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A dendroecological method to evaluate past caribou (*Rangifer tarandus* L.) activity[1,2]

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Abstract: Records of population changes of caribou come from various sources (historical accounts, hunting and trading statistics, herd surveys) that are typically incomplete and discontinuous in time and space. Here we propose a new method for the evaluation of past caribou activity using tree-ring records from boreal and subarctic conifer stands. The age-frequency distributions of trampling scars produced by caribou hooves on surficial roots and low branches of erect and stunted conifers are used as an index of the passage of caribou through stands during the snow-free period. To verify if changes in the age structure of trampling scars correspond to changes in abundance of caribou movement, we analyzed factors influencing production and loss of scars at two lichen-woodland sites in northeastern Québec-Labrador (Canada). The detailed analysis of trampling scars in the first site indicates that the capacity of conifers to produce scars is maintained under a regime of repeated caribou traffic; scars were formed at new positions along the exposed roots and scars continued to be produced at a same position in a minimum time of one growing season, even after 15 years of caribou traffic. The influence of repeated caribou trampling on loss of scars was measured by comparing the age structure of scars of three vegetation groups (based on caribou trail network) with different intensities of use. The similarity of the age structures of the three groups showed that scar loss due to trampling was hardly detectable, which indicated that scar loss was low in comparison to the number of scars produced, even in the most used trails. Sampling of trampling scars during two successive years at the second site showed that the stability of the age structure of scars was not affected by moderate caribou traffic. Our results, therefore, indicate that most of the information deduced from the age structures of trampling scars comes from changes in caribou activity. The method opens the possibility of assessing caribou activity in time (several decades) and space over large areas of the boreal forest and the forest-tundra biomes.
Keywords: boreal forest, conifer roots, dendroecology, lichen woodlands, *Rangifer tarandus*, subarctic, tree rings.

Résumé: Notre connaissance de la dynamique des populations de caribou provient de diverses sources (documents historiques, données sur la chasse et le commerce, inventaire des troupeaux) qui livrent une information incomplète et discontinue dans l'espace et dans le temps. Nous présentons ici une méthode dendroécologique qui permet d'évaluer la fréquentation passée des milieux conifériens par le caribou au cours de la période sans neige. La fréquentation est évaluée au moyen de la structure d'âge des cicatrices de piétinement qui se forment sur les racines superficielles et les branches basses (chez les individus prostrés) des conifères sous l'impact des sabots de l'animal. Afin de vérifier si les fluctuations dans la structure d'âge des cicatrices correspondent à des changements dans la fréquentation, nous avons effectué une analyse des facteurs qui contrôlent la formation et la perte des cicatrices dans deux pessières à lichens du nord-est du Québec-Labrador (Canada). L'étude exhaustive des cicatrices dans un premier site indique que la capacité des conifères à produire des cicatrices se maintient sous un régime de fréquentation soutenu ; des cicatrices se sont formées à de nouvelles positions sur les racines exposées et des cicatrices superposées ont continué de se produire dans l'intervalle de temps minimum d'un an après 15 ans de fréquentation. L'influence du passage répété du caribou sur la perte des cicatrices a été étudiée dans le même site par la comparaison de la structure d'âge provenant de trois strates de végétation (définies d'après le réseau de sentiers de caribou) ayant connu une intensité différente dans la fréquentation. La similarité des structures d'âge permet difficilement de déceler la perte différentielle de cicatrices entre les trois strates, indiquant que cette perte est faible comparée au nombre de cicatrices produites et ce, même dans les sentiers fortement fréquentés. Grâce à l'échantillonnage des cicatrices deux années consécutives, on démontre que la fréquentation modérée du caribou au cours d'une année dans un second site d'échantillonnage n'a pas affecté la stabilité de la structure d'âge. Nos résultats suggèrent que la majeure partie de l'information contenue dans les structures d'âge de cicatrices est attribuable aux changements dans la fréquentation des sites par le caribou. Cette méthode offre la possibilité d'évaluer les patrons spatio-temporels d'activité du caribou dans la forêt boréale et la toundra forestière au cours des dernières décennies.
Mots-clés: cernes de croissance, dendroécologie, forêt boréale, pessière à lichens, racines de conifère, *Rangifer tarandus,* subarctique.

Introduction

Caribou (*Rangifer tarandus* L.) populations experience large fluctuations in size, density and distribution at different temporal and spatial scales. Herds have distinct seasonal distributions, often involving wide-ranging migrations associated with changes in animal density (Kelsall, 1968; Skoog, 1968; Parker, 1972; Gaare & Skogland, 1975; Klein & Kuzyakin, 1982; Thing, 1984; Vandal *et al.*, 1989; Russell, Martell & Nixon, 1993). Annual distribution and range of migratory movements vary according to the size of the herds over several decades (Skoog, 1968; Hemming, 1975; Meldgaard, 1986; Messier *et al.,* 1988). Because demographic data of caribou populations are severely impaired by the large and variable spatial and temporal scales to which the animals are tuned, our knowledge of herd dynamics is based on fragmentary information. A partial reconstruction of historical population trends is possible

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through the use of diverse documentary sources such as hunting and trading statistics, published accounts of explorers and naturalists, as well as company and mission journals (Elton, 1942; Vibe, 1967; Kelsall, 1968; Parker, 1972; Meldgaard, 1986; Fritz, Suffling & Younger, 1993).

In North America, the recent dynamics of caribou populations were assessed by aerial surveys of herds since the late 1940s (Banfield, 1954; Watson & Scott, 1956; Banfield & Tener, 1958; Siniff & Skoog, 1964; Bergerud, 1967; Kelsall, 1968; Parker, 1975). The surveys were used to evaluate the number of caribou, and their seasonal distribution and migratory patterns. Since the first aerial surveys, major improvements in the evaluation of herd sizes have relied on the use of aerial photography and radio-telemetry (Heard, 1985; Valkenburg *et al.,* 1985; Crête *et al.,* 1991; Couturier *et al*., 1996). Telemetric surveys of caribou equipped with radio-transmitters have also improved survey data on seasonal distribution, migratory movements and patterns of habitat use (Brown *et al.,* 1986; Curatolo, 1986; Vandal *et al.,* 1989; Russell, Martell & Nixon, 1993). Moreover, radio-telemetry has been increasingly used to estimate demographic parameters such as survival and parturition rates for the modeling of changing population size (Heisey & Fuller, 1985; Hearn *et al.,* 1990; Cameron *et al*., 1993; Fancy, Whitten & Russell, 1994; Crête *et al*., 1996). Despite clear improvement of survey techniques over the last two decades, however, the dynamics of caribou populations remain largely unknown.

Tree-ring data have been used to reconstruct past changes of animal populations such as moose (McLaren & Paterson, 1994), porcupine (Spencer, 1964; Payette, 1987), beaver (Bordage & Filion, 1988), hare (Sinclair *et al.,* 1993) and voles (Danell, Ericson & Jakobsson, 1981). Also, tree-rings are widely used to document the history of forest insect infestations (Mott, Nairn & Cook, 1957; Blais, 1962; 1965; Brubaker & Greene, 1979; Swetnam, Thompson & Sutherland, 1985; Swetnam & Lynch, 1989; 1993; Veblen *et al*., 1991; Jardon, Filion & Cloutier, 1994). The impact of animal activity on trees or shrubs is shown by reduced radial growth due to browsing or defoliation (moose and phytophagous insects), feeding scars (porcupine and voles), anomalous rings following browsing (hare), or improved radial growth in surviving trees following clearing by beaver.

