NRC Research Press

ARTICLE

Influence of climate on the growth of quaking aspen (*Populus tremuloides*) in Colorado and southern Wyoming

M.M. Dudley, J. Negron, N.A. Tisserat, W.D. Shepperd, and W.R. Jacobi

Abstract: We analyzed a series of increment cores collected from 260 adult dominant or co-dominant quaking aspen (*Populus tremuloides* Michx.) trees from national forests across Colorado and southern Wyoming in 2009 and 2010. Half of the cores were collected from trees in stands with a high amount of crown dieback, and half were from lightly damaged stands. We define the level of stand damage based on stand survey data in which lightly damaged stands had average crown dieback of 16% and heavily damaged stands averaged 41%. Upon analysis, two-thirds of the cores collected did not exhibit radial growth correlated with region-wide patterns (e.g., climate) and were classified as having a low cohesive response. The site variable most predictive of whether a stand exhibited high cohesive response or low cohesive response was site elevation, followed by aspect, slope, and canopy closure. Sites with high cohesive response stands were more likely to have aspen bark beetle damage, white rot, and Cryptosphaeria canker. We did not detect relationships between tree growth and summer precipitation from 1900–2008, but there was a relationship between growth and annual precipitation. A growth model included maximum May and July temperatures, as well as the current and previous year's annual precipitation.

Key words: aspen, *Populus tremuloides*, drought, increment, mortality.

Résumé : Nous avons analysé une série de carottes prélevées sur 260 peupliers faux-tremble (*Populus tremuloides* Michx.) adultes dominants ou codominants dans des forêts nationales à travers le Colorado et le sud du Wyoming en 2009 et 2010. La moitié des carottes ont été prélevées sur des arbres dans des peuplements sévèrement touchés par le dépérissement de la cime et l'autre moitié dans des peuplements légèrement endommagés. Nous avons défini le niveau de dommage du peuplement sur la base de données d'inventaire de peuplement selon lesquelles les peuplements légèrement endommagés avaient un taux moyen de dépérissement de 16 % alors que les peuplements sévèrement endommagés avaient un taux moyen de dépérissement de 41 %. Après analyse, les deux tiers des carottes ne montraient pas de corrélation entre la croissance radiale et des profils régionaux (p. ex. le climat) et ont été classées comme ayant une faible réponse cohésive. Parmi les variables de site, l'altitude prédisait le mieux la réponse cohésive du peuplement, suivie de l'exposition, de la pente et de la fermeture du couvert. Le peuplier faux-tremble avait plus de chance d'être endommagé par les scolytes, la carie blanche et le chancre cryptosphaérien dans les sites où les peuplements avaient une forte réponse cohésive. Nous n'avons pas détecté de relation entre la croissance des arbres et la précipitation estivale de 1900 à 2008, mais il y avait une relation entre la croissance et la précipitation annuelle. Un modèle de croissance incluait les températures maximum des mois de mai et juillet ainsi que la précipitation annuelle de l'année en cours et de l'année précédente. [Traduit par la Rédaction]

Mots-clés : peuplier faux-tremble, *Populus tremuloides*, sécheresse, accroissement, mortalité.

Introduction

Quaking aspen (*Populus tremuloides* Michx.) is the primary pioneer tree species and one of a few hardwood tree species found in forests throughout the southern Rocky Mountain region (Mueggler 1985). Following a disturbance event such as a stand-replacing fire, aspen colonize the area, either by seed or through sprouting from existing roots (Mueggler 1985; Barnes 1966). The success of this early-seral species is favored by widespread disturbance events, which often serve to reduce competing populations of late-seral conifer species (e.g., Kulakowski et al. 2013; Lankia et al. 2012; Krasnow and Stephens 2015). Aspen produces high numbers of suckers following stand-replacing fire or other disturbances (Scheier, and Campbell 1978; Perala 1995; Romme et al. 1995), with sucker densities greatest following a complete removal of the overstory. However, regeneration still occurs (though at lower densities) as gaps in the canopy are produced (Shepperd 1993; Shepperd and Smith 1993; Shepperd et al. 2001). Studies indicate that, as in most other tree species, growth rates of aspen are a function of climatic factors combined with various site and soil characteristics (Hogg et al. 2008, 2013). The impacts of drought on *P. tremuloides* includes a decrease in leaf size and leaf area index (LAI) and alteration of root water flow properties (Greitner et al. 1994; Siemens and Zwiazek 2003; Krishnan et al. 2006). Severely stressed individuals display an inhibition of root hydraulic conductivity as a result of an increase in the ratio of apoplastic to cell-to-cell water transport (Siemens and Zwiazek 2003). Anderegg et al. (2013) showed that aspen that have undergone drought stress and air embolism are more prone to cavitation during subsequent drought episodes.[1]

Received 2 March 2015. Accepted 21 July 2015.

