Respiration of the belowground parts of vascular plants: its contribution to total soil respiration on a successional glacier foreland in Ny-Ålesund, Svalbard

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As a part of the study on soil carbon flow in a deglaciated area in Ny-Ålesund, Svalbard (79°N), we estimated the contribution of the belowground respiration of vascular plants to total soil respiration in August 1996. Four study sites were set up along a primary successional series, ranging from newly deglaciated moraine to older moraine with well-developed vegetation cover. Respiratory activity of the belowground parts (roots + belowground stems) of three dominant species, *Salix polaris*, *Saxifraga oppositifolia* and *Luzula confusa*, was determined under laboratory conditions. The respiratory activity and the Q_{10} value of the respiration were higher in *S. polaris* than in the other two species. Total soil respiration rates measured in the field varied widely. The areas with dense vegetation cover tended to show high respiration rates. Belowground respiration of vascular plants was estimated based on the respiratory activity and biomass of the belowground parts at each study site. The contribution to the belowground respiration to total soil respiration was negligible in the early stages of succession. On the other hand, the respiration of the belowground parts contributed to a significant proportion (~29%) of the total soil respiration in the latter stages of succession.

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Introduction

Current global warming predictions indicate that warming will be more pronounced at high latitudes in the Northern Hemisphere (IPCC 1996). Northern ecosystems (arctic, boreal forests and northern bogs) are particularly sensitive to climatic change due to the large soil carbon pool and the predominance of permafrost (Oechel & Vourlitis 1994). Elevated temperature may increase the decomposition rate by stimulating soil microbial activity and by increasing soil active layer. Although, a number of studies recently have been carried out to predict the impact of climate change on the soil carbon flow in northern ecosystems (cf. Oechel & Vourlitis 1994), quantitative data of the soil carbon flow, especially for high arctic regions, is still limited.

In many of the studies on soil carbon flow, soil respiration has been used as an indicator of soil microbial activity and decomposition. However, in systems dominated by vascular plants, respiration of the belowground parts may contribute to a significant proportion of soil respiration. It has been reported that root respiration accounts for between 23 and 90% of the total soil respiration in forest ecosystems (Nakane et al. 1983; Ewel et al. 1987; Tate et al. 1993; Thierron & Laudelout 1996; Uchida et al. 1998), Belowground parts may compose more than 80% of the living biomass in tundra (Wielgolaski 1972). Billings et al. (1978) estimated that root and rhizome respiration contributed to 50 to 90% of the total soil respiration in an arctic meadow. Thus, in order to relate the soil respiration to the soil microbial activity, it is necessary to determine the contribution of the belowground parts to total soil respiration.

As a part of the soil carbon flow in different stages of primary succession in a deglaciated area in the high arctic zone, we aimed at estimating the contribution of the belowground parts of vascular plants to the total soil respiration. For this purpose, we measured (1) the respiration rates of

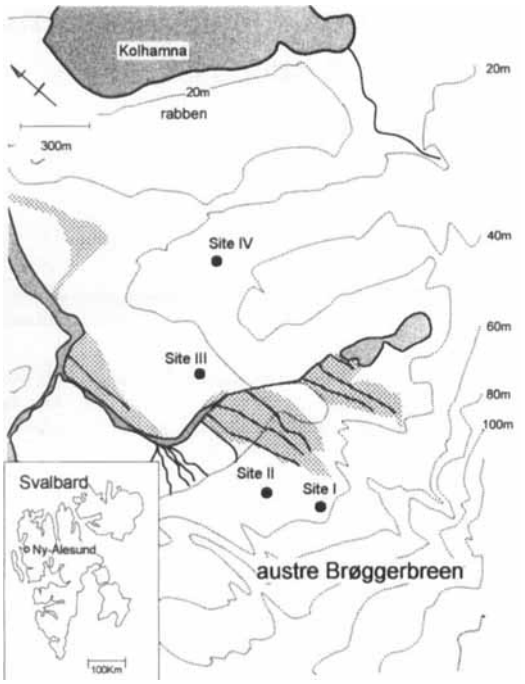

Fig. 1. Study sites in Ny-Ålesund, Svalbard.

belowground parts of dominant vascular plants, (2) the biomass of the belowground parts and (3) the total soil respiration rate in the field.

