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ORIGINAL ARTICLE

Climate variability and fire effects on quaking aspen in the central Rocky Mountains, USA

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ABSTRACT

Aim Our understanding of how climate and fire have impacted quaking aspen (*Populus tremuloides* Michx.) communities prior to the 20th century is fairly limited. This study analysed the period between 4500 and 2000 cal. yr BP to assess the pre-historic role of climate and fire on an aspen community during an aspen-dominated period.

Location Long Lake, south-eastern Wyoming, central Rocky Mountains, USA.

Methods Sedimentary pollen and charcoal were analysed to reconstruct the vegetation and fire history for a subalpine catchment currently dominated by lodgepole pine. Modern pollen-climate relationships were applied to the fossil pollen spectra to interpret past climate variability. Nonparametric ANOVA and Tukey HSD tests were used to determine whether the reconstructed climate and fire parameters were different throughout the study period.

Results The modern pollen-climate data suggest a *c.* 150-year long drought centred on 4200 cal. yr BP, which caused the aspen ecotone to shift upslope. Between 3950 and 3450 cal. yr BP, an anomalous period of abundant quaking aspen pollen (*Populus*) occurred at the study site. Optimal climatic conditions coupled with frequent fires facilitated local quaking aspen dominance for roughly 500 years. After 3450 cal. yr BP, *Populus* pollen declined coincident with a return to less frequent fires and conifer dominance. Reconstructed climate variables from 550 cal. yr BP to present suggest conditions were not favourable for quaking aspen establishment at Long Lake. The Tukey HSD test confirms that the period of abundant *Populus* pollen was significantly different than any other period during this study.

Main conclusions Quaking aspen shifted upslope in response to warmer temperatures, and persisted for roughly 500 years as a result of optimal climatic conditions and frequent fire events.

Keywords

aspen, climate variability, disturbance, drought, fire history, late Holocene, palaeoecology, pollen, Rocky Mountains, vegetation change

INTRODUCTION

Quaking aspen (*Populus tremuloides* Michx; hereinafter referred to as 'aspen') is the most widely distributed deciduous tree species in North America (Little, 1971; Perala, 1990). Despite its wide distribution, aspen are typically found where annual precipitation exceeds evapotranspiration and mean annual temperatures are relatively cool. Aspen do not function well where conditions are generally warm with low humidity levels (Jones *et al.*, 1985; Dang *et al.*, 1997; Morelli & Carr, 2011). Aspen are largely confined to lower elevations, or on south-facing slopes at higher elevations (Jones *et al.*, 1985).

Numerous studies have detailed the large-scale decline in aspen communities across parts of the western United States (US) (Kashian *et al.*, 2007; Hogg *et al.*, 2008; Worrall *et al.*, 2008, 2010, 2013; Rehfeldt *et al.*, 2009; Hanna & Kulakowski, 2012; Anderegg *et al.*, 2013a,b). However, aspen in

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other locations have thrived and expanded in western North America throughout the 20th century as a result of increased disturbances, mainly fire activity (Kulakowski *et al.*, 2004). Mueggler (1989) has shown that fire is critical for aspen regeneration and persistence in certain aspen ecosystems in western North America. Generally, aspen communities are thought to be either stable or seral, each being supported by distinct fire regimes (Jones & DeByle, 1985; Mueggler, 1989; Shinneman *et al.*, 2013). Within stable aspen ecosystems, lightning caused fires are uncommon (Jones & DeByle, 1985; Shinneman *et al.*, 2013) and the spread of fire is limited due to high moisture content within aspen stands (Smith *et al.*, 1993). However, within seral aspen ecosystems, conifers play an important role in fire susceptibility by increasing the amount of biomass in a stand and providing fuel ladders, which leads to increased fire-severity and stand-replacing crown fires (Brown & Debyle, 1987). However, both seral and stable aspen communities can burn when climatic conditions are favourable, and, in particular when aspen communities include conifers (Shinneman *et al.*, 2013).

Shinneman *et al.* (2013) reviewed primarily tree-ring-based studies to understand the relationship between aspen communities and historic fire regimes. Of 46 studies analysed, 12 reconstructed the mean fire return interval (FRI), and only one estimated fire rotation (> 140 years) near an aspen stand using stand-origin dates (Romme *et al.*, 2001). Despite their review, the natural range of variability of burning in aspen prior to the 20th century remains poorly understood, likely due to the fact that aspen stems are easily killed by surface fires and thus rarely form fire scars that could be used to reconstruct an accurate fire history from contemporary populations (Jones & DeByle, 1985; Brown & Debyle, 1987; Shinneman *et al.*, 2013).

Because aspen fire history reconstructions are limited to the age of extant wood when using dendrochronological methods, other sources of ecological and historical evidence are needed in order to understand the full range of natural variability of aspen dynamics (Rogers *et al.*, 2013). A palaeoecological approach that examines charcoal and pollen preserved in lake sediments is one methodology that provides a means to better understand the full range of natural variability of climate and fire in sustaining aspen populations. While aspen pollen (herein referred to as '*Populus*') is normally poorly preserved in sedimentary records, the record presented in this study contains an unusual amount of *Populus* pollen indicating an extremely high abundance of aspen on the landscape. This unique record allowed us to examine the possible climate–fire relationships on aspen abundance prior-to, during and after a period of anomalously high *Populus* pollen referred to as the *Populus* period. The *Populus* period is a unique vegetation transition period between 3950 and 3450 cal. yr BP when a lodgepole pine-dominated system transitioned to an aspen-mixed conifer forest in the Medicine Bow Mountains of south-eastern Wyoming (Carter *et al.*, 2013). The objectives of this study were to determine how aspen were influenced by climate variability, specifically warmer temperatures, and by fire.

MATERIALS AND METHODS

Study site

Long Lake (41° 30.099′ N, 106° 22.087′ W, 2700 m a.s.l.) is a small lake (*c.* 12 ha) with a 22 ha catchment (Dennison *et al.*, 2010) located in the Medicine Bow range of south-eastern Wyoming (Fig. 1). The modern forest surrounding Long Lake is dominated by lodgepole pine (*Pinus contorta*), with Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). The present-day aspen ecotone is *c.* 200 m a.s.l. downslope from Long Lake (Fig. 1).

Core recovery and chronology

A 4.85 m long core (LL07D) and 56 cm short core (LL07C) were collected in September 2007 (see Carter *et al.*, 2013). Sediments were transported back to the Records of Environment and Disturbance (RED) Lab at the University of Utah and refrigerated at 2°C.

Age-depth relationships were updated from Carter *et al.* (2013) with an additional ^{14}C accelerator mass spectrometry (AMS) date at depth 129 cm that now temporarily constrains the *Populus* period, and a caesium (Cs) peak date that provides modern temporal constraint (Table 1). The original ^{14}C AMS dates were converted to calibrated years using Calib 5.0.2. The newest ^{14}C AMS date was calibrated using Calib 7.0.1 (Reimer *et al.*, 2009). New age-depth relationships were determined using the classical age-depth model (Clam) with a smoothing spline and a smoothing parameter of 0.3 (Blaauw, 2010) (Fig. 2).

