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Physiological acclimation and growth response to partial shading in *Salix matsudana* in the Mu Us Sandland in China

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Abstract In a controlled experiment, *Salix matsudana* plants were subjected to uniform nonshading (F-S), partial shading (P-S) and uniform shading (U-S). The shoots of the plants in the F-S and U-S treatments were referred to as H-H and L-L, respectively. The plants in the P-S treatment had two kinds of shoots: (1) shoots under the nonshading treatment that were connected to others under the shading treatment (H-L). (2) Shoots under the shading treatment that were connected to others under the nonshading treatment (L-H). The physiological acclimation and growth response of the species to the partial shading were examined. The partial shading had significant effects on photosynthetic dynamics, transpiration and stomatal conductance, but no effect on instantaneous water use efficiency and maximum quantum yield. Water saturation deficit and coefficient of water loss were significantly smaller in the H-L shoots than in the H-H shoots. Leaf natality, leaf mortality and leaf turnover were greater in the H-L shoots than in the H-H shoots. In contrast, these three parameters were smaller in the L-H shoots than in the L-L shoots. The H-L shoots had significantly larger branching ratio, total branch length and shoot biomass than the H-H shoots. The L-H shoots had smaller branching ratio, total branch length and shoot biomass than the L-L shoots. Total plant biomass in the treatments increased as follows: F-S < P-S < U-S. Canopy productivity index was significantly higher in the P-S than in both F-S and U-S. Leaf weight ratio was also significantly affected by the light regime. These results suggest that the plants are able to respond to partial shading in their natural habitats when light is usually patchy

through modifying their physiology and growth in a manner of correlative inhibition between the H-L and the L-H shoots.

Keywords Correlative inhibition · Growth response · Partial shading · Physiological acclimation · *Salix matsudana*

Introduction

Spatial heterogeneity in the availability of resources essential for plants is among the inherent features of natural ecosystems. Its importance for ecological and evolutionary processes has been receiving considerable attention from ecologists (c.f. Stuefer et al. 1996). Among the environmental factors affecting plants, light is perhaps the most heterogeneously distributed in space and time (Carlton and Bazzaz 1998; Nicotra et al. 1999; Pearcy 1999). Therefore, individuals of a population may grow in different microhabitats in terms of light conditions. The responses of plants to high versus low uniform light conditions have been well documented (e.g. Bjorkman 1981; Caldwell and Pearcy 1994; Pearcy 1999). Moreover, in nature, the scale on which light condition shows patchiness may be small and thus the interconnected parts of single plants may grow under different light conditions (Caldwell and Pearcy 1994). Understanding of the response of whole plants to patchy light (or partial shading) environments requires more evidence.

Salix matsudana is a dominant tree species in the Mu Us Sandland located in the Ordos Plateau of Inner Mongolia, a semi-arid area of China that has vegetation composed of a variety of herbs, and woody species (Li 1990; Zhu and Bao 1993; Zhang 1994). It is fast-growing and light-demanding (EBFC 1984). The heterogeneous structure of its canopy fosters spatial heterogeneity in light availability not only for young plants in the undergrowth but also for its own different parts (e.g. shoots). Interconnected shoots (branches) of individual *S. matsudana* plants grow under different light conditions. According

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to space economy (Bloom et al. 1985), in general, an individual's adaptation to environmental heterogeneity should maximize profit to the whole individual when resources are unevenly distributed in space. Growing in a patchy light environment, interconnected parts (e.g. shoots) of individual plants may show a correlative inhibition (Novoplansky et al. 1989; Prati et al. 1997; Stoll and Schmid 1998), whereby the performance of the whole plant is enhanced. Therefore, it is predicted that, as an individual plant of *S. matsudana* grows under partial shading conditions, its unshaded shoots are enhanced while its shaded shoots are depressed.

To test the prediction, physiological (e.g. gas exchange, fluorescence and water traits), morphological (e.g. branch architecture) and growth (e.g. length, biomass and productivity) modification of the cuttings in response to partial shading was examined in a controlled experiment with *S. matsudana* young individuals.