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[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2015-0092.

Forest health researchers have documented stand mortality in southern Utah and Idaho (Guyon and Hoffman 2011), Arizona (Fairweather et al. 2008; Zegler et al. 2012), the Pacific Northwest (Flowers and Kohler 2011), the Carson National Forest in New Mexico (J. Jacobs, personal communication, 2015), and the boreal aspen forests of Alberta and Saskatchewan (Brandt et al. 2003; Hogg et al. 2002, 2008). Worrall et al. (2008) first observed rapid overstory dieback in Colorado in 2005 and coined the term "sudden aspen decline" (SAD) based on the observation that stands with dying overstory lacked a significant regeneration response (Worrall et al. 2008). Based on aspen health data from an extensive Colorado and southern Wyoming study (Dudley et al. 2015), we concluded that acute drought was most likely the inciting factor causing a marked increase in select secondary damage agents and overstory mortality. In that study, we found that heavily damaged stands with over 38% overstory mortality were consistently warmer and drier during the period directly preceding and during the episode of dieback, 2000–2006, than lightly damaged stands (Dudley et al. 2015). Trees growing on sites with suboptimal growing conditions such as those with shallow soils and drier sites tend to be more responsive to climatic events than trees growing on more favorable sites (Fritts 1976; Stokes and Smiley 1968). Chronologies from tree species closely related to quaking aspen (e.g., plains cottonwood) and from species with similar wood structure (e.g., *Betula* species) have demonstrated that these species respond to climatic events with increased or decreased radial growth (Edmondson et al. 2014; Levanič and Eggertsson 2008). Further, previous studies on the impact of various environmental, site, and biotic agents on aspen growth indicate that drought, frost, defoliation (by forest tent caterpillar, *Malacosoma disstria* Hübner), and poor site conditions all have a negative influence on annual growth (Hogg et al. 2002, 2008; Strain 1966; Cooke and Roland 2007; Ireland et al. 2014; Leonelli et al. 2008).

To date, there are no chronologies available for *P. tremuloides* from the International Tree Ring Data Bank (NOAA, ITRDB), but several studies have utilized aspen increment cores and cross sections to age stands (Elliott and Baker 2004) and to produce regional chronologies (Hogg and Schwarz 1999; Hogg and Bernier 2005). Quaking aspen are often difficult to cross-date, due in part to the wood structure (diffuse-porous), which can make ring boundaries difficult to determine, as well as the formation of false rings or complete lack of ring formation during some years (Speer 2010; P.M. Brown, personal communication, 2011). In this study, we examined a set of tree cores collected from 97 aspen stands throughout the mountainous regions of Colorado and southern Wyoming.

The main questions that we wished to answer included the following. (*i*) Are some aspen stands predisposed by site, stand, or geographic conditions to produce a highly cohesive radial growth pattern in response to changes in precipitation or temperature? (*ii*) Are there differences in drought impacts on radial growth by region? (*iii*) Do any variables have a larger impact on increment growth than others? (*iv*) Can inferences be made about current and future aspen health (i.e., presence of various diseases and insects) from radial growth and site characteristics?

Materials and methods

Study area

In 2009 and 2010, we established 97 aspen health survey plots on five national forests to assess the impact of current and future disturbances by diseases, insects, and climate (Fig. 1). Approximately half of our survey plots were established in aspen stands classified as heavily damaged, and half were in lightly damaged stands (though not as a paired-plot design), based on 2008–2009 USDA Forest Service aerial survey data. Aerial surveyors annually map four categories of aspen stand damage or dieback. These include (1) aspen stands currently undergoing an apparent defoliation or foliage discoloration event, (2) stands with thinning crowns on at least 25% of adult aspen, (3) stands with moderate (<50% of stems) levels of overstory mortality, and (4) stands with high (>50% of stems) levels of overstory mortality (Krist, 2005). We combined damage categories 1 and 2 into a "lightly damaged" group and categories 3 and 4 into a single category for placement of plots in heavily damaged stands. We later verified that heavily damaged stands had much higher rates of overstory dieback than lightly damaged stands (38% and 14%, respectively) (Dudley et al. 2015).