In this paper, we propose a dendroecological method for the evaluation of past caribou activity during the snow-free period using tree-ring records from boreal and subarctic conifer stands. The method is based on debarking lesions (trampling scars) produced by caribou hooves on surficial roots and low branches of conifers. Wood lesions are dated dendrochronologically and age-frequency distributions of trampling scars are used as an index of the passage of caribou in conifer stands. Use of the age structure of trampling scars rests on two premises. First, the number of trampling scars produced annually is proportional to the intensity of caribou activity, *i.e*., more scars are formed when more animals pass through the site. Second, any changes in the age structure of trampling scars correspond to changes in the rate of scar formation. Because there is no count of caribou passing through lichen woodlands that can be linked to the abundance of trampling scars, we analyzed factors influencing the production and loss of trampling scars at two sites in order to verify the premises. Our analysis of the age structure of trampling scars was based on an exhaustive sampling of scars in a lichen woodland used by caribou each year for at least the last 15 years (sampling years: 1992 and 1993). Several points were considered in the analysis. First, the record of the passage of caribou was documented by an analysis of the number, distribution and age of root scars. Whether the recorded damage decreases with repeated root trampling by caribou also was considered. Second, the effect of age of roots on the age structure of trampling scars was evaluated. Third, the influence of repeated caribou walking on exposed roots was measured by comparing the age structure of trampling scars from trails with different intensities of use. Fourth, anatomical changes in the wood structure of exposed roots associated with disturbance by caribou were dated to check for a delay between root exposure and scar formation, to identify the various stages of trail development and use, and the periods of disturbance of the lichen cover by caribou. Finally, a second site was selected to evaluate the impact of caribou traffic during two successive years on the stability of the age structure of trampling scars.

Material and methods

Study area

Our method was developed in northeastern Québec-Labrador in the summer range areas of the Rivière George herd. These areas have been heavily used by caribou during past decades due to the recent expansion of the herd (Messier *et al*., 1988). The two study sites are old-growth lichen woodlands located 50-60 km south of Kangiqsualujjuaq on the south coast of Ungava Bay. The region, dominated by tundra vegetation, is located in the forest-tundra bordered to the east by the shrub tundra of the Rivière George plateau (Payette, 1983). It has been used by caribou in spring and summer since at least the 1970s (Messier *et al*., 1988, Crête *et al*., 1991, Couturier *et al*., 1996). The study sites are crossed by migrating caribou, and caribou occupy the area during calving time and in summer. Note that distribution and migratory patterns of the Rivière George herd have changed markedly across the summer range during the last decades (Messier & Huot, 1985). For instance, the calving areas were located west and south of the two study sites during the 1970s and 1980s (Messier *et al*., 1988), but since the end of the 1980s, the sites have been inside the calving grounds (Crête *et al*. 1991, Couturier *et al*., 1996).

The Rivière George site (RG) is located on a sandy river terrace (58° 12' N, 65° 48' W). The postfire lichen woodland has a 20% tree cover dominated by black spruce, with frequent tamarack and white spruce (Figure 1a). Dominant trees are about 10 m in height, and the oldest individuals are at least 150 years old. Ground vegetation is dominated by lichens and shrubs. The shrub cover (< 10 %) is composed of dwarf birch (*Betula glandulosa* Michx) and heath (*Ledum groenlandicum* Retzius and *Vaccinium vitis-idaea* L.). Lichens cover about 80% of the stand, with about 25% of dead thallii. *Cladina stellaris* (Opiz) Brodo is the dominant species with 30% cover, followed by *C. rangiferina* (L.) Harm. and *Stereocaulon paschale* (L.) Hoffm., both with 10% cover; the tallest thallii average 3 cm in height.

The Lac De Caen site (LC) is located on a rocky hill covered by till, 13 km northeast of the RG site at the altitudinal limit of conifer stands (58° 17' N, 65° 38' W; altitude 250 m). The site is occupied by an old-growth black spruce krummholz (30% cover), with trees about 1-1.5 m in height (Figure 1b). Like all the conifer stands on the Rivière George plateau, this site has been heavily used by caribou. The lichen cover is completely destroyed (< 5% cover, with live thallii ≤ 0.5 cm high), shrubs have been heavily browsed, and the organic and mineral soil layers are exposed at several places.

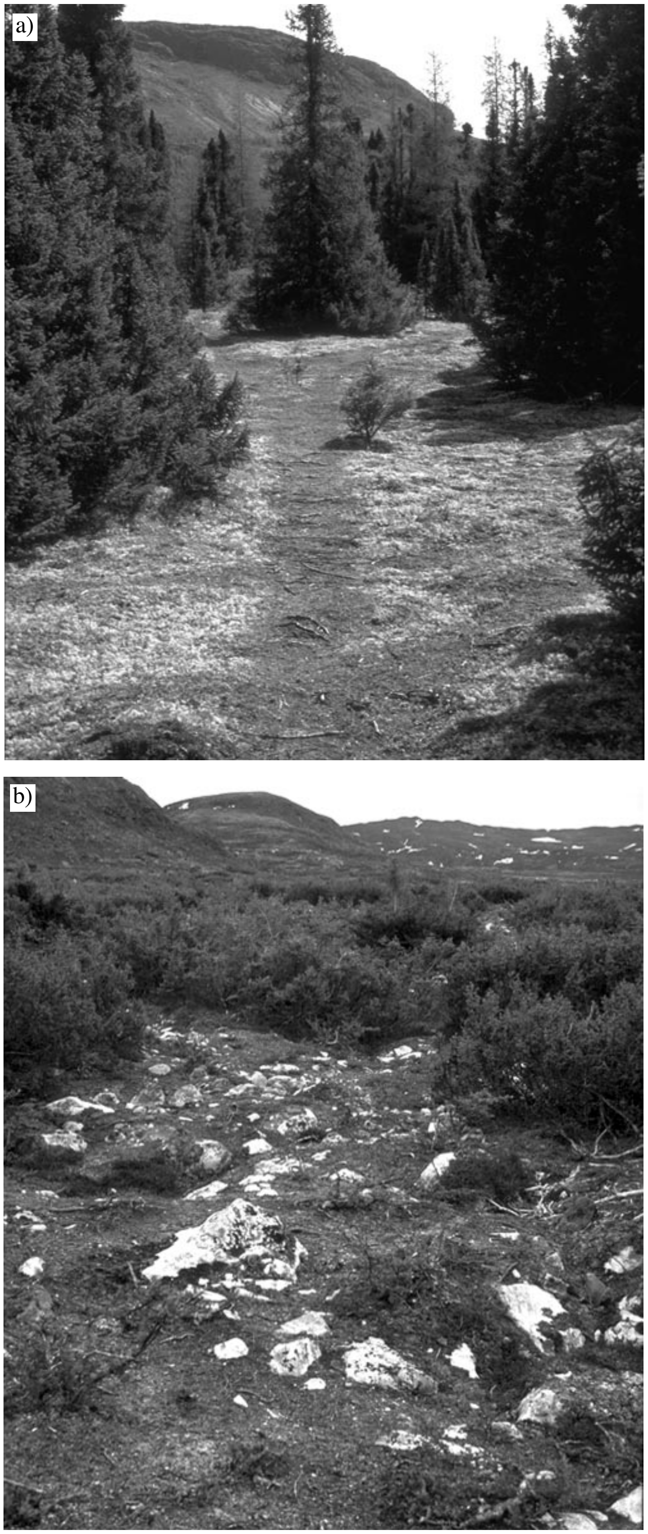

FIGURE 1. a) Caribou trails crossing the lichen-spruce woodland at the RG site. b) Krummholz stand in the LC site with severe damage to the ground vegetation by caribou trampling and grazing.

