Slope Aspect Mediates Fine-Scale Tree Establishment Patterns at Upper Treeline during Wet and Dry Periods of the 20th Century

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Slope aspect mediates fine-scale tree establishment patterns at upper treeline during wet and dry periods of the 20th century

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Abstract

Previous research collectively demonstrates the importance of taking local moisture availability and biotic threshold responses into account when seeking to reveal the ecological manifestations of climate change within upper treeline ecotones. Yet dendroecological studies that explicitly address the role of slope aspect in this context are non-existent. In this paper, we examine whether slope aspect and related temperature-precipitation interactions mediate abrupt increases in tree establishment and pulses of upper treeline advance (≥ 10 m) on contrasting north- and south-facing slopes during wet and dry periods of the 20th century. We used regime-shift analysis to quantify episodic changes in the rate of tree regeneration at each site ($p < 0.05$). We employed a climatic water deficit approach to define fine-scale moisture conditions to compare with dendroecological data from opposite aspects on eleven mountain peaks along a latitudinal gradient in the U.S. Rocky Mountains. Regime-shift analysis measured abrupt, yet asynchronous increases in tree establishment across contrasting slope aspects on 10 of 11 mountain peaks. Upper treeline advance was significantly greater ($p < 0.05$) during drought on north-facing slopes. On south-facing slopes, ecotonal dynamics varied more with respect to fluxes in the climatic water deficit; namely because of differences in local hydroclimate regimes. Collectively, these results underscore the importance of considering both slope aspect and temperature-moisture interactions when elucidating climate-vegetation interactions within upper treeline ecotones.

Introduction

Ongoing trends and future climate change scenarios for high-elevation regions of western North America foretell the predominance of warm and dry conditions as diminished snowpack retention accompanies rising temperatures and increased evaporative demand (Barnett et al., 2008; Clow, 2010; Cowell and Urban, 2010; Pederson et al., 2011). Corresponding drought-level water deficits are expected to impact an increasing proportion of ecosystem processes through the triggering of abrupt regime-shift changes (Anderson et al., 2009). A regime shift refers to the tipping point or measurable change stemming from an ecological threshold response to broad-scale climate forcing, internal feedbacks related to more fine-scale interactions, or a combination of the two (Williams et al., 2011). Consequently, elucidating the relative role of regime shifts in driving spatiotemporal changes in ecosystem processes, such as tree regeneration within upper treeline ecotones, is scale dependent (Elliott, 2012a, 2012b). For instance, we know that the combination of drought and warmer temperatures in the early 1950s triggered a region-wide extrinsic regime-shift increase in the rate of tree establishment, leading to varying degrees of treeline advance along a latitudinal gradient in the U.S. Rocky Mountains (Elliott, 2012a). What remains unknown, however, is how fine-scale moisture gradients produced by differences in slope aspect regulate the ecological expression of broad-scale drought conditions across upper treeline ecotones in the Rocky Mountains. Understanding this is essential because the spatial heterogeneity of mountain environments will undoubtedly create complex responses to changes in climate (e.g., Shafer et al., 2005).

Despite the classic designation as a temperature-limited ecotone (see Körner, 2012), the relative influence of temperature on tree regeneration at a specific study site is contingent on spatial scale, with fine-scale, site-specific attributes capable of facilitating, modulating, or possibly overriding the influence of more broad-scale climate inputs (Malanson et al., 2007; Holtmeier, 2009; Kullman and Öberg, 2009; Elliott, 2011; Stueve et al., 2011; Case and Duncan, 2014). Furthermore, accumulating evidence from multiple spatial scales, ranging from an individual site to broad regions, underscores the importance of considering both temperature and precipitation in governing regeneration dynamics at upper treeline (Weisberg and Baker, 1995; Rochefort and Peterson, 1996; Hessl and Baker, 1997; Lloyd and Graumlich, 1997; Daniels and Veblen, 2004; Elliott, 2012a; Moyes et al., 2013). The slope aspect mediation of seedling survival (Weisberg and Baker, 1995; Germino et al., 2002), snowpack accumulation/growing season length (Minnich, 1984; Rochefort and Peterson, 1996), spatial pattern of tree establishment (Elliott and Kipfmueller, 2010), climate-pattern-feedback interactions (Elliott, 2011), and demographic processes required for upper treeline advance (Danby and Hik, 2007; Elliott and Kipfmueller, 2011; Dang et al., 2015) all reinforce the crucial role local-scale moisture regimes play in shaping regeneration dynamics at upper treeline. It is therefore surprising that much of what we currently know about how slope aspect modifies the response of trees at upper treeline to climate variability originates from dendroclimatological studies concerned with annual ring-width formation rather than from dendroecological studies focused on the spatiotemporal patterns of tree regeneration (Tranquillini, 1979; Villalba et al., 1994; Leonelli et al., 2009; Kipfmueller and

Salzer, 2010; Bunn et al., 2011; Salzer et al., 2014). This is an important distinction because climate parameters favorable for annual growth are often uncoupled from successful seedling/tree establishment and related treeline advance (Daniels and Veblen, 2004; Holtmeier and Broll, 2005; Fajardo and McIntire, 2012).

Although these research efforts collectively demonstrate the importance of taking fine-scale moisture availability and biotic threshold responses into account when testing for the ecological manifestations of climate change within upper treeline ecotones, dendroecological studies that explicitly address the role of slope aspect in this context are nonexistent (but see Suarez and Kitzberger, 2010, for montane zone). As a result, the goal of this research is to determine how contrasts in slope aspect and related temperature-precipitation interactions mediate the rate of tree establishment and pulses of treeline advance during both dry and wet periods of the 20th century. To do this, we use a macroecological framework to examine the individual site-level data from the regional-scale synthesis presented in Elliott (2012a). The purpose of this is to determine whether reciprocal temperature-moisture interactions relate to abrupt increases in tree establishment at finer spatial scales and if this varies by slope aspect. Study sites were originally stratified by slope aspect and confined to north- and south-facing slopes.

Ascertaining the influence of temperature-moisture interactions on tree regeneration within upper treeline ecotones is challenging because traditional moisture indices derived from instrumental precipitation data or proxy reconstructions do not necessarily reflect the amount of moisture actually available to plants. Thus, we employ a Thornthwaite-based climatic water deficit approach to define "wet" and "dry" conditions during the 20th century. Calculating the climatic water deficit is particularly suitable in this circumstance because

(1) it takes into account the complex exchanges of energy and water at the surface, which more accurately conveys soil moisture available to plants, and (2) it signifies the quantity of water needed to fulfill evaporative demand and, in doing so, measures absolute drought independent of local site vegetation (Stephenson, 1998).

We hypothesize that slope aspect will have a pronounced influence on site-level climate-vegetation interactions and corresponding regime-shift changes in regeneration dynamics, therefore leading to uneven threshold switches between opposite slope aspects. Given the expected differences in bioclimatic conditions on contrasting slope aspects, we also hypothesize that drought-like conditions will disproportionately favor demographic processes on more mesic, north-facing slopes where moisture is seldom limiting. Taken at large, the purpose of this study is to gain a more refined understanding of how fine-scale regeneration dynamics within these climatically sensitive ecosystems will likely respond to climate variability in general and drought in particular.

