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Cale A.C. Gushulak, Christopher K. West and David R. Greenwood

Cale A.C. Gushulak and David R. Greenwood, Department of Biology, Brandon University, 270 18th Street, Brandon, Manitoba, R7A 6A9, Canada

Christopher K. West, Department of Geological Sciences, University of Saskatchewan, 114 Science Place, Saskatoon, Saskatchewan, S7N 5E2, Canada

Corresponding author: David R. Greenwood (e-mail: greenwoodd@brandonu.ca).

Current address: Department of Earth Sciences, University of Western Ontario, London, Ontario, N6A 5B7, Canada, cgushula@uwo.ca
Paleoclimate and precipitation seasonality of the Early Eocene McAbee megaflora, Kamloops Group, British Columbia

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Abstract: Early Eocene fossil floras from British Columbia are a rich resource for reconstructing western North American early Cenozoic climate. The best known of these floras reflect cooler (MAT \( \leq 15^\circ C \)) upland forest communities in contrast to coeval (MAT \( \geq 18^\circ C \)) forests in lowland western North American sites. Of particular interest is whether Early Eocene climates were monsoonal (highly seasonal precipitation). The McAbee site is a \( 52.9 \pm 0.83 \) Ma 0.5 km outcrop of bedded lacustrine shale interbedded with volcanic ash. In this report two historical megaflora collections, that were collected independently from different stratigraphic levels and/or laterally separated by \( \sim 100-200 \) m in the 1980s (US) and 2000s (BU) are investigated to: (1) assess whether they represent the same leaf population, (2) assess whether a combined collection yields more precise climate estimates, and (3) reconstruct paleoclimate to assess the character of regional Early Eocene precipitation seasonality. Combined, the two samples yielded 43 dicot leaf morphotypes. Analysis of leaf size distribution using ANOVA showed no difference between the 2 samples and they were combined for climate analysis. Climate analysis using leaf physiognomy agrees with previous estimates for McAbee and other regional megafloras, indicating a warm (MAT \( \sim 8-13^\circ C \)), mild (CMMT \( \sim 5^\circ C \)), moist (MAP >100 cm.a\(^{-1}\)) but summer-wet, non-monsoonal climate. Additionally, we recommend that climate analyses derived from leaf fossils should be based on samples collected within a stratigraphically constrained quarry area to capture a snapshot of climate in time rather than time-averaged estimates derived from multiple quarry sites representing different stratigraphic levels within a fossil site.

key words: paleobotany, Eocene, Okanagan Highlands, paleoclimate, precipitation seasonality
Introduction

The Early Eocene was the warmest time of the Cenozoic, and includes a sustained period of warmth, the Early Eocene Climatic Optimum (EECO; 50–52 Ma; Zachos et al. 2008) with terrestrial Mean Annual Temperatures (MAT) in North America ranging from 9–24 °C and possibly as high as 35 °C depending on the paleontological climate proxy used (Greenwood and Wing 1995; Greenwood et al. 2010; Huber and Caballero 2011; Schubert and Jahren 2011; West et al. 2015). Worldwide the environment was largely tropical during the Early Eocene with thermophilic organisms such as alligators and palms, and warm-wet climates extending into the Arctic (Greenwood et al. 2010; Eberle and Greenwood 2012; Eldrett et al. 2014). However, there appears to be two overall climate regimes: ever-wet, (consistent precipitation year round), and monsoonal (highly seasonal precipitation) (Schubert and Jahren 2011; Huber and Goldner 2012; West et al. 2015).

Early Eocene fossil floras from British Columbia and Washington State, coined the Okanagan Highlands, provide a window into the climate of the Early Eocene at mid-latitudes (e.g., Smith et al. 2010, 2012; Archibald et al. 2011, 2014), where modelling has identified highly seasonal precipitation in the North American continental interior and ever-wet regimes on the west coast and adjoining area of British Columbia (Huber and Goldner 2012). The southern Okanagan Highlands sites are 200–300 km inland today (Fig. 1) with a dry climate (annual precipitation < 40 cm.a⁻¹; e.g., climate normals for Kamloops (28 cm.a⁻¹), Merritt (32 cm.a⁻¹) and Princeton BC (35 cm.a⁻¹) from Environment Canada, http://climate.weather.gc.ca/climate_normals/index_e.html). In the Early Eocene the Okanagan Highlands fossil sites are reconstructed as upland floras with paleoelevations around 0.8–1.3 km or higher (Wolfe et al. 1998; Tribe 2005; Smith et al. 2009). The Okanagan Highlands Early
Eocene fossil assemblages are characterized by a mix of temperate and tropical organisms as opposed to the predominantly tropical floras found in coeval lowland sites of the Chuckanut and Huntingdon formations (Mustoe and Gannaway 1997; Archibald and Farrell 2003; Archibald et al. 2011; Breedslovetrout et al. 2013; Eberle et al. 2014; Mathewes et al. this volume). The Okanagan Highlands floras have been interpreted as being analogous to modern day highland forests of Central America in which climate and vegetation become increasingly temperate as elevation increases (Greenwood et al. 2005; Moss et al. 2005; Smith et al. 2012; Mathewes et al. this volume).

Paleoclimate has been studied at several British Columbia Early Eocene sites with MAT estimates ranging from 10–15 °C (Archibald and Mathewes 2000; Greenwood et al. 2005; Smith et al. 2009, 2012; Dillhoff et al. 2013; Mathewes et al. this volume). The winters have been interpreted from both plant and insect proxies as mild and frost free with Cold Month Mean Temperature (CMMT) estimates for these sites ranging from 0–5 °C, to perhaps as high as 8°C (Greenwood et al. 2005; Moss et al. 2005; Dillhoff et al. 2013; Archibald et al. 2014; Mathewes et al. this volume). Precipitation estimates based on nearest living relatives and leaf physiognomy have been used to reconstruct Mean Annual Precipitation (MAP) over 100 cm.a⁻¹ for most of the Okanagan Highlands floras (Greenwood et al. 2005; Smith et al. 2012; Dillhoff et al. 2013; Mathewes et al. this volume). Overall, the climate of the Okanagan Highlands area during the Early Eocene has been described as upper microthermal to lower mesothermal with mesic humid conditions (Moss et al. 2005; Smith et al. 2009, 2012; Dillhoff et al. 2013; Mathewes et al. this volume). It is unknown, however, whether Early Eocene climate for the Okanagan Highlands, including that of McAbee, was ever-wet or monsoonal.
West et al. (2015) defined a summer monsoon for the Early Eocene Arctic where winter 24-hour darkness restricts the growing season to the summer months using the Zhang and Wang (2008) index for a region where the summer daily rate of precipitation is equal to 3 mm/day or more (i.e., 3 warmest months precipitation >28 cm), and the ratio of summer to annual precipitation exceeds 55%. Huber and Goldner (2012) for their modelling of Eocene precipitation regimes used a simplification of the Zhang and Wang (2008) index, defining monsoonal climates as being highly seasonal precipitation regimes where summer wet season precipitation was >70% of the annual total. In the Eocene Arctic, West et al. (2015) proposed that the summer light season precipitation = Growing Season Precipitation (GSP), allowing discrimination of monsoonal or non-monsoonal conditions using CLAMP. At McAbee’s paleolatitude the light regime poses no restriction on plant growth. As we cannot discriminate between a summer or winter wet season using CLAMP, we seek to reject a null hypothesis of monsoonality (i.e., highly seasonal precipitation) using a modification of the simpler definition of Huber and Goldner (2012) for monsoonal climates as being highly seasonal precipitation regimes where wet season precipitation >70% of the annual total.

