ARCTIC
VOL. 68, NO. 1 (MARCH 2015) P. 69–78
http://dx.doi.org/10.14430/arctic4453

High-Latitude Yukon Boreal-Cordilleran Grassland Plant Communities

Wayne L Strong[1]

(*Received 13 January 2014; accepted in revised form 10 June 2014*)

ABSTRACT. High-latitude (61.9˚–62.8˚ N) graminoid plant communities located near the northern limit of boreal forest occurrence in the Carmacks–Pelly Crossing area of Yukon were sampled and classified, and four sociations were recognized: *Calamagrostis purpurascens* (purple reedgrass), *Hesperostipa comata* (needle-and-thread grass), *Poa glauca–Artemisia frigida* (glaucous bluegrass–pasture sagewort), and *Pseudoroegneria spicata–Artemisia frigida* (bluebunch wheatgrass–pasture sagewort). These plant communities occurred primarily on south-southwest slopes (180˚–230˚) with 45%–75% gradients. Relative to southern Canada mixedgrass prairie, Yukon grasslands were likely species poor, had less total canopy cover, and produced less than half as much aboveground herb biomass (typically 200–300 kg/ha). The distribution of the sociations appeared limited to ~60˚–65˚ N latitude in the Yukon-Alaska region. *Calamagrostis* was the most abundant and widespread grassland sociation in the study area. The four sociations occupied less than 4% of the Carmacks–Pelly Crossing landscape, although they represented the most extensive high-latitude boreal grassland vegetation in Canada (≥ 2600 ha) and they were among the most northerly in North America.

Key words: Beringia; boreal; ecology; grassland; palaeovegetation; plant community; sociation

RÉSUMÉ. Les communautés de plantes graminoïdes en haute latitude (61,9˚-62,8˚ N) situées près de la limite nord du milieu de forêt boréale dans la région de Carmacks-Pelly Crossing, au Yukon, ont fait l’objet d’un échantillonnage et d’un classement. Cela a permis de reconnaître quatre sociations : *Calamagrostis purpurascens* (calamagrostis pourpre), *Hesperostipa comata* (stipe comateuse), *Poa glauca-Artemisia frigida* (pâturin glauque-armoise douce) et *Pseudoroegneria spicata-Artemisia frigida* (agropyre à épi-armoise douce). Ces communautés de plantes se manifestaient surtout sur les versants du sud et du sud-ouest (180˚-230˚) comportant des gradients variant entre 45 % et 75 %. Comparativement à la prairie mixte du sud du Canada, les herbages du Yukon comportaient vraisemblablement peu d’espèces et un moins grand couvert au total, et ils produisaient moins de la moitié de biomasse épigée (généralement entre 200 et 300 kg/ha). La répartition des sociations semblait limitée à la latitude ~60˚-65˚ N de la région du Yukon-Alaska. Dans l’aire visée par l’étude, *Calamagrostis* était la sociation d’herbage la plus abondante et la plus généralisée. Les quatre sociations occupaient moins de 4 % du paysage de Carmacks-Pelly Crossing, même si elles représentaient la végétation d’herbage boréal la plus vaste en haute latitude au Canada (≥ 2600 ha) et qu’elles figuraient parmi les sociations les plus au nord de l’Amérique du Nord.

Mots clés : Béringie; boréal; écologie; herbage; paléovégétation; communauté de plantes; sociation

Traduit pour la revue *Arctic* par Nicole Giguère.

INTRODUCTION

The grassland or Prairie biome of interior North America extends northward to ~54˚ N latitude in western Canada (Ecoregions Working Group, 1989). Grass-dominated communities, however, are not restricted to this biome. They also occur among conifer forests on favorable site conditions in the mountains of southwestern Alberta (Stringer, 1973; Holland and Coen, 1982; Grande Cache Coal Company, 2001), northern British Columbia (Seip and Bunnell, 1985; Pojar, 1986), and southwest Yukon (Hoefs et al., 1975; Vetter, 2000; Chambers, 2010). Grass-dominated vegetation was also relatively common among mixedwood forests, as far north as ~58˚ in the Peace River district of northwestern Alberta until the mid-1900s. Since that time, however, most of these grasslands have been converted to agricultural cropland or replaced by forest vegetation (Moss, 1952; Wilkinson and Johnson, 1983; Strong et al., 2009). Today, grassland remnants are largely confined to steep southerly slopes such as those along the Peace River Valley.

In forested boreal and cordilleran landscapes, grass-dominated vegetation typically occurs as small isolated entities of two distinct ecological types: meadows and grasslands. Meadows occur where early summer flooding results in site moisture that exceeds the needs of the associated terrestrial plants, but conditions become much drier during the remainder of the growing season (Mueller-Dombois and Ellenberg, 1974:481). *Calamagrostis*

[1] Arctic Institute of North America, 2500 University Drive NW, Calgary, Alberta T2N 1N4, Canada; present address: Yukon Research Centre, Yukon College, 500 College Drive, PO Box 2799, Whitehorse, Yukon Y1A 5K4, Canada; wstrong@yukoncollege.yk.ca

canadensis (marsh reedgress), *Calamagrostis stricta* (northern reedgrass), and *Deschampsia cespitosa* (tufted hairgrass) are characteristic meadow taxa in forested landscapes. In contrast, grasslands (including dryland *Carex* spp. or xerophytic sedge stands) are associated with sites that create severe physiological moisture stress for plants. These sites include steep southerly slopes that have rapid lateral drainage and accentuated evaporation, coarse-textured surficial materials with poor water-holding capacity, and saline (Wilkinson and Johnson, 1983) and alkaline soils (Schwarz and Wein, 1997) with adverse soil chemistry. Grasslands that occur on steep slopes are the focus of this study.

