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Scientific paper

Chemical property of live and dead leaves of tundra plant species in Oobloyah Valley, Ellesmere Island, high arctic Canada

Takashi Osono^{1*}, Akira Mori¹, Masaki Uchida^{2,3} and Hiroshi Kanda^{2,3}

 ¹Graduate School of Agriculture, Kyoto University, Kitashirakawa Oiwake, Sakyo-ku, Kyoto 606-8502
 ²National Institute of Polar Research, Kaga 1-chome, Itabashi-ku, Tokyo 173-8515
 ³Department of Polar Science, School of Multidisciplinary Sciences, The Graduate University for Advanced Studies (SOKENDAI), Kaga 1-chome, Itabashi-ku, Tokyo 173-8515
 *Corresponding author. E-mail: fujijun@kais.kyoto-u.ac.jp

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Abstract: The chemical property of live and dead leaves was investigated regarding 14 plant species, including shrubs, forbs, graminoids, and mosses. Leaves were collected from a deglaciated terrain in Ellesmere Island, high arctic Canada. The contents of organic chemical components (lignin, total carbohydrates, extractives), carbon, and nutrients (N, P, K, Ca, Mg) were examined and compared among the species. In general, forbs had high content of nutrients and low content of carbon and organic chemical components; shrubs had high content of carbon and lignin and low content of nutrients; graminoids had high content of total carbohydrates and low content of lignin and nutrients. Principal component analysis showed separation of clusters of shrubs, forbs, graminoids, and mosses. The trend was generally similar between live and dead leaves.

key words: glacier foreland, leaf, lignin, nitrogen, phosphorus

1. Introduction

The chemical property of leaves is an important aspect of leaf traits of plants; it represents the ecophysiological activity, nutritional status, and strategy for nutrient acquisition of plants, and the quality as food resources for herbivore animals and decomposer organisms (Chapin, 1989; Kudo, 1999; Aerts and Chapin, 2000; Berg and McClaugherty, 2003). Chemical properties of leaves thus provide basic information for the understanding of arctic ecosystems, where plant growth is strongly limited by such environmental factors as low temperature, low moisture, low nutrient availability, and a short growing season (Svoboda and Freedman, 1994). Chemical properties of leaves of arctic plants have been studied in relation to growth form, mycorrhizal status, seasonal changes, soil conditions, and climatic gradients (Skre *et al.*, 1975; Wielgolaski *et al.*, 1975; Maessen *et al.*, 1983; Nams and Freedman, 1987a; Woodley and Svoboda, 1994; Michelson *et al.*, 1996; Kudo *et al.*, 2001; Kume *et al.*, 2003). Few studies, however, have examined the contents of both organic chemical components and nu-

trients at the same time, and more studies are needed that compare the chemical properties across arctic plants of various growth forms.

The purpose of the present study was to investigate the chemical property of live and dead leaves of 14 plant species, including deciduous and evergreen shrubs, forbs, graminoids, and mosses, in Oobloyah Valley, Ellesmere Island, high arctic Canada. The study area was a well-vegetated proglacial field that can be divided into several habitats for plant exploitation based on soil moisture conditions and establishment periods after deglaciation. Plants of different growth forms, such as shrubs, forbs, graminoids, and mosses, were encountered along these gradients (Kojima, 1991, 1999; Okitsu *et al.*, 2004; Ueno and Kanda, unpublished data; Osono *et al.*, unpublished data). Leaves of these plants were collected, and contents of organic chemical components (lignin, total carbohydrates, extractives), carbon, and nutrients (N, P, K, Ca, Mg) were examined and compared among the species. Principal component analysis was used to ordinate the 14 plant species based on the chemical property of leaves, to examine the similarity of chemical property between species or growth forms.

2. Study area

The study was carried out in a deglaciated terrain in the southern front of Arklio Glacier of the Kreiger Mountains, located on the right bank of the Arklio River. The area is near the mouth of Oobloyah Valley, about 6 km east of Oobloyah Bay $(80^{\circ} 50'N, 82^{\circ} 45'W)$, Ellesmere Island, Nunavut, Canada. The area is rich in well-preserved moraines. No climate data are available in the study area, but the climate, as represented by the weather station at Eureka $(80^{\circ} 00'N, 85^{\circ} 56'W)$, located 130 km south of the study area, is extremely harsh. The annual mean temperature is -19.7° C, and the monthly mean temperature of the warmest (July) and coldest (February) months is 3.3° C and -38.0° C, respectively. Annual precipitation is 64 mm (Atmospheric Environmental Service, 1982; after Kojima, 1994).