Materials and methods

The species and the study site

Salix matsudana Koidz. (Salicaceae) is widely distributed throughout northern China. It is a cold- and drought-tolerant tree species and possesses a regular branching pattern (EBFC 1984). Its catkins and buds are initiated simultaneously in April, its span of fructification lasts from May through June, and its defoliation ends in October (EBFC 1984; Li 1990). The species is considered an appropriate tree species to combat desertification in the Mu Us Sandland due to its capacity to grow in desertified environments (Li 1990; Zhu and Bao 1993).

The experiment was conducted at the Ordos Sandland Ecological Station (110°15'E 39°34'N, 1,247 m a.s.l.) in the Mu Us Sandland in China, where the mean annual precipitation is 388 mm, 70% of which falls in July, August and September, the mean annual temperature is 6°C, and the potential evapotranspiration rate may approach 2.0 (Zhang 1994).

Experimental design

On 6 April 1999, we collected 200 2-year-old twigs (ca. 15 cm in length) from the same mature maternal *S. matsudana* plant. Subsequently, the twigs were grown in growth containers (ca. 9 dm³), one twig per container. The containers were filled with homogenized topsoil from local natural habitats. Only two opposite buds per twig 1 cm above the soil surface were allowed to develop to new shoots and the rest of the buds were pruned. Thus, all the experimental plants shared the same genotype. Forty-five days following the cutting, 60 of the cuttings with two similar shoots (ca. 5 cm in length, three or four leaves) were chosen and randomly grouped into three categories (treatments) (Fig. 1).

1. Plants grew under uniform unshaded conditions (treatment F-S) and both interconnected opposite shoots were unshaded (H-H).
2. Plants grew under uniform shaded conditions (treatment U-S) and both interconnected opposite shoots were shaded (L-L).
3. Plants grew under partially shaded conditions (treatment P-S). One of the interconnected opposite shoots was the shoot under the unshaded treatment and connected to the shoot under the shaded treatment (H-L); the other was the shoot under the shaded treatment and connected to the shoot under the unshaded treatment (L-H).

Each treatment had 15 replicates. Two layers of neutral shade cloth changeable in both length and width to accommodate shoot

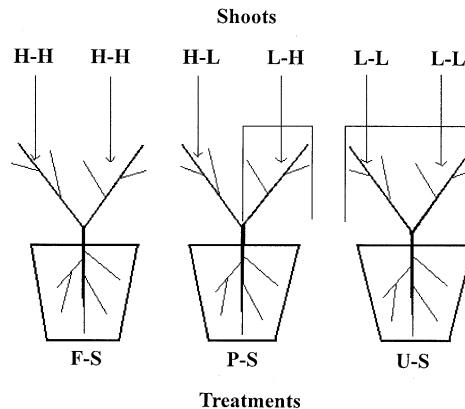


Fig. 1 Illustrative diagram of experimental design. F-S, P-S and U-S stand for uniform unshaded, partial shading and uniform shaded treatment, respectively. The interconnected opposite shoots growing under the F-S were unshaded shoots (H-H). The interconnected opposite shoots growing under the U-S were shaded shoots (L-L). Plants growing under the P-S had two kinds of shoots, one of which was the shoot under the unshaded treatment and connected to the shoot under the shaded treatment (H-L); the other was the shoot under the shaded treatment and connected to the shoot under the unshaded conditions (L-H)

growth were used in the P-S and U-S. Photosynthetically active radiation (PAR) was measured throughout the experiment with a quantum sensor (ADC, Hoddesdon, England). Two layers of neutral shade cloth reduced PAR by ca. 40% of the full sunlight. During the experiment the plants were provided with a nutrient solution (1.467g l⁻¹ NH₄NO₃, 0.775g l⁻¹ NaH₂PO₄·2H₂O, and 0.976g l⁻¹ KCl) and watered as needed. The experiment ran from 22 May to 1 September 1999.

Measurements

During the experiment the number of natal leaves and dead leaves was labeled and recorded daily. Leaf natality [natal leaves per day (no. day⁻¹)], leaf mortality [dead leaves per day (no. day⁻¹)], and leaf turnover (ratio of total dead leaves to total natal leaves (no. no.⁻¹)) were calculated.

