Colonization of the polar willow *Salix polaris* on the early stage of succession after glacier retreat in the High Arctic, Ny-Ålesund, Svalbard

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Abstract

The polar willow (*Salix polaris*), predominant in the late successional stage in deglaciated areas of Ny-Ålesund, Svalbard, is rarely found in the early stage, when purple saxifrage (*Saxifraga oppositifolia*) dominates. To elucidate the pattern and the mechanism of successional change from the *Saxifraga* stage to the *Salix* stage, we examined the distribution pattern, size structure and habitat conditions of a colonizing *Salix* population in the seral stage where *Salix* was invading *Saxifraga*-dominated sites. The present distribution pattern and aerial photographs taken in the past suggest that *Salix* colonization at this site commenced within the last 70 years. We found 115 *Salix* individuals (22 male, 13 female and 80 unknown) in a 30 m × 30 m quadrat on the seral stage. Although the largest individual had a size of 2000 cm^2 (length × maximum width), the majority (84%) of individuals were smaller than 100 cm^2. The seedling size distribution, as inferred from the leaf scar number, indicated that annual recruitment was slight. Of the individuals observed about 75% had colonized bare ground; only four individuals grew within *Saxifraga* colonies. No significant difference was found in soil characteristics (water content, and carbon and nitrogen concentrations) between the seral stage and the earlier stage prior to colonization by *Salix*. These results suggest that difficulties in seed production, germination and/or seedling establishment of *Salix*, rather than soil formation by preceding species (*Saxifraga*), limits the early-stage colonization by *Salix*.

Glacier retreat is occurring widely in the Arctic, including the High Arctic (Green 2005; Kohler et al. 2007). Some evidence suggests that many glaciers in western Svalbard are losing mass at an increasing rate (Kohler et al. 2007). Glacier retreat provides new habitats for plant colonization, where organic matter accumulates. Information related to colonization rates of plants, especially dominant species, and their limiting factors is critically important for predicting how ecosystems in deglaciated areas will respond to future climate change.

In a deglaciated area in Ny-Ålesund, Svalbard, purple saxifrage (*Saxifraga oppositifolia* L.) colonizes bare ground as early as a few years after deglaciation (Kume et al. 1999). Several traits enable this species to be the first colonizer in the area: high fecundity, the ability to form adventitious roots from shoot fragments (Kume et al. 1999) and low leaf nitrogen content, which might facilitate their establishment on nutrient-poor substrates (Muraoka et al. 2008). In addition, *Saxifraga oppositifolia* is known to have two growth forms—prostrate and semi-erect—that are adapted to maximize growth in different habitat conditions (Crawford et al. 1995).

In contrast, the polar willow (*Salix polaris* Wahlenb.), a dwarf shrub with creeping subterranean shoots or occurring in a moss carpet, predominates in the late successional stage, but it is rarely found in the early stage, where *Saxifraga oppositifolia* dominates (Kume et al. 1999; Nakatsubo et al. 1998; Nakatsubo et al. 2005; Muraoka et al. 2008). This species has high leaf photosynthetic capacity, and plays a crucial role in carbon sequestration in the deglaciated ground (Muraoka et al. 2002). Muraoka et al. (2008) estimated that the contribution of *Salix polaris* is as high as 12 times that of the pioneer plant *Saxifraga oppositifolia*. Therefore, invasion by *Salix polaris* during the early stage is important not only in terms of community structure but also for carbon sequestration in this area. To date, however, the pattern and the mechanism of the successional change from the *Saxifraga* stage to the *Salix* stage have been undocumented.

This study specifically examined the seral stage—between the early and the late successional stages—during which *Salix polaris* colonizes *Saxifraga*-dominated sites. We examined the distribution pattern, size structure and habitat conditions of colonizing *Salix* populations in the seral stage to study the colonization rate of *Salix* and its limiting factor(s).

Materials and methods

The study site was situated in the glacier foreland of Austre Brøggerbreen, near Ny-Ålesund, on the fjord Kongsfjorden in Svalbard (78.5°N, 11.5°E). In the Kongsfjorden area, the retreat rates of glaciers ending on land are reportedly about 10–20 m per year (Svendsen et al. 2002). The rate of retreat of Austre Brøggerbreen determined in our field study agrees with these values: the recession was about 30 m between 2003 and 2005, and about 60 m between 2003 and 2008. The annual mean air temperature and precipitation in this area between 2001 and 2008 were, respectively, −4.2°C and 433 mm. The ground begins to be free of snow in early July; snow begins to accumulate in mid-September.

