Taihangia rupestris, a rare herb dwelling cliff faces: responses to irradiance

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Abstract

We studied the responses of gas exchange, leaf morphology, and growth to irradiance in *Taihangia rupestris*, a naturally rare herb inhabiting only vertical cliff faces. In low irradiance (LI, 10 % of full sun) *T. rupestris* had lower net photosynthetic rate (P_N) and produced much less leaves, total leaf area, and biomass than in high (HI, full sun) or medium irradiance (MI, 50 % of full sun). P_N of *T. rupestris* was higher in HI than in MI on August 8, but lower in HI than in MI on September 22. *T. rupestris* had shorter petioles and lower leaf area ratio, and produced more but smaller and thicker leaves in HI than in MI. In HI the fast production of new leaves may guarantee *T. rupestris* to maintain higher P_N at the whole plant level and thus accumulate more biomass at harvest, although the single-leaf P_N may become lower as found on September 22. Hence *T. rupestris* possesses a latent capacity to acclimate and adapt to full sun. Irradiance, therefore, may not be a responsible factor for the restricted distribution of *T. rupestris* on vertical cliffs.

Additional key words: cliff-inhabiting plant; gas exchange; growth; irradiance; leaf morphology; net photosynthetic rate; restricted habitat; stomatal conductance; transpiration rate; water use efficiency.

Introduction

Plant species are able to deal with the changing environments by adjusting physiological, morphological, and growth responses (Bazzaz 1996, Matos *et al.* 1998, Gamper *et al.* 2000, Vats *et al.* 2002). However, this ability varies among species (Boardman 1977, Bazzaz 1979, 1996, Xiong *et al.* 2000, Meir *et al.* 2002). It is generally believed that plant species from habitats with large environmental variations possess a large ability of photosynthetic acclimation and morphological adaptation, whereas those from habitats with relatively stable conditions tend to have a small ability (Berry and Björkman 1980, Björkman 1981, Xiong *et al.* 2000). Endemic plant species with a restricted habitat, therefore, may show a rather limited ability of acclimation and adaptation to the changing environments (Björkman 1981, Baskin and Baskin 1988, Larson *et al.* 2000). Examples include *Petrophytum cinerascens* which grows only on steep rocky outcrops and sandy soils along the Columbia River in eastern Washington, USA (Moore *et al.* 1998), and *Deschampsia antarctica* which is limited to the maritime region along the west coast of Antarctica (Xiong *et al.* 2000). Both species demonstrated no photosynthetic acclimation to temperature changes (Moore *et al.* 1998, Xiong *et al.* 2000).

Cliffs are the natural habitats of a number of rare and endemic plant species, such as *Kunzea sinclairii*, *Centaurea corymbosa*, *Adiantum capillus-veneris*, *Dianthus gratianopolitanus*, *Sorbus domestica*, and *Pyrus cordata* (Colas *et al.* 1997, 2001, Larson *et al.* 2000, de Lange and Norton 2004). The environmental conditions on cliffs are much more stable and have been affected much less by competition, grazing, fire, and human activities than non-cliff habitats such as grasslands and forests (Bunce 1968, Larson *et al.* 2000, Colas *et al.* 2001, de Lange and Norton 2004). Therefore, it is expected that naturally rare plant species dwelling cliffs may display a rather limited ability of acclimation and adaptation when facing the changing environments.

In the recent decades, numerous studies on cliff plants have been carried out (for review see Larson *et al.* 2000), but most of them have focused on patterns and descriptions of vegetation (*e.g.* Collins *et al.* 1989, Nuzzo 1996,

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Cooper 1997, Farris 1998, Booth and Larson 1998, 2000, Haig *et al.* 2000). Detailed eco-physiological studies on individual plant species have received little attention (but see Bartlett and Larson 1990, Moore *et al.* 1998). Even less is known about the eco-physiological, morphological, and growth responses to environmental changes with regard to naturally rare species inhabiting only vertical cliff faces. This information may be important for the understanding of the distribution and for the conservation of the rare species on cliffs (Bartlett and Larson 1990).

