American Journal of Botany 91(3): 422–429. 2004.

Caribou-induced changes in species dominance of lichen woodlands: an analysis of plant remains[1]

Stéphane Boudreau and Serge Payette[2]

Centre d'études nordiques and Département de biologie, Université Laval, Québec City, Canada, G1K 7P4

Plant communities in northern Quebec-Labrador, Canada have been severely grazed and trampled since the early 1980s by the increasingly large George River caribou herd (GRCH). To evaluate changes in species dominance associated with caribou disturbance, we compared past and present ground vegetation from 14 lichen woodlands. Plant remains from superficial organic horizons indicate that ground vegetation was largely dominated by lichens (especially *Cladina*) before the onset of caribou disturbance. In enlargments of aerial photos taken before 1975 (i.e., prior to maximum size of the GRCH), all sites were free of caribou trails and were dominated by a continuous lichen (*Cladina*) carpet. Principal components analysis showed that partial or complete destruction of the *Cladina*-dominated lichen carpet was the most striking change in ground vegetation. Severe trampling degraded superficial organic horizons, subsequently exposing mineral soil in heavily used sites. With reduced caribou activity in the 1990s, exposed ground was colonized by crustose lichens and *Cladonia*. Sites that faced severe grazing but light trampling were recolonized mainly by small podetia of *Cladina stellaris* sprouting from the lichen litter. However, patterns of post-caribou disturbance lichen succession differed from those of post-fire succession, because species from different successional stages are present at the same time in a stand and also because caribou can modify the successional trajectory at any time.

Key words: aerial photos; caribou disturbance; *Cladina*; George River caribou herd; grazing; lichen succession; plant remains; trampling.

Through selective grazing, herbivores are one of the most important factors shaping plant communities in tropical as well as in temperate and cold regions (McNaughton, 1983; Oksanen and Oksanen, 1989; Oksanen and Virtanen, 1995; Oksanen et al., 1995; Augustine and McNaughton, 1998; Suominen and Olofsson, 2000). Species composition, biomass, and plant architecture are among the main components of plant communities that can be affected by herbivory (McNaughton, 1984). Although of significance in several instances, herbivore trampling has received much less attention. Trampling from large herds of migratory caribou seems to be a major disturbance factor in the Arctic and the Subarctic. Indeed, lichen woodlands, a dominant vegetation type of the boreal forest (Kershaw, 1978), are particularly vulnerable to such disturbance (Ukkola, 1995). Repeated use of the same path by caribou results in trail formation as trampling rapidly destroys the lichen carpet. When trampling and grazing effects are combined, thick lichen carpets may disappear almost completely in a relatively short period (Morneau and Payette, 1998).

The George River caribou herd (GRCH) experienced a rapid demographic growth between the early 1960s and the mid-1980s (Messier et al., 1988), when it reached a relative stability at approximately 700 000 individuals (Couturier et al., 1996) before declining during the 1990s (Boudreau et al., 2003). With the increasing number of caribou in the summer habitat of the GRCH, lichen woodlands faced sustained herbivore pressure. Extensive surveys of the summer habitat of the GRCH indicated that all lichen woodlands showed signs of caribou disturbance as revealed by dense trail networks and degradation of the lichen carpet (Fig. 1a, b, c).

Fruticose lichens are vulnerable to destruction by trampling during dry periods (Pegau, 1970; Bayley, 1976; Oksanen, 1978; Bayfield et al., 1981; Haapasaari, 1988; Biermann and Daniels, 1997). Recovery of damaged ground vegetation from caribou disturbance may be a slow process (Haapasaari, 1988) because the growth rate of the dominant lichen species (mostly *Cladina* spp.) is very low, i.e., 3–6 mm/yr (Scotter, 1963; Pegau, 1968; Ouzilleau and Payette, 1975).

Several studies on the impact of caribou on vegetation have compared sites with different herbivory histories: ungrazed vs. grazed sites (Moser et al., 1979; Klein, 1987; Henry and Gunn, 1991; Manseau et al., 1996) and exclosure sites vs. grazed sites (Ouellet et al., 1993; Väre et al., 1995, 1996). Such studies provide useful information on plant–caribou relationships but some limitations are apparent. Comparisons between ungrazed and grazed sites are based on the assumption that vegetation composition of the sites being compared was initially the same, an assumption generally difficult to assess. Such comparisons can be misleading when trying to identify vegetation change through time.

Exclosure studies are the best way to evaluate change in vegetation composition (or recovery patterns) associated with herbivore removal (Watkinson et al., 2001). However, processes involved in vegetation degradation caused by herbivores cannot be studied directly using this approach. Furthermore, exclosure studies may not be ideal when working with slow-growing species like lichens. A more straightforward approach to identify changes in species dominance is to use vegetation composition of the same site at two different periods, before and after herbivore disturbance.

[1] Manuscript received 5 June 2003; revision accepted 30 October 2003.

The authors thank Hydro-Québec, the Natural Sciences and Engineering Research Council of Canada (NSERC), and the Department of Indian and Northern Affairs for financial support. S. Boudreau received scholarships from the Fonds pour la Formation de Chercheurs et l'Aide à la Recherche (Fonds FCAR) and the Association of the Canadian Universities for Northern Studies (ACUNS). The authors acknowledge the assistance of C. Morneau, S. Desaulniers, C. Lambert, M. Longchamps, P. Morin, and J. Théau in the field and the laboratory, and the statistical advice of G. Houle and H. Crépeau. Thoughtful comments on an earlier draft by G. Houle, D. Coxson, P. Crittenden and an anonymous referee were greatly appreciated.

[2] E-mail: serge.payette@bio.ulaval.ca.