Several authors have studied the vegetation and succession pattern in the glacier foreland of Austre Brøggerbreen (Nakatsubo et al. 2005; Ohtsuka et al. 2006), and of a neighbouring glacier (Hodkinson et al. 2003). *Saxifraga oppositifolia* is the most common pioneer plant in the newly deglaciated moraines of Austre Brøggerbreen, although it also occurs in later stages. Late stages are dominated by various species, including mosses, such as *Sanionia uncinata* (Hedw.) Loeske and *Aulacomnium turgidum* (Wahlenb.) Schwaegr., and vascular plants, such as *Saxifraga oppositifolia*, *Salix polaris*, *Dryas octopetala* L. and *Luzula confusa* Lindeb. The early stage (*Saxifraga* stage) and the later stages of succession are divided spatially by the floodplain (Fig. 1). A recent study (Nakatsubo et al. 2008) showed that part of the later stage had developed on a raised beach deposit.

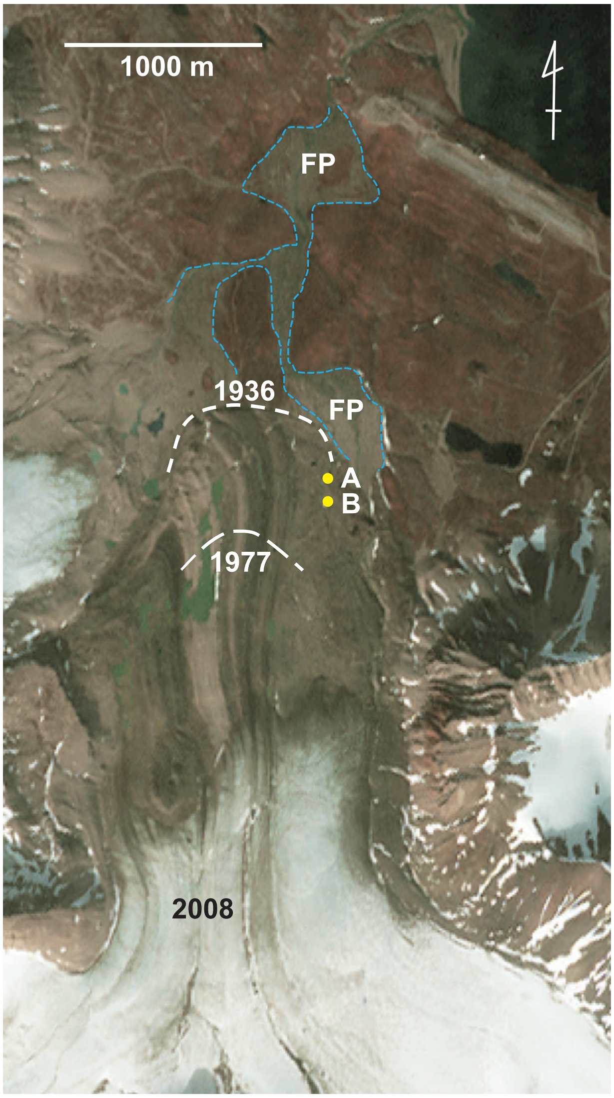

Fig. 1 Satellite image showing the study site in the glacier foreland of Austre Brøggerbreen, near Ny-Ålesund, Svalbard. Locations of the two quadrats (A and B), the glacier front terminus in 1936 and 1977, and the floodplain (FP) are also shown; they were determined using aerial photographs from the Norwegian Polar Institute.

Although *Salix* was rare in the early stage, colonization of scattered individuals of *Salix* was observed in the old part (near the floodplain) of the early stage. This stage is hereafter designated as the "seral stage". Early in August 2008, a 30 m × 30 m quadrat (quadrat A) was set in the seral stage. The distance between quadrat A and the front of the Austre Brøggerbreen glacier was about 1 km. For comparison, another 30 m × 30 m quadrat (quadrat B), within which no *Salix* was observed, was set in the upper (more recently deglaciated) site of the deglaciated area.

The two quadrats were situated in the middle of the two lateral moraines (west and east ridges) of Austre Brøggerbreen (Fig. 1). The respective vegetation coverage ratios (mainly *Saxifraga oppositifolia*) of quadrats A and B were about 3 and <1%, respectively. Accurate positions of these quadrats were determined using a portable GPS receiver (Trimble GeoXT GPS unit; Trimble Navigation, CA, USA) and a satellite image (Advanced Land Observing Satellite multi-spectral Advanced Visible Near Infrared 2 sensor image, acquired on 31 July 2008). Aerial photographs from the Norwegian Polar Institute were used to demarcate successive changes visually at the glacier front terminus in 1936 and 1977.