Pollen analysis

Pollen analysis was conducted to provide a high-resolution vegetation reconstruction. Long Lake serves as an excellent depositional environment with anoxic conditions that provided excellent pollen preservation, which is demonstrated by the overall high levels of preservation (calculated by the ratio of identified pollen to the tracer, *Lycopodium*) and the sheer abundance of *Populus tremuloides* pollen counted in this study. Individual 1-cm^{-3} pollen samples were processed contiguously between depths 1 through 36 cm (represents the modern period), and 94 through 176 cm (represents the period between 4500 and 2000 cal. yr BP) following standard acid-base methods (Faegri *et al.*, 1989). A known number of *Lycopodium* spores were added to each sample as an exotic tracer in order to quantify total pollen concentration values. A minimum of 300 pollen grains or *Lycopodium* tracers were counted per sample using light microscopy at 500X magnification. Pollen records are described in terms of influx and ratios. Pollen influx (particles cm^{-2} yr) provides information about individual pollen taxon abundance, while pollen ratios

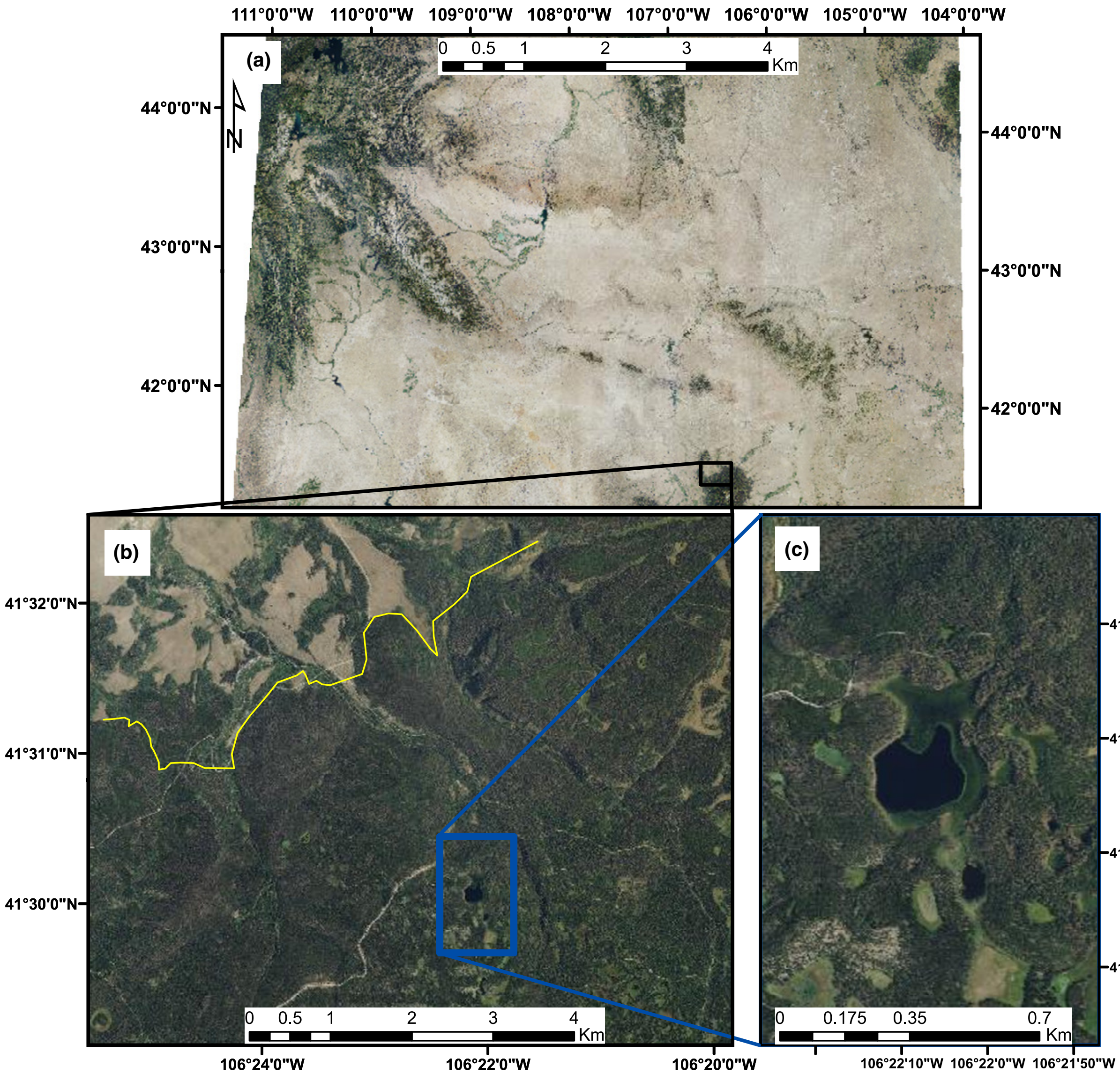

Figure 1 (a) Location of the study area located in the Medicine Bow Mountains of south-eastern Wyoming. (b) Image of the study site, Long Lake in relation to the modern aspen ecotone (yellow line), which is roughly 4 km and 200 m downslope from Long Lake. (c) Image of Long Lake, Wyoming. All images were made using 2012 NAIP imagery with a Universal Transverse Mercator Zone 13 map projection.

allow for comparison between two types of pollen taxon or a group of pollen taxa. In this study, genus names (i.e. *Populus*) are used when referring to pollen influx and/or ratios, while common names (i.e. aspen) are used when discussing environments. Two groups of ratios were compared in this study and were calculated using the formula $(a-b)/(a+b)$ (Maher, 1963, 1972); 1) a = total *Pinus* pollen, b = *Populus* pollen; and 2) a = the sum of all arboreal pollen (AP), b = the sum of all non-arboreal pollen (NAP) (see Table 2). The total *Pinus* pollen represents the sum of *Pinus* undifferentiated, *P.* subgenus *Pinus* and *P.* subgenus *Strobus* based on the modern phytogeography of the conifer species present in the Medicine Bow Mountains. Ratio data are presented in standard units where higher (lower) values indicate greater (lesser) abundance of *Pinus* pollen relative to *Populus* pollen, and AP pollen relative to NAP pollen.

Pollen zone boundaries were determined using Coniss (Grimm, 1987). Carter *et al.* (2013) identified three pollen zones prior-to, during and after the *Populus* period (LL: 9000–4000 cal. yr BP; LL:IV 4000–3100 cal. yr BP; and LL:V 3100–present (2007 CE) cal. yr BP). However, in this study we have added subzones to zones LL:IV and LL:V (LL:IVa, LL:4b–5a and LL:5b) in order to keep descriptions consistent with previous descriptions (Carter *et al.*, 2013), but also reflect the new age-depth model discussed in the 'Core Recovery' section (see Table 1). Subsequent analytical methods discussed below will also be presented based on the new subzones.

Table 1 Summary of age-depth relations for Long Lake, Wyoming used by Carter *et al.* (2013). Dates with a '*' symbol indicate new dates that were used to refine the age-depth model used in this study, particularly the ^{14}C date at depth 129 cm, which was used to constrain the upper age of the *Populus* period. The *Populus* period is characterized as a unique vegetation transition period when a lodgepole pine-dominated forest transitioned to a mixed conifer-quaking aspen forest between 3950 and 3450 cal. yr BP.

