

Carbon Isotope Discrimination in Diverging Growth Forms of *Saxifraga oppositifolia* in Different Successional Stages in a High Arctic Glacier Foreland

Authors: Kume, Atsushi, Bekku, Yukiko S., Hanba, Yuko T., and Kanda, Hiroshi

Source: Arctic, Antarctic, and Alpine Research, 35(3) : 377-383

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: [https://doi.org/10.1657/1523-0430\(2003\)035\[0377:CIDIDG\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2003)035[0377:CIDIDG]2.0.CO;2)

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Carbon Isotope Discrimination in Diverging Growth Forms of *Saxifraga oppositifolia* in Different Successional Stages in a High Arctic Glacier Foreland

Atsushi Kume,*

Yukiko S. Bekku,†

Yuko T. Hanba,‡ and

Hiroshi Kanda§

*Department of Forest and Forest Products Sciences, Faculty of Agriculture, Kyushu University, Sasaguri, Kasuya Fukuoka 811-2415, Japan. akume@attglobal.net

†Department of Primary Education, Tsuru University, Tsuru 402-8555, Japan.

‡Research Institute for Bioresources, Okayama University, Kurashiki 710-0046, Japan.

§National Institute of Polar Research, Itabashi 173-8515, Japan.

Abstract

We investigated carbon isotope discrimination of two morphs of *Saxifraga oppositifolia* and other plant species in a glacier foreland in the High Arctic at Ny-Ålesund, Svalbard, Norway. At this site, soil conditions vary considerably along with the progress of primary succession within a small area. We compared growth forms and $\delta^{13}\text{C}$ values, which reflect long-term leaf gas exchange characteristics, of plants growing in different successional stages with different soil conditions. Even though the soil mass water content (water mass/dry mass) increased from 10% to 140% with the progress of succession, the water and nitrogen content of the soil had negligible effects on the $\delta^{13}\text{C}$ values of the observed species. The $\delta^{13}\text{C}$ values were determined mainly by species and growth forms. We compared two morphs of *S. oppositifolia*, the prostrate form (P-form) and the cushion form (C-form), on the same riverbank in the glacier foreland. Regardless of the successional stage, the $\delta^{13}\text{C}$ values of the C-form were about 2‰ more negative than those of the P-form. The ground cover area per plant mass (GA) of the C-form was less than 30% that of the P-form, and the product of GA and stomatal conductance appears to be an important factor in the relationship between transpiration and photosynthesis of a whole plant. We suggest that the relationship between GA and the root mass fraction is a crucial factor affecting the water utilization in high arctic environments. We also examined the relationship between life form and water utilization for other phototrophs, including lichens, mosses, narrow-leaved grasses, perennials, and shrubs.

Introduction

With the progress of global warming, newly deglaciated areas are increasing in high arctic regions (IPCC, 2001). On deglaciated moraines, which consist of pure mineral soil, pioneer species are immediately invading and becoming established (Matthews and Whittaker, 1987). Just after deglaciation, the soil contains almost no carbon or nitrogen, and its ability to hold water is relatively poor (Bekku et al., 1999). However, with the progress of primary succession, the soil develops and the soil water condition is drastically improved. The established dominant pioneer species will be replaced by late-successional species. The succession implies that there will also be changes in the patterns of water utilization of plants. In a glacier foreland, the rate of soil development is slow because of the low temperatures and short growing season. The physical perturbation and other disturbances caused by soil freezing have strong effects on soil forming (Fitzpatrick, 1997). As a result, two contrasting extreme microclimatic environments, damp environments (snowbed) with a short growing season and dry environments (ridge) with a long growing season, can be adjacent to one another (Crawford, 1997). Plants receive sunlight directly in summer, and soil freezes in winter. Thus, proper utilization of water through biophysical (e.g., Campbell and Norman, 1998) and physiological control is crucial for plants growing in such extreme polar desert environments.

In the glacier foreland in the high arctic Ny-Ålesund area in Svalbard, Norway, contrasting soil conditions are associated with different stages of succession within a small area. In this area, these are several types of phototrophs: lichens, mosses, narrow-leaved grasses,

perennials and shrubs. Comparisons of different successional stages make it possible to examine the relationships between soil development and water utilization of plants with different life forms.

The purple saxifrage, *Saxifraga oppositifolia*, is a long-lived perennial herb with wide circumpolar distribution (Hultén and Fries, 1986) and one of the first colonizers after glacial recession. Abbott et al. (2000) showed that *S. oppositifolia* has been surviving at high latitudes throughout the Pleistocene. *Saxifraga oppositifolia* is morphologically variable, and two morphs (Rønning, 1996), the prostrate form (P-form) and the cushion form (C-form), can be distinguished by their shoot elongation characteristics (Kume et al., 1999). Brysting et al. (1996) concluded that the high levels of morphological and ecological variation within *S. oppositifolia* in Svalbard were not taxonomically significant but rather local ecocline evolution was occurring independently in different sites.

Brysting et al. (1996) showed that the median of the five longest stem internode length for each plant was closely related to the growth form. We also found that the stem internode lengths of shoots determine various growth characteristics of the plant (Kume et al., 1999). The P-form's rate of colony expansion on the bare ground was several times faster than that of the C-form, partly because of the P-form's longer shoots. Shoot fragments of the P-form root easily and quickly become established. However, the C-form had a larger number of flowers per biomass than did the P-form, which caused greater seed production. These comparisons showed that the growth forms and reproductive characteristics were closely related. The P-form had an advantage in vegetative propagation by shoot fragments, while the C-form had an advantage in sexual reproduction.

