Fire, Terrestrial Lichens, and the Itcha-Ilgachuz Caribou

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ABSTRACT

This paper presents 11 testable hypotheses pertaining to terrestrial lichens, forest dynamics, and woodland caribou on the Chilcotin Plateau of south-central British Columbia. Based on preliminary studies conducted in the lodgepole pine forests of the Very Dry, Cold subzone of the Sub-boreal Pine–Spruce biogeoclimatic zone (SBPSxc), it is suggested that caribou and terrestrial forage lichens are linked in a positive-feedback continuum dependent in the long term on periodic surface fire. The possibility is raised that fire suppression may adversely affect woodland caribou in this subzone. Further work is required.

Key words: caribou, Chilcotin, foraging, fire, terrestrial lichens.

As a result of increasing pressure from forestry interests, the lodgepole pine forests of British Columbia's Chilcotin Plateau have been the subject of considerable debate in recent years. At issue is the sustainability of the Itcha-Ilgachuz caribou. During the winter months these animals derive a significant portion of their carbohydrate intake from lichens (Cichowski 1989). In many regions, both arboreal lichens (*Bryoria*) and terrestrial lichens (*Cladina*, *Cladonia*, *Stereocaulon*) are utilized, though in the driest subzone of the Sub-boreal Pine–Spruce zone (SBPSxc), only terrestrial lichens are available for consumption (Goward et al. 1999).

Several studies have been conducted on caribou-lichen relations in the Itcha-Ilgachuz area, though none has been published and only 2 pertain specifically to the SBPSxc (Cichowski 1989, Miège and Goward 1999). For the present purposes, however, the most important study is certainly that of Cichowski (1989), who has shown that: 1) caribou make use of this subzone during the winter months; 2) foraging caribou exhibit a strong preference for open, mature pine stands with a canopy cover of <10–15%; 3) *Cladonia*, *Stereocaulon*, and, especially, *Cladina* are more highly sought after by caribou than other terrestrial lichens; and 4) caribou are able to detect the presence of these lichens beneath the winter snowpack—presumably as a result of a highly developed sense of smell. All of these observations are pertinent to the present study.

This paper has 2 primary objectives: to advance various "propositions" concerning lichen succession and caribou use in undisturbed lodgepole pine forests in the Very Dry, Cold subzone of the Sub-boreal Pine–Spruce zone; and to formulate these propositions into a general hypothesis on the relationships among terrestrial lichens, caribou, and their habitat.

STUDY AREA

The study area is located at 52°29'N, 124°25'W on the Chilcotin Plateau, near the Itcha-Ilgachuz Mountains in the Fraser Plateau ecoregion (Demarchi 1993), roughly 40 km northwest of Puntzi Lake, and at an elevation of 1,200–1,300 m above sea level. Topographic relief is minimal, reflecting the plateau basalts that underlie the region. Bedrock, however, is largely obscured by a deep mantle of locally derived glacial tills and moraines. Soils are generally coarse-textured and weakly developed.

The climate can be characterized as cold and dry. Average mean monthly temperatures vary between -12°C in January and 12°C in July (Steen and Coupé 1997). Frost has been recorded in every month. Reflecting the existence of a strong rain shadow in the lee of the Coast Mountains, precipitation is much lower here than at similar elevations elsewhere in the province. At nearby Puntzi Mountain, for example, annual precipitation is only 317 mm. During the winter months, snowpacks accumulate to depths of about 50 cm.

Forest cover is rather uniform in the SBPSxc. In mesic sites, the tree layer consists entirely of lodgepole pine (*Pinus contorta*), with an understory comprising dwarf juniper (*Juniperus communis*), soopalallie (*Shepherdia canadensis*), and kinnikinnick (*Arctostaphylos uva-ursi*), among others. The ground layer is composed primarily of macrolichens, including Icelandmoss (*Cetraria ericetorum*),

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L. M. Darling, editor. 2000. Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk, Kamloops, B.C., 15 - 19 Feb.,1999. Volume Two. B.C. Ministry of Environment, Lands and Parks, Victoria, B.C. and University College of the Cariboo, Kamloops, B.C. 520pp.

reindeer lichens (mostly *Cladina arbusucula*), pixie-cup lichens (mostly *Cladonia ecmocyna*, *C. cervicornis*, *C. cornuta*, *C. gracilis*, and *C. phyllophora*), pelt lichens (*Peltigera* spp.), and foam lichens (mostly *Stereocaulon alpinum*).