Depth (cm)	UGAM #	Source material	Age (^{14}C yr BP)	Age (cal yr BP) with 2 sigma range
1		Date collected		−57
13*		Cesium peak		−10
29	3249	*Pinus contorta* needle	50 ± 35	31–139
49	3710	*Abies lasiocarpa* needle	845 ± 30	688–796
88	2772	*Pinus contorta* needle	1730 ± 35	1549–1714
129*	17695	Pollen	3380 ± 25	3560–3649
156	3032	*Pinus contorta* needle	3510 ± 30	3698–3864
232	2774	*Pinus contorta* needle	6460 ± 45	7275–7435
249	3031	*Abies lasiocarpa* needle	8110 ± 50	8976–9152
323.5	2775	*Pinus flexilis* needle	9630 ± 50	10,774–11,180
449	3478	*Abies lasiocarpa* needle	10400 ± 50	11,975–12,386

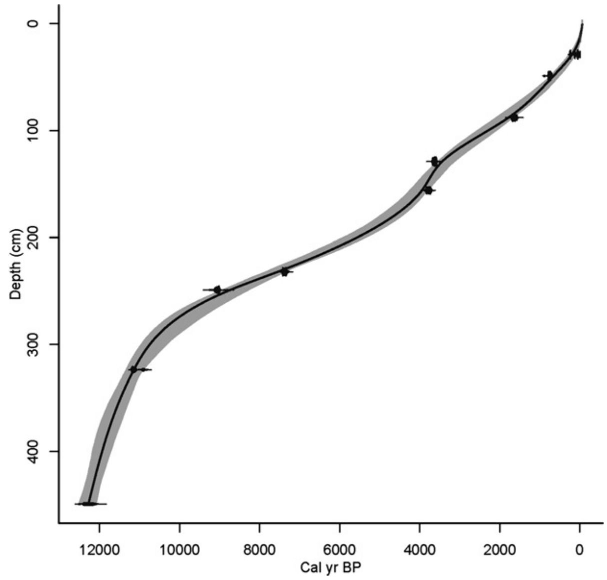

Figure 2 New age-depth model updated from Carter *et al.* (2013) from Long Lake, Wyoming. The age-depth model was constructed using the classical age-depth model (CLAM) with a smoothing spline and a smoothing parameter of 0.3.

Charcoal analysis

Macroscopic charcoal was used to reconstruct the fire history. Individual 5-cm^{-3} charcoal samples were analysed contiguously between depths 1 through 36 cm, and 94 through 176 cm following standard methods (Long *et al.*, 1998). Sediments were screened through 125 µm and 250 µm sieves as fraction sizes > 250 µm do not travel far from their source and represent local fire activity within the catchment (Clark, 1988; Gardner & Whitlock, 2001). Total charcoal counts were converted into charcoal concentrations (particles cm^{-3}) and then transformed to charcoal influx (CHAR; particles cm^{-2} yr). Charcoal samples were interpolated using the median sample resolution (25 years) using the CharAnalysis program (Higuera *et al.*, 2009; Huerta *et al.*, 2009). The CHAR time series was decomposed into two components; a slow moving background component which represents the continual input of charcoal from varying local and extra-local fire activity, and a peaks component, which represents instantaneous charcoal input into the lake from a local fire event. The background component was determined using a 500-year Lowess smoother robust to outliers. The peaks component was determined using residuals, and the 99th percentile of a locally fit Gaussian mixture model to identify peaks. A minimum count test using a $P < 0.05$ was used to determine whether peaks were statistically different from non-peak charcoal counts (Higuera *et al.*, 2010). Additionally, the peaks component used a signal-to-noise value > 3 (Kelly *et al.*, 2011). Fire return interval (FRI), or the number of years between each fire episode, was smoothed using a 1000-year moving window. Fire peak magnitude (particles cm^{-2} episode) represents the amount of charcoal produced above the background charcoal level for each fire episode.

Climate reconstruction

The modern pollen analogue approach (Overpeck *et al.*, 1985) was used to apply modern pollen-climate relationships to the fossil pollen spectra as a means to interpret past climatic conditions (Minckley, 2003; Whitmore *et al.*, 2005; Williams *et al.*, 2006; Minckley *et al.*, 2008; Williams & Shuman, 2008). Two temperature variables, mean temperature of the warmest month (MTWA) and mean temperature of the coldest month (MTCO), and two moisture variables, the ratio of actual evapotranspiration to potential evapotranspiration (AE/PE) and annual precipitation (AnnP) were selected for the climate reconstruction. We also used two bioclimate variables, growing season precipitation (GSP), which is the sum of the reconstructed precipitation from April through September, and the annual dryness index (ADI), using the ratio of growing degree-days (5° base) to annual precipitation, which Worrall *et al.* (2013) and Rehfeldt *et al.* (2009) suggest are

Table 2 List of arboreal pollen (AP), which are tree species, and non-arboreal pollen (NAP), which are herbs and shrubs used in the AP:NAP ratio. The AP:NAP ratio was calculated using the equation $(a-b)/(a+b)$, where a represents the sum of all AP, and b represents the sum of all NAP, and was used to infer changes in canopy density through time.

Arboreal pollen	Non-arboreal pollen			
Total *Pinus*	Amaranthaceae	*Cercocarpus*	Loranathaceae	Rosaceae
Abies	*Ambrosia*	*Chickory*	Malvaceae	Rubiaceae
Picea	*Amelanchier*	*Ephedra*	Onagraceae	*Salix*
Pseudotsuga	*Artemisa*	*Eriogonum*	Poaceae	*Sarcobatus*
Acer	Apiaceae	Fabaceae	Polymoniaceae	Schrophulaceae
Populus	Asteraceae	Fagaceae	Polygonaceae	*Shepherdia*
Betula	Brassicaceae	*Juniperus*	Ranunculaceae	*Thalictrum*
Celtis	Caryophyllaceae	Lamiaceae	Rhamnaceae	
	Ceanothus	Liliaceae	*Ribes*	

Table 3 Results from the Tukey HSD test, which was used to identify which pairs of zones exhibited significant differences based on climate variables, fire history variables and aspen (*Populus*) pollen influx data. The six climate variables used in this study include, mean temperatures of the warmest month (MTWA), mean temperature of the coldest month (MTCO), annual precipitation (AnnP), growing season precipitation (GSP), the ratio of actual evapotranspiration to potential evapotranspiration (AE/PE), and annual dryness index (ADI). Two fire history variables included in this statistical analysis included charcoal accumulation (CHAR) and fire return interval (FRI). Zones analysed in this study include LL:III 4500–3950 cal. yr BP; LL:IVa 3950–3450 cal. yr BP; LL:4b–5a 3450–2000 cal. yr BP; and LL:5b 550 cal. yr BP to present.

