Composition and function of biological soil crust communities along topographic gradients in grasslands of central interior British Columbia (Chilcotin) and southwestern Yukon (Kluane)

Janet Marsh, Sabine Nouvet, Paul Sanborn, and Darwyn Coxson

Abstract: Grasslands in the rainshadow of the Chilcotin (British Columbia) and St. Elias (Kluane, Yukon) mountain ranges of western Canada are characterized by widely spaced clumps of bunchgrass and sage, between which can be found lichen-dominated biological soil crusts (BSC). Our examination of Chilcotin and Kluane grasslands showed differential BSC development along topographic gradients, favoring those sites with lower levels of soil disturbance. Lichen species richness was greatest in upper topographic positions, that is, on valley side terraces in the Chilcotin and esker slopes in Kluane. Common BSC lichens in both grasslands included *Acarospora schleicheri*, *Caloplaca tominii*, *Collema tenax*, *Diploschistes muscorum*, *Fulgensia bracteata*, *Phaeorrhiza nimbosa*, *Placidium squamulosum*, and *Psora decipiens*. Chilcotin BSC additionally contained many *Cladonia* species (e.g., *C. carneola*, *C. chlorophaea*, *C. pyxidata*), particularly where vegetation had encroached on BSC. The potential for nitrogen fixation by *Collema*-dominated crusts in Kluane was examined using acetylene reduction assays (ARA) and soil surface microclimate monitoring. ARA activity was highly dependent upon the duration of wetting events, reaching C_2H_4 levels up to 63 μmol·m^{-2}·h^{-1}after 40 h of hydration. Given the abundance of *Collema*-dominated crusts in Kluane and the optimal conditions for ARA activity that are reached during wetting–drying transitions, we hypothesized that BSC communities potentially make an important contribution to ecosystem nitrogen budgets. Enrichment in total and mineralizable N, as well as ^{15}N natural abundance values, was consistent with N fixation making an important contribution to soil N pools in these ecosystems. Both Chilcotin and Kluane BSC had similar spongy microstructures that contrasted with the platy microstructures of the underlying surface mineral soils, but only the latter site showed micromorphological evidence of burial of mosses and other BSC components by continuing loess deposition. BSC may have performed similar roles in analogous steppe-like ecosystems that existed under full-glacial conditions in the unglaciated areas of eastern Beringia in Alaska and Yukon.

Key words: acetylene reduction, Beringia, biological soil crusts, lichen diversity, *Collema tenax*.

Résumé : Les prairies des régions montagneuses ombrophiles de Chilcotin (Colombie-Britannique) et de St-Elias (Kluane, Yukon), dans l'ouest canadien, sont caractérisées par des touffes de graminées cespiteuses et d'armoises espacées, entre lesquelles on peut trouver des encroûtement biologiques édaphiques (BSC) dominés par des lichens. Les observations des auteurs dans les prairies de Chilcotin et de Kluane montrent des développements différentiels des BSC, le long de gradients topographiques, favorisant les sites avec des degrés moindres de perturbation du sol. La richesse en espèces lichéniques est plus importante dans les sites topographiques plus élevés, ceci sur les terrasses du côté de la vallée à Chilcotin et sur les pentes des eskers à Kluane. Dans les deux prairies, les lichens usuels des BSC incluent les *Acarospora schleicheri*, *Caloplaca tominii*, *Collema tenax*, *Diploschistes muscorum*, *Fulgensia bracteata*, *Phaeorhiza nimbosa*, *Placidium squamulosum* et *Psora decipiens*. Les BSC de Chilcotin comportent en plus plusieurs espèces de *Cladonia* (p.ex. *C. carneola*, *C. chlorophaea*, *C. pyxidata*), surtout où la végétation envahit les BSC. Les auteurs ont examiné le potentiel de fixation d'azote dans les encroûtements dominés par des *Collema* à Kluane, en utilisant des tests de réduction de l'acétylène (ARA), et ont suivi le microclimat à la surface du sol. L'activité ARA dépend fortement de la durée des épisodes humides, atteignant 63 μmol C_2H_4·m^{-2}·h^{-1} après 40 h d'hydratation. Compte tenu de l'abondance des encroûtements dominés par les *Collema* à Kluane, et des conditions optimales pour l'activité ARA qui sont atteintes au cours des transitions humide–sec, les auteurs avancent l'hypothèse que les communautés BSC pourraient apporter une importante contribution aux budgets azotés de ces écosystèmes. L'enrichissement en N total et minéralisable, et les valeurs de l'abondance naturelle en ^{15}N sont congruentes avec l'idée que la fixation de l'azote apporte une importante contribution aux pools azotés du sol dans ces écosystèmes. Les BSC de Chilcotin aussi bien que de Kluane montrent des microstructures spongieuses similaires qui contrastent avec les microstructures lamellaires des minéraux des sols sous-jacents, mais seulement le dernier site présente des preuves de l'enterrement des mousses et autres composantes des BSC par une déposition continue de loess. Les BSC pourraient avoir joué des rôles similaires dans des écosystèmes analogues, qui ont existé sous de conditions de pleine gla-

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ciation sur les surfaces non glacées, dans le Beringia oriental, en Alaska et au Yukon.

Mots clés : réduction de l'acétylène, Beringia, croûtes biologiques édaphiques, diversité lichénique, *Collema tenax*.

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Introduction

Biological soil crusts (BSC), also called cryptogamic or microbiotic soil crusts, are present throughout arid natural grassland ecosystems. These inconspicuous crusts on the soil surface are variously composed of bacteria, cyanobacteria, green algae, mosses, liverworts, microfungi, and lichens. In some plant communities, these living organic crusts, which often cover all soil surfaces not occupied by vascular plants, may comprise up to 70% of the living plant cover (Evans and Johansen 1999). BSC perform many ecological functions, including promoting soil structure formation, protecting the soil surface from water and wind erosion, increasing water infiltration and retention, and providing habitat for other species (Belnap et al. 2001*a*, 2001*b*). The role of crusts in supplying nitrogen (N) to N-limited grasslands and arid-land ecosystems is particularly important (Billings et al. 2003).

Most BSC studies in North America have focused on desert or shrub–steppe grasslands from intermountain valleys in the western United States, or in wet polar and alpine environments (Blundon and Dale 1990; Liengen and Olsen 1997; Gold et al. 2001). Fewer studies have examined BSC communities from intermountain basins in Western Canada (Rosentreter and Belnap 2001), even though these communities have been noted in several ecological studies on shrub-steppe grasslands in subarctic environments (Walker et al. 1991; Dickson 2000; Zazula et al. 2002).

In both the Kluane Lake area of southwestern Yukon and the Chilcotin region of central interior British Columbia, major grassland complexes are found in the rain shadow of coastal mountain ranges. In the Kluane area, grassland communities have developed on south-facing slopes of glaciofluvial terraces and eskers, with up to 30 m of local relief along the southeastern shore of Kluane Lake. These grassland ecosystems have been shaped by Holocene loess deposition, resulting in silty surface soils that have a high pH because of the deposition of calcium carbonate-rich loess (Laxton et al. 1996). In the Kluane grasslands, loess deposition continues, fed by deflation of sediments from the unvegetated floodplain of the nearby Slims River (Laxton et al. 1996). As a result, the Kluane grasslands may provide one of our closest modern analogues to the loess-influenced Beringian steppe–tundra, which may have dominated much of Alaska and the Yukon during full-glacial conditions (Lloyd et al. 1994; Laxton et al. 1996; Schweger 1997; Vetter 2000). In the Chilcotin region, grasslands reach their greatest development along terraces in the Fraser River valley, occurring over a 600 m elevational gradient from valley rim to bottom. These grasslands occupy a variety of morainal and glaciofluvial landforms, but soil surface horizons on all but the steepest slopes have formed in a pervasive veneer of silty aeolian deposits. Unlike in the Kluane Lake area, aeolian activity is largely inactive in the modern Chilcotin landscape, being restricted to localized cliff-top dune formations adjacent to eroding canyon walls.

Both the Chilcotin and Kluane grasslands are dominated by bunchgrass communities that have extensive areas of exposed soil between widely spaced bunchgrass or shrub (*Artemisia*) species. Although it has been noted that soil surfaces in these grasslands are colonized by BSC communities (Meidinger and Pojar 1991; Vetter 2000), their community composition and ecological role have not previously been examined. We now report on lichen and bryophyte community structure in BSC communities from the Chilcotin and Kluane grasslands, placing particular attention on the influence of topographic position on BSC composition. We also examine the functional importance of BSC communities in these grasslands, looking at soil chemical and structural properties underlying soil crusts, and in the Kluane grasslands examining the potential for nitrogen fixation using acetylene reduction assays (ARA).

We hypothesized that Chilcotin and Kluane BSC communities would contain elements of both arctic–alpine and grassland–desert lichen and moss floras. Although physiological response patterns (ARA activity) of the dominant BSC lichen *Collema tenax* have previously been examined in shrub–steppe deserts of the western United States, there is presently no information available on the potential role of *Collema* in British Columbia and Yukon grasslands, an important information gap given the quite different climate and soils of these two regions. Our documentation of BSC microclimate will allow us to characterize representative conditions under which crust metabolic activity occurs and compare these operating environments against those documented at lower latitudes. We expected that British Columbia and Yukon BSC communities would have higher concentrations of organic matter and associated nutrients than the underlying mineral soils, as previously found in shrub–steppe deserts in the western United States (Belnap et al. 2001*a*). In particular, N-related soil properties should be consistent with the presence of N-fixing BSC components (i.e., BSC should have total and available N concentrations that are higher than those in the underlying mineral soil and ^{15}N natural abundances close to those of the atmosphere). We also expected BSC to have microstructures that differ from those in the underlying mineral soil; and where active deposition of loess occurs, this should be expressed in micromorphological evidence of previously buried BSC communities. For the Kluane site, a potential analogue of the full-glacial Beringian steppe–tundra, evidence for the roles of BSC in this modern grassland may suggest that existing models of Beringian ecosystem functioning need refinement.

