

Response of photosynthesis in *Shaniodendron subaequale* to soil water status

Chun-Lei Yue^{1,*}, Shui-Hu Jin², Jie Chang³ & Hong Jiang¹

¹⁾ International Institute for Earth System Science, Nanjing University, Nanjing 210093, P. R. China (*e-mail: chunlei@chinaacc.com)

²⁾ Zhejiang Forestry College, Linan 311300, P. R. China

³⁾ College of Life Science, Zhejiang University, Hangzhou 310029, P. R. China

Received 25 Nov. 2005, revised version received 14 Feb. 2006, accepted 17 Feb. 2006

Yue, C.-L., Jin, S.-H., Chang, J. & Jiang, H. 2006: Response of photosynthesis in *Shaniodendron subaequale* to soil water status. — *Ann. Bot. Fennici* 43: 389–393.

The Chinese endemic and endangered *Shaniodendron subaequale* (Hamamelidaceae) is restricted to a narrow distribution area, where drought frequently occurs. In order to find out soil water demand of the species, we studied its photosynthesis and other ecophysiological traits in response to soil water availability. The results showed that, when relative water content was 60%, *S. subaequale* had the maximal photosynthetic rate and highest light saturation point. Below 60% of soil water holding capacity, mean photosynthesis rate, mean transpiration rates, mean water use efficiency and mean stomatal conductance remarkably decreased with decreasing soil water content. Significant reduction of *S. subaequale* leaf area followed that of soil water content, but at the same time the chlorophyll content increased. The study indicated that relatively wet soil was more favourable for *S. subaequale*. Separation of its actual water niche from an optimal water niche can partly account for its endangered status.

Key words: endangered species, photosynthesis, *Shaniodendron subaequale*, water availability, water use efficiency

Introduction

Shaniodendron subaequale (Hamamelidaceae) is endemic to eastern China, and is one of the critically endangered species in the country (Wei *et al.* 1994). It was listed in *Directory of State Key protected Wild plants* in 1999. *Shaniodendron subaequale* was first found in the south of Jiangsu Province in 1935. However, it was not until the 1990s that this species was re-found in Yixing in Jiangsu province, Anji and Linan in Zhejiang Province, and Shucheng, Jixi and Jinzhai in Anhui Province. At present,

seedlings of *S. subaequale* are extremely rare, and the maximal population only consists of about 100 individuals (Hao *et al.* 2000). In the field, this species is mainly restricted to gravelly areas in valleys and barren areas near mountain ridges, where drought frequently occurs (Hao *et al.* 2000), although some individuals also grow beside mountain rivulets.

In recent years there were many reports in the literature about plant response to soil water status (Abril *et al.* 1998, Tsuji *et al.* 2003, Gindaba *et al.* 2004). Drought causes changes in biomass accumulation, growth rate and many

other physiological or structural traits (Arora *et al.* 2001, Chaitanya *et al.* 2003), which are important as they can contribute to the capability of competition, ecological distribution (Bell 1999) and thus existence of plants (Garg *et al.* 2001). Photosynthesis is known to be very sensitive to environmental stress. When soil water availability is limited, photosynthetic rate often limits plant growth (Huang *et al.* 2000).

Studies of *S. subaequale* have been focused on its taxonomy and anatomy (Deng *et al.* 1992, Fang *et al.* 1996, 1997, Hao *et al.* 1996, Li *et al.* 1997), but little has been known about its ecophysiological characteristics. In order to find out the soil water demand of this species, we studied its photosynthesis rate and other related ecophysiological characteristics in a greenhouse. Based on the experimental results, actual water niche and optimal water niche of this species was analyzed, and the relationship between water niche and the endangered status is discussed. This study can increase the understanding of endangering mechanisms and assist in the development of approaches to conserving this endangered species.

Material and methods

Plant material

The study site is located in the experiment base of Zhejiang Forestry Academy (120°12'E, 30°16'N; 50 m above sea level). In December 2003, 16 five-year-old seedlings of *S. subaequale* of uniform size were selected from the nursery in Longwangshan Natural Protection Zone. They were randomly transplanted into pots (height 30 cm, upper diameter 25 cm, one plant per pot) filled with the same forest soil. The pots were placed outside a greenhouse.