Plot selection

Ranger districts were sampling units within each national forest, with one to four districts sampled per forest. Districts were selected for sampling if they contained large areas of aspen-dominated forests, as determined by examination of forest type data (based on a remotely-sensed vegetation data layer; http://gapanalysis.usgs.gov/gaplandcover/). All spatial data processing and extraction was performed using ArcGIS 10.0 desktop software (ESRI, Redlands, California, USA). Potential survey points in lightly and heavily damaged stands were generated using the "Create Random Points" tool in ArcToolbox. Point locations greater than 1 km from a road were eliminated from consideration. Further, final plot locations were chosen from the remaining points to represent a wide range of aspen stands and elevations. Survey points were uploaded to handheld GPS units (Garmin eTrex Legend, Garmin International, Ltd., Olathe, Kansas, USA). Potential survey stands were to consist of at least 50% aspen stems and be at least 120 × 20 m in size or another potential site was located. Each plot consisted of a 100 m long transect, which was established starting at the randomly generated GPS point and oriented in such a way as to roughly bisect the stand of interest. Three circular (8 m radius), fixed-area (201 m^2) subplots were established along the 100 m transect by selecting three numeric locations from a list of randomly generated numbers. One adult dominant or co-dominant tree was cored in each subplot for a maximum of three increment cores per transect.

