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Comparison of community structure and growth between the alpine dwarf shrubs *Rhododendron aureum* and *R. brachycarpum* on the Yatsugatake range, central Japan

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Rhododendron aureum and *R. brachycarpum* are species of the Japanese alpine zone whose altitudinal zonation was determined by the last glacial stage. We compared the ecological features of the two species in a mixed community on the Yatsugatake range. A productive structure diagram showed that *R. brachycarpum* can absorb light efficiently by arranging its leaf mass in an upper layer and developing a more horizontal orientation of both the shoots and individual leaves in comparison with *R. aureum*. The C/F ratio for *R. brachycarpum* was 6.52, and was almost the same value (5.99) in a mixed community. The ratio for *R. aureum* was lower (2.50) and decreased to 0.77 in a mixed community. Since *R. aureum* cannot gain sufficient light in a mixed community, its tree-ring width here was about half of that in a pure community, and there was also a decrease in the number of leaves. These results suggest that *R. brachycarpum* shows superior substance production in a mixed forest.

長沼慶拓，崎尾　均，増沢武弘：八ヶ岳連峰における高山矮性低木キバナシャクナゲとハクサンシャクナゲの群落構造と成長量の比較

日本の高山帯に生育するキバナシャクナゲとハクサンシャクナゲの標高に沿った分布は最終氷期以降に形成されてきたと見られる。本研究では八ヶ岳連峰において，2種の生育特性を比較し，分布が重なる場所での競争関係について調査した。ハクサンシャクナゲの方がキバナシャクナゲに比べ，葉群をより上層に広げるとともに，シュートや個葉をより水平に展開するために，光を効率よく獲得できていることが，生産構造図によって示唆された。ハクサンシャクナゲのC/F比は純群落では6.52あるのに対し，2種が混生しても5.99とほぼ同じ値であった。一方キバナシャクナゲは純群落で2.50，混生群落では0.77と大きく減少した。混生群落のキバナシャクナゲは十分に光を得られないため，年輪幅が純群落の約半分となり，葉数も減少していた。これらの結果はハクサンシャクナゲが物質生産の上で優位であることを表している。

Introduction

It is predicted that the global warming observed in recent years will lead to marked effects on climate and vegetation, especially in polar regions and the alpine zone (Mitchell et al., 1990; Maxwell, 1992; Grabherr et al., 1994; Oechel and Vourlitis, 1994). In the case of alpine plants, many scientists have reported direct effects such as increases in CO_2 concentration and temperature, leading to an increment of biomass and other changes in physiological activity or phenology (Havstrom et al., 1993; Suzuki and Kudo, 2000; Wada et al., 2002). Although accumulation of such data is important, a more pressing field of research is the competition between species that plays a key role in determining dominance in the face of climate change. Although research on the influence of climatic fluctuation on vegetation has led to many reports on subalpine zone conifers (Rochefort et al., 1994; Amy and William, 1997; Frederick and Daniel, 2002), there have been few studies of alpine dwarf shrubs.

The zonation between *Rhododendron brachycarpum* and *R. aureum* developed after the last glacial stage. *R. brachycarpum* is distributed from the subalpine to the alpine zone, whereas *R. aureum* occurs at higher sites, especially those exposed to wind. However, on part of the ridgeline at 2,600 m or more on Mt. Tatsugatake, the distribution of *R. brachycarpum* has shown an upward shift in recent years, with an extension of the area occupied by *R. aureum* (Masuzawa 2005). It is suggested that competition exists between the two species at the site where both distributions are mixed. After warming, in the narrow alpine zone of the Japanese Islands, alpine species like *R. aureum* may be driven to higher altitudes and perhaps eventually disappear altogether.

This study was planned to compare the community structure of the two species. In particular, the study set out to explore quantitatively the influence of competition for light on the relationship between the two species. Since light, which is one of the critical determinants affecting plant performance, comes directionally from above, larger plants have suppressive effects on smaller

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ones by shading them (Kikuzawa and Umeki, 1996). Generally, stratification is unclear in the alpine zone because plant height is regulated by strong winds. Research on this topic will help to clarify the weakness or adaptation of alpine vegetation to some environmental changes.