Zones compared	Peaks	FRI	CHAR	AnnP	GSP	ADI	AE/PE	MTCO	MTWA	*Populus*
LL:III & LL:IVa	0.659	< 0.001	< 0.001	0.106	0.508	0.088	< 0.001	0.195	0.453	< 0.001
LL:Iva & LL:Ivb	0.627	< 0.001	< 0.001	0.007	0.381	0.011	0.007	0.183	0.067	< 0.001
LL:IVb & LL:Va	0.609	< 0.001	0.602	0.999	0.080	0.773	0.434	0.052	0.602	0.002

important bioclimate predictors for the presence or absence of aspen. *Populus* pollen abundance was not used in the association between modern and fossil pollen assemblages because it currently is not a part of the modern pollen data set. Climate reconstructions were based on the weighted average modern climate values from the seven closest pollen analogues for each fossil spectra (see Minckley *et al.*, 2008; Williams & Shuman, 2008). Climate analogues were calculated using squared cord distances, and results were presented as anomalies from present-day reconstructed climate. Standard deviation of the means for all reconstructed climate variables was calculated using the weighted averages, and error was reported for the first standard deviation.

Statistical analysis

The Kruskal–Wallis rank sum test was used to assess differences between subzones based on the six climate variables (MTCO, MTWA, AnnP, AE/PE, GSP and ADI), two fire history variables (CHAR and FRI), and *Populus* pollen influx. The Kruskal–Wallis rank sum test was chosen for this analysis because the residuals were not normally distributed. Tukey's Honest Significance Difference (HSD) test was used to identify which pairs of subzones exhibited significant differences (Table 3).

RESULTS

Zone LL:III Pre-Populus period (4500 & 3950 cal. yr BP)

The high abundance of *Pinus* pollen (mean = 5658 grains cm^{-2} yr) and non-arboreal pollen (NAP) (mean = 3346 grains cm^{-2} yr) indicated a lodgepole pine forest with abundant understorey vegetation (Fig. 3b). Low *Populus* pollen (mean = 55 grains cm^{-2} yr) indicated the aspen ecotone was not proximal to the lake. Fire activity was low (n = 2) during this zone. CHAR averaged 1.5 particles cm^{-2} yr, and peak magnitude averaged 148 particles cm^{-2} episode (Fig. 4b). Reconstructed temperature variables indicated modern-like temperatures (MTWA mean = 15°C ± 1.6; MTCO mean = −9°C ± 1.2), and relatively high precipitation (AE/PE mean = 0.47 ± 0.3; AnnP mean = 442 ± 57 mm; GSP mean = 347 ± 31 mm) (Fig. 5).

However, between 4300 and 4100 cal. yr BP, *Picea* pollen (mean = 152 grains cm^{-2} yr), *Populus* pollen (mean = 63 grains cm^{-2} yr) and NAP pollen (mean = 3861 grains cm^{-2} yr) all increased coincident with a decrease in AE/PE (mean = 0.43 ± 0.3), AnnP (mean = 394 ± 58 mm), GSP (mean = 330 ± 42 mm) and an increase in MTWA (mean = 16°C ± 1.8) and MTCO (mean = −8°C ± 1.1), which indicated a drought. High ADI (mean = 0.45 ± 0.17) further indicated warmer and drier conditions during this time.

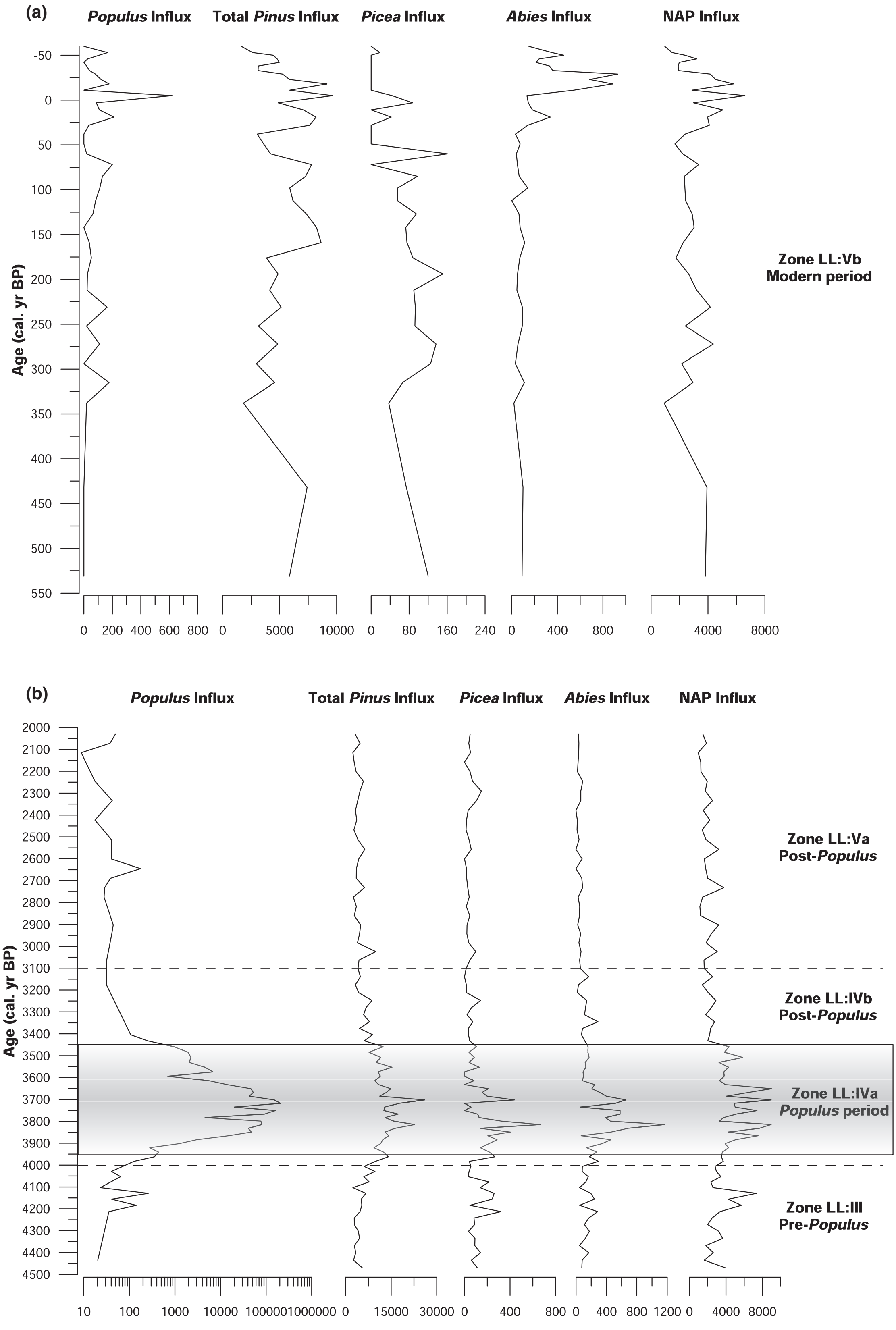

Figure 3 Pollen influx (particles cm^{-2} yr) diagram for Long Lake, Wyoming. Note the change in scale in *Populus* pollen influx between (a) the modern period, and (b) the *Populus* period, which is plotted on a logarithmic scale. The dashed lines represent the original zone boundaries that once defined the *Populus* period (Carter *et al.*, 2013). The shaded gray scale box indicates the new *Populus* period ages used in this study.