Methods

STUDY AREA

Moving from north to south along an ~1000 km latitudinal gradient, our study area encompasses four approximately linear mountain ranges that form the easternmost extent of upper treeline environments in the Rocky Mountains from ~44°–35°N: (1) Bighorn, (2) Medicine Bow, (3) Front Range, and (4) Sangre de Cristo (Fig. 1). This latitudinal gradient bisects a precipitation dipole at approximately 40°N, where opposite moisture conditions
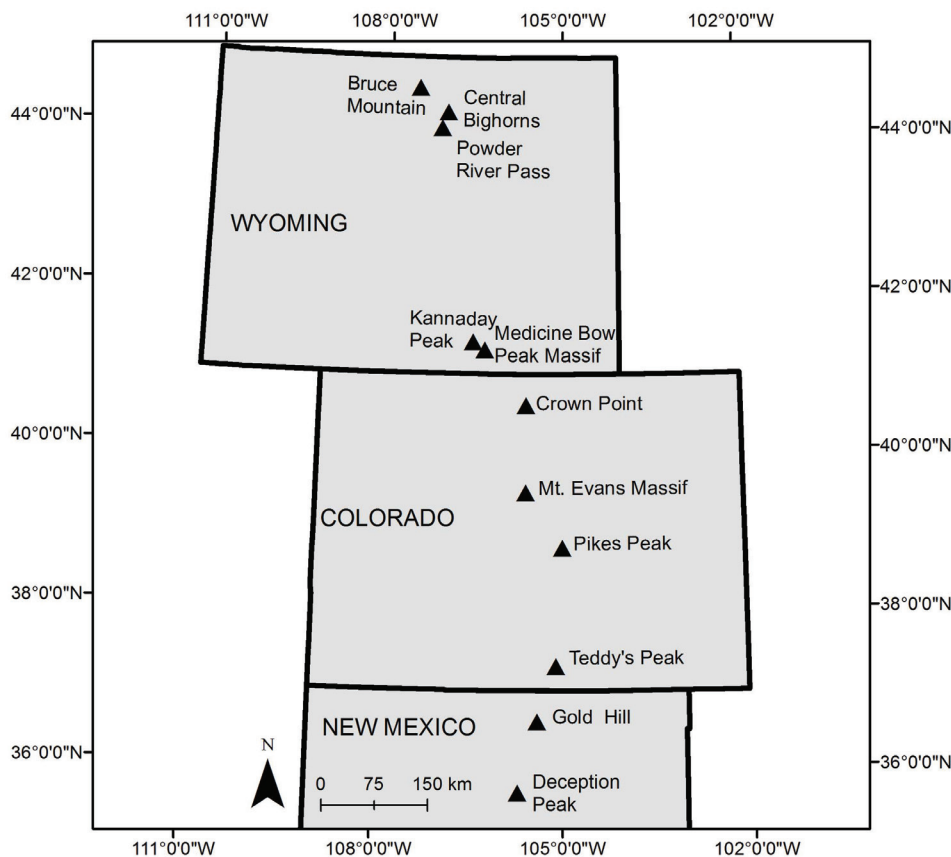

FIGURE 1. Study area map. Triangles denote the mountain peaks where we placed study sites on opposite north- and south-facing slopes. The lone exception to this is in the central Bighorn Mountains, where study sites were on two peaks in close proximity to each other.

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TABLE 1

Study site characteristics.

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(Subregion) Study site	Mountain range	Lat (°N)	Long (°W)	Elev.[a] (m)	AWC (mm)	Annual precipitation[b] (mm)	Cool season[c] (%)	MAT (°C)	Annual PET (mm)	Annual AET (mm)	Annual deficit (mm)
(Central Rocky Mountains)											
Bruce Mountain (BM)	Bighorn	44.6	107.5	3003	75	780.1	52.5	0.15	280	255	25
Central Bighorns (CB)	Bighorn	44.3	107.0	2990	75	748.8	48.4	0.08	270	254	16
Powder River Pass (PR)	Bighorn	44.1	107.1	3005	75	692.2	51.5	–0.26	259	238	21
Kannaday Peak (KP)	Medicine Bow	41.4	106.5	3213	75	938.6	61.6	2.00	339	303	36
Medicine Bow Massif (MB)	Medicine Bow	41.3	106.3	3327	75	1204.0	65.0	–0.61	259	248	11
(Southern Rocky Mountains)											
Crown Point (CP)	Front Range	40.6	105.6	3421	69	757.6	57.3	1.11	294	278	16
Mt. Evans Massif (EM)	Front Range	39.5	105.6	3581	73	596.8	44.2	0.42	276	268	8
Pikes Peak (PP)	Front Range	38.8	105.0	3605	50	737.4	33.7	1.17	289	285	4
Teddy's Peak (TP)	Sangre de Cristo	37.3	105.1	3653	60	797.9	49.5	1.96	306	299	7
Gold Hill (GH)	Sangre de Cristo	36.6	105.4	3662	120	801.6	40.2	1.29	297	295	2
Deception Peak (DP)	Sangre de Cristo	35.7	105.7	3725	117	927.2	38.9	2.01	308	306	2

[a]Elevation refers to mean value of outpost tree (term after Paulsen et al., 2000) on contrasting south- and north-facing slopes.

[b]Climate values derived from 1895–2010 mean values; precipitation and temperature data for water budget summary obtained from PRISM Group, Oregon State University (http://www.prism.oregonstate.edu) .

[c]Cool season (%) refers to proportion of cool season precipitation (November–April) compared to total annual precipitation and is an approximate measure of snow.

Abbreviations: AWC = soil available water capacity, MAT = mean annual temperature, PET = potential evapotranspiration, AET = actual evapotranspiration.

often exist to the north and south of this parallel, especially during El Niño events that normally cause above-average precipitation below 40°N and dry conditions above (Dettinger et al., 1998). This boundary coincides with differences in synoptic climatology as well, with more frequent intrusions of maritime Pacific air masses to the north of 40° in the winter and a stronger summer monsoon influence to the south (Mitchell, 1976). For this reason, we classify mountain ranges north of 40° as the Central Rocky Mountains (Bighorn and Medicine Bow) and ranges to the south as the Southern Rocky Mountains (Front Range and Sangre de Cristo).

The floristic composition of upper treeline ecotones is co-dominated by Engelmann spruce (*Picea engelmannii*) and sub-alpine fir (*Abies lasiocarpa*) along the entire latitudinal gradient. Higher proportions of spruce exist in the south and fir becomes more dominant toward the north, particularly in the Bighorn Mountains. Other tree species include Rocky Mountain bristlecone pine (*Pinus aristata*) on south-facing slopes in the Sangre de Cristo and Front Range mountains and lodgepole pine (*P. contorta*) on more xeric sites in the Bighorn, Medicine Bow, and northern Front Range mountains.