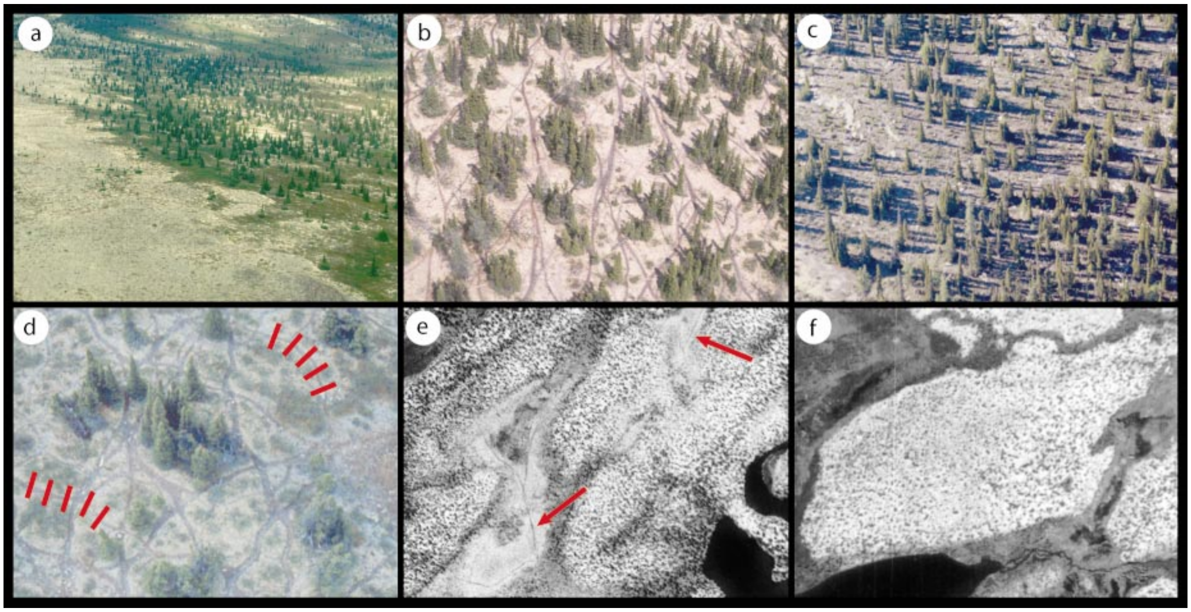

Fig. 1. Lichen woodlands of the summer habitat of the George River caribou herd (GRCH), northeastern Québec-Labrador, Canada (a) undisturbed, (b) with well-developed trail network, (c) after destruction of lichen carpet, (d) sampling scheme along trail, (e) caribou trails in fen peatland, site 118, (f) site 33.

In this study, we analyzed plant remains to identify the relative abundance of ground species prior to caribou disturbance. Conventional plant macrofossil analysis is conducted generally on lake sediment or peatland samples where the decomposition process is slow (Warner, 1990). Although plant remains are rarely preserved in terrestrial soils (Andersen, 1986), conditions at our study sites slowed down the decomposition process (e.g., cold temperatures and short frost-free growing seasons, excessively drained soils and short time lag [about 25 yr] between the onset of caribou disturbance and sampling). As a result, most of the vegetation destroyed by caribou was still present and identifiable in the superficial organic layers.

The main objective of this study was to identify potential shifts in species dominance of ground vegetation of lichen woodlands in the summer habitat of the GRCH in response to caribou grazing and trampling. To do so, we reconstructed the vegetation composition of 14 sites prior to caribou disturbance and evaluated the severity of disturbance based on the amplitude of compositional changes between past and present vegetation.

MATERIAL AND METHODS

Study area—The study area covers most of the summer habitat of the GRCH. Of the 14 sites sampled, eight sites were located within the calving ground. Four sites were outside the calving ground but still within the range of the summer habitat and the remaining two sites were located in the winter habitat (at the edge of the summer habitat) in the vicinity of Schefferville (Fig. 2). One of these two sites was used as control because no evidence of caribou disturbance was found, a condition rarely met in the study area.

All studied sites were selected at random among a set of 30 potential stands. All stands corresponded to old-growth conifer stands (Table 1) dominated by black spruce (*Picea mariana* [Mill.] B.S.P.), with white spruce (*Picea glauca* [Moench] Voss) and eastern larch (*Larix laricina* [DuRoi] K. Koch) as secondary species. The tree cover varied between 10 and 40%. All the woodlands studied were growing on well-drained soils, which at one time supported a dense lichen carpet. All sites showed evidence of caribou disturbance except the control site.

Sampling—Plant remains in superficial organic horizons and present plant cover were used to evaluate plant composition of the lichen woodlands prior to and after caribou disturbance. For both data sets, ground cover was used to evaluate the relative abundance of each species. The ground vegetation was surveyed using the line-intercept method (Mueller-Dombois and Ellenberg, 1974). Two trails were selected at each site, and five 2 m long transects were placed perpendicular to each trail. The center of each transect corresponded to the middle of the trail, allowing the recording of ground vegetation in the trail (30–70 cm large) and in the woodland proper. The first transect in each trail was positioned at random, and the other four transects were placed systematically at 2-m intervals (Fig. 1d).

Linear surveys of present vegetation were performed in each trail along the five transects. Plants were tallied along each 2-m transect using 20 10-cm long sections. The linear cover (cover classes: <1%, 1.1–10.0%, 10.1–20.0%, etc.) of living plants (lichens, mosses, low shrubs, etc), litter, and mineral soil crossing the transect was determined for each 10-cm section. Thus, the survey in each trail was based on 100 measurements used for the calculation of species relative cover. Based on each of the 20 sections/transect, the mean cover of living plants, litter, and mineral soil along each transect was calculated, using the central value of the cover class rather than the cover class itself (e.g., cover class 10.1–20.0% replaced by 15%).

Plant remains were recovered in each trail for transects #1, #3, and #5 thought to be representative of the plant macrofossil assemblage at each site. Plant remains correspond to dead plant parts directly attached to living plants (as in the case of the decaying basal part of *Cladina podetia*) or buried in the uppermost 1 cm of the organic horizon (F horizon). The position and good preservation of plant remains in the uppermost part of the organic horizon indicate their young age and recent burial relative to the long-term development of the vegetation cover at each site. Along each transect, contiguous slices (10-cm long, 5-cm wide) of living plants and the underlying organic horizons were extracted. The samples were then carefully packed to preserve the original stratigraphy. In the laboratory, samples were dried at room temperature and plant remains were exposed by removing the living plants.