Materials and methods

Study sites

Chilcotin grassland communities were sampled in

Junction Sheep Range Provincial Park (JSRPP) near the junction of the Fraser and Chilcotin Rivers, British Columbia (Table 1). The park's landscape is represented by the following three variants or subzones of the British Columbia Ministry of Forests biogeoclimatic ecosystem classification (Steen and Coupe 1997). (*i*) Lower Grassland (Very Dry Hot Bunchgrass Subzone, Fraser Variant BGxh3) dominated by bluebunch wheatgrass (*Agropyron spicatum*) and big sagebrush (*Artemisia tridentata*). (*ii*) Middle Grassland (Very Dry Warm Bunchgrass Subzone, Alkali Variant – BGxw2), dominated by bluebunch wheatgrass (*Agropyron spicatum*) and needle-and-thread grass (*Stipa comata*). (*iii*) Upper Grassland (Very Dry Mild Interior Douglas-Fir Subzone – IDFxm), dominated by short-awned porcupinegrass (*Stipa curtiseta*) and pussytoes (*Antennaria* sp.). Lower grasslands have a much warmer and drier local climate, with mean annual temperatures almost 2 °C higher than those of upper grasslands (Table 2). Most precipitation in the Chilcotin falls as winter snow or spring rain; this differs from Columbia Basin perennial grasslands, where precipitation predominantly occurs as winter and spring rains (Belnap et al. 2001*b*).

In the Lower Grasslands at JSRPP, Brown Chernozemic soils have formed on sandy fluvial and glaciofluvial parent materials, while the Dark Brown Chernozemic soils of the Middle and Upper Grasslands have formed predominantly on medium-textured morainal deposits (Valentine et al. 1987). Despite this diversity of underlying surficial materials, soil Ah horizons and BSC crusts have usually formed in the surface silty aeolian veneer that occurs across the elevation range of grasslands at JSRPP.

The Kluane grasslands (Table 1) are found in the rainshadow of the St. Elias Mountains in the southwestern Yukon. They have been characterized as having a semi-arid, continental climate (Laxton et al. 1996). At the Kluane Lake Research Station, temperatures range from an average high of 17.6 °C in summer to a low of –21.8 °C in winter (Fig. 1; Arctic Institute of North America, unpublished data). Most precipitation falls in the summer as rain; between 1974 and 1981, there was an average of 34 d of precipitation per year, with a mean annual precipitation of 325 mm. Dominant vascular plants in the Kluane grasslands include pasture sage (*Artemisia frigida*), tufted sedge (*Carex filifolia*), and purple bluejoint (*Calamagrostis purpurascens*) (Vetter 2000). Many of the esker complexes in the Kluane Lake region run from northwest to southeast, parallel to the St. Elias Mountain ranges. As a result the southwest facing slopes, which face prevailing winds and receive high solar loading, are characterized by open grasslands, while the shaded slopes of each esker see an abrupt transition to closed canopy white spruce (*Picea glauca*) at each ridgeline. Lower slope positions on the southwest facing esker slopes see a more gradual transition from grassland to shrubs and deciduous trees, with species such as *Rosa acicularis*, *Shepherdia canadensis*, and *Populus tremuloides* common. Soils of the grassland slopes consist of Humic Regosols and Melanic Brunisols, with carbonates present at the surface, reflecting the continuing incorporation of calcareous loess. On mid- to upper slope sites, the surface veneer of loess usually ranges from 5 to 30 cm in thickness.

Biological soil crust sampling

BSC species composition (lichens and brophytes) of Chilcotin grasslands was assessed in study plots placed in each of upper, middle, and lower elevation environments (Table 1). Plot placement at each topographic position (upper, middle, or lower) was stratified into sites dominated by bunchgrass communities versus those dominated by big sagebrush communities. At each site type, three 100 m^2 circular plots were laid out (5.64 m in diameter) for a total of nine plots. Sampling in Kluane BSC communities was adapted to meet the smaller scale relief of esker complexes. Sample plots for BSC species composition were laid out on the south- to southwest-facing slopes of nine eskers. These plots were also 100 m^2 in size, but they were laid out as belt transects, 2 m wide by 50 m long. Three of these belt transects were placed on each esker, one in a upper slope position (5 m from esker ridge crest), one in a mid-slope position (15 m downslope from the esker ridge crest), and one in a lower slope position (25 m downslope from the esker ridge crest). In both Chilcotin and Kluane locations, sites with evidence of recent soil disturbance were excluded.

Within both Kluane and Chilcotin sites, a survey-based visual search approach was used to assess lichens and bryophytes found within each plot (after Goward 1996). BSC samples were collected at each plot location for later verification of species identifications. Lichen nomenclature follows Esslinger (1997), while bryophyte nomenclature follows the North American list from the Missouri Botanical Garden (http://mobot.mobot.org/W3T/Search/most.html).

Percent soil surface cover of dominant BSC components was also assessed in Kluane grasslands. On each esker, 10 belt transects were placed at 5 m intervals, each running from the ridge crest to the bottom of each esker. At 2 m intervals along these transects, three 10 cm^2 quadrats were surveyed for BSC cover using a modified Daubenmire scale. BSC was assessed in 6 "functional group" categories. These were (1) cyanolichen-dominated soil crusts (predominantly *Collema tenax*), (2) chlorolichen soil crusts (composed mainly of green-algal biont lichens, e.g., *Cladonia* spp., *Fulgensia bracteata*, *Diploschistes muscorum*, *Physconia muscigena*), (3) bryophytes, (4) exposed soil surfaces (which may still contain free-living cyanobacteria), (5) grasses, and (6) forbs. Average cover for each functional group category was subsequently calculated for four slope positions: esker ridge (0–2 m), upper esker (2–10 m), middle esker (10–20 m), and lower esker (20–30 m).

Acetylene reduction assays

ARA activity was assessed during each precipitation event for Kluane BSC communities, from 16 June to 16 August 2004, using the methods of Stewart et al. (1967). Each set of ARA assessments was based on 6–8 replicate crust samples (destructive sampling) placed in 200 mL glass cuvettes for ARA incubations. Sampled crusts were approximately 1 cm thick and 7 cm in diameter; this corresponds to the mean size of the small mounds that characterize surface BSC structure in these grasslands. Crust segments selected for ARA sampling had a dominant cover of the dark cyanolichen *Collema tenax*. Samples were maintained at close to ambient environmental conditions during ARA incubations. Comparisons of BSC temperature (between incu-

Table 1. Location, elevation, slope, aspect, and vegetation type for the study plots in Chilcotin and Kluane grasslands.

Site No.	Latitude (N)	Longitude (W)	Elevation (m a.s.l.)	Slope (%)	Aspect (°)	Dominant vascular vegetation
Chilcotin lower elevation plots (2002 and 2003)						
G1	51°44′30″	122°24′16″	358	0	na	Bluebunch wheatgrass (*Agropyron spicatum*)
G2	51°44′36″	122°24′16″	386	2	160	Bluebunch wheatgrass
G3	51°44′38″	122°24′16″	387	2	160	Bluebunch wheatgrass
S9	51°44′35″	122°24′47″	392	0	na	Big sagebrush (*Artemisia tridentata*)
S10	51°44′31″	122°24′44″	395	0	na	Big sagebrush
S11	51°44′29″	122°24′40″	351	0	na	Big sagebrush
Chilcotin mid-elevation plots (2002 and 2003)						
G4A	51°46′3″	122°24′38″	722	5	90	Bluebunch wheatgrass
G4B	51°46′4″	122°24′38″	725	7	160	Bluebunch wheatgrass
G5	51°46′1″	122°24′43″	729	15	330	Bluebunch wheatgrass
S12	51°45′22″	122°24′59″	651	0	na	Big sagebrush
S13	51°45′28″	122°25′3″	662	0	na	Big sagebrush
S14	51°45′28″	122°25′3″	663	0	na	Big sagebrush
Chilcotin upper elevation plots (2002 and 2003)						
G6	51°46′58″	122°25′12″	927	13	150	Short-awned porcupine grass (*Stipa curtiseta*)
G7	51°46′59″	122°25′13″	927	8	240	Short-awned porcupine grass
G8	51°47′53″	122°26′59″	917	17	290	Short-awned porcupine grass
S15	51°47′1″	122°25′12″	790	15	180	Big sagebrush
S16	51°47′0″	122° 25 12″	782	12	90	Big sagebrush
S17	51°47′17″	122°26′0″	900	0	na	Big sagebrush
Kluane crust and soil sampling sites (2003)						
3	61°10′4″	138°25′37″	798	45	225	
4	61°10′11″	138°26′4″	800	40	180	
5	61°9′43″	138°23′35″	812	0	na	
6	61°4′2″	138°21′57″	825	0	na	
7	61°1′43″	138°29′36″	788	0	na	
9	61°4′0″	138°22′35″	828	0	na	
10	61°2′55″	138°23′17″	807	70	225	
12	61°1′9″	138°29′28″	819	20	225	
Kluane crust sampling sites (2004)						
Peninsula site	61°1′42″	138°29′36″	786	29.5	220	
Silver City site	61°2′20″	138°21′40″	815	29.5	220	
Kluane esker plots (2004)						
1	61°2′98″	138°22′10″	823	26	220	Pasture sage (*Artemisia frigida*), tufted sedge (*Carex filifolia*), and purple reedgrass (*Calamagrostis purpurascens* var. *purpurascens*)
2	61°10′15″	138°26′50″	829	29	200	
3	61°10′22″	138°26′38″	825	28	182	
4	61°2′20″	138°21′40″	815	29.5	220	
5	61°2′25″	138°22′60″	815	29	210	
6	61°4′26″	138°22′10″	817	25	205	
7	61°3′88″	138°21′45″	798	32	162	
8	61°10′38″	138°26′95″	805	31.5	200	
9	61°2′19″	138°22′40″	818	37	200	

Note: Chilcotin site numbers at which crust and soil samples were collected are underlined. na, not available.