HYDROCLIMATOLOGY

We used the Precipitation-elevation Regressions on Independent Slopes Model (PRISM) climate data website (PRISM Group, Oregon State University, http://www.prismclimate.org, created 1 June 2010) to access monthly climate data (temperature and precipitation) for each mountain peak in the study area. These data were selected to compensate for the dearth of available high-elevation weather stations and because they take into account the dominant role of elevation and topography in dictating climatic conditions throughout mountain environments (Daly et al., 2008). Given our emphasis on ecological changes at upper treeline within the context of the climatic water budget, we focused on the main climate inputs for high-elevation areas of the Rocky Mountains, including mean annual air temperature (MAT) and cool season (November–April) precipitation (Table 1, Fig. 2). Broad geographic patterns of these two climate variables reveal more uniform conditions among mountain peaks in the Bighorn and Sangre de Cristo Mountains, whereas more pronounced variability exists within the Front Range and especially the Medicine Bow Mountains (Fig. 2). Not surprisingly, the same general spatial patterns emerge when assessing how these inputs combine to form the climatic water deficit, with the notable trend of increased aridity along a south-north gradient (excluding Kannaday Peak [KP], Fig. 2).

Cool season precipitation represents a conservative estimate of total snowfall accumulation and makes up a majority of moisture delivered to upper treeline environments in the Central Rocky Mountains (55.8%; Table 1). In contrast, it only accounts for 43.9% of annual precipitation in the Southern Rockies (Table 1), with the lowest percentages in the Sangre de Cristos where monsoon-derived rainfall (July–September) surpasses monthly snow totals accrued during the cool season (Elliott, 2011). This explains why, despite receiving roughly equal amounts of cool season precipitation, mountain peaks in the Bighorns typically experience more severe climatic water deficits during the summer growing season
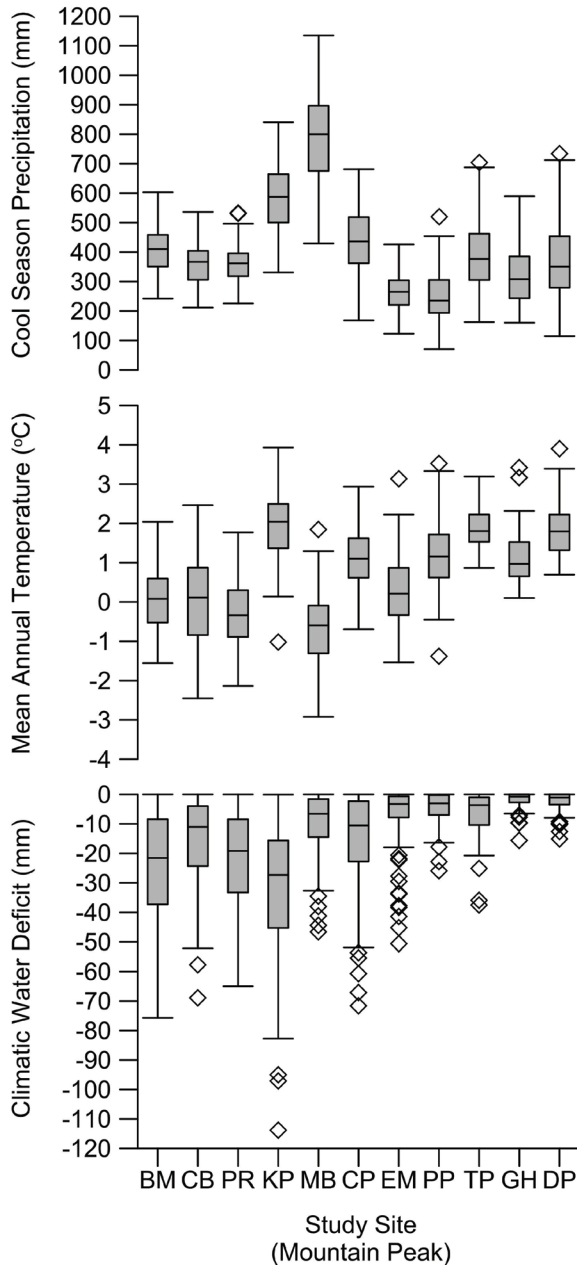
FIGURE 2. Box-and-whisker plots of 20th-century (1900–1999) cool season precipitation (November–April), mean annual temperature, and climatic water deficit for each site arranged along a north-south (left-right) gradient. Diamonds represent values outside the interquartile range (e.g., outliers). All precipitation and temperature data are from PRISM Group, Oregon State University (http://www.prism.oregonstate.edu).

= –0.01 °C; Table 1). Temperature trends during the 20th century indicate widespread warming throughout the study area with minimum temperatures consistently ≥0.5 °C above the century-long mean (1900–1999) from ca. 1940–2007 (e.g., Elliott, 2012a). Maximum temperature, on the other hand, peaked in the mid-1950s and subsequently decreased during the latter half of the 20th century (Elliott, 2012a). From a long-term perspective, recent temperature increases in the Bighorn and Medicine Bow Mountains equal the intense warmth experienced during the early- to mid-Holocene (11,000–6000 years before A.D. 1950) when summer insolation was greater than present (Shuman, 2012).

FIELD METHODS

Field data for this study were collected at the same time and followed the same systematic design described by Elliott (2011), which essentially focused on locating mountain peaks with climatic treeline boundaries (see Holtmeier and Broll, 2005; Butler et al., 2007) on both north- and south-facing slopes (azimuths 135° to 225° and 315° to 45°, respectively). In total, eleven mountain peaks were sampled and at each site (*n* = 22) nested-belt transects were placed through the entire ecotone boundary on contrasting north and south aspects, extending from the outpost tree (term after Paulsen et al., 2000) downslope to below timberline. Here treeline is defined as the variable-length transition zone between the uppermost limit of individual trees with an upright growth form and timberline, the elevational limit of closed-canopy forest. The length of each transect varied depending on the upward position of the outpost tree and transect width was divided into two parts to ensure an adequate number of saplings to calculate age corrections and analyze regeneration patterns. Total transect width above timberline was 40 m, and below timberline, the width was reduced to 20 m to accommodate for the general increases in tree density. For illustrations of this transect design, please refer to Elliott and Kipfmueller (2010). Krummholz were not sampled because of the different microclimatic influences on establishment compared to upright trees (Holtmeier, 2009).

DENDROECOLOGICAL DATA

We collected age-structure data by extracting two increment cores at 30 cm above the ground from all living trees (≥5 cm diameter at breast height [dbh]) along the transect. Every sapling (<5 cm dbh, ≥1.2 cm diameter at ground level [dgl]) within the transect was harvested at ground level. Sections were taken from 10–15 saplings growing in both open and closed-canopy environments to determine a correction factor for age-at-coring height for trees above and below timberline, respectively (cf. Veblen, 1992). Seedlings (<1.2 cm dgl) were inventoried as alive or dead throughout the transect and excluded from the age-structure data.

Tree cores and sapling cross sections were prepared following standard procedures for dendrochronology (Stokes and Smiley, 1996). Pith estimators were used to geometrically determine the number of missed rings when the pith was not obtained during field sampling (Applequist, 1958). Dates of tree establishment were calculated based on tree age at the time of sampling (summer of 2007 or 2008) and by adding the appropriate age to coring-height correction. Age to coring-height corrections were calculated by taking the mean age at 30 cm of harvested saplings and adding it to the age of the cross-dated individual tree cores collected from the same height. Age corrections were further stratified by species, mountain range, and position relative to timberline to account for the differ-

(Fig. 2). Furthermore, vegetation in the Bighorns rely almost exclusively on isolated convective storms during the growing season (e.g., rather than the Southwest Monsoon), which generally fail to replenish evaporative demand.