Materials and methods

Study sites

This study was carried out within the Japan–Norway cooperative study "Ecosystem Change at the Glacier-edge Areas in the Arctic". The glacier austre Brøggrebreen is located near Ny-Ålesund in the northwestern part of Spitsbergen, Svalbard (79°N), Norway. In 1994, four permanent plots (Sites I, II, III and IV) were set up along a primary successional series in the deglaciated area of austre Brøggrebreen. Some soil properties of these study sites are summarised in Table 1.

Site I was the youngest site situated on a newly deglaciated moraine. Only isolated small plants such as *Saxifraga oppositifolia* L. grew at this site. The coverage of vascular plants was very small (<1%), but black crusts of cyanobacteria and several species of bryophytes partially covered the ground (cf. Minami et al. 1996).

At Site II, small patches of vascular plants such as *Saxifraga oppositifolia*, *Poa alpina* L. and *Draba* spp. were found, though the coverage of the plants was still low (<10%).

Site III was characterised by a patterned ground composed of small polygons (Fig. 2). The diameter of each polygon ranged from about 50 to 100 cm. A mixed community of bryophytes and vascular plants (Mv) covered the marginal part of the polygons, whereas the central part consisted of almost bare ground (Bg). Black crust of cyanobacteria and lichens (Cl) covered the area between Mv and Bg. The percentage cover of Mv, Cl and Bg was 53, 30 and 17%, respectively.

Site IV was similar to Site III except that the black crust entirely covered the central part of the polygons. Relative coverage of Mv and Cl was 45 and 55%, respectively.

Belowground respiration

The respiratory activity of the belowground parts (roots + belowground stems) of the dominant three species, *Salix polaris* Walenb., *Saxifraga oppositifolia* and *Luzula confusa* (Hartm.) Lindeb., was determined in the laboratory at Ny-Ålesund. *S. polaris* is reported to be an ectomycorrhizal species while the other two species are non-mycorrhizal in Spitsbergen (Väre et al. 1992). Unless otherwise noted, these species will henceforth be referred to by their generic names. The plants were dug out with adhering soil and brought to the laboratory. After they were washed carefully to remove soil particles, the aboveground part was cut off. The sample, about 1–6 g in dry weight, was placed on a filter paper in a petri dish (Ø = 7 cm). The sample and the filter paper were wetted with water occasionally to prevent desiccation. Five replicate samples of each species were stored at temperatures of 6 ± 3°C until the respiration measurement. This temperature condition was similar to the soil temperature in the field.

The respiration rate of the belowground parts was measured using an open-flow gas exchange system with an infrared gas analyzer (IRGA) (LI-6252, LI-COR, NE, USA). A detailed description of this system appeared in Bekku et al. (1997). The IRGA was calibrated using a standard gas containing 431 ppm CO_2 (GL Sciences, Tokyo, Japan) and CO_2-free air prior to the measurement.

Table 1. Some soil properties of the study sites.

Site	Thickness of O horizon (cm)	C %*	N %*	C/N*	pH* (H_2O)	Soil water content** (%)
I	0	1.6	0.02	80	6.7	11
II	0	1.8	0.05	36	6.7	21
III	0–3	7.0	0.37	19	5.8	92
IV	1–3	14.5	0.83	17	5.7	130

* Average of 0–5 cm layer.
** (Fresh weight–Dry weight)/Dry weight; determined on 27–30 July 1996.

The petri dish with the sample was placed in a cylindrical chamber (Ø = 9 cm, h = 3.5 cm) connected with the system. Ambient air containing 347–350 ppm CO_2 was flowed into the system at the rate of 0.51 min^{-1}. During the measurement of the respiration, the chamber was placed in a portable refrigerator or a water bath to control the temperature conditions. The temperature in the chamber was monitored using a copper-constantan thermocouple. Unless otherwise noted, the temperature in the chamber was controlled at 8 ± 0.5°C.

In previous studies (e.g. Tate et al. 1993), it was reported that plant roots showed a high respiration rate immediately after the sampling. Therefore, we monitored the respiration rate at 1, 4, 7 and 9 days following the sample collection.

Temperature dependence of the respiration was also examined by changing the temperature from 2 to 12°C at every 3–4°C interval. About 4–6 hours were required to obtain the temperature-respiration curve of each sample. In some experiments, the temperature was again decreased from 12 to 2°C to determine whether a hysteresis occurred or not. Hysteresis was not observed in any of the cases.

After the respiration measurements, the samples were freeze-dried to calculate the dry weight.