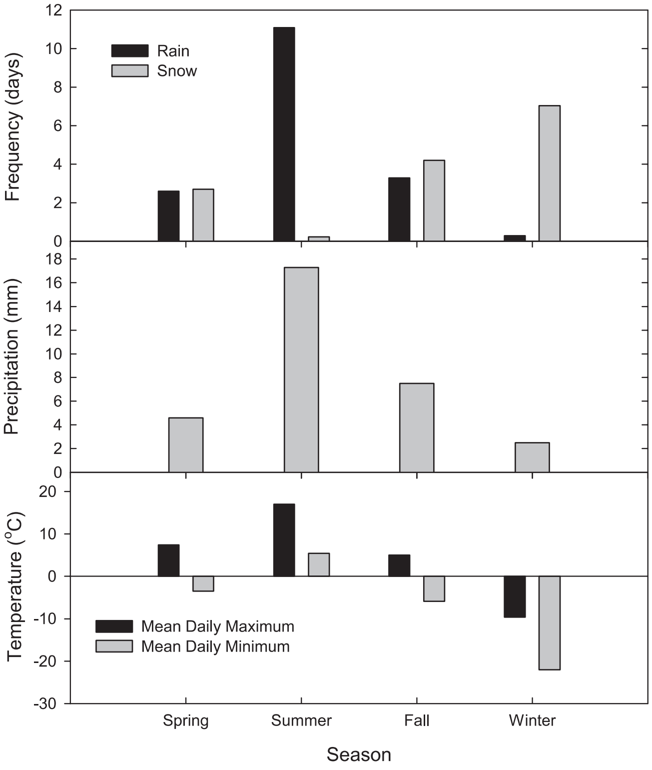
bation samples and adjacent undisturbed esker surfaces) were conducted with fine wire thermocouples. Light intensities were measured with a quantum sensor (LI-COR, Lincoln, Nebraska, USA), while thallus water content was assessed gravimetrically (destructive sampling of separate BSC replicates). We found that during periods of darkness incubation bottles placed on the soil surface maintained crust samples near to or at ambient environmental conditions (<2 °C difference in temperature). During daylight hours, incubation bottles were placed within an open top water bath, with BSC surface temperatures maintained within 5 °C of the ambient temperature (and usually within 2 °C of ambient temperature).

The temperature and light response patterns of ARA in *Collema*-dominated BSC samples was determined on-site using freshly collected crust samples. These BSC samples were

Table 2. Climatic characteristics of selected biogeoclimatic subzones and variants relevant to grasslands in central interior British Columbia (Steen and Coupe 2000).

	Very Dry Hot Bunchgrass Subzone, Fraser Variant (BGxh3)	Very Dry Warm Bunchgrass Subzone, Alkali Variant (BGxw2)	Very Dry Mild Interior Douglas-Fir Subzone (IDFxm)
Mean annual precipitation (mm)	330	345	392
Mean annual temperature (°C)	5.9	5.0	4.0
Frost-free days	182	169	163

Fig. 1. Mean frequency of days with precipitation (measured as rain or snow), mean daily precipitation, and mean daily maximum and minimum air temperatures during spring (April–May), summer (June–August), fall (September–November), and winter (December–March) periods, 1974–1981, at the Kluane Lake Research Station.



given a pre-incubation dark hydration exposure of 8 h (mimicking wetting by late evening precipitation events). Neutral density screening and a temperature-controlled water bath were used to maintain hydrated BSC samples at 5, 15, 25, and 35 °C and 0, 100, and 600 μmol·m^{-2}·s^{-1} photosynthetically active radiation (PAR). A second set of incubations was conducted to determine the time course recovery of ARA activity, where freshly collected BSC samples were rehydrated and held in darkness at 5, 15, and 25 °C.

BSC microclimate measurements

Soil surface microclimate measurements (thallus hydration status, incident light at thallus surface, and thallus temperature) were conducted on *Collema*-dominated crusts at Kluane (site 9) from 15 June to 15 August 2004. Fine wire thermocouple arrays (0.003 inches) were installed in three crusts located at mid-slope positions. Thermocouple tips were inserted in the upper lichen cortex, immediately below the crust surface. LI-COR quantum sensors were used to measure photosynthetically active radiation. Crust hydration status was determined by the placement of impedance clips across thallus surfaces (Coxson 1991). Observations of BSC microclimate were made during 10 precipitation events, which resulted in periods of hydration ranging from 2 to 43 h for BSC communities.

Soil sampling and analysis

Two types of samples were collected at 10 of the Chilcotin sites (Table 2): (1) the living portion of the crust and the approximately 1.0 cm thickness of adhering mineral soil and (2) the upper 10 cm of the soil A horizon directly beneath the crust sample. Samples were air-dried, sieved (<2 mm), and analyzed for total C and N (LECO CHN-600 elemental analyzer, St. Joseph, Michigan, USA), total S (LECO SC-132 S analyzer), mineralizable N (ammonium extracted after 2 week anaerobic incubation at 30 °C), extractable P (Bray P1 method; Kalra and Maynard 1991), cation exchange capacity, exchangeable cations ($BaCl_2$ method; Hendershot and Duquette 1986), and pH (1:2 soil:solution ratio, in 0.01 mol·L^{-1} $CaCl_2$). Field testing of crusts and surface soils indicated that carbonates were not present, so total C can be taken as consisting largely of organic C.

During an initial reconnaissance in 2003, we examined eight grassland sites along a 20 km transect along the southern and southeastern shore of Kluane Lake, corresponding to the inferred gradient of loess deposition previously studied by Laxton et al. (1996). BSC and underlying mineral soil were sampled from mid- to upper slope positions as at JSRPP, with the modification that the soil sampling depths ranged from 5 to 18 cm because of variation in surface mineral horizon thicknesses. Subsequent intensive sampling in 2004 was conducted at two sites within 8 km of the Slims River delta (Table 1). Four bulk samples (at least 10 cm × 10 cm) of BSC and its layer of adhering mineral soil (approximately 1–2 cm thick) were collected from a 0.3 ha sample plot at both sampling sites. The bulk samples were subdivided by depth, with the uppermost 5 mm of BSC removed with a razor blade and analyzed separately from the lower portion of mineral material in the crust. The Kluane crust and mineral soil samples were air-dried, sieved (<2 mm), and analyzed for total C and N (Fisons NA1500 NC analyzer, Beverly, Massachusetts, USA), inorganic C (Bundy and Bremner 1972), and mineralizable N (2003 samples only). Organic C was calculated as the difference between total C and inorganic C. Carbonates were present in all Kluane soil and BSC samples, so pH was not measured because it is buffered near pH 8.3 in calcareous soils (Bohn et al. 1979).

^{15}N natural abundance ($\delta^{15}N$) for all BSC and soil sam-

Table 3. Presence and absence records for lichens and mosses in Chilcotin sampling plots (lower, middle, and upper bench positions).

	Bunchgrass sites									Big Sagebrush sites								
	Lower			Middle			Upper			Lower			Middle			Upper		
	G1	G2	G3	G4a	G4b	G5	G6	G7	G8	S9	S10	S11	S12	S13	S14	S15	S16	S17
Lichens																		
Acarospora schleicheri			x				x							x		x	x	x
Caloplaca jungermanniae										x		x						
Caloplaca cerina																x	x	x
Caloplaca tominii	x	x												x		x	x	x
Candelariella reflexa			x															
Candelariella terrigena																		x
Catapyrenium cinereum											x				x	x		
Cladonia sp.										x								
Cladonia borealis										x								
Cladonia cariosa					x	x	x	x	x	x	x	x			x	x	x	x
Cladonia carneola						x	x											
Cladonia chlorophaea	x	x	x			x						x		x				
Cladonia crispata						x												
Cladonia fimbriata									x									
Cladonia macrophyllodes	x						x	x	x									
Cladonia multiformis														x				
Cladonia phyllophora	x			x	x	x												
Cladonia pocillum	x	x	x	x	x	x	x	x	x	x	x	x	x		x		x	x
Cladonia pyxidata	x	x	x	x	x	x	x	x	x	x		x		x				
Cladonia symphycarpia		x	x	x						x	x	x	x	x		x		x
Collema cristatum	x	x																
Collema undulatum																		x
Collema tenax	x	x	x	x	x			x	x	x	x		x		x	x	x	x
Diploschistes muscorum	x	x	x	x	x		x	x	x	x	x	x	x	x	x		x	x
Endocarpon pusillum			x	x										x				
Fulgensia bracteata											x	x		x		x	x	
Lecanora hageni									x									
Parmelia sulcata										x								
Peltigera didactyla		x	x				x	x		x							x	x
Peltigera lepidophora	x	x	x					x	x	x	x							
Peltigera rufescens								x	x	x	x	x					x	
Phaeorrhiza nimbosa	x						x	x								x	x	x
Phaeorrhiza sareptana											x			x		x		x
Physconia muscigena				x			x			x		x	x		x	x	x	
Placidium squamulosum		x	x				x			x	x					x	x	x
Psora cerebriformis		x	x										x	x		x	x	x
Psora decipiens		x	x							x	x	x		x	x	x		
Psora himalayana							x								x		x	
Psorostichia sp.					x			x										

Table 3 (*concluded*).

	Bunchgrass sites									Big Sagebrush sites								
	Lower			Middle			Upper			Lower			Middle			Upper		
	G1	G2	G3	G4a	G4b	G5	G6	G7	G8	S9	S10	S11	S12	S13	S14	S15	S16	S17
Toninia ruginosa subsp. *ruginosa*							x											
Toninia tristes														x				x
Xanthoparmelia wyomingica												x	x	x	x	x	x	x
Mosses																		
Polytrichum juniperinum									x									
Tortula ruralis	x	x									x	x				x	x	

ples from both study areas was determined by continuous flow – elemental analysis – isotope ratio mass spectrometry (CF-EA-IRMS) technology at the Isotope Science Laboratory, University of Calgary, Calgary, Alberta, using a Finnigan Mat Delta+XL mass spectrometer interfaced with a Carlo Erba NA 1500 elemental analyzer (CE Elantech, Inc., Lakewood, New Jersey, USA).

Intact samples of BSC and the underlying surface soil were collected in sampling tins, freeze-dried, and impregnated under vacuum with epoxy resin; thin sections (30 µm thick) were prepared for examination with a petrographic microscope.

