

# Growth performance of *Cladina stellaris* following caribou disturbance in subarctic Québec<sup>1</sup>

Stéphane BOUDREAU & Serge PAYETTE<sup>2</sup>, NSERC Northern Research Chair, Centre d'études nordiques and Département de biologie, Université Laval, Québec G1K 7P4, Canada, e-mail: serge.payette@bio.ulaval.ca

**Abstract:** *Cladina stellaris* is a dominant lichen species of old-growth lichen-spruce woodlands in subarctic Québec, where the continuous lichen carpet persists for several decades in the absence of disturbance. The lichen carpet is, however, vulnerable to caribou (*Rangifer tarandus*) disturbance under dry site conditions. Through grazing and trampling, large herds of migratory caribou reduce *C. stellaris* abundance and modify ground vegetation composition. Here, we have evaluated the age and growth performance of *C. stellaris* in relation to the recent activity of the George River Caribou Herd (GRCH). We measured the age, length, and growth rate of *C. stellaris* podetia in and near caribou trails in 15 lichen-spruce woodlands across the summer habitat. The age of lichens, used to evaluate the initial period of lichen recruitment following the decline of the GRCH, indicated that lichen recovery began in the early 1990s in heavily disturbed sites, whereas comparisons between the age structure of border and trail lichens also suggested that the southern part of the calving ground was still heavily used in the early 1990s. Length and growth rate of *C. stellaris* thallus were closely associated with severity of caribou disturbance, as inferred from the residual ground cover of terrestrial lichens. Growth performance of *C. stellaris* during the initial stage of lichen recovery varied according to the spatial use of the summer habitat by caribou, with better performance at the edge of the summer and winter habitats and reduced performance in the extensively used calving ground. The analysis of growth performance of *C. stellaris* provides new insights on lichen-spruce stand recovery associated with caribou disturbance.

**Keywords:** caribou disturbance, *Cladina stellaris*, ecological succession, lichen growth, lichen-spruce woodland, northern Québec, subarctic.

**Résumé :** *Cladina stellaris* est l'espèce lichénique dominante des vieilles pessières à lichens au Québec subarctique, où le tapis de lichens persiste pendant plusieurs décennies en l'absence de perturbation. En conditions sèches, le tapis de lichens est toutefois vulnérable aux perturbations par le caribou (*Rangifer tarandus*), qui réduit alors l'abondance de *C. stellaris* et modifie la composition du parterre végétal. Nous avons évalué l'âge et la performance (la croissance) des podétions de *C. stellaris* en relation avec l'activité récente du troupeau de caribous de la rivière George (TRG). Nous avons déterminé l'âge et mesuré la longueur et le taux de croissance des podétions de *C. stellaris* échantillonnées en bordure et dans les sentiers de 15 pessières à lichens réparties dans l'habitat estival du TRG. L'âge des lichens, qui sert à déterminer la période initiale de recrutement suivant le déclin de l'activité du caribou, montre que la reprise lichénique s'est amorcée au début des années 1990 dans les sites les plus dégradés. La comparaison des structures d'âge des lichens de bordure et de sentier suggère que la partie sud de l'aire de mise bas était fortement utilisée au début des années 1990. La longueur et le taux de croissance de *C. stellaris* sont associés à la sévérité de la perturbation par le caribou. La croissance de *C. stellaris* dans les stades initiaux de la reprise lichénique varie selon l'utilisation spatiale de l'habitat d'été par le caribou, la croissance étant meilleure à la frontière entre les habitats estival et hivernal et plus faible dans l'aire de mise bas. L'analyse de la croissance de *C. stellaris* fournit donc des informations pertinentes sur la reprise lichénique associée aux perturbations engendrées par le caribou.

**Mots-clés :** *Cladina stellaris*, croissance des lichens, perturbations engendrées par le caribou, pessière à lichens, Québec nordique, succession écologique, zone subarctique.

**Nomenclature:** Marie-Victorin, 1995; Brodo, Duran Sharnoff & Sharnoff, 2001.

## Introduction

Lichen woodlands are a dominant vegetation type throughout the North American boreal forest (Kershaw, 1978), where successional patterns are mainly driven by fire and caribou (*Rangifer tarandus*) disturbance. Fire is a major disturbance factor controlling the structure and functions of boreal and subarctic ecosystems (Rowe & Scotter, 1973; Payette, 1992). Ground vegetation of lichen-dominated stands in parts of Fennoscandia and Spitsbergen is mainly influenced by reindeer grazing and trampling (Haapasaaari, 1988; Oksanen & Oksanen, 1989;

Ahti & Oksanen, 1990; Oksanen & Virtanen, 1995; Suominen & Olofsson, 2000; van der Wal *et al.*, 2001).