Two historically and independently collected fossil leaf collections from the McAbee site (Figures 1 and 2; coordinates 50° 47.831’ N, 121° 08.481’ W, 586 m elevation, using a Garmin™ GPS, July 30, 2015) were examined for this study. The University of Saskatchewan (US) collection was made by J.F. Basinger in the late 1980s, and was used for initial leaf physiognomic estimates of climate for McAbee (e.g., Greenwood and Wing 1995; Greenwood et al. 2005; Smith et al. 2010, 2012). The Brandon University (BU) collection was made by S.B. Archibald in the early 2000s. Neither collection was made within a site stratigraphy (J.F. Basinger and S.B. Archibald, pers. comm., Sept. 4, 2015). The McAbee main site (Fig. 2) is an
approximately 0.5 km stretch of lacustrine shale interbedded with volcanic ash and tephra
referred to as the McAbee beds, an unnamed unit within the Tranquille Formation of the
Kamloops Group (Ewing 1981; Read and Hebda 2009; Hebda 2012). Volcanic rocks from the
Dewdrop Formation, the upper-most unit within the Kamloops Group, overlie the McAbee beds
in outcrop (Fig. 2). Radiometric dating on volcanic ash layers within the McAbee beds using the
\(^{40}\text{Ar} - ^{39}\text{Ar}\) method estimated the age of the McAbee fossil beds at 52.9 ± 0.83 Ma (Archibald et
al. 2010), thus representing environments just prior to the EECO (50-52 Ma; Zachos et al. 2008).
The fossil bearing sediments from this site represent a local near-shore environment (Read and
Hebda 2009), thus the fossil megaflora represent a lake-shore forest flora due to specific
transport and taphonomic properties of leaves (Greenwood 1992; Burnham 1994; Steart et al.
2002).

The original collections from the McAbee site (e.g., Hills 1965; Verschoor 1974; Wilson
1977; Manchester 1991) were sampled from a limited area of outcrop encompassing where the
University of Saskatchewan collection was made (Fig. 2, 'US'), and from an outcrop of the
McAbee beds 4 km west (Wilson 2008). These earlier collections were made from a series of
small benches cut into the strata \textit{in situ}, or were recovered from scree float derived from these
exposures (J.F. Basinger and S.B. Archibald, pers. comm., Sept. 4, 2015). In the late 1990s a
road was bulldozed at the base of the fossil-bearing sediments (Wilson 2008; Read and Hebda
2009; Hebda 2012). Subsequent to the road construction, collecting and description of fossil
plants was from outcrop exposed in the cut faces above the road bed (e.g., Dillhoff et al. 2005).
All of these collections treated the McAbee beds as a single assemblage (the 'McAbee beds
flora'), not accounting for any differences in taxonomic composition or relative abundance of
taxa between subsequent levels within the site stratigraphy (1–10 m) or lateral variation over 0.5
km within the beds (Read and Hebda 2009). Work at the Early Eocene Falkland Okanagan Highlands site (Fig. 1), in similar lithologies to the McAbee beds, has demonstrated significant differences in taxonomic composition and also leaf physiognomy over a stratigraphic depth of 2.9 m, likely reflecting 6000–8000 years of lake sedimentation and climate change (Smith et al. 2009, 2012). Recent survey work has shown considerable differences in plant taxon dominance and presence-absence between stratigraphic levels and laterally within the McAbee beds (Read and Hebda 2009; Hebda 2012 see Fig. 2 (A & B) and Table 1 herein), matching in part the Falkland observations. It is not known, however, whether the leaf assemblage physiognomy such as mean leaf size, a key character for estimating precipitation - varies between stratigraphic levels at McAbee.

Parauthochthonous leaf assemblages - assemblages of leaves transported short distances down-stream or laterally within a lake - show a smaller mean leaf size than an authochthonous assemblage - those directly deposited beneath the trees such as near shore lake - due to preferential loss with transport of larger leaf size classes within and between leaf taxa (Roth and Dilcher 1978; Greenwood 1992, 2007; Steart et al. 2002). These same patterns have been seen in Eocene lake sediment leaf assemblages over short stratigraphic distances of <5 m (e.g., Greenwood 1991; Smith et al. 2009, 2012). At Falkland, Smith (2011; Smith et al. 2009, 2012) summed leaves from short stratigraphic spans, but recognized three separate units based on volcanic tuff marker beds and lithological breaks. However, as the lithologies in the three Falkland units were similar (and therefore the energy of deposition is comparable), changes in mean leaf size in the Falkland deposit between the three units were interpreted as being caused by changes in annual precipitation amounts over time (Smith et al. 2009, 2012). If similar differences between samples exist in the McAbee flora as were recorded for Falkland, combining
the historical McAbee collections may mask differences in mean leaf size, and therefore precipitation changes over the time interval between samples. This point is assessed here by comparing the mean leaf sizes of the US and BU collections.

The climate of McAbee has been previously studied using both fossil data and computer models resulting in: MAT estimates of 9.5 °C (Dillhoff et al. 2005), 10.1 °C (Smith et al. 2010), and 12.8 °C (Huber and Caballero 2011); MAP estimates ranging from 99 cm.a\(^{-1}\) (Smith et al. 2010) to 121 cm.a\(^{-1}\) (Dillhoff et al. 2005); and CMMT estimates ranging from -2 °C (Dillhoff et al. 2005) to 8 °C (Archibald et al. 2014), with a median estimate of 5.2 °C (Huber and Caballero 2011). In addition, the world climate regime model by Huber and Goldner (2012) places this area in an ever-wet climate, but this has not been demonstrated by direct analysis of paleontological climate proxies such as those provided by plant fossils.

The aims of this study therefore are: (1) to determine if the existing historical Brandon University and University of Saskatchewan collections statistically represent a similar leaf population (as measured by mean leaf size) in order to combine them for climatic analysis; (2) to determine if a combined collection yields more precise climatic estimates; (3) and to reconstruct the paleoclimate and precipitation seasonality of the McAbee megaflora to determine if this region of the Okanagan Highlands experienced a highly seasonal precipitation (i.e., 'monsoonal'), or ‘ever-wet’ climate regime.