The most frequently reported indigenous grassland community along the eastern slopes of the Canadian Cordillera is dominated by *Leymus innovatus* (hairy wild rye), often with *Arctostaphylos uva-ursi* (bearberry) as a codominant (e.g., Holland and Coen, 1982; Beckingham et al., 1996; Strong, 1996; Grande Cache Coal Company, 2001), and it occurs as far north as 59˚ N latitude (Seip and Bunnell, 1985). Such plant communities often represent less than 2% of the regional vegetation (e.g., Strong, 1996; Grande Cache Coal Company, 2001). Several studies have reported the occurrence of boreal and cordilleran grassland communities in northwestern Canada. *Hesperostipa spartea–Carex* spp.*–Artemisia frigida* (porcupine grass-sedge-pasture sagewort) communities on steep southerly slopes in the boreal forest zone of northern Alberta have been described by Wilkinson and Johnson (1983; ~56˚ N, 118˚ W) and Redmann and Schwarz (1986; ~59˚ N, 112.5˚ W). Pojar (1986) documented the occurrence of subalpine *Festuca altaica* (Altai fescue) and *Poa glauca–Carex supina* (glaucous bluegrass-weak arctic sedge) grasslands in north-central British Columbia (~57.6˚ N, 129˚ W), and Hoefs et al. (1975) recognized *Calamagrostis purpurascens* (purple reedgrass)*–Arctostaphylos uva-ursi*, *Carex filifolia* (threadleaf sedge)*–Artemisia frigida*, *Elymus violaceus* (wheatgrass), *Elymus × yukonensis* (Yukon wheatgrass)*–Artemisia frigida*, and *Festuca altaica* types on Sheep Mountain in Kluane National Park, southwestern Yukon (~61˚ N, 138.5˚ W). In contrast, Vetter (2000) found only *Carex filifolia–Artemisia frigida* vegetation near Aishihik-Sekulmun Lakes ~85 km to the northeast, whereas Chambers (2010) reported *Calamagrostis purpurascens*, *Carex duriuscula* (needleleaf sedge)*–Artemisia frigida*, and *Carex supina*-dominated communities in the Takhini Valley ~145 km east-southeast of Sheep Mountain. These examples convey some of the compositional diversity that exists among grasslands when they occur in tree-dominated landscapes.

In the northernmost portion of the Canadian boreal forest, an atypical concentration of grasslands has been recognized in Yukon from ~10 km south of Braeburn northward to Carmacks (Oswald and Senyk, 1977) and from Braeburn northward to the Stewart River (Smith et al., 2004) (Fig. 1). The latter study described these grasslands as "extensive" and a "notable feature" of the landscape, although they