Plant remains were then surveyed along the 20 10-cm lines of the 2-m transect. Each 10-cm line was divided in 1-cm sections, and plant cover was determined for each millimeter of 1-cm section under a dissecting microscope (40×, Fig. 3). Plant remains were identified at the genus level. Special attention was given to lichen and moss species because ground vegetation of lichen woodlands is largely dominated by different lichen and moss assemblages

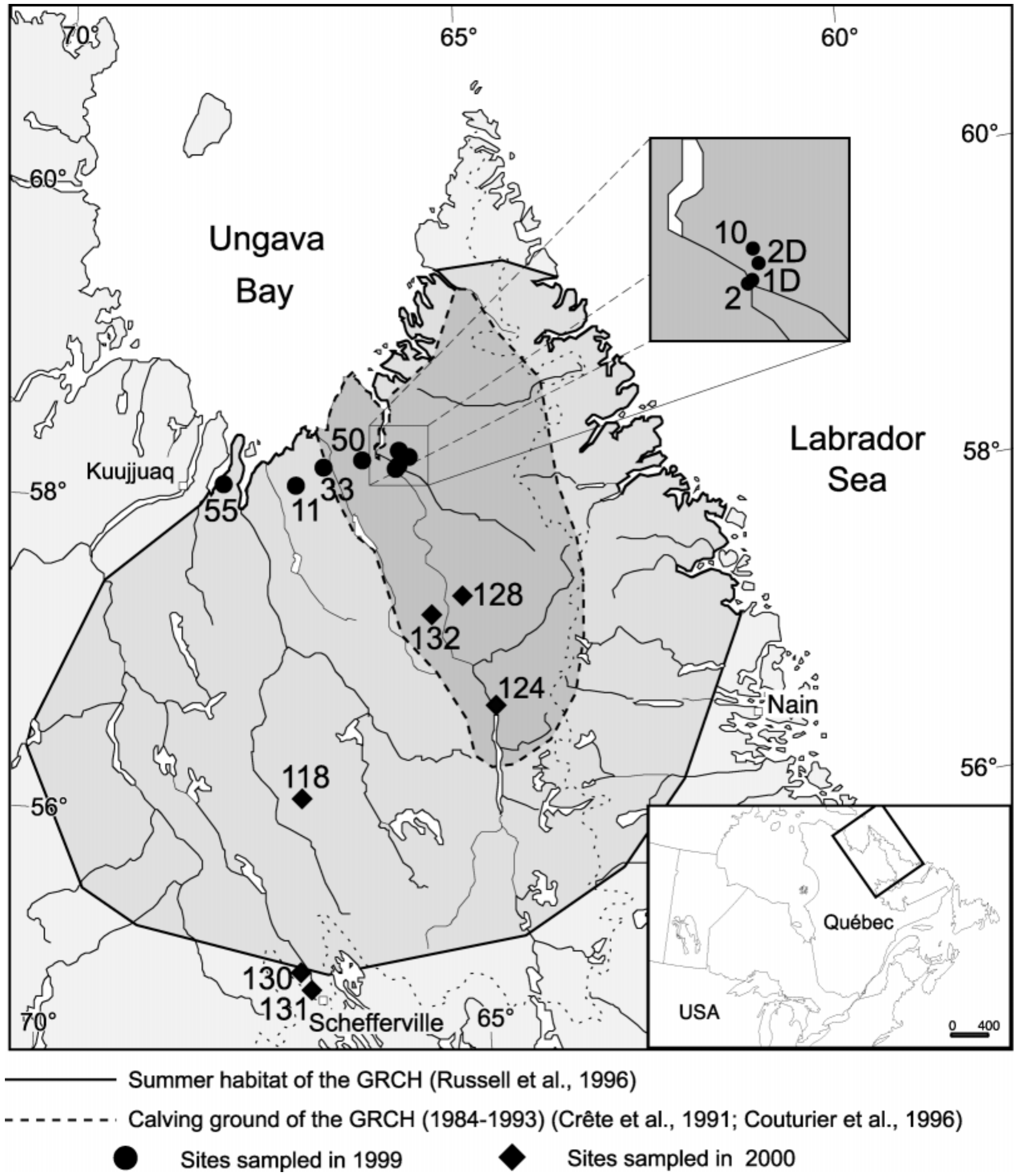

Fig. 2. Location of the study area, including calving ground and summer habitat of the George River caribou herd (GRCH), northeastern Québec-Labrador. Eight sites were sampled in 1999 (circle) and six in 2000 (diamond).

TABLE 1. Ground vegetation of study sites from aerial photos of northeastern Québec-Labrador, Canada.

Study sites	Latitude	Longitude	Vegetation type	Year of aerial photos	Ground vegetation
1D	58°12′	65°48′	Forest	1960	Continuous lichen carpet
2	58°11′	65°48′	Forest	1960	Continuous lichen carpet
2D	58°18′	65°38′	Krummholz	1960	Scarce lichen cover
10	58°22′	65°46′	Forest	1960	Continuous lichen carpet
11	58°06′	67°00′	Forest	1948	Continuous lichen carpet
33	58°12′	66°38′	Forest	1964	Continuous lichen carpet
50	58°14′	66°11′	Krummholz	1960	Continuous lichen carpet
55	58°08′	67°58′	Forest	1948	Continuous lichen carpet
118	56°02′	66°59′	Forest	1974	Continuous lichen carpet
124	56°40′	64°48′	Forest	1964	Continuous lichen carpet
128	57°22′	65°10′	Forest	1960	Continuous lichen carpet
130	54°57′	67°04′	Forest	1975	Continuous lichen carpet
131	54°51′	66°52′	Forest	1975	Continuous lichen carpet
132	57°12′	65°32′	Krummholz	1960	Continuous lichen carpet