Major changes in lichen and moss dominance occur during the post-fire recovery process, whereas only minor changes are generally recorded in vascular plants (Scotter, 1964; Bergerud, 1971; Maikawa & Kershaw, 1976; Black & Bliss, 1978; Johnson, 1981; Foster, 1985; Morneau & Payette, 1989). In western Canada, recovery proceeds along four successional stages dominated respectively by *Polytrichum* (0-20 y after fire), *Cladonia uncialis* and *Cladina stellaris* (21-60 y), spruce-*Stereocaulon paschale* (61-130 y), and spruce-mosses (> 130 y) as the tree canopy closes in the absence of fire (Maikawa & Kershaw, 1976). In subarctic Québec, recovery is somewhat differ-

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<sup>2</sup>Author for correspondence.

ent, with a five-stage succession dominated by mineral soil and crustose lichens (0-10 y), crustose lichens and *Polytrichum* (10-20 y), *Cladonia* species (20-30 y), *Cladina mitis* (30-90 y), and *C. stellaris* (> 100 y). *Cladina stellaris* is progressively replaced by mosses in the more humid climate of southeastern Labrador (Foster, 1985), whereas it is able to persist in the absence of fire in subarctic Québec (Payette *et al.*, 1985; Morneau & Payette, 1989; Payette & Morneau, 1993). Despite regional differences between the post-fire successional sequences, the progressive development of *C. stellaris* carpet is common to most subarctic lichen woodlands of North America.

Ground vegetation of lichen-dominated forests is also sensitive to caribou disturbance. Depending on the severity, caribou disturbance reduces lichen abundance and modifies species composition. Light to moderate grazing occurring in *C. stellaris*-dominated stands generally increases the abundance of *Stereocaulon paschale* and several *Cladina* species (Ritchie, 1959; Oksanen, 1978; Oksanen & Virtanen, 1995). Thick lichen mats can disappear rapidly with severe grazing or trampling (Morneau & Payette, 1998), as *C. stellaris* is particularly vulnerable under dry site conditions (Pegau, 1970; Bayley, 1976; Oksanen, 1978; Bayfield, Urquhart & Cooper, 1981; Haapasaari, 1988). Mineral soil also provides suitable conditions for different species of lichens (mainly crustose lichens and *Cladonia*), mosses, and herbs. Ground vegetation recovery after caribou disturbance is a long process, because of the slow growth of *Cladina* (growth rates of 3 to 6 mm·y<sup>-1</sup>; Scotter, 1963; Pegau, 1968; Ouzilleau & Payette, 1975).

Although lichen abundance can be reduced by severe caribou disturbance (Klein, 1968; Oksanen & Virtanen, 1995; Väre, Ohtonen & Oksanen, 1995; Väre, Ohtonen & Mikkola, 1996; Morneau & Payette, 1998), no data are available on the impact of caribou on the growth performance of *C. stellaris*. Age, length, and growth rate of lichen podetia may be useful parameters to evaluate vegetation recovery following caribou disturbance. Age of lichens may give an index of the time elapsed since the beginning of plant recovery following caribou activity. Growth patterns of individual podetia of *Cladina* species (Andreev, 1954) are usually divided into three different stages: accumulation, replacement, and decay. The accumulation stage (10-15 y) is characterized by the growth of the upper part of the podetium. During the second stage, corresponding to the replacement period, which can last for several decades, the lower part of the podetium decays. At this point, there is no change in the length of the living part of the podetium. Contrasted colour changes make it relatively easy to separate the living and dead parts of the podetium (Kershaw & Rouse, 1971). The last stage is characterized by rapid decay of the lower part of the lichen thallus. During this stage, the length of the living podetium decreases year after year. Branching occurs once a year, regardless of growth stage, and internodes grow for several years (generally between 5 and 7 y; Kärenlampi, 1971), according to site and weather conditions.

The main objective of this study is to evaluate the growth performance of *C. stellaris*, the main lichen ground species in lichen-spruce woodlands, during the

first stage of the recovery process associated with the declining activity of the George River Caribou Herd (GRCH) since the late 1980s (Boudreau *et al.*, 2003). The specific objectives of this study are to evaluate the relations between length and mean growth rate of *C. stellaris* podetia and severity of caribou disturbance, and the growth performance of *C. stellaris* during the initial period of lichen recruitment.

## Methods

### STUDY AREA

The study area includes the summer habitat of the GRCH in the northeastern part of Québec-Labrador. Of the 15 sites sampled, nine 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 two remaining sites were at the edge of the summer habitat, close to Schefferville (Figure 1). The sites were selected at random and corresponded to old-growth lichen woodlands dominated by black spruce (*Picea mariana*), with white spruce (*Picea glauca*) and eastern larch (*Larix laricina*) as secondary species. The tree cover varied between 10% and 40%. The sampled woodlands were on well-drained soils, which at one time supported a dense lichen mat. All sites showed evidence of variable caribou disturbance except one site (131) used as control.

### SAMPLING

Two caribou trails were selected at random at each site. At each trail, lichens were sampled along the border and in the trail proper using a randomly positioned transect (2 m × 8 m). Thus, a total of 57 plots (14 sites × 2 borders × 2 trails + control site) showing variable lichen cover were sampled. At the control site, lichens were sampled from two transects placed at random on the continuous lichen mat. In each plot, the longest 50 podetia of *Cladina stellaris* were recovered from a larger sample of lichen thallus. The podetia were assumed to be the oldest lichens to represent the initial period of lichen colonization following caribou disturbance. After sampling, lichens were moistened in plastic bags to avoid breakage.