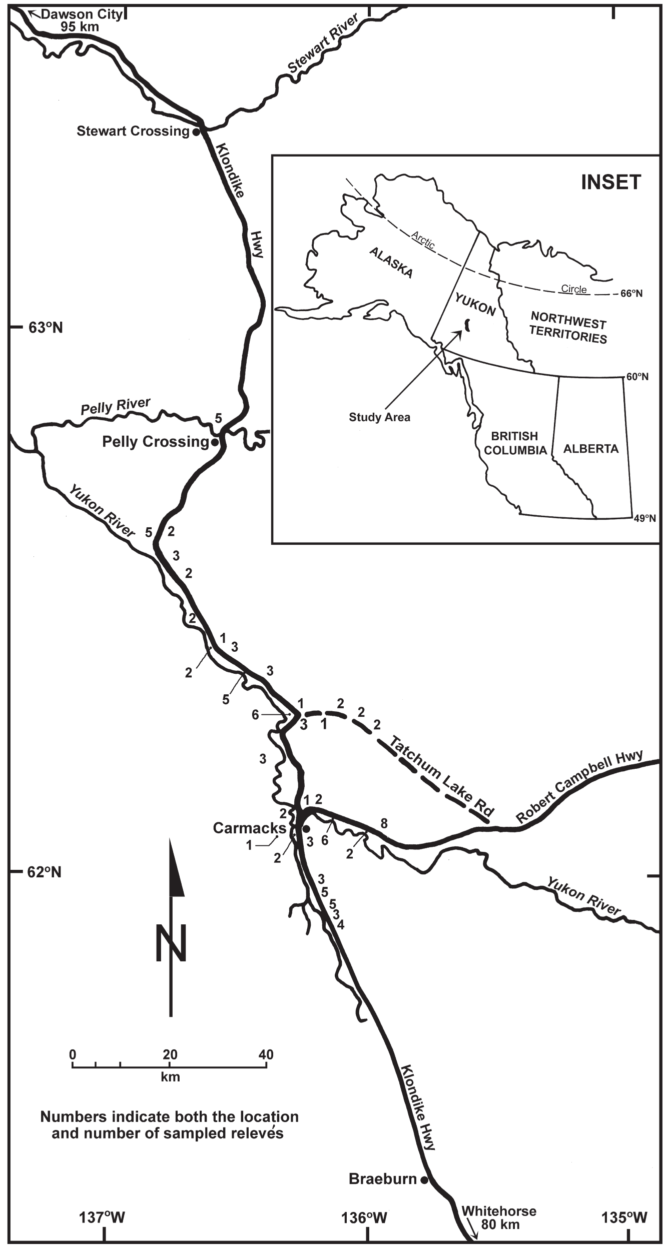

FIG. 1. Locations of sampled sites within the Carmacks–Pelly Crossing area. The inset indicates the location of the study area within Yukon and northwestern North America.

also occur elsewhere in southern Yukon (see Figs. 3 and 4 in Strong, 2013). In addition to creating diversity in forest-dominated landscapes, Yukon grasslands are also known to include rare endemic species such as *Nestotus macleanii* (Maclean's goldenweed), and prairie floristic elements such as *Hesperostipa comata* (needle-and-thread grass) and *Achnatherum richardsonii* (Richardson needlegrass) (Cody, 2000). Scudder (1997:50) considered grasslands to be the "most interesting and notable habitats in the Yukon" with respect to insect diversity. Yukon grasslands also represent an important but limited habitat for grazing ungulates (Strong et al., 2013).

Despite the purportedly common occurrence of grasslands on the central Yukon Plateau, little is known about the plant communities that form the vegetation except that they typically occur on steep southerly slopes. The goals of this study were therefore to (1) sample the botanical composition of the dry upland graminoid-dominated vegetation that occurs in the Carmacks – Pelly Crossing area of Yukon; (2) classify the resulting compositional summaries or relevés into distinct plant community types on the basis of species dominance (i.e., sociations); (3) determine the range of slope orientations and gradients that each occupies; and (4) estimate the aboveground productivity of herbaceous plants in each sociation.

MATERIALS AND METHODS

Study Area

The study area was limited to grassland polygons located near the Klondike Highway and connecting roads between Pelly Crossing and a point 20 km south of Carmacks, which represents a north-south distance of ~100 km (Fig. 1). The connecting roads included the easternmost portions of the poorly developed Nansen and Free Gold roads that are located immediately west of Carmacks, the western 16 km of the Tatchum Lake Road, and ~18 km of the Robert Campbell Highway along the Yukon River Valley, immediately east of Carmacks. The area included represents the more accessible portions of the region and the overlapping zones of grassland concentration recognized by Oswald and Senyk (1977) and Smith et al. (2004), as well as the core of the central Yukon Plateau.

Rounded mountain ridges with steep lower slopes and broad valleys typify the topography of the Carmacks – Pelly Crossing area. Maximum local relief is ~700 m, with a base elevation of 450 m above sea level. The study area is located within the westernmost portion of Wisconsinan glaciation (Dyke and Prest, 1987). Glacial fluvial deposits on valley bottoms and moraine on lower valley slopes are the most common surficial materials. Bedrock exposures often dominate upper slopes and the highest elevations (Klassen and Morison, 1987; Klassen et al., 1987). All of the study area is within Yukon's Northern Cordilleran Boreal ecoclimatic region, where seral *Populus tremuloides* (trembling aspen) and successionally more mature *P. tremuloides – Picea albertiana* ssp. *albertiana* (western white spruce) vegetation occupy well to moderately well drained sites at elevations below ~1200 m (Strong, 2013). *Pinus contorta* var. *latifolia* (lodgepole pine) vegetation forms only a small portion of the study area. *Picea albertiana* is the dominant late-successional tree on upland sites. The median temperatures are 10.8˚C for summer (May – September) and –18.8˚C for winter (November – March) (Strong, 2013). Most precipitation (177 of 279 mm) falls in summer, but ~72 cm of snowfall (~72 mm water equivalent) typically occurs during winter.

Field Sampling and Related Methods

Prior to field sampling, aerial photographs were searched for potential sampling areas, with attention focused primarily on larger grassland polygons. Relevé sampling was limited to locations within grassland polygons that had (1) xerophytic graminoids as the dominant plants, (2) a relatively uniform species composition, (3) a relatively uniform slope gradient and orientation, and (4) mineral soils without substantial evidence of active surface erosion, but (5) lacked a notable woody plant component and (6) occurred within a one-hour hike from a road or 20 minutes from another relevé. Grassland polygons larger than 2 ha in area were sometimes sampled in more than one location because of the spatial heterogeneity of the vegetation. If more than one relevé was sampled, they differed notably in species composition, or were more than 100 m apart, or had a greater than 20˚ difference in slope orientation, or more than 10% difference in slope gradient. One hundred relevés were sampled at 33 different locations in the study area (Fig. 1).