Data analysis

Diversity statistics for BSC lichens and bryophytes were calculated using the EcoSim program (Gotelli and Entsminger 2001). Species richness was calculated as the number of species present at each site. The Shannon–Wiener index was used to give an indication of species richness and evenness. The Dominance index was used to show the proportion of the site that was dominated by the most common species. A nested ANOVA was calculated on these diversity statistics to determine the effect of site type (bunchgrass versus big sagebrush in Chilcotin plots) or topographic position (all sites).

Cluster analysis of BSC species plots was performed in PC-ORD version 4.0 (McCune and Mefford 1999), using a relative Sorenson distance measure (nearest neighbor distance measure).

Chemical properties of BSC and underlying mineral soils (Chilcotin 2002 and Kluane 2003 samples) and of upper and lower crust components (Kluane 2004 samples) were compared by one-way ANOVA using SYSTAT version 10 software (SPSS Inc., Chicago, Illinois, USA)

Results

Big sage versus bunch grass dominated plots at the Chilcotin sites had similar species richness, with 31 species of lichens and mosses in the bunchgrass dominated site types versus 34 species in the big sage dominated sites (Table 3). Sites in upper topographic positions had the highest number of species, irrespective of site type, followed by lower topographic positions; with mid-position sites having the lowest species richness. Upper slope positions were also the most species rich in Kluane plots, with 36 taxa located in upper slope positions, compared with 22 and 19 taxa, respectively, in mid- and lower-slope positions (Table 4). Taxa common to both Chicotin and Kluane BSC plots included *Acarospora schleicheri*, *Caloplaca tominii*, *Collema tenax*, *Diploschistes muscorum*, *Fulgensia bracteata*, *Phaeorrhiza nimbosa*, *Physconia muscigena*, *Placidium squamulosum*, and *Psora decipiens* (Table 5). Species specific to each site type were found in both big sage and bunchgrass plots at Chilcotin. Characteristic species of the bunchgrass plots included several *Cladonia* species (*C. carneola*, *C. crispate*, *C. fimbriata*, *C. macrophyllodes*, *C. phyllophora*, and *Cladonia symphycarpia*), while the big sagebrush sites contained species such as *Caloplaca jungermanniae*, *Candelariella terrigena*, *Fulgensia bracteata*, and *Xanthoparmelia wyomingica*. Kluane BSC communities were dominated by

Table 4. Presence and absence records for lichens and mosses in Kluane sampling plots (lower, middle, and upper esker positions).

	Slope position site No.									
	Lower								Middle	
	Y2L	Y3L	Y4L	Y5L	Y6L	Y7L	Y8L	Y9L	Y1M	Y2M
Lichens										
Acarospora schleicheri		x					x			x
Aspicilia sp.										
Buellia elegans		x	x		x			x		x
Caloplaca cerina						x				
Caloplaca jungermanniae										
Caloplaca tominii	x	x	x	x	x	x	x	x	x	x
Cetraria aculeate										x
Cetraria ericetorum										
Cladonia chlorophaea										
Cladonia pocillum										
Cladonia pyxidata										
Collema tenax		x	x	x			x	x	x	x
Collema undulatum	x				x					
Dermatocarpon intestiniforme									x	x
Diploschistes muscorum			x						x	
Flavocetraria cucullata										
Flavocetraria nivalis										
Fulgensia bracteata			x	x	x			x	x	
Lecanora epibryon										
Peltigera didactyla										
Peltigera rufescens										
Phaeorrhiza nimbosa	x	x	x	x	x	x	x	x	x	x
Physconia muscigena			x			x	x		x	x
Placidium squamulosum	x									
Psora cerebriformis										
Psora decipiens	x	x	x	x	x	x	x	x	x	x
Psora himalayana		x	x		x		x	x	x	x
Psora montana	x		x					x		
Psora tuckermanii			x							
Squamarina lentigera										
Toninia sedifolia			x		x					
Toninia tristes subsp. *canadensis*										
Xanthoparmelia chlorochroa	x	x	x	x	x	x	x		x	x
Xanthoparmelia somloensis										
Mosses										
Bryum argenteum										
Tortula ruralis	x		x		x	x	x	x	x	x

cyanolichen soil crust components (*Collema*), particularly in mid-slope positions, where cover exceeded 50% (Fig. 2). Chlorolichen soil crusts, with species such as *Buellia elegans*, *Diploschistes muscorum*, *Phaeorrhiza nimbosa*, and *Psora decipiens*, or bare ground, were the next most common groups found in each slope position.

A significant effect of topographic position was confirmed by ANOVA on the Shannon–Wiener diversity indices (Tables 5 and 6) for both the Chilcotin and Kluane BSC communities. In the Chilcotin plots, site type was also a significant predictor for Shannon-Wiener diversity index measurements. Significant effects on the Dominance index were seen for all site and topographic position combinations (Table 6), with Dominance indices greatest in the mid-elevation Chilcotin plots and lower slope Kluane plots.

The first hierarchical division of the cluster analysis clearly discriminated between Kluane and Chilcotin study plots (Fig. 3). The second hierarchical division in the Chilcotin plots separated bunchgrass from sagebrush dominated sites, with the exception of sites G2, G3, and G4a. Further divisions of the Yukon plots tended to cluster lower slope unit sites together, although this patterning was not consistent across sites.

The summer of 2004 saw prolonged periods of dominance by high pressure in the southwestern Yukon, with most precipitation events resulting from late day or nighttime convective shower activity. The mean length of BSC hydration episodes in summer 2004 was 24 h, with a median hydration length of 15.6 h. A pattern of nighttime wetting is evident for data collected from 30 June to 13 July (Fig. 4), where the transition from dry to wet, at the start of precipitation events, and back to dry again, as skies clear, is abrupt for

							Upper								
Y3M	Y4M	Y5M	Y6M	Y7M	Y8M	Y9M	Y1U	Y2U	Y3U	Y4U	Y5U	Y6U	Y7U	Y8U	Y9U
x			x		x		x	x	x			x		x	
													x		
x	x	x	x	x	x	x		x	x	x	x	x	x	x	x
														x	
										x					
x	x	x	x	x	x	x		x	x	x	x	x	x	x	x
	x		x	x	x			x	x	x	x	x	x	x	x
														x	
							x								
												x			
							x								
x	x	x	x		x	x	x	x	x	x	x	x		x	x
				x									x		
	x	x	x		x			x		x	x	x	x		x
	x	x	x		x		x			x	x	x		x	x
												x			
								x	x			x			
	x	x	x		x	x	x			x	x	x	x		x
							x								
							x								
										x	x				
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
x				x	x		x	x	x	x	x	x	x	x	
				x		x			x						
x	x	x			x									x	
x	x	x		x	x	x	x		x	x	x	x	x	x	
x	x	x		x	x	x			x	x	x	x	x	x	
x	x	x		x	x			x	x	x				x	
	x													x	
							x								x
	x						x								
										x					
x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
x															
							x			x					
	x		x			x	x		x	x	x	x	x	x	

BSC communities. When hydrated, crusts rarely exceeded 20 °C (Fig. 5). A small, but significant exception to this pattern occurs, however, during the final stages of drying, when hydrated crusts can briefly reach temperatures near 30 °C under clearing skies (Figs. 4 and 5). Surface temperatures of desiccated crusts commonly reached 60 °C or more under full sun conditions, resulting in extreme diel temperature fluctuations.

ARA incubations during precipitation events showed a clear pattern of physiological recovery after wetting (Table 7). Observed ARA rates ranged from 0.6 to 63 $\mu mol \cdot m^{-2} \cdot h^{-1}$, the former during an early morning incubation shortly after crusts had become hydrated, and the latter after a full day's hydration under optimal conditions. Low, but still appreciable ARA activity was observed in incubations that occurred during the nighttime period (typically after wetting). This pattern of continued ARA activity under darkness was confirmed under controlled conditions (Fig. 6), where BSC segments held under temperatures representative of night-time field conditions (<10 °C) had increasing ARA rates throughout the exposure period. ARA activity was optimal at 25 °C, in a series of incubations held under temperature- and light-controlled conditions, falling when crust temperatures were held at 35 °C.

The Chilcotin BSC differed significantly ($p < 0.05$) from the underlying 0 to10 cm deep mineral soil in the majority of the properties examined, with concentrations of total C, N, and S, and available P that were approximately twofold higher (Table 8). pH was significantly lower in the crusts than the underlying soil, but cation exchange capacity and exchangeable cations showed no significant differences. Mineralizable N was eightfold higher in the crusts relative

Table 5. Species indices (mean ± SE and *n*) by slope position (lower, middle, upper) for Chilcotin and Kluane grasslands and species specificity for site type (Bunchgrass, Big Sagebrush, Esker) in each location.