In the laboratory, the main axis of each *C. stellaris* podetium was exposed by cutting all secondary axes. The main axes were then scanned and measured with Image Analysis Software (Object-Image 1.62p7). The number of internodes and the total length of each podetium were measured. Podetia were rejected when it was not possible to accurately determine the number of internodes due to irregular morphology (caused mostly by caribou trampling). First used by Andreev (1954), who monitored the growth of forage lichens over several years, the number of internodes is now widely used to determine the minimum age of *C. stellaris* podetia, based on the assumption that one internode corresponds to one year of growth (Scotter, 1963; Pegau, 1968; Kärenlampi, 1971; Ouzilleau & Payette, 1975). We have validated the value of this assumption by determining the age of *C. stellaris* podetia growing in two recently burned sites (1991 and 1995) in the Parc-des-Grands-Jardins near Baie-St-Paul, Québec). *Cladina stellaris* podetia originating from parts

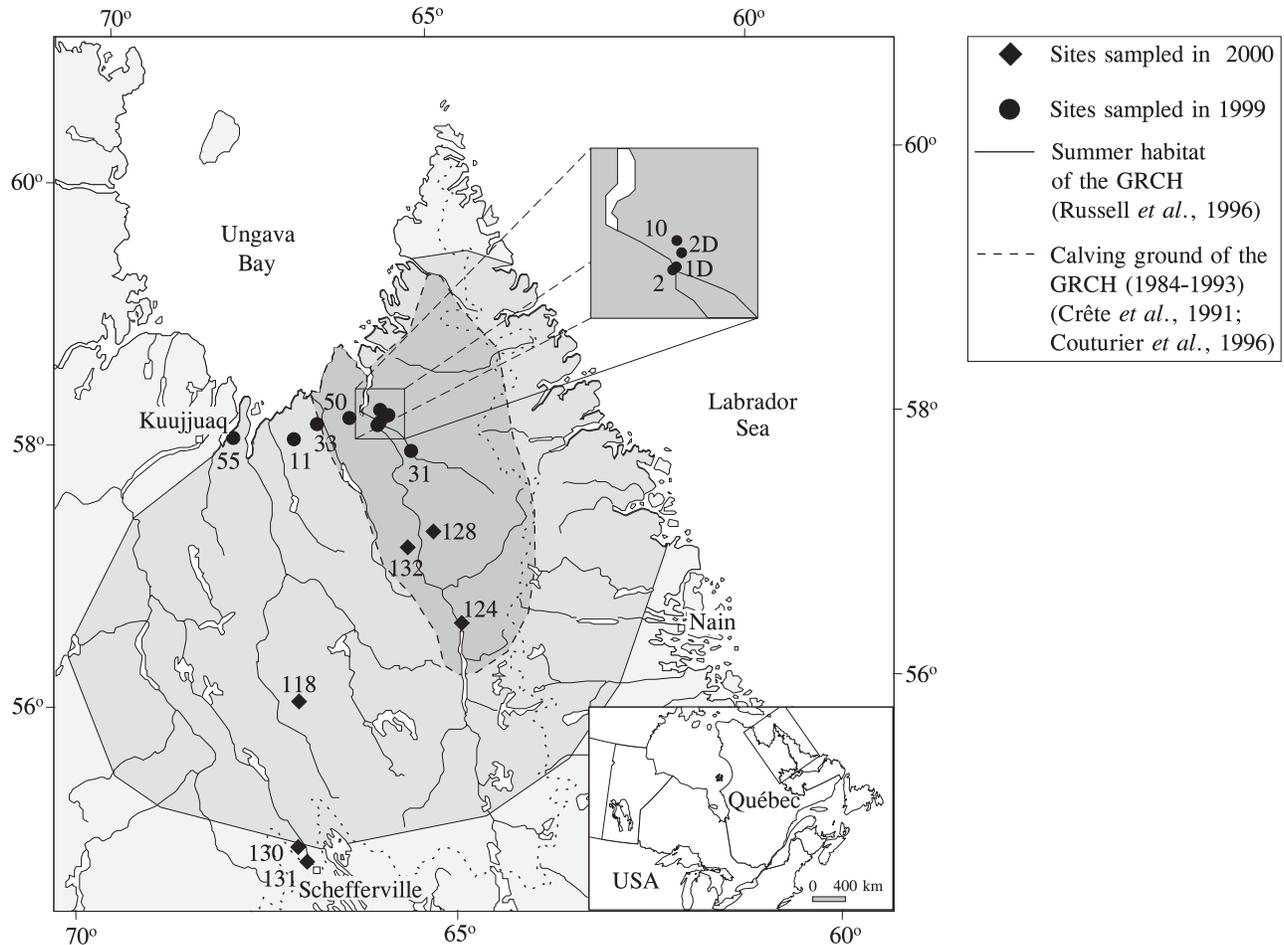


FIGURE 1. Location of the sampled sites. Nine sites were sampled in 1999 and six sites were sampled in 2000.

of the lichen mat that survived the two fires were harvested in September 1999, and our results were in full compliance with Andreev's assumption stated above. The mean growth rate of *Cladina* was then calculated based on the ratio of podetium length (L) to the number of internodes (I) (L/I ratio; Kärenlampi, 1971). Although the L/I ratio is less indicative of the growth rate than biomass (Palmqvist, 2000), it is the only method that allows us to go back in time.