Taihangia rupestris Yü & Li (Rosaceae) is a naturally rare, cliff-inhabiting perennial herb endemic to the southern part of the Taihang Mountains of China. It occurs mostly in the small crevice on the faces of the north-facing cliffs at altitudes ranging from 600 to 1 500 m a.s.l, where direct sunshine can not be received (Yu and Li 1983, Shen 1994, Lu *et al.* 1995). This paper deals with a pot experiment in which *T. rupestris* was grown in three irradiances. We aim to address how physiology, morphology, and growth of *T. rupestris* are affected by irradiance.

Materials and methods

Plant: *Taihangia rupestris* Yü & Li is self-compatible and possesses both bisexual and unisexual male flowers. The bisexual flowers can produce seeds which may develop into new plants in greenhouse conditions, but this species was rarely observed to produce seeds and establish seedlings in its natural habitat (Shen 1994, Lu *et al.* 1995). Lu (1996) found that, when temperature was too low, the pistils of the bisexual flowers of *T. rupestris* tended to abort and thus a high proportion of male flowers could be formed. *T. rupestris* can reproduce vegetatively by forming short rhizomes which develop roots and leaves at the tips. However, for lack of soil on vertical cliff faces, this ability is limited. The new vegetative plants can only be produced very close to the mother plant and extend along the crevice on the vertical cliff faces (Tang 2004).

Experiment design: 18 clones of *T. rupestris* were collected and used as the experiment material. On April 27, 2002, three vegetatively-produced, similar-sized plants from each of the 18 clones were grown in 16-cm-diameter pots filled with sand and peat mixture (1 : 1 in volume). After one month's growth for recovery, all the experimental plants were standardized by removing all the leaves except the youngest, unexpanded ones. Three plants from each clone were then randomly subjected to three irradiances. The high irradiance (HI) was 100 % of the full sun. The medium (MI) and low irradiance (LI), provided by shading nets, were *ca*. 50 % and 10 % of the full sun, respectively. The experiment was conducted outdoors at the Institute of Botany, the Chinese Academy of Sciences, Beijing, China. During the experiment all the plants were watered as needed and fertilized every 10 d with 20 cm^3 full strength N-P-K nutrient solution (4.373 g NH_4NO_3, 2.063 g NaH_2PO_4, and 2.876 kg KCl per m^3).

Gas exchange: On August 8, 2002, a sunny day in the middle of the growth season, we measured net photosynthetic rate (P_N), transpiration rate (E), and stomatal conductance (g_s) simultaneously at 2-h intervals from 06:30 to 18:30. Since leaf turnover rate of *T. rupestris* seemed much faster in HI than in MI and LI on September, we selected another sunny day (September 22, 2002) and conducted the second measurements on the diurnal patterns of gas exchange in *T. rupestris*. All measurements were done on fully expanded young leaves under full sun with a *LCA-4* portable gas exchange analyzer (*Analytical Development Company, ADC,* Hoddesdon, England). Four replicated plants were used for these measurements. Water use efficiency (WUE) was calculated as P_N/E.

Growth and leaf morphology: From the start of the experiment, the number of leaves per plant was counted every 8 to 12 d. On October 12, 2002, five mature leaves from each plant were sampled and each leaf was separated into lamina and petiole. The area, length, and width of each lamina were measured with a leaf area meter (*CI-202, CID,* Vancouver, Washington, USA), and the length of each petiole was measured with a ruler. After measurement, all parts of these leaves were dried and weighted. The remaining parts of each plant were separated into roots, laminae, and petioles, and weighed after drying at 80 °C for 48 h. Specific lamina area (SLA, lamina area/lamina mass), specific petiole length (SPL, petiole length/petiole mass), leaf area ratio (LAR, total leaf area/total plant mass), and leaf mass ratio (LMR, total leaf mass/total plant mass) were derived.

Data analysis: One-way repeated-measures analysis of variance (rmANOVA; Ende 2001) followed by pair-wise contrasts was used to compare the differences in gas exchange parameters and number of leaves among the three irradiance treatments. One-way ANOVA followed by Student-Neuman-Keuls multiple comparisons (Sokal and Rohlf 1981) was employed to test the differences in growth and leaf morphology traits among the three irradiance treatments. *SAS* software package was used for all analyses (SAS Institute 1999).