Geographic patterns of MAT generally correspond to latitudinal position (excluding KP), with the warmest temperatures in the Sangre de Cristo Mountains (mean = 1.8 °C) at the southern end of the transect and lowest on the northern end in the Bighorns (mean

ent growth rates of saplings in open (e.g., above timberline; mean = 19.5 yr) versus more closed-canopy conditions (e.g., below timberline; mean = 32.3 yr). All cross-dating was achieved by using the visual list method proposed by Yamaguchi (1991). Tree establishment dates were grouped into five-year intervals for the period 1900–2000. Further details of age to coring-height calculations can be found in Elliott (2012a).

CLIMATIC WATER DEFICIT

To assess the role of temperature-precipitation interactions via the climatic water deficit on regeneration dynamics at upper treeline during the 20th century, we used a Thornthwaite-based method to model the climatic water budget (Thornthwaite and Mather, 1955; Hamon, 1963; Dingman, 2002). Following Stephenson (1998), climatic water deficit represents the limits placed on evapotranspiration by water availability and thus renders it a suitable proxy for the length and severity of absolute drought conditions. Inputs for this model include latitude, mean monthly temperature and precipitation, and soil water holding capacity. Monthly temperature and precipitation data inputs were obtained from the PRISM website (http://www.prismclimate.org). Soil available water capacity (AWC) data were obtained for sites in the Southern Rocky Mountains through the Natural Resources Conservation Service (NRCS) Web Soil Survey (http://websoilsurvey.nrcs.usda.gov/app/HomePage.htm). Data are incomplete or unavailable for our study sites in the Medicine Bow and Bighorn mountain ranges. Yet, given that water stress is common at upper treeline because of generally thin soils with a low moisture-holding capacity (Sveinbjörnsson, 2000), we compensated for this by assigning an AWC of 75 mm for these sites. This value equals half the saturation level of 150 mm typical of more well-developed soils (cf. Cowell and Urban, 2010). In the case of different AWC values between soils above and below timberline, we used the mean. Precise climatic water deficit calculations for each site rather than each mountain peak were not possible given the spatial resolution of PRSIM data (4 km resolution), which typically meant that both aspects were contained within a single climate grid.

Climatic water deficit data are produced in the form of a continuous monthly time series (e.g., 1900–2000), along with a suite of other climatic water budget variables (e.g., potential evapotranspiration [PET] and actual evapotranspiration [AET]) that are influenced by both current and antecedent soil moisture conditions. PET is a measure of the water that could be lost to the atmosphere, assuming the available heat energy (temperature), and AET is the actual moisture lost to the atmosphere from soil and vegetation (Cowell and Urban, 2010). An advantage of the Thornthwaite-based approach is the limited input requirements in comparison to the robust output, whereas drawbacks stem from the exclusion of local-scale data such as wind, humidity, and land cover (Stephenson, 1998). These data, however, are typically unavailable for high-elevation treeline sites and this method is arguably the most appropriate for examining broad regions (cf. Vörösmarty et al., 1998).

DATA ANALYSIS

Of central importance to this study is classifying temporal variations in the climatic water deficit as wet or dry during the 20th century. To do this, we standardized annual deviations from the 20th-century mean (1900–1999) and averaged these to create z-score pentads in order to match the minimum temporal resolution of the age-structure data. The rationale for this was to create five-year periods of relatively wet (+ anomaly) or dry (– anomaly) soil moisture conditions to examine how given deficit regimes (e.g., wet or dry) align with regime shifts in tree establishment and associated upper treeline advance on contrasting slope aspects.

According to Williams et al. (2011), a "phenomenalogical" regime shift takes place when a variable of a system changes abruptly compared to rates of past change. This relatively broad definition permits the statistical verification of regime-shifts by identifying a change point in time when sudden changes happen to key ecological variables (Anderson et al., 2009; Williams et al., 2011), such as the rate of tree establishment. Thus, for the purposes of this research, we used regime-shift analysis as a tool to quantify statistically significant changes in the rate of tree establishment rather than for arguing about the potential unprecedented nature of population-level controls on tree establishment. This is largely due to the fact that our age-structure data are confined to the 20th century and therefore unable to justify the uniqueness of these changes at the centennial scale. To test for regime-shift changes in the rate of tree establishment, we used a sequential algorithm developed by Rodionov (2004). This is a data-driven method where an a priori hypothesis on the timing of regime shifts is not needed and sequential t-tests are conducted on time series data to detect regime-shift changes (Rodionov, 2004). A regime-shift change is identified when the cumulative sum of normalized deviations from the mean value of a potential new regime is significantly different from the mean of the current regime (Rodionov, 2004). We used a 0.05 significance level to quantify statistically significant deviations in the age-structure data and to guard against spurious regime shifts that may appear in the middle of a time series (Overland et al., 2008), we visually verified that the regime-shift analysis fit the clear visual trends present (Elliott, 2012a). We selected a 10-year interval to detect regime-shift changes in the age-structure data (Elliott, 2011).

To assess the total distance of upper treeline advance, we reconstructed the uppermost elevation of the outpost tree along the transect for each five-year period during the 20th century (1900–1995 age classes). We then stratified the values based on whether a given advance occurred during "wet" or "dry" pentads to quantitatively compare the influence of climatic water deficit conditions on this process using a Mann-Whitney U Test. This nonparametric procedure tests for statistically significant differences in the median value of a time series. We also employed this method to test for significant shifts in the elevational extent of treeline on contrasting north- and south-facing slopes during wet and dry periods. We evaluated overall treeline advance using a 10 m increase as the minimum criterion (Liang et al., 2011). The rationale for a dual analysis of ecological regime-shift changes with pulses of upper treeline advance is to evaluate two separate lines of evidence regarding the extent to which upper treeline ecotonal dynamics are driven by abrupt, threshold-type changes.