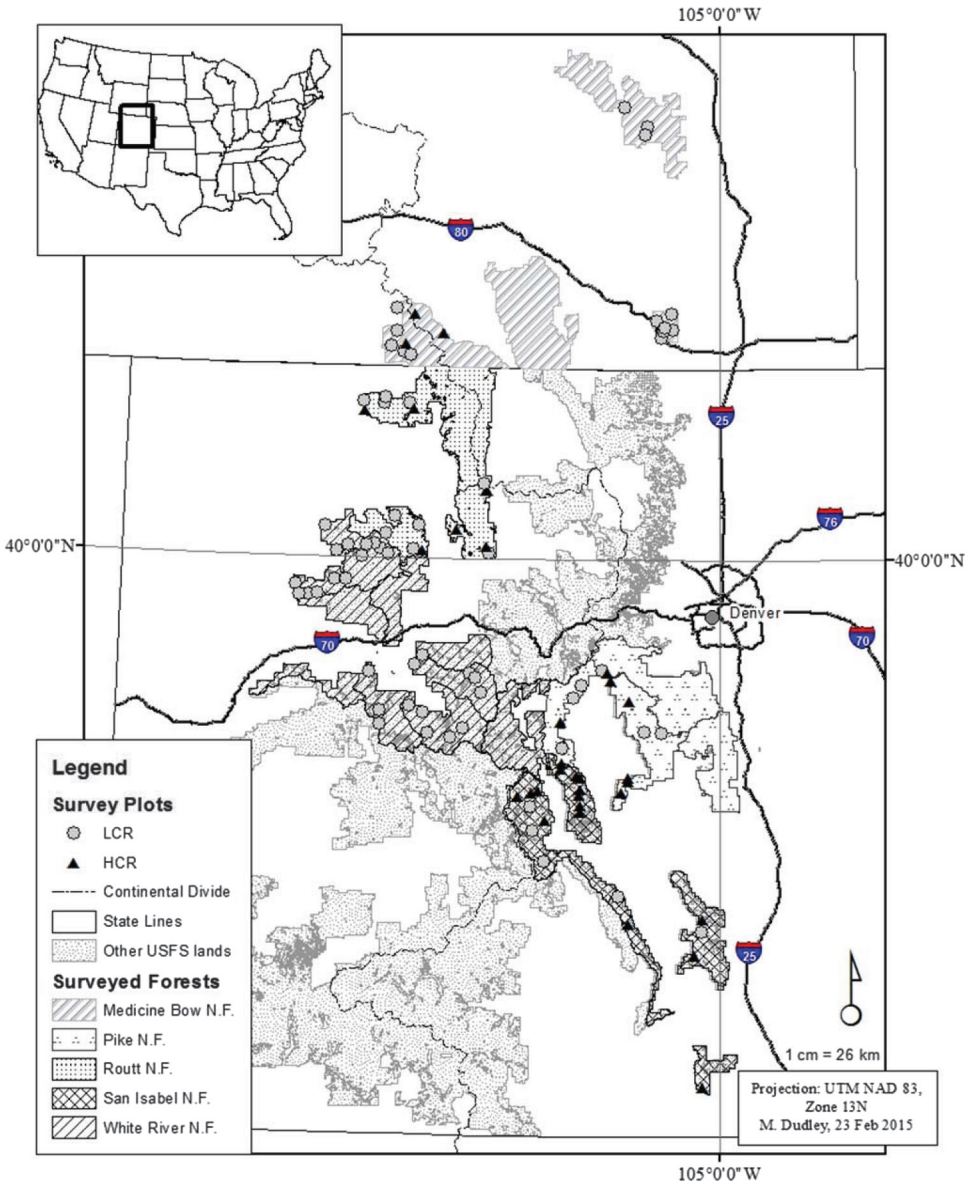
Site and stand data

Stand-level data recorded during core collection included aspect, percent slope, elevation, stand structure, and percent live stems. In each subplot, the first 10 adult aspen (≥12 cm diameter at breast height (DBH)) were assessed for percent crown dieback and disease and damage agents. We used morphological characteristics such as the type of fruiting body and pattern of cankers on the stem to identify specific canker diseases and morphology and placement of conks to identify decay fungi. Likewise, we examined trees for general signs of wood borer attack (*Saperda calcarata* Say or *Agrilus liragus* Barter & Brown), which included tunneling, exit holes, and brown-stained bark. However, damage was not attributed to either species specifically. Presence of aspen bark beetles (*Trypophloeus populi* Hopkins, 1915, or *Procryphalus mucronatus* (LeConte, 1879)) was determined based on the presence of small (<1 mm) exit holes on the bark, cracked bark over galleries, or both.

Increment core sampling and preparation

One adult dominant or co-dominant tree (≥12.0 cm) was cored, using a 5 mm increment borer, at breast height (1.4 m from the base of the tree) in each subplot for a total of 260 increment cores. Trees selected for sampling were living and either healthy or with mild to moderate evidence of disease or damage but did not show signs or symptoms of white rot fungus (*Phellinus tremulae* (Bondartsev) Bondartsev & P.N. Borisov), as cores from rotten trees would be unreadable. Some subplots (31) did not contain any adult aspen, and thus cores were not collected from these locations. Increment cores collected within the same national forest (and later grouped together as a chronology) were no more than

Fig. 1. Survey area and increment core collection sites in Colorado and southern Wyoming, 2009–2010. A high cohesive response (HCR) plot refers to whether one or more of the trees sampled per transect were responsive to region-wide climate signals. Low cohesive response (LCR) trees were not responsive to region-wide climate signals.



100 miles apart, and most were within 40 miles of each other. Although cored trees occurred on sites with varying elevation, aspect, and slope steepness, a previous analysis of aspen health, size, and mortality did not reveal major differences among these classifications, and thus we did not stratify our samples by elevation or aspect (Dudley et al. 2015). Cores were air-dried for one week before being glued to wooden mounting blocks with the vascular tissue vertical. Cores were sanded progressively with 150 or 220 and then 400 and 600 grit sandpaper to produce a smooth surface with cell and fiber structures clearly visible (Speer 2010). A few cores were broken, discolored, or otherwise unreadable and were omitted from measurement and analysis.

Skeleton plot construction

Cross-dating using the skeleton plot technique (Stokes and Smiley 1968; Swetnam 1985), a graphical technique for comparing ring width, was used to establish an accurate tree age. A master skeleton plot (tree ring chronology), which was representative of all cores within a sampling area (ranger district) and contained a series of reference years, was then constructed. This allowed the identification of missing rings and elimination of false rings (Stokes and Smiley 1968).

Annual ring measurement

Annual rings widths were measured using an increnometer (Velmex, Inc., Bloomfield, N.Y., USA), a digital counter, and associated software program (MEASURE J2X, VoorTech Consulting, Holderness, New Hampshire, USA). The raw data was then checked and statistically cross-dated using the software program COFECHA (Holmes 1983; Grissino-Mayer 2001) to first determine the correlation between three cores (series) collected within the same transect. These triplicates were then compared with others collected within the same ranger district. All raw core data were standardized using a segment length of 30 years, with a 15-year overlap between increments. Core series with correlations of less than 0.42 were examined and corrected (using the software program EDRM; see Grissino-Mayer 2001) or were placed in the low cohesive response (LCR) group and excluded from further climate–

growth analysis if their correlations remained <0.42 or if they were responding to some growth driver (e.g., possible insect outbreaks or successional processes) other than climate. We are using the terms "low cohesive response" and "high cohesive response" (HCR) to describe groups of trees that respond together in a similar manner to climatic influences. We also examined each series' mean sensitivity rating (Speer 2010), although this measure was not used in this study to divide series into HCR (i.e., those trees responding to climate effects) and LCR groups (Appendix Table A2). For each national forest, the master chronology (i.e., a dataset that contains series with the highest possible correlations) represented samples within a distinct geographic area. Series collected from the Medicine Bow and Routt National Forests were combined into a single category due to their relative proximity to each other and to create a larger sample size.