When both C-form and P-form plants were growing on the same moist riverbank in Svalbard, their net photosynthesis rates per shoot mass were similar (Kume et al., 1999), but when they were growing in different habitats, their net photosynthesis rates per biomass were different (Crawford et al., 1993, 1995). It is expected that these growth form differences are related to the manner of water utilization and growing conditions. Kume et al. (1999) showed that the plant surface area per biomass varied significantly with the growth form and growing conditions, but the root mass fraction was not affected by growing condition and growth form, though the root fraction was highly correlated with plant size. Therefore, *S. oppositifolia* may adapt to the various water environments in the High Arctic by existing in different growth forms. It is noted that the separation of genetical and environmental factors in the morphogenesis is sometimes difficult. For example, it is well documented that the C-form plants develop a taproot, while the P-form plants develop a fibrous root system (e.g. Crawford et al., 1993; Rønning, 1996). However, the root system of *S. oppositifolia* changed easily and it appeared to be mainly dependent on the growing environment (Teeri 1973; Kume et al. 1999).

In C₃ plants, the leaf carbon isotopic composition is related to long-term plant water use (e.g., Farquhar et al., 1982; Ehleringer and Cooper, 1988). The extent of the fractionation of carbon isotopes depends on the partial pressures of CO₂ at the site of Rubisco relative to the atmosphere (C_i/C_a) and discrimination against ¹³CO₂ during photosynthesis decreases with increasing physical restriction. The isotope composition (δ¹³C) reflects long-term leaf gas exchange characteristics and can be used to examine the effects of growth form differences on the pattern of water utilization. We compared δ¹³C values of the plants growing in different successional stages and different moisture conditions in a deglaciated area at Ny-Ålesund, Svalbard. The object was to reconsider the significance of the different growth forms of *S. oppositifolia*, studied in Kume et al. (1999). In addition, we measured and compared the δ¹³C values of other vascular plant species and mosses growing sympatrically in order to understand how the ecophysiological characteristics of these plants are related to their survival in the environment of Svalbard.

Materials and Methods

STUDY SITES

The East Brøgger Glacier is located near Ny-Ålesund in the northwestern part of Svalbard, Norway (78°55'N, 11°51'E). The annual mean air temperature and amount of precipitation in this area are about -5.7°C and 490 mm, respectively. The maximum monthly mean air temperature is about 5°C in July and August, and the minimum monthly mean air temperature is about -15°C in January. The snow-free period ranges from 1 to 2 mo and varies considerably year by year.

We set up 4 study sites (Sites 1, 2, 3, and 4) along a primary successional series of the glacier foreland (Fig. 1). Site 1 was the youngest, situated on a newly deglaciated moraine, about 100 m from the tip of the glacier. Only isolated plants such as *S. oppositifolia* were observed. The total coverage of vascular plants was less than 1%, and black crusts of cyanobacteria and several species of bryophytes partially covered the ground (Minami et al., 1996). Site 2 was about 300 m from the glacier, and the coverage of *S. oppositifolia* was greater. *Poa alpina* var. *vivipara* and *Draba alpina* were observed. The coverage of the plants was less than 10%. Site 3 was on a small moraine where approximately 17% of the ground was bare, 30% is covered with black crust, and 53% is covered with mosses and vascular plants (mainly *S. oppositifolia*, *Salix polaris*, *Luzula confusa*, and *Sanionia uncinata*). Site 4 was on the oldest moraine about 1200 m from the glacier. The ground at Site 4 was patterned by small polygons.

Almost all the ground was covered with black crusts, lichens, mosses, and vascular plants (mainly *Salix polaris*, *Luzula confusa*, and *Sanionia uncinata*). The coverage of *Saxifraga oppositifolia* decreased, and *Salix polaris* was dominant. These sites were the same used by Nakatsubo et al. (1998) and Bekku et al. (1999). Nakatsubo et al. (1998) measured soil and root respiration and soil water content at each site. Bekku et al. (1999) measured microbial biomass at each site. Throughout all successional stages, there was a positive high correlation between soil C or N content and microbial biomass with correlation coefficients of 0.91 and 0.85, respectively. Those studies also measured vertical profiles of C, N, and microbial biomass in the soil. With the progress of succession, C and N contents increased in the soil surface layer (0–1 cm).

Because the height of most of the vegetation was lower than 10 cm, the δ¹³C value might be affected by soil respiration. Nakatsubo et al. (1998) showed soil respiration rates at Site 1 to 4 and seasonal variation of soil respiration rates early July to mid August at Site 2 and 3. The soil respiration rates in the latter stages of succession (Site 3 and 4) were usually higher than those in the earlier stages (Site 1 and 2) but the maximum rate is quite small (less than 60 mg CO₂ m⁻² h⁻¹ at most). Thus, the effects of soil respiration can be assumed negligible.

To compare the effects of the different moisture environments on the growth form, Site 5 was set up on a riverbank about 600 m from the glacier. There were large patches of *S. oppositifolia*, and P-form and C-form plants grew in close proximity within the same homogeneous habitat (cf. Kume et al., 1999). Site 6 was set up on a dry moraine ridge, a polar semidesert ecosystem about 3.5 km north of the glacier containing many small patches of *S. oppositifolia* and *Dryas octopetala*. The snow-free period was about 2 wk longer than that of other sites.