Results

ECOLOGICAL REGIME SHIFTS

Regime-shift analysis measured a significant increase in the rate of tree regeneration ($p < 0.05$) at 77.2% of sites sampled ($n = 17/22$, Figs. 3 and 4). The primary spatiotemporal attributes of these threshold responses include the following: (1) regime shifts were concentrated during the latter half of the 20th century (1945–1985 age classes), and (2) the initial triggering was asynchronous between opposite north- and south-facing slopes on all but one peak ($n = 10/11$, Figs. 3 and 4).
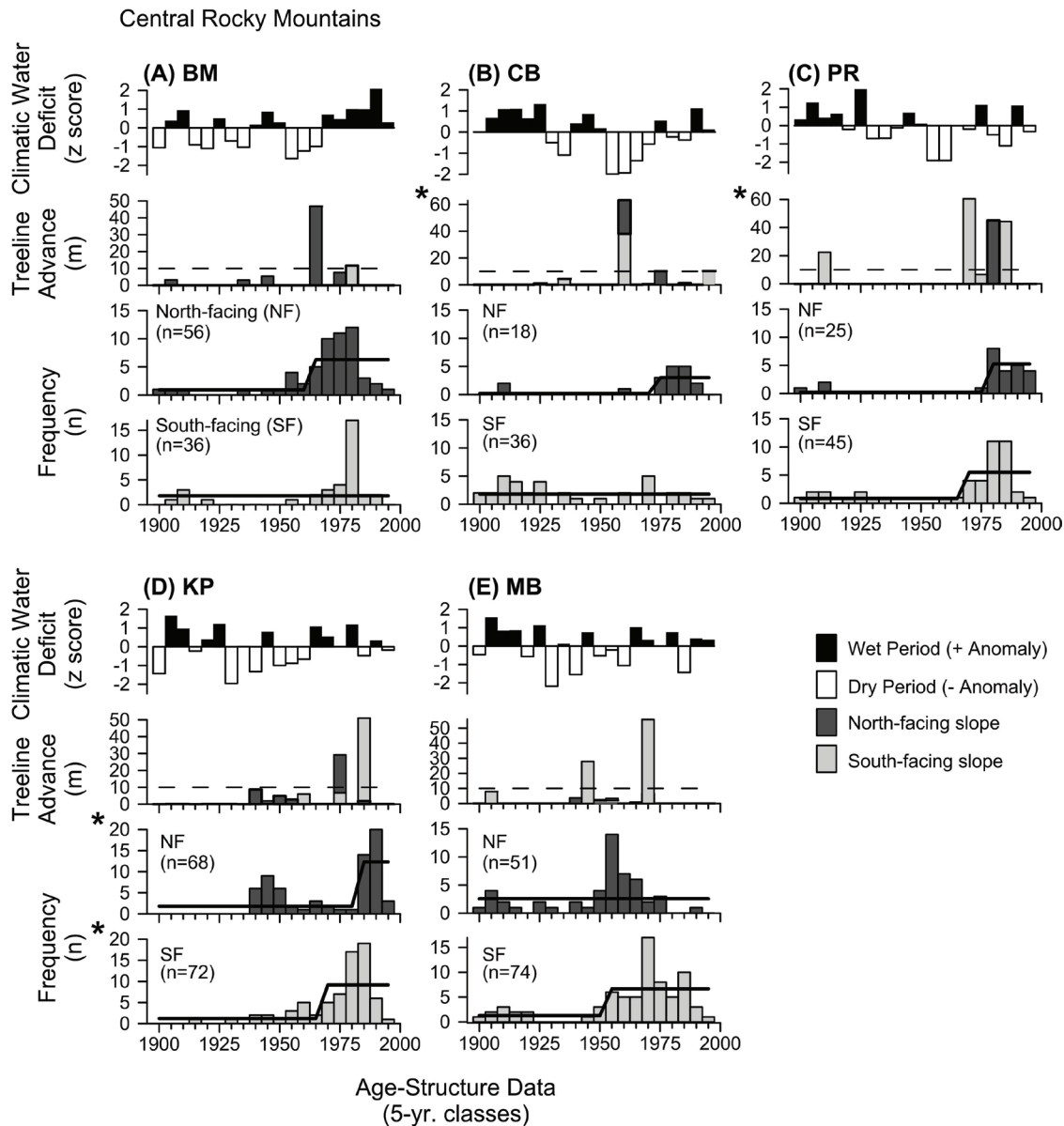
FIGURE 3.   Data from the Central Rocky Mountains showing 5-year phases (wet or dry) of the climatic water deficit (z-scores), pulses of upper treeline advance (m), and north- and south-facing age-structure data (*n*). Phases of the climatic water deficit are plotted with respect to the 20th century mean (1900–1999). The dashed line on the treeline advance graphs represents the 10 m minimum criterion used and the bold lines superimposed on the age-structure data represent the results of regime-shift analysis ($p = 0.05$). Refer to Table 1 for specific site information. An asterisk refers to a non-uniform axis.

Drought conditions coincided with 64.7% ($n = 11/17$) of regime-shift increases in tree regeneration and this was the most pronounced on north-facing slopes ($n = 7/11$, Figs. 3 and 4). On the other hand, 50% of regime shifts on south-facing slopes aligned with wet conditions ($n = 4/8$, Figs. 3 and 4), which were most prevalent in the Front Range ($n = 3/3$ sites; Fig. 4, parts A–C). The south-facing slope of Medicine Bow Peak Massif therefore provides an interesting comparison because, unlike xeric slopes on nearby peaks (e.g., Kannady and sites in the Front Range), dry conditions evidently favor regime-shift increases in tree establishment (Fig. 3, parts D–E, and Fig. 4, parts A–C). Collectively, spatiotemporal patterns along the latitudinal gradient suggest that demographic processes on north-facing slopes were most responsive to drought conditions, whereas regeneration dynamics varied more on south-facing slopes with respect to fluxes in the climatic water deficit.

PULSES OF UPPER TREELINE ADVANCE

Pulses of upper treeline advance (≥ 10 m) occurred 28 times during the 20th century, and 85.7% ($n = 24$) were confined to the period 1945–1995. These pulses were spread among every mountain peak except Mount Evans Massif in the Colorado Front Range and were more frequent on south-facing slopes, especially in the Medicine Bow and elsewhere in the Front Range (Figs. 3 and 4). The overall mean distance (± 1 SD) of treeline advance was 54.0 m (± 44.2 m), and given the nearly ubiquitous nature of it, there was no significant difference between the distance of advance on