The final detrended chronologies for (1) Medicine Bow and Routt National Forests, (2) Pike National Forest, and (3) San Isabel National Forest were produced using the program ARSTAN (Cook 1985). A 25-year smoothing spline was used to remove autocorrelative influences on growth (i.e., growth trends not related to climate such as tree age). This relatively short spline was chosen due to the relatively short life-span of aspen; the chronology used in this study covers 108 years. A similar approach had previously been used to examine climatic influences on the growth of a similarly short-lived species, *Betula pubescens* Ehrh. (Levanič and Eggertsson 2008). The residual chronology, which contains no autocorrelation, was used in this analysis for each national forest, as it is most appropriate for regression analysis (Speer 2010). An individual series' inclusion in the final chronology was determined based on the expressed population signal (EPS), an indication of whether an observed signal (i.e., trend) is dominated by the stand or single tree (Wigley et al. 1984) (Appendix Table A2), as well as running *r*-bar ($\bar{r}$), a measure of the common signal strength in a series (Appendix Table A2) (Speer 2010). Any one series that resulted in an EPS value of less than 0.80 was excluded from the final chronology (Wigley et al. 1984; Youngblut and Luckman 2013). Chronologies for each national forest (Appendix Figs. A5–A7) were constructed by importing data into a single spreadsheet using the computer program YUX (Grissino-Mayer 2001).

Of the 260 cores collected, cross-dated, and measured, two-thirds were excluded from the climate–growth analyses due to lack of response to clearly identifiable growth variable (i.e., climate) (low series correlations in COFECHA). Only those cores designated as HCR were used in analyses with climate variables. This included cores from 18 trees on the Medicine Bow and Routt National Forests, 21 trees on the Pike National Forest, and 30 trees on the San Isabel National Forest. Although sample depth for this study is lower than the average used in other dendroclimatological studies, it is comparable to other recent dendroclimatological studies (Levanič and Eggertsson 2008; Weijers et al. 2012; Decaulne et al. 2012; Dawadi et al. 2013).

Maximum temperature and precipitation data

All site-specific climate data used in this study were obtained from spatial PRISM (Parameter Regression Independent Slopes Model) datasets (Daly et al. 2002, 2008). Monthly and annual weather data over a time span of 109 years (1900–2008) were downloaded as a series of 800 m resolution grids from the PRISM climate group's website (http://prism.oregonstate.edu). Site-specific weather data were extracted for each plot location using the "Sample" tool within ArcToolbox. Data for sample locations were selected and averaged together by national forest to match the locations of cores included in the final three chronologies. Precipitation data were compiled and used in three ways: (*i*) an annual dataset from 1900–2008; (*ii*) a monthly dataset from 1950–2008; and (*iii*) a three-month running average from 1950–2008. We chose the time period 1950–2008 because our original analysis included El Nino Southern Ocean (ENSO) surface temperature data (National Oceanic and Atmospheric Administration (NOAA), Climate Prediction Center, http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ensoyears.shtml, accessed May 2014) for this same time period. Maximum temperature data were compiled for the months of May, June, July, and August from 1900–2008.

Soil and geologic data

Soil survey data for the four national forests included in the study was downloaded from the digital general soil map of the United States (STATSGO2) as statewide ESRI shapefiles from the USDA Natural Resources Conservation Service, Geospatial Data Gateway site (USDA, NRCS; https://gdg.sc.egov.usda.gov/GDGOrder.aspx). This dataset includes soil series associations for each polygon, as well as geologic data. Soil series and geologic formations of interest were selected by intersecting each layer with core collection plot locations and then exporting the tabular data of the resulting shapefile. Characteristics of the dominant three soil series for each area were used in analyses and included parent material, particle size class, mineralogy class, cation exchange capacity (CEC) class, depth of the "A" horizon(s), and total soil depth.