Materials and Methods

Plant materials

R. aureum is an evergreen dwarf shrub 10–20 cm high, which possesses a trunk running horizontally with frequent branches. *R. brachycarpum* is an evergreen shrub 1–3 m high in the subalpine zone, but becomes dwarved in the alpine zone. Both are palaearctic species. On the Yatsugatake mountain range, dwarf *R. brachycarpum* grows on the ridgeline stretching from Mt. Yoko-dake to Mt. Iou-dake. It is often confused with *R. aureum* or may occur as an intermediate hybrid, but the two species can be distinguished by differences in the base of the leaf and in the time of flowering.

Both species are long-lived and grow clonally;moreover, their branches are largely prostrate and become progressively buried in the ground. Since it is difficult to identify genetic individuals in the field, one above-ground part was defined as one ramet. All ramets in a quadrat were counted.

Research site

The Yatsugatake range, which is located in the central part of the main Japanese island, Honshu, and belongs to the Mt. Fuji volcanic zone, has become part of Yatsugatake-Chushinkogen Semi-National Park. In the northern part of the Yatsugatake range, the vegetation is primary coniferous forest, whereas in the southern part there is a rocky ridgeline focusing on the main peak, Mt. Aka-dake. Mt. Iou-dake is located at the northernmost tip of the southern Yatsugatake range, and is characterized by widespread areas of bare volcanic rock.

The investigation site was established at Akaiwa-no-kashira (2,680 m asl) on the northwest slope of Mt. Iou-dake (Fig. 1). The neighborhood has much vegetation cover and many alpine plants. Evergreen dwarf shrubs, such as *Empetrum nigrum* var. *japonicum* and *R. aureum*, are distributed near the ridgeline, while *R. brachycarpum* and *Pinus pumila* are mostly distributed over the lower part of the slopes. The angle of the slope is about 30°.

Temperatures at the study area (ca. 2,680 m asl) were estimated from temperatures recorded at Hara AMeDAS (1,017 m asl, approximately 10 km from the study area) using a lapse rate of −0.6℃ per 100-m increment in altitude. Values for precipitation were also based on the data for Hara AMeDAS. The mean monthly temperature in the coldest month (January) was −14.4℃, that for the warmest month (August) was 11.3℃. Although the mean annual temperature has fluctuated, overall there has been an apparent tendency for it to increase (Fig. 2). The mean annual precipitation is 1,477 mm. However, considering the snow in winter, it seems probable that the value for precipitation at the investigation site is higher. Precipitation fluctuates sharply between years and there has been no clear tendency for it to change overall.

Methods

A belt transect (vertical × horizontal = 10 × 2 m) was established from near the ridgeline to the lower part of the northwest slope of Akaiwa-no-kashira because both species are distributing to some degree, and ups and downs by geographical features are few at this slope. This transect was divided into 10 sections, from the upper to the lower part, in August 2003 (Fig. 3), and the vegetation cover ratio of emergent species was measured in every section.

A productive structure diagram was constructed in August for the typical community of each species in order to provide a comparison between the two. We collected ten shoots for growth analysis. The length and width of leaves on these shoots were measured, and an estimated leaf area was obtained by considering the leaf as an ellipse. In addition, these leaves were dried for three days at 80℃ and the dry weights were measured. The linear regression equations between temporary leaf area and dry weight were determined for both species (Table 1). The stem segment was assumed to be a cylinder and the equation relating estimated volume to dry weight was determined similarly to that for the leaf. Quadrats measuring 50 × 50 cm were established in the pure communities in sections 3 and 9 of the transect, and each quadrat was divided vertically by strings at 5-cm intervals. The length and width of the leaf and diameter and length of the stem section were measured in every layer, and the dry weight was estimated using the above-mentioned equations. Moreover, photosynthetic photon flux density (PPFD) was measured in each layer using a photon sensor (PAR-02, PREDE Co.) and recorded using a data logger (LOGGER L810A, UNIPULSE Co.). These sensors were oriented in a vertical direction. PPFD was monitored every 1 minute for 1 hour, the values were summed, and relative PPFD was calculated from that value. A productive structure diagram was constructed for the mixed community, which was located in section 6 of the transect. I defined a pure community