CHARACTERISTICS OF TRAMPLING SCAR AND SCAR DATING

Caribou trampling scars are formed on surficial roots (Figure 2a) and low branches during the snow-free period. In forest stands the scars are exclusively formed on roots, whereas in krummholz stands they are also found on branches and leaning stems. The scars result from local debarking after the impact of caribou hooves that cause cambium death and radial growth to stop (Figure 2b). The xylem can be exposed at the time of impact or later when dead bark is shed; sometimes the xylem is completely covered by resin. Caribou trampling scars are easily recognized by their shape and position on roots. They are round, elliptic or slightly elongated in shape with neat margins. The scars are located at the top or the sides of exposed roots, particularly along caribou trails. They can occur at various places along the roots and at the same position, as superposed scars (Figure 2a, 2c). Secondary growth at the periphery of the lesion gradually overgrows the scar. However, xylem may remain exposed for several years, especially when superposed scars are produced. The size of scars is a function of the diameter of roots. Several scars (diameter < 1 cm) can be formed on small roots. No evidence was found for other biotic or abiotic factors producing these scars in the study area. Similar scars can be produced by other ungulates or as a result of human disturbance, as observed on hiking paths. However, the Rivière George area is a pristine region and no other species of ungulate is present.

The age of a scar is determined by the number of annual rings added after the lesion formed. The rings must be cross-dated because some rings may be absent from the sampled cross-sections. Cross-dating is a procedure based on the variability of the structure of rings (width, density, etc.) to correctly identify the year of formation (Fritts, 1976). The exact year of scar formation is determined only when the lesion is produced during xylem growth (cell division) (Figure 2b). Even when all the rings are cross-dated, there is a ± 1-year error inherent in the dating when scars are formed during the seasonal dormant phase of cambium. Hence, dating spans two calendar years, *i.e.*, the fall of one year and the spring of the next. The year of scar formation was attributed to the most recent year.

CHANGES IN WOOD STRUCTURE OF ROOTS

Many exposed roots along caribou trails produce stem-like annual rings. Typical root rings are composed of a few cell layers with the latewood (the later formed cells, radially flattened) relatively similar to earlywood (isodiametric cells) in colour and wall thickness, and forming only a small portion of the ring. In many scarred roots, such rings are

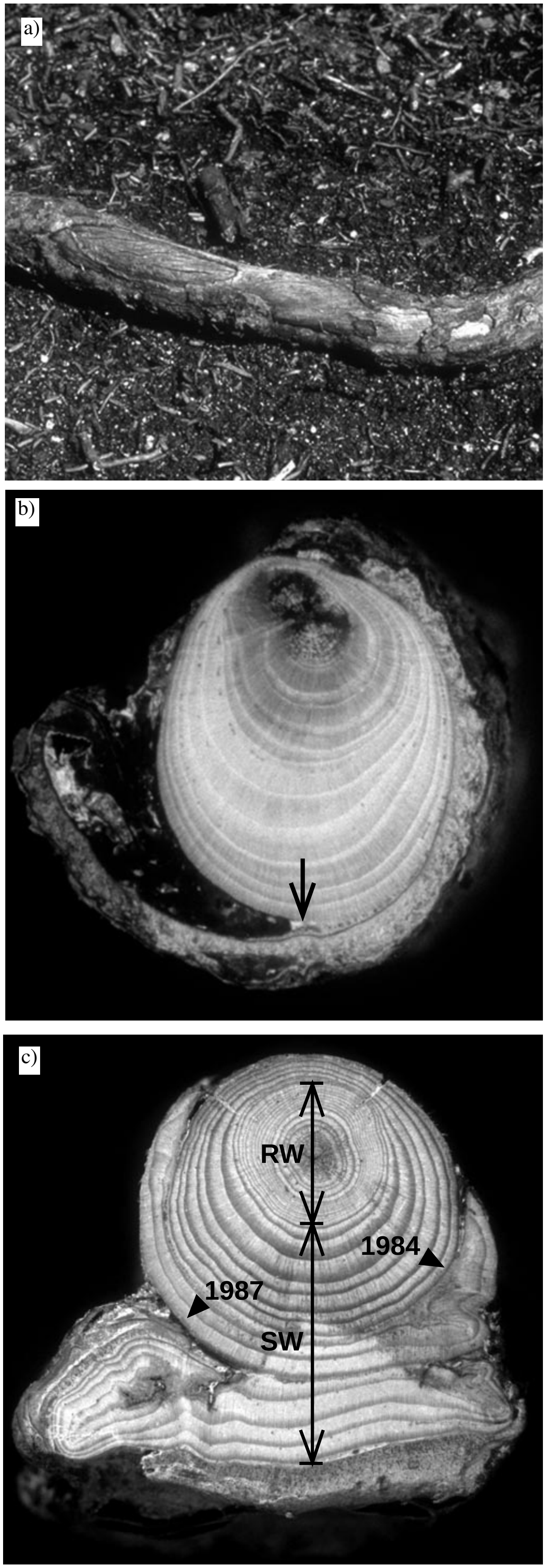

FIGURE 2. Caribou trampling scars on conifers. a) Superposed trampling scars with exposed xylem on a surficial black spruce root. b) Cross-section of a root locally debarked by caribou trampling. The scar was formed during the period of ring formation of the sampling year (arrow). c) Cross-section of a root showing two trampling scars and an abrupt transition in wood structure between root wood (RW) and stem wood (SW) that occurred in 1977.

followed by wider ones having latewood cells that differ markedly from earlywood cells by a brownish colour and a dense structure. This results from the presence of tracheids that are smaller and have thicker cell walls (Figure 2c). The distinction between root wood and stem wood is general in gymnosperms; root xylem normally differs from stem xylem in having a smaller proportion of latewood, larger tracheids with thinner cell walls, and little or no difference in wall thickness across the annual ring (Fayle, 1968; Timell, 1986). The anatomical changes of wood discussed here (Figure 2c) are associated with the exposure of roots following the destruction of lichen cover by caribou; stem-like wood initiation does not result from scar formation because these two events are not always simultaneous. In general, burial or exposure of woody plants induces a rapid modification of wood structure (Patel, 1965; Timell, 1986; Cournoyer & Bégin, 1992; Cournoyer & Filion, 1994). Exposed roots readily adopt the anatomical structure of stem wood; roots produce xylem similar to that of shoots during the same season the exposure occurred (Patel, 1965; Fayle, 1968). Fayle (1968) reported that exposure of conifer roots causes the formation of smaller tracheids and an increase in radial growth.

SAMPLING OF TRAMPLING SCARS IN RG SITE

Sampling was done in a quadrat (40 m $\times$ 40 m) randomly positioned near the centre of the lichen woodland. The vegetation was mapped according to caribou use. The vegetation cover was divided into three groups based on the caribou trail network and the amount of vegetation disturbance (Figure 3). Group 1 corresponded to well-developed trails with exposed organic and mineral soils, lichen debris and other plant detritus. Group 2 included weakly-developed trails composed of lichen debris and litter, small live thallii (< 1 cm) and locally exposed organic soils. The trails were generally short (< 10 m) and located near physical obstacles like spruce clones, fallen trees and boulders, thus causing the caribou to converge as they moved. The trails often ended in open areas, gradually fading into the lichen cover, resulting in a typically discontinuous pattern (Figure 3). Caribou trails (groups 1 and 2) ranged between 25 and 45 cm in width. Group 3 included the relatively undisturbed vegetation cover delineated by spruce clones (Figure 3). All the trails and conifers ≥ 2 m high were mapped on a grid at intervals of 1 m (1600 1 m^2 cells).