Species composition sampling and canopy cover estimation for each relevé were based on five 100 cm × 100 cm quadrats located at 2.5 m intervals along a 15 m transect. The lower left corner of the first quadrat was located at the 2.5 m mark on each transect. For each relevé, a transect was placed in the center of a vegetation stand that by visual survey was judged to have a relatively consistent structure and species composition. Transects were aligned parallel to the terrain contour, with the quadrat frame held horizontal during sampling (cf. Beers, 1969; Abella et al., 2004). Ocular estimation was used to gauge the percent canopy cover of individual species (*sensu* Daubenmire, 1968). The larger-than-normal quadrat size for grassland sampling (cf. Wilkinson and Johnson, 1983; Redmann and Schwarz, 1986) was used to accommodate the tussock habit and large size (e.g., up to 70 cm tall foliage; Cody, 2000) of locally common *Calamagrostis purpurascens*. A short transect was used to minimize the topographic variability that could occur within a relevé, so a specific slope orientation and gradient might be linked to each plant community. Furthermore, the short transects helped minimize the amount of physical site damage caused by sampling. Slope orientation and gradient were determined for each relevé using a compass and clinometer, and location and elevation, with a hand-held global positioning system device. June 22 solar insolation (kJ/m^2) input was estimated by regression analysis of total daily values (Buffo et al., 1972), with adjustments for the location, slope orientation, and slope gradient for each relevé. Plant nomenclature follows ITIS Partners (2013) for vascular plants, except for *Picea* spp. (Strong and Hills, 2006) and lichens (Esslinger, 2014).

The vegetation at selected relevés was sampled to estimate aboveground plant biomass availability. To ensure at least five biomass estimates were available for each plant community type in the final vegetation classification, relevés were stratified into five tentative plant community types on the basis of general species compositions. Ten relevés were selected at random from the two more common plant community types and five from each of the other three types, for a total of 35 samples. The tentative relevé classification was discarded after the biomass sampling was completed. Biomass sampling followed the same design used for relevé composition sampling. The current summer's growth of herbaceous plants was clipped within 3 cm of the ground surface and separated into graminoids and forbs. The collected material was air-dried in paper bags for approximately three weeks in a warm environment and then oven-dried at 60˚C for 24 hours prior to weighing. Vegetation composition sampling was conducted from 24 June to 9 July 2013, and biomass sampling from 5 to 11 August. The latter was completed before the anticipated first late-summer frost, which typically occurs in mid to late August, as indicated by Carmacks meteorological data for 1981 – 2012 (Environment Canada, 2014).

An estimate of grassland areal extent in the Carmacks – Pelly Crossing study area was determined for a corridor 5 km wide centered on the three main access roads (a total area of ~840 km^2). Mapping of individual grassland polygons was done through stereoscopic interpretation of aerial photographs and the plotting of polygons at a map scale of 1:50 000. The mapped polygons included all sampled grassland polygons, as well as some judged unsuitable for sampling for whatever reason and those that were not readily accessible (e.g., across a river). The areal extent of the individual grassland polygons and the study area was determined by planimeter measurement.

Data Analysis

A cluster analysis based on Ward's method and relative Euclidean distance was used to aggregate relevés according to similarities in species composition and abundance (McCune and Mefford, 1999). The groups recognized in the resulting dendrogram were scrutinized for consistency in composition and then classified according to dominant species, i.e., sociations *sensu* G.E. Du Rietz (Mueller-Dombois and Ellenberg, 1974). The closest North American approximations to this classification approach are represented by the proposed Canadian System of Vegetation Classification (Strong et al., 1990) and the system used in Alaska (Viereck et al., 1992). Two relevés that were ambiguous with respect to sociation membership were excluded from classification. Detrended correspondence analysis (McCune and Mefford, 1999) was used to illustrate the compositional relationship among individual relevés and the distinctiveness of each sociation. The degree of ordination explanation was based on relative Euclidean distance. Constancy was defined as the percent occurrence of a taxon among relevés. Dominance concentration of taxa in individual relevés was estimated using the algorithm presented by Strong (2002).

Prior to statistical analysis, data were tested for normality using the Kolmogorov-Smirnov one-sample test. Because most variables were not normal distributed, Kruskal-Wallis tests were used to identify compositional and site condition differences among sociations. Nonparametric Scheffé rank tests at the $\alpha = 0.05$ level (Miller, 1966: formula 110) were used to identify differences between individual sociations. Paired groups with normally distributed values were compared using t-tests. All statistical analyses were based on STATISTICA software (Statsoft, 1995) except Scheffé rank tests, which were assessed manually.