We chose five similar leaves developing during the treatments from each kind of shoots for the following physiological measurements on 25 August and 29 August: net photosynthetic rate (P_n), transpiration (E), stomatal conductance (g_s), atmospheric CO₂ concentration (C_a), substomatal CO₂ concentration (C_i), air temperature, leaf temperature, and PAR. They were determined at 1-h intervals with an open flow gas exchange system (LCA-4, ADC, Hoddesdon, England) from 0600 through 2000 hours. Before every set of gas exchange measurements, the infrared gas analyzer calibration was checked against a CO₂ standard, and the humidity sensor was calibrated using a dew point generator. Night respiration (R_n) was determined from 2000 to 2100 hours. Instantaneous water use efficiency (WUE_i) was calculated as the ratio of P_n to E (Gibson 1998).

Chlorophyll-*a* (Chl *a*) fluorescence was measured on the same leaves used in the gas exchange measurements. After at least 20 min of dark adaptation, the minimal level of Chl *a* fluorescence (F_0) was measured with a Plant Efficiency Analyzer (Hanstech, UK) and the maximal level of Chl *a* fluorescence (F_m) was induced by a 1 s saturating flash provided by the Plant Efficiency Analyzer. Variable Chl *a* fluorescence (F_v) equals F_m minus F_0 . From the various fluorescence levels, the maximum quantum yield of PSII electron transport (F_v/F_m) was calculated (Adams et al. 1990).

On 31 August, we collected 20 fully developed leaves from each type of shoot, and determined their fresh weights as quickly

as possible. Subsequently we put the leaves into water for at least 24 h to saturate them. Saturation weights of the leaves were determined; subsequently the saturated leaves were kept at room air temperature to lose water until leaf masses remained relatively constant. Leaf weight was determined once per 24 h during the course of water loss. Finally the leaves were oven-dried at 85°C for 48 h and then weighed. The curves of water loss versus time were created based on the cumulative amount of water loss against time (He 2001). Water saturation deficit was calculated as described by Beadle et al. (1993). Coefficient of water loss (k) was estimated with linear regression using the first four or five points of the water loss versus time curves (He 2001).

At the end of the experiment, we counted the number of branches and measured branch angle with a protractor and branch length with a ruler. All plants were harvested and then were separated into roots, stems, and leaves. The harvested materials were finally oven-dried at 85°C for 48 h and then weighed. Branch angle, branching ratio (Fisher 1986), total branch length, shoot biomass, total plant biomass, leaf weight ratio (leaf biomass/total plant biomass), and canopy productivity index (net biomass increase per unit of leaf area) (Norby 1996) were determined.

Data analyses

Three contrasts (i.e. contrast 1, H-H vs L-L; contrast 2, H-L vs H-H; and contrast 3, L-H vs L-L) were performed (planned comparisons, contrast option in SAS 1985). In order to reveal the contrasting effects of partial shading on H-L and L-H, both H-H and L-L were used as controls. Significant differences between the related characteristics within a contrast were determined with pairwise comparison (SAS 1985).

At the whole-plant level, total plant biomass, leaf weight ratio, and canopy production index were statistically analyzed using one-way analysis of variance with a t -test based on the General Linear Model (SAS 1985).

Results

Only the gas exchange measured on 25 August is presented here because the patterns of gas exchange were highly similar on 25 August and 29 August. There were marked differences in the changes in P_n between shoots (Fig.2). For example, there were differences in midday depression (i.e. timing and intensity) and in peak of P_n . At ca. 0600 hours, P_n in the H-H, H-L, L-H, and L-L shoots was -1.66 ± 0.12 , -1.23 ± 0.09 , 0.69 ± 0.08 , and $0.88\pm 0.09 \mu\text{mol m}^{-2}\text{s}^{-1}$, respectively. Night respiration in the H-H, H-L, L-H, and L-L shoots was 1.75 ± 0.14 , 1.33 ± 0.11 , 1.24 ± 0.10 , and $1.08\pm 0.09 \mu\text{mol m}^{-2}\text{s}^{-1}$, respectively. There was no significant difference in gas ex-