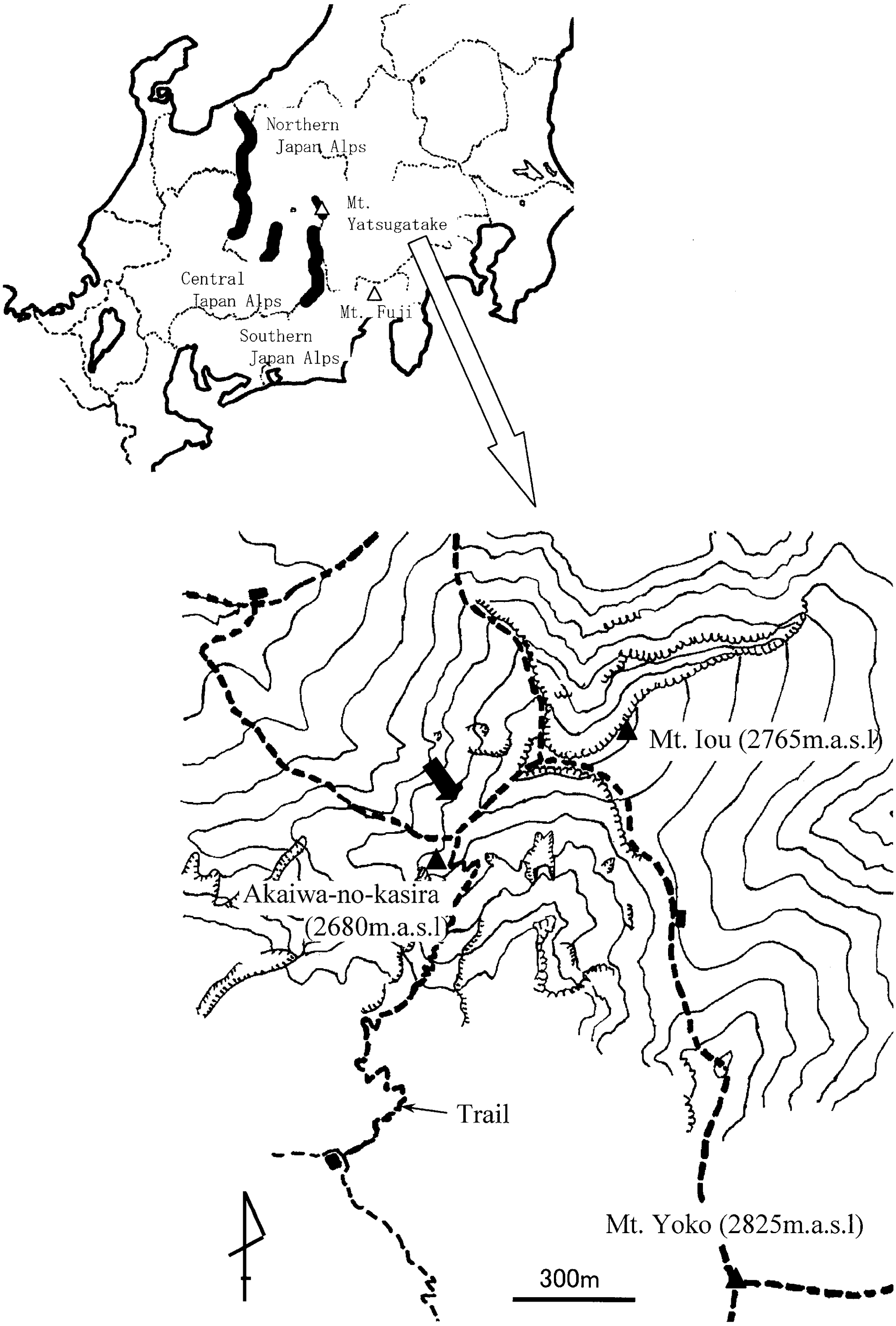

Fig. 1 **The location of Yatsugatake range. 1 : 50000 map of the area around the research site. The arrow shows the study slope. Contours are shown at 50-m intervals.**

as a place where the canopy was composed of only one species, and defined a mixed community as a place where both species grew together in a vertical direction.