SAMPLES

In the Ny-Ålesund area, two morphs of *Saxifraga oppositifolia* were recognized: the prostrate form (P-form) and the cushion form (C-form). Although the existence of intermediate growth forms was pointed out by Brysting et al. (1996), typical P-form plants have long-internode shoots. We used the third internode length of shoots as a key for distinguishing between the two forms. A plant having shoots of the third internode length longer than 6 mm was categorized as P-form (Kume et al., 1999). The distributional pattern of the two morphs in the glacier foreland was described in Kume et al. (1999). On 30 and 31 July 1999, which is near the end of the growing season in Ny-Ålesund, 3 to 5 individuals of each growth form of *S. oppositifolia* and other species growing on each site were arbitrarily selected. These plants were immediately put in a deep freezer and then freeze-dried. The green parts of the samples were milled with a coffee mill modified for small samples (KTG-0001, Koizumi-Seiki Co., Osaka, Japan). Carbon isotope ratios in plant dry matter were measured for subsamples containing 100–200 μg of carbon with a system combining an elemental analyzer (EA1108, Carlo-Erba, Italy) for combustion of the samples, an interface (Finnigan MAT Confro, Bremen, Germany), and a stable isotope ratio mass spectrometer (Finnigan MAT 252, Bremen, Germany). The mean reproducibility for isotope ratio measurement was ±0.08‰ (n = 26).

STATISTICS

Data are presented as mean ± one standard error (SE). The statistical significance in the effects of sites and growth forms on δ¹³C values was assessed the two-way analysis of variance. All statistical analyses were carried out using the StatView 5.00 (SAS Institute, Inc.).

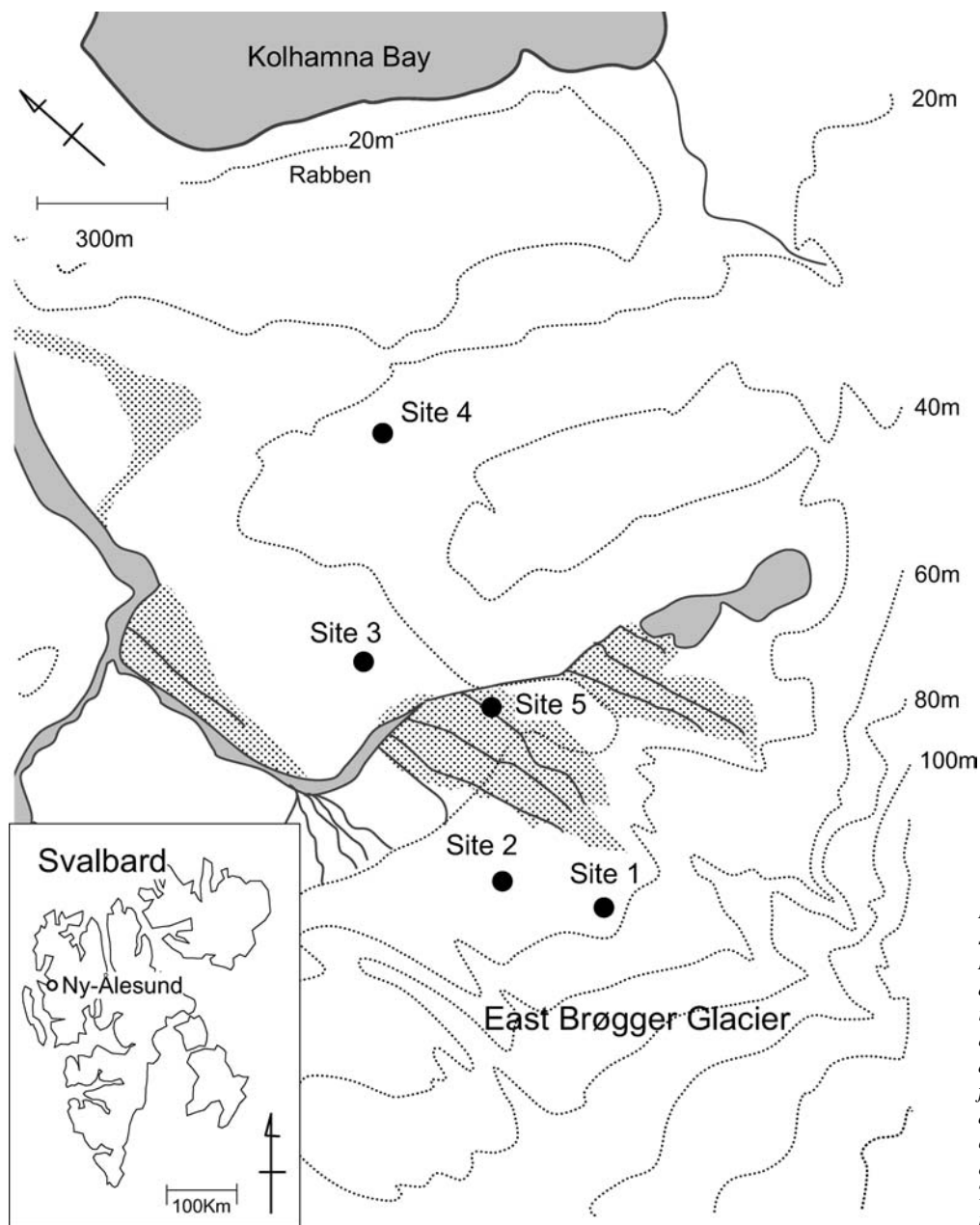


FIGURE 1. Locations of study sites in the glacier foreland of East Brøgger Glacier in the Ny-Ålesund area, Svalbard. Site 6 is not shown; it is about 500 m north of the edge of this map. The tip of the glacier is at 50 m a.s.l. Dotted areas are floodplains and wet areas. Gray areas are water. The melted glacier water flows northward and enters the sea at Kolhamna Bay. The Japanese observation station is at Rabben.