Results

Diurnal patterns of gas exchange: On both August 8 and September 22, the diurnal changes in P_N (Fig. 1*A, B*) and WUE (Fig. 1*G, H*) of *T. rupestris* all demonstrated the typical bimodal curves, with two peaks appearing at around 08:30 and 16:30, respectively. The diurnal patterns of E and g_s were bimodal on September 22 (Fig. 1*D, F*), but tended to be bell-shaped on August 8 (Fig. 1*C, E*).

Daily means of gas exchange: Irradiance significantly affected P_N and WUE of *T. rupestris* on both measuring dates (Table 1). On August 8, P_N of *T. rupestris* was higher in HI than in MI and LI, but did not differ significantly between MI and LI (Table 1, *A*). On September 22, however, *T. rupestris* showed the highest P_N in MI and the lowest in LI (Table 1, *B*). On August 8, WUE increased significantly with increasing irradiance (Table 1, *A*). On September 22, however, WUE in HI and MI did not differ, but were significantly higher than in LI (Table 1, *B*). A significant effect of irradiance on E and g_s of *T. rupestris* was found on September 22, but not on August 8. On September 22, E and g_s were markedly higher in MI than in HI, but did not differ between HI and LI (Table 1, *B*).

Growth: Irradiance had a marked effect on biomass, total leaf area, number of leaves, LAR, and LMR of *T. rupestris*. About one month after the start of the experiment (*i.e.* on June 28) the number of leaves started to differ among the three irradiance treatments, and at harvest the number of leaves in HI was 0.49 and 2.73 times greater than that in MI and LI, respectively (Fig. 2*E*). With increasing irradiance, biomass increased greatly at harvest (Fig. 2*A*). Total leaf area and LMR did not differ between treatments HI and MI, but were significantly greater in HI and MI than in LI (Fig. 2*B, D*). LAR in MI and LI did not differ, but was significantly greater than in HI (Fig. 2*C*).

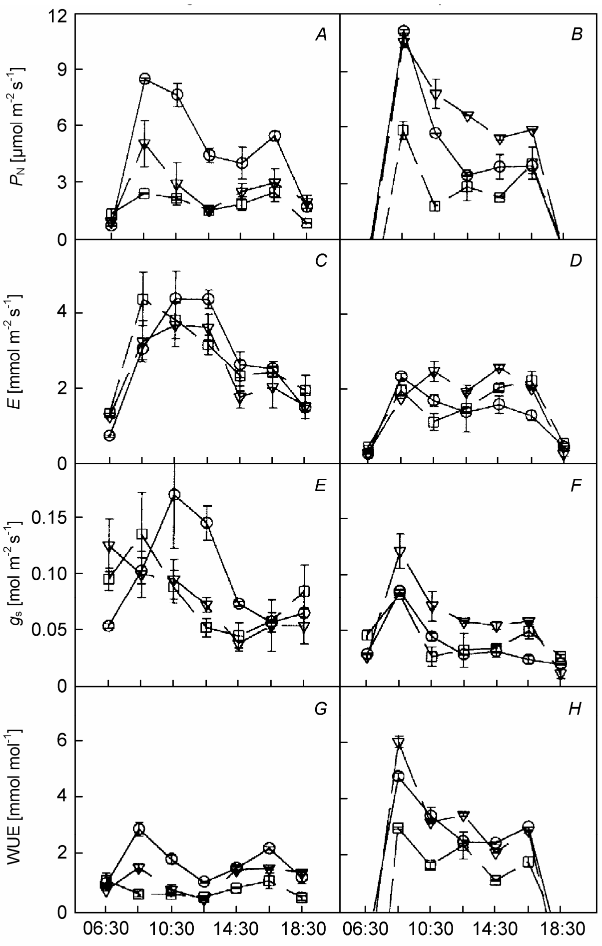

Fig. 1. Diurnal patterns of net photosynthetic rate, P_N (*A, B*), transpiration rate, E (*C, D*), stomatal conductance, g_s (*E, F*), and water use efficiency, WUE = P_N/E (*I, J*) of *Taihangia rupestris* measured on August 8 and September 22, 2002, respectively. *Circles, triangles, and rectangles* stand for high, medium, and low irradiance, respectively.