RESULTS

Grasslands represented at least 2600 ha or 3% – 4% of the terrestrial vegetation within the 5 km wide study corridor along the main access roads in the Carmacks – Pelly Crossing area. In total, 100 grassland polygons were mapped, with upper quartile values (Q_3 – maximum) of 27 to 345 ha. Both the size and the frequency of grassland polygons appeared to diminish with increasing distance from the highways. The sampled grasslands were located between 61.9˚ and 62.8˚ N latitude. Relevés were distributed throughout the study area, with one notable exception: the five most northern relevés were sampled near Pelly Crossing, which was ~19 km northeast of the next nearest location (Fig. 1). The next potentially available grassland polygon to the north was located ca. 70 km away, immediately north of Stewart Crossing. Most of the polygons visited were dominated by a single type of grassland community, but at least one other community was often present because of variation in site conditions and topographic position (e.g., toe versus middle and upper slopes). Variable site conditions also tended to create differences in plant densities and composition within communities. Most sampled polygons had mineral matter (sandy loam to loamy sand texture) in the uppermost portion of their soil profile, with bedrock often within 1 m of the ground surface. No evidence of permafrost was observed. Stunted and scattered individuals and small clones of *Populus tremuloides* sometimes occurred in conjunction with grassland areas, but well-developed forest vegetation occurred only at the margins.

Sociations

Four grass-dominated sociations were recognized among 98 relevés in the final classification (Table 1): *Calamagrostis purpurascens* (purple reedgrass, Fig. 2), *Pseudoroegneria spicata – Artemisia frigida* (bluebunch wheatgrass – pasture sagewort), *Hesperostipa comata* (needle-and-thread grass), and *Poa glauca – Artemisia frigida* (glaucous bluegrass – pasture sagewort). The cluster analysis groupings that represented the first three sociations formed in the dendrogram at the 13% or less amalgamation error level, whereas the *Poa* sociation formed at the 23% error level. Cluster amalgamation was discontinued after formation of the latter group. Three percent chaining occurred within the dendrogram. *Calamagrostis* was the most frequently sampled sociation (49%, Table 1), but field observations suggested that it probably comprised at least

TABLE 1. Species composition, site characteristics, and net primary productivity of boreal grassland sociations in the Carmacks – Pelly Crossing area in Yukon, Canada. Group comparisons are based on Kruskal-Wallis tests. See Table 2 for list of other occurring taxa.

	Sociation				
	Calamagrostis purpurascens	*Pseudoroegneria spicata – Artemisia frigida*	*Hesperostipa comata*	*Poa glauca – Artemisia frigida*	*p*-value
Taxonomic Composition[1]	Average percent cover [SD] constancy, Scheffé test[2,3]				
Androsace septentrionalis	+[+]6a[4]	+[+]3a	+[+]1a	+[+]7a	0.003
Anemone patens	2[4]5b	+[+]0a	0a	1[2]5a	< 0.001
Artemisia frigida	4[3]9a	8[6]9ab	3[4]7a	12[11]9b	< 0.001
Calamagrostis purpurascens	44[11]10b	+[1]1a	+[+]2a	+[+]1a	< 0.001
Carex spp.[5]	3[5]6a	+[1]2a	+[1]5a	13[11]10b	< 0.001
Carex supina	2[5]4ab	+[2]a	+[+]2ab	8[11]7b	< 0.001
Hesperostipa comata	0a	0a	49[20]10b	+[+]1a	< 0.001
Penstemon gormanii	1[1]6	2[2]7	1[1]4	1[1]6	0.245
Poa glauca	+[1]2a	+[1]2a	0a	18[14]10b	< 0.001
Potentilla pensylvanica	1[1]7a	1[1]6a	+[1]2a	2[3]7a	0.047
Pseudoroegneria spicata	+[1]2a	30[14]10b	0a	2[3]a	< 0.001
Cladonia spp. (as squamules)	1[2]5ab	+[1]2a	+[1]5ab	10[18]6b	0.023
Flavocetraria cucullata	2[2]9a	4[6]8a	4[5]9a	11[10]10b	0.002
Botanical Characteristics	Average [SD] Scheffé test				
Total plant cover (%)	63[14]b	48[16]a	63[18]b	73[19]b	< 0.001
Bare ground (%)	36[20]b	50[18]b	31[17]ab	17[15]a	< 0.001
Taxa richness per relevé	9.5[3.1]b	6.4[2.6]a	6.5[2.7]ab	9.6[2.5]b	< 0.001
Vascular plant richness per relevé	8.1[3.0]b	5.2[2.0]a	5.0[1.0]a	8.1[4.0]b	< 0.001
Dominance concentration[6]	0.63[0.08]b	0.52[0.12]a	0.61[0.17]ab	0.49[0.08]a	< 0.001
Site Characteristics	Average [SD] Scheffé test				
Elevation (m)	618[92]	565[42]	579[51]	591[54]	0.111
Slope (%)	57[13]b	67[12]b	58[7]ab	49[10]a	< 0.001
Aspect (˚)	205[13]	213[32]	182[24]	195[10]	0.075
June 22 solar insolation (kJ/m^2)	3.0[0.3]ab	2.7[0.4]a	3.0[0.2]ab	3.2[0.2]b	< 0.001
Number of relevés	49	25	8	16	
Net Primary Productivity (kg/ha)	Average [SD] Scheffé test				
Graminoids	298[88]b	168[32]a	248[71]ab	130[70]a	< 0.001
Forbs	48[27]	61[51]	42[51]	109[61]	0.058
Total	346[91]b	229[38]a	290[117]ab	239[59]ab	0.016
Number of samples[7]	10	9	5	10	

[1] Includes taxa that occurred in 50% or more of the relevés in one or more sociations.