Results

$\delta^{13}\text{C}$ OF *SAXIFRAGA* *OPPOSITIFOLIA*

In all study sites, $\delta^{13}\text{C}$ of *S. oppositifolia* was distinctly different between the two growth forms (Fig. 2, Table 1). At each site, $\delta^{13}\text{C}$ differed by about 2‰ between the two growth forms. The $\delta^{13}\text{C}$ values of the C-form were always more negative and ranged from -28‰ to -30‰ , while those of the P-form ranged from -26.5‰ to -28‰ . With the progress of succession (from Sites 1 to 4), the water and nitrogen content in the soil increased distinctly, but $\delta^{13}\text{C}$ of both growth forms significantly increased (Fig. 2, Table 1). At Site 5, where the two growth forms grow sympatrically on the moist riverbank, the $\delta^{13}\text{C}$ value of the C-form was 3‰ more negative than that of the P-form. The C-form plant was hardly observed at Site 4, which was the latest successional site and the wettest site, while the P-form plant was not observed at Site 6, which seemed to be the driest site.

$\delta^{13}\text{C}$ OF EACH SPECIES AT EACH SITE

The $\delta^{13}\text{C}$ values for the dominant vascular plants, mosses and lichens at each site are shown in Figure 3. At Site 1, only *S. oppositifolia* was present in sufficient amounts for sampling. At all other sites, the $\delta^{13}\text{C}$ values of the P-form were more positive than the $\delta^{13}\text{C}$ values of all other species. On the other hand, $\delta^{13}\text{C}$ of the C-form tended to be more negative than the $\delta^{13}\text{C}$ values of the other species. Narrow-leaved grasses (*Poa* and *Luzula*) had small $\delta^{13}\text{C}$ values. *Salix polaris* and mosses (*Sanionia uncinata* and *Aulacomnium turgidum*) had intermediate $\delta^{13}\text{C}$ values regardless of the site. The lichen *Cetrariella delisei* had quite positive $\delta^{13}\text{C}$ values at Site 6, a dry site, and negative values at Site 4, a moist site. This result suggested that *C. delisei* was strongly affected by the moisture conditions on the soil surface, but more samples may be required to confirm this hypothesis.

Most of the variance in $\delta^{13}\text{C}$ values was due to the species or

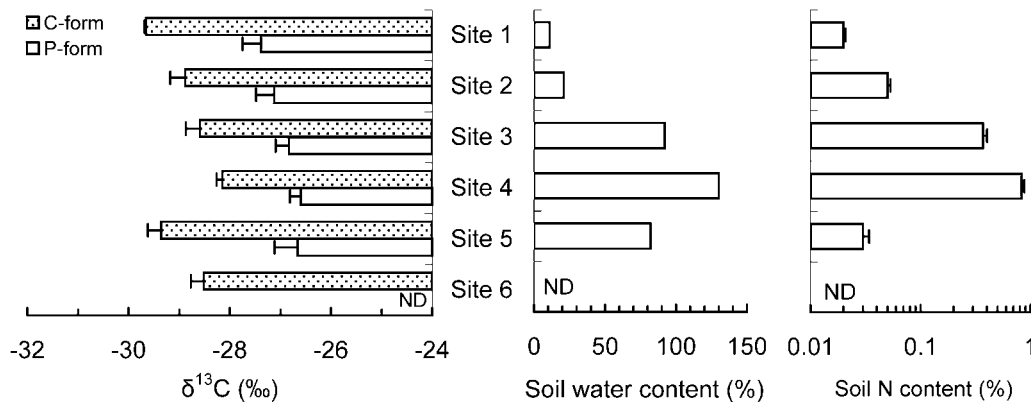


FIGURE 2. $\delta^{13}\text{C}$ value of the two growth forms of *S. oppositifolia*, soil water contents, and soil nitrogen contents at each study site. Sites 1 to 4 represent sequential stages in succession: Site 1 is the youngest and Site 4 the oldest. P-form plants (\square) and C-form plants (\square) were growing in close proximity within the same habitat at Site 5. P-form plants were not observed at Site 6, which is the driest site. The soil mass water contents (water mass/dry mass) and nitrogen contents contained in the soil between 0- and 2-cm depths are from Nakatsubo et al. (1998) and Bekku et al. (1999).

growth form. Even though the soil mass water contents of the study sites varied from 10% to 140% and the soil nitrogen contents varied from 0.02% to 0.85% (Fig. 2), the variance among individuals and the variance in the same species among the sites were both small. The average $\delta^{13}\text{C}$ values of the observed species at Sites 1–6 were -28.5 , -28.5 , -28.4 , -28.6 , -28.6 , and -28.0 ‰, respectively. The difference among the sites was less than -0.6 ‰ and no significant correlation was detected. The $\delta^{13}\text{C}$ values for a given species or growth form varied only slightly among the study sites.

Discussion

WATER UTILIZATION OF THE TWO MORPHS OF *SAXIFRAGA OPPOSITIFOLIA*

Our results show that $\delta^{13}\text{C}$ value of the P-form plants was always the most positive among all species, indicating severe physical restrictions (including stomatal restriction) of CO_2 uptake in photosynthesis. The $\delta^{13}\text{C}$ value of the P-form plants also suggested the highest water use efficiency. On the other hand, $\delta^{13}\text{C}$ value of the C-form of *S. oppositifolia* was always more negative than that of the P-form, indicating that the physical restrictions in photosynthesis were small, at least at the individual leaf level. These results show that $\delta^{13}\text{C}$ depends on the growth form rather than on the soil conditions. Though Körner et al. (1991) concluded that a range of 4‰ is to be expected within a single community of C_3 plant species, the difference in $\delta^{13}\text{C}$ between C-form and P-form was significant and consistent.

