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Summer Climatic Moisture Balances for Yukon Xerophytic Grassland Slopes and Their Late-Wisconsinan Counterparts: Are Present-Day Grasslands Beringian Relicts?

Wayne L Strong[1]

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ABSTRACT. Summer climatic moisture balances (precipitation – potential evapotranspiration) for topographic slopes favored by present-day xerophytic boreal grasslands (SSW aspects with 61%–65% gradients) in southwest Yukon were compared to their unglaciated late-Wisconsinan (14 000–12 000 cal yr BP) Beringian counterparts. The purpose was to determine whether present-day grasslands are ecologically plausible Beringian relicts or analogues. The Beringian climate was represented by meteorological stations with average July temperatures 4˚C colder than those of present-day grassland areas; all were from Arctic locations. The most commonly occupied grassland slopes received maximum local solar radiation and likely represented the warmest topographic positions in the landscape. Their summer evapotranspiration demands exceeded the 200 mm moisture supply by 189 mm. The same slopes had late-Wisconsinan summer moisture balances of −57 to −101 mm because of colder and shorter growing seasons. Moisture balances for late-Wisconsinan SSW slopes were similar to those of present-day WNW–NW aspects, which do not support grasslands. Differences in moisture deficits indicated present-day xerophytic grasslands were improbable Beringian in situ relicts or analogues. Alternatively, it was hypothesized that present-day *Calamagrostis purpurascens* communities developed during the Holocene Thermal Maximum (11 000–9000 cal yr BP), whereas *Hesperostipa comata* communities formed less than 3000 years ago after postglacial migration of the species from central North America.

Key words: Beringia; climate; evapotranspiration; grassland; moisture balance; palaeovegetation; solar radiation; Late Wisconsinan; Yukon

RÉSUMÉ. Le bilan hydrique climatique pour la saison d’été (précipitations moins évapotranspiration potentielle) des pentes topographiques favorisées par les herbages boréaux xérophytes actuels (aspects SSO avec pentes de 61 % à 65 %) dans le sud-ouest du Yukon a été comparé à celui de leurs homologues béringiens dénués de glace du Wisconsinien tardif (de 14 000 à 12 000 années cal. BP). L’objectif consistait à déterminer si les herbages actuels sont des relictes béringiens écologiquement plausibles ou des analogues. Le climat béringien a été représenté par des stations météorologiques avec des températures moyennes de 4 ˚C plus froides en juillet que celles des zones d’herbages actuelles. Tous les emplacements étaient dans l’Arctique. Les pentes d’herbages les plus couramment occupées recevaient un rayonnement solaire local maximal et représentaient vraisemblablement les positions topographiques les plus chaudes du paysage. Pendant l’été, leurs demandes d’évapotranspiration ont dépassé l’apport d’humidité de 200 mm dans une mesure de 189 mm. Pour les mêmes pentes, le bilan hydrique du Wisconsinien tardif pour la saison d’été s’établissait de - 57 mm à - 101 mm en raison des températures plus froides et des saisons de croissance plus courtes. Le bilan hydrique des pentes SSO du Wisconsinien tardif ressemblait à celui des aspects ONO-NO actuels, qui ne peuvent pas soutenir les herbages. Les différences en matière de déficit hydrique indiquaient que les herbages xérophytiques actuels étaient d’improbables relictes béringiens in situ ou des analogues. Autrement, on a supposé que les communautés actuelles de *Calamagrostis purpurascens* se sont formées pendant le maximum thermique de l’Holocène (de 11 000 à 9 000 années cal. BP), tandis que les communautés de *Hesperostipa comata* se sont formées il y a moins de 3 000 ans, après la migration postglaciaire des espèces du centre de l’Amérique du Nord.

Mots clés : Béringie; climat; évapotranspiration; herbages; bilan hydrique; paléovégétation; rayonnement solaire; Wisconsinien tardif; Yukon

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INTRODUCTION

Grass-dominated plant communities have been reported at various locations in southwest Yukon (Hoefs et al., 1975; Oswald and Senyk, 1977; Vetter, 2000; Chambers, 2010; Conway and Danby, 2014; Strong, 2015), despite the cold, high-latitude (> 60˚ N) boreal-cordilleran climate (Fig. 1). These grasslands occur primarily on steep southerly slopes (Lloyd et al., 1994; Vetter, 2000; Strong, 2015), which are among the warmest and ecologically driest in the region.

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

FIG. 1. A southwest-facing grassland slope north of Carmacks along the Yukon River, with a 60%–70% gradient. *Calamagrostis purpurascens* (purple reedgrass) was the dominant community type, with *Pseudoroegneria spicata* (bluebunch wheatgrass) inclusions. Although some grasslands are associated with river slopes, many occur on nearby hillsides.