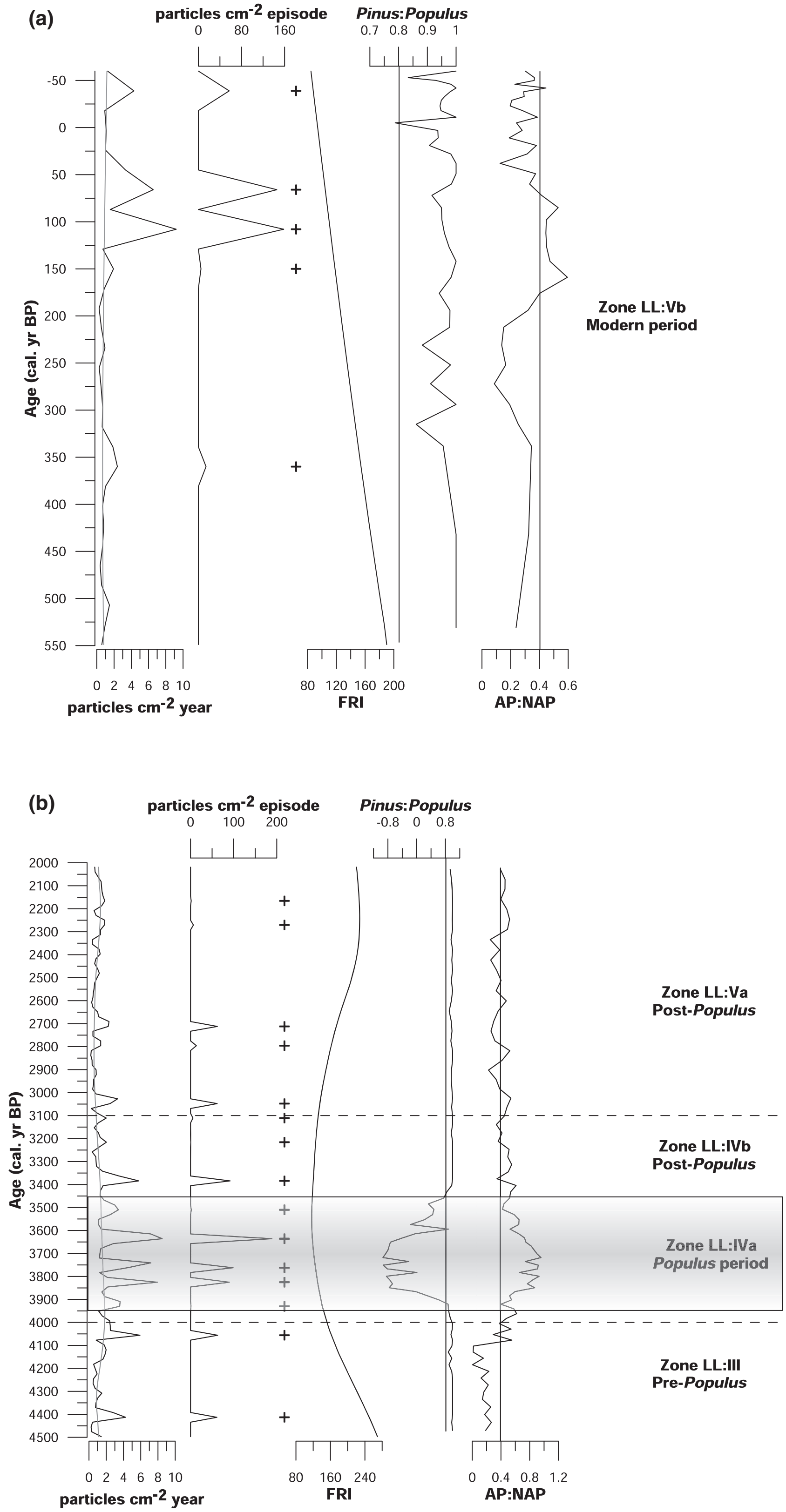

Figure 4 Fire history and pollen ratio diagram for Long Lake, Wyoming during (a) the modern period, and (b) the *Populus* period. From left to right; CHAR (particles cm^{-2} yr) (black), indicating instantaneous charcoal input into the lake from a local fire event when it exceeds the background (gray), which represents the continual input of charcoal from varying local and extra-local fire activity; Peak magnitude (particles cm^{-2} episode) represents the number of charcoal particles associated with each fire peak, which is represented by the '+' symbol; *Pinus*:*Populus* and AP:NAP ratios were used to compare the dominant canopy species, as well as compare the canopy to understorey. The dashed lines represent the original zone boundaries that once defined the *Populus* period (Carter *et al.*, 2013). The shaded gray scale box indicates the new *Populus* period ages used in this study.

Zone LL:IVa the populus period (3950 & 3450 cal. yr BP)

Based on the best fit CLAM age model, the *Populus* period occurred between 3950 and 3450 cal. yr BP, but minimum and maximum ages ranged between 4141 and 2900 cal. yr BP. The abrupt yet significant increase in *Populus* pollen (mean = 40,101 grains cm^{-2} yr) distinguished this zone (Fig. 3b), which was significantly different than the pre-