Experimental design

In early April 2004, when *S. subaequale* began sprouting, all seedlings were randomly assigned into four groups, and each group was subjected in the greenhouse to one of four treatments,

expressed in terms of relative soil water content (RWC), which is a percentage of soil water holding capacity: (1) W_{80} , water was withheld until the RWC dropped to 80% and then water was added thoroughly to saturation; (2) W_{60} , water was withheld until the RWC dropped to 60% and then water was added thoroughly to saturation; (3) W_{40} , water was withheld until the RWC dropped to 40% and then water was added thoroughly to saturation; (4) W_{20} , water was withheld until the RWC dropped to 20% and then water was added thoroughly to saturation. Watering was performed after sunset.

After three months of treatments, incident photosynthetic photon flux density (PPFD), air temperature (T_a), net photosynthetic rate (P_N), transpiration rate (E), and stomatal conductance (g_s) were determined with a portable gas exchange system (LCA-4, Analytical Development Company, Hoddesdon, England) on three consecutive clear days. The diurnal course of gas exchange was monitored at 1-h intervals. Water use efficiency (WUE) was calculated as P_N/E . P_N was recorded after steady data was reached, there being four replications. The response of P_N to step changes in PPFD was examined. A series of PPFD ranging from 0 to 1700 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was produced by gradually altering the light intensity of an attached light source. There were four replications for each PPFD. Light saturation point and light compensation point were estimated by fitting the data to a model function expressed as a quadratic equation (Prioul & Chartier 1977). Immediately after photosynthesis measure was finished, chlorophyll content was determined by the method described by Ping and Liu (1992). Leaf area was measured using a leaf area meter (Li-cor 3000) and leaves were dried at 80 °C for at least 72 h and weighed to calculate the specific leaf area (SLA, leaf area/leaf mass).

Data analysis

Statistical analysis was conducted using Microsoft Excel 2000 and SPSS 8.0 for Windows. All data were tested for significant effects of the treatments using a one-way ANOVA with mean values.

Results

Response of photosynthesis to PPFD

Soil water status greatly affected response of photosynthesis to PPFD in *S. subaequale* (Table 1). The difference in P_{\max} was significant among all treatments, of which W_{60} had the highest P_{\max} , slightly greater than W_{80} . When RWC was smaller than 60%, P_{\max} decreased significantly following a decrease in soil water content, and the P_{\max} in W_{60} was 2.6 times that of P_{\max} in W_{20} . There was also a significant difference in light saturation point among the treatments, of which that in W_{60} was highest. When RWC was below 60%, light saturation point greatly decreased with decreasing soil water content. However, the difference in light compensation point among the treatments was small, ranging from $15 \mu\text{mol m}^{-2} \text{s}^{-1}$ to $25 \mu\text{mol m}^{-2} \text{s}^{-1}$. These results indicate that W_{60} was optimal for photosynthesis of *S. subaequale*.

Diurnal course of photosynthesis

A typical diurnal course of photosynthesis for one day with uninterrupted sunshine and temperatures being stable around 36° between 10:00 and 16:00 is presented in Fig. 1. All treatments displayed a diurnal pattern for net photosynthesis that was typical for a tree with a peak early in the day followed by a later decline. P_N differed among treatments with W_{80} and W_{60} being similar and always more than double the rates for W_{40} and W_{20} . E and g_s showed very similar patterns to P_N . Mean transpiration rates were 2.26 and $2.23 \text{ mmol m}^{-2} \text{ s}^{-1}$ for W_{80} and W_{60} , respectively,

and about 60% of these values for W_{40} and W_{20} . When RWC was below 60%, g_s greatly decreased following the decrease in soil water content. The similar patterns for P_N and E are shown clearly in the WUE, which combines these, and which was remarkably similar for all treatments and also constant for most of the day. These results show the plant has excellent stomatal control.

Leaf area and chlorophyll content

There was a highly significant difference in leaf area and SLA among the treatments (Table 2). Leaf area significantly decreased with decreasing soil water content. The value in W_{80} was almost 3 times that in W_{20} . SLA increased with decreasing soil water content. Significant differences in chlorophyll content between different treatments were observed. Decreased soil water content resulted in an increase in chlorophyll content. Chlorophyll *a* content had little response to soil water content, but chlorophyll *b* greatly increased with decreasing soil water content, resulting in a significant decrease in chlorophyll *a*/chlorophyll *b* ratio.

