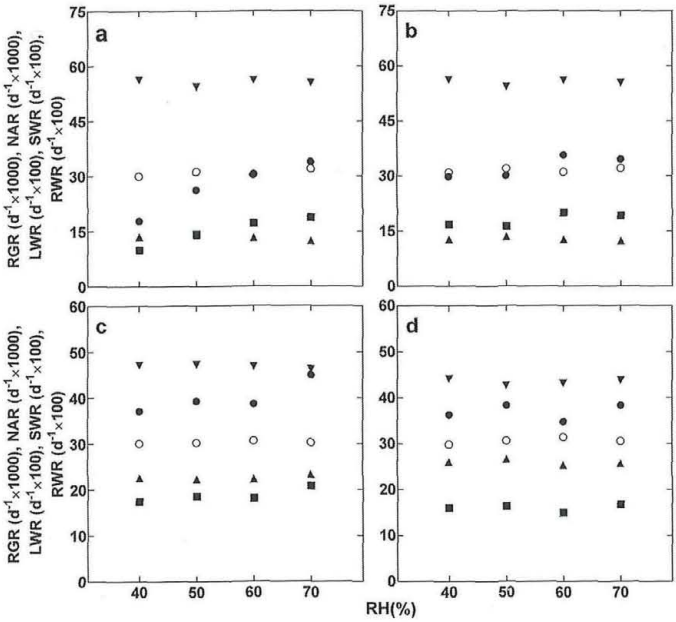

Fig. 2. Effect of relative air humidity (RH) on some of the plant growth parameters of four Chinese conifer tree species (a, *P. massoniana*; b, *P. tabulaeformis*; c, *P. orientalis* and d, *C. lanceolata*). ■, RGR; ●, NAR; ▼, LWR; ▲, SWR; ○, RWR. Data are means of 10 plants in each treatment for each species.

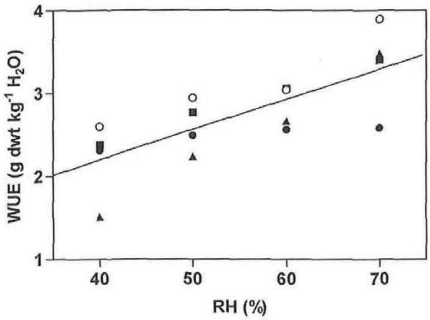

Fig. 3. Linear relationship between plant water use efficiency (WUE) and relative air humidity (RH) of four Chinese conifer tree species (▲, *P. massoniana*; ■, *P. tabulaeformis*; ○, *P. orientalis*; ●, *C. lanceolata*). Data represent the integrated WUE measured on 12 plants. The line represents the linear relationship between WUE and RH for the four species. The equation for the line is; WUE = 0.0365RH + 0.74, R^2=0.56, P = 0.001.

Results also showed that there was a tight positive correlation between WUE and Δbiomass within each species for two species (*P. massoniana*, r = 0.991, *P* = 0.009; *P. orientalis*, r = 0.9956, *P* = 0.004), but not in the other two species. Compared to plant growth, WUE was more sensitive to RH in all the four species. WUE was higher under higher RH conditions. This is in agreement with the general model that WUE is negatively related to VPD (ZHANG & NOBEL 1996) and most of the previous experimental results (MARSDEN & al. 1996, ZHANG & NOBEL 1996, BALL & al. 1997). The increased WUE under higher RH in the present study suggests that there was no trade-off between water use efficiency and growth under different RH for these four species.

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