

Variations of leaf traits of an alpine shrub *Sieversia pentapetala* along an altitudinal gradient and under a simulated environmental change

Yasuhiro Taguchi* and Naoya Wada**

Department of Biosphere Science, Faculty of Science, Toyama University,
Gofuku 3190, Toyama 930-8555

Abstract: We investigated intraspecific variations of leaf traits such as number of leaves, leaf size, leaf mass per shoot, leaf mass per area (LMA) and leaf nitrogen concentration (leaf N), in a deciduous alpine dwarf shrub *Sieversia pentapetala* (L.) Greene (Rosaceae), along an altitudinal gradient in the Tateyama Range, Toyama Prefecture, central Japan. We also observed the change in leaf traits under simulated environmental amelioration using an open-top chamber (OTC). Three study sites were established at different altitudes (1900–2800 m a.s.l.) and the OTC was installed at the highest elevation site. Snow-free duration and foliage period decreased with altitude. The number of compound leaves per shoot and individual leaf size (compound leaf area) significantly decreased, resulting in reduction of leaf mass per shoot with altitude. LMA decreased, while leaf N increased significantly with altitude. Under simulated environmental amelioration (increased temperature), number of leaves, individual leaf size, and leaf mass per shoot increased significantly. LMA showed significantly higher values and leaf N lower values in the OTC manipulated shoots compared with controls. In other words, leaf mass and LMA decrease and leaf N increases under harsh conditions. These variations and changes in leaf traits seemed to be adaptive responses to severe growth conditions to maintain positive carbon balance.

key words: altitudinal gradient, deciduous leaf, leaf nitrogen, LMA, OTC

Introduction

Environmental conditions for growth and reproduction of plants are generally considered to become severe with increasing altitude: *i.e.* air temperature, nutrient availability in the soil, partial pressure of CO₂, length of snow-free period and then favorable growing season decrease, while wind speed, intensity of solar radiation and UV increase. These variations of environmental factors may strongly affect not only net production but also leaf traits of plants (Woodward, 1979, 1983, 1986; Körner *et al.*, 1986, 1989; Körner, 1989; Kudo, 1995, 1996; Bowman *et al.*, 1999). Among leaf traits, leaf life-span, leaf mass per area (LMA) and leaf nitrogen concentration (leaf N) are particularly important and useful parameters for evaluating growth responses to varying environmental conditions in a single plant species (*e.g.* Kudo, 1999 for review).

When the length of the favorable growing season is shortened with increasing

* Present address: Graduate School of Environmental Earth Science, Hokkaido University, Sapporo 060-0810.

** E-mail address: wada@sci.toyama-u.ac.jp

altitude, deciduous plants behaving reduction of leaf construction cost and enhancement of photosynthetic efficiency are considered “adaptive” based on the carbon balance hypothesis (Chabot and Hicks, 1982; Kikuzawa, 1991; Kudo, 1996). This is because deciduous plants require positive carbon gain within a restricted growing period to maintain the cost-benefit balance of the carbon economy. Generally, LMA is positively related to leaf thickness, toughness and construction cost (Givnish, 1988; Williams *et al.*, 1989), and leaf N is strongly positively correlated with maximum photosynthetic capacity on a leaf-weight basis (Field and Mooney, 1986; Reich *et al.*, 1991). Therefore, we expect LMA to decrease and leaf N to increase with altitude for deciduous plants when those adaptively respond to the shortened growing period along an altitudinal gradient.

Not only the length of the growing season but also other environmental factors such as temperature and nutrient availability change with altitude. However, most factors appear to force plants to reduce the carbon gain by photosynthesis with increasing altitude. Higher concentration of leaf nitrogen may lead to higher efficiency of carbon gain by photosynthesis, and lower leaf construction cost seems to compensate for the short photosynthetic period in deciduous plants on the basis of the carbon budget at higher elevation habitats. Thus, lower LMA and higher leaf N at higher elevation habitats could also be considered as one of the adaptive traits under harsh conditions for deciduous plants (*e.g.* Kudo, 1996). In the present study, we tested this prediction in a deciduous alpine shrub *Sieversia pentapetala* (L.) Greene (Rosaceae), ranging from *ca.* 1900 m to *ca.* 2800 m above sea level in the Tateyama Range, central Japan.