Besides being incongruent with the regional vegetation, these grasslands have gained special attention because they have been declared or suggested to be either relicts or analogues of vegetation that existed in unglaciated Beringia during the last 2000 years of the Late Wisconsinan (e.g., Lausi and Nimis, 1985; Edwards and Armbruster, 1989; Yurtsev, 2001; Swanson, 2006; Berman et al., 2011; Conway and Danby, 2014). However, the vegetation in the Yukon portion of Beringia and in adjacent Alaska toward the end of the last major continental glaciation event has been interpreted as tundra (Cwynar and Ritchie, 1980; Anderson et al., 1988; Alfimov and Berman, 2001; Bunbury and Gajewski, 2009; Vermaire and Cwynar, 2010) or tundra with steppe/grassland inclusions (Young, 1982; Edwards and Armbruster, 1989; Elias and Crocker, 2008; Berman et al., 2011).

If present-day Yukon grasslands are relicts of the now extinct Beringian biome, it implies they had a consistent long-term floristic composition and a continuous in situ existence prior to the Holocene, which in southwest Yukon, judging by the rise in *Betula* (birch) abundance, began after 12 000 calendar years before present (cal yr BP) (Anderson et al., 1988; Vermaire and Cwynar, 2010). This relationship applies whether they developed during the Late Wisconsinan (~30 000–12 000 cal yr BP) or the Middle Wisconsinan (50 000–30 000 cal yr BP, Blinnikov et al., 2011), when mammoth-steppe may have existed (e.g., Zazula et al., 2007). If present-day grasslands are botanical and ecological analogues of pre-Holocene vegetation, it would be necessary for present-day xerophytic grasslands to have existed in the Beringian landscape on sites other than those that they currently occupy. Community relocation would have involved the migration of individual species to present-day sites, presumably in response to a change in climate that made the original Beringian locations ecologically unfavorable.

Plant communities as components of vegetation can be sensitive ecological entities. Modest modification of growing season temperatures or precipitation or their pattern of occurrence, or an alteration of site conditions, can initiate long-term changes in floristic composition, which can lead to the development of different community types. Therefore, particular environmental conditions are associated with individual plant community types within a given geographical area. This fact suggests that present-day community types should be associated with the same thermal and moisture regimes as their Beringian counterparts.

The objective of this analysis was to model the summer climatic moisture balances of grassland slopes in Yukon today and those in what was easternmost Beringia around 14 000–12 000 cal yr BP (a period hereafter referred to as "late-Wisconsinan") to determine whether they might have been similar. Climate moisture balance (precipitation – potential evapotranspiration) was chosen for modeling because moisture availability and the pattern of its occurrence influence the types of plant communities that form within a landscape. Climatically, for example, grasslands typically have severe late summer moisture deficits compared to forests, shrublands, or tundra, rather than being associated with a specific thermal regime or a particular amount of summer or annual precipitation, and they are sensitive to short- and long-term changes in their moisture balance (e.g., Coupland, 1961). A finding that the summer moisture balances of the present day and the late-Wisconsinan were similar on the same slopes would corroborate the interpretation that present-day grasslands in what was Beringia are ecological relicts. The reverse result would reduce the range of vegetation diversity thought to have occurred within the late-Wisconsinan landscape of southwest Yukon.

MATERIALS AND METHODS

Study Area

The geographical area of consideration was limited to the western portion of Yukon into which Beringia (Duk-Rodkin et al., 2002) extended south of the Ogilvie Mountains (Fig. 2). The northern boundary of this area roughly corresponds to the most northerly extent of boreal forest in Yukon. Subarctic vegetation occurs at higher latitudes (Strong, 2013). Mountainous terrain occurs in much of the area. In the present-day landscape, *Populus tremuloides* (trembling aspen), mixed *P. tremuloides* and *Picea* spp. (spruce), and *Picea* spp. forest stands, in association with Brunisolic soils, occur in the Carmacks area and farther south, as part of the Northern Cordilleran Boreal ecoclimatic region (Strong, 2013). In contrast, upland sites to the west and north are dominated by *Picea* forests that often occur in association with Cryosolic soil (Northern Cordilleran High Boreal ecoclimatic region).