The angle of the petiole and branching were measured in September 2003 as an index of light conditions for the leaf. The angle between the petiole and under the branch was measured with a protractor for about 30 leaves, and also between the main trunk and 30 branches.

The next step was to analyze the growth of the two species in the pure and mixed community in order to assess the influence of competition on elongation and radial growth. These samples were collected outside the tran-

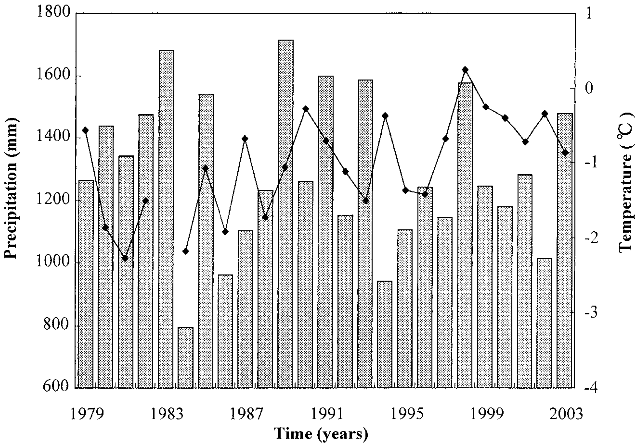

Fig. 2 The temperature and precipitation at the study area were estimated from temperature recorded at Hara AMeDAS. The data for mean temperature in 1983 were not recorded. ◆ Temperature ▩ Precipitation

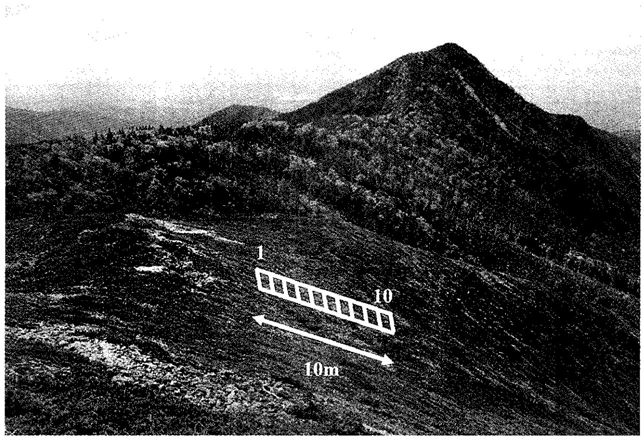

Fig. 3 The research site located on the Northwestern slope of the Yatsugatake range. Established quadrats are shown by white lines.

Table 1 The equations for estimation of leaf and stem dry weight. These equations were used to make the productive structure diagram.

	R. aureum		*R. brachycarpum*	
	Eq.	r^2	Eq.	r^2
temporary leaf area vs. dry weight	y = 0.448x-1.546	0.885	y = 0.414x-15.77	0.921
temporary stem volume vs. dry weight	y = 1.567x-15.44	0.954	y = 1.586x-4.094	0.911

(n = 30)

sect. Since the scales and bud scars of both species remain for many years, the age of a branch can be determined up to about ten years. In pure communities of each species, and in mixed communities, ten branches were collected respectively in August 2004 to represent a ten-year period, and the annual elongation and the number of leaves were measured. The mean values were calculated for each community. In addition, the stem cross-section was measured in a 10-μm section at the base of a ten-year branch, and the mean annual radial growth over the ten years was estimated by measuring the tree-ring width. The stems were boiled to soften them, and then cut with a microtome. Cross-sections were stained with 1% safranin for three hours, dehydrated with ethanol to allow penetration of the xylem, and then mounted on slides glasses with Canada balsam. The widths of the tree-rings in the stem sections were measured from the center of the stem in 4 directions using a transmission microscope. The mean values were calculated for each stem and in each community.