Table 1. Daily means (± 1 SE) of net photosynthetic rate, P_N [µmol m^{-2} s^{-1}], transpiration rate, E [mmol m^{-2} s^{-1}], stomatal conductance, g_s [mol m^{-2} s^{-1}], and water use efficiency, WUE = P_N/E [mmol mol^{-1}] of *Taihangia rupestris* measured on (*A*) August 8 and (*B*) September 22, 2002. Within one column, numbers sharing the same letters are not different at $p \leq 0.05$. HI, MI, and LI stand for high, medium, and low irradiance, respectively.

	(*A*) August 8				(*B*) September 22			
	P_N	E	g_s	WUE	P_N	E	g_s	WUE
HI	4.64 a (0.24)	2.73 a (0.23)	0.0951 a (0.0113)	1.64 a (0.07)	3.87 b (0.14)	1.29 b (0.07)	0.0380 b (0.0012)	1.87 a (0.08)
MI	2.56 b (0.51)	2.44 a (0.33)	0.0767 a (0.0083)	1.09 b (0.02)	4.97 a (0.08)	1.62 a (0.05)	0.0579 a (0.0007)	1.74 a (0.12)
LI	1.80 b (0.14)	2.77 a (0.14)	0.0797 a (0.0079)	0.72 c (0.09)	1.76 c (0.16)	1.41 ab (0.11)	0.0430 b (0.0034)	0.07 b (0.16)

Leaf morphology: A marked effect of irradiance was found on petiole length, SPL, area per leaf, and SLA (Table 2). Petiole length was significantly greater in MI than in HI, but did not differ between HI and LI (Table 2). SPL was much greater in LI than in HI and MI, but did not differ between HI and MI (Table 2). Area per leaf was larger in MI than in HI and LI (Table 2). SLA decreased significantly with increasing irradiance (Table 2).

Discussion

Contrary to the expectations, *T. rupestris* displayed remarkable responses of gas exchange, leaf morphology, and growth to the changing irradiance in the present study, despite the fact that it only inhabits a rather restricted habitat of the vertical cliff faces (Shen 1994, Lu *et al.* 1995).

Although the diurnal patterns of P_N in *T. rupestris* were similar in the three irradiance treatments, the daily means differed significantly (Fig. 1*A, B*; Table 1). In addition, the effects of irradiance on P_N differed between the two measuring dates, with *T. rupestris* showing a higher P_N in HI than in MI on August 8 but a reverse pattern on September 22 (Fig. 1*A, B*). These results suggest that the ability of *T. rupestris* to acclimate photosynthetically to full sun varies with time. Zhang *et al.* (2003) also reported that the shade-tolerant herb *Paeonia suffruticosa* displayed photosynthetic acclimation to full sun after one month of growth, but did not after two months. They proposed that long-term exposure to full sun might have damaged the photosynthetic apparatus of the species (Zhang *et al.* 2003).

This hypothesis, however, may not hold true for *T. rupestris* in the present study, as biomass and the number of leaves at harvest were much greater in HI than in MI and LI (Fig. 2*A, E*). The differences in P_N between August 8 and September 22 may reflect a complex physiological and morphological adaptation of *T. rupestris* to the seasonal changes in irradiance (Matos *et al.* 1998).

Plants would maintain, or even increase, the carbon uptake after they have acclimated to a new environment (Bazzaz 1996). Besides these physiological responses, various morphological and growth changes may occur to balance the carbon economy during this process (Bazzaz 1979, 1996, Yu *et al.* 2002, Yu and Dong 2003). At harvest, *T. rupestris* in LI had much less biomass, leaves,

Table 2. Means (± 1 SE) of petiole length, PL [cm], specific petiole length, SPL [m kg^{-1}], area per leaf, LA [cm^2], and specific lamina area, SLA [m^2 kg^{-1}] of *Taihangia rupestris* in the three irradiances. Within one column, numbers sharing the same letters are not different at $p \leq 0.05$. Treatment codes are as in Table 1.