	Chilcotin						Kluane		
	Bunchgrass			Big Sagebrush			Esker		
Index	Lower	Middle	Upper	Lower	Middle	Upper	Lower	Middle	Upper
Shannon–Wiener	1.535±0.080, *n*=3	1.221±0.045, *n*=3	1.840±0.056, *n*=3	2.005±0.108, *n*=3	1.399±0.251, *n*=3	2.153±0.019, *n*=3	2.304±0.080, *n*=8	2.547±0.091, *n*=8	2.719±0.040, *n*=8
Dominance	0.078±0.010, *n*=3	0.131±0.000, *n*=3	0.086±0.007, *n*=3	0.070±0.011, *n*=3	0.103±0.033, *n*=3	0.057±0.002, *n*=3	0.1021±0.0077, *n*=8	0.0807±0.0079, *n*=8	0.0663±0.0027, *n*=8
Species richness	13.00±1.5, *n*=3	7.67±0.1, *n*=3	11.67±1.0, *n*=3	14.67±2.5, *n*=3	11.00±4.5, *n*=3	17.67±0.5, *n*=3	10.2500±0.9014, *n*=8	13.1250±1.1090, *n*=8	15.2500±0.5901, *n*=8
Species specific to each site type	*Candelariella reflexa*, *Cladonia carneola*, *Cladonia crispata*, *Cladonia fimbriata*, *Cladonia macrophyllodes*, *Cladonia phyllophora*, *Collema cristatum*, *Lecanora hageni*, *Polytrichum juniperinum*, *Psorostichia* sp., *Toninia ruginosa*			*Caloplaca jungermanniae*, *Caloplaca cerina*,* *Candelariella terrigena*, *Catapyrenium cinereum*, *Cladonia borealis*, *Cladonia multiformis*, *Collema undulatum*,* *Collema tenax*,* *Fulgensia bracteata*,* *Parmelia sulcata*, *Phaeorrhiza sareptana*, *Toninia tristes*,* *Xanthoparmelia wyomingica*			*Bryum argenteum*, *Buellia elegans*, *Cetraria aculeata*, *Psora montana*, *Psora tuckermanii*, *Squamarina lentigera*,[†] *Xanthoparmelia chlorochroa*, *Xanthoparmelia somloensis*		
Species common to both Kluane and Chilcotin locations .	*Acarospora schleicheri*, *Caloplaca cerina*, *Caloplaca tominii*, *Candelariella terrigena*, *Collema undulatum*, *Collema tenax*, *Diploschistes muscorum*			*Fulgensia bracteata*, *Peltigera didactyla*, *Peltigera rufescens*, *Phaeorrhiza nimbosa*, *Physconia muscigena*, *Placidium squamulosum*			*Psora cerebriformis*, *Psora decipiens*, *Psora himalayana*, *Toninia tristes*, *Tortula ruralis*		

*Species specific to Big Sagebrush sites in comparison with other Chilcotin plot types, but also recorded in Kluane plots.

[†]Not observed in Chilcotin sample plots, but found elsewhere in Chilcotin grasslands.

to the mineral soil, while ^{15}N natural abundance ($\delta^{15}N$) was lower in the BSC than in the underlying mineral soil. For a subset of these properties, the 2003 Kluane samples showed the same general relationships, though the only significant difference was for mineralizable N, which was approximately fivefold higher in the crusts relative to the underlying mineral soil (Table 8). The more intensive 2004 sampling at Kluane revealed significant differences in total N concentrations and ^{15}N natural abundance between the uppermost 5 mm and the remainder of the crust, with $\delta^{15}N$ values close to atmospheric in the upper portion (Table 8).

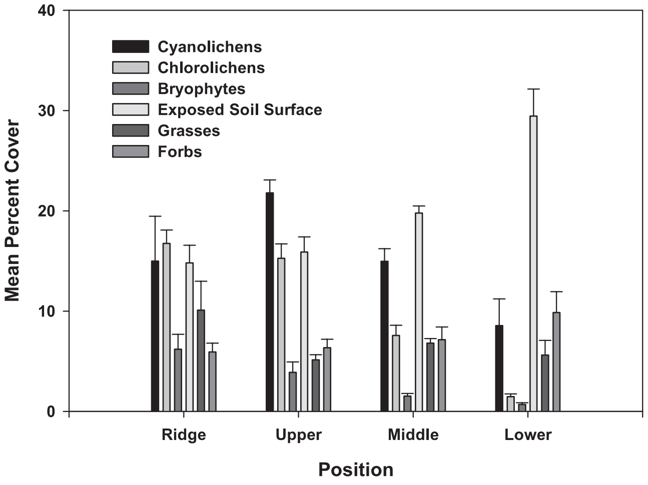
Thin sections of BSC and underlying surface mineral soil horizons showed similarities in microstructure between the Chilcotin and Kluane study areas, and a predominance of silt-sized mineral particles (<50 µm in diameter) (Fig. 7). In both cases, the crusts displayed a more porous version of the spongy microstructure (Figs. 7*a*, 7*c*–7*e*, 7*g*) found in the underlying mineral soil, with the latter also having a pronounced platy microstructure at 2 cm or greater depth from the surface (Fig. 7*h*). Both recognizable plant detritus and dark brown, amorphous humified materials appeared to be more abundant within approximately 1 cm of the surface (Fig. 7*g*), corresponding to the typical thickness of the C- and N-enriched zone found beneath BSC in these study areas. Herbaceous plant roots also occurred within the uppermost, organic matter-enriched zone within 1 cm of the surface, particularly in the Chilcotin thin sections (Fig. 7*e*). However, the Chilcotin crusts displayed less intermingling of mineral and living (or recently living) crust components at the crust surface, and this was particularly evident when viewed in polarized light (Fig. 7). In contrast, the BSC from Kluane had recognizable fragments of both mosses and lichens dispersed throughout the uppermost 1 cm.(Figs. 7*f*, 7*g*). In addition, dark brown, crudely laminated structures, occurred up to 2 cm below the surface, although it was not determined whether these consisted of organic matter or clays (Fig. 7*h*).

Discussion

The diversity of BSC communities reflects both immediate physical environments, including factors such as the availability of moisture, gradients of temperature and light, and soil physiochemistry; as well as previous site history, including the intensity and frequency of previous disturbance events and their influence on successional changes in BSC communities.

Two major types of disturbance event dominate Chilcotin and Kluane grasslands. Fire was historically a reoccurring event in both grassland communities. There was abundant evidence of previous fires in both locations, including charring on big sagebrush stems in the Chilcotin grasslands and on remnant white spruce stumps along esker ridgelines in Kluane. Although some authors suggest that the southwestern Yukon grasslands represent an intermediate successional stage prior to the development of xerophytic white spruce forests (Lausi and Nimis 1991), Vetter (2000) found that grassland boundaries (particularly on ridge crests) were quite stable, with few encroaching spruce seedlings, mirroring our own observations at Kluane. The Chilcotin grasslands, on the other hand, do contain encroaching Douglas-

Fig. 2. Percent cover (mean and SE) by slope position for major vegetation and soil elements in Kluane eskers.



fir seedlings. Comparisons with historical records indicate that many areas of the Chilcotin have been invaded by Douglas-fir forests, reflecting both previous periods of favourable climate for tree seedling recruitment and the influence of fire suppression in the historical era (Iverson 2001). Concerns over the loss of grassland to encroaching forest led British Columbia Parks to initiate controlled fires in JRSPP in 2001 (Alexander 2001). Most of our mid-elevation sampling plots fell within this area of controlled burn, as well as upper elevation sites 6 and 7.

The other major disturbance agent in both Kluane and Chilcotin grasslands is that of disturbance by mammals, both ungulates and rodents. Vetter (2000) found active soil erosion on many esker slopes in the southwestern Yukon grasslands, erosion that was initiated and (or) enhanced by the activity of arctic ground squirrels and feral horses. These factors were also present in the Kluane study sites, especially in lower slope positions. At the Chilcotin sites grazing by California Bighorn sheep, as evidenced by abundant fecal pellets and trampling of the soil surface, was particularly evident in the middle elevation positions. Although topographic position is a significant explanatory variable for species diversity in both Chilcotin and Kluane grasslands, we would conclude that this reflects more the previous history of disturbance (fire and trampling) in these particular topographic positions, than climatic variables (as was our a priori expectation). Both fire and grazing can have a significant negative influence on lichen and bryophyte diversity in BSC communities (Antos et al. 1983; Neff et al. 2005). Unfortunately, standard approaches for conducting retrospective studies on fire successional history, using known dated sites (time since last fire) are not available in these grasslands, where previous fire history (with the exception of the 2001 controlled burn at JRSPP) remains undocumented. Nonetheless, the lower topographic positions at the Chilcotin site have apparently experienced a much longer fire return interval, as evidenced by the development of large stature individuals of *Artemisia tridentata* that do not show fire scars.

Upper grassland plots in the Chilcotin study area had the greatest species richness, particularly plots that were not included in recent controlled burns (four of the six upper

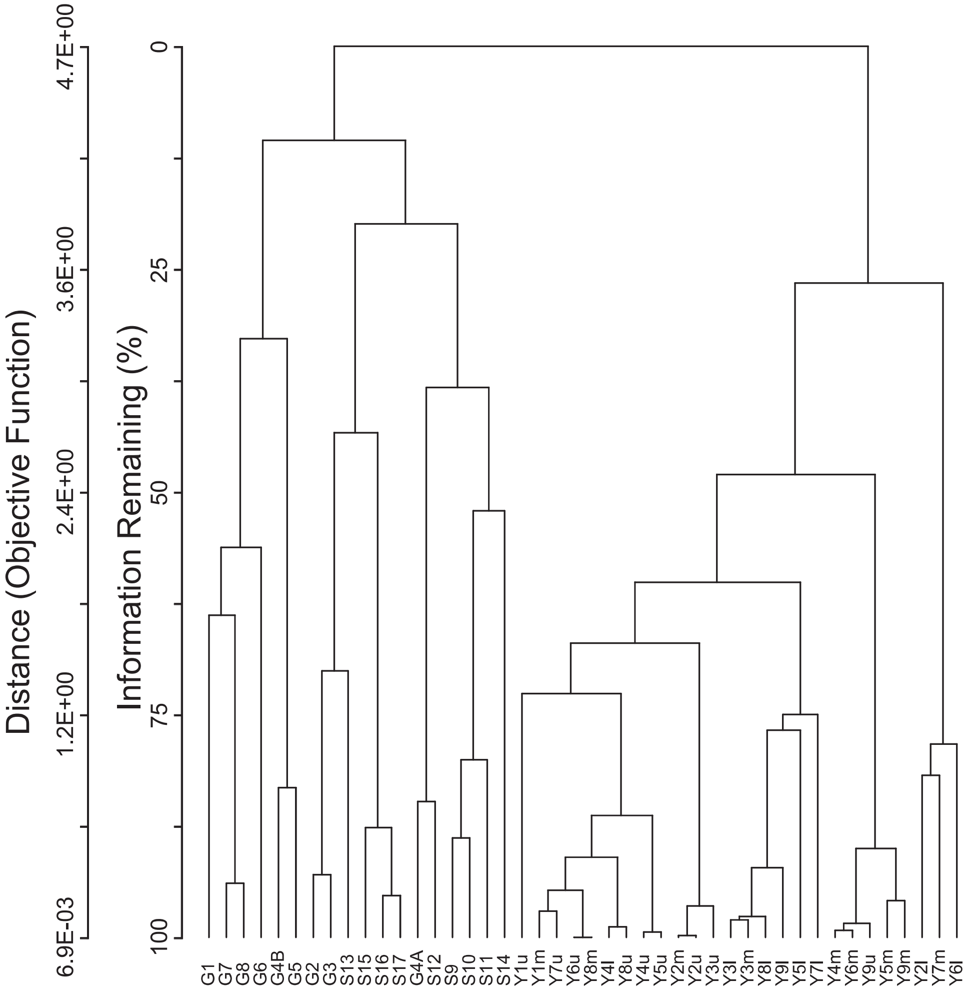
Table 6. Analysis of variance for diversity indices by habitat and slope position in Chilcotin and Kluane grasslands.