Trampling scars on live parts of conifers (all roots) were cross-sectioned. Scars were identified based on their external features (exposed xylem, resin accumulation). All roots exhibiting growth anomalies that could correspond to overgrown lesions were checked. Roots buried under plant debris on trails were exhumed to check for scar location. Root cross-sections were finely sanded and scars were dated under the binocular microscope. The year of scar formation

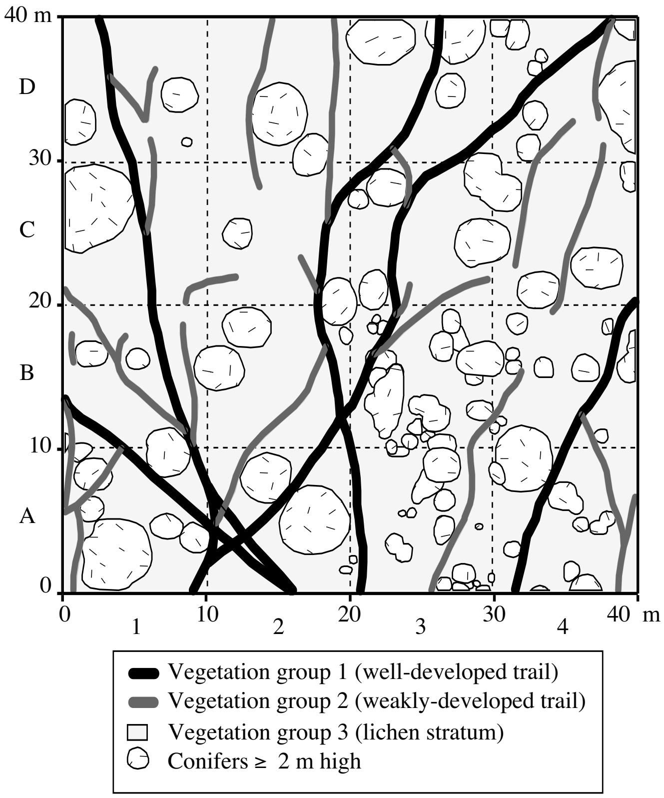

FIGURE 3. Network of caribou trails in a 40 m × 40 m quadrat in RG site.

was determined by cross-dated rings formed before and after the damage based on patterns of ring width and diagnostic light rings (Filion *et al*., 1986). In our samples, light rings were frequent in 1956, 1969, 1972 and 1978, and were present in both typical root wood and stem-like wood. Cross-dating was facilitated because several scars were located on the root system of the same individual. Damage was classified as to whether or not it occurred during the period of xylem growth. When cross-dating was unsuccessful, the rings between the lesion and the bark were counted to obtain a minimum age. All the scars collected in 14 out of 16 plots (each plot: 10 m × 10 m within the quadrat) were dated (excluding plots 1C and 1D; Figure 3). Only scars from groups 2 and 3 were studied in plots 1C and 1D.

Each scar was numbered according to its position in the quadrat, the trail and the root, and also according to its date of formation relative to that of other scars on the same cross-section of root, with scars numbered in an increasing order from the oldest to the most recent. Exposed roots (few decimetres in length) were also numbered according to their position within the quadrat. The diameter of live roots with or without scars and of dead roots located on the trails (vegetation groups 1 and 2) were measured. Root age was determined in a sub-sample of live, scar-bearing roots (n = 261) located along 65 m of well-developed caribou trails. Only a minimum age was calculated for many roots because of cross-dating problems due to reduced secondary growth typical of the period preceding root exposure.

The anatomical changes associated with root exposure were examined on roots from well-developed trails (vegetation group 1) and from the lichen stratum (vegetation group 3) to establish the chronology of trail development and disturbance of the lichen cover. All roots where the vegetational cover was classified as group 3 were examined, whereas in the case of group 1 we analyzed a subsample of roots collected along 59 m of trails in a 20 m × 20 m sub-quadrat (plots 2A, 2B, 3A and 3B; Figure 3). The sub-sample included about 35% of all well-developed trails. Because the analysis of anatomical change was performed *a posteriori* on root cross-sections sampled for scar dating, exposed non-scarred roots were not studied. All the cross-sections of each sampled root were examined (the number of cross-sections per root was a function of the number of scars present). Root and stem-like wood rings were identified and dated in each cross-section. Both types of wood were readily identified under the binocular microscope according to latewood features (Figure 2c). In order to qualify as stem-like wood, the major part of the ring circumference included stem-like latewood. Abrupt anatomical change corresponded to a stem-like ring preceded by a root ring; an anatomical change was qualified as gradual when at least one ring showed intermediate characteristics between root wood and stem wood. The periods of anatomical transition were compiled for each root. The transition was usually synchronous among different cross-sections of a given root, minimizing the errors associated with a variable number of samples per root.

MINIMUM SAMPLE SIZE FOR THE ESTIMATION OF THE AGE STRUCTURE OF TRAMPLING SCARS

The large number of trampling scars recorded in the RG site was used to determine the appropriate sample size for the estimation of the age structure of scars. This was done by multiple sampling of different sample sizes of scars amongst all the scars dated with certainty. Multiple sampling was done on root cross-sections instead of individual scars because sampling in the field does not permit independent selection where superposed scars occur. One hundred samples of 50, 100, 150, 200, 300, and 500 root cross-sections were randomly chosen among the 1545 sections bearing scars dated with certainty.

SHORT-TERM VARIATION IN THE AGE STRUCTURE OF TRAMPLING SCARS AT LC SITE

The LC site, located at the centre of the calving grounds in 1993 (Couturier *et al*., 1996), was sampled in two consecutive years; July 1992 and August 1993. For both sampling dates, trampling scars were collected in 6 different 100 m^2 quadrats (10 m × 10 m) positioned along two parallel transects (3 quadrats per transect). The transects and the quadrats within each transect were 20 m apart. During the first sampling, the quadrats were placed by starting from a point randomly chosen near the centre of the stand. During the second sampling, the quadrats were juxtaposed to those of 1992 along the transects. All the trampling scars on living conifer roots and branches were sampled in each quadrat, although the scars were dated in only one randomly selected quadrat per sampling year. The two selected quadrats were 120 m apart.

Results

TRAMPLING SCARS IN RG SITE

NUMBER AND DISTRIBUTION OF SCARS AND ROOTS

A total of 2377 trampling scars was recorded on live roots in the 1400 m^2 quadrat. Most scars (90%, *n* = 2137) were located on trails which occupied a small part of the total area available to caribou (Figure 3); 74% of all scars (*n* = 1756) were located on well-developed trails (vegetation group 1) and 16% (*n* = 381) on weakly-developed trails (vegetation group 2). The average number of scars per metre of trail in group 1 (10.6 scars/m; 166 m of trail) was five-fold that of group 2 (2.2 scars/m; 173 m of trail). In the lichen stratum (vegetation group 3), the scars (10%, *n* = 240) were on scattered roots protruding above the ground.

About 70% (*n* = 930) of the 1326 exposed live roots on the trails were in vegetation group 1. Thus, there were 2.5 times more exposed roots per metre of trail in group 1 (5.6 roots/m) than in group 2 (2.3 roots/m). The number of scars per root (0 to 19) averaged 1.9 in group 1 and 1 in group 2. The proportion of scarred roots was comparable between both types of trails: 62% (*n* = 581) of live roots in group 1 and 56% (*n* = 220) in group 2 had at least one scar. A similar proportion also applies to dead roots with 10% (*n* = 101) and 9% (*n* = 37) of roots in groups 1 and 2, respectively. Therefore, the distinction between both types of trail based on vegetation characteristics is also correlated with the larger number of exposed roots and scars per root in well-developed trails.

Most of the exposed live roots on the trails were less than 1 cm in diameter (74.5%), and only 6.6% were greater than 2 cm (42.8%, 31.7%, 13.2%, 5.7%, and 6.6% of roots were in the < 5 mm, 5-10 mm, 10-15 mm, 15-20 mm, and ≥ 20 mm diameter classes, respectively). By comparison, 68% of all scars were on roots less than 1 cm and 6% on roots greater than 2 cm (28.5%, 39.6%, 18.4%, 7.6%, and 6.0% of scars were on roots < 5 mm, 5-10 mm, 10-15 mm, 15-20 mm, and ≥ 20 mm in diameter, respectively). Scars were underrepresented in roots less than 5 mm because the proportion of scarred roots was much less (47.4%) than in roots greater than 5 mm (69.5%). Small roots are more likely killed by caribou trampling, as suggested by the higher proportion of dead roots in roots less than 5 mm (15%) than in samples made up of roots of a larger size (4.8%).