Next, we investigated the effects of simulated environmental amelioration using an open-top chamber (OTC) on leaf traits such as LMA and leaf N. The OTC increases air temperature *ca.* 1–2°C per day throughout the summer, June and July (Wada, 2000). This amelioration of thermal environment may affect not only leaf mass (Wada, 2000) but also leaf traits of alpine plants (Suzuki and Kudo, 1997, 2000). A previous study on *S. pentapetala* demonstrated that leaf mass per shoot significantly increased in the OTC manipulated shoots during three growing seasons than in controls (Wada, 2000), indicating that net production through photosynthesis increased under the amelioration. This suggests that leaf mass and construction cost (*i.e.* LMA) may increase in the ameliorated growth condition, resulting in lower leaf N in the OTC manipulated shoots than in controls. In other words, we expect that LMA is lower and leaf N is higher in controls than in plants inside the OTC if leaves could plastically change their traits under the simulated environmental change, because plants growing outside the OTC (controls) may experience more stressful conditions and restricted carbon gain due to lower temperature. The second aim of this study is to clarify the responses of leaf traits of *S. pentapetala* to the simulated environmental change as predicted above.

Materials and methods

This study was carried out in the Tateyama Range, Toyama Prefecture, central Japan (36°33'N, 137°26'E). In 1999, we established three study sites at different altitudes: Midagahara (1910 m a.s.l.), Murodo (2460 m a.s.l.), and Johdo (2820 m a.s.l.) (Fig. 1). Midagahara is located in the sub-alpine zone. In slope habitats where the