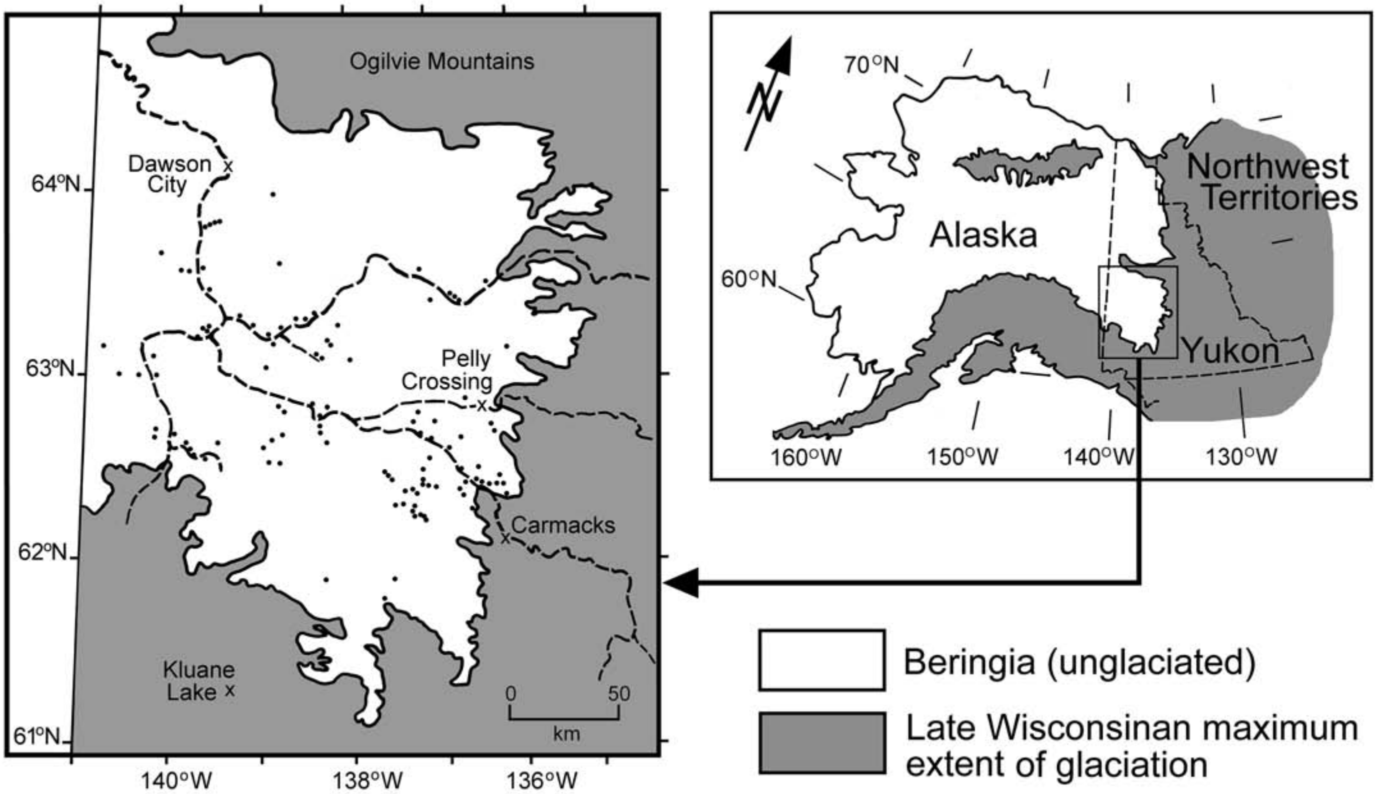

FIG. 2. Locations of xerophytic grasslands in the unglaciated portion of southwest Yukon where Beringia once occurred. The late-Wisconsinan limits of glaciation were based on Duk-Rodkin et al. (2002) and Dyke et al. (2003). Dots indicate known and possible locations of present-day xerophytic grasslands in the area formerly occupied by Beringia. These locations were identified based on the interpretation of aerial photographs. Dashed lines represent the Yukon River and its major tributaries.

Grasslands are scattered throughout southwest Yukon, but when both the former Beringia (Fig. 2) and glaciated landscape occurrences are considered, they are most abundant near Carmacks (cf. Strong, 2015). *Calamagrostis purpurascens* (purple reedgrass), *Hesperostipa comata* (needle-and-thread grass), *Pseudoroegneria spicata* (bluebunch wheatgrass), and *Poa glauca* (glaucous bluegrass), each in combination with *Artemisia frigida* (pasture sagewort), form xerophytic grassland communities in the Carmacks region (Strong, 2015) and farther west. In contrast, *Carex* (sedge) species such as *C. duriuscula*, *C. supina*, and especially *C. filifolia* are also common immediately south of the area formerly represented by Beringia in the vicinities of Aishihik Lake (Vetter, 2000), Takhini Valley (Chambers, 2010), and southern Kluane Lake (M.A. Vetter, pers. comm. 2016). *Calamagrostis purpurascens*, *P. glauca*, and *A. frigida* are amphi-Beringian species and are known to inhabit alpine and Arctic as well as boreal environments (Hultén, 1968; Walker et al., 1991; Czerepanov, 1995), whereas *H. comata*, *P. spicata*, and *C. filifolia* are considered mid-continental prairie species (Scoggan, 1978).

Climate Data

Meteorological stations 2100300 (Carmacks – 62˚06′ N, 136˚11′ W) and 2100301 (Carmacks CS – 62˚07′ N, 136˚11′ W) (Environment Canada, 2017) were used to characterize 1981 – 2010 temperature and precipitation conditions in the Carmacks area (Fig. 2). Data from the two stations were merged to form a single summary because the meteorological record for station 2100301, which was more continuous and complete, did not start until late 1999, and station 2100300 was discontinued in 2008. Linear regression based on overlapping 2000 to 2008 records was used to adjust for systematic differences between these stations.

Daily maximum and minimum temperatures and daily precipitation data were collated for April – September, or months with average temperatures above 0˚C in the Carmacks area. Mean daily temperatures were calculated by averaging maximum and minimum values. Missing maximum and minimum temperatures were estimated by regressing Carmacks and Pelly Ranch (2100880, Environment Canada, 2017) daily station data. The Pelly Ranch meteorological station (62˚50′ N, 137˚19′ W), located ~90 km north of Carmacks and ~38 km west of Pelly Crossing, has one of the longest and most complete records in the region. Missing precipitation values were few (< 2%) and were not estimated because of concerns about the reliability of the predicted values.