686 / Arctic, Antarctic, and Alpine Research
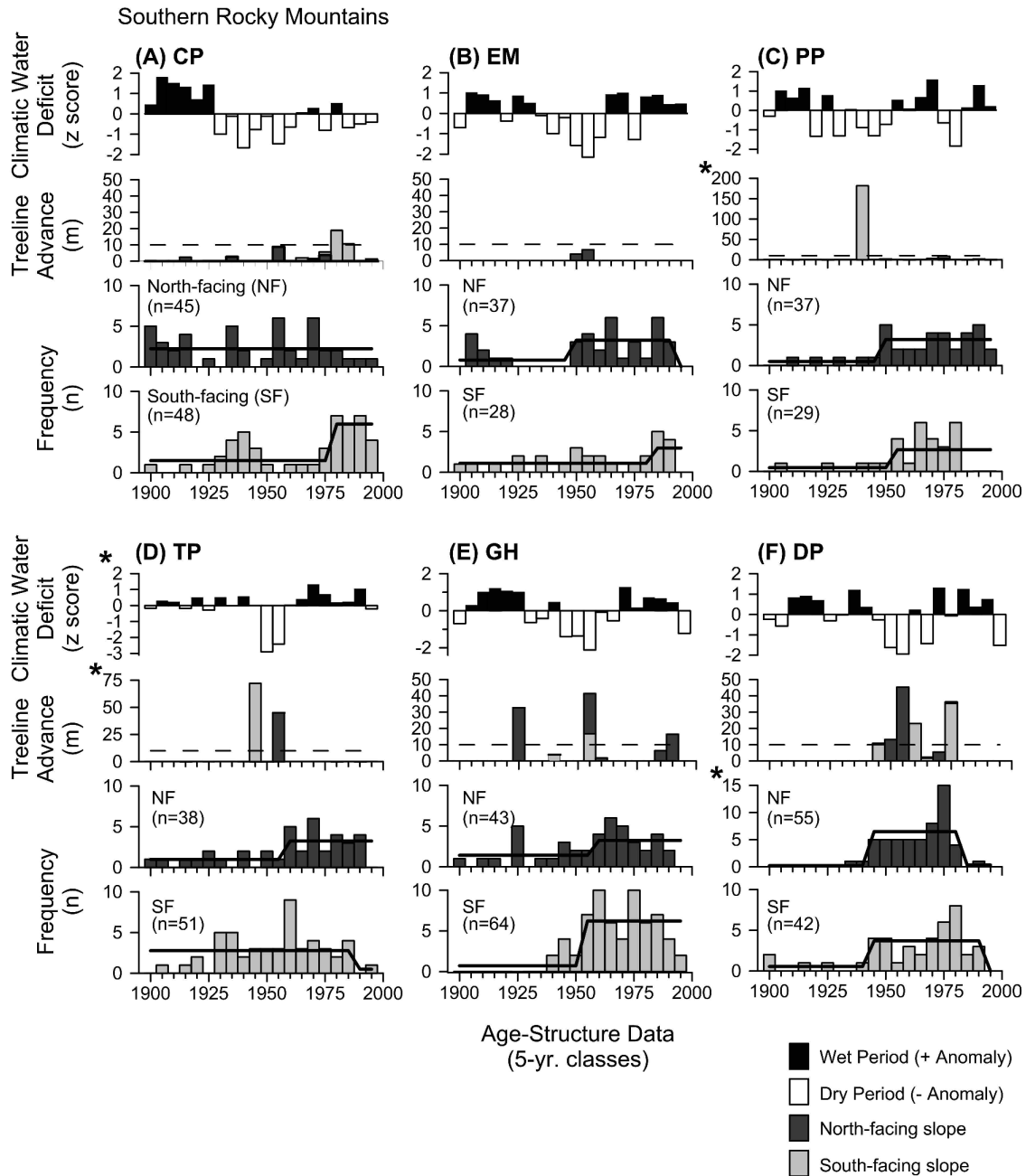
Southern Rocky Mountains

FIGURE 4.   Data from the Southern Rocky Mountains showing 5-year phases (wet or dry) of the climatic water deficit (z-scores), pulses of upper treeline advance (m), and north- and south-facing age-structure data (n). Phases of the climatic water deficit are plotted with respect to the 20th century mean (1900–1999). The dashed line on the treeline advance graph represents the 10 m minimum criterion used, and the bold lines superimposed on the age-structure data represent the results of regime-shift analysis ($p = 0.05$). Refer to Table 1 for specific site information. An asterisk refers to a non-uniform axis.

north- and south-facing slopes ($p = 0.212$, Fig. 5). From a temporal perspective, the median distance of upslope advance was significantly greater ($p = 0.001$) during the latter half of the 20th century compared to the first (24.8 m vs. 0.3 m, respectively).

Upper treeline advance was more frequent during drought (57.1%, $n = 16/28$), and although not statistically significant ($p = 0.146$), elevational increases were nearly twice as large during drought versus wet periods (35.6 m vs. 18.5 m, respectively, Fig. 5). On more mesic north-facing slopes, however, treeline advance was significantly greater ($p = 0.049$) during dry periods with more than a fourfold difference in median distances of upslope migration (26.6 m vs. 6.4 m, respectively). South-facing slopes exhibited the widest range of variability (range of advance = 0–187.0 m), and similar to opposite north-facing slopes, this was greater during dry periods than wet (43.5 m vs. 24.8 m, respectively, Fig. 5). Alternatively, two key exceptions exist on south-facing slopes (sites MB and TP) where treeline advanced more than 60 m under wet conditions (Fig. 5). Results from reconstructing the history of upper treeline advance
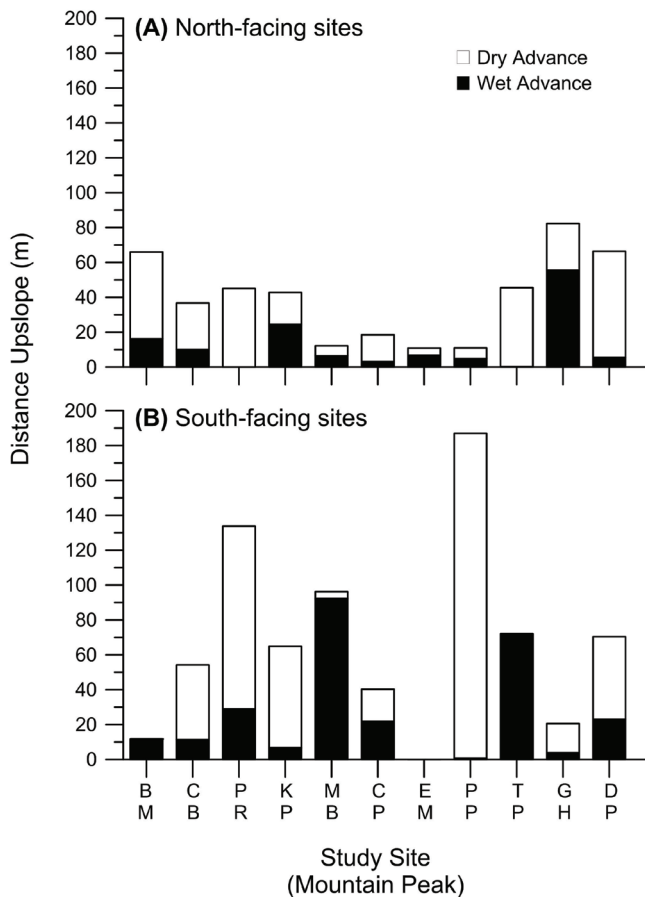
GRANT P. ELLIOTT AND C. MARK COWELL / 687

FIGURE 5. **Stratified distance of upper treeline advance at each site along the latitudinal gradient based on wet or dry climatic water deficit conditions. See Table 1 for site abbreviations.**

during the 20th century highlight the critical role drought plays in facilitating these processes, particularly on north-facing slopes.

Discussion

To our knowledge, this study represents the first regional-scale attempt to elucidate the combined influence of temperature and precipitation via the climatic water deficit on abrupt threshold changes at upper treeline across contrasts in slope aspect and fine-scale moisture regimes. The combined results from this research clearly illustrate the importance of not only considering slope aspect, but also temperature and local moisture when seeking to ascertain the ecological manifestations of climate change within upper treeline ecotones. Perhaps most compelling, however, is that although the spatiotemporal patterns of demographic responses to climate vary along the latitudinal gradient, a majority of measured changes happened during periods of drought (60.0%, *n* = 27/45) during the mid to late 20th century. This is particularly noteworthy considering that, up to this point, drought has primarily been viewed as a severe limiting factor to both successful regeneration dynamics and treeline advance within upper treeline ecotones (Weisberg and Baker, 1995; Hessl and Baker, 1997; Lloyd and Graumlich, 1997; Moyes et al., 2013). The remaining spatiotemporal variability in ecological responses to climate can be explained by examining slope aspect within the framework of local hydrocli-

mate regimes (sensu Rochefort and Peterson, 1996; Daniels and Veblen, 2004).