**Materials and Methods**

**Fossil Flora**

The first of the two fossil samples examined in this study was collected by S.B. Archibald in the early 2000s and is currently curated at Brandon University (BU). This collection
consists of 143 specimens—none of which have been used in previous climatic studies. The second collection was made by J.F. Basinger in the 1980s, and was previously curated at the University of Saskatchewan (US). Part of this collection (49/124 specimens) was loaned to Brandon University for this study and had been previously analysed for paleoclimate by Greenwood and Wing (1995), Greenwood et al. (2005), Smith et al. (2010, 2012), and also reported for leaf size analysis in Dillhoff et al. (2013). The prior paleoclimate and taxonomic analyses by Dillhoff et al. (2005) of the McAbee flora were based on leaves collected from multiple quarries (Fig. 2) and housed in the Thompson Rivers University collection. The two collections used in this study were excavated at single quarries but were at different stratigraphic levels and/or laterally separated from each other within the McAbee site (Figs. 2 & 3). This required the collections to be analyzed to show if they represent statistically similar leaf populations. The TRU collection was not available for analysis.

**Leaf Morphotyping**

The fossil leaves of both the BU and US collections were separated into distinctive morphotypes (Figs. 4 & 5) based on leaf characters defined in the Manual of Leaf Architecture (MLA; Ellis et al. 2009). The morphotype process serves to organize a fossil flora into distinct categories, which act as an approximation of a biological species, and as such does not require an in depth taxonomic analysis of the fossil flora (Ellis et al. 2009; Yang et al. 2011, 2015). Important morphological characteristics considered in this process include: leaf size, margin type, apex shape, base shape, and venation. Each morphotype is defined using the character scores of multiple leaves representative of the morphotype, entered into the MLA pro forma. Scores of leaf size class for each leaf morphotype were made using both the leaf size classes from the MLA (Ellis et al. 2009) and those used in CLAMP (Yang et al. 2011, 2015).
Photographs of examples of these morphotypes were taken using a Nikon D3200 DSLR 24 megapixel digital camera with a Nikon 55–200 mm DX VR lens and were slightly modified to remove lens geometric aberration, and to optimize contrast and brightness using the image editing feature of the camera.

**Statistical Analyses**

Statistical analyses were performed on the two collections in order to determine if they represent statistically similar or different leaf populations so that they may be combined during climatic analysis. To test this, the average area in mm$^2$ of each leaf morphotype from both collections was directly measured using the equation:

(1) Leaf Area = Length × Width × 0.67 (Cain and Castro 1957; Greenwood 1992).

The leaf area data was analyzed using two one-way ANOVA tests in Microsoft®-Excel 2007’s data analysis function. The first ANOVA test included all specimens in both collections in order to determine the base statistical difference of the two collections. The second ANOVA excluded all fossils that were deemed incomplete (broken specimens or those missing features) in order to remove any statistical imprecision which would have occurred in measuring incomplete specimens.

**Leaf Margin Analysis (LMA)**

A strong correlation has been repeatedly observed between the percentage of woody dicot species with toothed or untoothed leaf margins and MAT (Bailey and Sinnott 1916; Wolfe 1979; Wilf 1997; Greenwood et al. 2004; Peppe et al. 2011). To conduct the Leaf Margin Analysis (LMA) the morphotypes were scored using a binomial scale of non-toothed vs. toothed
consistent with the recommendation of Wilf (1997). The LMA equation (2) of Wing & Greenwood (1993) was applied, where LMP is the percent of non-toothed leaves in a flora. The global LMA equation (3) of Peppe et al. (2011) was also applied in our analysis, and is derived from a global set of 92 sites that represent more diverse vegetated environments than used to derive the original LMA equation, but has a much greater standard error (Peppe et al. 2011). This is intended to counteract the regional variances that have been observed between MAT and the proportion of untoothed leaves found in a flora (Gregory-Wodzicki 2000; Greenwood et al. 2004; Royer et al. 2012).

(2) \( \text{MAT} = 1.141 + (30.6 \times LMP) \)

(3) \( \text{MAT} = 4.60 + (20.4 \times LMP) \)

**Leaf Area Analysis (LAA)**

For LAA, each morphotype was measured indirectly using the Raunkiaer-Webb size class templates provided by the Manual of Leaf Architecture (Ellis et al. 2009) and then analyzed to generate an estimate for MAP. In addition, the smallest and largest specimens from each morphotype were directly measured using equation (1), averaged, and analyzed to estimate MAP. In morphotypes where there was only one fossil, that measurement was used as the average area of the morphotype. Morphotypes containing damaged or incomplete fossils that could not be directly measured were excluded from the analysis, although future work will incorporate these fragmentary specimens into the analysis using the leaf vein density scaling method (Sack et al. 2012; Merkhofer et al. 2015).

In LAA, each measurement of leaf area size, both indirect and direct yielded a specific natural log value that was used to calculate the mean area of each morphotype. These natural log
averages were then used to find the mean natural log of leaf area size (MLnA) of each collection, which were used to estimate MAP. Equation (4) (Wilf et al. 1998), was used on the direct and indirect measurements from both the BU and combined collections to estimate the MAP. In addition, we applied the global LAA equation (5) from Peppe et al. (2011), to the set of direct measurements although this equation has lower precision due to a large standard error.

\[
(4) \ln(\text{MAP}) = 0.548 \times \text{MLnA} + 0.768
\]

\[
(5) \ln(\text{MAP}) = 0.283 \times \text{MLnA} + 2.92
\]

**CLAMP (Climate Leaf Analysis Multivariate Program)**

Similar to LMA and LAA the Climate Leaf Analysis Multivariate Program (CLAMP) utilizes the evolutionary adaptations of leaves to their respective environments. This relationship has been observed and quantified in a dataset of leaf characteristics from floras around the world (Wolfe 1995; Spicer et al. 2004). CLAMP has been further refined through the use of globally gridded climate data (New et al. 2002; Spicer et al. 2009), which through the use of canonical correspondence analysis (Wolfe et al. 1997) allows for a best fit of the fossil physiognomy onto the physiognomy of modern floras in a 3-dimensional plot of 31 leaf characteristics. Since CLAMP is based on multiple leaf characters and their correlation with modern climates, it generates data on precipitation seasonality and growing season which LMA and LAA cannot provide (Yang et al. 2011, 2015). Fossils were scored and analyzed based on guidelines from CLAMP Online (Yang et al. 2011; http://clamp.ibcas.ac.cn).

The fossil floras were initially analyzed using the PhysgGlobal378 data set, which includes 378 modern vegetation sites from around the world (e.g., North America, Japan, East Asia, Southern Africa, Southern Asia, India, New Zealand, and Australia) (Yang et al. 2015).
The large increase in climates represented in the PhysgGlobal378 data set results in a decrease in the precision of the climate predictions (Yang et al. 2015). However, the utility of this data set lays in indicating which subset of the CLAMP data sets should be used for analysis (Yang et al. 2015). Results from the analysis using the PhysgGlobal378 data indicated that the McAbee fossil was distant in physiognomic space from the monsoonal South Asian and Indian vegetation. The Physg3brcAZ_GRIDMet3brAZ dataset consists of 144 modern sites that are primarily from temperate Northern Hemisphere localities (e.g., North America, Japan) but excludes cold temperature sites (Yang et al. 2011). This dataset was selected for the primary analysis of the McAbee fossil flora as it is based on vegetated sites from non-monsoonal climates; the climate regime previously modelled for this region (Huber and Goldner 2012). The climate data generated from CLAMP include temperature estimates (MAT, Warm Month Mean Temperature (WMMT), CMMT), precipitation estimates (Growing Season Precipitation, Mean Month Growing Precipitation, amount of precipitation in the three wettest months and three driest months) and other climate data (Growing Season Length, Relative Humidity, and Specific Humidity).