To represent climatic conditions in eastern Beringia during the late-Wisconsinan, the Environment Canada (2017) historical meteorological database was searched

TABLE 1. Estimated differences between present-day and late-Wisconsinan July temperatures in the Yukon portion of eastern Beringia.

Location	Basis for estimate	Time frame (k cal yr)	July average temperature differential (˚C)	Source
Trout Lake	Chironomids	15.2–14.3	2–4	Irving et al., 2012: Fig. 2a
Trout Lake	Pollen	> 14.7	≤ 5	Fritz et al., 2012
Hanging Lake	Chironomids	~16.5	5	Kurek et al., 2009
Antifreeze Pond	Chironomids	~16.2	2.2–3.6	Barley, 2004
Eastern Beringia	Pollen	18–12	4	Viau et al., 2008: Fig. 7

for western Canada stations with 1981 – 2010 (±1 yr) average July temperatures ~4˚C colder than Carmacks (i.e., analogue stations). The differential for eastern Beringia estimated by Viau et al. (2008) was similar to estimates from localized studies in the Yukon region (Table 1).

The same meteorological variables were compiled for the Beringia climate analogues as for the Carmacks stations. When daily temperatures were missing (gap of < 1% of a record, typically 1 or 2 days), the values were estimated by averaging (for 1 missing day) or prorating (for > 1 missing day) the difference between the values just before and just after the data gap. Daily temperatures of each analogue station were adjusted to create July averages of 11.9˚C (i.e., Carmacks average of 15.9˚C – 4˚C) by adding a correction (i.e., 11.9˚C – station July average) to all values. Averages of both adjusted daily temperatures and daily precipitation were used to represent the late-Wisconsinan April – September climate of Beringia in southwest Yukon.

Evapotranspiration

Potential daily evapotranspiration (ET) was estimated using the Hargreaves-Samani algorithm (Samani, 2000; Moeletsi et al., 2013):

$$ET = 0.0135 \times KT \times (T_{max} - T_{min})^{0.5} \times (T_{ave} + 17.8) \times Ra \times 0.408,$$

where KT represents an assumed value of 0.17, which relates differences in solar radiation to the temperature of interior continental locations (Samani, 2000); T_{ave}, T_{max}, and T_{min} are average, maximum, and minimum daily air temperatures (˚C), respectively; Ra is extraterrestrial radiation (MJ m^{-2}), and 0.408 converts MJ m^{-2} of energy to millimetres of evaporation per day (Moeletsi et al., 2013). The advantages of this algorithm are that it requires only basic meteorological variables and is simple to calculate. It also produces results that are strongly correlated with the Thornthwaite (Hargreaves and Samani, 1985) and more demanding Penman-Monteith ($r > 0.92$, Moeletsi et al., 2013) methods. Moisture balances were calculated for each day of April through September. Present-day balances were estimated for grasslands on the basis of median slope gradients and orientations, level sites, and slopes at a right angle (+90˚) and opposite (+180˚) to the median slope orientation. The slope data were derived from field measurements.

The non-scattered and unreflected portion of extraterrestrial solar radiation (Ra) that reaches the ground surface (i.e., direct radiation) was estimated using an online calculator (http://www.meteoexploration.com/products/SolarCalculator.html). This software program incorporates latitude, longitude, elevation, calendar date, time zone, atmosphere visibility (assumed clear sky), ozone thickness, relative humidity (assumed 60%), average daily temperature, albedo—assumed to be 0.25 for all scenarios (Briegleb and Ramanathan, 1982) and 0.168 as an alternative level for tundra vegetation (Williamson et al., 2016)—slope orientation, and slope gradient into the calculation of kWh m^{-2} of direct radiation. The resulting kWh m^{-2} were converted (multiplied by 3.6) to MJ m^{-2} to accommodate the ET equation and for analysis purposes.

The reference location for all solar radiation calculations approximated the study area centroid (63˚ N, 138˚ W) at an elevation of 600 m. It was assumed that present-day and late-Wisconsinan sites with the same topographic conditions received identical amounts of direct solar radiation. Slope orientation and gradient values for the solar radiation calculations were based on class midpoints of each variable's frequency distribution. Daily ozone thickness was extrapolated from Environment Canada (2007) monthly maps using polynomial regression modeling ($R = 0.996$, $n = 6$).

The precipitation component of Beringian moisture balances was based on (i) daily analogue values and (ii) daily analogue values reduced by 37% to approximate a 100 mm reduction in annual precipitation during the late-Wisconsinan (cf. Viau et al., 2008: Fig. 6a; Fritz et al., 2012: Fig. 6).