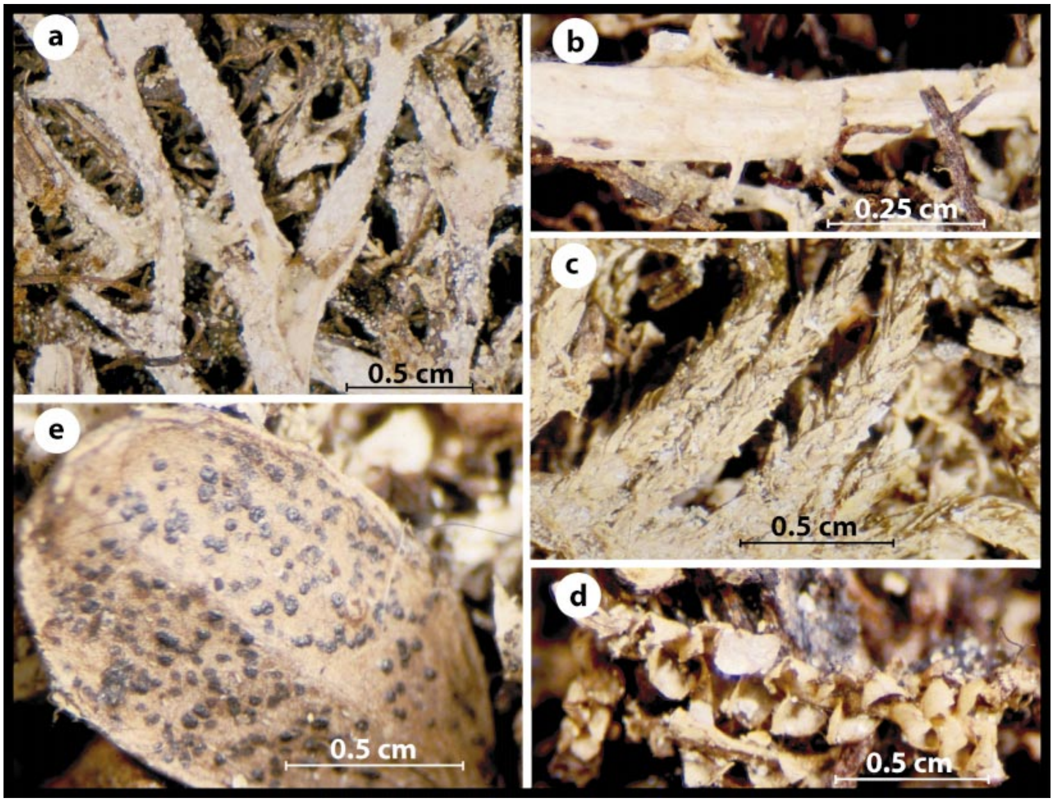

Fig. 3. Plant remains from organic horizons of lichen woodlands in the summer habitat of the George River caribou herd (GRCH), northeastern Québec-Labrador. Clockwise from top left: *Cladina*, *Stereocaulon*, *Pleurozium*, *liverworts*, and *Vaccinium*.

rather than by vascular plants. However, shrubs and herbs were also identified and surveyed when present. Plant cover prior to caribou disturbance was then reconstructed using plant remains from the six surveyed 2-m transects.

Enlargments of aerial photographs, taken between 1948 and 1975, were used to identify the major components of ground vegetation of the studied lichen woodlands prior to caribou disturbance and to evaluate caribou activity based on trail networks and photo-interpreted vegetation composition. Distribution of lichen cover and presence of caribou trails were compared to present conditions in the 14 studied woodlands to validate the analysis of plant remains and present plant cover.

Data analysis—Principal component analysis (PCA) on plant remains and present vegetation data was conducted to evaluate changes in the relative abundance of the different plants as a result of caribou disturbance over the last 25 yr (mixed effects of grazing and trampling). Relative abundance of species in the present ground vegetation was calculated using living plant cover only. Litter and exposed mineral soil were excluded from the current ground cover data in order to homogenize past and present vegetation data sets. Because we used standardized data, the PCA was performed on the covariance matrix. Scores were then calculated using the centered variables instead of the standardized ones (SAS 6.12, Cary, North Carolina, USA).

RESULTS

Ground vegetation—Living ground vegetation covered between 30 and 96%, from the most disturbed site to the control site, the remaining surface being litter and mineral soil (Table 2). However, for most sites (nine out of 14), ground cover varied between 40 and 65%. Lichens were the major component of the vegetation (55–93% cover). *Cladina*, *Cladonia*, and *Stereocaulon* were dominant plants, while other lichens (*Alectoria*, *Cetraria*, *Nephroma*, *Peltigera*, and several crustose lichens) were rare, even though their relative abundance reached 10% at some sites (e.g., *Cetraria* in site 50). Companion plants were mosses and liverworts (0–27%), shrubs (5–24%), and herbs (0–4%). *Dicranum* was the most abundant of the moss and liverwort group, and *Vaccinium* and *Empetrum* were the most abundant of the shrub group.

Plant remains—Plant remains were divided into the same four groups: lichens, mosses and liverworts, shrubs and herbs. A smaller number of taxa were recorded in the plant-remain samples (Table 3). Lichens were the most represented group, with a relative cover varying from 46 to 98% (>72% in 13 of 14 sites). The lichen component consisted of three genera, *Cladina* (mainly *C. stellaris*), *Stereocaulon* (*S. paschale*), and *Cladonia* (several species). No other lichens were identified in the plant-remain assemblages. Plants of the moss and liverwort group were the same as those recorded in present ground vegetation (with the exception of *Racomitrium*) and varied from 0 to 41% (<23% in 13 of 14 sites). Shrub (*Vaccinium* spp. and *Ledum groenlandicum*, 0–13%) and herb (*Lycopodium*, 0–1%) remains were less represented.

The overall ground vegetation composition reconstructed from plant remains was compared to vegetation cover interpreted from enlarged aerial photographs (Fig. 1e, f). In the latter, ground vegetation was mainly dominated by a continuous lichen carpet interspersed with spruce trees at all sites but one (Table 1). A systematic aerial photo-interpretation of the study sites (lichen woodlands and fen peatlands) prior to 1975 indicated the presence of only sparse caribou trails, particularly in peatlands (Fig. 1e, f).