**Results**

**Leaf Morphotyping**

After scoring the leaf architectural features of a total of 192 fossil leaves, 43 distinct morphotypes were defined using the character set and pro forma of Ellis et al. (2009). Of these, 29 were unique to the BU collection, 3 were unique to the US collection, and 11 were present in both collections (Table 1\(^c\)). These data show different taxonomic assemblages between these two

\(^c\) Tables S1 & S2, online supplementary materials
collections is typical of the differences observed between quarry sites in the McAbee beds (Read and Hebda 2009; Hebda 2012). Photographs of specific morphotypes are presented in Figures 4 and 5. Several morphotypes were identified: *Sassafras hesperia* (Fig. 4A & B); both collections), *Acer* (Fig. 4C; BU), *Betula leopoldae* (Fig. 4D; BU), *Fagus langevinii* (Fig. 5A), *Comptonia columbiana* (Fig. 5C & F; BU), and *Ulmus* (Fig. 5I; both collections). *Fagus langevinii* (Fig. 5A), was found to be the most common morphotype in both collections with 17 of 143 specimens in the BU collection and 14 of 49 specimens in the US collection. Other leaf morphotypes were only tentatively identified: *Cercidiphyllum / Joffrea* (not illustrated), cf. *Vitis* (Fig. 4E), cf. *Crataegus* (Fig. 4F), cf. Bignoniaceae (Fig. 4G, likely also present as seeds), cf. *Decodon* (Fig. 4H), cf. *Neviusia* (not illustrated), cf. *Tetracentron* (not illustrated), cf. *Fraxinus* (Fig. 5B), and cf. Platanaceae (Fig. 5G).

**Statistical Analyses**

The numerical values for the ANOVA tests are as follows: ANOVA test 1 statistical value 1.95, critical value 4.03; ANOVA test 2 statistical value 2.26, critical value 4.13. Both statistical tests found that the BU collection and US collection were not statistically different in terms of leaf area. Details of the tests can be found in Tables 2 and 3. This allows for the combination of the two collections into the larger combined collection. Subsequent climatic tests (LMA and LAA) showed that the BU collection agreed with the originally published US collection (Greenwood and Wing 1995) showing the two collections likely experienced similar climates despite being separated by an unknown length of time. This stability of climate through time also allows for the blending of the two collections in the combined collection. Furthermore, when plotted in physiognomic space by CLAMP, the BU collection and combined collection
occur very near to each other (Fig. 6) showing that the two collections have near identical 
physiognomies and that the creation of the combined collection was justified.

Leaf Margin Analysis

In the BU collection 23% (9/40) of all morphotypes were found to be non-toothed while 
26% (11/43 morphotypes) of the combined collection was found to be non-toothed\(^d\). The 
estimate for MAT for the BU collection using equation (2) was \(8.2 \pm 2.0 \degree C\) and \(9.3 \pm 4.8 \degree C\)
using equation (3). The combined collection yielded the results of \(9.2 \pm 2.0 \degree C\) using equation (2)
and \(9.9 \pm 4.8 \degree C\) using equation (3) (Table 4).

Leaf Area Analysis

The MLnA values for both the BU and combined collections were 7.3 and 7.1 when 
using the indirect and direct measurements respectively\(^e\). These values are similar to the MLnA 
values found for the US collection, which were 7.2 and 6.9 in this study and reported to be 7.0 
(direct measurement of US collection) in Dillhoff et al. (2013). Table 4 shows the MAP 
estimates for the BU and combined collection using equation (4) on both the indirect and direct 
measurements and equation (5) on the direct measurements. A wet climate (>100 cm.a\(^{-1}\)) is 
suggested by all the estimates, but the indirect measurements yielded higher estimates than the 
direct measurements when using equation (4). Estimates using equation (5) were highest of all 
(>130 cm.a\(^{-1}\)) but had large errors (Table 4). The differing number of morphotypes in each 
collection likely caused the small difference in the MAP estimate between the BU and combined 
collections.

\(^d\) Tables S3 & S4, online supplementary materials. 
\(^e\) Tables S5 & S6, online supplementary materials.
The completeness statistics for BU and the combined collections were high (0.807 / 81% and 0.814 / 81%)\(^f\), which indicates that the results generated by CLAMP are statistically significant under the method’s parameters (Yang et al. 2011). The analysis is statistically significant due to the high number of morphotypes (>20) that were analyzed (Wolfe 1993; Spicer et al. 2005; Yang et al. 2011). Some examples of climate estimates generated by CLAMP for the BU collection are (Table 5): MAT 13.1 ± 2.1 °C, CMMT 5.0 ± 3.4 °C, and Growing Season Precipitation (GSP) 130 ± 32 cm. The same estimates for the combined collection are: MAT 12.9 ± 2.1 °C, CMMT 5.1 ± 3.4 °C, and GSP 130 ± 32 cm. All errors are standardized and provided by the CLAMP analysis (Yang et al. 2011).

Figure 6 shows the BU and combined collections plotted in multi-dimensional space against modern data points from the CLAMP analysis. This is achieved using canonical correspondence analysis (CCA) which ordinates the data (CCA axes 1 and 2), which shows the environmental vectors (Kovach and Spicer 1996; Spicer 2000; Yang et al. 2011, 2015). The vectors point in the extremity of that specific characteristic, but do not form an average in which the results lie due to the multi-dimensional nature of the analysis. The placement of the BU and combined collection in physiognomic space shows that both collections experienced wet, but non-monsoonal conditions as the three dry months (THREE_DRY), the three wet months (THREE_WET), and mean growing season precipitation per month (MMGSP) vectors all point in the same direction which indicates no major seasonal change in precipitation. This assessment is supported by numerical estimates of the three driest months data generated by CLAMP (Table 5) which shows that; (1) the three driest months received ~30 cm, or approximately one quarter

\(^f\) online supplementary materials.
of the total estimated precipitation; (2) the three wettest months’ received ~60 cm, only twice the amount of the three driest months; and (3) MAP >100 cm.a⁻¹ (Table 5). These data indicate that there was slight seasonality in terms of precipitation but no markedly wet or dry seasons. Thus, conditions at McAbee during the Early Eocene were not highly seasonal under the definition applied (THREE_WET >70% of MAP), and thus not monsoonal.

Discussion

McAbee Climate Interpretations

Precipitation seasonality is a climatic feature that is often overlooked in paleoclimatic reconstructions, but is essential to understanding ancient environments and ecosystems (Huber and Golder 2012; Eldrett et al. 2014; West et al. 2015). Huber and Goldner (2012) modeled Early Eocene climate and mapped climate regimes across the Eocene globe, and were able to highlight two major precipitation patterns: ever-wet and monsoonal (i.e., as defined by Huber and Goldner (2012) for their model as the ratio of summer to annual precipitation > 70%:).