The current leaves in the upper layer of the community have a brownish discoloration during winter. The rate of color change for the two species was measured in a 50×50-cm quadrat in each pure community on the belt transect, respectively.

Results

Vegetation structure

Vegetation in the established transect was characterized by the following ten species: *R. aureum*, *R. brachycarpum*, *Sorbus sambucifolia*, *Chamaepericlymeum canadense*, *Arctous alpina*, *Pinus pumila*, *Empetrum nigrum* var. *japonicum*, *Vaccinium vitis-idaea* var. *minus*, *Cetraria ericetorum*, *Cladonia nigripes*. Although bare ground occupied 10-30% of sections 1-3, the lower quadrats were covered by vegetation (Fig. 4). The number of species was lower in the lower sections. *R. aureum* occurred in sections 2-6, with the highest cover ratio in section 5. There were no ramets of *Rhododendron* species in section 1. *R. brachycarpum* occurred in sections 6-10, with the highest cover in section 9. Two *Rhododendron* species were present together only in section 6, with a low cover ratio. *R. aureum* increased from section 3, and 235 ramets were present in section 5. The number of *R. brachycarpum* ramets also increased similarly from section 6 to the lower sections. There were few ramets of either species in section 6. In all quadrats, the number of ramets of *R. brachycarpum* was three times higher than that of *R. aureum*.

Difference in productive structure and recent growth rate

The leaf layer of the pure *R. brachycarpum* community was higher and thicker than that of *R. aureum* (Fig. 5). The light that had passed through the leaf layer of *R. brachycarpum* was decreased to 10% in terms of relative PPFD 30 cm above the ground. Although the biomass of both species was decreased in the mixed community, the ratio of the decrease was more pronounced for *R. aureum*. In the mixed community, the leaf layer of *R. brachycarpum* was above that of *R. aureum*. The biomass of non-photosynthetic organs of *R. aureum* was very small.

In the pure community, the leaf area index (LAI) of *R. brachycarpum* was 2.07, which was about three times higher than that of *R. aureum* (Table 2). In the mixed community, the LAI was 1.35 – about five times higher

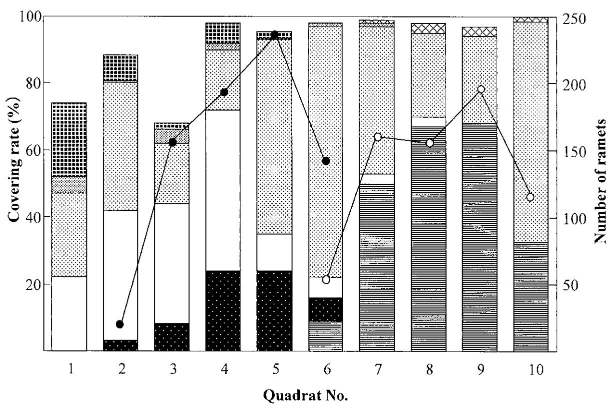

Fig. 4 Distribution of the two species on the slope. Covering data were obtained from the area of plants in each (2 m^2) quadrat. ▩ *R. aureum* ▤ *R. brachycarpum* ● Number of R. aureum ramets ○ Number of R. brachycarpum ▨ *Pinus pumila* ▢ *Arctus alpine* ▧ *Sorbus sambucifolia* □ Other dwarf shrub ▦ Moss and Lichen