Arklio Glacier has developed at least five glacial moraines (moraines in relative ages of 1, 2, 3, 4, and 5) with different development periods since the Last Glacial (Hasegawa *et al.*, 2004; Fig. 1). Relative ages of the moraines were estimated based on geomorphological observations, and relative dating was estimated by means of weathering rind thickness and lichenometry (Hasegawa *et al.*, 2004; Okitsu *et al.*, 2004). Moraines located just below Arklio Glacier consist of fresh, sharp ridges that apparently originated during the Little Ice Age, whereas moraines located in the outermost part of the study area, which has a fairly gentle slope, have had their morphology modified by cryogenic processes. Moraines of intermediate ages lie between the "Little Ice Age" moraines and the outermost moraines, and still show clear moraine morphology.

Okitsu *et al.* (2004) reported the vegetation development on the upper parts of moraines. The "Little Ice Age" moraines were covered thoroughly with fresh, sharpedged rocks, and the colonization of vascular plants, mosses, and lichens is very limited, with plant coverage of less than 1% of the surface. The plant cover was higher in the older moraines, and increased to 61% in the outermost moraines. The dominant vascular species on these moraines included *Salix arctica*, *Dryas integlifolia*, and *Cassiope tetragona*. Two mosses: *Racomitrium lanuginosum* and *Hylocomium splendens*, were

also dominant on these moraines (Ueno and Kanda, unpublished data). The vegetation that is developed in the study area is similar to the *Cassiope*-dominated dwarf shrub heath in the low arctic, according to Okitsu *et al.* (2004). This vegetation type is relatively uncommon in the high arctic, which is generally represented by polar desert with sporadic occurrence of vascular plants (Nams and Freedman, 1987b), and it is commonly called a "polar oasis" (Svoboda and Freedman, 1994).

In the study area, mesic habitats were distinguishable on depressions between some moraines (Fig. 1) that were characterized by higher accumulation of deposited till and deeper soil depth, and by higher coverage and a higher number of vascular plant species than xeric habitats on the upper parts of moraines (Osono *et al.*, unpublished data). Soil moisture contents in mesic habitats were consistently higher than in xeric habitats, despite the increase of soil moisture contents in xeric habitats in relation to the developmental periods (Osono *et al.*, unpublished data). The dominant species in mesic habitats include not only shrubs: *S. arctica, D. integlifolia,* and *C. tetragona*, but also forbs, such as *Oxyria digyna, Pedicularis lanata*, and *Polygonum viviparum*; graminoids, such as *Carex* spp. and *Arctagrostis lactifolia*, and mosses, such as *H. splendens* (Ueno and Kanda, unpublished data; Osono *et al.*, unpublished data). Relative ages of mesic habitats can be estimated with reference to the relative ages of nearby moraines, unless the local topography was modified by glacio-fluvial activities (Hasegawa *et al.*, 2004).

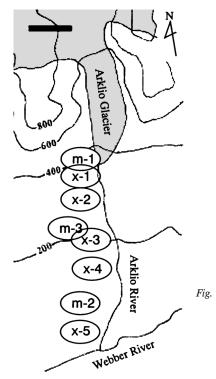


Fig. 1. Schematic representation of the distribution of eight habitats with different moisture conditions and development periods. x-1 and m-3, for example, indicate xeric habitat in relative age 1 and mesic habitat in relative age 3, respectively. Circles show the approximate area of sample collection. The bar indicates 1 km.

3. Materials and methods

3.1. Collection of leaves

In the study area, eight habitats were distinguished with difference in soil moisture conditions and relative ages: five xeric habitats on the upper parts of moraines in relative ages of 1, 2, 3, 4, and 5, and three mesic habitats on depressions in relative ages of 1, 2, and 3 (Fig. 1). Geomorphological observations suggested that the area between moraines in relative ages of 4 and 5 on the right bank of the present Arklio River was the former outwash plain of the Arklio River and corresponded to relative age 2 (Hasegawa *et al.*, 2004).