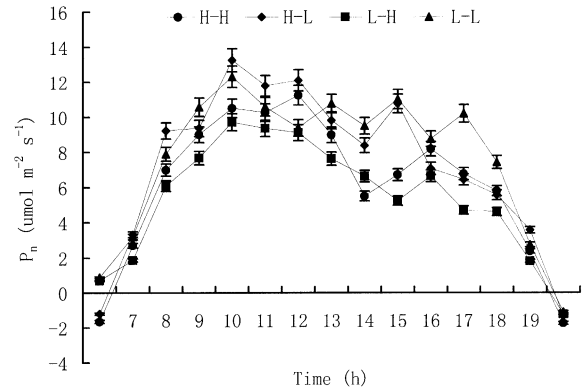


Fig. 2 Changes in net photosynthetic rate (P_n) with time. Data are means (± 1 SE) ($n=5$). The shoots are coded as in Fig. 1

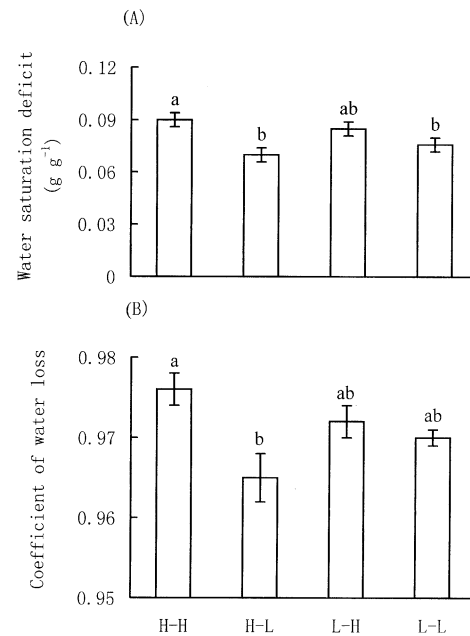


Fig. 3 Changes in (A) water saturation deficit and (B) coefficient of water loss of the leaves. Data are means (± 1 SE) ($n=20$). The bars followed by the same letter are not significantly different at $P=0.05$. The shoots are coded as in Fig. 1

Table 1 The physiological characteristics measured. Data are means (± 1 SE) ($n=5$). The values within a row followed by the same superscript are not significantly different at $P=0.05$. (H-H, H-L, L-H and L-L are the same as in Fig. 1. P_n , E , g_s , C_i/C_a , WUE_i

Variable	H-H	H-L	L-H	L-L
P_n ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	7.18 ± 0.19^b	8.46 ± 0.21^a	5.91 ± 0.13^c	8.45 ± 0.27^a
E ($\text{mmol m}^{-2} \text{s}^{-1}$)	4.61 ± 0.12^b	6.04 ± 0.21^a	4.03 ± 0.18^b	4.90 ± 0.22^b
g_s ($\text{mol m}^{-2} \text{s}^{-1}$)	0.34 ± 0.04^{bc}	0.53 ± 0.06^a	0.27 ± 0.06^c	0.48 ± 0.05^{ab}
C_i/C_a (mmol mmol ⁻¹)	0.75 ± 0.04^a	0.57 ± 0.03^b	0.67 ± 0.04^{ab}	0.72 ± 0.04^a
WUE _i (mmol mol ⁻¹)	1.52 ± 0.11^a	1.42 ± 0.15^a	1.43 ± 0.13^a	1.69 ± 0.10^a
F_v/F_m	0.86 ± 0.01^a	0.85 ± 0.02^a	0.86 ± 0.01^a	0.86 ± 0.01^a

and F_v/F_m stand for net photosynthetic rate, transpiration, stomatal conductance, substomatal CO_2 /atmospheric CO_2 concentration, instantaneous water use efficiency, maximum quantum yield, respectively)