TABLE 2. Present vegetation composition (percent cover) of the study sites given in Table 1.[a]

Vegetation type/species	Site													
	131	130	55	118	11	33	2D	10	132	50	1D	2	128	124
Plant cover (%)	95.9	76.6	43.8	48.8	48.7	29.9	41.1	58.2	35.6	50.6	86.7	62.5	57.4	45.4
Lichens														
Alectoria	—	—	—	—	—	—	—	—	—	0.8	—	—	—	—
Cetraria	0.3	0.1	0.4	0.1	0.1	0.2	2.1	0.4	8.0	10.2	0.1	0.4	1.8	4.9
Cladina	86.2	86.5	86.7	64.4	33.1	32.5	29.6	24.6	21.5	6.8	43.8	36.1	19.3	15.5
Cladonia	2.0	1.9	5.6	5.4	31.7	13.6	21.8	44.1	21.9	30.7	6.9	5.3	16.3	16.4
Crust. lichens	—	0.8	—	—	0.5	5.8	3.2	2.2	1.7	6.0	—	2.4	1.8	6.7
Nephroma	—	—	—	—	1.8	—	—	—	—	0.2	—	—	—	—
Peltigera	—	—	—	—	—	—	—	—	—	—	0.1	—	—	—
Stereocaulon	1.1	+	0.6	2.3	0.3	9.3	2.1	0.9	3.0	0.7	27.6	12.3	23.0	25.2
Mosses														
Dicranum	0.1	—	0.9	6.9	8.5	5.7	9.8	14.4	15.1	7.6	5.4	4.3	21.4	11.7
Pleurozium	0.4	—	—	2.2	—	1.0	7.9	0.1	—	0.1	2.5	15.7	0.8	1.5
Polytrichum	—	—	—	0.2	—	1.0	0.6	3.6	0.3	2.1	—	—	0.5	1.9
Racomitrium	—	—	—	—	—	0.2	—	—	—	4.4	—	—	—	—
Liverworts	0.4	—	0.3	0.4	2.9	3.4	8.9	—	3.9	7.8	2.2	5.6	2.3	1.7
Shrubs														
Arctostaphylos	—	—	—	—	—	—	—	—	1.4	—	—	—	—	—
Betula	—	0.9	—	—	—	1.0	0.4	0.8	—	0.1	0.5	—	1.7	—
Empetrum	0.8	6.6	—	4.0	9.1	11.4	—	6.6	7.6	9.3	—	—	—	9.7
Ledum	0.3	—	0.2	—	0.5	—	—	—	2.2	0.2	0.1	—	—	0.6
Potentilla	—	—	—	—	—	—	—	—	—	—	0.1	0.2	—	—
Salix	—	—	—	—	—	—	—	0.1	—	1.2	—	—	—	—
Vaccinium	8.0	2.8	4.8	13.2	10.7	11.0	12.9	1.9	13.5	10.4	10.6	17.2	10.8	4.1
Herbs														
Carex	—	—	0.7	—	—	—	0.6	0.1	—	0.7	—	0.6	—	—
Coptis	0.1	—	—	—	—	—	—	—	—	—	—	—	—	—
Cornus	—	—	—	0.6	0.5	—	—	—	—	—	—	—	—	—
Deschampsia	0.1	—	—	—	—	3.7	—	—	—	—	+	—	0.3	—
Loiseleuria	—	—	—	—	—	—	—	—	—	0.6	—	—	—	—
Lycopodium	0.5	0.4	—	0.4	0.3	0.2	0.1	—	—	—	—	—	—	—
Rubus	—	—	—	—	—	—	—	—	—	0.1	—	—	—	—

[a] A + indicates less than 0.1% cover.

TABLE 3. Past vegetation composition (percent cover) of the study sites given in Table 1 based on plant remains.[a]

Vegetation type/species	PCA group[b]													
	1st site										2nd site			3rd site
	131	130	55	118	11	33	2D	10	132	2	1D	124	128	50
Lichens														
Cladina	83.5	95.9	97.7	82.4	90.5	89.5	81.9	73.9	86.6	67.7	44.7	36.2	47.6	40.9
Cladonia	0.4	—	0.2	—	0.4	—	—	0.5	0.1	—	2.9	—	—	4.6
Stereocaulon	8.1	2.6	0.4	2.1	1.0	2.6	1.7	0.9	2.2	9.4	26.6	36.0	28.0	0.6
Mosses														
Dicranum	0.6	+	0.8	1.2	3.7	0.9	4.2	16.4	7.8	0.8	12.6	11.4	12.1	22.5
Pleurozium	0.5	0.2	0.1	0.5	—	0.9	3.5	0.7	—	11.3	9.3	2.3	0.9	1.1
Polytrichum	0.2	—	0.2	—	—	0.4	—	0.3	0.1	—	0.4	0.8	—	—
Liverworts	1.1	0.3	0.2	0.7	2.4	2.3	6.7	5.6	0.5	5.8	0.3	6.0	5.1	17.7
Shrubs														
Ledum	+	0.2	—	0.1	0.6	—	0.7	1.3	0.4	0.1	0.9	3.0	—	6.4
Vaccinium	4.5	0.9	0.5	13.0	1.3	3.4	1.2	0.5	2.3	4.8	2.2	4.3	6.4	6.3
Herbs														
Lycopodium	1.1	+	—	—	0.1	—	—	—	—	—	—	—	—	—

[a] A + indicates less than 0.1% cover.
[b] PCA groups include lichens, mosses and liverworts, shrubs, and herbs.