Seasonality, however, is not limited to variable precipitation patterns, but may also be the result of seasonal changes in temperature (e.g., this study) or light regime (e.g., West et al. 2015).

The MAT results generated by equation (2) for the BU collection and the combined collection agree with each other, the MAT result from Greenwood and Wing (1995), and the results from using equation (3) (Table 4). The indirect and direct methods of measuring leaves for LAA yielded different results for annual precipitation (MAP) for the BU and combined collections, but are concordant due to the method’s large error estimates. They also agree with results from the US collection (Greenwood and Wing 1995; Table 4). The difference between the direct and indirect measurement estimates of MAP is caused by the direct method’s inability to
utilize damaged specimens. Several morphotypes (17/40- BU collection; 14/43- combined collection) from each collection were not analyzed using direct measurements for this reason. In addition, taphonomic bias affects LAA estimates as smaller leaves are more likely to be preserved (Greenwood 1991, 1992; Steart et al. 2002) which suggests that the upward error values of LAA estimates are more likely to reflect the actual climate as smaller leaves indicate a drier climate. Vein density scales with leaf size offering a solution to the problem of fragmented leaves (Sack et al. 2012; Merkhofer et al. 2015), and future work will apply this approach to the McAbee flora.

The results from the CLAMP analysis indicate a warm (MAT ~13 °C), mild (CMMT ~5 °C), and wet (GSP ~130 cm) climate for both the BU and combined collections. Differences in the estimates between the methods are because CLAMP uses 31 leaf characters for analysis (Wolfe 1993; Spicer 2000; Yang et al. 2011, 2015). The MAT and CMMT results generated by CLAMP are mostly consistent with other published results for Okanagan Highlands sites (Archibald and Mathewes 2000; Archibald et al. 2005; Greenwood et al. 2005; Smith et al. 2009, 2012; Dillhoff et al. 2013; Mathewes et al. this volume). The one exception is the CMMT estimate of -2 °C by Dillhoff et al. (2005) from CLAMP, which based on the presence of both palm pollen and bruchine beetles, would appear an underestimate. These and other data from plant and insect fossils from other Okanagan Highlands sites suggest McAbee winters would likely have been mild and frost-free for much of the season (Greenwood et al. 2005; Smith et al. 2012; Archibald et al. 2014; Mathewes et al. this volume; Moss et al. this volume).

Archibald et al. (2014) identified palm-seed feeding bruchine beetles at McAbee, 'constraining CMMT to >8 °C' on the basis of the higher temperatures at which palms experience lethal freezing damage under Eocene high pCO₂, citing experimental trials with the cold tolerant
palms *Chamaerops humilis* and *Trachycarpus fortunei* by Royer et al. (2002). However: (1) Royer et al. (2002, p. 965) recommended an adjustment of ‘at least +1.5 to +3 °C’ to the plant NLR derived CMMT (palms in this case), not 'CMMT >8 °C', which represents the upper limit of adjustment assuming a minimum CMMT for palms of 5 °C (Greenwood and Wing 1995); and (2) based on more precise analyses of the modern distribution limits of palms, the lower limit for CMMT for palms has been calculated as < 5 °C (Walther et al. 2007 for *Trachycarpus fortunei*; Fang et al. 2011 for 7 species of Chinese palms\(^g\); Archibald et al. 2014 for *Washingtonia filifera*). According to data listed by Fang et al. (2011; summarised in Table S7) some palms may naturally grow where CMMT is as low as 1.3°C, with these authors listing the lower limit of CMMT for *T. fortunei* as -3.2 °C. This much lower CMMT for *T. fortunei* seems out of step with all other temperature limit data for palms, and so we accept the higher CMMT value of 2.2 °C for this species from Walther et al. (2007). Allowing for the revised lower CMMT’s provided for palms as noted here, the pCO\(_2\)>800 ppm adjusted CMMT for palms (i.e., Royer et al. 2002) is conservatively in the range 4.3 °C (1.3 from Fang et al. 2011+ 3.0) to 5.2 °C (2.2 from Walther et al. 2002 + 3.0). In our view, constraining McAbee CMMT to >8 °C is not appropriate as our estimate of 5.1 ± 3.4 °C from CLAMP overlaps within its errors with the revised palm CMMT lower limit, with the presence of palms indicating CMMT range of 4.3 – 8.5 °C. Combining the temperature results from the physiognomic analyses (LMA, LAA, and CLAMP) provides a MAT range of ~8-13°C, a WMMT of ~21 °C, and a CMMT of ~5 °C.

The MAP estimates generated by LAA using equations (4) and (5) overlap when the error values are considered and the results are not statistically different (Table 4). The MAP estimates are similar in value with the GSP estimates generated by CLAMP; the estimated ~8 month

\(^g\) Table S7, online supplementary materials.
growing season (Table 5) may also represent the time period being captured for both MAP and GSP. Both methods suggest a wet (MAP >100 cm.a\(^{-1}\)) climate for McAbee. The conditions for a monsoonal climate are not indicated by the results, as defined by Huber and Caballero (2012), as the wettest portion of the year received ~50% (i.e., <70%) of the total precipitation, i.e. the precipitation was not highly seasonal. Non-monsoonal conditions are further indicated by canonical correspondence analysis (Fig. 6) and the (THREE_DRY) three driest months’ estimate (Table 5). This interpretation agrees with the global climate model by Huber and Goldner (2012), which placed the Okanagan Highlands sites in an ever-wet, not monsoonal condition. Precipitation estimates of ~30 cm in the three driest months and ~60 cm of precipitation in the three wettest months shows some precipitation seasonality, but does not resolve the time of year that was the 'dry season'. These data (Table 5) would suggest a climate similar to the modern day North Pacific coast of North America (e.g., Vancouver BC (from Environment Canada, http://climate.weather.gc.ca/climate_normals/index_e.html), MAT 9.9 °C, CMMT 3 °C, WMMT 17.4 °C, MAP 117 cm.a\(^{-1}\), THREE_WET 50 cm, THREE_DRY 12 cm; Portland OR (from NOAA, http://www.ncdc.noaa.gov/cdo-web/datatools/normals), MAT 12.0 °C, CMMT 4.2 °C, WMMT 20.3 °C, MAP 92.2 cm.a\(^{-1}\), THREE_WET 42.8 cm, THREE_DRY 8.2 cm), but with wetter dry seasons than the modern sites. The megaflora of the McAbee collections indicates some level of temperature seasonality as they contain deciduous trees such as *Fagus*, and fossil leaves found in mats on the exposed shale surfaces are consistent with seasonal leaf-fall. Cool average winter temperatures and a non-permanent growing season (Table 5) show that the McAbee EECO forest was seasonal with respect to temperature, and that precipitation was also seasonal with a wet and a dry season (THREE_WET ~60 cm vs. THREE_DRY ~ 30 cm).
The Early Eocene Okanagan Highland floras, including the McAbee flora, represents a time of rapid evolution and the early radiation of many dicot families (DeVore et al. 2005). The fine scale preservation of lake sediments of these localities may allow these diversification events to be studied in great detail during the warmest part of the Cenozoic. An unbiased census approach for fossil collecting is critical for observing and identifying these fine-scale patterns or trends in diversity of fossil plant communities and the reconstruction of fossil climates (Greenwood 1991; Greenwood and Basinger 1993; Wilf et al. 2003, 2005; Iglesias et al. 2007; Smith et al. 2009).