Discussion

In the field *S. subaequale* mainly grows in gravelly areas of valleys and barren areas near mountain ridges, where the soil water content is low and drought is frequent. However, our results show that the plant is clearly not in a preferred water niche. When RWC was below 60%, mean photosynthesis rate, mean transpiration rate, mean water use efficiency and mean

Table 1. Maximal photosynthetic rate, light compensation point and saturation point of *Shaniodendron subaequale* under different soil water treatments. Values are means \pm SE.

Water treatments	Maximal net photosynthetic rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Light compensation point ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Light saturation point ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
W_{80}	11.00 ± 0.98	23 ± 2	796 ± 37
W_{60}	11.78 ± 0.64	18 ± 4	1135 ± 110
W_{40}	7.79 ± 0.93	19 ± 3	697 ± 76
W_{20}	4.48 ± 0.67	16 ± 4	590 ± 32

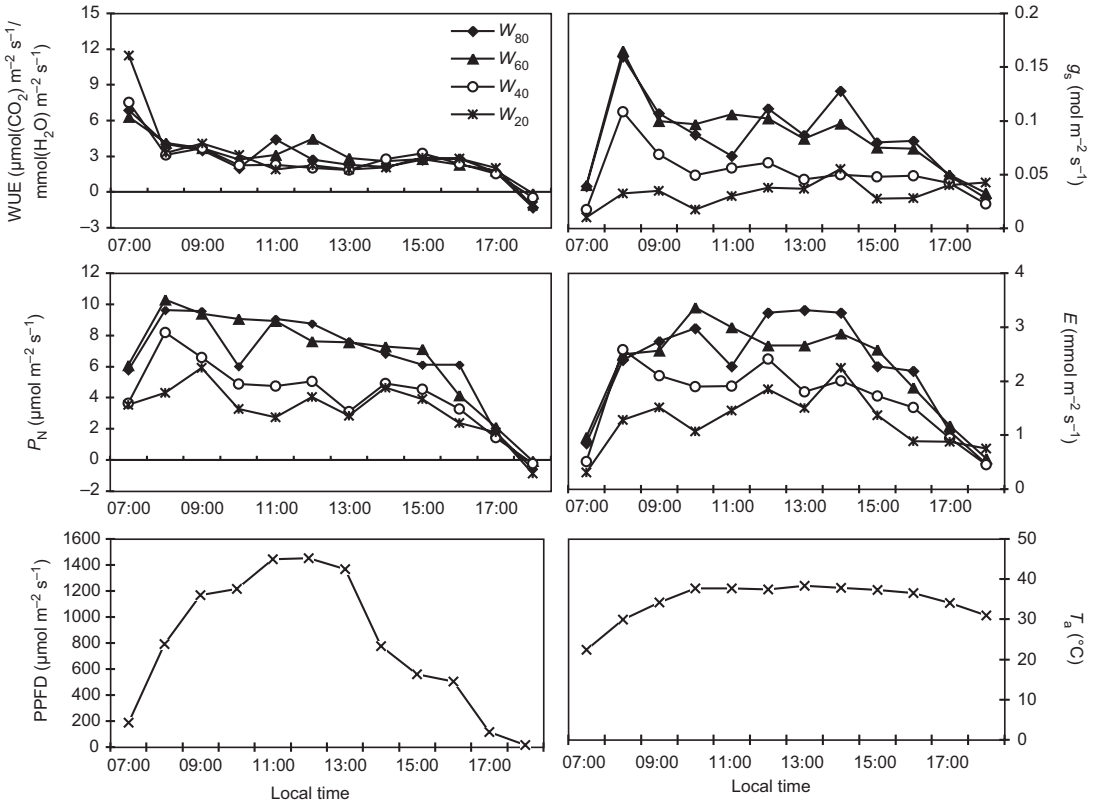


Fig. 1. Diurnal changes of photosynthetic photon flux density (PPFD) and air temperature (T_a), net photosynthetic rate (P_N), transpiration (E), water use efficiency (WUE), and stomatal conductance (g_s) of *Shaniodendron subaequale* in different soil water status.

stomatal conductance markedly decreased with decreasing soil water content, indicating that W_{60} appears to be optimal for the species.