The quadrats were subdivided into 5 m × 5 m subquadrats, and the size, sex and position of each *Salix* plant within the subquadrat was recorded. Because the *Salix* colony shape varied widely, the length (L) and the maximum width (W) of the ground covered by each colony was measured: L × W was used as the plant size index. A preliminary study indicated that there was a highly significant relationship between the index (L × W) and the colony size (area) determined from photographs with an image scanner ($r = 0.99$; $P < 0.001$). The sex of each (male, female or unknown) was determined according to inflorescence. Seed production in female inflorescences of the current (2008) and previous year (2007) were also recorded. Individuals smaller than 1 cm^2 were recorded as "seedlings". To determine the seedling age, we collected all seedlings and counted leaf scars under a binocular microscope. At that time, the presence of mycorrhiza was also recorded.

We examined the relation of *Salix polaris* to *Saxifraga oppositifolia* colonies. Each *Salix* individual was classified into one of the following three categories based on its position relative to *Saxifraga*: (1) *Salix* colony growing within the *Saxifraga* colony; (2) *Salix* colony growing close to *Saxifraga* (with at least one branch of the two species crossed); (3) *Salix* colony colonizing bare ground.

To examine the study site soil characteristics, soil samples of the 0–3 cm layer were collected from 18 randomly selected subquadrats in each quadrat. Fresh weights of these samples were measured to obtain their water contents later. They were freeze-dried and brought back to Japan. The total carbon and nitrogen contents of the soil were measured using a CN analyser (Sumigraph NC-22; Sumika Chemical Analysis Co., Tokyo, Japan).

Results and discussion

Colonization of *Salix polaris* on the seral stage was observed only within 200 m of the riverbank. Although five isolated individuals of *Salix* were found between the two quadrats (A and B), we were unable to find any *Salix* individual between quadrat B and the glacier front.

The aerial photograph taken in 1936 showed that the glacier front was near the riverbank; the study site was covered entirely by the glacier at that time. By 1977, when another photograph was taken, the site was left exposed by the glacier (Fig. 1). Although the site might have been subjected to disturbances after deglaciation, these data suggest that colonization of *Salix* commenced within the last 70 years. This rapidity of colonization is faster than some late successional species in other glacier forelands, e.g., *Betula nana* in a glacier foreland in mainland Norway (Whittaker 1993). However, although *Saxifraga oppositifolia* invaded near to the glacier front, *Salix* colonization was limited to the older part of the moraine, which suggests that the *Salix* invasion speed is insufficient to keep up with the recession speed, which was estimated as about 10–20 m annually (Svendsen et al. 2002).

This pattern of colonization of *Salix polaris* and *Saxifraga oppositifolia* in our study site is somewhat different from that reported for the neighbouring glacier, Midre Lovénbreen (Hodkinson et al. 2003), where isolated small seedlings of *Salix* were found in a pioneer site of as young as 2 years (Hodkinson et al. 2003). However, successional changes in frequency of occurrence and in ground cover were slower in *Salix* than in *Saxifraga* (Hodkinson et al. 2003: figs. 2, 3), which also suggests a limited ability of *Salix* to colonize pioneer sites.

In quadrat A we found 115 *Salix* individuals (22 male, 13 female and 80 unknown, including seedlings), although the total coverage of *Salix* was less than 1%. The largest individual was 2000 cm^2 (L × W), but most (84%) of the individuals were smaller than 100 cm^2 (Fig. 2a). The size structure of the colonizing population (Fig. 2a) resembles an inverted J-shaped size distribution: a population structure with a relatively constant juvenile supply (Mori et al. 2006). However, the fraction of individuals larger than 100 cm^2 was very small, and the size distribution of the large individuals is discontinuous. Moreover, analysis of leaf scars revealed that the age of the small individuals classified as seedlings varied widely, ranging from less than 5 years to greater than 20 years (Figs. 2b, 3). Half of the seedlings had more than five leaf scars. Because most seedlings had two or three green leaves, it is estimated that most seedlings were older than several years. These results indicate that annual recruitment was quite limited: not more than 10 individuals in the 30 m × 30 m quadrat.