The McAbee collections have been traditionally treated as a single assemblage (the ‘McAbee beds flora’), not accounting for any differences in taxonomic composition or relative abundance of taxa between subsequent levels within the McAbee site stratigraphy or lateral variation over 0.5 km within the beds (Read and Hebda 2009). This, however, can limit the use of the flora for observing fine scale patterns and trends in regional diversity that may be preserved in the geological record. Previous work conducted at the EECO Falkland OH site has demonstrated significant differences in taxonomic composition and leaf physiognomy, and therefore climate, over a stratigraphic depth of 2.9 m (Smith et al. 2009, 2012). Based on sedimentation rates at the Horsefly BC site (0.36–0.47 m per 1000 years; Wilson and Bogen 1994; Barton 1998), Smith et al. (2012) calculated that the ~3 m they sampled for megaflora represented ~6000-8000 years of lake history.

Recent survey work has shown considerable differences in plant taxon dominance and presence-absence between stratigraphic levels and laterally within the McAbee beds (Read and Hebda 2009; Hebda 2012; see Fig. 2 & 3, and Table 1 herein), matching in part the Falkland observations of Smith et al. (2009, 2012). The results of this present McAbee study have shown
that the average area of leaves was similar over distance and through time, suggesting a stable climate regime. The size of the collections poses a problem when interpreting diversity and species composition of the McAbee flora. The different morphotypes unique to each collection (Table 1), however seems to suggest that diversity and species composition of the lake-side forest may have been changing regionally over time. Although, local leaf physiognomy may have been constrained to specific architectural elements correlated to regional climate. These observations reinforce the need for census style collection methods for fossil floras, including McAbee.

The combined collection and McAbee climate stability

The BU and the US collections were not statistically different in terms of leaf area, and the univariate climatic estimates (LMA, LAA) from the BU collection agreed with previously published work on the US collection (Greenwood and Wing 1995). This suggests that the climate and the environment were relatively stable over time. This interpretation, of little change in physiognomy (and hence climate) at McAbee coupled with change in taxonomic composition contrasts with Smith et al.’s (2009) observed pattern for the nearby Falkland site. The apparent stability of climate for the McAbee site requires more study, both to confirm the pattern and to ascertain its cause. For this present study, however, only a portion of the US collection (49/124 specimens) was available for climatic analysis. Analysis of this small collection generated erroneous results that did not agree with the previously published data or the results from the BU collection. This is likely a result due to a small number of morphotypes in this partial collection (14) compared to the previous study (24; Greenwood and Wing 1995). In order to minimize uncertainties and potential errors, it is recommended that at least 20 morphotypes be available for an adequate climate reconstruction (Wolfe 1993; Spicer et al. 2005; Yang et al. 2011).
The differences between the two collections may also be the result of the sampling techniques utilized. The BU collection was collected over several weeks with the majority of found specimens collected. The US collection, however, was made over the span of a few days with “high quality” specimens being preferentially collected. Neither collection, however, was census sampled. As the BU collection represents the majority of flora found, the results are likely more representative of the actual McAbee EECO flora and therefore climate, even if this collection is not a true census sample.

Despite the success in this study, census sampling is still preferred method for fossil leaf collection for future climatic analyses based on leaf physiognomy, as a short sequence of strata may contain a rapidly changing flora with leaf size differing between successive layers in response to regional shifts in precipitation or taphonomic effects (Greenwood 1991; Smith et al. 2009, 2012). Census sampling has been applied to other North and South American fossil floras (see Greenwood and Basinger 1993; Wilf et al. 2003, 2005; Iglesias et al. 2007; Smith et al. 2009, 2012), and the further application of this collection method to the Okanagan Highlands floras will allow further testing and comparison to these Eocene fossil floras found across the Americas.

**Conclusions**

The two fossil collections (BU and US), are not statistically different in terms of leaf area, which allowed them to be combined for additional climate analysis. The statistical similarities and agreement between MAT and MAP estimates of the BU and total US collection suggests that the environment of McAbee was relatively stable over this time with respect to precipitation despite there being distinct taxonomic changes between the collections. The combined collection
likely yielded more precise climatic estimates compared to the BU collection due to the greater number of morphotypes included in its climatic analysis, but the BU collection represents a more constrained view of the climate as opposed to the time averaged combined collection. This method of combining collections that are separated in time, however, cannot be utilized in all cases due to the possibility of taxonomic or climatic changes occurring through a relatively small amount of deposition. Census collecting should be used to gain the most precise and time constrained climatic estimates in the future.

Leaf physiognomic analysis using LMA, LAA, and CLAMP show that the climate of McAbee during the EECO was microthermal (MAT ~8–13 °C, WMMT ~21 °C) with mild winters (CMMT ~5 °C) and high levels of precipitation (MAP ~100–130 cm.a⁻¹). In terms of seasonality, precipitation was relatively constant year-round with the driest portion of the year receiving approximately 50% of the amount of precipitation as the wettest. There is no evidence to suggest there were monsoonal or highly seasonal precipitation during this time. Therefore our data agree with the climatic modelling by Huber and Goldner (2012) that the interior area of British Columbia experienced an ever-wet climate regime during the Early Eocene.

Acknowledgements

We thank Bruce Archibald and Jim Basinger for the loan of their McAbee collections, and for assistance with field work. D.R.G. acknowledges the support from a discovery grant from the Natural Sciences and Engineering Research Council of Canada (DG-311934) and a Committee for Research and Exploration grant from the National Geographic Society (9652-15). C.K.W. acknowledges financial support from the University of Saskatchewan. C.A.C.G. gives additional thanks to Pamela Rutherford of Brandon University for assistance in statistical analysis and Bob
Spicer (Open University) for assistance with the CLAMP analysis set-up. Special thanks to Markus Sudermann for taking the leaf morphotype images presented in this paper, and for field assistance to D.R.G. and C.K.W. at the McAbee fossil beds in 2015. This work was completed as part of an undergraduate thesis by C.A.C.G. Constructive and thoughtful reviews by Dana Royer and Dan Peppe led to important improvements to the paper.

References


Moss, P.T., Greenwood, D.R., and Archibald, S.B. 2005. Regional and local vegetation community dynamics of the Eocene ‘Okanagan Highlands’ (British Columbia


Figure Captions

Fig. 1. Map of British Columbia showing the Early Eocene Okanagan Highlands fossil sites (open circles) and nearby cities (small filled circles). Star signifies the study area. Modified from Dillhoff et al. (2013; Fig. 1).