METHODS

The observations upon which this paper are based were made during the development phase of a sampling protocol for the rapid assessment of caribou habitat in the SBPSxc (Goward et al. 1999). Field work was conducted during August 1998, and yielded 24 plots, each consisting of 10 subplots. The subplots measured 4 X 4 m, and were laid out along a transect at 8-m intervals in forest stands judged to be vegetationally homogeneous. The plots were evenly distributed among 3 forest age-classes: 40–60 years, 70–100 years, and >150 years. The raw data resulting from these plots are presented in Goward et al. (1999) and will not be repeated here.

RESULTS AND DISCUSSION

In this section, 11 testable "propositions" will be advanced concerning the ecological relationships among terrestrial lichens, caribou, and the pine woodlands that support them. These propositions have been derived from the field work reported in detail in Goward et al. (1999).

Proposition 1

At genus level, *Cladina*, *Cladonia*, and *Stereocaulon* are not limited in undisturbed pine forests of the SBPSxc by extremes of within-stand lighting.

Goward et al. (1999) found that cover values in the forage lichen genera *Cladina*, *Cladonia*, and *Stereocaulon* vary little with differing degrees of exposure to light. For example, no consistent cover value differences were observed between pine stands spaced at 0.5 m and stands spaced at 4 m. Only at spacings of >4 m were significant trends observed (i.e., a distinct increase in *Cladina* and *Stereocaulon* versus a corresponding decrease in *Cladonia*); but such trends can probably be attributed to the foraging behaviour of caribou (see Proposition 5), and are not necessarily to be construed as an ecophysiological response to exposure.

Proposition 2

Tree spacing in mesic pine stands is positively correlated with stand age.

As a rule, lodgepole pine stands become increasingly open as they mature. In the SBPSxc, Goward et al. (1999) found that tree spacing in 50-year-old forests varies between 0.5 m and 2–3 m, whereas spacing in 200-year-old forests varies between 2 m and 4–5 m.

Proposition 3

The perimeters of *Cladina* and *Stereocaulon* colonies differ markedly between open stands (in which thalli with uneven, or indeterminate, perimeters predominate) and closed stands (in which thalli with even, or determinate, perimeters predominate).

Cladina and *Stereocaulon* characteristically take the form of roughly circular colonies. Generally the perimeters of such colonies are well delimited ("determinate"), though in some cases a more ragged ("indeterminate") perimeter develops. In the SBPSxc, at least, indeterminate colonies predominate in forest openings, yet are comparatively rare in closed forest stands in which tree spacing is <3–4 m.

Proposition 4

The existence of indeterminate colony perimeters in *Cladina* and *Stereocaulon* can be attributed largely to the foraging behaviour of caribou.

Determinate colony outlines in *Cladina* and *Stereocaulon* can probably be taken as "standard" for the genera. By contrast, indeterminate outlines appear to reflect disturbance in 1 form or another. Potential disturbance mechanisms in the SBPSxc might include seasonal "churning" (Yarranton 1975), trampling, hailstones, and the ground-feeding activities of birds. None of these phenomena, however, accord with the striking observation (Goward unpubl.) that indeterminate colonies occur most frequently within the distribution area of caribou. If only for this reason, caribou can be assumed to represent a key element in the development of indeterminate outlines. Foraging caribou cause lichen fragments to be displaced outward beyond the margins of the lichen colonies being foraged (H. Armleder, B.C. Ministry of Forests, pers. comm.). Casual observation suggests that many of these fragments soon establish as small "satellite" colonies around the larger "parent" colony. Presumably it is the eventual merging of such colonies with the parent colony that confers upon the latter a ragged, indeterminate outline.

Proposition 5

Foraging by caribou favours the rapid development of *Cladina* and *Stereocaulon* "supercolonies" (to >75 cm in diamter).

The merging of parent colonies with their satellite colonies results in an accelerated rate of expansion for the population as a whole. This accelerated growth leads to the development of lichen "supercolonies"—indeterminate lichen colonies much larger than unforaged, determinate colonies growing nearby. Because supercolonies are probably highly attractive to foraging caribou, their accelerated growth rates are doubtless maintained over long periods. In the SBPSxc, *Cladina* supercolonies have been measured at up to 6 m across; by contrast, determinate colonies seldom attain a diameter of >25–30 cm.