AGE STRUCTURE OF TRAMPLING SCARS

The age structure of scars shows that the site has been used by caribou on a yearly basis since at least 1975 (Figure 4). The number of scars formed was high between 1984 and 1990 (95% of all scars), with peaks in 1985 and 1988 that represented 49% of all sampled scars. Prior to this period, the highest frequencies were in 1981 and between 1975 and 1979. The age structure of scars (Figure 4) was constructed based only on scars that could be dated with certainty, *i.e.*, 80% (*n* = 1898) of all the scars sampled in the 1400 m^2 quadrat. The frequency distribution of the minimum age of scars that were excluded from the compilation of the age structure of the scar population because of uncertain dating (20%; *n* = 479) is similar to that of scars dated with certainty. The minimum age of scars with uncertain dating was less than 16 years (scar formation in 1976) in 99% of the cases and less than 9 years (scar formation in 1983) in 96% of the cases. So, nothing suggests that scars with uncertain dating were older than the others.

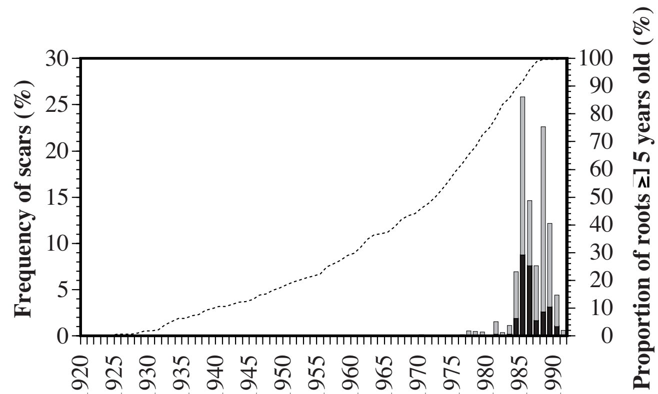

FIGURE 4. Age structure of trampling scars in RG site and proportion of roots ≥ 5 years old each year (broken line). Black portion of columns correspond to scars formed during ring development.

Of all the scars dated with certainty, 27% (*n* = 518) were formed during the growing season (Figure 4). As the exact year of formation was known only for these scars, the annual variations of the number of scars may be modified based on a minimum age (early spring damage) or a maximum age (autumn damage) of scar formation. Maximum frequencies of scar formation occurred in 1984 and 1987 when the maximum age of scars is used.

INFLUENCE OF ROOT AGE

In order to assess the influence of root age on the age structure of scars, we assumed a scar first occurs on a root at least 5 years old; scar formation on the first five rings of a root was exceptional. The proportion of roots at least 5 years old was computed for each year to evaluate the number of potential scar-bearing roots according to age (Figure 4). For instance, 59% of scar-bearing roots in 1992 were at least 5 years old in 1975. The age structure of scars weighted in relation to the number of potential scar-bearing roots did not differ from the non-weighted age structure (Kolmogorov-Smirnov [KS], $p > 0.05$), suggesting that the number of scars per year varied independently of root age.

SPATIAL VARIATION IN AGE STRUCTURE OF TRAMPLING SCARS

The age distributions of scars were relatively similar among all the 100 m^2 plots. In each plot, more than 77% of scars were formed during the 1984-1990 period, and over 43% of the total were formed in 1985 and 1988. In every case, maximum frequency corresponded to one of the two latter years. The percent of similarity (or Czekanowski's index of similarity; Pielou, 1984) between the frequency distributions averaged 75%. The average similarity increased to 83% when only plots with more than 100 scars dated with certainty were considered (*n* = 8).

The age structure of scars from the three vegetation groups showed a bimodal distribution with peaks in 1985 and 1988 (Figure 5). However, the frequency distribution of scars from well-developed trails (group 1) differed from those placed in groups 2 and 3 (KS, $p < 0.01$ in both cases). The distributions in the former case had a higher frequency and smaller annual variations between 1984 and 1990 than corresponding data for those from groups 2 and 3 which were similar (KS, $p > 0.05$). A notable trend among the age structures is the increase in the proportion of scars formed before 1980, with 1% in group 1, 2.5% in group 2, and 6% in group 3.

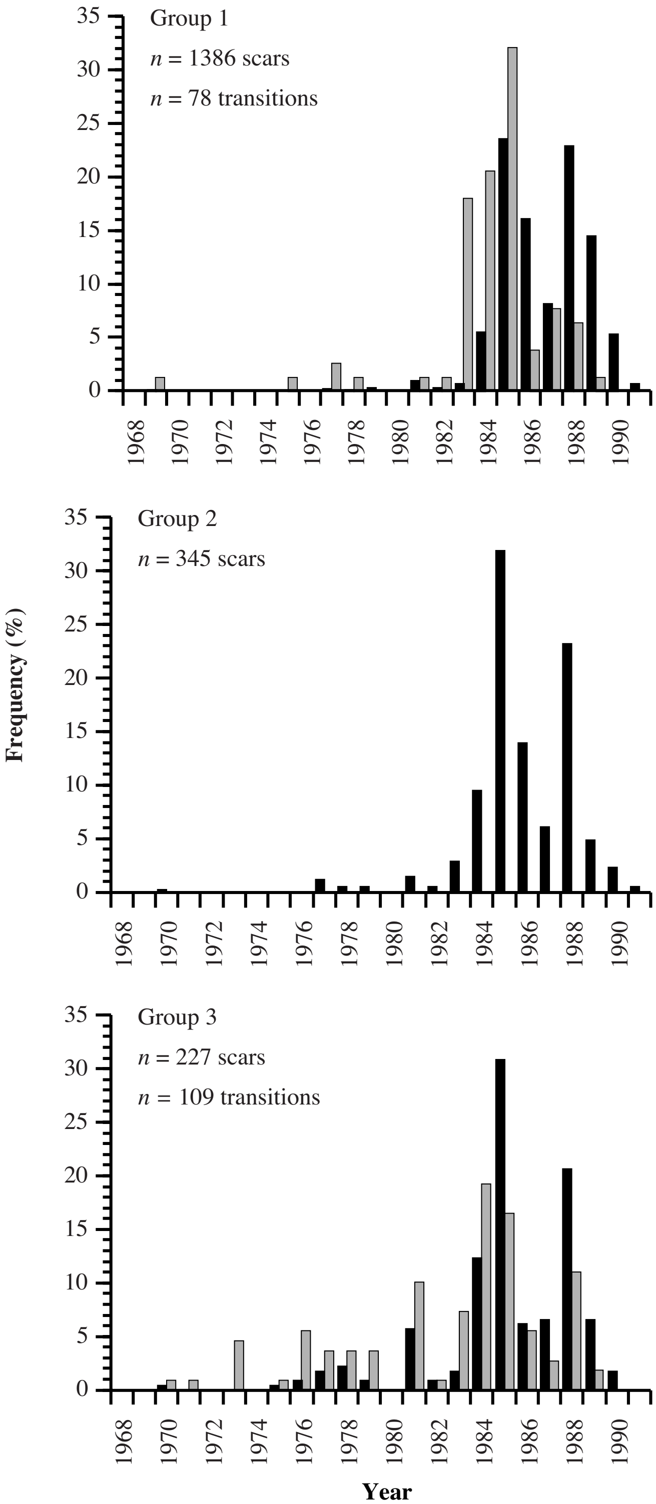

FIGURE 5. Age structure of trampling scars (black columns) and frequency distribution of the first year of stem-like wood in scarred roots (gray columns) from three stratified vegetation groups in RG site. Stem-like wood was not examined in roots of vegetation group 2.