Statistical analysis

Site and stand comparisons: HCR or LCR tree presence

All statistical analyses were performed using SAS 9.4 and Jmp Pro software packages (The SAS Institute Inc., Cary, North Carolina). Stand and site conditions from HCR and LCR core collection plots were first examined with the categorical regression tree (CRT) function within Jmp Pro software. Potential variables for use in later logistic regression models were selected based on the LogWorth score (where LogWorth = –log(*P* value)). The minimum LogWorth score accepted was 1.0, equal to a *P* value of 0.10. Splitting values (nodes) were established to maximize LogWorth scores. A 0.10 *P* value was chosen for this and other analyses in this study due to lack of significance of some measures at the $P = 0.05$ level; thus, for the sake of continuity, we chose a cutoff of $P = 0.10$. The likelihood of a stand containing HCR trees was also modeled as a logistic regression with a Spearman correlation coefficient of various site and stand variables of interest with the PROC LOGISTIC program.

Site and stand characteristics: stand structure and disease or insect presence

Site and stand descriptive data, including basal area per hectare, average stand health status score (an index value of 1 to 5, where 1 represents a completely healthy tree and 5 represents a long-dead tree), percent dead crown, percent live adult aspen stems (≥12.0 cm DBH), and percent conifer encroachment, were analyzed at the plot level. Additionally, the presence of several common canker diseases (e.g., Cytospora canker (*Cytospora* spp.), sooty bark canker (*Encoelia pruinosa* (Ellis & Everh.) Torkelson & Echkblad), black canker (*Ceratocystis populicola* Johnson, Harrington & Engelbrecht), and Cryptosphaeria canker (*Cryptosphaeria ligniota* (Fr.) Auersw.)), white trunk rot (*Phellinus tremulae* (Bondartsev) Bondartsev & P.N. Borisov) disease, and two types of insect damage (wood borers and aspen bark beetles) were analyzed at the plot level. All variables were analyzed as mixed linear models in PROC GLIMMIX. Least-squares estimates were calculated for each variable by ranger district within national forest, continental divide position (east or west), stand type (healthy or damaged), and tree response type (HCR or LCR). Means were considered significant if $P \leq 0.10$.

Climatic comparisons: precipitation and maximum temperature

The residual chronology was analyzed as annual incremental growth by maximum monthly temperature (May–August), total annual precipitation, and national forest. An initial examination of the data included simple Spearman correlation coefficients

Table 1. Spearman correlation coefficients and *P* values for correlations between ring width indices (of high cohesive response series) and three-month average precipitation values from 1950–2008 by national forest.

	December–February	January–March	February–April	March–May	April–June	May–July	June–August	July–September	August–October	September–November	October–December	November–January
Medicine Bow and Routt National Forests												
Spearman	0.07	0.16	**0.22**	0.16	**0.24**	0.21	0.15	0.08	0.03	0.05	0.10	0.07
P value	0.60	0.23	**0.0971**	0.22	**0.0729**	0.11	0.25	0.53	0.85	0.73	0.43	0.59
Pike National Forest												
Spearman	0.02	0.12	**0.36**	**0.35**	**0.41**	**0.30**	0.16	0.07	–0.00	–0.04	0.012	–0.06
P value	0.90	0.36	**0.0052**	**0.0121**	**0.0013**	**0.0196**	0.22	0.62	0.98	0.74	0.93	0.65
San Isabel National Forest												
Spearman	0.02	0.14	0.19	0.10	0.09	–0.08	–0.04	–0.15	**–0.23**	–0.09	0.02	0.05
P value	0.89	0.28	0.14	0.47	0.51	0.55	0.76	0.25	**0.0776**	0.49	0.87	0.71
n	58	59	59	59	59	59	59	59	59	59	59	59

Note: Means in bold indicate significance at $P = 0.10$; *n* = number of years.

between increment and climate data, calculated in the PROC CORR program.

Ring width indices (RWI) were also modeled with climatic data by year and national forest with the PROC MIXED and PROC REG programs. Maximum temperature was analyzed as monthly values (May–August) over 108 years (1900–2008), and precipitation was analyzed as annual values for the same time period. In addition to the year-to-year RWI and temperature and precipitation analyses, we also modeled yearly RWI with the previous year's total precipitation (i.e., "lagged" precipitation). These models utilized categorical temperature and precipitation data. Categories were determined by calculating 1.67 and 2 standard errors from the mean (approximately equivalent to 90% and 95% confidence intervals (CI) and to *P* values of 0.10 and 0.05, respectively) based on precipitation and temperature means by national forest (Table 1). Values between the 90%–95% CI represented the "mild" categories (e.g., mildly warm or mildly dry), and values beyond the 95% CI represented the more severe category (e.g., very warm or very dry). Values that fell within the 90% CI limits were considered to be within the normal range. Variables included in the random statement for all models performed were precipitation (current or lagged) and temperature (month) within year.