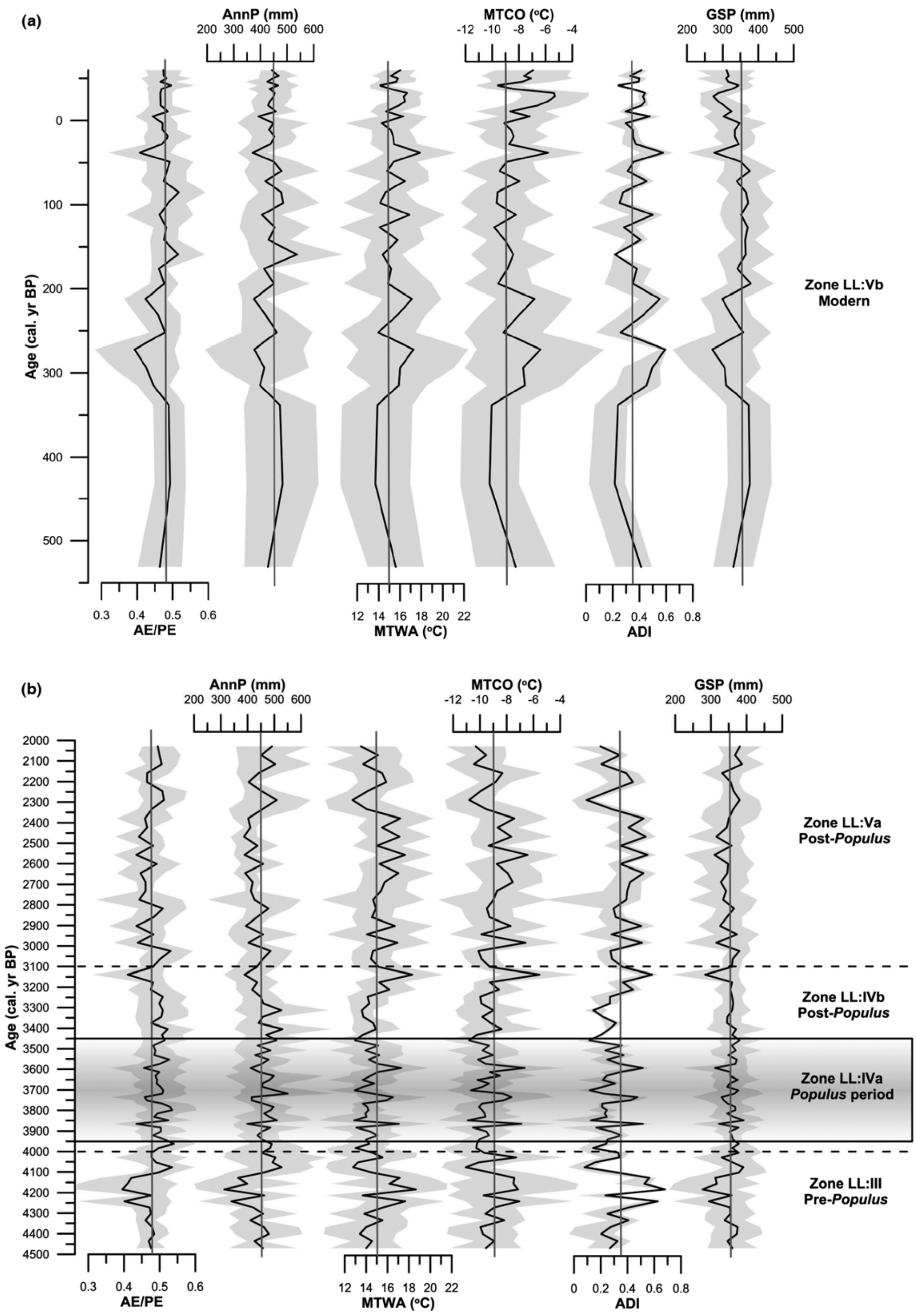

Figure 5 Reconstructed climate variables using modern pollen-climate relations from Long Lake, Wyoming for (a) the modern period, and (b) the *Populus* period. From left to right; AE/PE is the ratio of actual evapotranspiration to potential evapotranspiration; AnnP is reconstructed annual precipitation; MTWA and MTCO are the mean temperature of the warmest and coldest months; ADI is reconstructed annual dryness index (Rehfeldt *et al.* (2009); GSP is growing season precipitation (Worrall *et al.*, 2013). The dashed lines represent the original zone boundaries that once defined the *Populus* period (Carter *et al.*, 2013). The shaded gray scale box indicates the new *Populus* period ages used in this study.

Populus period zone ($P < 0.001$) (Table 1). Total *Pinus* pollen (mean = 13,571 grains cm^{-2} yr), *Abies* pollen (mean = 333 grains cm^{-2} yr), *Picea* pollen (mean = 162 grains cm^{-2} yr) and NAP pollen (mean = 5171 grains cm^{-2} yr) all increased during this zone, likely a result of increased precipitation (AE/PE mean = 0.50 ± 0.2; AnnP mean = 468 ± 35 mm; and GSP mean = 358 ± 19 mm). The reconstructed ADI values (mean = 0.28 ± 0.11) also suggested wetter-than-previous conditions (Fig. 5b). Fire activity increased during the *Populus* period ($n = 5$) with a mean FRI of 109 years, which was significantly different than the pre-*Populus* period ($P < 0.001$). CHAR (mean = 3.0 grains cm^{-2} yr) and peak magnitudes (mean = 225 particles cm^{-2} episode; range = 31 & 549 particles cm^{-2} episode) both increased during this zone (Fig. 4b). Temperatures were similar to that experienced prior to the drought between 4300 and 4100 cal. yr BP, with a mean MTWA of 15°C ± 1.2 and a mean MTCO of −9°C ± 1.1 respectively.

Zone LL:IVb & LL:Va Post-Populus period (2000 & 3450 cal. yr BP)

The significant decline in *Populus* pollen (mean = 30 grains cm^{-2} yr) defined the end of aspen dominance and the beginning of this zone. Total *Pinus* pollen (mean = 4767 grains cm^{-2} yr), *Abies* pollen (mean = 63 grains cm^{-2} yr), *Picea* pollen (mean = 43 grains cm^{-2} yr) and NAP pollen (mean = 2005 grains cm^{-2} yr) also gradually decreased (Fig. 3b). Fire activity was abundant ($n = 8$), and the FRI lengthened to 166 years. However, two fire episodes (2271 and 2166 cal. yr BP) failed to meet the > 3 signal-to-noise value, which justifies peak analysis. CHAR (mean = 1.2 particles cm^{-2} yr) and peak magnitudes (mean = 80 particles cm^{-2} episode; range = 1.0 and 183 particles cm^{-2} episode) both decreased during this zone (Fig. 4b). Temperatures during the post-*Populus* period remained similar to the *Populus* period, while precipitation decreased slightly (AE/PE mean = 0.48 ± 0.3; AnnP mean = 443 ± 39 mm; GSP mean = 351 ± 22 mm). Reconstructed ADI values increased (mean = 0.35 ± 0.12), suggesting slightly drier-than-previous conditions (Fig. 5b).

Zone LL:Vb The Modern period (550 cal. yr BP & present)

The high abundance of total *Pinus* pollen (mean = 5376 grains cm^{-2} yr) and NAP pollen (mean = 3006 grains cm^{-2} yr) suggested a landscape dominated by lodgepole pine with abundant understorey vegetation. Low *Populus* pollen (mean = 81 grains cm^{-2} yr) suggested that the aspen ecotone was located downslope from Long Lake (Fig. 3a). Fire activity was abundant ($n = 6$) and frequent (FRI = 110 years). CHAR (mean = 1.6 particles cm^{-2} yr) and peak magnitude (mean = 112 particles cm^{-2} episode; range = 1.10 to 260 particles cm^{-2} episode) declined from the previous zone (Fig. 4a). Climate was similar to temperature and precipitation conditions reconstructed for the pre-*Populus* and post-*Populus* periods (Fig. 5a).

A brief warm and dry period occurred between 49 and 28 cal. yr BP (1901–1922 CE) (MTWA mean = 16°C ± 1.4; MTCO mean = −7.8°C ± 1.7; AE/PE mean = 0.46 ± 0.5; AnnP mean = 419 ± 43 mm) (Fig. 5a), In addition, ADI (mean = 0.44 ± 0.12) increased from the previous zone, which further suggested drier conditions.

DISCUSSION

The modern distribution of aspen is dependent upon climate and other environmental conditions, such as aspect and slope (Morelli & Carr, 2011). Disturbances such as wildfire have also been shown to exert strong control on aspen regeneration (Kulakowski *et al.*, 2004). However, the long-term natural range of variability of aspen–climate–fire relationships and the distribution of palaeo-aspen is not well understood. Typically, because *Populus* pollen is poorly preserved, there have been few studies that have been able to offer insights of pre-20th century conditions that are necessary to fill in the knowledge gap regarding aspen–climate–fire relationships. The results of this study suggest that warmer temperatures influenced the upslope shift of aspen communities, while a frequent fire regime helped maintain aspen prevalence. These results enhance our understanding about aspen–climate–fire relationships, and provide valuable information that can help land managers anticipate future changes in aspen distributions (Worrall *et al.*, 2013).