In July 2003 and July 2004, we collected live and dead leaves of 14 plant species, including four species of shrubs, four of forbs, four of graminoids, and two of mosses (Table 1). These species were dominant species in the study area (Okitsu *et al.*, 2004; Ueno and Kanda, unpublished data; Osono *et al.*, unpublished data). Leaves were collected in five xeric and three mesic habitats where the species were frequently encountered according to Table 1. *Carex* spp. included several species, such as *C. misandra*, *C. stans*, *C. nardina*, and *C. atrofusca*, but they were not distinguished from each other in this study. Live leaves and attached dead leaves were collected from five well-established individuals of shrub, forb, and graminoid. In mosses, live, senescent, and dead parts are usually difficult to distinguish or determine, and they are generally referred to as green, yellow, and brown parts, according to color (Nakatsubo, 1990). Green parts on the surface of a colony, and brown parts beneath yellow parts of mosses, were thus collected from five well-developed colonies of moss. These green and brown parts of mosses are are are are usually developed colonies of moss. These green and brown parts of mosses were air-dried in the study site and were taken back to the laboratory in Japan within

					Mesic	Number of			
Species	1	2	3	4	5	1	2	3	samples
Shrubs									
Salix arctica	0	0	0	0	0	0	0	0	8
Vaccinium uliginosum	-	-	0	0	0	-	-	-	3
Dryas integlifolia	0	0	0	0	0	-	-	-	5
Cassiope tetragona	-	0	0	0	0	-	-	-	4
Forbs									
Papaver lapponicum	0	0	0	0	0	0	0	0	8
Epilobium latifolium	0	-	-	-	-	0	-	-	2
Oxyria digyna	-	-	-	-	-	-	0	0	2
Polygonum viviparum	-	-	-	-	-	-	0	0	2
Graminoids									
Carex spp.	-	0	0	0	-	-	0	0	5
Luzula confusa	-	-	0	-	0	-	-	0	3
Arctagrostis lactifolia	-	-	-	-	0	-	0	0	3
Alopecurus alpinus		-	-	-	-	-	-	0	1
Mosses									
Racomitrium lanuginosum	-	0	0	0	0	-	-	-	4
Hylocomium splendens	-	-	-	-	-	-	-	0	1

Table 1. Plant species and material studied.

one month after collection.

3.2. Chemical analyses

The leaves from five individuals of a single species in each habitat were combined to make one sample. The leaves were then oven-dried at 40°C for one week, followed by grinding in a laboratory mill, to make particles that would pass through a 0.5-mm screen. Lignin and extractive contents were measured by sulfuric acid digestion and alcohol-benzene extraction, respectively (King and Heath, 1967). Total carbohydrate content was measured by a phenol-sulfuric acid method (Dubois *et al.*, 1956). Total C and total N contents were measured by automatic gas chromatography (NC analyzer SUMIGRAPH NC-900, Sumitomo Chemical Co., Osaka, Japan). After acid wet oxidation in HNO₃+HClO, an ascorbic acid method was performed for P (Olsen and Sommers, 1982); flame photometry was performed for K, and atomic absorption was performed for Ca and Mg. Details of the methods were described by Osono and Takeda (2004a, b, 2005). The contents were expressed in percentage (w/w). The original data of live and dead leaves are listed in Appendices 1 and 2, respectively.

No "true" lignin has been found in moss, but other phenolic cell wall material has been found (Erickson and Miksche, 1974). For the purpose of the present study, however, the term sulfuric acid-insoluble lignin is used for "lignin-like substances" of moss, even if not fully correct.

3.3. Statistical analysis

Principal component analysis was used to ordinate the plant species based on chemical property (contents of lignin, total carbohydrates, extractives, C, N, P, K, Ca, and Mg) of live and dead leaves (Systat, 1992).