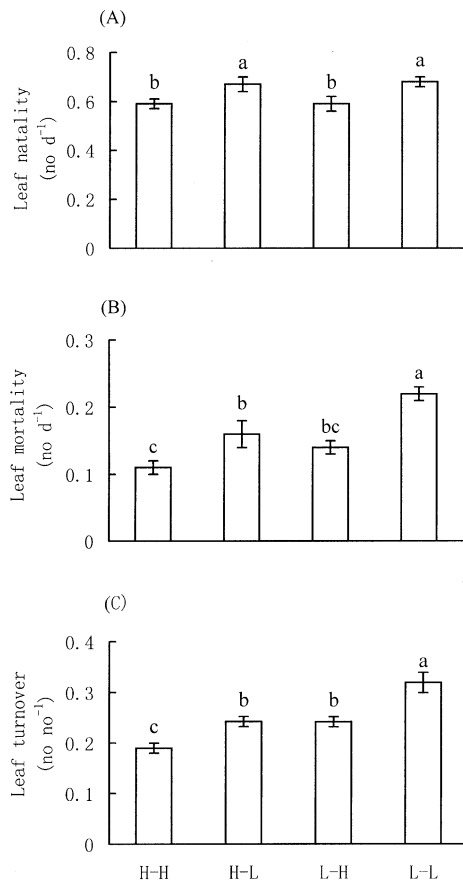
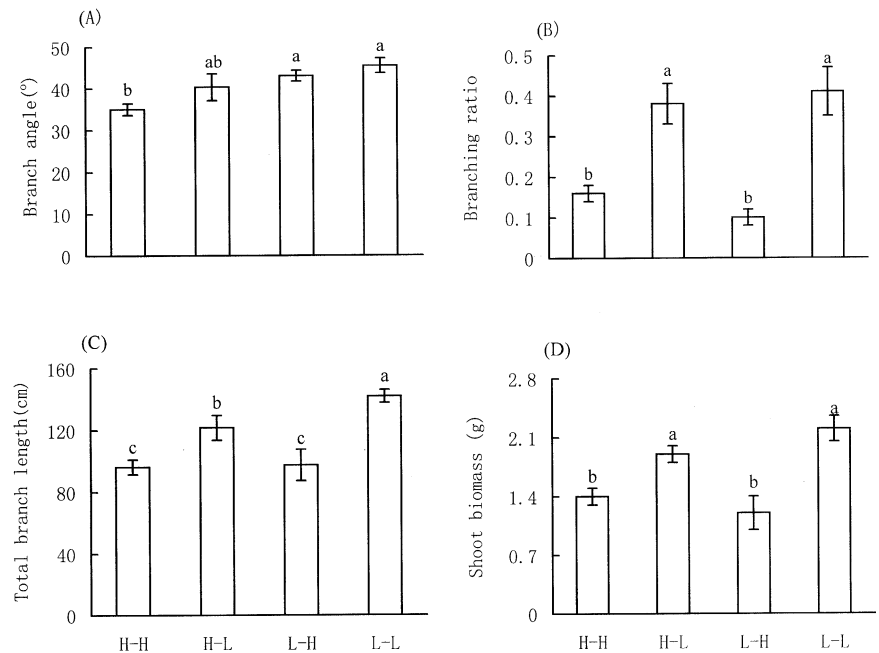


Fig. 4 Changes in (A) leaf natality, (B) leaf mortality and (C) leaf turnover. Data are means (± 1 SE) ($n=10$). The bars followed by the same letter are not significantly different at $P=0.05$. The shoots are coded as in Fig. 1

Fig. 5 Changes in (A) branch angle, (B) branching ratio, (C) total branch length and (D) shoot biomass. Data are means (± 1 SE) ($n=10$). The bars followed by the same letter are not significantly different at $P=0.05$. The shoots are coded as in Fig. 1



change between the H-H and the L-L shoots except for P_n (Table 1). The H-L shoots had higher P_n , E and g_s than the H-H shoots, while the former had lower C_i/C_a than the latter (Table 1). The L-H shoots had lower P_n and g_s than the L-L shoots; there was no significant difference in the other gas exchange between them (Table 1). F_v/F_m did not show significant differences between the four kinds of shoots (Table 1).

Water saturation deficit (WSD) was greater in the H-H shoots than in the L-L shoots, whereas no significant difference in k was found between them (Fig. 3A, B). WSD and k were significantly smaller in the H-L shoots than in the H-H shoots; there were no significant differences in WSD and k between the L-H and the L-L shoots (Fig. 3A, B).

Leaf natality, leaf mortality and leaf turnover were significantly lower in the H-H than in the L-L shoots; these three indices were significantly higher in the H-L than in the H-H shoots; the differences between the L-H and the L-L shoots in these three parameters showed the same patterns as those between the H-H and the L-L shoots (Fig. 4A–C).