Total soil respiration in the field

Five areas representing typical vegetation cover at each site were selected for the measurements of total soil respiration. The aboveground parts of vascular plants and the green bryophyte layer were cut off. Two or three days prior to the measurement, a cylindrical soil collar (Ø = 10.5 cm) was carefully driven into the soil at a depth of 1 cm in each area (cf. Fig. 2). The soil respiration chamber (LI-6000-09, LI-COR, NE, USA) was placed on the soil collar and the soil respiration rate was measured using a portable infrared gas analyzer (LI-6200, LI-COR, NE, USA). A detailed description of this system is given in Rochette et al. (1991, 1992).

In the previous year of this study (1995), seasonal variations of soil respiration rate were studied at the same sites as those in this study. However, no clear seasonal change of the rate was observed from early July to mid August (Fig. 3). In this study, therefore, the measurement of soil respiration was carried out in early August (3 August 1996).

After the measurement of soil respiration, the belowground parts within the soil collar were collected. They were separated into species and were freeze-dried to obtain the dry weight.

Results and discussion

Belowground respiration rate differences

Fig. 4 shows the changes in the respiratory activity of the belowground parts in *Salix*, *Saxifraga* and *Luzula* following sample collection. The respiration rate of *Salix* was highest immediately after sample collection, possibly due to injury by excision and disturbance. It then decreased rapidly and no significant change was observed 4 days after sample collection. Such changes were not apparent in the respiratory activity of *Saxifraga* and *Luzula*.

In this measurement, the aboveground parts were cut from the belowground parts, so no assimilates and no nutrients reached the belowground parts. Nevertheless, no apparent decline in

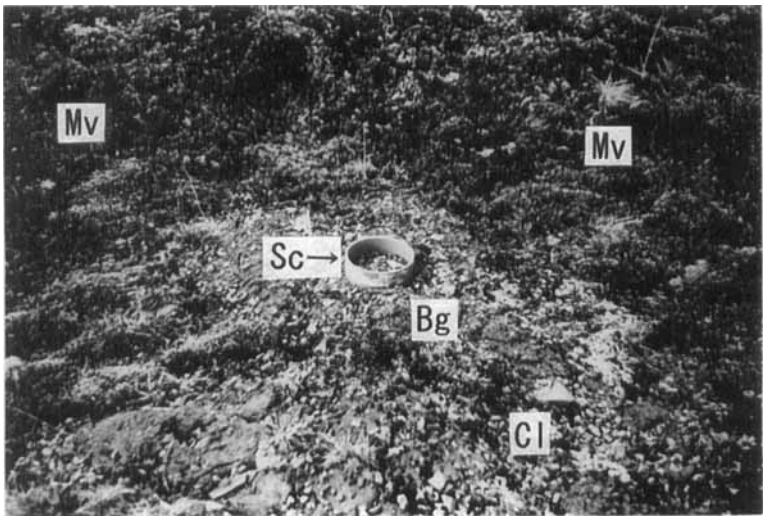

Fig. 2. Study site (Site III) on the old moraine in Ny-Ålesund, Svalbard. Bg = bare ground, Cl = crust of cyanobacteria and lichens, Mv = mixed community of bryophytes and vascular plants, Sc = soil collar used for soil respiration measurements (ϕ = 10.5 cm).

the respiration rate was observed at least from 4 to 9 days after sample collection. Moreover, the materials used in the measurements regenerated new organs (see below). These results agree with the previous reports that plant roots excised from main stem could survive and maintain their respiratory activity for more than 10 days (e.g. Tate et al. 1993; Uchida et al. 1998).

The respiratory activity in the stable phase (4–9 days) of *Salix* and *Saxifraga* was within the range of root respiration in arctic plants reported by Earnshaw (1981), though Skre (1975) reported much higher values for some tundra plants. However, in this study, the respiration rates differed widely between the species; the average respiration rate was much higher in *Salix* than in *Saxifraga* and *Luzula* (Table 2). This higher respiration rate in *Salix* may be partly due to its well-developed belowground stem. The belowground stem of *Salix* appeared to have a high activity; excised belowground stem of *Salix* could regenerate new leaves and roots within a week in the laboratory. On the other hand, regeneration of new organs from the belowground parts was much slower in the other species.

The Q_{10} values of the respiration obtained in this study (Table 2) were similar to those of many arctic plants so far reported (Skre 1975; Billings et al. 1978; Earnshaw 1981). However, as in the case of the respiration activity, the Q_{10} values differed significantly between the species in this study; *Salix* showed the largest Q_{10} value which reflects its high sensitivity to temperature.