#### DATA ANALYSIS

We compared the age structure of lichens in the trail *versus* that in the border for each of the 28 trails sampled (14 sites, 2 trails per site) using a Kolmogorov-Smirnov test. The control site was excluded from this analysis, because of absence of caribou trails. Linear regressions were performed to evaluate the relations between length and mean growth rate (L/I ratio) of *C. stellaris* podetia and lichen cover in trails and borders, respectively. Because ground vegetation at all sites was dominated by a continuous *Cladina* carpet prior to the onset of caribou activity, disturbance severity was measured as the percentage of terrestrial lichen cover (*Cladina*, *Cladonia*, and *Stereocaulon*) remaining, a small cover percentage being associated with severe disturbance. To compare growth performance of *C. stellaris* among the study sites, border podetia from the two transects at each site were

pooled as they represent the woodland proper. In addition to the L/I ratio, we calculated annual internode growth, as the lichens were of different age (according to time elapsed since caribou disturbance). Because our results show that each internode grows for 7 to 9 y (Figure 2), we applied growth models of 7, 8, or 9 y (Table I). ANOVAs were used to compare total length (L), mean growth rate (L/I ratio), and annual internode growth of border lichens between sites. Multiple comparisons were performed using least square means tests (LSM; SAS 6.12, Cary, North Carolina, USA).

## Results

#### AGE OF LICHENS

For most plots, the median value of the year of the initial period of colonization (1990-1993) corresponded to the onset of the declining trend in GRCH activity (Figure 3). The age of lichens varied between 3 y and 21 y, but lichens over 16 y old were rare. The age range within a plot generally varied from 6 y to 9 y. Significant differences were found in 17 out of the 25 comparisons (Kolmogorov-Smirnov test) between the age structure (frequency distribution of internodes) of border and trail lichens (Table II, Figure 3). When significant differences were found, the age structures of trail lichens were always younger than those of border lichens. Moreover,

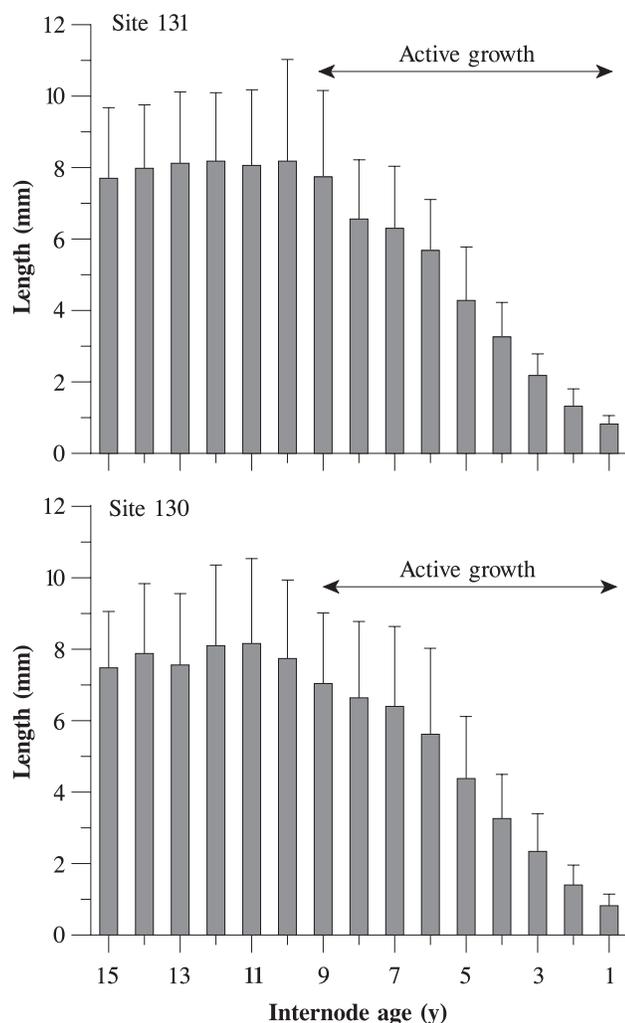


FIGURE 2. Internode length in relation to internode age (mean + SD).

six out of eight comparisons showing no significant differences between the two age structures were from sites located in the southern part of the calving ground.

#### PODETIIUM CHARACTERISTICS AND CARIBOU DISTURBANCE SEVERITY

The remaining fruticose lichen cover, used here as an index of caribou disturbance from heavily disturbed to least-disturbed plots, ranged between 5% and 85% (5% to 85% in the borders and 5% to 60% in the trails). Podetium length and L/I ratio in border ( $r^2 = 0.81$ ,  $P < 0.001$  and  $r^2 = 0.82$ ,  $P < 0.001$ , respectively) and trail ( $r^2 = 0.54$ ,  $P < 0.001$  and  $r^2 = 0.53$ ,  $P < 0.001$ , respectively) plots were significantly associated with disturbance severity (Figure 4).

#### GROWTH PERFORMANCE OF LICHENS

Border lichens were representative of the lichens distributed across the woodlands and varied in length between 15.9 and 80.5 mm. Two major groups were determined based on presence (group 1) or absence (group 2) of the decaying basal part of the podetium. The first group was divided into two subgroups based on podetium length. Subgroup 1a (sites 130 and 131) had the

TABLE I. Number of growing internodes  $\cdot y^{-1}$  according to duration of active growth of each internode (7, 8, or 9 y).

Internode	7 years		8 years		9 years	
	Total number of internode growth years		Total number of internode growth years		Total number of internode growth years	
	Ind. <sup>1</sup>	Cum. <sup>2</sup>	Ind.	Cum.	Ind.	Cum.
1 (youngest internode)	1	1	1	1	1	1
2	2	3	2	3	2	3
3	3	6	3	6	3	6
4	4	10	4	10	4	10
5	5	15	5	15	5	15
6	6	21	6	21	6	21
7	7	28	7	28	7	28
8	7	35	8	36	8	36
9	7	42	8	44	9	45
10	7	49	8	52	9	54
11	7	56	8	60	9	63
12	7	63	8	68	9	72
13	7	70	8	76	9	81
14	7	77	8	84	9	90
15 (oldest internode)	7	84	8	92	9	99

<sup>1</sup> Ind: Number of growth years of individual internode.