4. Results

4.1. Chemical property of leaves

Figure 2 shows the chemical property of live and dead leaves of 14 plant species. Lignin content in live and dead leaves was higher in shrubs and *Polygonum viviparum* than in the other forbs, graminoids, and mosses. The total carbohydrate content in live and dead leaves was higher in graminoids and mosses than in shrubs and forbs. Extractives content in live leaves was highest in *Dryas integlifolia* and *Cassiope tetragona*, whereas the difference was small in dead leaves. The C content in live and dead leaves was similar among species, but *O. digyna* had lower content. Nitrogen and phosphorus contents in live leaves were lowest in *C. tetragona* and mosses, whereas the differences were small in dead leaves. The K content in live leaves was highest in *O. digyna* and lowest in *C. tetragona* and mosses but the difference was small in dead leaves. The Ca content in live and dead leaves was higher in some forbs than in the other species. The Mg content in live leaves was also higher in *O. digyna* and *P. viviparum* than in the other forbs, shrubs, graminoids, and mosses, whereas the difference was small in dead leaves.

4.2. Principal component analysis

Principal component (PC) analysis was used to ordinate these species based on

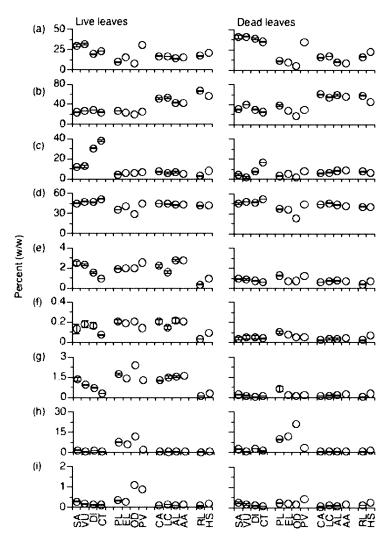


Fig. 2. Chemical property of leaves. ○live leaves, ●dead leaves. Values indicate means±se in% (w/w).
(a) lignin, (b) total carbohydrates, (c) extractives, (d) carbon, (e) nitrogen, (f) phosphorus, (g) potassium, (h) calcium, (i) magnesium. SA Salix arctica, VU Vaccinium uliginosum, DI Dryas integlifolia, CT Cassiope tetragona, PL Papaver lapponicum, EL Epilobium latifolium, OD Oxyria digyna, PV Polygonum viviparum, CA Carex spp., LC Luzula confusa, AL Arctagrostis lactifolia, AA Alopecurus alpinus, RL Racomitrium lanuginosum, HS Hylocomium splendens.

chemical properties (Fig. 3). The first two principal components accounted for 70% (live leaves) and 66% (dead leaves) of the total variance in the data (Table 2).

In live leaves, the first principal component (PC1) accounted for 49% of the total variance, and it was significantly positively correlated with N, P, K, Ca, and Mg contents, and significantly negatively correlated with lignin and C contents. PC2 accounted for 21% of the total variance, and it was significantly positively correlated with lignin and N contents, and significantly negatively correlated with total carbohydrate

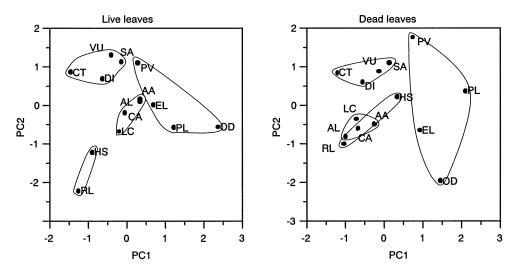


Fig. 3. Scatter plot of PC1 and PC2 of live and dead leaves. Abbreviations are the same as in Fig. 2.

Table 2.	Result of the principal component analysis on leaf properties of 14 plant species.
	***P < 0.001, **P < 0.01, *P < 0.05.

	Loading								
	Live 1	eaves	Dead	leaves					
Variable	PC1	PC2	PC1	PC2					
Lignin	-0.54 *	0.62 *	-0.27	0.84 ***					
Total carbohydrates	-0.45	-0.73 **	-0.53	-0.27					
Extractives	-0.50	0.49	-0.61 *	0.21					
Carbon	-0.83 ***	0.51	-0.70 **	0.66 **					
Nitrogen	0.56 *	0.60 *	0.68 **	0.60 *					
Phosphorus	0.75 **	0.30	0.82 ***	0.22					
Potassium	0.94 ***	0.15	0.70 **	0.15					
Calcium	0.84 ***	-0.13	0.76 **	-0.45					
Magnesium	0.70 **	0.11	0.66 *	0.48					
Proportion (%)	48.8	21.2	42.7	23.7					

contents. In dead leaves, PC1 accounted for 43% of the total variance, and it was significantly positively correlated with N, P, K, Ca, and Mg contents, and significantly negatively correlated with extractives and C contents. PC2 accounted for 24% of the total variance and was significantly positively correlated with lignin, C, and N contents.