DROUGHT AND TREE REGENERATION AT UPPER TREELINE

Results from this study offer key insight into how effective slope aspect is in modulating the interactions of broad-scale temperature inputs with more fine-scale moisture conditions and, by extension, the susceptibility of demographic processes to abrupt switches during drought at upper treeline. It has been suggested that in the presence of drought, climatically sensitive ecosystems, such as upper treeline ecotones, may be predisposed to threshold-induced regime shifts that coincide with more steady increases in temperature that help undermine system stability (Foley et al., 2003; Scheffer and Carpenter, 2003). Indeed, this type of "drought-triggering" scenario explains the abrupt regime-shift increases in regeneration dynamics at upper treeline from a regional perspective along this same latitudinal gradient during the early 1950s (1950–1954 age class) when rising temperatures coincided with a sharp reduction in snowfall (Elliott, 2012a). The finer scale results derived from individual mountain peaks in this study, however, offer a notable refinement to the drought-triggering hypothesis; namely, that within the context of warmer temperatures, the likelihood of drought events triggering an ecological regime shift in tree establishment at upper treeline varies by slope aspect. Thus, the slope aspect mediation of ecological regime-shift changes in tree regeneration reinforces the critical control it exerts on both temperature-precipitation and climate-vegetation interactions in high-elevation mountain environments.

From an ecoclimatological standpoint, however, it is important to consider that "drought" in this case primarily stems from reduced snowpack rather than a persistent reduction in growing-season precipitation, which is more typical at lower elevations where snow constitutes a lower proportion of annual moisture. Correspondingly, a reduction in snowpack likely prolongs favorable growing season conditions, which has facilitated both tree regeneration and upper treeline advance in the Swedish Scandes (Kullman, 2002) and Canadian Rocky Mountains (Luckman and Kavanagh, 1998). Although growing season length has been previously identified as a chief constraint on demographic processes at upper treeline, findings from this study provide new evidence suggesting that the ecological impacts of these conditions on tree demography are not uniform and are, instead, often contingent on slope aspect.

The slope aspect mediation of abrupt changes in upper treeline ecotonal dynamics can be explained by examining how the interactions between soil thermal regimes and snow often vary across a single mountain peak. For example, Körner and Paulsen (2004) demonstrated the importance of soil temperature thresholds in governing the elevational extent of tree regeneration, and although they reported insignificant temperature differences between contrasting slope exposures, this was likely the result of placing measuring devices underneath shaded canopies. In addition to necessary temperature requirements, studies suggest that the amount of snowfall and subsequent snowpack accumulation can severely limit the length of the growing season and thus rates of successful tree establishment within upper treeline ecotones (Minnich, 1984; Hättenschwiler and Smith, 1999), particularly on windward (Rochefort and Peterson, 1996) and/or north-facing slopes (Elliott and Kipfmueller, 2011). In fact, an important linkage between persistent snowpack and critical soil temperatures was recently made in southeastern Tibet, where researchers identified a 20–30 day delay in the onset of nec-

essary soil warming on more shaded north-facing slopes compared to opposite south-facing slopes during the spring (Liu and Luo, 2011). This finding likely corresponds to accelerated rates of soil formation on north-facing slopes compared to south-facing slopes where increased climatic water deficits coupled with higher solar insolation impede pedogenic processes (Shickoff, 2005). Thus, although soil is one of the most complex site factors at upper treeline (Holtmeier, 2009), we conclude that regeneration processes are evidently unencumbered by late-lying snowpack during periods of drought, especially on north-facing slopes, and therefore able to respond more abruptly to the spatiotemporal alignment of favorable temperature and moisture conditions.

ROLE OF LOCAL HYDROCLIMATE

Evidence for demographic processes responding rapidly to drought in normally snow-heavy environments exists on north-facing slopes in the Bighorns (sites BM, PR), Medicine Bows (site KP), and Front Range (sites EM, PP) along with south-facing slopes on the other peak in the Medicine Bows (site MB) and Crown Point (CP) in the Front Range (Figs. 2–5). In some cases, however, results from this research imply that even in the presence of 20th century warming and during periods of drought, regeneration dynamics on north-facing slopes continue to be impeded by snow accumulation. This is the most discernible on the north-facing slope of Medicine Bow Peak Massif and Crown Point where regime shifts and pulses of treeline advance were absent. Coincidentally, both of these mountain peaks typically receive a high proportion of annual precipitation from snow, and the ecological impacts of this are almost certainly amplified on north-facing slopes (Table 1), which bolsters the likelihood of snow limiting tree regeneration and related biotic responses to climate variability in these hydroclimate settings dominated by snow.

Despite the widespread evidence for snow-limited tree establishment at upper treeline during wet periods along the latitudinal gradient, some instances remain where this is evidently not the case; most notably on south-facing slopes in the Front Range and on Kannaday Peak in the Medicine Bow Mountains (KP) where regime-shift increases coincide with wet conditions. Ecophysiological studies from the Rocky Mountains suggest that seedlings growing within upper treeline ecotones are consistently subject to combinations of high sun exposure and related rises in soil temperature that ultimately limit rates of establishment (Broderson et al., 2006; Moyes et al., 2013), especially on more xeric south-facing slopes (Weisberg and Baker, 1995; Germino et al., 2002). The predominance of clustered spatial patterns of tree establishment above timberline on south-facing slopes in this area provide further evidence for frequent moisture stress (Elliott and Kipfmueller, 2010). As for Kannaday Peak, tree regeneration is clearly operating under the influence of a much warmer and drier climate than that of neighboring Medicine Bow Peak Massif (Table 1, Fig. 2). In contrast to the frequent snow limitations for tree establishment on north-facing slopes, these interactions highlight the importance of wet conditions in maintaining regeneration dynamics on xeric south-facing slopes, which supports previous work from the northern Front Range (Hessl and Baker, 1997). More generally, these results provide broad-scale support for findings on Mount Ranier in the Cascades (Rochefort and Peterson, 1996) and in the Andes Mountains of northern Patagonia (Daniels and Veblen, 2004) where the relative influence of temperature-precipitation interactions were contingent on both slope aspect and local hydroclimate regimes. More specifically,

this spatial variability portends uneven ecological responses to drought across upper treeline ecotones.

DATA LIMITATIONS

As with any study that relies on static age-structure data and modeled climate-variable data (e.g., climatic water deficit), a brief discussion of potential limitations is appropriate in order to fully justify our interpretations of the results.

AGE-STRUCTURE DATA

Although the dendroecological results from this study illustrate explainable patterns along a latitudinal gradient in the Rocky Mountains, there are inherent limitations to the interpretation of static age-structure data (Veblen, 1992; Johnson et al., 1994). For instance, statistically significant pulses of upper treeline advance were most concentrated during the latter half of the 20th century, which might just reflect a loss of evidence from earlier advances through tree mortality. Furthermore, successful tree establishment is dependent on rates of survival and mortality, with abrupt regime-shift changes resulting from above-average establishment and subsequent survival and/or low mortality. Equally important, the expected frequency of living trees naturally decreases through time, therefore making it more likely for regime-shift changes to occur more recently. Yet, dead seedlings only accounted for 3% of the total recorded ($n = 11/366$) and evidence of previous tree mortality was lacking from every site, with the critically important caveats that it is nearly impossible to fully understand seedling regeneration dynamics through a single season of fieldwork at each site and because of how quickly dead ones fully decompose. This is noteworthy considering that evidence of previous mortality, in the form of standing dead trees/snags, can persist on the landscape for several decades in these high-elevation environments.