Best subset regression analysis of increment data with maximum temperature and current or lagged precipitation was performed using the GLMSELECT function in SAS. The model selection method used was stepwise, and selection criteria were based on AIC_c, an adjusted version of AIC (Akaike information criterion).

Finally, we analyzed annual precipitation data by 10-year increments from 1900–2008 for differences between HCR and LCR series, as well as between these series within healthy or heavily damaged stands, and by national forest. All means used were least-squares means, and significant differences were compared at the $P = 0.10$ level.

Results

Site and stand comparisons: HCR versus LCR trees

Examination of ARSTAN output data indicated that the majority of cored trees did not respond uniformly to climatic influences over the 108-year period. After we had verified that there were no cross-dating or measurement errors, we examined which, if any, site factors contributed to this phenomenon. For sites on the White River National Forest, either most of the cores collected were LCR or the standardized chronologies had expressed population signal (EPS) values of less than 0.80 and were excluded. Mean sensitivity rating was high (0.30–0.37) for nearly all of the series examined, even when a series' correlation coefficient was below the threshold level (0.42). Categorical regression analysis revealed four predictors of whether a site would produce HCR or LCR trees. Regression tree nodes (splits) were based on (*i*) site elevation, (*ii*) site percent slope, (*iii*) site aspect, and (*iv*) canopy closure (Fig. 2). Of these, site elevation was the single best predictor of whether a stand would produce HCR or LCR trees ($P = 0.0003$). Sites at high elevations (above 2836 m) tended to have fewer LCR trees overall, and steep, high-elevation sites with open canopies were significantly more likely to produce HCR trees than similar sites with closed canopies (Fig. 2). The second split, on slope category, indicated that HCR trees were not detected on sites with low percent slope (<6%) and occurred on less than 40% of high-elevation sites with steep slopes ($P = 0.028$) (Fig. 2). Site aspect was also a significant predictor of response type; sites with LCR trees did not occur on sites with northeast, east, or southeast aspects ($P = 0.078$) (Fig. 2). Sites with closed canopies were more likely to produce LCR trees ($P = 0.023$) (Fig. 2).

Site and stand characteristics: stand structure and disease or insect presence

We detected no meaningful differences in site or stand descriptive variables (basal area per hectare, health status score, percent dead crown, percent live stems, number of adult aspen stems per hectare, or percent conifer encroachment) among sites producing HCR trees and those producing LCR trees (Appendix Table A1; Appendix Figs. A1–A4). We did detect differences in frequency of select damage agents between the two tree response types (Fig. 3). White trunk rot, Cryptosphaeria canker, and aspen bark beetles were more prevalent among sites with HCR trees than those with LCR trees (Fig. 3).

Climatic comparisons: precipitation and maximum temperature

There were significant relationships between three-month precipitation averages and RWI (based on Spearman correlation coefficients), and this varied by national forest (Table 1). Annual precipitation amounts generally decreased with latitude (i.e., Medicine Bow and Routt National Forests receive more precipitation than Pike and San Isabel National Forests) (Fig. 4A). Correlations between precipitation and growth were positive and strongest for sites on the Medicine Bow and Routt and Pike National Forests for the precipitation three-month averages for February–April, April–June, and May–July. On the Pike National Forest, there were also significant, positive correlations between increment growth and the precipitation averages for March–May (Table 1). Among series collected from sites on the San Isabel National Forest, growth was negatively correlated with precipitation averages from August through October of the same year (Table 1). Negative correlations were detected between growth and maximum May and June temperatures for sites on the Medicine Bow and Routt National Forests and maximum May temperatures for sites on the Pike National Forest (Table 2).

Fig. 2. Categorical regression tree of plots containing likelihood of high cohesive response (HCR) or low cohesive response (LCR) series (i.e., increment cores) occurring in plots with various site, stand, and soil characteristics. Grey and white bars indicate the proportion of transects (with up to three cores per transect) exhibiting LCR or HCR. $N = 70$; $R^2 = 0.381$; splits = 4. MB-RT, Medicine Bow and Routt National Forests; PI, Pike National Forest; SI, San Isabel National Forest.