[2] Constancy classes: 0[0 – 5%]; 1[6 – 15%]; 2[16 – 25%]; 3[26 – 35%]; 4[36 – 45%]; 5[46 – 55%]; 6[56 – 65%]; 7[66 – 75%]; 8[76 – 85%]; 9[86 – 95%]; and 10[96 – 100%].

[3] Sociations with the same Scheffé rank test letter do not differ at the $\alpha = 0.05$ level.

[4] A "+" represents a value of less than 0.56.

[5] Includes *C. supina*, *C. duriuscula*, *C. filifolia*, *C. obtusata*, and *C. aurea*.

[6] Based on a scale of 0 to 1, in which 1 represents maximum species dominance concentration (Strong, 2002).

[7] Two samples were excluded from analysis because they were unclassified with respect to sociation membership (Fig. 3).

two-thirds of the grassland vegetation. *Hesperostipa* vegetation appeared the least abundant.

The *Calamagrostis*, *Pseudoroegneria*, and *Hesperostipa* sociations were easily differentiated on the basis of a single high-constancy species that had 30% – 50% canopy cover (Table 1; cf. Fig. 3). On a relative basis, these dominant species individually represented at least two-thirds of the total plant cover in their respective sociations. The *Poa* sociation was compositionally more heterogeneous, with four taxa having more than 86% constancy and individual average canopy cover values of 10% – 18% (Table 1). This greater compositional diversity was reflected in the greater dispersion of *Poa* relevés in ordination space compared to the other sociations (Fig. 3). The *Calamagrostis*, *Hesperostipa*, and *Pseudoroegneria* sociations also had more than one high-constancy taxon, but the other taxa had much less cover than the dominant one. In addition to greater *Poa glauca* canopy cover than the other communities, the *Poa* sociation was also distinguishable by its greater proportion of *Flavocetraria cucullata* (curled snow lichen) and *Cladonia* (fruticose lichens) squamule cover. The two relevés excluded from the classification had botanical composition that was intermediate between the *Pseudoroegneria* and *Poa* sociations judging by their position within the detrended correspondence analysis ordination (Fig. 3). Neither excluded relevé contained a grass species with more than 5% canopy cover.

Plant heights within the four sociations seldom exceeded 40 – 45 cm, except that flowering stalks sometimes reached 1 m tall. Average total plant canopy cover of sociations

FIG. 2. An example of the *Calamagrostis purpurascens* sociation from the Carmacks–Pelly Crossing area of Yukon. Note the tussock growth habit of the grass and the common occurrence of exposed mineral soil. The vegetation sampling frame is 1 m wide and the shovel is ~1 m tall.

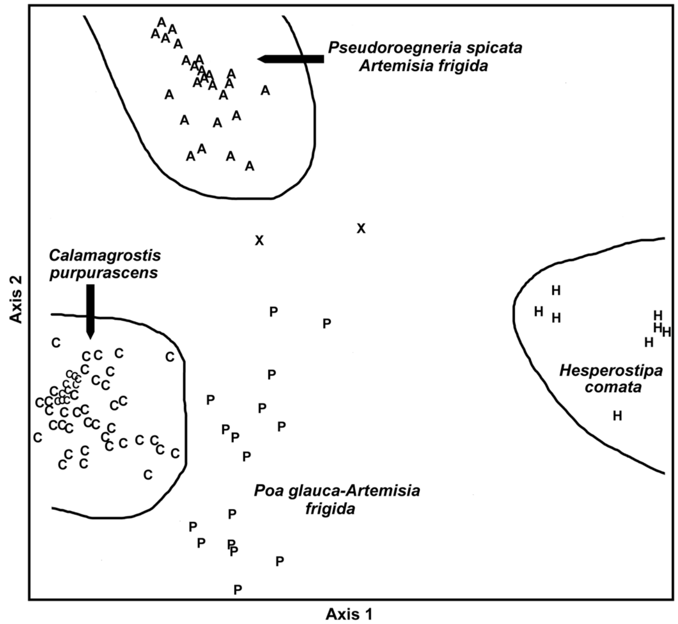

FIG. 3. Detrended correspondence analysis ordination of grassland relevés from the Carmacks–Pelly Crossing area of southern Yukon, Canada. Axes 1 and 2 explained 63% of the variance in botanical composition among 100 relevés. The letter X represents unclassified relevés.

ranged from 48% to 73%, with the *Poa* sociation having the greatest cover (Table 1). The *Calamagrostis* and *Poa* sociations contained on average ~9.5 taxa per relevé, whereas the *Pseudoroegneria* sociation averaged 6.4 taxa, which was significantly fewer ($p < 0.001$). According to Scheffé rank tests, the *Hesperostipa* sociation was intermediate in total species richness, although the average number of taxa was essentially the same as that of the *Pseudoroegneria* sociation (Table 1). This inconsistency likely stems from the small *Hesperostipa* sample. Dominance concentration among sociations was moderate, but greatest in the *Calamagrostis* sociation. The least amount of bare ground was associated with the *Poa* sociation, in part because it included abundant ground lichens (Table 1).