When the water utilization of a whole plant is considered, the transpirative water consumption (TWC) is determined by the product of surface area per biomass (SA) and average conductance to water vapor of the leaf surface (g_l). Both SA and g_l may be important for TWC. Because the two growth forms had similar root mass fraction and root types (taproot or fibrous root) when growing in the same habitat (Kume et al., 1999), the manner of water utilization of *S. oppositifolia* is determined by stomatal openness and biophysical characteristics of aboveground growth forms. C-form plants only have shoots with a short internode length (<6 mm), and the upper and the lower leaves imbricate each other. Some leaves of P-form plants are thin and flat shaped, but all the leaves of C-form plants are thick and fleshy. According to Kume et al. (1999), C-form plants are able to adjust their SA to soil moisture conditions by changing the degree of leaf overlap: SA has a value of about $50 \text{ cm}^2 \text{ g}^{-1}$ in dry environments and $100 \text{ cm}^2 \text{ g}^{-1}$ in damp environments. P-form plants have long internode shoots with thin, detached leaves. The SA of P-form plants is

about $100 \text{ cm}^2 \text{ g}^{-1}$. At Site 5, a damp riverbank, where both growth forms grow sympatrically, the C-form and the P-form had similar SAs (about $100 \text{ cm}^2 \text{ g}^{-1}$). However, the difference in the $\delta^{13}\text{C}$ values between the two growth forms was the largest among the sites. These facts suggest that the P-form leaf's innate physical restriction of CO_2 uptake is larger than that of the C-form.

In the net photosynthesis rate per SA, Kume et al. (1999) could not detect any differences among the single shoots of different forms when they were measured under field conditions with an open-flow infrared gas analysis system (LI-6400, LI-COR, Inc., Lincoln, Nebraska, U.S.A.). However, the C_i/C_a ratio of the P-form was about 0.72, and that of the C-form was about 0.82. These results agree with the $\delta^{13}\text{C}$ analysis and raise the possibility that the P-form had lower water consumption than the C-form under the damp conditions at Site 5, even though their net photosynthetic rates were similar. However, this assumption must be incorrect. Water consumption at the whole plant level must be less in the high-density cushion form than in the low-density prostrate form. The ground cover area per biomass of P-form plant is the largest among the plants growing in Ny-Ålesund. The average ground cover area per biomass (GA) of the P-form was about $240 \text{ cm}^2 \text{ g}^{-1}$, whereas GA of the C-form was at most $70 \text{ cm}^2 \text{ g}^{-1}$ in the moist sites and less than $30 \text{ cm}^2 \text{ g}^{-1}$ in the dry sites (Kume et al., 1999). The conductance of water vapor of the boundary layer of the plant surface can be assumed equal because all of these colonies spread on the ground and have similar aerodynamic resistance. Therefore, the P-form's effective evaporative surface area is over 4 times larger than that of the C-form, and the demand of transpiration per biomass of P-form plants may be markedly larger than that of C-form plants. At the whole plant level, the C-form plant is self-shaded and has small conductance per biomass because of its high plant (area) density.

Nakatsubo (1994) obtained similar results in moss colonies of different area densities and pointed out the importance of GA in restricting water loss from moss colonies. TWC is more accurately given by $\text{GA} \times g_l$ than by $\text{SA} \times g_l$, and $\delta^{13}\text{C}$ is mostly affected by GA. Despite the small differences among different shoot forms in the net photosynthesis rate per SA, it is expected that the whole-plant photosynthesis per biomass of P-form plants is markedly larger than that of C-form plants. This conclusion is in accordance with the results of Crawford et al. (1993). They showed that the two growth form plants had different photosynthesis rates per biomass (the P-form was about $2.3 \mu\text{molCO}_2 \text{ g}^{-1} \text{ min}^{-1}$, and the C-form was about $1.3 \mu\text{molCO}_2 \text{ g}^{-1} \text{ min}^{-1}$). Crawford and Wolf (1999) also provided a value of the ^{13}C isotope discrimination ratio (Δ) for *S. oppositifolia* in the High Arctic ($-19.5\% \pm 0.32$, $n = 8$). If the ^{13}C value of surround-

TABLE 1

ANOVA for the $\delta^{13}\text{C}$ values of *Saxifraga oppositifolia*. Effects of site (Sites 1–4) and growth form (C-form and P-form) were detected (see Fig. 2), but no interaction was detected

Effect	df	MS	F	P
Site	3	1.58	9.9	0.0006
Growth form	1	18.5	116.1	<.0001
Site * growth form	3	0.20	1.3	0.32
Residual	16	0.16		

ing environment ($\delta^{13}\text{C}$ of air) was assumed -8‰ , their $\delta^{13}\text{C}$ will be -27.5‰ and well accord with our results.

Körner (1999) showed that the differences in life form had negligible effects on $\delta^{13}\text{C}$ in alpine plants. One reason is that, he did not consider the relationships among SA, GA, *gl*, root mass fraction, and life forms. More appropriate life form evaluation might be needed to understand the effects of different life form on $\delta^{13}\text{C}$.

ADAPTIVE SIGNIFICANCE OF GROWTH FORMS OF SAXIFRAGA OPPOSITIFOLIA

In the High Arctic, the growing season in areas where snowbeds occur, about 30 days, is significantly shorter than that on snow-free ridges, about 50 days (Crawford 1997). Usually P-form plants are dominant in snowbeds, that is, damp areas with a short growing season. In such environments, P-form plants have an advantage because of their high productive efficiency, while C-form plants are not able to produce enough photosynthate to survive in the short growing season. Nonetheless, at Site 6, which was the driest site but also the one with the longest expected growing season, the number of C-form plants increased significantly. This result may be because the GA of P-form plants is so large that it is difficult to decrease TWC by decreasing *gl* alone in extreme dry conditions. At the base of the East Brøgger Glacier, there is plenty of meltwater from the glacier, and the growing season is relatively long compared to that in areas where snowbeds occur. These conditions may enable the sympatric growth of C- and P-form plants.