Scatter plots of PC1 and PC2 of live and dead leaves showed clusters of different growth forms (Fig. 3). In live leaves, PC1 separated forbs from graminoids, shrubs, and mosses, and further graminoids from mosses; and PC2 separated shrubs, graminoids, and mosses from each other, and forbs from mosses. In dead leaves, PC1 separated forbs from shrubs, graminoids, and mosses; and PC2 separated shrubs from graminoids and mosses.

5. Discussion

This study showed the chemical property of live and dead leaves of 14 plant species, which were markedly different between growth forms. PC1 positively correlated with inorganic nutrients, and negatively with C and organic chemical components; it separated forbs rich in nutrients and poor in C and organic chemical components, from shrubs, graminoids, and mosses. PC2 positively correlated with lignin, C, and N, and negatively with total carbohydrates; it separated shrubs rich in lignin and poor in total carbohydrates, from graminoids poor in lignin and mosses rich in total carbohydrates. These differences among growth forms were consistent with previous reports on the chemical property of arctic plant leaves (Wielgolaski et al., 1975; Maessen et al., 1983). The levels of N, K, and Mg contents at the study area were similar to those reported by Maessen et al. (1983) from an Alexandra Fjord lowland oasis approx. 200 km south east of Oobloyah Bay, but live and dead leaves of forbs had half the content of P and a tenfold higher content of Ca compared with the findings of Maessen et al. (1983). The reason for the difference is unclear but may be attributable to the difference in geological situations between the locations. Besides, the present study showed not only nutrient contents but contents of organic chemical components in both vascular plants and mosses. Our data indicated that Polygonum viviparum was similar to deciduous shrubs in terms of organic chemical composition of live and dead leaves, and that graminoids and mosses were similar in terms of low nutrient content and intermediate lignin content of dead leaves.

The effect of soil moisture condition and establishment periods after deglaciation on the chemical property of plant leaves was not determined in the present study, but generally the effect seems smaller than the difference between growth forms. In *S. arctica*, however, the contents of N and P are generally higher in live and dead leaves from mesic habitats compared with leaves from xeric habitats (Appendices 1 and 2). In fact, some previous studies indicated the effect of soil moisture condition on the chemical property of plant leaves within individual species (Karlsson, 1985; Woodley and Svoboda, 1994) and changes in chemical property in the course of primary succession (Matthews, 1992). Further studies are thus needed on the effects of soil moisture conditions and establishment periods after deglaciation on the chemical property of leaves and the related implications for development in the high arctic ecosystem.