CLIMATIC WATER DEFICIT

We plotted standardized deviations of both annual temperature (MAT) and precipitation (Precip) relative to the 20th century mean to see if the resulting climatic water deficit (CWD) phases (wet or dry) were logical, particularly for the Central Rocky Mountains where data are unavailable and sites were assigned an AWC value of 75 mm (Fig. 6). Given that "wet" or "dry" phases are all produced by plausible combinations of temperature and precipitation, our results suggest that the assignment of this value does not fundamentally alter the calculation of the climatic water deficit.

Conclusions

Results from this research support our first hypothesis regarding the pronounced influence of slope aspect on temperature-precipitation interactions and related ecological responses to climate. The confirmation of our second hypothesis, however, appears to be contingent on local hydroclimate regimes. For example, abrupt demographic responses to drought were most common on north-facing slopes, but in relatively cool areas with heavy snowfall totals (e.g., Medicine Bow Peak Massif), drought is capable of ameliorating conditions on more xeric south-facing slopes as well. Moreover, evidence from the south-facing side of Medicine Bow Peak Massif suggests that although drought favors regime-shift increases in tree establishment, wet conditions may be more impor-
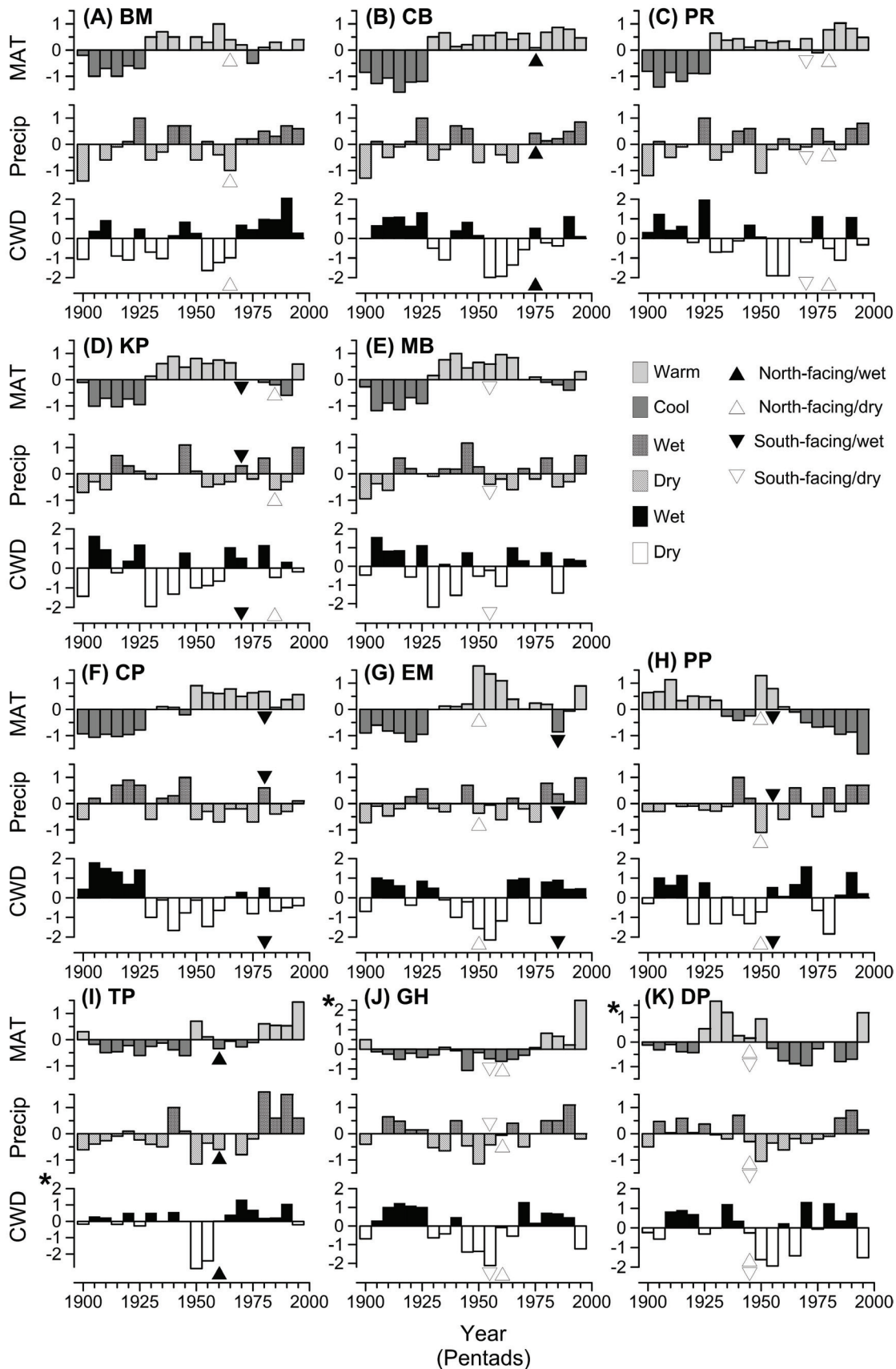
FIGURE 6. Standardized pentad values for mean annual temperature (MAT), annual precipitation (Precip), and the climatic water deficit (CWD) in comparison to regime-shift changes in tree establishment (triangles). These data illustrate how the assignment of 75 mm for available water holding capacity (AWC; see Table 1) in the Central Rocky Mountains aligns with what would be expected in terms of temperature and precipitation inputs given a "wet" or "dry" classification. Positive or negative anomalies are with respect to the 20th century mean (1900–1999).

tant for episodes of treeline advance. A similar switch in moisture conditions between regime shifts in regeneration dynamics (wet) compared to pulses of treeline advance (dry) exists on neighboring Kannaday Peak (Figs. 3 and 5). Taken together, this suggests that separate bioclimatic conditions may favor abrupt increases in demographic processes compared to the upslope migration of the outpost tree.

What this means for regeneration dynamics at upper treeline within the context of projected changes in climate therefore depends on how slope aspect mediates local hydroclimatic conditions. Continued rises in temperature coupled with further reductions in snowpack (e.g., Clow, 2010; Pederson et al., 2011), for example, will most likely continue to favor demographic processes on north-facing slopes in all but the snowiest environments unless drought-like deficits persist long enough to undergo a regime-shift change toward drier conditions that help alleviate current snow limitations. From a global change ecology standpoint, this research suggests that upper treeline ecotonal dynamics on north-facing slopes may remain more closely aligned with variations in climate and thus serve as a more accurate barometer for gauging climate-vegetation interactions moving forward. Ultimately, the cumulative evidence presented here strongly suggests that in order to fully elucidate the ecological impacts of climate variability in high-elevation treeline ecotones, both slope aspect and temperature-moisture interactions should be considered.

Acknowledgments

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