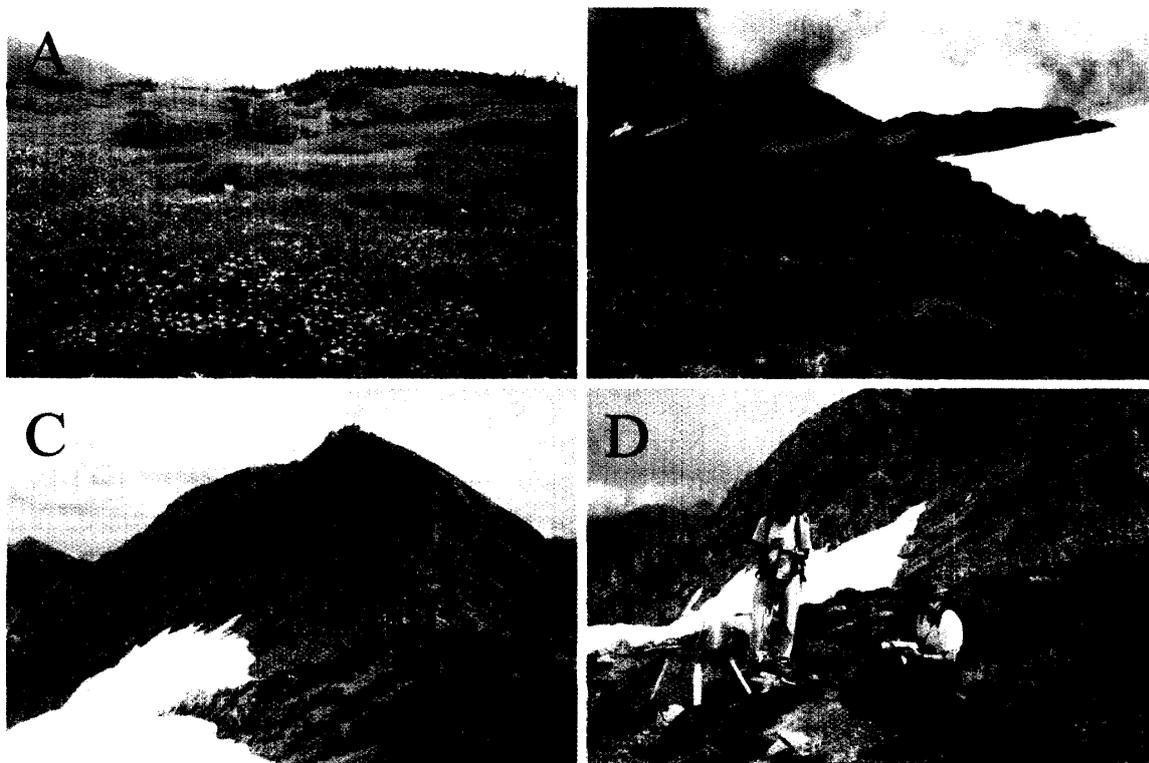


Fig. 1. Landscapes of three study sites in the Tateyama Range, Toyama Prefecture, central Japan. A, Midagahara (1910 m a.s.l.); B, Murodo (2460 m a.s.l.); C and D, Johdo (2820 m a.s.l.). Open-top chambers (OTCs) were installed in the summer of 1996 (D).

soil moisture is relatively low, conifers and deciduous trees such as *Abies mariesii* Masters, *Betula ermanii* Cham. and *Sorbus commixta* Hedl. are common. In topographically flat habitats where the soil moisture is relatively high, mire and snow-bed alpine plant communities dominate; such as *Fauria crista-galli* (Menz.) Makino, *Sanguisorba tenuifolia* var. *purpurea* Trautv. et Mey., *Sieversia pentapetala* (L.) Greene, *Calamagrostis longiseta* Hack., *Moliniopsis japonica* (Hack.) Hayata, *Sasa kurilensis* Makino, *Scirpus hondoensis* Ohwi, *Carex paupercula* Michx., *C. blepharicarpa* Franch. and *Eriophorum vaginatum* L. The study site at Midagahara was chosen on the mesic habitats dominated by *S. pentapetala* without conifers and deciduous trees (Fig. 1A). Murodo and Johdo are located in the alpine zone. *Sieversia pentapetala* is a dominant species and coexists with *Phyllodoce aleutica* A. Hell., *P. nipponica* Makino, *Empetrum nigrum* L., *Schizocodon soldanelloides* f. *alpinus* Maxim., *Anemone narcissiflora* var. *nipponica* Tamura, *Fauria crista-galli*, *Peucedanum multivittatum* Makino, *Pinus pumila* Regel, and many grasses and sedges in the snow-bed vegetation at Murodo (Fig. 1B). The vegetation of Johdo consists mainly of *Empetrum nigrum*, *Loiseleuria procumbens* Desv., *Pinus pumila*, *Gentiana algida* Pallas and *Potentilla matsumurae* Th. Wolf in wind-exposed habitats; *S. pentapetala* occurs with *Empetrum nigrum*, *Phyllodoce aleutica*, *Anaphalis alpicolain* Makino, *Carex flavocuspis* Fr. et Sav. and grasses in wind-swept and snow-bed habitats (Fig. 1C, D).

At each site, we established five 50 cm × 50 cm quadrats in *S. pentapetala* dominated patches, and the phenology from leaf emergence to senescence was observed weekly

from snowmelt in early June to snowfall in early to mid-October 1999. The snow-free period at each site was recorded and leaf life-span in the quadrats was estimated not on an individual leaf basis but on a patch (individual plant) basis as the “foliage period” from the weekly observations. Leaf samples were collected from twenty fruiting shoots (at almost the same developmental stage) of *S. pentapetala* ($n=20$) around the quadrates at each study site: after 55 days (2 August) from snowmelt (8 June) at Midagahara, after 66 days (20 August) from snowmelt (15 June) at Murodo, and after 60 days (29 August) from snowmelt (30 June) at Johdo, respectively. For each shoot sample, we measured leaf area by using a scanner connected with a personal computer (NIH Image ver. 1.62) and leaf dry weight was measured by an electronic balance (AC 211S, Sartorius Co. Ltd., Tokyo, Japan) after drying at 80°C for 48 h. Leaf nitrogen concentration was analyzed by a CN corder (MT-700, Yanaco Co. Ltd., Kyoto, Japan).