	Chilcotin						Kluane					
Indices	Variable	Sum of squares	df	Mean square	*F* ratio	*P*	Variable	Sum of squares	df	Mean square	*F* ratio	*P*
Shannon–Wiener	Habitat[a]	0.343	1	0.343	7.910	0.016	Slope position[b]	0.697	2	0.349	8.010	0.003
	Slope position[b]	0.839	2	0.420	9.676	0.003						
Dominance	Habitat[a]	0.002	1	0.002	6.787	0.023	Slope position[b]	0.005	2	0.003	7.496	0.003
	Slope position[b]	0.008	2	0.004	12.341	0.001						
Species richness	Habitat[a]	60.500	1	60.5	9.000	0.011	Slope position[b]	100.750	2	50.375	7.902	0.003
	Slope position[b]	98.778	2	49.389	7.347	0.008						

[a] Grassland or Big Sagebrush.

[b] Lower, middle, or upper.

Fig. 3. Cluster analysis for Chilcotin and Yukon BSC species plots. Site details are provided in Tables 3 and 4.



grassland plots). In these areas crustose lichens such as *Lecanora hageni* had begun to colonize grass litter. The lichens *Cladonia pyxidata* and *Peltigera lepidophora* were also abundant at these upper grassland sites. The proximity of Douglas-fir forests likely has allowed woodland lichen species such as *Cladonia fimbriata* and the moss *Polytrichum juniperinum* to occur here. *Xanthoparmelia wyomingica* was associated only with big sagebrush sites in the Chilcotin, possibly reflecting a preference for more acidic sites (Goward et al.1994) under big sagebrush canopies and (or) the greater proportion of open soil in the JSRPP big sagebrush sites. In contrast, *X. chlorochroa*, and in one site *Xanthoparmelia somloensis*, were found in the Kluane sites. This abundance of vagrant lichens in both locations is reminiscent of Great Plains grasslands, where *Xanthoparmelia* and other foliose lichens are dominant crust components (Belnap et al. 2001*b*).

Lower topographic positions in the Chilcotin plots did not show evidence of recent fire (charring, reduction of litter). Further they contained many individual big sagebrush and rocky mountain juniper (*Juniperus scopulorum*) of exceptional stature. The presence of *Acarospora schleicheri* in many of the Chilcotin and Kluane plots suggests the presence of late-successional BSC communities (Belnap et al. 2001*b*). Other BSC species that have been described as late-successional indicators for sagebrush steppe in the United States, for example, *Texosporium sancti-jacobi* (McCune and Rosentreter 1992), are beyond their northern range limit at the Chilcotin and Kluane sites.

Overall, many of the BSC species recorded in each of our sites had clear affinities with BSC communities from the western United States. The dominance by *Collema tenax*, and widespread presence of other species, such as *Caloplaca tominii*, *Diploschistes muscorum*, and *Psora decipiens*, is common to many BSC-dominated steppe grasslands from the Columbia and intermountain basins (St. Clair et al. 1993; McCune 1994). Other steppe indicators, such as *Fulgensia bracteata*, were found in both Chilcotin and Kluane locations, though only in the big sagebrush sites at Chilcotin (and *Squamarina lentigera* in upper slope positions at Kluane). Each of the major morphological groups that comprise BSC lichens (Eldridge and Rosentreter 1999; Belnap et al. 2001*b* were found in the Chilcotin and Kluane sites, with crustose, gelatinous, and squamulose lichens often growing together in close proximity on the small mounds that characterized BSC surface morphology in both locations.

The Kluane and Chilcotin sites each contained several taxa that were not found in the other location, particularly in the Chilcotin grasslands, where 20 site-specific taxa were found (mainly *Cladonia* in the bunchgrass sites). This pro-

Fig. 4. Kluane soil crust microclimate, 30 June – 12 July 2005.

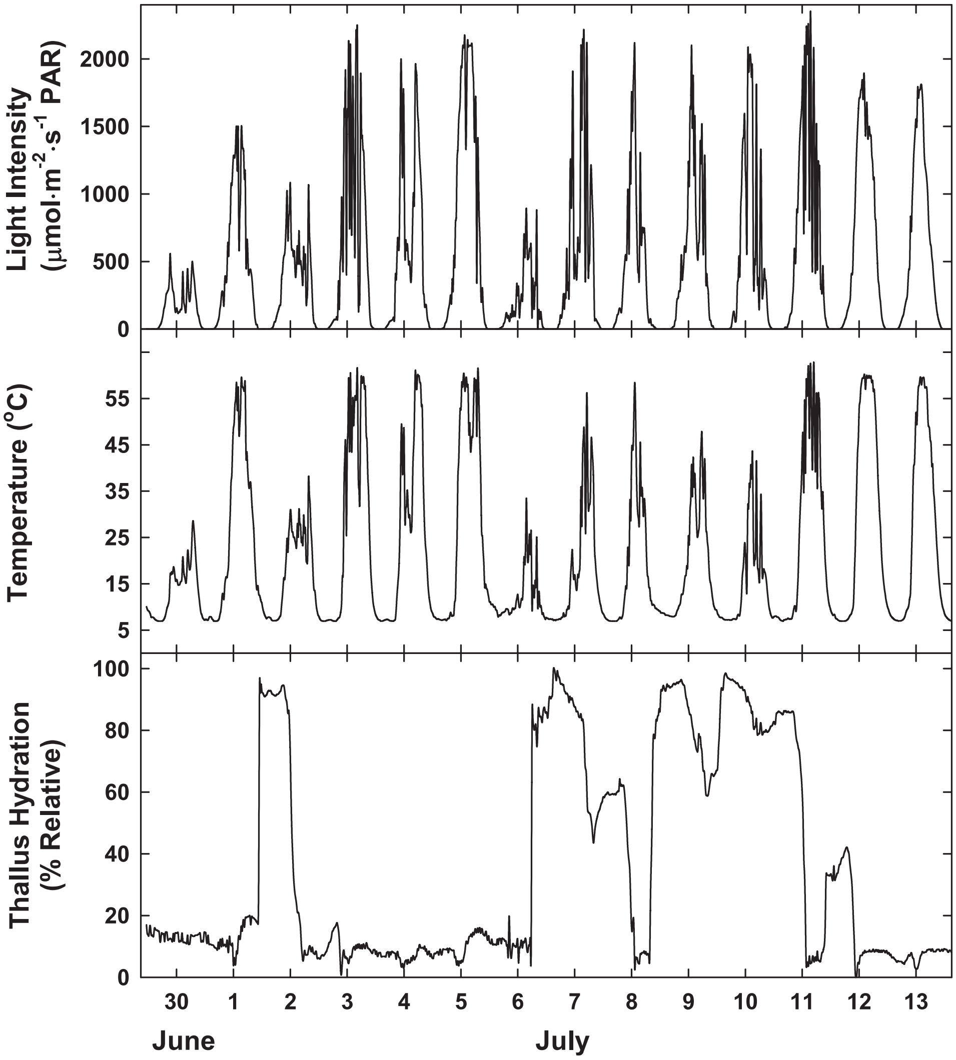
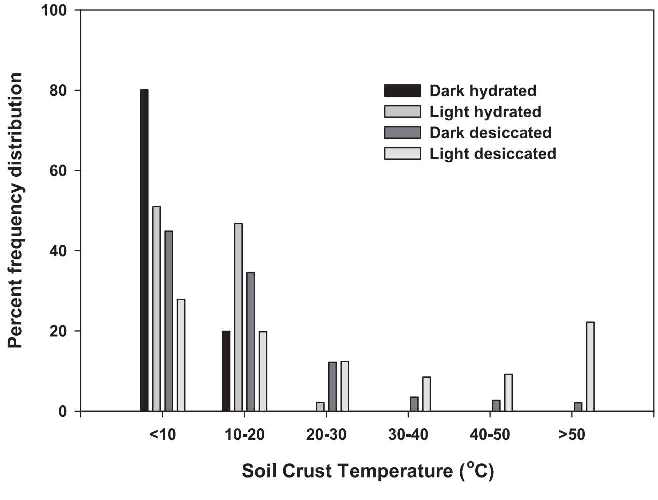


Fig. 5. Soil crust temperature frequency distribution for hydrated and desiccated crusts under light ($>10\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PAR) and dark field conditions.



vided a strong basis for the first hierarchal division of the Chilcotin from Kluane sites by cluster analysis. The Kluane plots contained relatively fewer site-specific taxa (only 8). Some of these were species with arctic–alpine affinities (e.g., *Cetraria aculeata*, *Flavocetraria cucullata*, and *Flavocetraria nivalis*), and others were steppe lichens, common in western United States grasslands, but not found in the Chilcotin plots. An important factor in interpreting this trend in the Kluane BSC data set may be the affinity of many grassland species from the Yukon with Great Plains flora (Vetter 2000), possibly reflecting species exchanges along ice-free corridors in glacial times. As an example, McCune (1994) characterizes *Buellia elegans* as a calcareous steppe indicator in the Columbia Basin. We did not find this species in JRSPP, a disjunct grassland of the northern Fraser basin. It was present, however, in the Kluane study plots, and it is found further south along the east slope of the Rockies in grasslands from Alberta (Thomson 1997).