<sup>2</sup> Cum: Cumulative number of internode growth years for a podetium of  $n$  internodes.

following characteristics: length of 79.6-80.5 mm and mean growth rate of  $5.6 \text{ mm} \cdot \text{y}^{-1}$ . Both sites were located at the fringe of the summer and winter habitats (Figure 5). In subgroup 1b (sites 1D, 2, 118), mean length varied from 37.9 to 51.2 mm and mean growth rate ranged from 3.3 to  $4.9 \text{ mm} \cdot \text{y}^{-1}$ . Two of the sites were located in the calving ground, while the other one was in the southern part of the summer habitat. Group 2 included sites with mean podetium length  $< 22.0 \text{ mm}$  and mean podetium growth rate ranging between 1.9 and  $2.7 \text{ mm} \cdot \text{y}^{-1}$ . All the sites of group 2 were located in the calving ground or just outside the calving ground along the Ungava Bay coast. Significant inter-site differences were found for the two variables ( $P < 0.001$ ). Intra-group differences also were found based on LSM tests (Figure 5). Growth per internode per year (Table III) showed the same pattern as the L/I ratio. However, differences between sites were less pronounced when considering the growth per internode per year than the L/I ratio (about two times higher *versus ca* three times higher in the control site than in sites with the lowest growth performance).

## Discussion

Age, length, and mean growth rate of *Cladina stellaris* podetia were used to date the initial period of lichen colonization following the decrease of the GRCH's activity and also to evaluate the growth performance of this dominant lichen species during the initial stage of lichen recovery across the summer habitat of the herd.

#### INITIAL PERIOD OF LICHEN RECRUITMENT

The age of podetia was used to date the initial period of lichen recruitment, lichen age being closely related to the time elapsed since cessation of caribou disturbance. However, the age of lichens can only be determined accu-