Regarding propagation by seeds, vegetative propagation might play some role in *Salix* colonization. Reportedly, *Salix polaris* can form roots from shoot fragments, but this capability is rather limited compared with

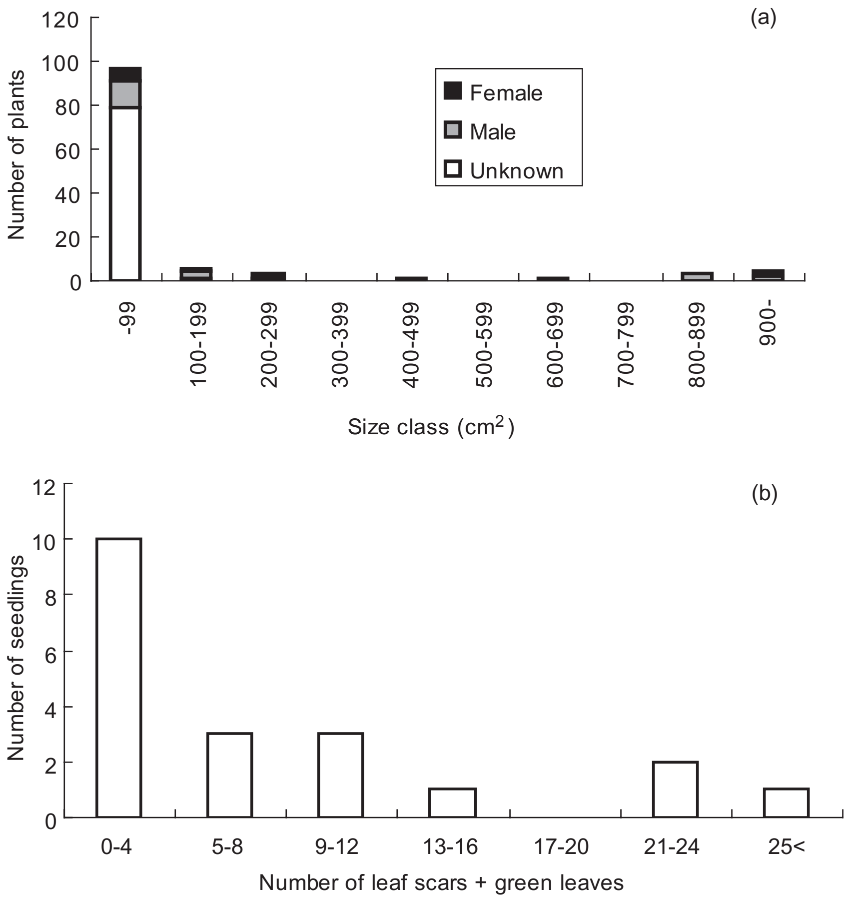

Fig. 2 Size distribution of the *Salix polaris* population at the study site. (a) The size distribution of *Salix* individuals found in quadrat A ($n = 115$). Sizes are expressed as the product of the length (L) and the maximum width (W) of the colony. (b) The size distribution of seedlings based on the number of leaf scars, excluding cotyledons.

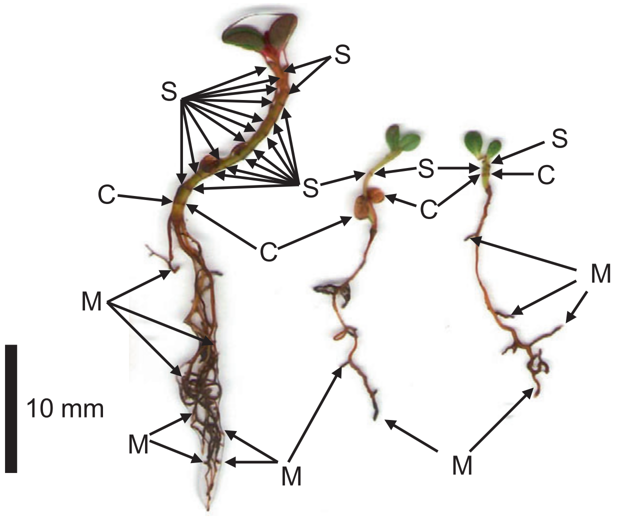

Fig. 3 *Salix* seedlings of different ages: S, leaf scar; C, cotyledon or its leaf scar; M, mycorrhizal roots.

that of *Saxifraga oppositifolia* with its prostrate growth form, which has high rhizogenesis ability and which spreads vegetatively by shoot fragments (Kume et al. 1999). Apparently, the short above-ground part of *Salix* is unsuitable for propagation by shoot fragments. In fact, we were unable to find any rooted fragments of *Salix* in our study site. This difference in vegetative propagation might partly explain why *Salix* is rare in the early stage, and why *Saxifraga oppositifolia* dominates.