At Johdo, the highest elevation site, an open-top chamber (see Wada *et al.* (1998) and Wada (2000) in detail) was installed in the summer of 1996 (Fig. 1D). Inside this OTC, 10 fruiting shoots were collected on 26 August 1999 (the fourth year after the OTC set up); and leaf dry mass per shoot, LMA and leaf N were measured by the method described above. These leaf traits were compared with samples collected outside the OTC around five quadrats ($n=20$) at Johdo as mentioned above.

Ambient air temperature at 30 cm above the ground was measured automatically at 1 h intervals during the growing season at each study site, by using a data logger (HOBO H8 Pro, Onset Computer Co., Pocasset, MA, USA). However, we could not record air temperature at Midagahara, so we estimated air temperature by calculating from actual data at Murodo on a basis of the altitudinal lapse rate (0.6°C 100 m⁻¹ a.s.l.). Ambient air temperature at 5 cm above the ground inside and outside the OTC at Johdo was measured by using temperature data loggers (KADEC U-II, Kona System Co. Ltd., Sapporo, Japan) at 1 h intervals during the growing season.

Results

Altitudinal variation

Table 1 shows ambient air temperature at 30 cm above the ground in July, August and September 1999, at three study sites (mean \pm SD). Ambient temperatures at Midagahara were estimated values. Snow free periods in 1999 were 19 wk at Midagahara, 18 wk at Murodo and 16 wk at Johdo, respectively. Foliage periods were 16 wk at Midagahara, 13 wk at Murodo and 11 wk at Johdo, respectively (Fig. 2), indicating the shortened growing length and decreasing leaf life-span with increasing altitude. Leaf emergence and senescence occurred synchronously, with less variation among quadrats within each study site. Leaf emergence at Midagahara occurred 1 wk after the snowmelt, and that at Murodo and Johdo occurred 2 wk after the snowmelt.

The number of compound leaves per shoot and individual leaf size (average value of compound leaf area per shoot) significantly decreased with altitude ($P=0.012$, $n=60$, by the Kruskal-Wallis test for number of leaves, and $P<0.001$, $F=9.35$, $n=60$, by one-way ANOVA for leaf size; Table 2). As a consequence, leaf mass per shoot significantly decreased with altitude ($P<0.001$, $n=60$, by the Kruskal-Wallis test; Fig. 2), suggesting limited growth at the higher elevation site. LMA also decreased with

Table 1. Ambient air temperature ($^{\circ}\text{C}$, mean \pm SD) at 30cm above the ground in July, August and September 1999 at three study sites.

Study site	Midagahara* (1910 m)	Murodo (2460 m)	Johdo (2820 m)
July	15.4 \pm 1.6	12.1 \pm 1.6	10.5 \pm 1.6
August	16.5 \pm 1.5	13.2 \pm 1.5	11.4 \pm 1.4
September	13.9 \pm 1.9	10.6 \pm 1.9	9.4 \pm 1.6
Average	15.3 \pm 1.8	12.0 \pm 1.8	10.6 \pm 1.6