There are many reports on the relationship between soil water content and photosynthesis, but effect of soil water on light saturation point has seldom been investigated. Recently, studies on the endangered species *Woonyoungia septentrionalis* found that its light saturation point

decreased following the decrease in soil water content (Zeng *et al.* 2004). In the present study, light saturation point decreased with decreasing soil water content when RWC was below 60%, indicating that soil water content can affect the light adaptation range of a plant.

With the decrease of soil water content, chlorophyll content of *S. subaequale* increased, but net photosynthetic rate decreased, which perhaps

Table 2. Leaf area, SLA and chlorophyll content of *Shaniodendron subaequale* under different soil water treatments. Values are means \pm SE. Different letters express significant (at $p < 0.05$, Student-Newman-Keuls test) difference between water treatments.

Water treatment	W_{80}	W_{60}	W_{40}	W_{20}	P (ANOVA)
Leaf area (cm ²)	12.45 \pm 2.24 ^a	9.44 \pm 2.69 ^{ab}	7.35 \pm 0.41 ^b	4.76 \pm 0.94 ^c	0.0051
SLA (dm ² g ⁻¹)	1.547 \pm 0.178 ^a	1.414 \pm 0.067 ^a	1.652 \pm 0.077 ^{ab}	2.020 \pm 0.268 ^b	0.0106
Chlorophyll (mg g ⁻¹)	2.111 \pm 0.017 ^a	2.241 \pm 0.047 ^b	2.437 \pm 0.041 ^c	2.504 \pm 0.030 ^c	< 0.001
Chlorophyll <i>a</i> (mg g ⁻¹)	1.344 \pm 0.010 ^a	1.346 \pm 0.011 ^a	1.354 \pm 0.005 ^a	1.351 \pm 0.013 ^a	0.6303
Chlorophyll <i>b</i> (mg g ⁻¹)	0.766 \pm 0.012 ^a	0.894 \pm 0.053 ^b	1.083 \pm 0.036 ^c	1.153 \pm 0.028 ^c	< 0.001
<i>a/b</i>	1.755 \pm 0.027 ^a	1.509 \pm 0.094 ^b	1.252 \pm 0.038 ^c	1.172 \pm 0.031 ^d	< 0.001

contributed to the stomatal restriction induced by decreased leaf water content. The increased chlorophyll content improved plant's survival during drought. Leaf area plasticity is important for maintaining control of water use. In *Sorghum*, leaf area was significantly reduced under water stress, as reported by Blum (1996). In the present study, a reduction in leaf area of *S. subaequale* was also observed. Pereira and Chaves (1993) viewed stomatal closure as a short-term, and leaf area reduction as a long-term acclimation mechanism in response to soil water deficit.

Regarding photosynthesis, the optimal habitat for *S. subaequale* is where soil water and light are abundant. In fact, it is seldom distributed in such habitats, which may account for its weak competition ability. *Shaniodendron subaequale* is a heliophilic tree species as shown by its light saturation point and light compensation point, but its young seedlings grow much too slowly because of its dense timber, so it fails in competing with other tree species in a habitat where soil water and light are abundant. Thus the species is restricted to more adverse habitats. Its survival strategy should be regarded as competition-avoidance type. The clear difference between its existing water niche and optimal water niche can partly account for its endangered status.

Acknowledgements

This study was financially supported by grant 301225 from Zhejiang Provincial Natural Science Foundation of China and grant 2001CB309401 from The State Key Fundamental Science Funds of China. We wish to thank Lipeng Yu for providing us with the plant materials.