Grassland Distribution on Slopes

To determine the distribution of grasslands on slopes, the orientations and gradients of 18 arbitrarily selected grassland areas with a combined length of more than 12 km were measured in the Carmacks – Pelly Crossing region. Slope measurements were done in this general area because of poor access and the scarcity of grasslands elsewhere in the region. Slope measurements were made with a compass and clinometer at 40 m increments along the top edge of grasslands that had linear configurations and from the bottom edge of grasslands that had a conical shape. Slopes were characterized according to percent gradient (i.e., degrees of inclination/45˚ × 100).

TABLE 2. The range of slope orientations and gradients for southwest Yukon grasslands based on sampling in the Carmacks-Pelly Crossing region.[1]

	Percent slope												
Slope orientation (˚)	26–30	31–45	36–40	41–45	46–50	51–55	56–60	61–65	66–70	71–75	76–80	*n*	%
91–110	0	0	1	0	0	0	0	0	1	0	0	2	0.7
111–130	0	1	1	1	1	0	1	1	1	1	0	8	2.6
131–150	0	2	2	1	0	1	0	4	1	0	0	11	3.6
151–170	0	2	1	0	2	2	9	5	21	3	1	46	15.0
171–190	2	3	2	5	3	3	20	15	14	2	2	71	23.2
191–210	1	0	0	4	3	3	13	16	13	4	2	59	19.3
211–230	0	0	1	4	1	6	9	14	21	3	3	62	20.3
231–250	0	1	1	2	0	3	7	13	7	3	1	38	12.4
251–270	0	0	1	0	0	0	2	4	1	1	0	9	2.9
n	3	9	10	17	10	18	61	72	80	17	9	306	
%	1.0	2.9	3.3	5.6	3.3	5.9	19.9	23.5	26.1	5.6	2.9		100.0

[1] Box indicates where grasslands most frequently occurred (64.4%).

RESULTS

Grassland Slopes

Xerophytic grasslands in the Carmacks area were dominated by *C. purpurascens* communities that sometimes included stands of *P. spicata* (Fig. 1), whereas some locations west of Pelly Crossing had *H. comata* as the principal graminoid. The Carmacks – Pelly Crossing grasslands occupied southerly slopes that had compass orientations ranging from 95˚ to 268˚ (n = 306 measurements), of which 90% fell between 151˚ and 250˚ (Table 2). Seventy percent of slopes had gradients of 56% – 70% (Table 2). Analysis of medians indicates that grassland occurrences were centered on slopes with 191˚ – 210˚ or south-southwest (SSW) orientations and 61% – 65% gradients. Measured grasslands occurred between 490 and 725 m elevation, with others extending upward to 915 m. The latter occurrences were exceptions to the typical distribution.

Climate Regimes

May – September temperatures averaged 11.6˚C in the Carmacks region, with a July average of 15.9˚C. Average daily temperatures above 0˚C occurred from mid-April to early October (188 days). During May – September, the region received ~200 mm of precipitation, with a peak in July (Table 3). Total annual precipitation averaged 304 mm.

Three Nunavut locations had July average temperatures that approximated the expected value of 11.9˚C to represent Beringia: Baker Lake (station 2300500, 64˚18′ N, 96˚05′ W); Kugluktuk (station 2300903, 67˚49′ N, 115˚08′ W); and Lupin (stations 23026HN and 230N002, 65˚45′ N, 111˚15′ W). Kugluktuk deviated most from the expected July temperature and was the most northerly of the three stations (Table 3). After adjusting each station for its deviation from the expected July temperature, the three locations had summer temperature profiles similar to each other. Averaging the mean monthly temperatures for May to September gave a mean temperature of 5.2˚C for the Beringia-analogue climate during that five-month period. Continuous above 0˚C average daily temperatures occurred from the end of May to late September (122 days). May – September precipitation averaged 173 mm, with August the wettest month (Table 3). Total annual precipitation was 273 mm. The Beringia-analogue May – September climate was ~6.4˚C colder and received ~15% less precipitation than present-day Carmacks (Table 3).

Regardless of slope orientation, xerophytic grasslands with 61% – 65% gradients in the Carmacks area received at least 21.6 MJ m^{-2} of direct solar radiation on June 21 or the summer solstice (Fig. 3), but those on the most commonly occupied aspects received 24.1 to 25.1 MJ m^{-2}. Level and north-facing (0˚) slopes received 23.2 and 16.3 MJ m^{-2} of total direct solar radiation on June 21, respectively (Fig. 3).

Moisture Balances

Present-day grasslands on SSW aspects with 61% – 65% gradients had continuously increasing moisture deficits from 1 April to 21 September, which reached a maximum of −189 mm (Fig. 4). Subsequent September deficit values were similar to the maximum deficit. Slopes with the same gradient but located on 290˚ (west-northwest, WNW) and 20˚ (NNE) aspects had less severe moisture deficits than SSW slopes, with maxima of −86 and −37 mm, respectively (Fig. 4). Both slope orientations in the present day would typically be vegetated by forests. Unlike those for SSW aspects, the moisture deficits for WNW and NNE slopes reached maxima during the latter half of August and June, respectively, and then lessened (Fig. 4). The moisture balance for NNE slopes became positive after mid-September, whereas the others remained negative. Level sites had moisture balance profiles that were between those of SSW and WNW slopes (Fig. 4).