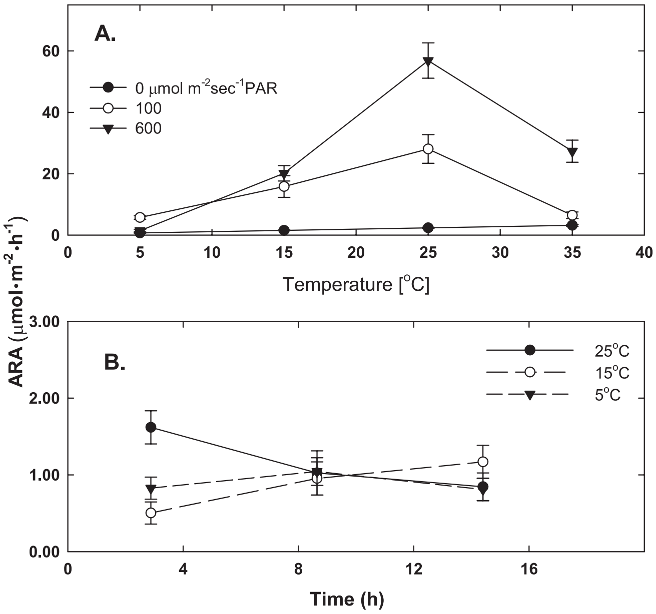
An important ecological role of BSC communities is their potential to support biological nitrogen fixation. Belnap (2002) found a strong correlation between the frequency and duration of prior precipitation events and the magnitude of realized nitrogenase activity on wetting, with nitrogenase

Table 7. Time course and environmental conditions during ARA soil crust incubations on Kluane eskers.

Wetting event	Incubation sequence during each wetting episode (incubation times)	Mean±SE ARA (μmol·m^{-2}·h^{-1})	Hours previously hydrated	Mean thallus temperature (°C)	Mean solar radiation (μmol·m^{-2}·s^{-1} PAR)
2 July	1 (07:30–15:00)	16.9±1.8	8*	21.8	553
6–7 July	1 (20:30–07:30)	3.3±0.3	1	11.72	195
7 July	2 (07:30–13:30)	4.0±0.7	12	18.31	637
8–9 July	1 (21:30–05:30)	2.9±0.3	1	11.8	11
9 July	2 (06:00–13:00)	22.3±3.3	9.5	18.2	474
9–10 July	3 (19:00–16:30)	63.0±6.4	22.5	29.32	971
30 July	1 (05:30–10:30)	0.6±0.2	3*	11.92	156.88
	2 (11:00–15:00)	15.5±2.8	8.5	24.93	263.97
31 July	1 (04:30–09:00)	4.6±1.9	2*	9.65	60.56
	2 (09:30–12:30)	8.5±1.1	7	9.65	424.62
1 August	1 (09:30–10:30)	3.4±0.9	1	23.2	741.87
2–3 August	1 (23:30–09:00)	3.7±0.9	1	9.33	53.42
3 August	2 (09:30–12:30)	1.2±0.1	9	12.74	267.47
11 August	1 (15:30–21:00)	7.0±0.7	1	12.8	71.27
11–12 August	2 (21:30–06:00)	7.5±0.7	7	9.9	8.22
12 August	3 (06:30–13:30)	7.5±1.9	16	12.33	157.39
12 August	4 (14:00–21:30)	17.6±4.1	23.5	17.52	268.23
12–13 August	5 (22:00–06:30)	14.2±1.6	31.5	10.3	12.96
13 August	6 (07:30–12:00)	22.5±3.7	41	17.08	488.74

*Pre-incubation hydration during previous evening or early morning.

Fig. 6. (A) Temperature and light response of acetylene reduction assay (ARA) in Kluane soil crusts. (B) Time response of ARA in dark after hydration at different temperatures.



activity only observed (in Utah study sites) if there had been a prior rain or snow event within the previous week. Although Kluane BSC communities were also sensitive to the duration of previous hydration events (threefold higher ARA rates after 24 h prior hydration), we did record ARA activity where the time since previous hydration events had been greater than 1 week (e.g., 30 July episode). This may reflect more severe soil surface microclimate conditions at Belnap's Utah sites. Belnap et al. (2004) further note that frequent short-duration hydration episodes can result in reduced viability of *Collema*-dominated BSC, possibly because of the loss of UV protective pigments. Our short-term data set would indicate that wetting events during summer 2004 would not have imposed this limitation on thalli; however, longer term (and multi-year) microclimate monitoring would be needed to confirm this trend.

Nonvascular cryptogams in northern boreal and montane environments face common limitations realizing potential net assimilation. During most periods of precipitation, when sufficient moisture is available to sustain metabolic activity, ambient temperature and light conditions fall well below optimum values (Kershaw and MacFarlane 1982; Coxson and Kershaw 1983*a*). However, on transition to full sun conditions, BSC thalli dry rapidly, even though temperature and light availability may briefly pass through optimal ranges. Optimizing physiological strategies to deal with these two extremes is difficult. Coxson (1987) found that this transition to full sun conditions resulted in short-term photoinhibition of net photosynthesis in the nitrogen-fixing forest floor lichen *Stereocaulon tomentosum*. *Collema*-dominated crusts from Kluane faced a similarly rapid transition from temperature- and light-limiting conditions to excess light and high temperature conditions. Still, over half of all daytime exposure by hydrated crusts was under cloud cover at temperatures of under 10 °C. Hydrated thalli were only exposed briefly to daytime temperatures of over 20 °C (only 2.2% of the time). By way of comparison, dry thalli face temperatures over 30 °C more than 30% of the time during daylight hours.

The observed ARA temperature optimum of 25 °C for *Collema* soil crusts is similar to that found in many north temperate cyanolichens (Coxson and Kershaw 1983*a*; Fritz-Sheridan and Coxson 1988). Lange et al. (1998) noted that

Table 8. Selected chemical properties of biological soil crusts and associated mineral soils at the Chilcotin and Kluane sites.

	Chilcotin (2002, n=10)				Kluane (2003, n=8)				Kluane (2004, n=32)			
	Soil		Crust		Soil		Crust		Lower crust		Upper crust	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Total C (%)	**1.38**	0.54	**4.14**	2.46	3.63	0.83	5.18	1.90	3.69	0.33	4.96	0.81
Inorganic C (%)					0.95	0.95	1.09	1.06	2.32	0.19	2.27	0.16
Total N (%)	**0.14**	0.05	**0.30**	0.15	0.24	0.10	0.32	0.15	**0.14**	0.03	**0.25**	0.07
Total S (mg·kg^{-1})	**165**	51	**303**	132								
Mineralizable N (mg·kg^{-1})	**30.0**	14.2	**247.0**	108.6	**46.5**	20.5	**251.7**	157.4				
Available P (mg·kg^{-1})	**6.6**	4.1	**14.0**	7.2								
pH (CaCl$_2$)	**6.88**	0.56	**6.04**	0.57								
Cation exchange capacity (cmol (+)·kg^{-1})	14.23	2.75	14.92	4.38								
Exchangeable Ca^{2+} (cmol (+)·kg^{-1})	9.73	1.59	9.83	2.82								
Exchangeable Mg^{2+} (cmol (+)·kg^{-1})	0.55	0.20	0.63	0.22								
Exchangeable K^{+} (cmol (+)·kg^{-1})	3.94	1.36	4.37	1.38								
δ^{15}N (‰)	**4.4**	1.1	**2.2**	0.8	3.1	1.5	2.2	1.7	**1.6**	0.8	**-0.2**	0.6

Note: Blank cells indicate properties that were not determined. Means in bold are significantly different between sample types within a site (one-way ANOVA, $p < 0.05$).

photosynthetic response patterns of *Collema* BSC crusts from Utah showed characteristics of an extreme "sun-adapted" plant, with tolerance of relatively high thallus temperatures when hydrated and optimum photosynthetic response observed near 35 °C. In the Kluane, *Collema* crusts with similar high temperature tolerance may favor brief periods of high N-fixation activity during transitional conditions, when crusts face full sun exposure before being desiccated. Although we do not know the degree to which thalli may acclimate to cooler spring snowmelt conditions, the work of Coxson and Kershaw (1983*a*) suggests that spring physiological responses may be relatively unchanged. Our surface impedance clips (that recorded thallus hydration under field conditions in *Collema* crusts) did not show any evidence of crust rewetting during early morning conditions of high ambient relative humidity. This is consistent with previous studies showing little or no metabolic response by cyanobacterial crusts to water vapor exposure (Stradling et al. 2002).

Given the relatively xeric nature of the Kluane rain-shadow environments (fewer than 18 d a year with rainfall) snowmelt events may also play an important role in providing conditions under which BSC net carbon assimilation and nitrogen fixation can occur. Coxson and Kershaw (1983*b*) demonstrated rapid recovery of ARA activity in *Nostoc* under snowmelt conditions. However, unlike southern Alberta, where Coxson and Kershaw (1983*a*) documented multiple snow deposition and melt events during the winter period, crusts at Kluane are covered in snow for a three to four month period each winter. The melt of winter snowpack from south facing esker slopes at Kluane in 2005 occurred during early April, though precipitation may fall as snow well into May. Conditions for nitrogen fixation activity may be suboptimal during many snowmelt events. However, solar loading in snow-melt pockets can result in surprisingly high crust temperatures. Coxson and Kershaw (1984) regularly documented temperatures of over 20 °C in *Caloplaca* BSC under a thin ice layer during full-sun late winter melt conditions.

Our focus on *Collema*-dominated crusts at Kluane will also bias our interpretation of overall BSC activity. In a comparison of ARA rates in different crust types, Belnap (2002) found that ARA rates were highest in "dark" *Collema*-dominated (lichenized) crusts, followed by rates in other cyanolichen crusts and finally by rates in so-called "light" crusts (dominated by free-living *Microcoleus* species). By this ranking our Kluane ARA estimates (from *Collema*-dominated crusts) would be biased towards higher ARA rates. However, given the relatively high proportion of *Collema*-dominated crusts on the Kluane eskers this may be quite representative of potential N-fixation activity.