CHANGES IN THE WOOD STRUCTURE OF ROOTS

Anatomical changes in root wood were analyzed based on a comparison of 108 roots from group 1 and 174 roots from group 3. The proportion of roots exhibiting stem-like wood was relatively similar in both groups. The transition from root wood to stem-like wood was recorded in 91% ($n = 98$) of all roots in group 1 and 83% ($n = 144$) in group 3. Abrupt transitions between both types of wood occurred in 73% and 67% of the roots from groups 1 and 3, respectively. Abrupt transitions were computed only in cases where rings were cross-dated, which corresponded to 80% of all transitions in group 1 and 88% in group 3. Our analysis has not included the intensity nor the extent of anatomical changes along the length of exposed roots.

Only one temporal event of anatomical change from root wood to stem-like wood occurred in roots, except in one root where two distinct phases of stem-like wood formation occurred (1957-1965 and 1976-1991), separated by a second phase of root wood formation. Stem-like wood formation had stopped in only four other roots, in each case at the end of the 1980s. In some instances, the transition from root wood to stem-like wood did not occur the same year in cross-sections of the same root. 7.4% of all roots showed two transition dates, and 1.2% showed three dates. The chronology of abrupt changes in root wood from groups 1 and 3 is based on frequency distribution of the first year of stem-like wood formation (Figure 5). Frequency distributions of samples from the two groups differed significantly (KS, $p < 0.01$). The transition between the two types of wood was synchronous in most roots of group 1, where stem-like wood formation started in 1983-1985 in 70.5% of all transitions. The period of stem-like wood formation in roots of group 3 was more variable, beginning at different dates, especially in 1981, 1984, 1985 and 1988. 23.9% of all transitions occurred between 1969 and 1979, as opposed to 6.4% in roots of group 1.

Stem-like wood in roots and trampling scars both formed during the same period (1969-1991). However, anatomical changes were not related to scar formation because stem-like wood initiation preceded the occurrence of the first scar in 60.8% of all roots exhibiting an abrupt transition. Among these roots, stem-like wood production began on the ring formed immediately after the first scar in 37.9% of all cases, whereas 1.3% showed a delay (≥ 1 annual ring) between the date of the oldest scar and the first year of stem wood initiation. Several roots (14%) bore scars without stem wood.

SUPERPOSED TRAMPLING SCARS ON ROOTS

The temporal sequence of scar formation at the same position on a root was used to assess the capacity of the surficial root system to record repeated caribou trampling. Among all scars analysed, 80.6% were the first formed at a given position along the root, with 80.4% of these (64.8% of the total) being the only one at that position. Thus, superposed scars comprised only 19.4% of the total number of scars, *i.e.*, 15.5% as second scar, 3.5% as third scar and 0.4% as fourth scar. The age distribution of superposed scars had a minor effect on the patterns of age structure of first scars (Figure 6). Their importance in the annual production of scars increased with repeated caribou use, reaching almost 60% in 1991 (Figure 6).

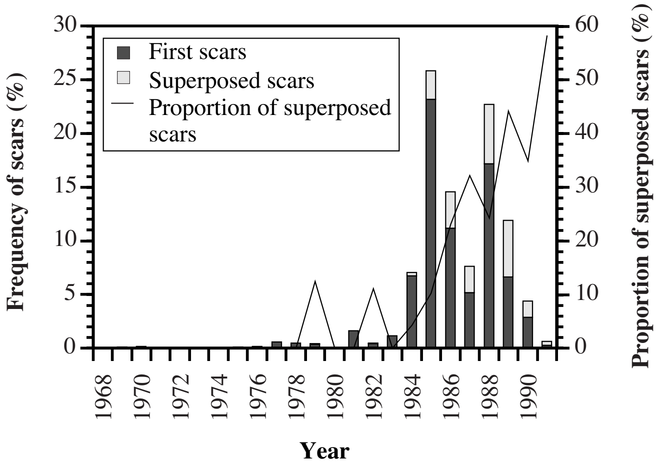

FIGURE 6. Proportion of superposed scars in the age structure of trampling scars in RG site.

The interval between two consecutive superposed scars was most often of one year (one annual ring), with their frequency rapidly decreasing with the length of the interval. The frequencies were 40.3%, 25.6%, 17.7%, 11.1%, and 3.7% in the 1-year, 2-year, 3-year, 4-year, and > 4-year intervals, respectively. A one-year interval corresponds to the minimum time between two consecutive scars, except when scars are separated by a ring incompletely developed, which occurred in 1.7% of cases. The short time lapse between superposed scars resulted from the sustained annual use of the site by caribou since the early 1980s. When considering the year of scar formation, superposed scars occurred most often the year following the date of the previous scar, except when the previous scar was formed in 1986. In the latter case, most of the next scars were produced in 1988. This reflects the high number of scars produced in the site in 1988 compared to those formed in 1987.

SAMPLE SIZE FOR DETERMINATION OF THE AGE STRUCTURE

Multiple sampling of different sample sizes of scars (Figure 7) indicates that, in each data set, the mean relative frequency obtained from 100 random drawings was an adequate estimate of the relative age frequencies of scars for the site, as estimated from all the sampled scars (n = 1948). The maximum error on the estimate of scar age frequency was 4.7% between 1984 and 1990 for all sets of sample sizes. The probability of identifying peak frequencies in 1985 and 1988 with a bimodal distribution around these age classes was high based on 200 cross-sections (about 250 scars). Overlapping of the intervals that included 95% (mean ± 1.96 SD) of the frequency estimates was low between the groups of years 1984-1987-1990, 1986-1989