The H-H shoots had significantly smaller branch angle, branching ratio, total branch length and shoot biomass than the L-L shoots (Fig. 5A–D). The H-L shoots had significantly larger branching ratio, total branch length and shoot biomass than the H-H shoots, while there was no significant difference in branch angle between them (Fig. 5A–D). The differences between the L-L and the L-H shoots in branch angle, branching ratio, total branch length and shoot biomass showed the same patterns as those between the H-L and the H-H shoots (Fig. 5A–D).

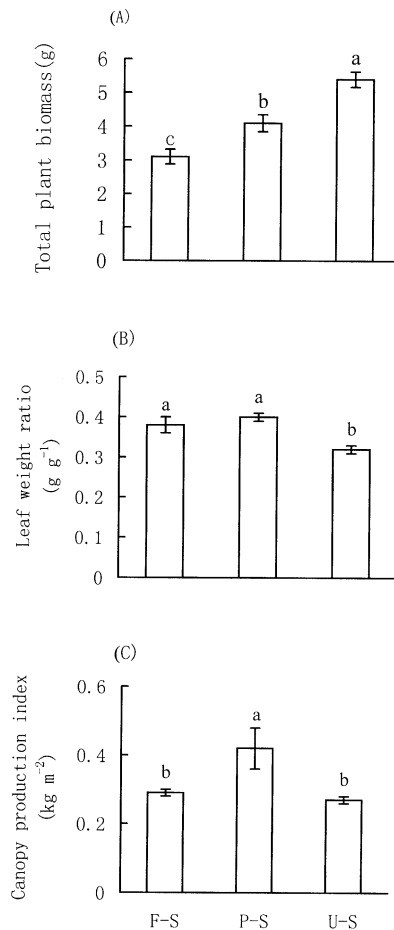


Fig. 6 Changes in (A) total plant biomass, (B) leaf weight ratio and (C) canopy productivity index. Data are means (\pm SE) ($n=10$). Bars followed by the same letter are not significantly different at $P=0.05$. The treatments are coded as in Fig. 1

At the whole-plant level, light availability increased in the following order: U-S < P-S < F-S. Total plant biomass significantly increased with decreasing light availability (Fig. 6A). Leaf weight ratio was significantly higher in the F-S and P-S than in the U-S, but it did not show significant differences between the F-S and the P-S shoots (Fig. 6B). The canopy productivity index of plants growing under P-S was significantly greater than that of plants growing under F-S and U-S while it exhibited no significant difference between F-S and U-S (Fig. 6C).

Discussion

Growth of the H-L shoots was enhanced whereas that of the L-H shoots was depressed due to the partial shading. This indicates a correlative inhibition occurring in *Salix matsudana*, as previously found in the herbaceous plants *Pisum sativum* and *Rhinanthus serotinus* (Novoplansky et al. 1989; Prati et al. 1997) and in a woody plant *Pinus*

sylvestris (Stoll and Schmid 1998). There have been two possible explanations for this correlative inhibition. One is dynamic competition in *Pisum sativum* (Sachs and Novoplansky 1997) and the other is “negative” physiological integration between the sun shoots and shade shoots in *Pinus sylvestris* (Stoll and Schmid 1998). Our results concerning physiology may provide a third possible explanation that the H-L shoots have higher photosynthetic product accumulation than the L-H shoots (see below).

On the other hand, such a correlative inhibition process greatly enhances the canopy productivity index of the plants growing in partially shaded environments compared with the homogeneous light environments, and therefore plants under a patchy light condition have higher potential to produce organic matter on per unit leaf area basis. This may be adaptive for *S. matsudana* to grow in its natural habitats with a heterogeneous light supply. Thus the prediction proposed in the Introduction was supported by our results to a great extent.

Interestingly, although there was no significant difference in shoot biomass between the L-H and the H-H shoots, shoot biomass of the H-L shoots was significantly greater than that of the H-H shoots (Fig. 5D). Therefore, total plant biomass was significantly smaller in the F-S than in the P-S (Fig. 6A). In contrast, total plant biomass was significantly greater in the U-S than in the P-S owing to the L-H being depressed by the partial shading (Figs. 5D, 6A). Growth differences between the H-H and the L-L shoots indicate that the *S. matsudana* cuttings under 60% of full sunlight grew better than those under full sunlight. This explains why its seedlings often appear under the dense canopy of mother trees rather than in gaps in natural conditions.