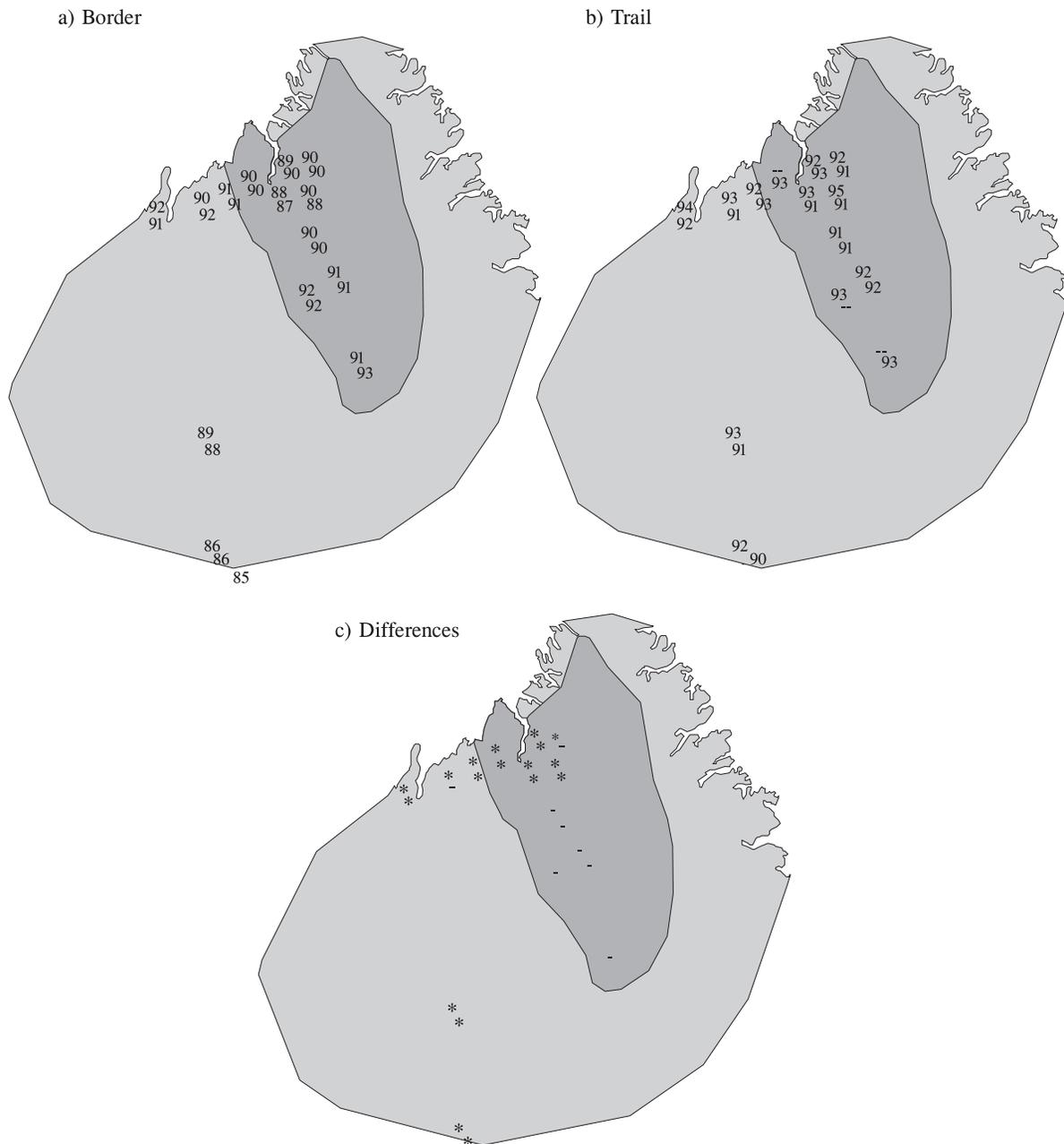


FIGURE 3. Median value of the initial period of lichen recruitment in a) the border and b) the trail, and c) results of Kolmogorov-Smirnov tests (at  $P = 0.05$ ) for each trail in relation to location of the study sites (\* = significant differences, - = no significant differences; dark grey: GRCH calving ground; pale grey: GRCH summer habitat).

rately when lichen is still in the first growth stage, *i.e.*, when the basal portion is not decaying, which is the case in heavily disturbed sites. In most of these sites, the initial period of lichen recruitment following caribou disturbance was in the late 1980s and early 1990s (Figures 3 and 4), after the onset of decline of caribou activity (Boudreau *et al.*, 2003). Lichen recruitment is likely associated with better podetium survival due to the decline in caribou activity during the 1990s.

Comparisons between the age structures of border and trail lichens were used as an index of caribou activity at the site scale. The absence of significant differences between age structures is likely associated with similar

caribou activity in both environments. In lightly disturbed sites, the age structures of trail lichens were always younger than those of border lichens. However, border lichens do not represent the first cohort established following the decrease of caribou activity, because the lichen carpet was not destroyed. The situation is different when considering sites where both border and trail lichens were recently established and are still in the first growth stage, as revealed by the absence of decaying basal podetia. For sites located in the southern part of the calving ground, the initial period of lichen recruitment in the border micro-environment was somewhat delayed (Figure 4), resulting in non-significant differences between border

TABLE II. Kolmogorov-Smirnov test on the age structure of *Cladina stellaris* podetia in and along caribou trails.

Site		<i>n</i> (border/trail)	Maximum difference observed	Critical value	Verdict
2D	1	(56/30)	0.311	0.307	S
	2	(39/19)	0.302	0.380	NS
10	1	(41/37)	0.428	0.308	S
	2	(66/58)	0.564	0.244	S
11	1	(37/28)	0.678	0.340	S
	2	(43/43)	0.140	0.293	NS
31	1	(41/36)	0.308	0.310	NS
	2	(41/39)	0.175	0.304	NS
33	1	(53/23)	0.424	0.339	S
	2	(38/32)	0.416	0.326	S
50	1	(25/0)			
	2	(35/17)	0.534	0.401	S
55	1	(41/22)	0.563	0.359	S
	2	(37/29)	0.346	0.337	S
124	1	(25/0)			
	2	(24/31)	0.210	0.369	NS
128	1	(39/27)	0.288	0.340	NS
	2	(36/18)	0.361	0.392	NS
132	1	(20/5)	0.450	0.679	NS
	2	(49/0)			
1D	1	(89/41)	0.869	0.256	S
	2	(56/67)	0.496	0.246	S
2	1	(63/37)	0.790	0.281	S
	2	(36/43)	0.694	0.307	S
118	1	(43/40)	0.753	0.461	S
	2	(43/45)	0.298	0.290	S
130	1	(44/29)	0.829	0.325	S
	2	(40/32)	0.788	0.322	S

Comparisons were not possible for trails at site 50-1, site 124-1, and site 132-2 because *Cladina stellaris* podetia were absent.

and trail age structures. These data suggest that caribou activity was still relatively important in this area even after the GRCH started to decline.

#### DISTURBANCE SEVERITY AND GROWTH PERFORMANCE

The cover of fructicose lichens of the 57 plots was used as an index of caribou disturbance severity because prior analyses of plant remains and old aerial photos showed that ground vegetation of lichen-spruce woodlands was dominated by a continuous lichen carpet prior to the onset of caribou disturbance (Boudreau & Payette, 2004). Moreover, van der Wal *et al.* (2001) showed that there is a strong relation between cover of fructicose lichens and reindeer pellet density. Because lichens are poikilohydric organisms, *i.e.*, unable to control their water status (Hyvärinen & Crittenden, 1998; Palmqvist, 2000), and because growth occurs only when moisture is sufficient, even at low temperatures (Kershaw & Rouse, 1971; Nash, 1996), growth rate is closely linked to the ability of the lichen thallus to retain moisture. In lightly disturbed sites, the continuous lichen mat was likely more efficient at retaining moisture for a longer period than the scarce lichen cover in heavily disturbed sites. As a result, lichens had a longer period of active growth. Length and growth rate of lichen thallus are both strongly associated with caribou disturbance severity. However, the relation is stronger in borders than in trails. The lower growth performance of *C. stellaris* in trails was associated with a greater cover of exposed mineral soil, which reduces ambient soil and air moisture.