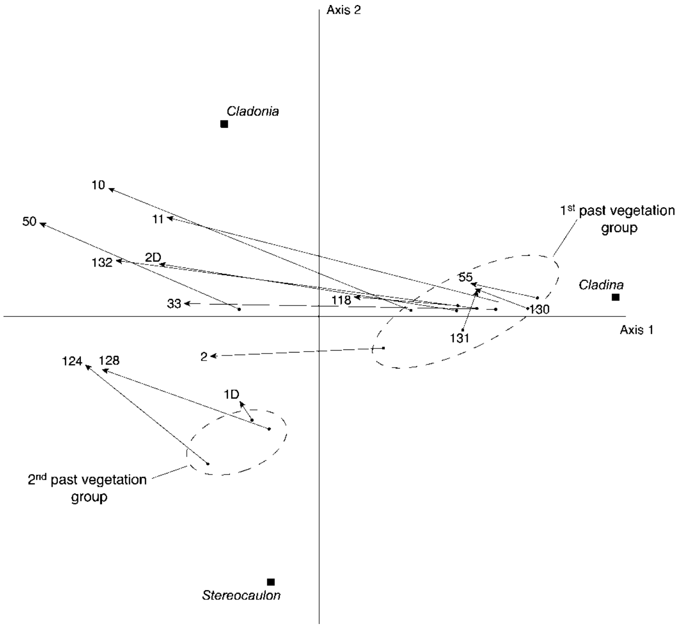

Fig. 4. Principal component analysis using plant remain and present vegetation data of lichen woodlands of the summer habitat of the George River caribou herd (GRCH), northeastern Québec-Labrador. Past and present vegetation composition of each site are represented by a circle and an arrowhead, respectively. (Broken line: group based on past vegetation.)

PCA analysis—Principal component analysis was used to ordinate the study sites according to composition of ground vegetation before and after caribou disturbance (Fig. 4). The first two axes of PCA explained 91.4% of the variance. Axis 1 (79.4% of the variance) was positively correlated with *Cladina* (score of 0.92) and negatively correlated with *Cladonia* (−0.29) cover. Axis 2 explained an additional 12% of the variance and was positively correlated with *Cladonia* (0.57) and negatively correlated with *Stereocaulon* (−0.79) covers.

Based on plant remains, two natural groups of sites were identified. The first group was composed of *Cladina*-dominated sites, and the second group included sites with high *Stereocaulon* cover (Table 2). The position of site 50 in the PCA reflected a somewhat unique past ground cover, with mosses and liverworts as important as lichens.

Position of the sites in the PCA analysis, based on present vegetation, was directly linked to the relative abundance of the different lichens, in relation to the severity and type (trampling or grazing) of caribou disturbance. Four major vegetation types were identified: *Cladina*-dominated ground vegetation; reduced *Cladina* and increased *Cladonia* cover; reduced *Cladina* cover with no increase of *Cladonia*; and finally, reduced *Cladina* and *Stereocaulon* cover combined with an increase of *Cladonia*.

DISCUSSION

In this study, we used a new approach to evaluate caribou-induced changes in ground species dominance over a short period based on macrofossil analysis. The use of this paleoecological method was possible because plants prior to caribou disturbance were still identifiable in the organic topsoil. Our sampling scheme was designed to evaluate the most important botanical changes relative to present composition of ground vegetation as it was based on the analysis of the extensive trail networks crossing the studied lichen woodlands. Although relative species abundance is thought to be representative of the ground vegetation of the lichen-spruce woodlands, we need to point out that no consideration was given to trail densities.

Past and present vegetation data—Prior to caribou disturbance, the ground vegetation of most lichen woodlands was largely dominated by lichens. Most of the sites (10/14) were dominated by *Cladina* species typical of late-successional stages (Hustich, 1951; Ahti, 1959; Bergerud, 1971; Auclair, 1983; Morneau and Payette, 1989). Based on the *Cladina* dominance, sustained growth conditions in absence of ground disturbance was likely during the decades preceding growth of the GRCH. However, *Stereocaulon*-dominated sites were probably associated with light caribou disturbance. *Stereocaulon* typically increases to the detriment of *Cladina* in response to light disturbance (Ritchie, 1960; Scotter, 1964; Ahti and Hepburn, 1967; Haapasaari, 1988). Some of the factors likely to explain *Stereocaulon* abundance on disturbed sites are better trampling resistance (Haapasaari, 1988), thalli less thoroughly eaten by caribou (Haapasaari, 1988), and faster growth rate (Hustich, 1951). More recent quantitative work in northern Finland (Kärenlampi, 1971; Crittenden et al., 1994; Kytöviita and Crittenden, 2002), however, indicates that several *Cladina* species are growing faster than *Stereocaulon*.

Aerial photo interpretation of the sites prior to 1975 corroborates our plant-remain data, which suggested the dominance of a continuous lichen (*Cladina*) carpet before the period of caribou disturbance. Although the identification of the dominant species from aerial photos cannot be validated directly, continuous lichen carpets in northeastern Canada have always been reported to be *Cladina*-dominated in field surveys (Hustich, 1951; Bergerud, 1971; Morneau and Payette, 1989; Riverin and Gagnon, 1996). Also, according to aerial photos, no caribou trails were present in the studied sites prior to 1975. Although seldom-used trails could have been overlooked, only a few well-developed trails, particularly in fen peatlands, were present at the time the aerial photos were taken. Obviously, trail networks at that time were ill-developed in comparison to now, which strongly suggests the absence of significant caribou disturbance at that time.

Degradation process—Ground vegetation faced severe trampling and grazing pressures as caribou density increased in the summer habitat following the rapid growth of the GRCH. The most striking impact of caribou disturbance was the destruction of the lichen carpet, as reported elsewhere (Manseau et al., 1996; Morneau and Payette, 1998), resulting in a directional shift in species dominance, from *Cladina*-dominated vegetation to more complex and diverse lichen assemblages accompanied by mosses, shrubs, and herbs.

The dominant ground species in stands with light or moderate disturbances had no major change, because destruction of the lichen cover was restricted to caribou trails. Although light and moderate trampling can favor short-distance lichen dissemination (Heinken, 1999), severe trampling can have deleterious effects on lichens. At the landscape scale, degradation of ground vegetation in lichen woodlands of the summer habitat is closely associated with severe trampling. For lichen species other than those in the genera *Cladina* and *Stereocaulon*, the impact of caribou disturbance on ground vegetation can be compared to that of forest fire. By destroying the lichen cover, caribou trampling causes mineral soil to be exposed, thereby creating favorable conditions for the establishment of crustose lichens and several early successional *Cladonia* species. The relative abundance of mosses and dwarf shrubs generally increases with the destruction of the lichen carpet, although to a lesser extent.