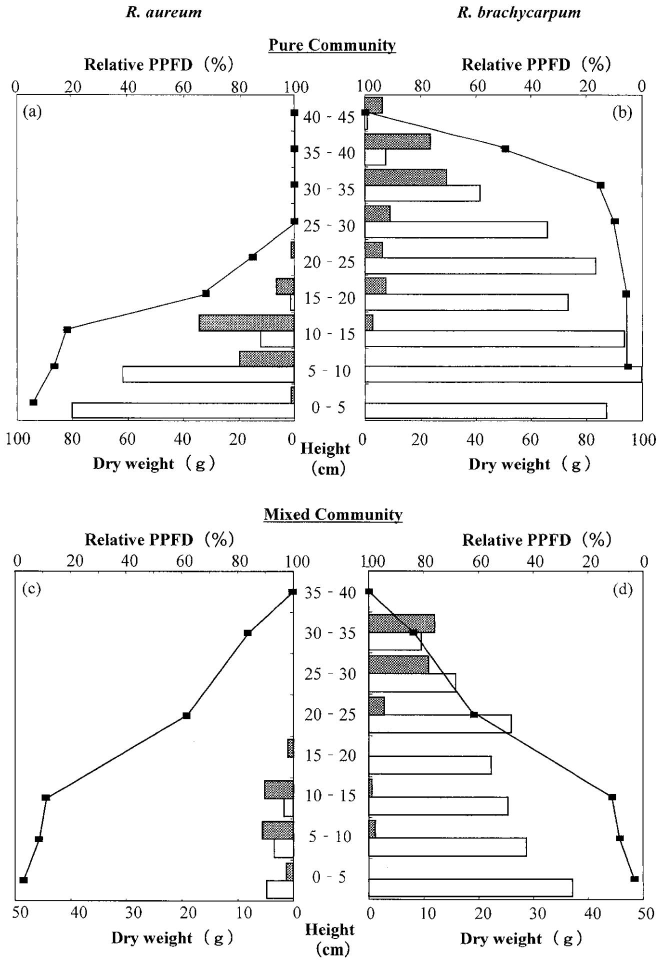

Fig. 5 Productive structure diagram. Pure community of *R. aureum* (a), *R. brachycarpum* (b), mixed community of *R. aureum* (c), *R. brachycarpum* (d).
▩ Photosynthetic organ □ Non-photosynthetic organ -■- Relative PPFD

Table 2 LAI and C/F ratio in the communities. These values were estimated for each quadrat (0.25m^2).

Community	LAI	C/F ratio
Pure community		
R. aureum	0.68	2.50
R. brachycarpum	2.07	6.52
Mixed community		
R. aureum	0.28	0.77
R. brachycarpum	1.35	5.99