Proposition 6
Two alternative successional pathways can be discerned in the SBPSxc: one confined to densely stocked stands, and dominated by *Cladonia*, and the other restricted to open stands, and dominated by *Cladina* and, to a lesser extent, *Stereocaulon*.

Apparently related to the foraging behaviour of caribou, stand-level terrestrial lichen succession in the SBPSxc tends to follow 1 of 2 alternative successional pathways. In the first pathway, characteristic of densely spaced stands, *Cladonia* dominates the forest floor at each successional stage, while *Cladina* and *Stereocaulon* are restricted to small, rather localized populations. By contrast, the second successional pathway is restricted to more open stands, where *Cladonia* predominates in early successional stages, but is later gradually replaced by extensive supercolonies of *Cladina* and, to a lesser extent, *Stereocaulon*.

Proposition 7
Expanding *Cladina* and *Stereocaulon* colonies invariably outcompete adjacent colonies of *Cladonia*.

As mentioned earlier, foraging caribou are assumed to act as an important mechanism of short-distance dispersal for *Cladina* and *Stereocaulon*. During foraging, many fragments are dispersed onto nearby lichen mats consisting of other genera. In time the resulting new colonies overgrow—and thereby kill—the lichens that support them. Such a dispersal strategy, which can be described as "scatter-and-smother," owes its success to 3 attributes of *Cladina* and *Stereocaulon*: 1) a brittle thallus; 2) an ability to proliferate laterally; and 3) an ability to maintain apical growth long after the death of the basal portions of the thallus.

Proposition 8
In the absence of disturbance, competition from kinnikinnick and other shrubs can be expected to increase over time.

Eight species of shrubs and 9 species of herbs have been recorded as ground cover in the SBPSxc (Goward et al. 1999). Of these, however, only kinnikinnick and, to a lesser extent, dwarf juniper vigorously compete for space with terrestrial lichens. Kinnikinnick is a much-branched, evergreen, ground-hugging shrub capable of producing solid mats over the forest floor. Expanding outwards, it successfully overrides any terrestrial lichens with which it comes into contact. No evidence of die-back has been observed in this species, whether through disease, insects, or adverse weather. Given sufficient time, then, kinnikinnick is probably an important limiting factor to terrestrial lichen cover.

Proposition 9
Stand-replacing fires generally result in densely stocked regenerating stands of little direct benefit to foraging caribou.

Lodgepole pine regeneration is strongly linked to the occurrence of wildfire (e.g., Lotan and Critchfield 1990). In the SBPSxc, stand-replacing fires generally replace old, well-spaced pine stands with densely stocked pioneer stands (Goward et al. 1999). Apparently for this reason, young pine stands are generally avoided by caribou, which have been shown to favour a more open stand structure (Cichowski 1989). Only after a prolonged period of self-thinning, usually lasting 100–120 years (Goward et al. 1999), do lodgepole pine stands become sufficiently open to attract the attention of these animals; and only then do their foraging activities begin to direct lichen succession toward a predominance of *Cladina* and *Stereocaulon*.

Proposition 10
Surface fires generally do not affect tree spacing.

In contrast to stand-replacing fires, surface fires generally do not promote the establishment of pine seedlings at high density. The reason for this is not clear, but may involve an inability on the part of seedlings to compete for moisture with the roots of pre-existing trees. The net result, in any event, is that pre-fire canopy spacing is maintained.

Proposition 11
Surface fires temporarily favour forage lichens through the creation of large openings on the forest floor suitable for lichen colonization prior to the reestablishment of kinnikinnick and other vascular shrubs at competitive levels.

Based on preliminary studies of fire scars, pine stands in the SBPSxc have in the past been subjected to surface fire at intervals of roughly 50–100 years (Goward et al. 1999). With each burn the ground vegetation is more or less returned to an early seral stage, and in the resulting temporary absence of competing vascular plants, lichen mats soon begin to dominate the forest floor. *Cladina* and *Stereocaulon*, for example, can apparently establish to impressive cover values (as "supercolonies") in as little as 40–50 years after fire (e.g., Yarranton 1975), whereas *Cladonia* achieves stand-level dominance even sooner. In the absence of further disturbance, however, this "lichen phase" of forest succession is likely to be short-lived: by about 60–100 years after fire, kinnikinnick and other ground-dwelling vascular species can begin to outcompete the lichens for space (Goward et al. 1999). In theory, this trend would then continue either until a continuous vascular cover had been achieved, or until it was interrupted by fire or other agents of disturbance.