Late Holocene climate variability and fire effects on aspen in the Medicine Bow Mountains

Prior to the *Populus* period, the reconstructed AE/PE, AnnP and MTWA variables are suggestive of decreased effective moisture and increased temperatures for *c.* 150 years between 4300 and 4100 cal. yr BP (Fig. 5b). The AP:NAP pollen ratio is indicative of a lodgepole pine-dominated forest at Long Lake. However, an abrupt increase in *Populus* pollen influx around 4200 cal. yr BP suggests that the aspen ecotone was responding to warmer and drier conditions, as aspen do not function well in these conditions. Therefore, the aspen ecotone likely began shifting upslope closer to Long Lake as a result of the drought. Limited moisture likely inhibited fire activity during this warm drought. However, persistent dry conditions on a multi-decadal-to-centennial scale could also potentially limit fuels in subalpine forests (see Calder *et al.*, 2015).

The inferred drought centred on 4200 cal. yr BP not only affected the Long Lake catchment, but also affected Little Windy Hill Pond (elevation 2980 m a.s.l.) 8 km upslope from Long Lake. During this drought, Little Windy Hill Pond experienced a slight increase in *Picea* pollen, which suggests that the subalpine forest may have also migrated upslope in response to the drought (Minckley *et al.*, 2012).

However, because there were no large-scale changes in the vegetation composition at Little Windy Hill Pond, this could also suggest that upper tree line was largely unaffected by the drought. Similar to Long Lake, Minckley *et al.* (2012) attribute the long fire-free period at Little Windy Hill Pond to low effective moisture.

Regional responses to the drought centred on 4200 cal. yr BP include widespread dune reactivation at the Ferris Dune Field roughly 80 km north-west of Long Lake (Stokes & Gaylord, 1993), and lower lake levels at Upper Big Creek Lake in northern Colorado roughly 69 km south-west of Long Lake (Shuman *et al.*, 2015). Warm and dry conditions were also recorded in a $\delta^{13}C$ and $\delta^{18}O$ isotope record from a speleothem from Minnetonka Cave on the Utah/Idaho border roughly 430 km west of Long Lake (Lundeen *et al.*, 2013). Similarly, Booth *et al.* (2005) also present evidence of an abrupt and severe drought from the mid-continent of North America. Enhanced El Niño Southern Oscillation (ENSO) variability and/or more persistent La Niña-like conditions have been hypothesized as possible mechanisms for the drought in the mid-continent of North America *c.* 4200 cal. yr BP (Forman *et al.*, 2001; Menking & Anderson, 2003; Booth *et al.*, 2005; Barron & Anderson, 2011), which potentially explains the widespread drought response recorded throughout the Rocky Mountain region.

However, immediately following the drought around 4100 cal. yr BP, the reconstructed temperature and precipitation variables suggest a change from drought-like conditions to wetter-than-previous conditions (Fig. 5b). Shuman *et al.* (2009) document above average lake levels *c.* 4000 cal. yr BP, which they suggest reflects a snow-dominated precipitation regime. Anderson (2011) documented a change from a rain-dominated precipitation pattern to a more snow-dominated pattern in the Rocky Mountains around 4100 cal. yr BP. The shift in hydroclimate around 4100 cal. yr BP to a more snow-dominated precipitation regime could potentially explain the wetter-than-previous conditions identified at Long Lake. Abrupt changes in climate directly influence vegetation composition, which subsequently influences wildfire activity (Marlon *et al.*, 2009). In this case, the abrupt change from warm and dry conditions to cooler and wetter-than-previous conditions around 4100 cal. yr BP led to an increase in both biomass (i.e. fuel) and fuel connectivity. Subsequently, this led to more fire activity at Long Lake, which is demonstrated by a fire event at 4100 cal. yr BP (Fig. 4b).

At the beginning of the *Populus* period around 3950 cal. yr BP, pollen-based climate reconstructions suggest continued wetter-than-previous conditions with high annual precipitation and average temperatures (Fig. 5b). Increased moisture likely led to an increase in forest productivity, indicated by the increases in *Pinus*, *Abies*, *Picea* and NAP pollen influxes (Fig. 3b). However, it is the dramatic increase in *Populus* pollen influx and the *Pinus*:*Populus* ratio that is truly unique in our record, indicating a switch from a lodgepole pine-dominated forest to a mixed forest abundant with aspen for roughly 500 years (Fig. 3b). Since aspen are typically located where annual precipitation exceeds evapotranspiration and mean annual temperatures are relatively cool, the optimal climatic conditions experienced during the *Populus* period created a suitable environment for aspen establishment at Long Lake. Once established, persistent aspen populations were likely related to both shorter FRIs (*c.* 109 years) and increased fire severity. The increase in conifer forest density likely increased local fire severity by creating fuel ladders (Cumming, 2001), which is demonstrated by several large peak magnitude fire events. Our data are consistent with fire-supported aspen persistence at Long Lake during the *Populus* period. The timing of increased FRI at Long Lake appears to be a regional phenomenon. Higuera *et al.* (2014) documented an increase in the FRI (*c.* 77 years/fire) in Rocky Mountain National Park (roughly 257 km south of Long Lake) during the same time as the *Populus* period. The authors conclude that the increase in FRI was likely a result in the switch from rain-dominated precipitation to snow-dominated precipitation regimes beginning around 4100 cal. yr BP.

Immediately following the end of the *Populus* period around 3450 cal. yr BP, pollen-based climate reconstructions show a return to climatic conditions experienced prior to the drought. As a result, conditions were no longer suitable for aspen at Long Lake. *Populus* pollen influx decreased dramatically, and the *Pinus*:*Populus* ratio indicates an abrupt return to a lodgepole pine-dominated forest. FRI lengthened and fire events became more infrequent than those experienced during the *Populus* period. The lengthening of the FRI is within the natural range of FRIs within lodgepole pine forests, which vary between 50 and 400 years depending on the region of Wyoming (Arno, 1980; Millspaugh *et al.*, 2000; Minckley and Shriver, 2011).

Modern climate variability and fire influences on aspen in the Medicine Bow Mountains

Over the past 550 years, the ecosystem at Long Lake has been dominated by lodgepole pine, with Engelmann spruce and subalpine fir located on more mesic soils. Climatic conditions are currently not conducive for aspen establishment at Long Lake. According to the data from the USDA Forest Service Forest Inventory and Analysis (FIA) program (Gillespie, 1999), the average elevation of aspen is roughly 200 m lower in elevation than Long Lake. However, aspen does exist in small stands close to Long Lake and at higher elevations on south-facing slopes (Fig. 6). This is significant because it demonstrates that aspen can exist at higher elevations in the Medicine Bow Mountains, but that its occurrence is likely dependent on warmer temperatures characteristic of south-facing slopes.