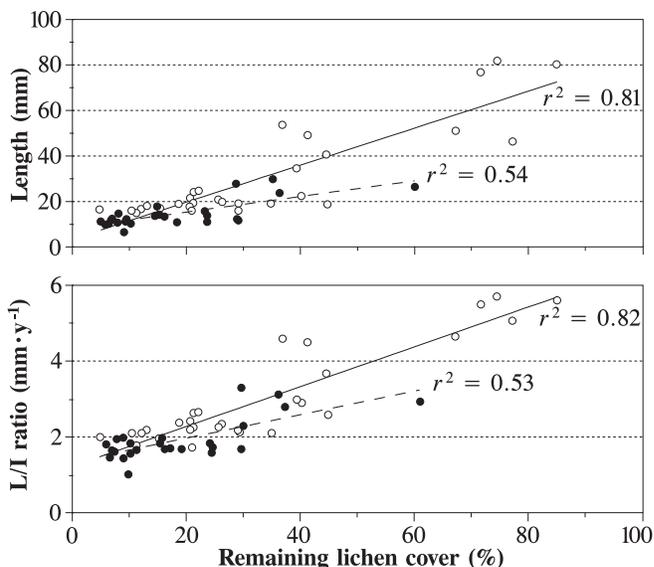


FIGURE 4. Relation between length and mean growth rate and lichen cover (open dots: border plots; black dots: trail plots; solid line: regression line for border plots; broken line: regression line for trail plots).

#### GROWTH PERFORMANCE ACROSS THE SUMMER HABITAT

The growth performance of *C. stellaris* was determined based on two complementary methods: the conventional one, called the L/I ratio, used in many studies (Scotter, 1963; Pegau, 1968; Karenlampi, 1971; Ouzilleau & Payette, 1975), and a new one based on annual growth of internode. The gradients in the growth performance from the two methods are in good agreement. Length and growth rate of border lichens, representative of the woodland proper, allowed us to classify the sites along a *C. stellaris* growth performance gradient. Moreover, spatial patterns in growth performance should reflect the spatial use of caribou over the summer habitat.

Lichens with podetia showing decaying basal parts are lichens that experienced light to moderate disturbance. Long growth (*ca* 80 mm) and high growth rate ( $5.6 \text{ mm} \cdot \text{y}^{-1}$ ) of lichen podetia are representative of old-growth lichen woodlands at the southern edge of the summer habitat, not disturbed during the last 100 y at least. The growth performance of these lichens is comparable to those in other old-growth lichen-dominated woodlands (Scotter, 1963; Pegau, 1968; Ouzilleau & Payette, 1975). Intermediate growth performance is mainly associated with moderate caribou grazing, since moderate or heavy trampling would have destroyed the lichen carpet and exposed the mineral soil. In contrast, lichens established in the early 1990s showed reduced growth performance, with podetia showing anomalous characteristics due to poor growth conditions. Slow-growth lichens were from sites located in the calving ground area or along the Ungava Bay coast, where ground vegetation is broken by exposed mineral soils and colonized by *Cladonia*, *Cetraria*, and crustose lichens (Morneau, 1999).

The analysis of the growth performance of lichens increases our knowledge of the effect of trampling and grazing in lichen-dominated stands at the plant level. The age of *C. stellaris* podetia gives information on the initial