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Species	Growth	Moisture	Relative	Lignin	Total	Extrac-	· C	N	Р	K	Са	Mg
~P*****	form	condition	age	2.5	carbo-	tives	e	1.	-		- Cu	
			8-		hydrates							
Salix arctica	S	х	1	27.9	24.4	12.1	43.6	2.09	0.080	1.91	2.16	0.270
Salix arctica	S	x	2	32.6	25.9	11.5	46.2	2.20	0.049	1.07	1.21	0.257
Salix arctica	S	х	3	32.4	23.2	13.5	46.1	2.03	0.044	1.01	1.57	0.254
Salix arctica	S	х	4	32.9	23.4	11.2	45.9	2.10	0.038	1.08	1.51	0.304
Salix arctica	S	х	5	34.7	22.9	11.2	46.1	2.04	0.035	1.04	1.45	0.245
Salix arctica	S	m	1	23.6	27.3	11.1	44.5	3.26	0.324	1.56	1.77	0.350
Salix arctica	S	m	2	28.3	24.7	12.1	44.6	2.54	0.186	1.49	1.90	0.221
Salix arctica	S	m	3	26.1	22.6	10.8	44.2	3.31	0.317	1.61	1.48	0.356
Vaccinium uliginosum	S	х	3	33.5	27.2	9.4	46.6	2.45	0.256	0.97	0.63	0.165
Vaccinium uliginosum	S	х	4	31.1	27.9	14.6	47.3	2.10	0.137	1.02	0.67	0.122
Vaccinium uliginosum	S	x	5	31.0	26.2	13.5	48.9	2.35	0.161	0.90	0.69	0.195
Dryas integlifolia	ŝ	x	1	18.5	29.8	32.7	46.0	1.37	0.287	0.83	1.56	0.123
Dryas integlifolia	ŝ	x	2	20.7	27.0	29.2	46.9	1.57	0.146	0.71	1.76	0.124
Dryas integlifolia	ŝ	x	3	21.1	26.8	31.1	47.0	1.77	0.154	0.71	1.48	0.117
Dryas integlifolia	ŝ	x	4	17.9	30.7	30.5	47.6	1.28	0.118	0.65	1.61	0.086
Dryas integlifolia	Š	x	5	19.0	28.3	29.3	46.9	1.49	0.128	0.72	1.59	0.111
Cassiope tetragona	Š	x	2	23.5	24.6	38.5	50.3	0.95	0.090	0.31	0.74	0.114
Cassiope tetragona	s	x	3	23.8	25.8	36.8	51.5	0.89	0.073	0.36	0.59	0.105
Cassiope tetragona	s	x	4	22.5	22.6	39.0	51.6	0.94	0.066	0.31	0.83	0.099
Cassiope tetragona	ŝ	x	5	22.9	21.8	38.4	52.4	0.90	0.069	0.31	0.91	0.115
Papaver lapponicum	F	x	1	10.1	28.0	3.2	34.7	1.60	0.191	1.49	8.62	0.358
Papaver lapponicum	F	x	2	10.1	23.0	5.8	35.5	2.03	0.212	1.93	7.04	0.299
Papaver lapponicum	F	X	3	9.1	26.5	4.2	35.5	2.05	0.212	1.77	6.63	0.396
Papaver lapponicum	F	x	4	10.6	26.4	6.8	36.2	1.98	0.204	1.92	6.60	0.242
Papaver lapponicum	F	X	5	10.0	28.2	1.5	37.3	1.95	0.244	1.88	6.43	0.326
Papaver lapponicum	F	m	1	9.6	30.1	4.1	35.4	1.84	0.164	1.81	6.94	0.278
Papaver lapponicum	F	m	2	6.0	24.5	6.0	33.9	1.93	0.172		10.21	0.418
Papaver lapponicum	F	m	3	8.6	26.0	4.7	36.6	1.75	0.190	1.53	8.22	0.379
Epilobium latifolium	F	x	1	16.2	20.0	5.2	41.1	1.94	0.206	1.53	4.68	0.239
Epilobium latifolium	F	m	1	13.9	24.0	6.0	39.9	2.04	0.173	1.34	6.96	0.239
Oxyria digyna	F	m	2	7.1	18.2	6.4	27.4	1.79	0.263		12.70	1.128
Oxyria digyna Oxyria digyna	F	m	3	8.8	21.5	5.4	31.5	2.13	0.159		10.65	1.091
Polygonum viviparum	F	m	2	32.0	26.1	6.5	45.2	2.58	0.139	1.34	1.69	0.710
Polygonum viviparum	F	m	3	28.7	24.2	7.0	43.3	2.38	0.154	1.19	2.98	1.042
Carex spp.	G	x	2	15.9	51.0	8.4	43.4	1.87	0.127	1.19	0.46	0.070
Carex spp.	G	x	3	15.3	49.8	7.4	44.4	2.37	0.201	1.27	0.56	0.083
Carex spp.	G	x	4	15.5	56.5	6.1	44.5	2.02	0.201	1.27	0.50	0.081
Carex spp.	G	m	2	18.1	50.5	6.8	44.7	2.02	0.191	1.21	0.40	0.073
Carex spp.	G	m	3	18.7	49.6	7.6	45.3	2.57	0.280	1.37	0.26	0.088
Luzula confusa	G	x	3	16.3	55.6	3.8	44.0	1.75	0.128	1.69	0.46	0.141
Luzula confusa	G	X	5	16.4	49.5	5.6 7.6	44.8	1.51	0.126	1.40	0.50	0.141
Luzula confusa	G	m	3	16.5	53.0	6.4	43.3	1.46	0.130	1.40	0.30	0.131
Arctagrostis lactifolia	G	x	5	12.8	46.1	7.9	43.9	2.84	0.227	1.64	0.56	0.077
Arctagrostis lactifolia	G	m	2	12.8	40.1	7.4	41.9	2.64	0.227	1.41	0.76	0.077
Arctagrostis lactifolia	G	m	3	12.0	41.9	5.5	43.3	2.30	0.263	1.63	0.76	0.113
Alopecurus alpinus	G	m	3	15.5	41.0	5.5 5.4	43.0	2.79	0.203	1.63	0.55	0.115
			2	13.7	42.8 65.3	3.4 2.9	40.5	0.30	0.210	0.09	0.34	0.061
Racomitrium lanuginosum		X	3	18.8	65.5 68.7	2.9 3.8	40.5	0.30	0.032	0.09	0.24	0.061
Racomitrium lanuginosum		X	3 4				42.1	0.41	0.037	0.09	0.58	0.070
Racomitrium lanuginosum		x		15.6	67.2	2.7						
Racomitrium lanuginosum		x	5 3	16.9	66.1	2.9	42.5	0.34	0.032	0.10	0.28	0.065
Hylocomium splendens	M orb G gr	m minoid M	moss	21.1	56.8	8.1	42.0	0.89	0.095	0.33	0.86	0.157