Teeri (1972) showed that the uptake of dissolved oxygen during flooding was faster in the P-form than in the C-form. This difference may be because of the large GA of the P-form and suggests that another advantage of the P-form is its greater conductance at the whole-plant level.

The biophysiological characteristics of the whole-plant conductance may be significant only in the high arctic environment, where the competition for light is negligible during the growing season and where the plants spread only in two-dimensional space. Therefore, environmental changes such as global warming will affect the balance between the two growth forms by increasing three-dimensional competition (e.g., Stenström et al., 1997).

EFFECTS OF PRIMARY SUCCESSION

In both growth forms of *S. oppositifolia*, the $\delta^{13}\text{C}$ values increased slightly with increasing soil water content with the progress of succession from Sites 1 to 4 (Fig. 2). These results were puzzling because they suggested that the physical restrictions in photosynthesis of *S. oppositifolia* increased with increasing soil water availability. Even if the soil respiration affected the $\delta^{13}\text{C}$ values, the values should be decreased with increasing soil respiration. *Saxifraga oppositifolia* is the only vascular plant that occurs in all successional stages in Ny-Ålesund, although the population size decreased at the later successional stages, especially in C-form plants (Kume et al., 1999). One

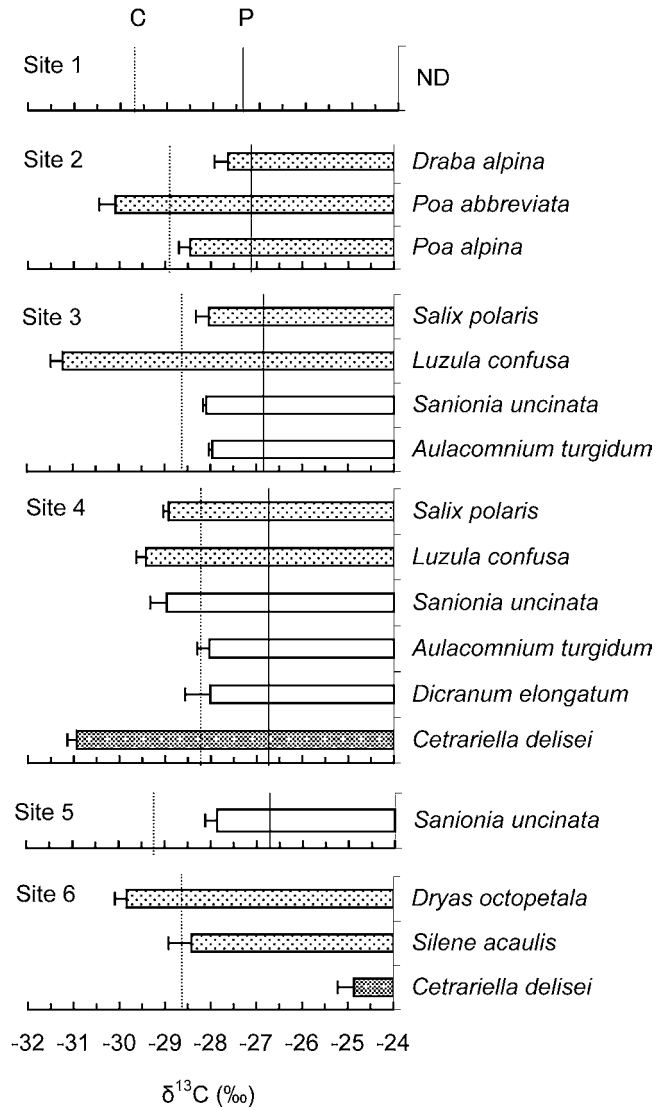


FIGURE 3. $\delta^{13}\text{C}$ values of dominant vascular plants (\square), mosses (\square), and lichens (\boxtimes) at each study site. Vertical solid lines indicate $\delta^{13}\text{C}$ values of the P-form of *S. oppositifolia*, and vertical dotted lines indicate those of the C-form. Site 1 is not shown because only *S. oppositifolia* was observed.

reason for the decrease in population size is that competition from other vascular plant species and mosses makes it more difficult to establish new seedlings at the later successional stages. Another possible reason is that there is an increase of GA per root mass of *S. oppositifolia* because of aboveground competition with other species. In later successional stages, the centers of the developed patches of *S. oppositifolia* were invaded by mosses, mainly *Sanionia uncinata*, which tended to cover the patches. To escape the mosses, *Saxifraga oppositifolia* might have to grow in the outer areas of a patch that had not yet been invaded by other species. Such activities should force *S. oppositifolia* to increase GA per biomass, hence decreasing the water supply per GA and increasing stomatal restriction. Therefore, *S. oppositifolia* might increase $\delta^{13}\text{C}$ with the progress of succession in spite of the increase in the soil water content.

GROWTH FORM VS. ROOT MASS FRACTION

The differences in the average $\delta^{13}\text{C}$ values of all the species growing at each site were quite small among the sites (Fig. 3), but the

reason was not clear. Narrow-leaved grasses and *Dryas octopetala* had small $\delta^{13}\text{C}$ values, which suggested a small stomatal restriction in photosynthesis. The grass species had quite large SA, and *D. octopetala* grew in the polar semidesert, a dry environment. We inferred that the small $\delta^{13}\text{C}$ of these plants was caused by their greater root mass fraction, which was about 2 to 5 times larger than the root mass fraction of *S. oppositifolia*. The deeper, well-developed roots of these grasses can provide enough water for their large TWC.