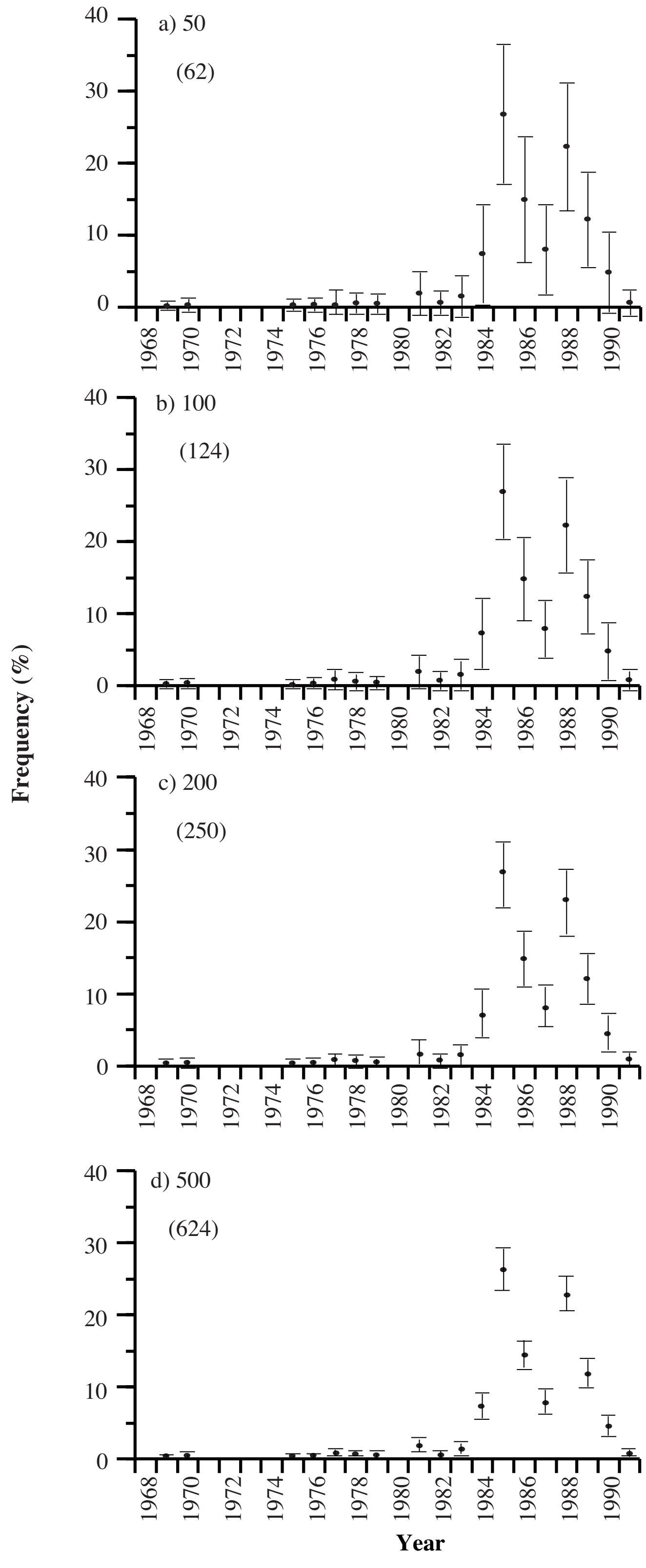

FIGURE 7. Mean and variability (± 1.96 SD; 95% of estimates) of the relative age frequency of trampling scars from multiple sampling of different sample sizes of root cross-sections: 50 (a), 100 (b), 200 (c), and 500 (d) cross-sections. These parameters were estimated from 100 random drawings of each sample size among all samples in RG site. The number in brackets is the mean number of trampling scars from each 100 drawings.

and 1985-1988 (Figure 7c). The standard deviation of relative frequencies of scars for 1984-1990, which was relatively constant within a given set of sample sizes, was used to show the increasing accuracy of scar frequency estimation as the number of scars increased (Figure 8). The mean standard deviation of 1984-1990 decreased steeply with number of scars until a sample size of 200 cross-sections was reached, at which point the curve slopes rapidly towards horizontal. Sample size beyond this number will increase only slightly the precision of the estimate. The age structure of scars can be adequately evaluated from a sample size of about 250 scars.

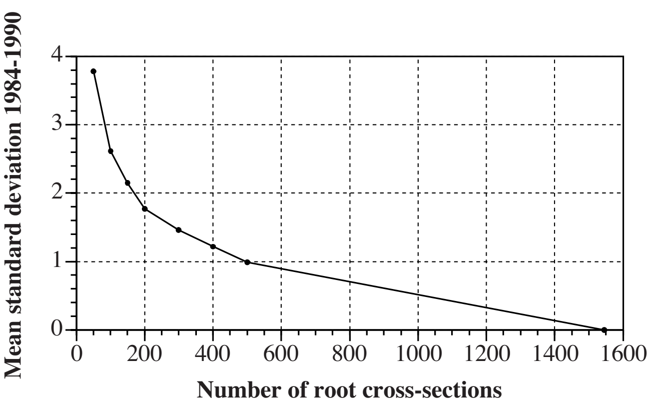

FIGURE 8. Mean annual standard deviation (SD) for the years 1984 to 1990 according to the number of root cross-sections (see text and Figure 7). The mean SD for each sample-size of root cross-sections is the mean of the 7 SD of 100 estimates of the relative annual frequency of trampling scars for the years 1984 to 1990.

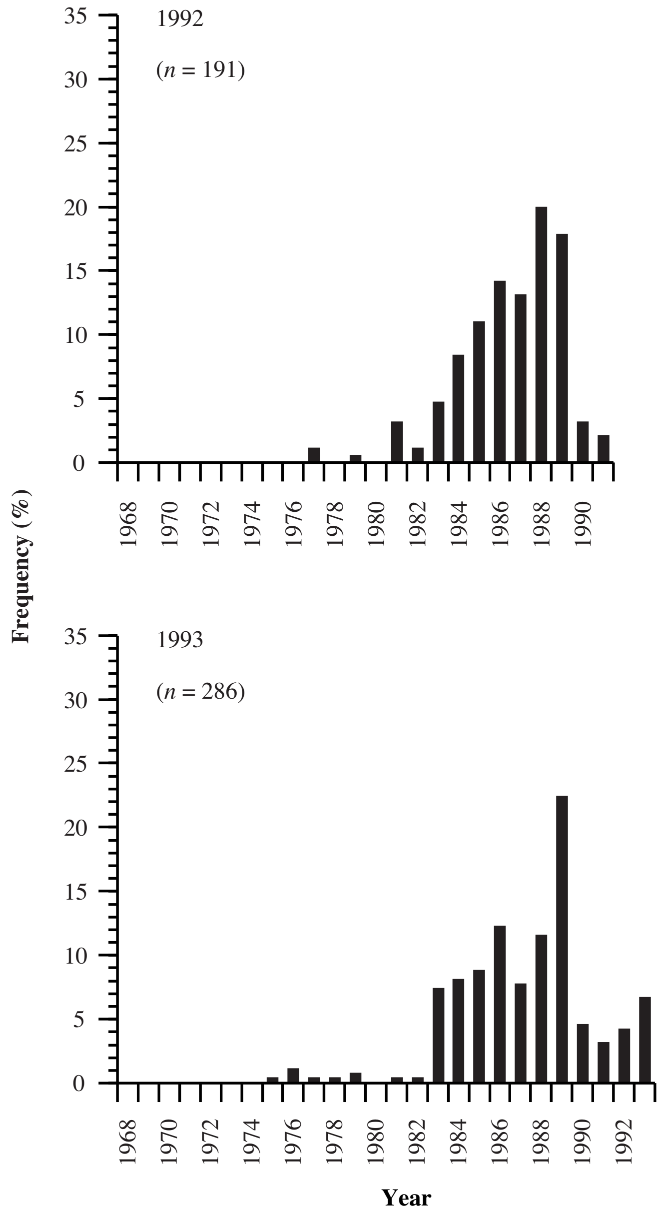

FIGURE 9. Age structure of trampling scars according to 1992 (a) and 1993 (b) samplings in LC site.

SHORT-TERM VARIATION IN THE AGE STRUCTURE OF TRAMPLING SCARS AT LC SITE

The age structures of the 1992 and 1993 samples were relatively similar over the period 1976-1991 (Figure 9; KS, $p > 0.05$): high frequencies of scars formed between 1983 and 1990 accounted for 89% of the scars sampled in 1992 and the corresponding figure in 1993 was 88.5%. During that period, both distributions showed the same increasing trend in numbers of scars. However, the maximum number of scars for the sampling in 1992 was in 1988, and 1989 for the sampling in 1993. The percentage of similarity between both distributions was 83%, *i.e.*, the same percentage for the age structures for those 100 m^2 quadrats where at least 100 scars were present at the RG site.

Discussion

PAST CARIBOU ACTIVITY DEDUCED FROM THE AGE STRUCTURE OF TRAMPLING SCARS

The use of trampling scars for the reconstruction of past caribou activity is based on scar production and scar loss through time. The loss of scars is mainly associated with death of the scar-bearing roots, and erosion or abrasion of xylem delineating the lesions by weather or hooves. The increasing difficulty of detecting scars as they aged (particularly the smaller ones), due to wood overgrowth or vegetation expansion over roots, is also a factor contributing to the loss of the scar record with time. A major factor influencing the trampling scar record is the repeated use of trails. Sustained caribou traffic contributes to scar loss by increasing mortality of roots and accelerating scar abrasion. The formation of new scars is also affected by the presence of older scars. For example, roots may be completely debarked at the surface exposed to trampling, thus limiting the production of new lesions. Conversely, the repeated use of trails by caribou will gradually expose new roots which are likely to be scarred.