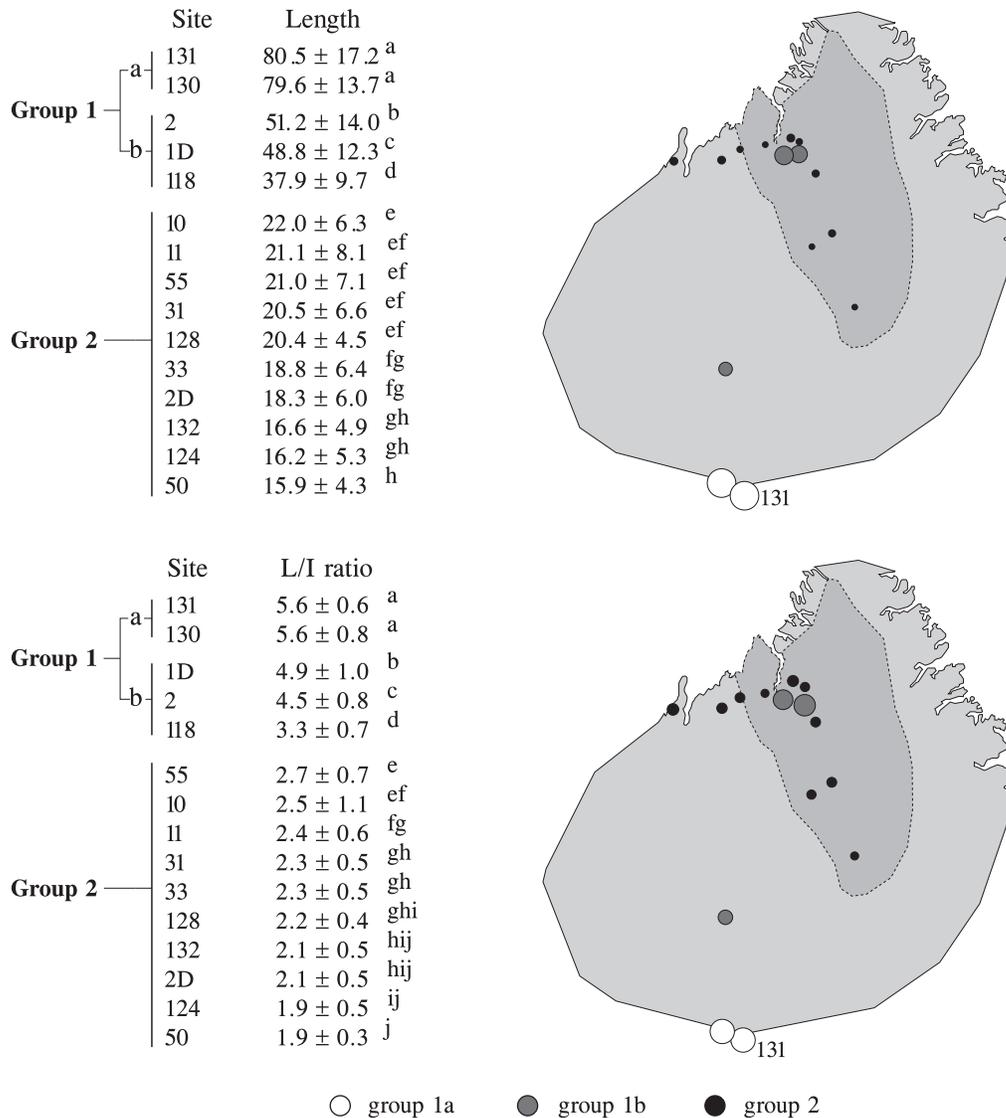


FIGURE 5. Border lichen growth performance in relation to location of the study sites. Symbol size is proportional to length and mean growth rate (different letters indicate significant differences according to LSM tests at  $P = 0.05$ ; dark grey: GRCH calving ground; pale grey: GRCH summer habitat).

period of lichen recovery in heavily disturbed sites. Our data show that there is a strong relation between growth performance of *C. stellaris* and severity of caribou disturbance. Spatial variations in growth performance are in agreement with the spatiotemporal use of the summer habitat by the GRCH. Growth rate of lichens has major implications for lichen recovery, particularly in heavily disturbed sites where plant recovery and growth performance of lichens are lowest.

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Table III. Performance of border lichen estimated with two different methods (L/I ratio and growth per internode per year, mean ± 1 SD).

Site	L/I ratio mm · y <sup>-1</sup>	Duration of internode growth (mm · internode · y <sup>-1</sup> )		
		7 years	8 years	9 years
131	5.6 ± 0.6 <sup>a</sup>	1.03 ± 0.12 <sup>a</sup>	0.94 ± 0.11 <sup>a</sup>	0.88 ± 0.11 <sup>b</sup>
130	5.6 ± 0.8 <sup>a</sup>	1.02 ± 0.17 <sup>a</sup>	0.94 ± 0.16 <sup>a</sup>	0.88 ± 0.16 <sup>b</sup>
1D	4.9 ± 1.0 <sup>a</sup>	1.03 ± 0.27 <sup>a</sup>	0.98 ± 0.28 <sup>a</sup>	0.95 ± 0.29 <sup>a</sup>
2	4.5 ± 0.1 <sup>c</sup>	0.90 ± 0.18 <sup>b</sup>	0.85 ± 0.18 <sup>b</sup>	0.81 ± 0.18 <sup>c</sup>
118	3.3 ± 0.7 <sup>d</sup>	0.66 ± 0.14 <sup>c</sup>	0.61 ± 0.14 <sup>c</sup>	0.59 ± 0.14 <sup>d</sup>
55	2.7 ± 0.7 <sup>e</sup>	0.67 ± 0.20 <sup>c</sup>	0.66 ± 0.20 <sup>c</sup>	0.65 ± 0.20 <sup>e</sup>
10	2.5 ± 1.1 <sup>ef</sup>	0.54 ± 0.12 <sup>d</sup>	0.52 ± 0.12 <sup>d</sup>	0.51 ± 0.13 <sup>f</sup>
11	2.4 ± 0.6 <sup>fg</sup>	0.54 ± 0.12 <sup>d</sup>	0.52 ± 0.12 <sup>d</sup>	0.51 ± 0.12 <sup>f</sup>
31	2.3 ± 0.5 <sup>gh</sup>	0.50 ± 0.14 <sup>de</sup>	0.49 ± 0.14 <sup>defg</sup>	0.48 ± 0.14 <sup>fg</sup>
33	2.3 ± 0.5 <sup>gh</sup>	0.53 ± 0.13 <sup>d</sup>	0.51 ± 0.14 <sup>de</sup>	0.51 ± 0.14 <sup>f</sup>
128	2.2 ± 0.4 <sup>ghi</sup>	0.47 ± 0.09 <sup>efg</sup>	0.45 ± 0.10 <sup>fgh</sup>	0.44 ± 0.10 <sup>gh</sup>
132	2.1 ± 0.5 <sup>hij</sup>	0.50 ± 0.13 <sup>def</sup>	0.49 ± 0.13 <sup>deg</sup>	0.49 ± 0.13 <sup>fg</sup>
2D	2.1 ± 0.5 <sup>hij</sup>	0.47 ± 0.11 <sup>efg</sup>	0.46 ± 0.12 <sup>fgh</sup>	0.45 ± 0.12 <sup>gh</sup>
124	1.9 ± 0.5 <sup>ij</sup>	0.45 ± 0.13 <sup>fg</sup>	0.43 ± 0.13 <sup>gh</sup>	0.43 ± 0.14 <sup>gh</sup>
50	1.9 ± 0.3 <sup>i</sup>	0.43 ± 0.11 <sup>g</sup>	0.42 ± 0.12 <sup>h</sup>	0.41 ± 0.12 <sup>h</sup>

Different letters indicate significant differences at  $P = 0.05$ .

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