SUMMARY HYPOTHESIS

While many of the above propositions clearly require further study, they do suggest a general hypothesis concerning the nature of terrestrial lichen ecology in the SBPSxc. In summary form, this hypothesis would posit that caribou and forage lichens (especially *Cladina* and *Stereocaulon*) are linked

in a positive-feedback continuum dependent for its maintenance on periodic surface fire or other mechanisms of disturbance. The details of this relationship are highly complex, but might be expressed as follows.

Terrestrial lichens constitute a primary winter food of caribou in open lodgepole pine stands throughout the SBPSxc. Foraging by these animals causes fragments of *Cladina* and *Stereocaulon* to become scattered beyond the perimeter of the colonies being foraged. Many of the fragments are scattered onto adjacent lichen mats consisting of other genera. Here they develop into expanding "satellite colonies" that override—and hence kill—the lichen mats on which they rest. Eventually the satellite colonies fuse with their originating "parent" colonies, thus considerably accelerating overall colony expansion. With repeated foraging, the resulting "supercolonies" can attain diameters of several metres in as little as 40–50 years. Unforaged colonies, by contrast, seldom attain a diameter of >25–30 cm; such colonies are generally associated with densely stocked stands, in which foraging by caribou is minimal.

Young lodgepole pine stands are generally rather densely stocked, and are hence avoided by foraging caribou. Yet because stand spacing tends to increase with increasing forest age, most stands can be expected to favour foraging by caribou by 100–120 years. In the meantime, competition by encroaching vascular shrubs, especially kinnikinnick, might be expected to render the forest floor unsuitable to extensive colonization by lichens. In fact, lichen supercolonies routinely do develop in old forest stands, suggesting that colonization by kinnikinnick is interrupted from time to time, possibly as a result of surface fire. In theory, surface fire would return the forest floor to early successional status at intervals of roughly 50–100 years, thus providing a temporary "window of opportunity" for the development of terrestrial forage lichens in the absence of competition from kinnikinnick. Different from stand-replacing fires, which generally initiate densely stocked regenerating stands, surface fires maintain open stand structure, and hence favour continued use by caribou.

CONCLUSION

This paper develops the hypothesis that the development of *Cladina* and *Stereocaulon* supercolonies in the SBPSxc may in part be dependent on periodic surface fire; and that, conversely, the long-term absence of surface fire (or other agents of disturbance) strongly favours increasing competition from vascular shrubs, and hence a decline in forage lichens. Here it can be added that periodic surface fire doubtless also tends to remove accumulated humus, and thus retards the establishment of well-developed soils. Well-developed soils are much less likely than poorly developed soils to support forage lichens at high abundance (Gaare 1995).

Many of the above assertions are, of course, highly preliminary; they are presented not as a guide to future management decisions, but as a stimulant to discussion and further research. Even so, the question must be raised whether the current policy of fire suppression in the SBPSxc is not likely to result in a long-term decline in available forage lichen habitat. Ahti and Hepburn (1967) have already proposed for northern Ontario that "light ground fire in pine-lichen woodlands would not interfere with the normal development of the pine, nor reduce the value of the current timber resource to any significant degree." Perhaps future research will lead to similar recommendations for some portions of the Chilcotin Plateau. Potential implications for other land-use decisions are beyond the scope of this paper, but warrant careful deliberation.

ACKNOWLEDGEMENTS

I wish to thank H. Armleder for continued support of the studies upon which this paper is based. D. Burgess provided capable assistance in the field. H. Armleder, S. Stevenson, and P. Williston provided pertinent literature. This paper has also benefited from constructive comment by H. Armleder, A. Arsenault, D. Burgess, S. Jovan, L. Kowalsky, D. Miège, and O. Steen. The project was supported by Forest Renewal British Columbia (FRBC) and the Williams Lake office of the British Columbia Ministry of Forests.

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