Analogue climate data indicate that SSW Beringian slopes with 61% – 65% gradients had moisture surpluses until early June which then became moisture deficits that

TABLE 3. Summary of the monthly meteorological record for Carmacks (Yukon) and three Arctic stations used to represent the climate of Beringia during the latter portion of the late-Wisconsinan.

Location	# of record years available 1980–2011	Percent missing values	Adjustments (°C)	April	May	June	July	August	September	May–September
				Present-day average monthly temperatures (°C)[1]						Average
Carmacks	30	14.8	–	1.0	8.2	13.8	15.9	13.2	7.0	11.6
Baker Lake	30	0.7	–	−17.1	−6.2	4.9	11.5	9.9	3.0	4.6
Kugluktuk	30	< 0.1	–	−16.3	−5.4	5.4	10.9	9.0	3.3	4.7
Lupin	30	0.6	–	−15.5	−5.6	6.4	11.7	8.8	2.0	4.7
			Average	−16.3	−5.7	5.6	11.4	9.2	2.8	4.7
				Adjusted temperatures to represent Beringia						Average
Baker Lake	–	–	+0.4°C[2]	−16.7	−5.8	5.3	11.9	10.3	3.4	5.0
Kugluktuk	–	–	+1.0°C[2]	−15.3	−4.4	6.4	11.9	10.0	4.3	5.6
Lupin	–	–	+0.2°C[2]	−15.3	−5.4	6.6	11.9	9.0	2.2	4.9
			Average	−15.8	−5.2	6.1	11.9	9.8	3.3	5.2
				Present-day total precipitation (mm)[1]						Total[3]
Carmacks	20	1.7	–	6.5	26.5	37.4	57.1	44.4	34.7	200
Baker Lake	30	0.9	–	14.7	14.1	22.8	40.5	53.1	46.6	176
Kugluktuk	30	< 0.1	–	10.3	13.2	15.9	39.8	46.6	35.3	151
Lupin	20	0	–	14.6	19.6	28.1	40.2	59.4	43.9	191
			Average	13.2	15.6	22.3	41.2	52.1	41.9	173

[1] Present-day data based on Environment Canada (2017).
[2] This amount was added to all daily values to create July average temperatures of 11.9°C or 4°C cooler than present-day to represent late-Wisconsinan conditions (Table 1).
[3] Totals and monthly values represent minima because missing daily values were not estimated.

reached −57 mm by mid-August (Fig. 4, upper Beringian limit). This moisture deficit was 30% that of present-day SSW values. Calculation of moisture balances on SSW slopes using albedos of 25% and 16.8% produced essentially the same deficits. The late summer daily moisture balance values for Beringian SSW slopes fall between those for present-day WNW and NNE slopes, but values for Beringian slopes were less negative during the early growing season (Fig. 4, upper limit).

A 37% reduction in summer precipitation to represent a 100 mm reduction in annual precipitation nearly doubled the moisture deficit of SSW Beringian slopes from −57 mm to −101 mm (Fig. 4, lower Beringia limit). The latter value was about half that of present-day SSW slopes. The range of late summer Beringian moisture deficits was similar to that of the moisture balances associated with present-day WNW slopes (Fig. 4). To achieve late summer moisture deficits similar to those of present-day southwest slopes, total Beringian May – September precipitation would need to be about 84 mm, or half the current average of 173 mm (Table 1).

DISCUSSION

Moisture Balance Modeling

The calculation of moisture balances is based on variation in temperatures and precipitation and an assumption of solar radiation constancy. However, solar radiation levels may have been 5% – 10% greater during the late-Wisconsinan than they are today (Berger and Loutre, 1991: Additional data, files 1 and 3). The maximum difference in radiation would have increased Beringia moisture deficits by an estimated 16 mm on SSW slopes (i.e., −57 mm to −73 mm). Therefore, 10% greater Beringian solar radiation would not have been sufficient to raise moisture deficits to present-day levels and create conditions suitable for the occurrence of xerophytic grasslands.

The modeled moisture balances assumed that October through March precipitation contributed nothing to the summer moisture supply and that all summer precipitation was available for evapotranspiration on grassland sites. In the present day, most winter precipitation as snow on steep SSW slopes would likely be lost to sublimation and spring surface runoff before soils thawed and plant growth commenced. Therefore, the effect of winter precipitation on present-day summer moisture balances would likely be minimal.