With the destruction of the *Cladina stellaris* carpet, the respective influences of trampling and grazing can be evaluated by looking at the sequence of lichen recovery. Present vegetation with small *Cladina stellaris* podetia (originating from sprouting of surviving lichen thalli) is possibly the result of the combined effects of heavy grazing (most living thalli removed) and light/moderate trampling (dead residual lichen carpet still present). However, the sequence of vegetation recovery with *Cladonia* and crustose lichens is likely initiated when heavy trampling that exposes the mineral soil ceases. Grazing severity is difficult to evaluate in this particular case because heavy trampling destroyed any former grazing evidence.

Lichen succession—All sampled sites were old-growth lichen woodlands (>200 yr old; Morneau, 1999), in an area with a long fire-return interval and rare recently burned stands. In absence of disturbance (fire and caribou), old-growth lichen woodlands are self-maintained during several centuries in northern Québec (Payette and Morneau, 1993).

Successional processes are still at an early stage at the caribou-disturbed sites as the activity of the GRCH only decreased in the early 1990s (Boudreau et al., 2003). Although comparisons can be made, successional trajectories for this type of disturbance are, for many reasons, more complex than those associated with fire disturbance: late successional lichen species are still present at every site, mineral soils are not always exposed and, more importantly, caribou can come back to a site and change the successional pathways anytime. Furthermore, plant composition in disturbed stands includes early (crustose lichens and *Cladonia*) and late (*Cladina stellaris* thalli and fragments dispersed in the stands) successional species. Such plant assemblages produce successional stands with high lichen diversity. In the absence of caribou activity, lichen succession will progress, with *Cladina* species becoming progressively dominant over the next 100 years until a thick *Cladina stellaris* carpet covers most of the ground surface (Morneau and Payette, 1989).

In conclusion, our results show that caribou disturbance plays an important role determining lichen abundance and diversity. Destruction of the *Cladina*-species-dominated lichen carpet allows other lichens, particularly species of early successional stages, to increase in abundance. However, the impact of caribou disturbance on mosses, shrubs, and herbs are less apparent, although small increases in relative cover were observed. Further research should emphasize the need to partition the respective influence of grazing and trampling in the degradation process.

LITERATURE CITED

AHTI, T. 1959. Studies on the caribou lichen stands of Newfoundland. *Annals of the Botanical Society Vanamo* 30: 1–44.

AHTI, T., AND T. L. HEPBURN. 1967. Preliminary studies on woodland caribou range, especially on lichen stands, in Ontario. *Research Report (wildlife)*, no. 74. Technical Series, Department of Lands and Forests, Toronto, Ontario, Canada.

ANDERSEN, S. T. 1986. Palaeoecological studies of terrestrial soils. *In* B. E. Berglund and M. Ralska-Jasiewiczowa [eds.], Handbook of Holocene palaeoecology and palaeohydrology, 165–177. John Wiley & Sons, Chicago, Illinois, USA.

AUCLAIR, A. N. D. 1983. The role of fire in lichen-dominated tundra and forest-tundra. *In* R. W. Wein and D. A. MacLean [eds.], The role of fire in northern circumpolar ecosystems, 235–256. John Wiley & Sons, New York, New York, USA.

AUGUSTINE, D. J., AND S. J. MCNAUGHTON. 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management* 62: 1165–1183.

BAYFIELD, N. G., U. H. URQUHART, AND S. M. COOPER. 1981. Susceptibility of four species of *Cladonia* to disturbance by trampling in the Cairngorm mountains, Scotland. *Journal of Applied Ecology* 18: 303–310.

BAYLEY, R. H. 1976. Ecological aspects of dispersal and establishment in lichens. *In* D. H. Brown, D. L. Hawksworth, and R. H. Bayley [eds.], Lichenology: progress and problems, 215–247. Academic Press, London, UK.

BERGERUD, A. T. 1971. Abundance of forage on the winter range of Newfoundland caribou. *Canadian Field-Naturalist* 85: 39–52.

BIERMANN, R., AND F. J. A. DANIELS. 1997. Changes in a lichen rich dry sand grassland vegetation with special reference to lichen-synusiae and *Campylopus introflexus*. *Phytocoenologica* 27: 257–273.

BOUDREAU, S., S. PAYETTE, C. MORNEAU, AND S. COUTURIER. 2003. Recent decline of the George River caribou herd as revealed by tree-ring analysis. *Arctic, Antarctic, and Alpine Research* 35: 187–195.

COUTURIER, S., R. COURTOIS, H. CRÉPEAU, L.-P. RIVEST, AND S. N. LUTTICH. 1996. The June 1993 photocensus of the Rivière George caribou herd and comparison with an independent census. *Rangifer Special Issue* 9: 283–296.

CRÊTE, M., L.-P. RIVEST, D. LE HENAFF, AND S. N. LUTTICH. 1991. Adapting sampling plans to caribou distribution on calving grounds. *Rangifer Special Issue* 7: 137–150.

CRITTENDEN, P. D., I. KALUCKA, AND E. OLIVER. 1994. Does nitrogen supply limit the growth of lichens? *Cryptogamic Botany* 4: 143–155.

HAAPASAARI, M. 1988. The oligotrophic heath vegetation of northern Fennoscandia and its zonation. *Acta Botanica Fennica* 135: 1–219.

HEINKEN, T. 1999. Dispersal patterns of terricolous lichens by thallus fragments. *Lichenologist* 31: 603–612.

HENRY, G. H. R., AND A. GUNN. 1991. Recovery of tundra vegetation after overgrazing by caribou in arctic Canada. *Arctic* 44: 38–42.

HUSTICH, I. 1951. The lichen woodlands in Labrador and their importance as winter pastures for domesticated reindeer. *Acta Geographica* 12: 1–48.

KÄRENLAMPI, L. 1971. Studies on the relative growth rate of some fruticose lichens. *Reports from the Kevo Subarctic Research Station* 7: 33–39.

KERSHAW, K. A. 1978. The role of lichens in boreal tundra transition areas. *Bryologist* 81: 294–306.

KLEIN, D. R. 1987. Vegetation recovery patterns following overgrazing by reindeer on St. Matthew Island. *Journal of Range Management* 40: 336–338.