Belowground respiration and soil respiration

The amount of biomass of the belowground parts of vascular plants was almost negligible in the earlier stages of succession (Sites I and II) (Table 3). There were several species of vascular plants such as *Saxifraga oppositifolia*, *Luzula confusa*, *Equisetum variegatum* Schleich. and *Oxyria digyna* (L.) Hill. in the latter stages of the succession (Sites III and IV). However, in most of the areas studied, *Salix polaris* predominated in the belowground biomass (Table 3).

Total soil respiration rates in the earlier stages of succession (Sites I and II) were usually lower than those in the latter stages (Sites III and IV). However, soil respiration rates comparable to those of the latter stages were detected in some areas (e.g. No. 7 at site II) (Table 3).

Average rate of total soil respiration was highest at Site III though the rate varied widely among the five areas studied. This large variation in the soil respiration rates was probably due to the heterogeneity of this site; the lowest rate ($12.8\ mgCO_2\ m^{-2}\ h^{-1}$) was observed in the central part of the polygon (No. 11), while high rates were restricted to the marginal parts of the polygons (Nos. 13 and 15) with a well-developed vegetation cover. Soil respiration rates in the areas

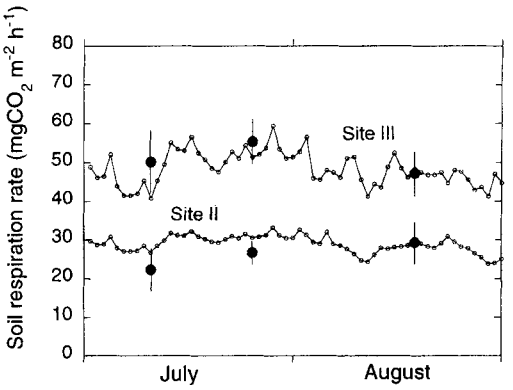

Fig. 3. Seasonal variations of soil respiration rate (SR) at Sites II and III in July and August 1995. Soil respiration rates were measured at the same study sites in the same manner as those in this study. Solid circles indicate the measured values (mean ± SD; n = 5). Open symbols show the rates estimated by the regression curves between SR and air temperature (AT) or soil temperature (ST). Site II: SR = 25.4 exp(0.0372*AT); Site III: SR = 37.2 exp(0.0624*ST).

Table 2. Respiration rates of the belowground parts (roots + belowground stems) and Q_{10} values of the respiration in the arctic plants.

Species	Respiration rate at 8°C* ($mgCO_2\ g^{-1}\ h^{-1}$)	Q_{10}** (5–12°C)
Salix polaris	0.175 (0.014)[a]	2.40 (0.05)[a]
Saxifraga oppositifolia	0.126 (0.039)[ab]	1.95 (0.25)[ab]
Luzula confusa	0.055 (0.015)[b]	1.65 (0.07)[b]

* Values indicate means of five samples with SE in parentheses.

** Values indicate means of three samples with SE in parentheses.

Means followed by the same letter within a column are not significantly different (Scheffe's test, $P > 0.05$).

covered with a black crust (Cl) gave intermediate values (Nos. 12 and 14).

At Site IV, areas Nos. 17 and 19 corresponded to the mixed community of bryophytes and vascular plants (Mv), and areas Nos. 16, 18 and 20 to the areas covered with a black crust (Cl). However, there was no distinct difference in the soil respiration rate between the two vegetation types (Mv and Cl). The range of total soil respiration was smaller at Site IV (33.6–47.4 $mgCO_2\ m^{-2}\ h^{-1}$) than at Site III (12.8–96.4 $mgCO_2\ m^{-2}\ h^{-1}$).

Because of the wide variation within each site, the difference in soil respiration rate between sites was not significant (ANOVA, $P > 0.05$). On the other hand, the effect of vegetation types on soil respiration rate was highly significant (ANOVA, $P < 0.001$).

The total soil respiration rates obtained in these study sites were much lower than those reported for Alaskan arctic tundra (Billings et al. 1978; Oberbauer et al. 1986). This is possibly because of the thin O horizon in these study sites (Table 1).

The respiration rates of the belowground parts of the vascular plants in the field were estimated based on the amount of biomass (Table 3) and respiration rate per dry weight (Table 2). The respiration rates were corrected for the field temperature using the Q_{10} value (Table 2). Since the amount of belowground biomass of each species other than *Salix* was small, the mean value of the respiration rates of *Saxifraga* and *Luzula* (0.091 $mgCO_2\ g^{-1}\ h^{-1}$) was used to calculate the rates for the other species. For these species, mean Q_{10} value of the two species (1.8) was also used to estimate the respiration rate at the field temperature.