Belnap (2002) further notes that the presence of light BSC is often indicative of past surface disturbance and can result in areas with much lower nitrogen fixation potential. This may be a concern in many of the Kluane eskers, especially on mid- and lower-slope positions, where heavy grazing by horses has resulted in many localized areas of soil erosion. Although evidence of widespread grazing (by California bighorn sheep) was also noted present in the Chilcotin, it was at much lower levels of intensity (based on disturbance of soil surfaces). Yeager et al. (2004) suggests that it can

Fig. 7. Thin section micrographs of biological soil crusts (BSC) and underlying mineral soil at the Chilcotin and Kluane study areas. All images were acquired in plane light, except as noted. Scale bar = 1 mm. (*a*–*e*) Chilcotin. (*a*) Site 8-1, detail of upper portion of BSC. (*b*) Site 6-1, platy microstructure in Ah horizon at a depth of 4 cm. (*c*) Site 1–3, detail of upper portion of BSC. (*d*) Same view as Fig. 7*c* but in polarized light. Note bright white birefringent silt grains below lichen crust components. (*e*) Site 3-1, detail of BSC. Note proximity of root (arrow) to crust surface. (*f*–*h*) Kluane. (*f*) Peninsula site. Note partial burial of moss crust components (arrow). (*g*) Silver City site. Note numerous dark organic fragments dispersed throughout spongy matrix below living crust components. (*h*) Peninsula site. Note dark lamination (arrow) 2 cm below crust surface.

take upwards of several decades before soil surface environments are sufficiently stabilized by early successional cyanobacteria such as *Microcoleus vaginatus* before colonization by *Collema*-dominated crusts can occur. This transition from *Microcoleus* to *Nostoc* or *Scytonema* as dominant cyanobacterial crust components was accompanied by the development of a pinnacled surface topography that characterizes mature crusts.

At the Chilcotin sites, the pattern of elevated concentrations of C and nutrients (N, S, P) in the crusts was consistent with that found in other arid or semi-arid ecosystems (Harper and Pendleton 1993; Belnap et al. 2001*c*; Smith et al. 2002). Although N-fixation rates were not measured at this study area, the twofold enrichment in total N concentration likely reflects N inputs by N-fixing crust components, particularly free-living *Nostoc* colonies and *C. tenax* crusts, both of which were abundant in the Chilcotin BSC.

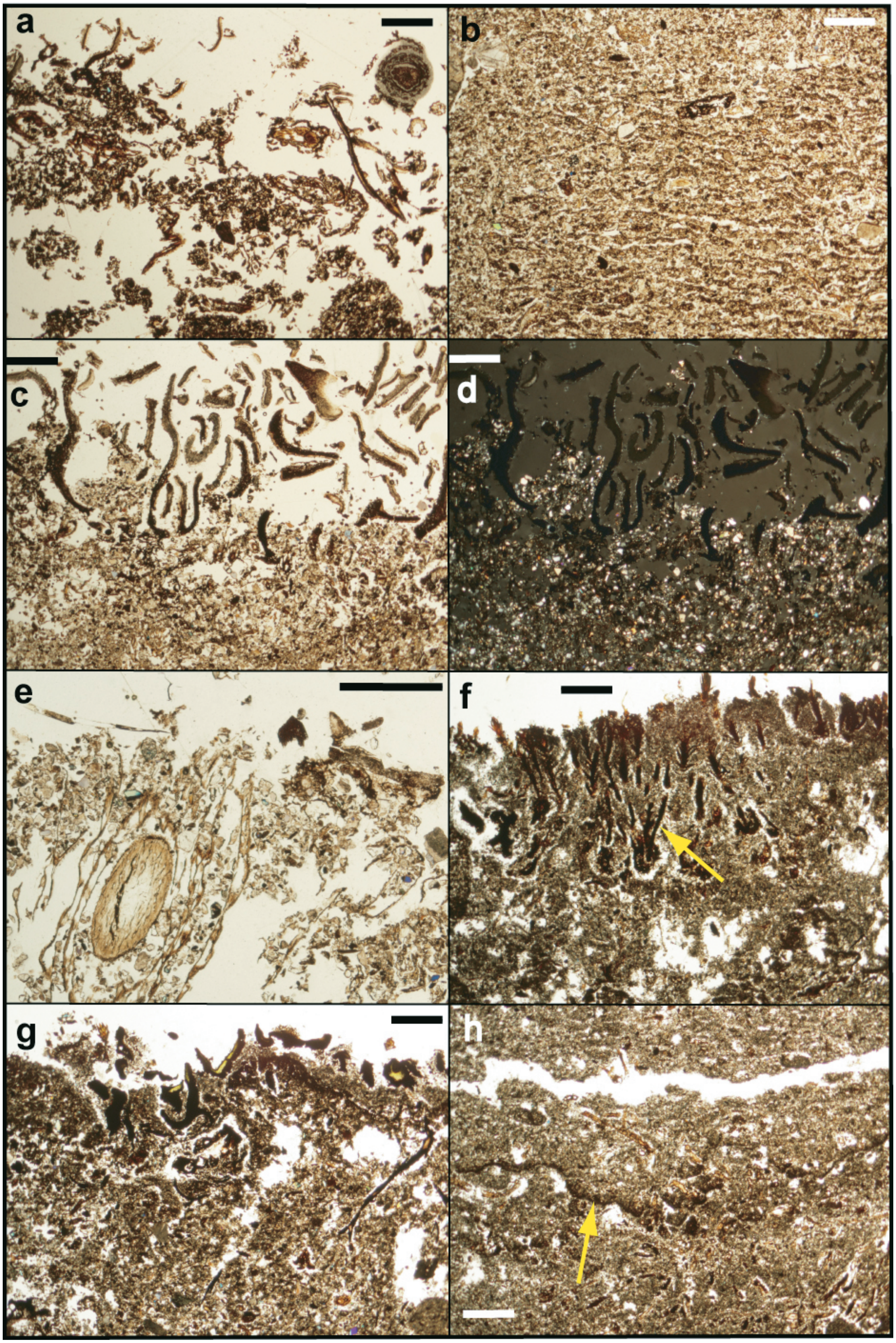
N-fixation activity in the crusts was also suggested by ^{15}N natural abundance values (δ^{15}N) that were significantly lower than in the underlying mineral soils and close to the range (–2% to 2 ‰) suggested by Evans and Lange (2001) as indicating significant N inputs from fixation. The degree of difference in mineralizable N concentrations between crusts and soils greatly exceeded that reported for other steppe ecosystems (Smith et al. 2002), and although different incubation procedures were used in the earlier study, such findings suggest that crust N pools are particularly labile.

The observed lower pH values in these crusts relative to the underlying soil parallels findings elsewhere (Pérez 1997; Smith et al. 2002). Although Belnap et al. (2001*c*) cited evidence that photosynthetic BSC organisms locally increase the pH of their surrounding medium, the acidity in the Chilcotin samples could be contributed by other BSC components and their metabolic activities, such as production of organic acids by lichens (Banfield et al. 1999). This acidification may potentially enhance chemical weathering of minerals, contributing to the observed improvement in phosphorus availability. This pH depression may also account for the lack of significant differences in cation exchange capacity and exchangeable cation concentrations between crust and soils, as a result of lower dissociation of pH-dependent exchange sites associated with BSC organic matter. Greater soil phosphorus availability at BSC microsites may also result from secretion of P-freeing compounds, such as oxalic acid, by lichenized fungi (Chen et al. 2000).

For the 2003 Kluane Lake samples, the less distinct differences between crust and soil chemical properties may reflect both a smaller sample size and the confounding effects of more heterogeneous soil environments resulting from differences in loess deposition rates along the 20 km transect from the Slims River delta. Nevertheless, mineralizable N concentrations displayed a degree of enrichment in the crusts that was almost as great as that observed in the Chilcotin study area. The more intensive 2004 sampling was conducted at sites that are at the high end of the inferred loess deposition continuum at Kluane Lake (Laxton et al. 1996). This greater homogeneity in soil-forming environments may be responsible for the clear expression of N enrichment within the uppermost portion of the crusts, paralleled by δ^{15}N values that were clearly within the range associated with N-fixation at other sites (Evans and Ehleringer 1993; Evans and Belnap 1999; Russow et al. 2004).

Soil thin sections from both study areas indicated that BSC had spongy, porous microstructures differing consistently from the underlying surface mineral soils, with the typical platiness of the latter usually being attributed to formation of ice lenses (Van Vliet-Lanöe 1985). At Kluane, the greater degree of intermingling of mineral material and recognizable BSC components, such as mosses, suggests that crust burial is occurring by the continuing inputs of loess from the adjacent Slims River floodplain. A similar sediment-trapping effect by mosses was also inferred from thin sections of Australian BSC by Belnap (2001). The origin of the darker laminations deeper within the crust is uncertain, although somewhat similar features were noted in micrographs of Chinese BSC and considered to be sedimentary structures (Hu et al. 2003). This continuing process of deposition and burial is consistent with the apparently deeper dispersal of crust-derived detritus into the surface mineral soil at Kluane than in the Chilcotin sections, perhaps accounting for the less pronounced contrast in C and N concentrations between BSC and mineral soils at the former study area.

These findings suggest that lichen-dominated biological soil crust communities have important roles in stabilizing loess-influenced soils and contributing biologically fixed N in rain-shadow grasslands of central interior British Columbia and southwestern Yukon. Further studies are needed to quantify these N inputs, and the contribution of BSC to soil organic matter and nutrient dynamics in these ecosystems. A more complete understanding of the roles of BSC in modern grasslands in northwestern Canada will also have implications for models of the ecological functioning of full-glacial ecosystems in ancient Beringia. Although current concepts (Schweger 1997) recognize the central importance of edaphic factors for the productivity of steppe-like Beringian ecosystems, the contribution of nonvascular components to loess stabilization and nutrient cycling has not been reflected in these models. Equally important, these results suggest that a large body of prior research on biological soil crusts from desert and grassland environments of the western United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States may now have application to sage–steppe grasslands from rain-shadow environments of interior British Columbia and the Yukon, where many of the same lichen taxa give rise to biological soil crust formation.

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