Several factors might explain the small annual recruitment of *Salix polaris* at this study site. Seed availability can be a limiting factor of plant colonization in this area. Cooper et al. (2004), who examined the composition and density of soil seed banks in Svalbard, reported that *Salix polaris* is common in vegetation, but was a poor germinator in seed bank trials. At our study site, seven of the 13 females failed to bear seeds in 2008 (Table 1), suggesting the difficulty in seed set in this area. Additionally, we were unable to find even a single seedling around some female plants (Table 2), which suggests limited germination and/or high seedling mortality in the field. Slow initial growth rate, as indicated by the analysis of leaf scars (Figs 2b, 3), might also contribute to the slow colonization of *Salix* at this site.

It has been suggested that facilitation, the process by which colonizing species improve the environment for later successional species, is among the major successional mechanisms in severe environments (Chapin et al.

Table 1 Seed production of each female *Salix polaris* plant.

Individual females	Seed production 2007	2008	Presence of seedlings around the female[a]
1	+	+	+
2	+	+	+
3	+	+	+
4	+	−	+
5	+	−	+
6	+	−	−
7	+	+	−
8	−	−	+
9	+	+	−
10	+	+	+
11	−	−	+
12	+	−	−
13	+	−	−

[a] Distance from the female to each seedling was less than 1 m.

Table 2 Colonizing site of *Salix polaris* in relation to *Saxifraga oppositifolia* within the 30 m × 30 m quadrat.

Colonizing site	Number of *Salix* individuals
Within a *Saxifraga* colony	4
Close to *Saxifraga*[a]	25
Bare ground	86

[a] With at least one branch of the two species crossed.

Table 3 Some soil characteristics of the two 30 m × 30 m quadrats. Mean values of soil samples (0–3 cm depth) collected from 18 randomly selected subquadrats (5 m × 5 m) are shown with the SD.

Soil characteristics	Quadrat A	Quadrat B
Water content[a]	0.15 ± 0.06	0.15 ± 0.06
Carbon concentration (%)	0.56 ± 0.21	0.48 ± 0.17
Nitrogen concentration (%)	0.03 ± 0.01	0.03 ± 0.01

[a] Water content = (fresh weight – dry weight)/dry weight.

1994). If this applies to our study site, it is expected that the late successional species (*Salix*) colonizes sites where the early successional species (*Saxifraga*) has already been established. Our results did not support this hypothesis: about 75% of *Salix* individuals had colonized bare ground, although only four individuals grew within *Saxifraga* colonies (Table 2). This difference indicates that the presence of the preceding species is unimportant, at least for the initial stage of *Salix* colonization. Furthermore, no significant difference was found in soil characteristics (water content, and carbon and nitrogen concentrations) between the seral stage (quadrat A) and the *Saxifraga* stage (quadrat B) (Student's *t*-test, $P > 0.05$) (Table 3). We also examined the correlation between soil characteristics (water content, and carbon and nitrogen concentrations) and the number of *Salix* individuals in the subquadrats of quadrat A. The relation was not found to be significant ($n = 18$, $P > 0.05$). Therefore, it is unlikely that colonization of *Salix* was limited by soil development in our study site.

Another factor that might have affected the colonization of *Salix* is the presence of mycorrhizal fungi. Reportedly, colonization of mycorrhizal fungi facilitates subsequent seedling establishment of *Salix* species in a successional volcanic desert (Nara & Hogetsu 2004). At this study site, all *Salix* seedlings had ecotomycorrhiza. It is likely that whether the seedling was able to form a mycorrhizal association determined the survival of the seedling. This hypothesis should be tested through future study, including culture experiments.

To conclude, *Salix polaris* is a later colonizer of the deglaciated area than the pioneer *Saxifraga oppositifolia*. However, the presence of the preceding species—*Saxifraga*—is not a prerequisite of *Salix* colonization. The slight annual recruitment, which might be explained by low seed availability, difficulties in germination and/or seedling establishment, has limited the colonization rate of *Salix* at this study site. The colonization rate is insufficient to keep up with the speed of the glacier's recession. The loss of the glacier in this region has accelerated in recent years, in response to climate change (Nuth et al. 2007). Therefore, it is unlikely that *Salix* will make an important contribution to carbon sequestration in newly exposed sites unless future climate change considerably raises its colonization rate.

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