Appendix 1. Chemical property of live leaves. Values in % (w/w).

Growth form: S shrub, F forb, G graminoid, M moss. Moisture: x xeric, m mesic.

Species	Growth	Moisture	Relative	Lignin	Total	Extra		Ν	Р	K	Са	Mg
	form	condition	age		carbo-	tives	5					
					hydrates							
Salix arctica	S	х	1	40.2	30.9	6.5	44.6	0.92	0.055	0.33	2.62	0.138
Salix arctica	S	х	2	43.5	29.3	6.8	46.8	0.95	0.021	0.26	1.69	0.172
Salix arctica	S	х	3	44.9	29.8	5.3	46.5	0.81	0.009	0.12	1.99	0.143
Salix arctica	S	х	4	42.9	30.1	5.2	46.2	0.82	0.009	0.24	2.17	0.167
Salix arctica	S	х	5	42.6	25.6	5.5	45.8	0.82	0.009	0.26	2.40	0.215
Salix arctica	S	m	1	28.2	34.0	2.3	36.7	0.87	0.079	0.26	2.88	0.533
Salix arctica	S	m	2	41.6	34.7	1.3	46.8	1.24	0.055	0.11	2.93	0.187
Salix arctica	S	m	3	44.3	33.8	3.0	45.5	1.15	0.101	0.13	2.33	0.361
Vaccinium uliginosum	S	х	3	41.0	39.2	2.2	47.7	0.94	0.094	0.19	0.68	0.153
Vaccinium uliginosum	S	х	4	43.2	40.8	0.5	47.2	0.99	0.036	0.10	1.07	0.112
Vaccinium uliginosum	S	х	5	40.0	39.6	2.8	47.4	0.75	0.037	0.09	1.00	0.204
Dryas integlifolia	S	х	1	36.3	30.5	7.6	44.7	0.69	0.125	0.07	2.74	0.133
Dryas integlifolia	S	Х	2	40.1	30.0	8.4	48.0	0.79	0.034	0.04	2.49	0.096
Dryas integlifolia	S	х	3	41.5	29.5	7.6	47.8	0.79	0.032	0.05	2.28	0.077
Dryas integlifolia	S	х	4	38.6	29.0	7.9	46.7	0.67	0.034	0.07	2.85	0.072
Dryas integlifolia	S	х	5	37.8	32.6	7.6	47.7	0.78	0.038	0.07	2.55	0.091
Cassiope tetragona	S	х	2	35.6	25.6	16.8	52.6	0.65	0.050	0.09	1.15	0.071
Cassiope tetragona	S	х	3	35.5	24.9	17.2	52.7	0.65	0.047	0.10	0.80	0.078
Cassiope tetragona	S	х	4	34.7	24.2	17.0	51.3	0.63	0.039	0.09	1.23	0.076
Cassiope tetragona	S	х	5	34.0	26.2	16.0	50.5	0.61	0.041	0.10	1.36	0.074
Papaver lapponicum	F	х	1	13.3	42.2	1.7	36.7	1.13	0.078	1.01	9.75	0.204
Papaver lapponicum	F	х	2	14.0	43.0	1.3	38.7	1.37	0.123	0.35	9.20	0.148
Papaver lapponicum	F	х	3	13.7	35.2	2.9	38.3	1.69	0.183	1.04	9.80	0.194
Papaver lapponicum	F	х	4	11.1	40.8	2.2	38.6	1.21	0.102	1.55	9.10	0.126
Papaver lapponicum	F	х	5	9.4	36.9	6.4	37.2	1.20	0.123	0.39	10.96	0.153