* estimated values from data at Murodo

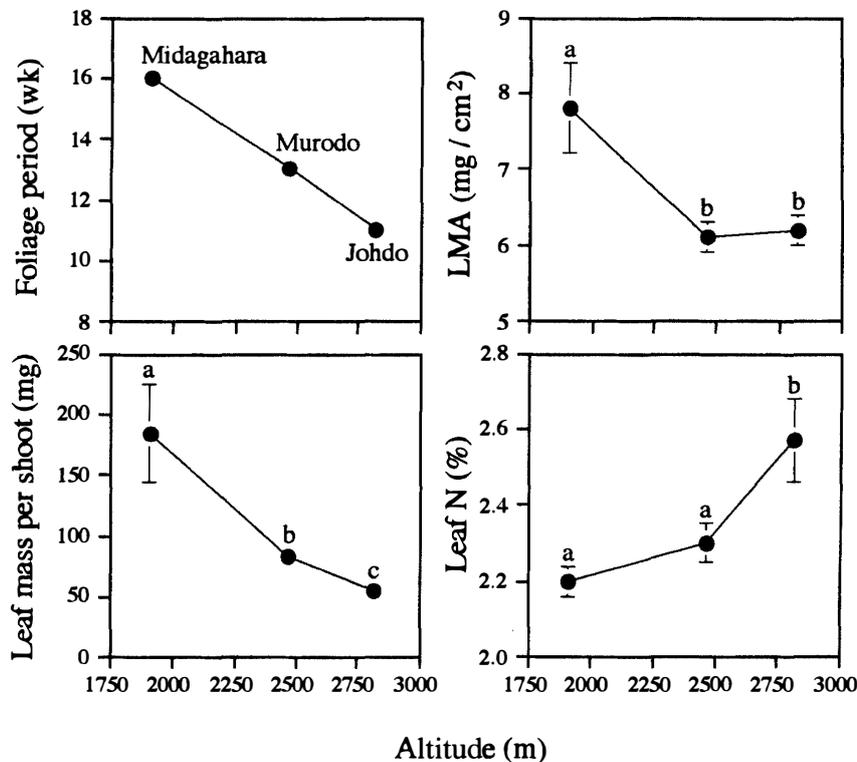


Fig. 2. Variations of foliage period, leaf mass per shoot, leaf mass per area (LMA) and nitrogen concentration (leaf N) of *Sieversia pentapetala* along an altitudinal gradient, at three study sites: Midagahara (1910 m a.s.l.), Murodo (2460 m a.s.l.) and Johdo (2820 m a.s.l.). Sample size of foliage period was 5 and of leaf mass per shoot, LMA and leaf N was 20 except for leaf N at Murodo ($n=16$). Vertical lines show SE. The same letters on SE lines indicate no significant difference between populations at the $P>0.05$ level (by the Mann-Whitney U test).

altitude ($P<0.001$, $n=60$, by the Kruskal-Wallis test; Fig. 2), but no significant difference was found between Murodo and Johdo ($P>0.05$, by the Mann-Whitney U test). In contrast to number of leaves, leaf size, leaf mass per shoot and LMA, leaf N significantly increased with altitude ($P<0.01$, $n=54$, by the Kruskal-Wallis test; Fig. 2), and leaves of *S. pentapetala* at Johdo showed significantly higher nitrogen concentra-

Table 2. The number of compound leaves per shoot (mean \pm SE, $n=20$) and individual leaf size (average value of compound leaf area per shoot (cm^2); mean \pm SE, $n=20$) at three study sites with different altitudes. The different letters on the numerals indicate a statistically significant difference at the $P<0.05$ level.

Study site	Midagahara (1910 m)	Murodo (2460 m)	Johdo (2820 m)
Leaf number*	17.3 \pm 1.5 ^a	13.6 \pm 0.7 ^{ab}	12.1 \pm 0.7 ^b
Leaf size (cm^2)**	1.21 \pm 0.10 ^a	0.97 \pm 0.07 ^{ab}	0.73 \pm 0.06 ^b

* Kruskal-Wallis test and Mann-Whitney U -test; ** One-way ANOVA and Scheff's F test

tions than those at Murodo and Midagahara ($P<0.05$, by the Mann-Whitney U test). These results support our predictions.

Simulated environmental change

Ambient air temperatures at 5 cm above the ground inside and outside the OTC are shown in Table 3. Temperature was *ca.* 2°C higher both in July and August, and *ca.* 1°C in September 1999 inside the OTC than the outside. Although quantitative measurements of leaf life-span were not performed in this experiment, we observed that leaf emergence was earlier and senescence was later in the OTC manipulated shoots than in controls. Thus, leaf life-span was extended by setting the OTC. The number of leaves, individual leaf size and leaf mass per shoot were significantly higher and larger in the OTC manipulated shoots ($n=10$) than in controls ($n=20$; Fig. 3), suggesting that the simulated amelioration of thermal environments positively affected the growth and net-production of *S. pentapetala*. As shown in an altitudinal gradient analysis, LMA oppositely changed with leaf N under the simulated amelioration (Fig. 3): LMA showed a higher but leaf N a lower value in the OTC manipulated shoots than in controls. Thus, LMA was higher and leaf N was lower under the more highly productive condition. These results indicate that LMA and leaf N of *S. pentapetala* could plastically change in response to an environmental change, and also support our predictions.