Our results indicate that most of the information deduced from the age structures comes from changes in the passage of caribou through the sites. Conifer roots are easily damaged by caribou trampling and their capacity to produce scars is maintained over the years despite sustained use of trails. This suggests that scar production on surficial roots in a given year is a function of the abundance of caribou movement. The loss of scars due to repeated caribou trampling and natural root mortality (associated with the long-term development of the root system) cannot explain the fluctuating patterns of the age structure of scars. We conclude that the changing scar frequency adequately reflects the fluctuations in the rate of scar production.

Trampling scars and caribou activity

The large number of scars on exposed roots in caribou trails reveals that trampling scars are easily produced. Repeated root trampling by caribou is recorded by the formation of adjacent and superposed scars that can be produced in a minimum time of one growing season. The high density of scars in sites RG and LC indicates that lichen woodlands are adequate places to obtain records of past caribou activity. In these stands a dense network of superficial roots develops in the thin organic soil layer (1-3 cm) beneath the lichen cover. Because the lichen cover is fragile, the roots are readily exposed by trampling. The exposure and scarring often occur simultaneously, as revealed by the absence of delay between stem wood initiation and scar formation on many roots at the RG site. Fresh scars were also observed on roots exposed in trails formed during the same season.

The sequence of scar formation on exposed roots at the RG site shows no clear trend towards a decrease in scar production caused by partially debarked roots. The gradual increase in the proportion of superposed scars with time was not related to changes in the number of scars. Scar formation continued on new parts of the roots in past years (> 50% of the scars were formed on new parts between 1989 and 1991). Years of heavy caribou traffic do not seem to have affected the capacity of roots to produce superposed scars, as indicated by the brief interval between two successive superposed scars, generally one year, regardless of the year of scar formation. Despite the large number of scars at the two studied sites, few roots exhibited a debarked zone large enough to prevent the formation of new lesions. Because most scars were small, bark could still be removed at the periphery of previous lesions. The capacity of the root system to record caribou activity may have decreased in large trails during the main periods of caribou migrations in the Rivière George area, where several surficial roots were destroyed or severely damaged.

Loss of scars with time

Scar loss is mainly due to root mortality because of caribou trampling or natural development of the root system. The effect of repeated use of trails on the scar record at the RG site was verified by stratified sampling based on the development stages of the trails. Marked differences in the number of scars, number of exposed roots and root mortality between the three stratified groups indicate different intensities of use. The small impact of caribou traffic on lichen vegetation of group 3 suggests that root mortality due to trampling was negligible over the time period of the study. The similarity of the age structures of scars on roots from the three groups shows that scar loss due to trampling is hardly detectable. The increase in the proportion of scars formed before 1980, from group 1 to group 3, is the only characteristic of these age structures that may reflect the influence of caribou traffic on the scar population. This trend may suggest that the destruction of the scars formed in the 1970s was proportional to caribou traffic in the 1980s (i.e., higher in roots from group 1 than in roots from groups 2 and 3). However, since the main trails were developed in the early 1980s (Figure 5), the stronger increase in number of scars from the 1970s to the 1980s in well-developed trails rather than in lichen stratum (where roots have been progressively exposed) may also indicate slightly different patterns of increase in caribou activity in these two strata. Scar loss along the most frequently used trails was low in comparison to the large number of scars produced. Similarly, caribou activity between July 1992 and August 1993 at the LC site, although relatively low, had a minor impact on the age structure of scars (Figure 9). The slight differences between the 1992 and the 1993 age distributions may largely reflect the spatial variability of the age structure of trampling scars.

Scar loss due to natural root mortality is most likely relatively constant with time. Both age structures of scar populations only cover a period of twenty years, and are marked by abrupt variations in scar frequency that reflect no gradual loss of scar records with time. In fact, most roots at the RG site developed well before the maximum period of scar production, suggesting that the natural mortality rate was much lower than the rate of scar formation in the 1970s and 1980s. The fading scar record as one goes back in time is, however, difficult to evaluate.

Past caribou activity at the RG site

The recent history of caribou activity at RG site may be reconstructed from the age structure of trampling scars, which indicates that the passage of caribou during the snow-free period began to increase around 1970, with a sustained increase in the late 1970s. A dramatic rise in the use of the site occurred during the 1980s, with a maximum between 1984 and 1989, followed by a sharp decrease around 1990. According to the age of scar-bearing roots, no other periods of abundant caribou movement occurred between 1940-50 and the 1970s. Therefore, the rare scars from the 1950s and 1960s suggest that summer use of the site was low at that time.

The disturbance history of the lichen cover and trail development may be reconstructed using the chronology of root exposure as recorded by the anatomical changes in root wood. The structure and species composition of the lichen cover at RG site (3 cm thick, dominated by *C. stellaris*, *C. rangiferina*, and *S. paschale*, with 35% of dead thallii) corresponded to a developmental stage associated with caribou use during the snow-free period. The lichen cover was relatively homogeneous outside the trails, instead of being patchy as would result from feeding craters in the snow. The wintering grounds of the Rivière George herd are actually located several kilometres west and south of the study sites (Messier *et al*., 1988; Vandal *et al*., 1989; Couturier *et al*., 1990). The prolonged period of low caribou activity before the 1970s suggests that the lichen cover was well developed (5-10 cm thick) and dominated by *C. stellaris*, similar to ground vegetation of lichen woodlands across wintering grounds in northern Québec and Labrador (Auclair, 1985; Morneau & Payette, 1989; Arseneault *et al.,* 1997). The recent stage of vegetation disturbance by trampling (and perhaps grazing) in areas classified as group 3 occurred during the 1970s and the 1980s with a peak around 1983-1985, when the main trails developed (Figure 5). The large number of scars formed after 1985 in group 1 indicates that caribou always used the same trails. The trails continued to develop afterwards, causing the exposure of more roots. At the time of sampling, the lichen cover in areas classified as group 3 was likely in a recovery stage.

AGE STRUCTURE OF TRAMPLING SCARS IN THE RIVIERE GEORGE-LAC DE CAEN AREA

The intensity of caribou use in recent years was very different between the two sites. The lichen carpet was completely destroyed by caribou trampling and grazing in LC site, while the ground vegetation in RG site was moderately disturbed. Despite marked differences in the intensity of habitat use, the age structures of trampling scars from these sites are largely similar, with an increase in scar frequency in the late 1970s and a period of high frequency of scar formation between 1983 and 1989 (Figures 4 and 9). The similarity in the age structures suggests a well-defined temporal pattern of use of the area by caribou. From a methodological point of view, the low variability in the age structures of trampling scars, despite differences in the intensity of caribou use, supports the hypothesis that variations in the age structure of scars are indicative of changes in caribou activity.

Conclusion

Our method provides an index to passage of caribou in conifer stands over the past decades. This index of past caribou activity in the two study sites can be evaluated from a few hundred scars, which require a few hours of field sampling per site and a few days of scar dating in the laboratory. The cross-dating procedure to date scar formation yields an accurate age-frequency of trampling scars (yearly data). Nevertheless, the annual frequencies of scars cannot be used as an index of annual caribou activity because of the error of one calendar year inherent to dating when scars are formed during the seasonal dormant phase of cambium. The main limitation of our method is that it is difficult to evaluate the loss of scars with time. As one goes back in time, caribou activity is increasingly underestimated by the age structure (assuming the capacity of conifers to produce scars remains constant with time). Consequently, scar data must be interpreted in terms of successive periods of increasing and decreasing caribou activity. One way to minimize the underestimation of past activity is to weight the age structure of scars according to the age of scar-bearing roots; the proportion of scars in a given age class is then corrected according to the proportion of older roots. This dendroecological method opens the possibility of assessing caribou activity in time and space over large areas. Increase or decrease in caribou density in an area probably results in concomitant changes in abundance of caribou movement. Therefore, the identification of common trends in age distributions of trampling scars between sites in a given area can lead to the identification of spatial and temporal patterns in caribou activity at the population scale. It then appears possible to identify changes in population size or to address the role of other environmental factors influencing habitat use.

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