Papaver lapponicum	F	m	1	11.7	38.6	2.6	35.9	1.11	0.068	0.38	6.09	0.316
Papaver lapponicum	F	m	2	7.2	31.7	4.1	34.3	1.13	0.091	0.19	11.15	0.339
Papaver lapponicum	F	m	3	8.6	34.3	5.1	35.9	1.30	0.086	0.23	10.78	0.266
Epilobium latifolium	F	х	1	10.9	29.9	6.2	39.1	0.74	0.073	0.20	8.69	0.158
Epilobium latifolium	F	m	1	8.2	25.0	4.8	33.9	0.69	0.085	0.19	14.85	0.269
Ôxyria digyna	F	m	2	4.2	16.1	2.3	23.3	0.70	0.056	0.13	20.86	0.183
Oxyria digyna	F	m	3	5.7	17.0	1.8	22.7	0.78	0.048	0.13	20.71	0.154
Polygonum viviparum	F	m	2	35.3	28.6	8.3	44.4	1.33	0.050	0.26	2.70	0.382
Polygonum viviparum	F	m	3	34.4	29.5	7.2	43.2	1.19	0.066	0.12	3.99	0.410
Carex spp.	G	X	2	16.2	60.7	4.8	44.3	0.58	0.019	0.09	0.51	0.038
Carex spp.	Ğ	x	3	14.7	60.3	6.5	43.9	0.70	0.032	0.19	0.69	0.038
Carex spp.	Ğ	x	4	14.8	59.4	5.0	44.0	0.59	0.023	0.12	0.75	0.036
Carex spp.	Ğ	m	2	15.4	63.0	7.6	44.6	0.53	0.023	0.13	0.80	0.040
Carex spp.	Ğ	m	3	17.0	57.4	7.1	44.5	0.60	0.046	0.12	0.58	0.066
Luzula confusa	G	x	3	16.9	55.3	5.8	46.6	0.80	0.035	0.17	0.65	0.084
Luzula confusa	G	X	5	16.9	53.2	7.2	45.2	0.64	0.028	0.08	0.69	0.068
Luzula confusa	G	m	3	16.7	54.9	6.9	44.9	0.70	0.020	0.17	0.55	0.120
Arctagrostis lactifolia	G	x	5	9.1	59.8	8.5	43.1	0.70	0.031	0.17	0.55	0.120
Arctagrostis lactifolia	G	m	2	9.1	61.9	8.3 8.4	42.9	0.65	0.042	0.22	0.95	0.059
Arctagrostis lactifolia	G	m	3	10.2	56.5	8.8	44.1	0.87	0.020	0.11	0.95	0.002
Alopecurus alpinus	G	m	3	8.6	55.3	8.7	44.1	0.87	0.055	0.18	0.82	0.121
	M		2	8.0 16.4	55.5 59.3	8.7 8.5	41.1 39.9	0.71	0.031	0.26	0.82	0.139
Racomitrium lanuginosum	M M	X	3	16.4	59.5 60.2	8.5 9.0	39.9 40.7	0.40	0.026	0.07	0.60	0.102
Racomitrium lanuginosum		X										
Racomitrium lanuginosum	M	x	4	16.0	55.6	7.1	39.3	0.42	0.033	0.09	1.00	0.149
Racomitrium lanuginosum	M	X	5	17.5	55.9	6.8	41.7	0.41	0.028	0.06	0.63	0.111
Hylocomium splendens	M Arb C are	m minoid M	3	22.7	45.3	6.5	39.8	0.70	0.076	0.28	1.28	0.249

Appendix 2. Chemical property of dead leaves. Values in % (w/w).

Growth form: S shrub, F forb, G graminoid, M moss. Moisture: x xeric, m mesic.