The possibility of all summer precipitation being available for evapotranspiration is a debatable

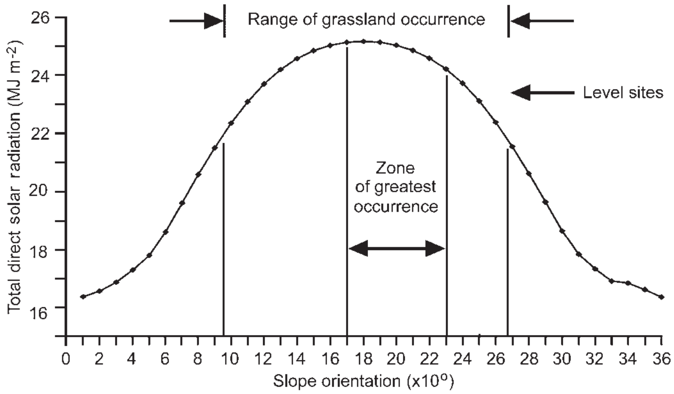

FIG. 3. Present-day June 21 direct solar radiation on slopes with 61%–65% gradients and different orientations at 63˚ N, 138˚ W, and 600 m elevation.

assumption. All water from low-volume precipitation events, as well as most water from prolonged moderate events, would probably be intercepted by plants or absorbed by the soil. Once the soil surface becomes saturated, however, a portion of the water for a given precipitation event could be lost for plant use as a result of surface runoff. Despite the steepness and high percentage of exposed mineral soil on grassland slopes (Strong, 2015), most slopes showed little or no evidence of surface erosion to indicate the common occurrence of summer precipitation runoff. If runoff does occur, it would enhance the moisture deficits of SSW slopes beyond the levels indicated in Fig. 4, more so for present-day than for Beringian sites, because the warmer conditions would accentuate evapotranspiration.

In conclusion, the moisture deficit models for SSW slopes vary according to the applied assumptions, but the Beringian scenarios indicate a moister-than-present environment even though those sites may have received only half as much precipitation (i.e., 173 mm × 0.63 = 109 mm versus 200 mm at present). Some reduction in the Beringian moisture deficit on SSW slopes could have occurred if July rather than August was the month of peak precipitation (Table 3), as it is in the present-day environment.

Beringia Vegetation

The location of all three Beringia-analogue meteorological stations within the Low Arctic of northern Canada (Ecoregions Working Group of Canada, 1989) indicates that Beringia was likely dominated by an Arctic climate and tundra vegetation during the late-Wisconsinan, which is consistent with localized palaeovegetation interpretations for the region (see Introduction). This conclusion assumes that July temperatures in Beringia were ~4˚C colder than present (Table 1). The complex terrain of western Yukon would have allowed plant community diversification based on differences in slope orientation and gradient, as well as in elevation. However, if "steppe" is defined as "prevalence of graminoids" and "xerophytes or mesoxerophytes (plants on dry soils)" (Yurtsev, 2001:166),

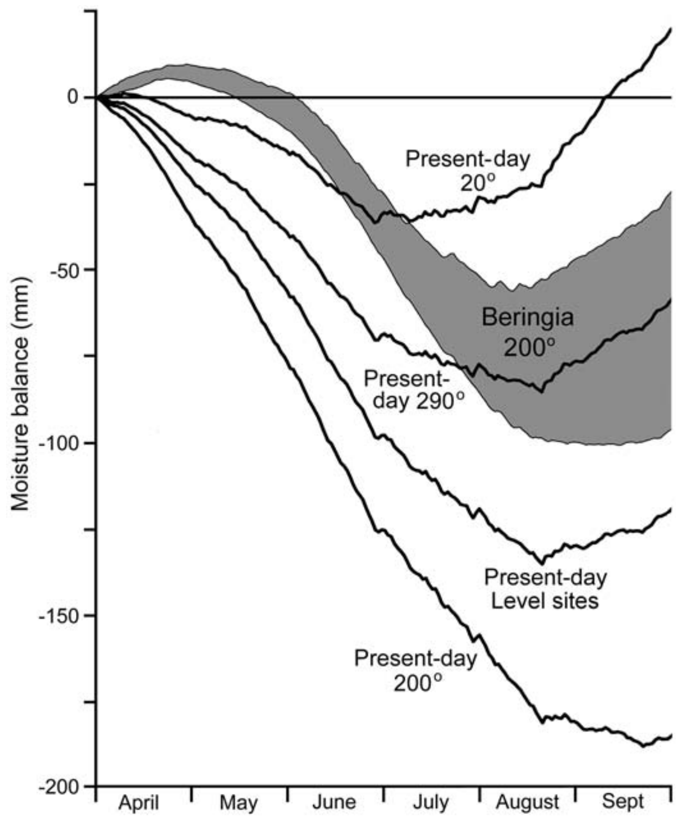

FIG. 4. Moisture balances (precipitation – potential evapotranspiration) for present-day grasslands slopes with 61%–65% gradients; 25% albedo; and 200˚ (SSW), 290˚ (WNW), and 20˚ (NNE) orientations, as well as level sites. Beringia moisture balances (shaded area) were determined for slopes with 200˚ orientations and a 25% albedo. The upper and lower limits of the Beringia moisture balances represent 0% and 37% reductions in precipitation relative to analogue climate values, respectively. Negative values represent moisture deficits.