	PL	SPL	LA	SLA
HI	2600±200b	2.1±0.2b	5.2±0.6b	1.12±0.4c
MI	3400±200a	2.8±0.2b	7.6±0.8a	1.65±0.4b
LI	2900±200ab	10.6±1.7a	4.1±0.3b	3.47±3.2a

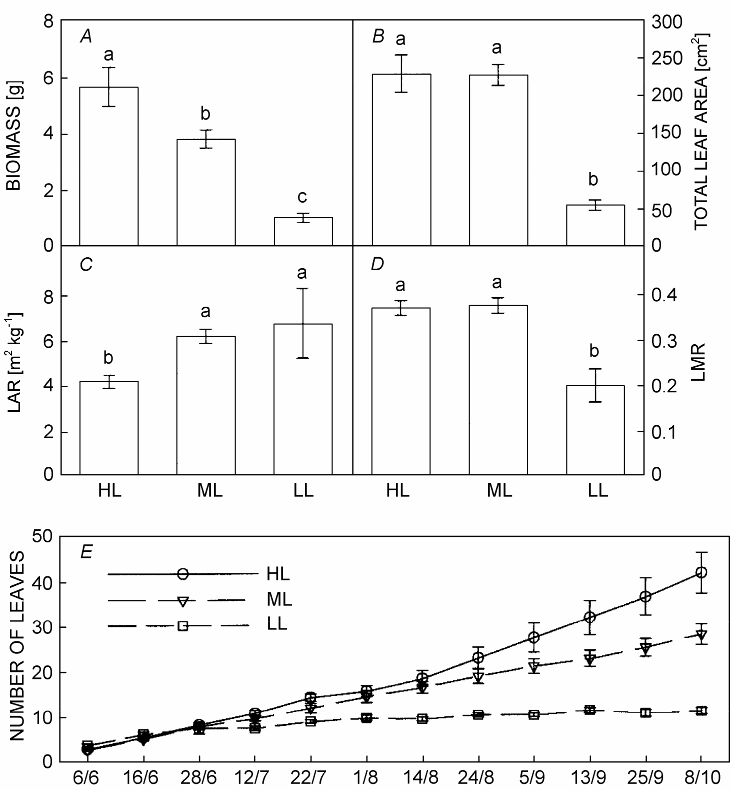

Fig. 2. Biomass (*A*), total leaf area (*B*), leaf area ratio, LAR (*C*), and leaf mass ratio, LMR (*D*) of *Taihangia rupestris* at harvest, and number of leaves on each measuring date (*E*). *Bars* sharing the same letters are not different at $p \leq 0.05$. Treatment codes are as in Table 1.

and total leaf area than in MI, and no significant elongation of petioles was detected (Fig. 2, Table 2). Some adaptive physiological (the decrease in g_s; Table 1, *B*) and morphological responses (the increase in SPL and SLA and the decrease in LMR; Fig. 2*D*, Table 2) of *T. rupestris* grown in LI did occur to enhance the whole plant P_N, but apparently they were far insufficient to compensate for the loss caused by LI (Yu and Dong 2003).

Although biomass and number of leaves of *T. rupestris* were greater in HI than in MI, the total leaf area did not differ (Fig. 2*A, B, E*). In addition, *T. rupestris* had longer petioles (Table 2), larger but thinner leaf laminae (Table 2), and higher LAR (Fig. 2*C*) in MI than in HI. These morphological and growth responses can increase photosynthetic energy capture at the whole plant level, and are thought to be adaptive for plants growing in environments with relatively low irradiance (Thompson *et al.* 1988, Yu and Dong 2003). Sims and Pearcy (1992) found that, with increasing leaf age, P_N of the sun leaves sharply decreased, but the shade leaves could keep higher P_N for much longer time. In the present study, *T. rupestris* produced in HI more leaves, but they were small and thick (Fig. 2*E*, Table 2). Thus, a quick formation of new leaves could probably ensure that *T. rupestris* in HI have a higher P_N at the whole plant level, although the single-leaf P_N may become lower as indicated on September 22.