Distribution and Site Conditions

Only the *Hesperostipa* sociation was not distributed throughout most of the study area, with seven of its eight relevés located east of Carmacks on the north side of the Yukon River Valley. South of Carmacks, only *Calamagrostis* vegetation was observed. Relevés occurred at elevations ranging from 497 to 872 m, with no significant difference among sociations (Table 1). Grasslands occurred on southerly aspects ranging from 90˚ to 270˚, but 72% (n = 71) occurred on south-southwest orientations (158˚–247˚), with quartile values of 180˚ and 230˚. No significant difference existed among grassland sociations with respect to slope orientation. *Calamagrostis* and *Pseudoroegneria* relevés occurred on the steepest slopes (Table 1), with 89% of all relevés having gradients of 45% to 75%. *Poa* relevés had the lowest slope gradients, with quartile values ranging from 45% to 56%.

Most grassland relevés had at least xeric moisture regimes due to the associated steep slopes and rapid lateral drainage. *Hesperostipa* vegetation, however, was typically associated with the toe of slopes, and therefore, it likely had somewhat moister (e.g., subxeric to submesic) regimes than upslope grasslands. On the basis of slope orientation and gradient values, *Pseudoroegneria* relevés were associated with the least amount of June 22 solar insolation; as a result, they likely had the coolest grassland environments. *Poa* vegetation occurred on the sites with highest insolation (Table 1). Observation suggested that *Pseudoroegneria* grassland communities were also typically associated with convex slopes, whereas *Calamagrostis* vegetation occupied concave slopes.

Herbaceous Biomass

No sampled relevé had a standing crop of herbaceous biomass greater than 485 kg/ha (excluding dead material from previous years) at the end of the 2013 growing season. Most relevés (n = 18 of 34) produced 200–300 kg/ha

TABLE 2. List of flora encountered in the Carmacks–Pelly Crossing grassland relevés that do not appear in Table 1.

Taxa	% constancy
Achillea millefolium	2
Arnica angustifolia	2
Artemisia campestris	3
Artemisia laciniata	1
Aster alpinus ssp. *vierhapperi*	4
Astragalus laxmannii var. *tananicus*	1
Astragalus agrestis	8
Astragalus australis	15
Boechera retrofracta	25
Bupleurum americanum	23
Castilleja yukonis	6
Cerastium arvense	1
Chamaerhodos erecta	17
Chamerion angustifolium	3
Elymus lanceolatus ssp. *psammophilus*	3
Erigeron glabellus spp. *pubescens*	4
Erysimum coarctatum	6
Festuca saximontana var. *saximontana*	2
Galium boreale	13
Juniperus horizontalis	1
Koeleria macrantha	6
Linum lewisii	4
Minuartia yukonensis	4
Nestotus macleanii	1
Oxytropis campestris ssp. *varians*	13
Phlox hoodii	4
Plantago canescens	6
Polemonium pulcherrimum	2
Potentilla nivea	6
Rosa acicularis	3
Saxifraga reflexa	3
Saxifraga tricuspidata	2
Solidago simplex	11
Stellaria longipes	1
Townsendia hookeri	1
Anticlea elegans	1
Cladonia amaurocraea	1
Flavocetraria nivalis	1
Peltigera rufescens	2
Psora decipiens	1
Xanthoparmelia wyomingica	2
Unidentified mosses	5

of total herbaceous biomass and 150–250 kg/ha of graminoid biomass. Graminoids comprised the bulk of the standing crop, although forbs constituted almost half in the *Poa* sociation (Table 1). Total graminoid biomass was greatest in the *Calamagrostis* and *Hesperostipa* sociations.

DISCUSSION

High-Latitude Boreal Grasslands

Eastern and central Canada lack high-latitude (> 60˚ N) boreal grasslands because the boreal biome extends northward only to ~53˚ N in eastern Canada and ~57˚ N in central Canada (Ecoregions Working Group, 1989). Grassland areas occur farther west in the boreal forests of the Northwest Territories, but they are rare, e.g., *Elymus trachycaulus–Muhlenbergia richardsonis* or slender wheatgrass-mat muhly (Thieret, 1959; Ecosystem Classification Group, 2010). North of 62˚ N, or at about the southern limit of the current study area, *Pseudoroegneria spicata* vegetation has been described as "abundant" on "widely separated" steep south-facing slopes in the Tanana River Valley near Fairbanks (64.7˚ N, 147.5˚ W) in central Alaska (Hansen, 1951). Kassler (1979) also reported occurrences of *P. spicata*, *Poa glauca*, and *Calamagrostis purpurpascens* communities up to 440 km farther west in the Galena area. In contrast, *Leymus innovatus* and *Festuca altaica* dominated grassland communities ~120 km southwest of Fairbanks (Hansen, 1951). Unfortunately, no data were available to determine the areal extent of grasslands for any of the areas. Immediately west of the Yukon boundary in east-central Alaska, however, *Calamagrostis purpurascens* and *Festuca altaica* communities have been reported in the Ogilvie Mountains (65.2˚ N, 141.8˚ W), where they comprised about two-thirds of the 468 ha of boreal-cordilleran grassland in the ~4120 km^2 Yukon-Charley Rivers National Preserve (Boggs and Sturdy, 2005; also see Edwards and Armbruster, 1989). Other grassland occurrences have been reported in Alaska, but they occur either south of 62˚ N or in nonboreal environments (e.g., alpine or Arctic ecosystems). Available information suggests that the Carmacks–Pelly Crossing boreal grasslands represent the most extensive occurrence in Canada, with an areal extent greater than 2600 ha, and they are among the most northerly grasslands in North America.