The estimated belowground respiration rate was almost negligible in the earlier stages of succession as in the case of the amount of biomass of the belowground parts (Table 3). In the latter stages of succession, estimated respiration rates varied widely among the five areas at each study site. At Site III, the respiration rates of the belowground parts showed a close correlation with the vegetation cover; high rates were restricted to areas with a well-developed vegetation cover (Nos. 13 and 15). The correlation between the respiration rate and the vegetation cover was less distinct at Site IV.

It appeared that the large site-to-site variation in the amount of biomass and respiration rate was inevitable in such heterogeneous habitats as those at the study sites. However, since the sampling areas were selected with consideration for the relative abundance of the vegetation types, the mean value of the respiration rates in the five areas could be regarded as the representative value for each site. The mean values of the percentage contribution of the belowground parts to total soil respiration at Sites I, II, III and IV were 0, 0.1, 29.4 and 23.0%, respectively. The values in the latter stages of succession (Sites III and IV) were comparable to those reported for

Table 3. Biomass of the belowground parts, total soil respiration (R_{total}) and estimated belowground respiration of vascular plants (R_{root}) at the four study sites (3 Aug. 1996).

Site	No.	Vegetation* cover	Soil** temp. (°C)	Biomass ($g\ m^{-2}$)		Respiration ($mgCO_2\ m^{-2}\ h^{-1}$)		$R_{root}/R_{total} \times 100$ (%)
				Salix	others	R_{total}	R_{root}	
I	1	Bg	9.3	0.0	0.0	8.3	0.0	0.0
	2	Bg	9.7	0.0	0.0	19.5	0.0	0.0
	3	Bg	9.4	0.0	0.0	18.1	0.0	0.0
	4	Bg	10.1	0.0	0.0	31.6	0.0	0.0
	5	Bg	11.1	0.0	0.0	0.0	0.0	0.0
II	6	Bg	7.2	0.0	0.0	32.6	0.0	0.0
	7	Bg	8.2	0.0	2.8	41.9	0.3	0.6
	8	Bg	8.6	0.0	0.0	21.3	0.0	0.0
	9	Bg	8.1	0.0	0.0	7.6	0.0	0.0
	10	Bg	8.5	0.0	0.0	20.6	0.0	0.0
III	11	Bg	7.6	4.2	1.4	12.8	0.8	6.5
	12	Cl	7.3	0.0	22.3	54.8	2.0	3.6
	13	Mv	6.2	352.0	0.0	81.2	52.6	64.8
	14	Cl	7.6	22.3	12.6	39.5	4.9	12.4
	15	Mv	6.9	345.0	33.5	96.4	57.7	59.8
IV	16	Cl	7.4	72.6	18.2	47.4	13.7	28.8
	17	Mv	5.9	117.3	4.2	37.6	17.4	46.4
	18	Cl	7.4	0.0	5.6	33.6	0.5	1.5
	19	Mv	6.3	46.1	2.8	38.6	7.2	18.6
	20	Cl	6.9	41.9	14.0	39.8	7.9	19.7

* Bg; bare ground, Cl; crust of cyanobacteria and lichens. Mv; mixed community of bryophytes and vascular plants.
** Soil temperature at 1 cm depth.

grassland ecosystems (Gupta & Singh 1981; Buyanovsky et al. 1987).

The soil respiration rates and respiratory activity of the belowground parts may change seasonally. However, the results obtained indicated that belowground respiration of vascular plants can contribute significantly to the soil carbon flow even in the high arctic zone, presumably due to the significant belowground carbon allocation in these plants.

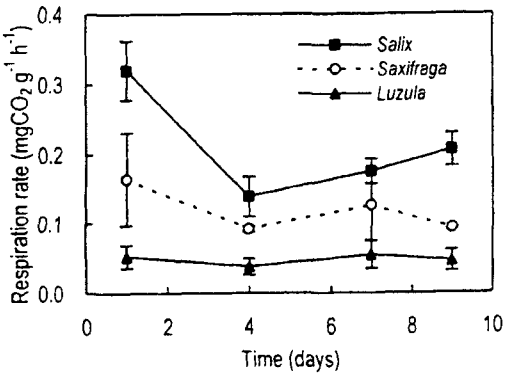

Fig. 4. Changes in the respiratory activity of the belowground parts of three arctic plants after sample collection. Temperature in the respiration chamber was controlled at 8 ± 0.5°C. Mean values of five samples are shown with SE.

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