In our study sites, all vascular plants except *S. oppositifolia* seemed to have different root mass fraction in different growth environments. Kume et al. (1999) showed that the root characteristics of *S. oppositifolia* were little affected by the growth form. In addition, the root mass fraction of *S. oppositifolia* was relatively small. For example, the root mass fraction of *S. oppositifolia* was about 0.20, and its coefficient of variation (CV, SD/mean) was 0.2. The mean ratio of *Draba alpina* was 0.35 and CV was 0.23; that of *Poa alpina* was 0.40 and CV was 0.25. For a plant to be established in the early stage of primary succession, it is essential for the roots to reach the safe layer in which the soil water content is stable, but root elongation is often disturbed by physical and meteorological events (Maruta, 1976). Thus, in newly deglaciated areas, where root development is often restricted, it may be beneficial for first colonizers, such as *S. oppositifolia*, to have two morphs with different aboveground growth forms or to be able to control the biophysical characteristics of growth forms in response to the variable severe growing conditions.

Even though stomatal restriction does not occur in mosses, the $\delta^{13}\text{C}$ values of mosses were similar to those of vascular C_3 plants, and the variances in the $\delta^{13}\text{C}$ values within individual species of mosses were relatively small. These results were similar to those of previous studies (Rundel et al., 1979; Teeri, 1981; Proctor, 1992). In Ny-Ålesund, high photosynthetic activities of mosses were observed only on rainy days or soon after rainfall, when moss water content was high (Uchida et al., 2002). Therefore, whole-plant conductance should be kept within a certain range during photosynthesis, and this should result in steady $\delta^{13}\text{C}$ values. As mentioned earlier, Nakatsubo (1994) pointed out the importance of differences in GA of each species in restricting water loss from moss colonies. The difference in GA causes the difference in the drying rate of the plant colonies and can readily affect the $\delta^{13}\text{C}$ values. The difference in $\delta^{13}\text{C}$ between the moss species may be caused by different colony densities, as is the case for *S. oppositifolia*. In Ny-Ålesund, the mosses, which do not have roots, tended to be more dominant than the vascular plants, which do. These facts emphasize the importance of the aboveground growth form in the high arctic environment.

ADAPTIVE SIGNIFICANCE OF POLYMORPHISM

Saxifraga oppositifolia had one of the broadest distributions near the lower end of the East Brøgger Glacier. It is also distributed widely in areas of receding glaciers in alpine regions of Europe, Asia, and North America (Hultén and Fries, 1986). In high arctic regions, contrasting extreme microclimatic environments are adjacent to each other. Polymorphism may be one of the adaptive characteristics for surviving under such a severe, mosaic environment. The photosynthesis, transpiration, and many other physiological and reproductive characteristics were significantly different between the two growth forms (Teeri, 1972; Crawford et al., 1995; Kume et al., 1999). Crawford et al. (1995) suggested that *S. oppositifolia* adapts to changing climates and survives glaciation by changing the frequencies of the two morphs. Various types of polymorphism are reported in *Dryas octopetala* (McGraw, 1995; Max et al., 1999), which showed much visible ecotypic variation throughout its wide polar range distribution (Elkington, 1971). Morphological variability or polymorphism within a species appeared to be one of the adaptive characteristics

of plants growing in the high arctic, as well as genetic flexibility (Brochmann and Håpnes, 2001), where the forces of selection vary spatially and temporally from short-term annual disturbances to long-term climatic oscillations.

Acknowledgments

We thank Dr. T. Masuzawa of Shizuoka University and Dr. Y. Ino of Waseda University for their encouragement and support. We thank Dr. T. Ueno of the National Institute of Polar Research for his assistance in Ny-Ålesund and Dr. H. Muraoka of Gifu University for advice and comments on the manuscript. We are grateful to the Center for Ecological Research, Kyoto University, for managing the measurements of carbon isotope ratio. We also thank the Norwegian Polar Institute for logistical support. This study was supported by a Grant in Aid for Scientific Research from the Ministry of Education, Science and Culture of Japan.