The concentration of grasslands in the Carmacks–Pelly Crossing area likely stems from the occurrence of northwest-southeast trending mountain ridges and the similarly aligned Yukon River Valley, in conjunction with relatively low elevations, and from the area's location in the lee of the Coast Mountains. The lee position creates a regional rain shadow, but lower elevations allow greater potential for adiabatic warming than at higher elevations; hence, there is a greater potential for evaporation. The effect of these circumstances was represented in a regional potential evaporation analysis conducted by Jätzold (2000), who found that a severe April–June moisture deficit occurred in and around the Yukon River Valley and the lower reaches of its main tributaries. Jätzold (2000) estimated that precipitation compensated for less than 25% of the potential early summer climatic moisture deficit, although this percentage varies with slope orientation and steepness. He equated the severity of deficits on steep south-southwest slopes to that of semi-desert environments in low latitudes. Similar moisture deficits were also associated with the Yukon-Charley Rivers National Preserve and the Tanana River Valley in central Alaska (see Fig. 2 in Jätzold, 2000).

Regional Plant Community Differences

The Carmacks–Pelly Crossing *Calamagrostis*, *Poa*, and *Pseudoroegneria* sociations appear taxonomically and ecologically analogous to the communities that occur in central Alaska, although Hansen (1951) described only one relevé per plant community type. There are no *Hesperostipa* *comata* plant communities in Alaska because the species is absent from the state's flora. All four Carmacks sociations appeared to be limited to locations between ~60˚ and 65˚ N latitude. The *Calamagrostis* sociation is the more widespread (Fig. 2), but probably represents less than 2% of the vegetation in southern Yukon. *Leymus innovatus*-dominant plant communities appeared to replace *Calamagrostis purpurascens* vegetation south of the sociation's distribution (cf. Hansen, 1951; Seip and Bunnell, 1985).

The Carmacks–Pelly Crossing sociations differed from other grasslands in various respects. In the Peace River district of northwest Alberta, for example, *Hesperostipa* vegetation was dominated by *H. spartea* rather than by *H. comata* (Wilkinson and Johnson, 1983). In addition, the *H. spartea*-dominant vegetation included large proportions of *A. frigida* (5%–11%) and presumably dryland *Carex* spp. (7%–21%), whereas *H. comata* comprised ~78% of the total plant cover in the Yukon sociation. Similarly, in the Canadian Prairie biome, *H. comata* mixedgrass vegetation typically includes 3–4 codominant graminoid taxa, each with 10%–15% canopy cover (Adams et al., 2004, 2005). Mixedgrass prairie also has greater total vascular plant cover than grasslands in the Carmacks–Pelly Crossing area (i.e., 79%–94% versus 44%–59%), as well as much greater annual aboveground herb biomass production (typically > 1000 kg/ha versus < 300 kg/ha, cf. Coupland, 1961; Adams et al., 2004, 2005). No prairie relevé data based on 5 m^2 of sampling area were available for a comparison of floristic richness. However, relevés based on 2 m^2 of sampled area from mixedgrass prairie in the Suffield National Wildlife Area of southeastern Alberta (Adams et al., 1997) did not differ from those in the Carmacks–Pelly Crossing area with respect to vascular plant richness (7.9 taxa per 2 m^2 of sampling area versus 7.1 taxa per 5 m^2 of sampling area, respectively, t-test, $p = 0.063$). If this 2.5× differential in sampling area could be rectified, it is very likely that the Carmacks grasslands would be less floristically diverse than their mixedgrass prairie physiognomic counterparts. These botanical differences likely reflect the ecological constraints imposed by a cold high-latitude climate compared to a mid-latitude climate. Vetter (2000:172) concluded appropriately that "Yukon and Alaska grasslands are more similar to each other than either [is] to the Great Plains [prairie] grasslands" in terms of both floristics and phytosociology, although both the Great Plains and the Carmacks–Pelly Crossing grassland soils are subject to similar Chernozemic soil development processes (Sanborn, 2010).

ACKNOWLEDGEMENTS

Scott Gilbert (Yukon College, Whitehorse) provided access to an analytical scale for weighing the biomass samples. Dr. Mary Vetter (Luther College, University of Regina) provided a comprehensive and constructive review that improved the manuscript.

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