Table 3. Ambient air temperature ($^{\circ}\text{C}$, mean \pm SD) at 5 cm above the ground in July, August and September 1999 inside and outside the open-top chamber at Johdo (2820 m a.s.l.).

OTC	Inside	Outside
July	13.4 \pm 2.7	11.1 \pm 2.0
August	14.8 \pm 2.6	12.7 \pm 1.8
September	11.5 \pm 1.4	10.4 \pm 1.9
Average	13.3 \pm 2.7	11.4 \pm 1.9

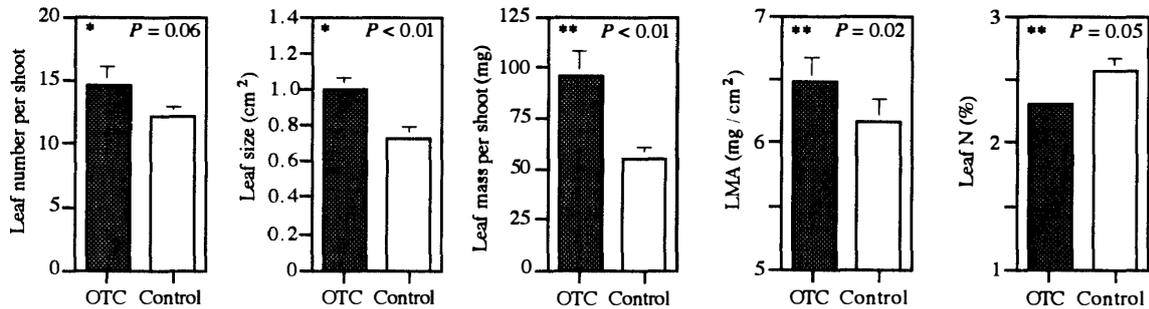


Fig. 3. Comparison of leaf traits of *Sieversia pentapetala* between OTC manipulated shoots ($n = 10$, solid bars) and controls ($n = 20$, open bars) at Johdo (2820 m a.s.l.). Vertical lines show SE. All values (leaf traits) significantly differ between OTC and control at the $P = 0.05$ level except for number of leaves which shows a marginally significant difference between them ($P = 0.06$). *, Student t -test; **, Mann-Whitney U -test.

Discussion

From the viewpoint of the carbon budget of deciduous plants, it seems to be reasonable to enhance the leaf N with increasing altitude in order to compensate for the carbon gain by photosynthesis within a restricted growing period under cool conditions (e.g. Woodward, 1986; Friend *et al.*, 1989; Kudo, 1996; Bowman *et al.*, 1999). *Sieversia pentapetala* behaved as decreasing LMA and increasing leaf N with altitude, under restricted growth conditions. These variations of leaf traits may enable *S. pentapetala* to occur across a wide altitudinal range from 1900 m to 2800 m above sea level in this study area. In an alpine snow-bed of the Taisetsu Mountains, Hokkaido, northern Japan, Kudo (1991) found that *S. pentapetala* had a wide distribution range along a snowmelt gradient. He also detected the intraspecific variations of leaf traits along the gradient: leaf life-span and LMA decreased while leaf N increased when the length of the growing period decreased, even in a short range of an altitudinal gradient (Kudo, 1992, 1996). This trend was also found in other deciduous alpine herbs *Peucedanum multivittatum* and *Potentilla matsumurae* (Kudo, 1996). Although environmental variations may be greater and other factors except for the season length and temperature might strongly affect variations of leaf traits in our study as compared with studies by Kudo (1991, 1992, 1996), the directional changes in leaf traits as shown in this study appear to be one of the adaptive responses to a limited growth condition in order to maintain the cost-benefit balance of the carbon economy in *S. pentapetala*.