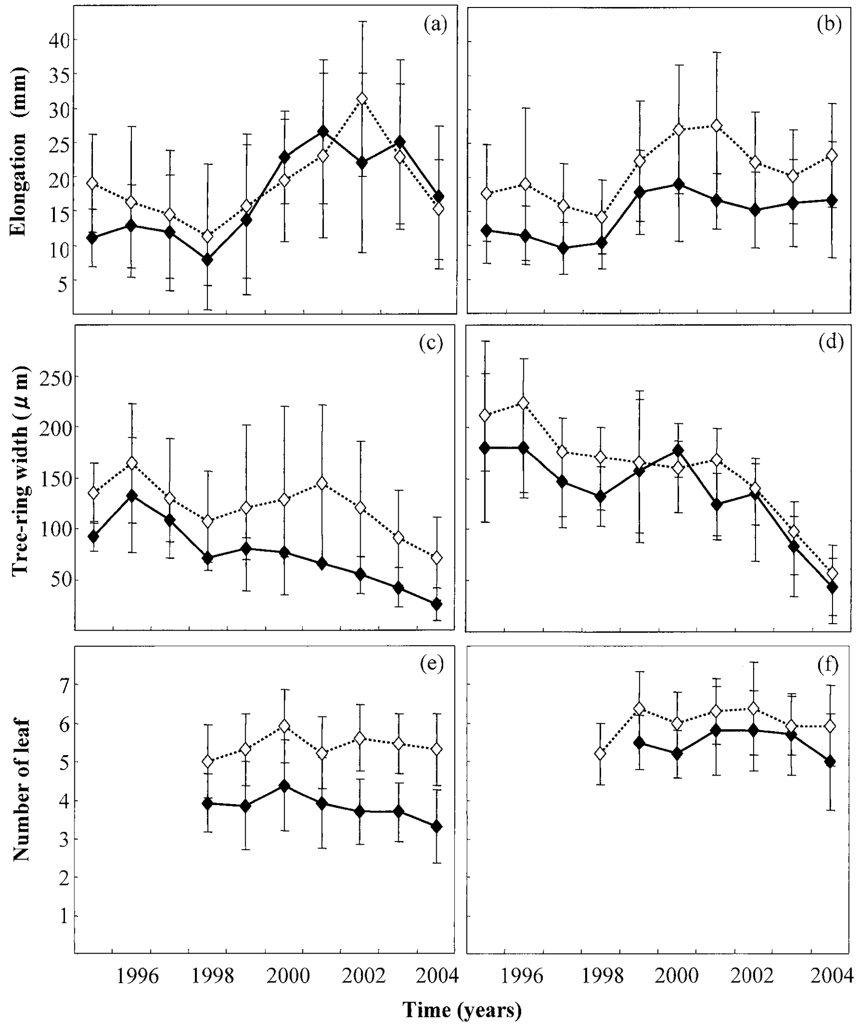

Fig. 6 Branch growth characteristics for ten years (n=10). Elongation of *R. aureum* (a), *R. brachycarpum* (b). Tree-ring width of *R. aureum* (c), *R. brachycarpum* (d). Leaf number of *R. aureum* (e), *R. brachycarpum* (f). ◇ Pure community ◆ Mixed community

Table 3 The angle of the petiole and branching in the two species. Mean values with standard deviations are shown; different letters on the numerals indicate a statistically significant difference by Mann-Whitney *U*-test ($P<0.0001$). n=30.

Species	Angle (°)	
	petiole	branching
R. aureum	154.7±12.3 [a]	145.8±10.5 [a]
R. brachyvarpum	123.2±6.4 [b]	119.5±12.1 [b]

than that of *R. aureum*. The C/F ratio (dry weight of non-photosynthetic organs/dry weight of photosynthetic organs) for *R. brachycarpum* was 6.52 in the pure community and 5.99 in the mixed community, showing a slight difference. In contrast, the ratio for *R. aureum* was only 2.50 in the pure community and decreased to 0.77 in the mixed community (Table 2). Since the angle between the petiole and branch of *R. brachycarpum* was less than that for *R. aureum* in the top layer of these communities (Table 3), it is suggested that *R. brachycarpum* tends to develop shoots and leaves with a more horizontal orientation than *R. aureum*.

In the mixed community, although the elongation of *R. aureum* was the same as in the pure community, the tree-ring width was about half, and the leaf number was markedly decreased. In contrast, *R. brachycarpum* showed almost the same value as that for the pure community (Fig. 6).

Brownish color change rate

The rate of change of the brownish discoloration in current leaves of *R. brachycarpum* was 47.1% in spring, which was higher than the value of 14.9% for *R. aureum*. The leaves that were discolored during winter dropped gradually until the following summer.

Discussion

There was a difference in the distribution between the two study species along the research slope. The range in which the two species occurred together was limited in plot 6 and the number of ramets was markedly decreased here (Fig. 4). We were unable to show that the present distribution of *R. brachycarpum* results from warming on the Yatsugatake range. Masuzawa (2005) showed that *R. brachycarpum* occurred in the vicinity of the ridgeline where *R. aureum* was generally distributed. This may suggest that the distribution area of *R. brachycarpum* has moved upward.

Comparison of the community structure showed that *R. brachycarpum* can arrange its leaves in a higher layer than *R. aureum* by considerable investment in trunk and branches, and so *R. brachycarpum* may absorb light efficiently by developing shoots and leaves with a more horizontal arrangement than *R. aureum*. The competition between the two species for light is important in the mixed site. This site represents the upper limit for *R. brachycarpum*, and the lower limit for *R. aureum*. Since *R. brachycarpum* maintained a large leaf area in the upper layer in the mixed community, *R. aureum* could not increase its biomass within a height of 20 cm or less as in a pure community. The influence of competition is reflected clearly in the C/F ratio (Table 2). Since *R. aureum* in the mixed community cannot obtain sufficient light as in a pure community, the relative investment in non-photosynthetic organs may decrease, and the plant cannot possibly maintain the same structure as in a pure community. The fact that tree-ring width and leaf number of *R. aureum* were markedly less in the mixed community may suggests that more production matter in *R. aureum* can be allocated to shoot elongation in order to meet the demand for light under shaded conditions. On the other hand, *R. brachycarpum* can grow under the same light conditions in both a mixed and a pure community, so perhaps tree-ring width and leaf number scarcely decrease (Fig. 6).