KYTÖVIITA, M.-M., AND P. D. CRITTENDEN. 2002. Seasonal variation in growth rate in *Stereocaulon paschale*. *Lichenologist* 34: 533–537.

MANSEAU, M., J. HUOT, AND M. CRÊTE. 1996. Effects of summer grazing by caribou on composition and productivity of vegetation: community and landscape level. *Journal of Ecology* 84: 503–513.

MCNAUGHTON, S. J. 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. *Ecological Monographs* 53: 291–320.

MCNAUGHTON, S. J. 1984. Grazing lawns, animal in herds, plant form, and coevolution. *American Naturalist* 124: 863–886.

MESSIER, F., J. HUOT, D. LE HENAFF, AND S. LUTTICH. 1988. Demography of the George River caribou herd: evidence of population regulation by forage exploitation and range expansion. *Arctic* 41: 279–287.

MORNEAU, C. 1999. Analyse dendroécologique de l'activité du caribou et perturbation de la végétation dans le nord-est du Québec-Labrador. Ph.D. dissertation, Université Laval, Québec City, Québec, Canada.

MORNEAU, C., AND S. PAYETTE. 1989. Postfire lichen-spruce woodland recovery at the limit of the boreal forest in northern Québec. *Canadian Journal of Botany* 67: 2770–2782.

MORNEAU, C., AND S. PAYETTE. 1998. A dendroecological method to evaluate past caribou (*Rangifer tarandus* L.) activity. *Ecoscience* 5: 64–76.

MOSER, J. M., T. H. NASH III, AND J. W. THOMSON. 1979. Lichens of Anaktuvuk Pass, Alaska, with emphasis on the impact of caribou grazing. *Bryologist* 82: 393–408.

MUELLER-DOMBOIS, D., AND H. ELLENBERG. 1974. Aims and methods of vegetation ecology. Wiley, New York, New York, USA.

OKSANEN, L. 1978. Lichen grounds of Finnmarksvidda, northern Norway, in relation to summer and winter grazing by reindeer. *Report of the Kevo Subarctic Research Station* 14: 64–71.

OKSANEN, L., J. MOEN, AND T. HELLE. 1995. Timberline patterns in northernmost Fennoscandia. Relative importance of climate and grazing. *Acta Botanica Fennica* 153: 93–105.

OKSANEN, L., AND T. OKSANEN. 1989. Natural grazing as a factor shaping out barren landscapes. *Journal of Arid Environments* 17: 219–233.

OKSANEN, L., AND R. VIRTANEN. 1995. Topographic, altitudinal and regional patterns in continental and suboceanic heath vegetation of northern Fennoscandia. *Acta Botanica Fennica* 153: 1–61.

OUELLET, J. P., D. C. HEARD, AND S. BOUTIN. 1993. Range impacts following the introduction of caribou on Southampton Island, Northwest Territories, Canada. *Arctic and Alpine Research* 25: 136–141.

OUZILLEAU, J., AND S. PAYETTE. 1975. Croissance de quelques lichens à caribou du genre *Cladonia* (sous-genre *Cladina*) en milieu subarctique, Nouveau-Québec. *Naturaliste canadien* 102: 597–602.

PAYETTE, S., AND C. MORNEAU. 1993. Holocene relict woodlands at the eastern Canadian treeline. *Quaternary Research* 39: 84–89.

PEGAU, R. E. 1968. Growth rates of important reindeer forage lichens on the Seward Peninsula, Alaska. *Arctic* 21: 255–259.

PEGAU, R. E. 1970. Effect of reindeer trampling and grazing on lichens. *Journal of Range Management* 23: 95–97.

RITCHIE, J. C. 1960. The vegetation of northern Manitoba. V. Establishing the major zonation. *Arctic* 13: 211–229.

RIVERIN, S., AND R. GAGNON. 1996. Dynamique de la régénération d'une pessière à lichen dans la zone de la pessière noire à mousses, nord du Saguenay-Lac-St-Jean. *Canadian Journal of Forest Research* 26: 1504–1509.

RUSSELL, J., S. COUTURIER, L. G. SOPUCK, AND K. OVASKA. 1996. Post-calving photo census of the Rivière George caribou herd in July 1993. *Rangifer Special Issue* 9: 319–330.

SCOTTER, G. W. 1963. Growth rates of *Cladonia alpestris*, *C. mitis*, and *C. rangiferina* in the Talston River region, N.W.T. *Canadian Journal of Botany* 41: 1199–1202.

SCOTTER, G. W. 1964. Effects of forest fires on the winter range of barren ground caribou in northern Saskatchewan. Wildlife Management Bulletin, series 1, no. 18. Canadian Wildlife Service, Ottawa, Ontario, Canada.

SUOMINEN, O., AND J. OLOFSSON. 2000. Impacts of semi-domesticated reindeer on structure of tundra and forest communities in Fennoscandia: a review. *Annales Zoologici Fennici* 37: 233–249.

UKKOLA, R. 1995. Trampling tolerance of plants and ground cover in Finnish Lapland, with an example from the Pyhätunturi National Park. *In* H. Heikkinen, B. Obrebska-Starkel and S. Tuhkanen [eds.], Environmental aspects of the timberline in Finland and in the Polish Carpathians, 91–110. Uniwersytet Jagiellonski, Krakow, Poland.

VÄRE, H., R. OHTONEN, AND K. MIKKOLA. 1996. The effect and extent of heavy grazing by reindeer in oligotrophic pine heaths in northeastern Fennoscandia. *Ecography* 19: 245–253.

VÄRE, H., R. OHTONEN, AND J. OKSANEN. 1995. Effects of reindeer grazing on understory vegetation in dry *Pinus sylvestris* forests. *Journal of Vegetation Science* 6: 23–30.

WARNER, B. G. 1990. Plant macrofossils. *In* B. G. Warner [ed.], Methods in Quaternary ecology, 53–64. Geoscience Canada Reprint Series 5. Geological Association of Canada, Stittsville, Ontario, Canada.

WATKINSON, A. R., A. E. RIDING, AND N. R. COWIE. 2001. A community and population perspective of the possible role of grazing in determining the ground flora of ancient woodland. *Forestry* 74: 231–239.