LMA decreased with altitude in this study (Fig. 2). Similar trends have been found in deciduous tree species (*Betula ermanii*, *B. platyphylla* var. *japonica* and *Quercus mongolica* var. *grosseserrata*) in Hokkaido (Kudo, 1996) and in an alpine perennial herb species *Frasera speciosa* Douglas (Gentianaceae) in Colorado (Bowman *et al.*, 1999). However, the opposite trend was generally recognized: leaf thickness and LMA increased with elevation (e.g. Körner and Diemer, 1987; Körner, 1989; Körner *et al.*, 1989). The stress of strong wind and low temperature is easily expected to increase with altitude. Strong wind may force plants to have physically tough leaves, resulting in high LMA. Körner *et al.* (1989) suggested that low temperature at high elevation

leads to increase cell wall thickness and leaf thickness. In the present study, the OTC manipulation reduced the wind and retained warmer air. If the influences of wind and cool temperature strongly act on leaf traits, LMA is expected to decrease inside the OTC in more wind-swept and warmer conditions. The results, however, showed an opposite tendency (Fig. 3). This suggests that increased temperature may lead to the higher carbon gain by photosynthesis (*i.e.* higher leaf numbers and larger leaf size and mass per shoot) and enable increase of the leaf construction cost, resulting in higher LMA under the amelioration, although decreased wind effects was expected to favor lower LMA. In other words, the ability to decrease LMA in more stressful conditions will enable plants to maintain the cost-benefit balance of the carbon economy.

Comparisons of leaf traits at Murodo with those at Johdo show us interesting trends. The increased temperature by the OTC manipulation at Johdo was *ca.* 2°C, which was almost the same as the difference of temperature between Murodo and Johdo (see Table 1 and 3). The difference of leaf mass per shoot between Murodo and Johdo was *ca.* 30 mg and that of leaf N between them was *ca.* 0.27%. Surprisingly, these values were mostly coincident with the difference between inside and outside the OTC: *ca.* 40 mg in leaf mass per shoot and *ca.* 0.27% in leaf N. In contrast, no significant difference of LMA between Murodo and Johdo was detected: the difference was only 0.06 (mg/cm²), while in the warming manipulation at Johdo, LMA was significantly higher inside the OTC than outside; and the difference was 0.318 (mg/cm²), showing five times as larger as the difference of LMA between Murodo and Johdo. These results suggest that leaf mass per shoot and leaf N directionally change in response to temperature and/or the growing season length, whereas LMA does not and may also be affected strongly by other environmental factors. This may be one of the reasons why LMA of some species increased (*e.g.* Kudo, 1996; Bowman *et al.*, 1999), and that of other species decreased with altitude (*e.g.* Körner and Diemer, 1987; Körner, 1989, Körner *et al.*, 1989).

In the present study, we unfortunately carried out the environmental manipulation at only one site, the highest elevation site. It is necessary to conduct environmental manipulations such as the length of the growing period, ambient air temperature and nutrient availability, at each different altitude. Such a field experiment may permit us to learn which factors strongly act on variations of leaf traits at each elevation.

Acknowledgments

We are grateful to Dr. Noboru Nishimura for his invaluable comments and encouragement throughout this study; Dr. Gaku Kudo for his advises to improve our manuscript. We also thank the members of our laboratory, "plant ecology", Toyama University, for their assistance in fieldwork. This study was partly supported by a grant from the Ministry of Education, Science and Culture, Japan (No. 09740580), for the second author (N. Wada).

References

Bowman, W.D., Keller, A. and Nelson, M. (1999): Altitudinal variation in leaf gas exchange, nitrogen and