it would seem unlikely that steppe or xerophytic grassland communities would have been components of the Beringian vegetation, for two reasons. First, grassland communities similar to those in the study area have been reported only as far north as the climatic tree line (Drew and Shanks, 1965) in Yukon or in nearby areas of Alaska (e.g., Lambert, 1968; Walker et al., 2001), but not farther north. This fact suggests that colder climates, such as those of Arctic tundra, would be outside the ecological tolerance limits of Yukon xerophytic grasslands. Second, the similarity in moisture balances between Beringian SSW aspects and present-day WNW to possibly NW aspects with the same topographic gradients indicates that SSW slopes during the Late Wisconsinan would not have supported xerophytic vegetation. These circumstances would not have excluded the occurrence of other, possibly more mesophytic graminoid-dominated communities or the scattered occurrences of species such as *C. purpurascens* in the Beringian landscape (cf. Walker et al., 1991). Swanson (2006) identified several grass species that could have formed communities on locally warm and possibly submesic tundra slopes, including *Calamagrostis canadensis* (marsh reedgrass), *Calamagrostis stricta* (narrow reedgrass), and *Alopecurus* spp. (foxtail), all of which have been reported in the Middle to Late Wisconsinan Beringian fossil flora (Zazula et al., 2006; Gaglioti et al., 2011; Wooller et al., 2011). A moist environment might also have allowed the common occurrence of forbs, as suggested by Willerslev et al. (2014).

Hesperostipa comata communities may not have existed in Beringia, judging by the species' absence in the known palaeoflora; this would certainly be true if *H. comata* was introduced, as suggested by Hultén (1968). Currently, this species is uncommon in Yukon and absent in Alaska (Hultén, 1968; Cody, 2000). *Pseudoroegneria spicata* and *C. filifolia* are also lacking in the Beringian floristic record, none is an amphi-Beringian species, and all three are phytogeographically affiliated with central North American prairie rather than high-latitude biomes.

A cold Beringian summer climate, the occurrence of moderate to low evapotranspiration moisture deficits (as opposed to severe deficits) on steep southerly slopes, and the possible absence of some key graminoid species suggest a limited likelihood that present-day Yukon grasslands are Beringian relicts. They are also implausible plant community analogues. For these grasslands to be analogues, the climate on low to moderate gradient slopes would have needed to be as warm and dry as present-day SSW slopes, which would be inconsistent with the occurrence of July temperatures 4˚C colder than at present. Such conditions would also be ecologically difficult to achieve while simultaneously maintaining modest moisture deficits on steep southerly slopes. Whereas Beringia might have received less precipitation than present-day grasslands (e.g., Viau et al., 2008; Fritz et al., 2012), moisture would have been physiologically more available to plants because cooler climatic conditions would have reduced evapotranspiration.

Present-day grasslands outside the former geographical limits of Beringia in southern Yukon are also neither relicts nor analogues because their occurrence within the zone of Wisconsinan glaciation means that they are of postglacial origin. These grasslands include most reported Yukon occurrences (e.g., Hoefs et al., 1975; Laxton et al., 1996; Vetter, 2000; Conway and Danby, 2014; Strong, 2015: more southern samples).

Alternative Origin Hypotheses

The only alternative to a Beringian origin of present-day xerophytic grasslands is development during the Holocene. A most logical temporal possibility would be development during the Holocene Thermal Maximum, which occurred from ~11 000 to 9000 cal yr BP (Kaufman et al., 2004). No other major period of prolonged warmer-than-present temperatures has since occurred (Viau et al., 2008). As well, *C. purpurascens* and *P. glauca* as amphi-Beringian species (Hultén, 1968; Czerepanov, 1995) in conjunction with *A. frigida* (Zazula et al., 2006, 2007) were already present in the Beringian flora to form postglacial grasslands.

A late Holocene origin of *H. comata* and *P. spicata*, as well as *C. filifolia* communities, would be a possibility if these species were postglacial migrants from south of the Laurentide glacial front in the central United States (cf. Dyke et al., 2003). The distance (~2300 km) and migration delays likely impeded the early Holocene development of these xerophytic grasslands on present-day sites. If the pattern of *Pinus contorta* (lodgepole pine) migration can be used as an indicator of movement by other species, then northward migration stalled along the southern Yukon border 10 000 to 6000 cal yr ago (Strong and Hills, 2013:1345). Therefore, xerophytic graminoids of prairie origin would not have been available to form grasslands in southwest Yukon during the Holocene Thermal Maximum. The arrival of prairie species in western Yukon might not have occurred until 3000 cal yr ago or less, after *P. contorta* reached the Carmacks areas.

CONCLUSIONS

The large and ecologically important difference between modeled late-Wisconsinan and present-day moisture balances (> 1.9×) make it unlikely that present-day xerophytic grasslands were present in eastern Beringia on the sites that they currently occupy in southwest Yukon. Therefore, present-day grasslands cannot be Beringian relicts, and their association with the warmest and driest of high-latitude boreal sites makes them unlikely analogues of plant communities that might have existed in an Arctic tundra environment. Instead, they more realistically represent plant communities of Holocene origin. The earliest and most logical time for xerophytic grassland to have developed in southwest Yukon would have been during the Holocene Thermal Maximum. Absence of key graminoids in the Beringian flora, as well as their phytogeographical affiliation with a biome that occurred south of the Laurentide glacial front during the Wisconsinan, indicates that two of the present-day grassland community types in southwest Yukon are likely of late Holocene origin.

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