References

- Abril, M. & Hanano, R. 1998: Ecophysiological responses of three evergreen woody Mediterranean species to water stress. — *Acta Oecol.* 19: 377–387.
- Arora, A., Singh, V. P. & Mohan, J. 2001: Effect of nitrogen and water stress on photosynthesis and nitrogen content in wheat. — *Biol. Plant.* 44: 153–155.
- Barathi, P., Sundar, D. & Reddy, A. R. 2001: Changes in mulberry leaf metabolism in response to water stress. — *Biol. Plant.* 44: 83–87.
- Bell, D. L. & Sultan, S. E. 1999: Dynamic phenotypic plasticity for root growth in *Polygonum*: a comparative study. — *Am. J. Bot.* 86: 807–819.
- Blum, A. 1996: Crop response to drought and the interpretation of adaptation. — *Plant Growth Regul.* 20: 135–148.
- Chaitanya, K. V., Jutur, P. P., Sundar, D. & Reddy, A. R. 2003: Water stress effects on photosynthesis in different mulberry cultivars. — *Plant Growth Regul.* 40: 75–80.
- Deng, M. B., Wei, H. T. & Wang, X. Q. 1992: *Shaniodendron*, a new genus of Hamamelidaceae from China. — *Acta Phytotaxon. Sinica* 30: 57–61. [In Chinese with English summary].
- Fang, Y. M. & Deng, M. B. 1996: Wood anatomy of *Shaniodendron subaequale* (Hamamelidaceae) and its systematic implication. — *J. Pl. Res. Environ.* 5(2): 50–54. [In Chinese with English summary].
- Fang, Y. M., Jin, Y. X., Deng, M. B. & Yang, Q. S. 1997: Macro and micro-structure leaves in shanidendron subaequale with consideration of its phylogeny. — *J. Pl. Res. Environ.* 6(3): 35–41. [In Chinese with English summary].
- Garg, B. K., Kathju, S. & Burman, U. 2001: Influence of water stress on water relations, photosynthetic parameters and nitrogen metabolism of moth bean genotypes. — *Biol. Plant.* 44: 289–292.
- Gindaba, J., Rozanov, A. & Negash, L. 2004: Response of seedlings of two *Eucalyptus* and three deciduous tree species from Ethiopia to severe water stress. — *For. Ecol. Manage.* 201: 119–129.
- Hao, R. M., Huang, Z. Y. & Liu, X. J. 2000: The natural distribution and characteristics of the rare and endangered plants in Jiangshu, China. — *Chinese Diversity* 8: 153–162. [In Chinese with English summary].
- Hao, R. M., Wei, H. T. & Liu, W. G. 1996: Floral morphology of *Shaniodendron subaequale* (Hamamelidaceae) and its taxonomic significance. — *J. Pl. Res. Environ.* 5(1): 38–42. [In Chinese with English summary].
- Huang, B. R. & Fu, J. M. 2000: Photosynthesis, respiration, and carbon allocation of two cool-season perennial grasses in response to surface soil drying. — *Plant Soil* 227: 17–26.
- Li, J. H., Bogle, A. L., Klein, A. S. & Pan, K. Y. 1997: Close relationship between *Shaniodendron* and *Parrotia* (Hamamelidaceae), evidence from its sequences of nuclear ribosomal DNA. — *Acta Phytotaxon. Sinica* 35: 481–493.
- Peng, Y. S. & Liu, E. 1992: Studies of method on extract chlorophyll *a* and *b*. — *Acta Agric. Univ. Pekinensis* 18(3): 47–50. [In Chinese with English summary].
- Priou, J. L. & Chartier, P. 1977: Partitioning of transfer and carboxylation components of intracellular resistance to photosynthetic CO₂ fixation: a critical analysis of the methods used. — *Ann. Bot.* 41: 789–800.
- Tsuji, W., Ali, M. E. K., Inanaga, S. & Sugimoto, Y. 2003: Growth and gas exchange of three sorghum cultivars under drought stress. — *Biol. Plant.* 46: 583–587.
- Wei, H. T. & Jin, N. C. 1994: Quantitative analysis of risk size of plant species: a case of *Shaniodendron subaequale*. — *J. Pl. Res. Environ.* 3(3): 1–8. [In Chinese with English summary].
- Zeng, X. P., Zhao, P., Cai, X., Sun, G. C. & Peng, S. L. 2004: Physioecological characteristics of *Woonyoungia septentrionalis* seedlings under various soil water conditions. — *Chinese J. Ecol.* 23 (2): 26–31. [In Chinese with English summary].