- phosphorus concentrations, and leaf mass per area in populations of *Frasera speciosa*. *Arct. Antarct. Alp. Res.*, **31**, 191–195.
- Chabot, B.F. and Hicks, D.J. (1982): The ecology of leaf life spans. *Ann. Rev. Ecol. Syst.*, **13**, 229–259.
- Field, C. and Mooney, H.A. (1986): The photosynthesis-nitrogen relationship in wild plants. On the Economy of Plant Form and Function, ed. by T.J. Givnish. Cambridge, Cambridge University Press, 25–55.
- Friend, A.D., Woodward, F.I. and Switsur, V.R. (1989): Field measurements of photosynthesis, stomatal conductance, leaf nitrogen and $\delta^{13}\text{C}$ along altitudinal gradients in Scotland. *Functional Ecol.*, **3**, 117–122.
- Givnish, T.J. (1988): Adaptation to sun and shade: A whole-plant perspective. *Aust. J. Plant Physiol.*, **15**, 63–92.
- Kikuzawa, K. (1991): A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern. *Am. Nat.*, **138**, 1250–1263.
- Körner, Ch. (1989): The nutritional status of plants from high altitudes. *Oecologia*, **81**, 379–391.
- Körner, Ch. and Diemer, M. (1987): In situ photosynthetic responses to light, temperature and carbon dioxide in herbaceous plants from low and high altitude. *Functional Ecol.*, **1**, 179–194.
- Körner, Ch., Bannister, P. and Mark, A.F. (1986): Altitudinal variation in stomatal conductance, nitrogen content and leaf anatomy in different plant life forms in New Zealand. *Oecologia*, **69**, 577–588.
- Körner, Ch., Neumayer, M., Menendez-Riedl, S.P. and Smeets-Scheel A. (1989): Functional morphology of mountain plants. *Flora*, **182**, 353–383.
- Kudo, G. (1991): Effects of snow-free period on the phenology of alpine plants inhabiting snow patches. *Arct. Alp. Res.*, **23**, 436–443.
- Kudo, G. (1992): Effect of snow-free duration on leaf life-span of four alpine plant species. *Can. J. Bot.*, **70**, 1684–1688.
- Kudo, G. (1995): Altitudinal effects on leaf traits and shoot growth of *Betula platyphylla* var. *japonica*. *Can. J. For. Res.*, **25**, 1881–1885.
- Kudo, G. (1996): Intraspecific variation of leaf traits in several deciduous species in relation to length of growing season. *Écoscience*, **3**, 483–489.
- Kudo, G. (1999): A review of ecological studies on leaf-trait variations along environmental gradients—in the case of tundra plants. *Jap. J. Ecol.*, **49**, 21–35 (in Japanese with English abstract).
- Reich, P.B., Uhl, C., Walters, M.B. and Ellsworth, D.S. (1991): Leaf life-span as a determinant of leaf structure and function among 23 Amazonian tree species. *Oecologia*, **86**, 16–24.
- Suzuki, S. and Kudo, G. (1997): Short-term effects of simulated environmental change on phenology, leaf traits, and shoot growth of alpine plants on a temperate mountain, northern Japan. *Global Change Biol.*, **3**, Suppl., 1, 108–115.
- Suzuki, S. and Kudo, G. (2000): Responses of alpine shrubs to simulated environmental changes during three years on a middle-latitude mountain, northern Japan. *Ecography* (in press).
- Wada, N. (2000): Responses of floral traits and increase in female reproductive effort to a simulated environmental amelioration in a hermaphrodite alpine dwarf shrub, *Sieversia pentapetala* (Rosaceae). *Arct. Antarct. Alp. Res.*, **32**, 208–211.
- Wada, N., Miyamoto, M. and Kojima, S. (1998): Responses of reproductive traits to short-term artificial warming in a deciduous alpine shrub *Geum pentapetalum* (Rosaceae). *Proc. NIPR Symp. Polar Biol.*, **11**, 137–146.
- Williams, K., Field, C.B. and Mooney, H.A. (1989): Relationships among leaf construction cost, leaf longevity, and light environment in rain-forest plants of the genus *Piper*. *Am. Nat.*, **133**, 198–211.
- Woodward, F.I. (1979): The differential temperature responses of the growth of certain plant species from different altitudes. II. Analysis of the control and morphology of leaf extension and specific leaf area of *Phleum bertolonii* D.C. and *P. alpinum* L. *New Phytol.*, **82**, 397–405.
- Woodward, F.I. (1983): The significance of interspecific differences in specific leaf area to the growth of selected herbaceous species from different altitudes. *New Phytol.*, **95**, 313–323.
- Woodward, F.I. (1986): Ecophysiological studies on the shrub *Vaccinium myrtillus* L. taken from a wide altitudinal range. *Oecologia*, **70**, 580–586.

(Received May 31, 2000; Revised manuscript accepted July 31, 2000)