Fig. 2. (A-C) The McAbee fossil beds site (taken 2005 and 2015). (A) View of main beds from highway (2005). Dotted line indicates outcrop exposure following a road that was cut into the lake sediments (approx. 0.5 km). Approximate locations of the sampling sites for the University of Saskatchewan (US) and Brandon University collections (BU) are shown, as is the location of 1 of 2 quarries sampled in 2015 (see (A) and (B) in this Figure). White stars indicate exposures favoured by mine operators (Read and Hebda 2009; Hebda 2012), and the likely source of fossils featured in reports of fossils collected after the road was constructed and curated in the Thompson Rivers University collection. The prominent hoodoos above the McAbee beds are weathered volcanics of the Dewdrop Formation. (B) Closer view of 2015 Quarry 1 site showing bench cut for quantitative 'census-style' sampling (dashed line), and prominent ash layer (arrow). Note red flagging tape marking location of a steel peg marker (= GPS point) near a hammer to the right of the man, and hoodoos above. (C) Close up view of beds sampled at red flagging tape shown in (B) and ash layer (arrow) used for dating (Moss et al. 2005).

Fig. 3. Synthetic or 'ideal' site stratigraphy based on lithological descriptions from Hebda (2012), showing approximate stratigraphic location of the US and BU historical collections, and sections 2 and 3 (numbering from Hebda 2012) reconstructed for the 2 separate quarries where these collections were made.
Fig. 4. (A-H) Examples of the leaf morphotypes from both collections I. MA0xx = McAbee leaf morphotype. (A & B) MA016 Sassafras hesperia; C, MA031 Acer sp.; D, MA029 Betula leopoldae; E, MA006 cf. Vitis; F, MA033 cf. Crataegus; G, MA019 cf. Bignoniaceae; H, MA036 cf. Decodon. Scale bar = 1 cm.

Fig. 5. (A-I) Examples of the leaf morphotypes from both collections II. MA0xx = McAbee leaf morphotype. (A) MA001 Fagus langevenii. (B) MA022 cf. Fraxinus. (C & F) MA017 Comptonia columbiana. (D) MA040 unknown leaf type. (E) MA002 unknown leaf type. (G) MA027 cf. Platanaceae. (H) MA036 unknown leaf type. (I) MA003 Ulmus okanaganesis. Scale bar = 1 cm.

Fig. 6. The BU collection (filled circle) and combined collection (filled square) in relation to modern data points in the CLAMP ordination using Canonical Correspondence Analysis (CCA axes 1 vs. 2). Groups Monsoonal A and Monsoonal B show modern monsoonal climates within the cloud. Monsoonal A represents modern arid to median climates (Arizona, California, Puerto Rico). Monsoonal B represents humid climates (Southern Japan, Tropical Pacific Islands). Ungrouped data represents the range of modern non-monsoonal environments. Main environmental vectors are plotted as labelled arrows. Labels are as follows going clockwise (Yang et al. 2011): WMMT- warm month mean temperature, GROWSEAS- growing season, MAT- mean annual temperature, CMMT- cold month mean temperature, ENTHAL- enthalpy, SH- specific humidity, GSP- growing season precipitation, MMGSP- mean month growing season precipitation, THREE_DRY- precipitation of the three driest months, THREE_WET- precipitation of the three wettest months, RH- relative humidity.
**Table 1.** The leaf morphotypes which are found in both collections, the Brandon University collection, and the University of Saskatchewan collection, and where known identified to genus or species.

<table>
<thead>
<tr>
<th>Both Collections</th>
<th>Brandon University Collection</th>
<th>University of Saskatchewan Collection</th>
</tr>
</thead>
<tbody>
<tr>
<td>MA 001 - <em>Fagus langevinii</em></td>
<td>MA 004</td>
<td>MA 041 - <em>Cercidiphyllum / Joffrea</em></td>
</tr>
<tr>
<td>MA 002</td>
<td>MA 005</td>
<td>MA 042</td>
</tr>
<tr>
<td>MA 003 - <em>Ulmus okanaganensis</em></td>
<td>MA 007 - cf. <em>Neviusia</em></td>
<td>MA 043</td>
</tr>
<tr>
<td>MA 006 - cf. <em>Vitis</em></td>
<td>MA 008</td>
<td></td>
</tr>
<tr>
<td>MA 016 - <em>Sassafras hesperia</em></td>
<td>MA 009</td>
<td></td>
</tr>
<tr>
<td>MA 018</td>
<td>MA 010</td>
<td></td>
</tr>
<tr>
<td>MA 022 - cf. <em>Fraxinus</em></td>
<td>MA 011 - <em>Comptonia columbiana</em></td>
<td></td>
</tr>
<tr>
<td>MA 026</td>
<td>MA 012</td>
<td></td>
</tr>
<tr>
<td>MA 029 - <em>Betula leopoldae</em></td>
<td>MA 013</td>
<td></td>
</tr>
<tr>
<td>MA 032</td>
<td>MA 014</td>
<td></td>
</tr>
<tr>
<td>MA 033 - <em>Crataegus sp.</em></td>
<td>MA 015</td>
<td></td>
</tr>
<tr>
<td></td>
<td>MA 017</td>
<td></td>
</tr>
<tr>
<td></td>
<td>MA 019 - cf. Bignoniaceae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>MA 020</td>
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<td></td>
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<td></td>
<td>MA 023</td>
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<tr>
<td></td>
<td>MA 024</td>
<td></td>
</tr>
<tr>
<td></td>
<td>MA 025</td>
<td></td>
</tr>
<tr>
<td></td>
<td>MA 027 - cf. Platanaceae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>MA 028 - cf. <em>Tetracentron</em></td>
<td></td>
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</table>
MA 030
MA 031 - Acer sp.
MA 034
MA 035
MA 036 - Decodon sp.
MA 037
MA 038
MA 039
MA 040
Table 2. One way ANOVA for all fossils in the Brandon University and University of Saskatchewan collections. Column 1- Brandon University Collection, Column 2- University of Saskatchewan collection, SS- sum of squares, df- degrees of freedom, MS, mean square between groups.

Anova: Single Factor

<table>
<thead>
<tr>
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<th>Variance</th>
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ANOVA

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<th>MS</th>
<th>F</th>
<th>P-value</th>
<th>F crit</th>
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<tbody>
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<td>3343879</td>
<td>1.951387</td>
<td>0.168371</td>
<td>4.026631</td>
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<tr>
<td>Within Groups</td>
<td>89106744</td>
<td>52</td>
<td>1713591</td>
<td></td>
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**Table 3.** One way ANOVA for complete fossils in the Brandon University and University of Saskatchewan collections. Column 1- Brandon University Collection, Column 2- University of Saskatchewan collection, SS- sum of squares, df- degrees of freedom, MS, mean square between groups.