References Cited

- Abbott, R. J., Smith, L. C., Milne, R. I., Crawford, R. M. M., Wolff, K., and Balfour, J., 2000: Molecular analysis of plant migration and refugia in the Arctic. *Science*, 289: 1343–1346.
- Bekku, Y., Kume, A., Nakatsubo, T., Masuzawa, T., Kanda, H., and Koizumi, H., 1999: Microbial biomass in relation to primary succession on arctic deglaciated moraines. *Polar Bioscience*, 12: 47–53.
- Brochmann, C., and Håpnes, A., 2001: Reproductive strategies in some arctic *Saxifraga* (Saxifragaceae), with emphasis on the narrow endemic *S. svalbardensis* and its parental species. *Botanical Journal of the Linnean Society*, 137: 31–49.
- Brysting, A. K., Gabrielsen, T. M., SrrlibrDten, O., Ytrehorn O., and Brochmann, C., 1996: The purple saxifrage, *Saxifraga oppositifolia*, in Svalbard: two taxa or one? *Polar Research*, 15: 93–105.
- Campbell, G. S., and Norman, J. M., 1998: *An Introduction to Environmental Biophysics*. New York: Springer-Verlag. 286 pp.
- Crawford, R. M. M., 1997: Habitat fragility as an aid to long-term survival in arctic vegetation. In Woodin, S. J., and Marquiss, M. (eds.), *Ecology of Arctic Environments*. British Ecological Society Special Publication No. 13. Oxford: Blackwell Scientific, 113–136.
- Crawford, R. M. M., Chapman, H. M., Abbott, R. J., and Balfour, J., 1993: Potential impact of climatic warming on arctic vegetation. *Flora*, 188: 367–381.
- Crawford, R. M. M., Chapman, H. M., and Smith, L. C., 1995: Adaptation to variation in growing season length in arctic population of *Saxifraga oppositifolia* L. *Botanical Journal of Scotland*, 41: 177–192.
- Crawford, R. M. M., and Wolfe, D. W., 1999: Temperature: cellular to whole-plant and population responses. In Luo, Y., and Mooney, H. A. (eds.), *Carbon Dioxide and Environmental Stress*. New York: Academic Press, 61–106.
- Ehleringer, J. R., and Cooper, T. A., 1988: Correlation between carbon isotope ratio and microhabitat in desert plants. *Oecologia*, 76: 562–566.
- Elkington, T. T., 1971: Biological flora of the British Isles: *Dryas octopetala* L. *Journal of Ecology*, 59: 887–905.
- Farquhar, G. D., O'Leary, M. H., and Berry, J. A., 1982: On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. *Australian Journal of Plant Physiology*, 9: 121–137.
- Fitzpatrick, E. A., 1997: Arctic soils and permafrost. In Woodin, S. J., and Marquiss, M. (eds.), *Ecology of Arctic Environments*. British Ecological Society Special Publication No. 13. Oxford: Blackwell Scientific, 1–39.
- Hultén, E., and Fries, M., 1986: *Atlas of North European Vascular Plants: North of the Tropic of Cancer*, Vol. 2. Königstein: Koeltz Scientific Books. 1172 pp.
- IPCC, 2001: *Climate Change 2001: The Scientific Basis—Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change* (eds. Houghton, J. T.,

- Ding, Y., and Griggs D. J.). Cambridge: Cambridge University Press.
- Körner, Ch., 1999: *Alpine Plant Life*. Berlin: Springer-Verlag. 338 pp.
- Körner, Ch., Farquhar, G. D., and Wong, S. C., 1991: Carbon isotope discrimination by plants follows latitudinal and altitudinal trends. *Oecologia*, 88: 33–40.
- Kume, A., Nakatsubo, T., Bekku, Y., and Masuzawa, T., 1999: Ecological significance of different growth forms of purple saxifrage, *Saxifraga oppositifolia* L., in the High Arctic, Ny-Ålesund, Svalbard. *Arctic, Antarctic, and Alpine Research*, 31: 27–33.
- Maruta, E., 1976: Seedling establishment of *Polygonum cuspidatum* on Mt. Fuji. *Japanese Journal of Ecology*, 26: 101–105.
- Matthews, J. A., and Whittaker, R. J., 1987: Vegetation succession on the Storbeen glacier foreland, Jotunheimen, Norway: a review. *Arctic and Alpine Research*, 19: 385–395.
- Max, K. N., Mouchaty, S. K., and Schwaegerle, K. E., 1999: Allozyme and morphological variation in two subspecies of *Dryas octopetala* (Rosaceae) in Alaska. *American Journal of Botany*, 86: 1637–1644.
- McGraw, J. B., 1995: Patterns, causes and ecosystem consequences. In Chapin, F. S., III, and Körner, Ch. (eds), *Arctic and Alpine Biodiversity: Patterns, Causes, and Ecosystem Consequences*, Ecological Studies Vol. 113. Berlin: Springer-Verlag, 33–43.
- Minami, Y., Kanda, H., and Masuzawa, T., 1996: The relationship between distribution of bryophytes and soil conditions on deglaciated arctic terrain in Ny-Ålesund. *Proceedings of the NIPR Symposium on Polar Biology*, 9: 307–312.
- Nakatsubo, T., 1994: The effect of growth form on the evaporation in some subalpine mosses. *Ecological Research*, 9: 245–250.
- Nakatsubo, T., Bekku, Y., Kume, A., and Koizumi, H., 1998: Respiration of the belowground parts of vascular plants: its contribution to total soil respiration on a successional glacier foreland in Ny-Ålesund, Svalbard. *Polar Research*, 17: 53–59.
- Proctor, M. C. F., Raven, J. A., and Rice, S. K., 1992: Stable carbon isotope discrimination measurements in sphagnum and other bryophytes: physiological and ecological implication. *Journal of Bryology*, 17: 193–202.
- Rønning O. I., 1996: The Flora of Svalbard 3rd ed. Norwegian Polar Institute, Oslo. 184pp.
- Rundel, P. W., Stichler, W., Zander, R. H., and Ziegler, H., 1979: Carbon and hydrogen isotope ratios of bryophytes from arid and humid regions. *Oecologia*, 44: 91–94.
- Stenström, M., Gugerli, F., and Henry, G. H. R., 1997: Response of *Saxifraga oppositifolia* L. to simulated climate change at three contrasting latitudes. *Global Change Biology*, 3: 44–54, Suppl. 1.
- Teeri, J. A., 1972: Microenvironmental adaptations of local populations of *Saxifraga oppositifolia* in the High Arctic. Ph.D. dissertation, Duke University, Durham, NC. 216 pp.
- Teeri, J. A., 1981: Stable carbon isotope analysis of mosses and lichens growing in xeric and moist habitats. *Bryologist*, 84: 82–84.
- Uchida, M., Muraoka, H., Nakatsubo, T., Bekku, Y., Ueno, T., Kanda, H., and Koizumi, H., 2002: Net Photosynthesis, Respiration, and Production of the Moss *Sanionia uncinata* on a Glacier Foreland in the High Arctic, Ny-Ålesund, Svalbard. *Arctic, Antarctic, and Alpine Research*, 34: 287–292.

Ms submitted July 2002