Our results suggest that *T. rupestris* possesses a broad tolerance to irradiance changes and retains the capacity to acclimate and adapt to full sun. Irradiance, therefore, may not be a factor responsible for the restricted distribution of *T. rupestris* on vertical cliff faces. Since water is likely to be a limiting factor for plant species on vertical cliff faces (Larson *et al.* 2000), growing on the faces of the north-facing cliffs may help *T. rupestris* to maintain water balance.

References

Bartlett, R.M., Larson, D.W.: The physiological basis for the contrasting distribution patterns of *Acer saccharum* and *Thuja occidentalis* at cliff edges. – J. Ecol. **78**: 1063-1078, 1990.

Baskin, J.M., Baskin, C.C.: Endemism in rock outcrop plant communities of unglaciated eastern United States: an evaluation of the roles of the edaphic, genetic and light factors. – J. Biogeogr. **15**: 829-840, 1988.

Bazzaz, F.A.: The physiological ecology of plant succession. – Annu. Rev. Ecol. Syst. **10**: 361-371, 1979.

Bazzaz, F.A.: Plants in Changing Environments: Linking Physiological, Population, and Community Ecology. – Cambridge University Press, Cambridge 1996.

Berry, J., Björkman, O.: Photosynthetic response and adaptation to temperature in higher plants. – Annu. Rev. Plant Physiol. **31**: 491-543, 1980.

Björkman, O.: The response of photosynthesis to temperature. – In: Grace, J., Ford, E.D., Jarvis, P.G. (ed.): Plants and Their Atmospheric Environment. Pp. 273-301. Blackwell, Oxford 1981.

Boardman, N.K.: Comparative photosynthesis of sun and shade plants. – Annu. Rev. Plant Physiol. **28**: 355-377, 1977.

Booth, B.D., Larson, D.W.: The role of seed rain in determining the assembly of a cliff community. – J. Veg. Sci. **9**: 657-668, 1998.

Booth, B.D., Larson, D.W.: Constraints on the assembly of cliff communities at the seed bank stage. – Ecoscience **7**: 326-335, 2000.

Bunce, R.G.H.: An ecological study of Ysgolion Duon, a mountain cliff in Snowdonia. – J. Ecol. **56**: 59-75, 1968.

Colas, B., Olivieri, I., Riba, M.: *Centaurea corymbosa*, a cliff-dwelling species tottering on the brink of extinction: a demographic and genetic study. – Proc. nat. Acad. Sci. USA **94**: 3471-3476, 1997.

Colas, B., Olivieri, I., Riba, M.: Spatio-temporal variation of reproductive success and conservation of the narrow-endemic *Centaurea corymbosa* (Asteraceae). – Biol. Conserv. **99**: 375-386, 2001.

Collins, S.L., Mitchell, G.S., Klahr, S.C.: Vegetation environment relationships in a rock outcrop community in southern Oklahoma. – Amer. Midland Naturalist **122**: 339-348, 1989.

Cooper, A.: Plant species coexistence in cliff habitats. – J. Biogeogr. **24**: 483-494, 1997.

de Lange, P.J., Norton, D.A.: The ecology and conservation of *Kunzez sinclairii* (Myrtaceae), a naturally rare plant of rhyolitic rock outcrops. – Biol. Conserv. **117**: 49-59, 2004.

Ende, C.N. von: Repeated-measures analysis: growth and other time-dependent measures. – In: Scheiner, S.M., Gurevitch, J. (ed.): Design and Analysis of Ecological Experiments. 2nd Ed. Pp. 134-157. Oxford University Press, Oxford 2001.

Farris, M.A.: The effects of rock climbing on the vegetation of three Minnesota cliff systems. – Can. J. Bot. **76**: 1981-1990, 1998.

Gamper, R., Mayr, S., Bauer, H.: Similar susceptibility to excess irradiance in sun and shade acclimated saplings of Norway spruce [*Picea abies* (L.) Karst.] and stone pine (*Pinus cembra* L.). – Photosynthetica **38**: 373-378, 2000.

Haig, A., Matthes, U., Larson, D.W.: Effects of natural habitat fragmentation on the species richness, diversity, and composition of cliff vegetation. – Can. J. Bot. **78**: 786-797, 2000.