Anova: Single Factor

**SUMMARY**

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<th>Average</th>
<th>Variance</th>
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<td>Column 2</td>
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<td>8339</td>
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**ANOVA**

<table>
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<th>Source of Variation</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P-value</th>
<th>F crit</th>
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<td>2379626</td>
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Table 4. Results for Leaf Margin Analysis and Leaf Area Analysis for the Brandon University collection and the combined collection compared to published data on the University of Saskatchewan collection from Greenwood and Wing (1995).

<table>
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<tr>
<td></td>
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<td>BU</td>
<td>BU</td>
<td>combined collection</td>
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<tr>
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<td></td>
<td>collection</td>
<td>collection</td>
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<td></td>
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<tr>
<td>LMA- (2)</td>
<td>MAT LMP</td>
<td>LMP 23% non-toothed</td>
<td>8.2 ± 2.0 °C</td>
<td>a 10.1 ± 2.0 °C</td>
<td>LMP 26% non-toothed</td>
<td>9.2 ± 2.0 °C</td>
</tr>
<tr>
<td>LMA- (3)</td>
<td>MAT LMP</td>
<td>LMP 23% non-toothed</td>
<td>9.3 ± 4.8 °C</td>
<td>b 12.8 ± 4.8 °C</td>
<td>LMP 26% non-toothed</td>
<td>9.9 ± 4.8 °C</td>
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<td>LAA- Indirect (4)</td>
<td>MAP MLnA 7.3</td>
<td>117 cm.a⁻¹ - 35, +51</td>
<td>N/A</td>
<td>MLnA 7.3</td>
<td>116 cm.a⁻¹ - 35, +50</td>
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<tr>
<td>LAA- Direct (4)</td>
<td>MAP MLnA 7.1</td>
<td>105 cm.a⁻¹ - 32, +45</td>
<td>c 99 cm.a⁻¹ -30, +43</td>
<td>MLnA 7.1</td>
<td>104 cm.a⁻¹ -31, +45</td>
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<td>LAA- Direct (5)</td>
<td>MAP MLnA 7.1</td>
<td>137 cm.a⁻¹ - 63, +116</td>
<td>N/A</td>
<td>MLnA 7.1</td>
<td>137 cm.a⁻¹ - 63, +116</td>
<td></td>
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</table>

a  new estimate using LMP data from Greenwood and Wing (1995) from the US collection

b  new estimate using LMP data from Greenwood and Wing (1995) from the US collection
c  estimate reported in Dillhoff et al. (2013) from the US collection
Table 5. Results from CLAMP analysis for the Brandon University collection and ‘Combined collection’. 5a, temperature estimates; 5b, seasonal precipitation; 5c, additional precipitation and humidity variable estimates.

### (5a)

<table>
<thead>
<tr>
<th>Collection</th>
<th>Mean Annual Temperature</th>
<th>Warm Month Mean Temperature</th>
<th>Cold Month Mean Temperature</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brandon</td>
<td>13.1 °C ± 2.1</td>
<td>21.0 °C ± 2.5</td>
<td>5.0 °C ± 3.4</td>
</tr>
<tr>
<td>Combined</td>
<td>12.9 °C ± 2.1</td>
<td>20.5 °C ± 2.5</td>
<td>5.1 °C ± 3.4</td>
</tr>
</tbody>
</table>

### (5b)

<table>
<thead>
<tr>
<th>Collection</th>
<th>Growing Season Precipitation</th>
<th>Growing Season Precipitation</th>
<th>Mean Month Growing Season Precipitation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brandon</td>
<td>7.7 Months ± 1.1</td>
<td>130 cm ± 32</td>
<td>18 cm ± 4</td>
</tr>
<tr>
<td>Combined</td>
<td>7.6 Months ± 1.1</td>
<td>130 cm ± 32</td>
<td>17 cm ± 4</td>
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</tbody>
</table>

### (5c)

<table>
<thead>
<tr>
<th>Collection</th>
<th>Three Wet Months</th>
<th>Three Dry Months</th>
<th>Relative Humidity</th>
<th>Specific Humidity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brandon</td>
<td>60 cm ± 23</td>
<td>31 cm ± 6</td>
<td>84.4% ± 8.6</td>
<td>12.5 g.kg(^{-1}) ± 1.7</td>
</tr>
<tr>
<td>Combined</td>
<td>62 cm ± 23</td>
<td>30 cm ± 6</td>
<td>84.4% ± 8.6</td>
<td>12.2 g.kg(^{-1}) ± 1.7</td>
</tr>
</tbody>
</table>
Fig. 1. Map of British Columbia showing the Early Eocene Okanagan Highlands fossil sites (open circles) and nearby cities (small filled circles). Star signifies the study area. Modified from Dillhoff et al. (2013; Fig. 1). 90x95mm (600 x 600 DPI)
Fig. 2. (A-C) The McAbee fossil beds site (taken 2005 and 2015). (A) View of main beds from highway (2005). Dotted line indicates outcrop exposure following a road that was cut into the lake sediments (approx. 0.5 km). Approximate locations of the sampling sites for the University of Saskatchewan (US) and Brandon University collections (BU) are shown, as is the location of 1 of 2 quarries sampled in 2015 (see (A) and (B) in this Figure). White stars indicate exposures favoured by mine operators (Read and Hebda 2009; Hebda 2012), and the likely source of fossils featured in reports of fossils collected after the road was constructed and curated in the Thompson Rivers University collection. The prominent hoodoos above the McAbee beds are weathered volcanics of the Dewdrop Formation. (B) Closer view of 2015 Quarry 1 site showing bench cut for quantitative ‘census-style’ sampling (dashed line), and prominent ash layer (arrow). Note red flagging tape marking location of a steel peg marker (= GPS point) near a hammer to the right of the man, and hoodoos above. (C) Close up view of beds sampled at red flagging tape shown in (B) and ash layer (arrow) used for dating (Moss et al. 2005).
Fig. 3. Synthetic or ideal site stratigraphy based on the lithological descriptions from Hebda (2012), showing approximate stratigraphic location of the US and BU historical collections, and sections 2 and 3 (numbering from Hebda 2012) reconstructed for the 2 separate quarries where these collections were made.

73x58mm (600 x 600 DPI)
Fig. 6. The BU collection (filled circle) and combined collection (filled square) in relation to modern data points in the CLAMP ordination using Canonical Correspondence Analysis (CCA axes 1 vs. 2). Groups Monsoonal A and Monsoonal B show modern monsoonal climates within the cloud. Monsoonal A represents modern arid to median climates (Arizona, California, Puerto Rico). Monsoonal B represents humid climates (Southern Japan, Tropical Pacific Islands). Ungrouped data represents the range of modern non-monsoonal environments. Main environmental vectors are plotted as labelled arrows. Labels are as follows going clockwise (Yang et al. 2011): WMMT- warm month mean temperature, GROWSEAS- growing season, MAT- mean annual temperature, CMMT- cold month mean temperature, ENTHAL- enthalpy, SH- specific humidity, GSP- growing season precipitation, MMGSP- mean month growing season precipitation, THREE_DRY- precipitation of the three driest months, THREE_WET- precipitation of the three wettest months, RH- relative humidity.

121x105mm (300 x 300 DPI)