For the plants growing under the heterogeneous light condition, biomass allocation to the H-L shoots was higher than that to the L-H shoots (data not shown). This allocation pattern is similar to “spatial division of labor” found in clonal plants (Hutchings and de Kroon 1994; de Kroon and Hutchings 1995) and may be a more economic allocation strategy (Bloom et al. 1985). The difference in leaf weight ratio between treatments (Fig. 6B) implies that biomass allocation to the leaves of the plants growing under partial shading condition was enhanced, which to some extent makes the leaves have a higher photosynthetic potential.

Fast leaf turnover can increase the maximum photosynthetic rate in sun plant species (Percy 1999). The partial shading accelerated leaf turnover in the H-L shoots compared with H-H shoots (Fig. 4C). Consequently maximum photosynthesis of the leaves was significantly higher in the H-L shoots than in the H-H shoots ($P<0.05$) (Fig. 2). Branch angle and branching ratio are usually considered to be indicators of adaptive strategy in woody plant species (Honda and Fisher 1978; Pickett and Kempf 1980; Fisher 1986). Higher branch angle, branching ratio and branch length might allow the H-L shoots to form a greater effective leaf area than the H-H shoots to intercept more light.

Physiological acclimation is indispensable to fully understand the adaptations of plants to patchy environments. Gas exchange is strongly restricted by stomatal behavior (e.g. Long et al. 1993; Gibson 1998). This viewpoint was supported by our results (Table 1, Fig. 2). F_v/F_m represents a good estimation of maximum photochemical efficiency (Adams et al. 1990). The differences in gas exchange and in Chl a fluorescence in response to the contrasting light environments (Table 1) indicate that changes in light environment might have different influences on “external” physiological pattern and “internal” physiological process. The differences in net photosynthesis at 0600 hours between the four kinds of the shoots (Fig. 2) imply that the light compensation point was lower in the L-H and the L-L shoots than in the H-L and the H-H shoots. In addition, the shoots could also respond to the contrasting light environments through other means, such as modification of the timing and intensity of mid-day depression, and change in the timing of the morning photosynthetic peak (Fig. 2). The H-L shoots had higher net photosynthesis and lower night respiration than the H-H shoots. In contrast, the L-H had lower net photosynthesis and higher night respiration than the L-L (Table 1, Fig. 2). As a result, partial shading might enhance photosynthetic product accumulation in the H-L shoots whereas it might depress that accumulation in the L-H shoots. This may explain why the H-L shoots grew better than the H-H shoots whereas the L-H shoots grew worse than the L-L shoots to some extent. On sunny days, particularly 1000–1700 (data not shown), leaf and air temperatures were higher by 1–2°C under the unshaded treatment than the shaded treatment due to differences in irradiation. Increased transpiration might enable the leaves in the H-L shoots to decrease their surface temperatures and simultaneously to accelerate their water losses. The drought-resistant and water-holding capacity of leaves tends to increase with decreasing WSD and k (Beadle et al. 1993; He 2001). The significant differences in WSD and k between the H-L and the H-H shoots (Fig. 3) suggest that the drought-resistant and water-holding capability of leaves was stronger in the H-L shoots than in the H-H shoots, which might advantageously allow the H-L shoots to be less vulnerable to water stress arising from higher transpiration.

The acquisition of heterogeneously distributed resources by plants through their foraging behavior has been studied extensively in clonal plants; hypotheses based on possible adaptations of clonal plants to heterogeneous distribution of resources have been developed with reference to the role of physiological integration, plastic changes in clone architecture, “division of labor”, and modification of the optimal balance between clonal propagation and recruitment from seed under variable growing conditions (Price and Marshall 1999). However, up to now very little effort has been paid to foraging behavior in a clonal plants and to comparison of foraging behavior between clonal and a clonal plants, which is vital to completely understand the adaptations of plants to heterogeneous environments.

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