Larson, W., Matthes, U., Kelly, P.E.: Cliff Ecology: Pattern and Process in Cliff Ecosystems. – Cambridge University Press, Cambridge 2000.

Lu, W.L.: [Development of sexual organs in *Taihangia rupestris* – different temperature requirements for both sexual organ development in a bisexual flower.] – Acta bot. sin. **38**: 174-179, 1996. [In Chin.]

Lu, W.L., Shen, S.H., Wang, F.X.: [Studies on reproductive biology of *Taihangia rupestris* II: investigation and study of sexual and asexual reproduction.] – Chin. Biodivers. **3**: 8-14, 1995. [In Chin.]

Matos, M.C., Matos, A.A., Mantas, A., Cordeiro, V., Vieira da Silva, J.B.: Diurnal and seasonal changes in *Prunus amygdalus* gas exchanges. – Photosynthetica **35**: 517-524, 1998.

Meir, P., Kruijt, B., Broadmeadow, M., Barbosa, E., Kull, O., Carswell, F., Nobre, A., Jarvis, P.G.: Acclimation of photosynthetic capacity to irradiance in tree canopies in relation to leaf nitrogen concentration and leaf mass per unit area. – Plant Cell Environ. **25**: 343-357, 2002.

Moore, D.J., Nowak, R., Nowak, C.L.: Photosynthetic acclimation to temperature and drought in the endemic chelan rockmat, *Petrophytum cinerascens* (Rosaceae). – Amer. Midland Naturalist **139**: 374-382, 1998.

Nuzzo, V.A.: Structure of cliff vegetation on exposed cliffs and the effect of rock climbing. – Can. J. Bot. **74**: 607-617, 1996.

SAS Institute: SAS/STAT User's Guide. Version 8. – SAS, Cary 1999.

Shen, S.: [Reproductive Biology of the Rare Species *Taihangia rupestris*.] – Ph.D. Thesis. Institute of Botany, Chinese Academy of Sciences, Beijing 1994. [In Chin.]

Sims, D.A., Pearcy, R.W.: Response of leaf anatomy and photosynthetic capacity in *Alocasia macrorrhiza* (Aeraceae) to a transfer from low to high light. – Amer. J. Bot. **79**: 449-455, 1992.

Sokal, R.R., Rohlf, W.J.: Biometry. – Freeman, San Francisco 1981.

Tang, M.: [Conservation biology of naturally rare, cliff-dwelling herb *Taihangia rupestris*.] – Ph. D. Thesis. Institute of Botany, The Chinese Academy of Sciences Beijing 2004. [In Chin.]

Thompson, W.A., Stocker, G.C., Kriedemann, P.E.: Growth and photosynthetic response to light and nutrients of *Flindersia brayleyana* F. Muell., a rainforest tree with broad tolerance to sun and shade. – Aust. J. Plant Physiol. **15**: 299-315, 1988.

Vats, S.K., Pandey, S., Nagar, P.K.: Photosynthetic response to irradiance in *Valeriana jatamansi* Jones, a threatened understorey medicine herb of Western Himalaya. – Photosynthetica **40**: 625-628, 2002.

Xiong, F.S., Mueller, E.C., Day, T.A.: Photosynthetic and respiratory acclimation and growth response of Antarctic vascular plants to contrasting temperature regimes. – Amer. J. Bot. **87**: 700-710, 2000.

Yu, F.H., Chen, Y.F., Dong, M.: Clonal integration enhances survival and performance of *Potentilla anserina*, suffering from partial sand burial on Ordos plateau, China. – Evol. Ecol. **15**: 303-318, 2002.

Yu, F.H., Dong, M.: Effect of light intensity and nutrient availability on clonal growth and clonal morphology of the stoloniferous herb *Halerpestes ruthenica*. – Acta bot. sin. **45**: 408-416, 2003.

Yu, T.T., Li, C.L.: [The systematic position of genus *Taihangia* in Rosaceae.] – Acta phytotaxon. sin. **21**: 229-235, 1983. [In Chin.]

Zhang, S., Ma, K., Chen, L.: Response of photosynthetic plasticity of *Paeonia suffruticosa* to changed light environments. – Environ. exp. Bot. **49**: 121-133, 2003.