Significance of the *Populus* period

The rapid rise to dominance, long persistence and rapid decline of an aspen community in the Long Lake core is unusual and provides an opportunity to examine prolonged aspen stand dynamics. Local dominance of aspen normally occurs

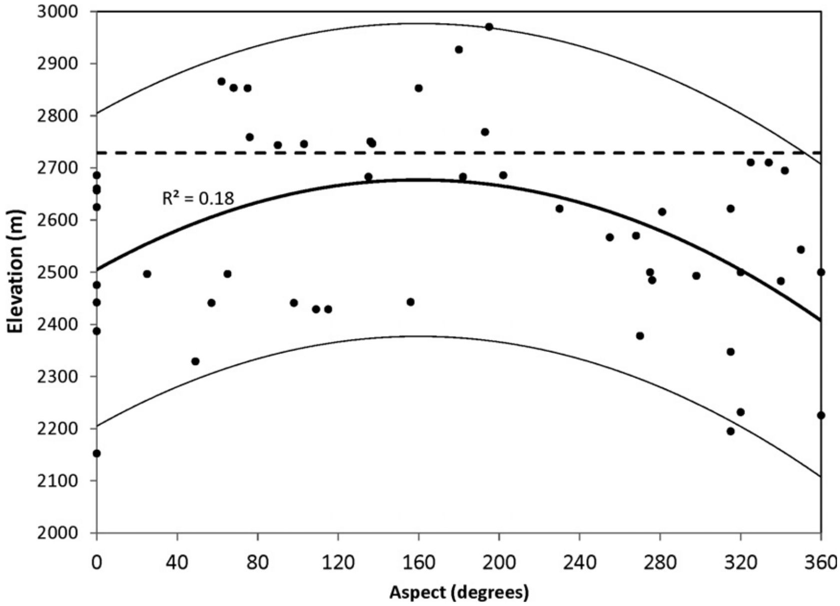

Figure 6 Diagram showing the relationship between quaking aspen, aspect, and elevation (m) on the north slope of the Medicine Bow Range, south-eastern Wyoming. The black dots represent the elevation of all USDA Forest Service Forest Inventory and Analysis (FIA) plots in the vicinity of Long Lake with aspen present. The horizontal dashed line indicates the elevation of the study site. The dark, solid line is a polynomial fit of the aspect-elevation relationship: Elevation (m) = 2505.0 + 2.15•Aspect −0.00674•Aspect^2; $n = 53$; $F = 5.37$; $P < 0.01$. The upper and lower arched lines represent ± 300 m from the fitted curve. The figure shows that the modern upper limit of aspen on north-facing slopes in the Medicine Bow Mountains is similar to the elevation at Long Lake. However, aspen does exist in small stands close to Long Lake and at higher elevations on south-facing slopes.

under two different general scenarios, depending upon the local climatic conditions. The first and most broad scenario is seral aspen, where aspen communities yield to spruce and fir *c.* 80 to 150 years after the onset of aspen dominance (Mueggler, 1985; Rogers, 2002). This occurs where annual precipitation exceeds evapotranspiration and mean annual temperatures are relatively cool, commonly at higher elevations. Under this scenario, relative pollen abundance between aspen and conifer species would be expected to oscillate on centennial time-scales. The other common scenario is that of the so-called 'stable aspen', which occurs when climatic conditions are too warm and dry to support late-succession conifers, but not too warm and dry for aspen since aspen do not function well in warm and dry conditions. Stable aspen are able to persist in the absence of disturbance or climate change (Morelli & Carr, 2011). In some areas, sites that support stable aspen are even too dry to support the establishment of aspen by seeding. However, in the Medicine Bow Mountains, and the nearby Uinta Mountains in Utah and Wyoming, aspen is presently seral in the upper end of its elevational range and stable in the lower end (Shaw & Long, 2007). In the lower end, aspen also forms the lower tree line either transitioning to sagebrush or occurring as islands that are topo-edaphically controlled. The modern upper limit of aspen on north-facing slopes in the Medicine Bow Mountains is similar to the elevation at Long Lake (Fig. 6, dashed line), indicating that aspen is primarily seral in the vicinity of the lake today. Identifying which of these two states was dominant during the *Populus* period is difficult as climatic conditions could have favoured stable aspen criteria, but frequent fire could have resulted in a persistent seral aspen state by resetting long-term succession patterns. However, the rapid increase and persistence of *Populus* pollen is more consistent with stable aspen in the immediate vicinity of Long Lake, and suggests that the aspen ecotone shifted upward at least 200 m at the onset of the *Populus* period, remained in that position for *c.* 500 years, and retracted to approximately the modern elevational range or lower.

It may be that understanding the natural range of variability between seral and stable aspen needs to be addressed independently, as each may respond to climate differently. For example, Anderegg *et al.* (2013a) and Worrall *et al.* (2013) attribute aspen mortality across much of the San Juan National Forest and southern Rocky Mountains to low soil moisture and high growing season temperatures. The mortality documented by Anderegg *et al.* (2013a) most likely took place in stable aspen stands located at lower tree line, and Worrall *et al.* (2013) state that mortality took place at low elevations. Because stable aspen is typically found at lower tree line, it is expected that recent mortality would be highest among aspen populations there. However, it is not understood whether the recent mortality among aspen in the western US. is within the natural range of variability, or whether the recent mortality is unprecedented.

CONCLUSIONS

The aim of this study was to understand the conditions that allowed for a period of aspen dominance in the Medicine

Bow Mountains between 3950 and 3450 cal. yr BP. This palaeoecological reconstruction offers invaluable insight regarding the natural range of variability of aspen ecosystems and a foundation for understanding modern declines and expansions of aspen stands. Kulakowski *et al.* (2013) suggest that understanding long-term aspen dynamics at finer spatial scales is necessary in order to understand how climate variability contributes to aspen mortality. While our study interpreted data from one catchment on the north end of the Medicine Bow Mountains, our study does offer the first high-resolution palaeo-aspen reconstruction for the area. The results from our study suggest that warming temperatures played an important role in the upslope shift of aspen, while frequent fire activity maintained aspen dominance.

Future climate–fire patterns of more frequent and severe fires are likely to favour the expansion of aspen to higher elevations because drought and warmer temperatures may inhibit aspen regeneration at lower elevations (Romme *et al.*, 2001; Elliott & Baker, 2004; Hanna & Kulakowski, 2012). Landhäusser *et al.* (2010) have already documented the expansion of aspen to higher elevations in Alberta, Canada because of disturbance and management practices, and suggest that these sites may become aspen-dominated if warming conditions persist with frequent disturbances. Because the *Populus* period is characterized by a frequent FRI with severe fires, these conditions may have aided in the persistence of stable aspen populations. While a few studies have documented the increase of aspen following fire (Kulakowski *et al.*, 2004), this differs from Morris *et al.* (2012) who document an increase in *Populus* pollen in the absence of fire activity in southern Utah. Therefore, additional palaeoecological reconstructions specifically conducted near the aspen ecotone are needed in order to futher improve our understanding of the natural range of variability of climate-fire-aspen relationships. This information can be used to inform management practices focused on either facilitating and/or inhibiting aspen migration in the face of climate change.

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BIOSKETCH

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