R. brachycarpum has an effective structure for light competition even when invading the alpine zone. Thus an alpine dwarf shrub like *R. aureum* is inferior when competing for light. However, in places where the snow cover is blown away by strong winds and where snowmelt is early, there are few *R. brachycarpum* ramets. The rate of change in brownish discoloration among the current leaves of *R. brachycarpum* was higher than that of *R. aureum* in spring. Therefore the elongation of *R. brachycarpum* may be limited in the upper range of the mixed community (Fig. 6). These characteristics may result from protection afforded by snow cover.

Although a temperature rise in recent years has been reported for the whole area, changes in precipitation, especially snowfall, are probably not uniform over the area and fluctuations are likely to become wider (IPCC, 2001). There has been a rise in temperature during the previous twenty years in the neighborhood of the investigation site. However, further research is necessary to determine whether *R. aureum* becomes restricted to a higher altitude or near the ridgeline as a result of competition.

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References

Amy, E.H. and William, L.B. (1997) : Spruce and fir regeneration and climate in the forest-tundra ecotone of rocky mountain national park, Colorado, U.S.A. Arctic, Antarctic, and Alpine Research 29 : 173-183.

Frederick, L.K. and Daniel, B.F. (2002) : A half century of change in alpine treeline patterns at glacier national park, Montana, U.S.A. Arctic, Antarctic, and Alpine Research 29 : 49-56.

Grabherr et al. (1994) : Climate effects on mountain plants. Nature 369 : 448p.

Havstrom, M., Callaghan, T.V., and Jonasson, S. (1993) : Differential growth responses of *Cassiope tetragona*, an arctic dwarf-shrub, to environmental perturbations among three contrasting high- and sub-arctic sites. Oikos 66 : 389-402.

IPCC (2001) : Climate Change 2001. The Scientific Basis. The Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC). Cambridge University Press.

Kikuzawa, k. and Umeki, K. (1996) : Effects of canopy structure on degree of asymmetry of competition in two forest stands in northern Japan. Ann Bot. 77 : 565-571.

Masuzawa, T. (2005) : Mountain topography and plant distribution on alpine zone:Mt. Fuji, Mt. Shirouma, Yatsugatake Mountain range and Mt. Apoi. Journal of Phytogeography and Taxonomy

53：131–137.
Maxwell, B. (1992)：Arctic climate. Potential for change under global warming. In Arctic Ecosystem in a changing climate (eds F.S. Chapin III, R.L. jeffries, J.R. Reynold & G.R. Shaver). Academic Press, San Diego：11–34.
Mitchell, J.F.B., Manabe, T., Tokioka, T. and Meleshk, V. (1990)：Equilibrium climate change. In Climate Change;The IPCC Scientific Assessment (eds J.T. Houghton, G.J. Jenkins & J.J. Ephraums). Cambridge University Press, Cambridge：131–172.
Oechel, W.C. and Vourlitis, G.L. (1994)：The effect of climate change on land Atomosphere feedbacks in arctic tundra regions. Trends in Ecology and Evolution 9：324–329.
Rochefort, R.M., Little, R.L., Woodward, A. and Peterson, D.L. (1994)：Changes in sub-alpine tree distribution in western North America, a review of climatic and other causal factors. Holocene 4：89–100.
Suzuki, S. and Kudo, G. (2000)：Responses of alpine shrubs to simulated environmental change during three years on a temperate mountain, northern Japan. Ecography 25：553–564.
Wada, N., Shimono, M., Miyamoto, M. and Kojima, S. (2002)：Warming effects on shoot developmental growth and biomass production in sympatric evergreen alpine dwarf shrubs Empetrum nigrum and Loiseleuria procumbens. Ecol. Res. 17：125–132.

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