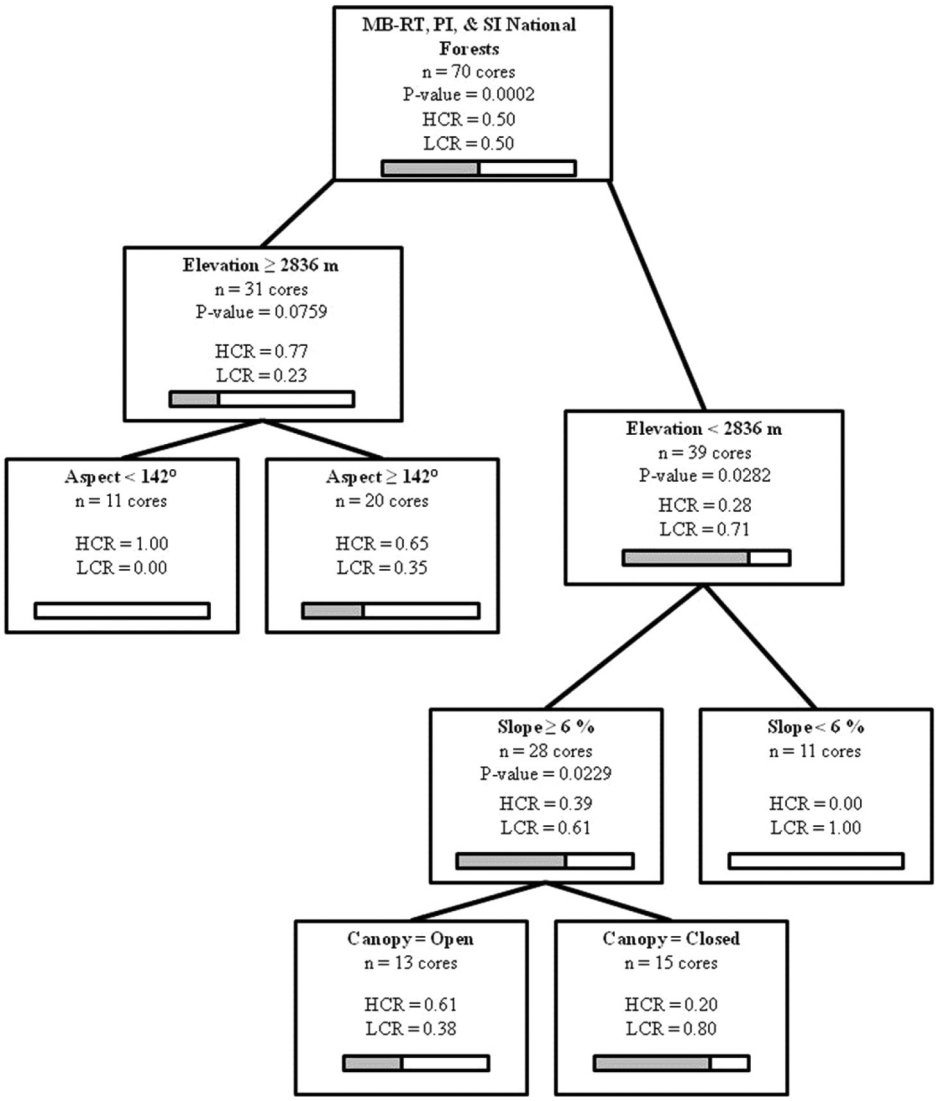


Fig. 3. Average occurrence of five common fungal diseases and two damaging insect groups on adult aspen by low cohesive response (LCR) or high cohesive response (HCR) tree type as recorded in a stand health survey during 2009–2010. All means are least-square means. Error bars represent LSD; bars that do not overlap are significantly different at $P = 0.10$. Damage agents included in the above categories are as follows: Cryptosphaeria canker, *Cryptosphaeria lignyota*; sooty bark canker, *Encoelia pruinosa*; black canker, *Ceratocystis populicola*; white tree rot (Phellinus conk), *P. tremulae*; Cytospora canker, *Cytospora chrysosperma* and *Cytospora notastroma*; wood borers *Agrilus liragus* and *Saperda calcarata*; and aspen bark beetles *Trypophloeus populi* and *Procryphalus mucronatus*.

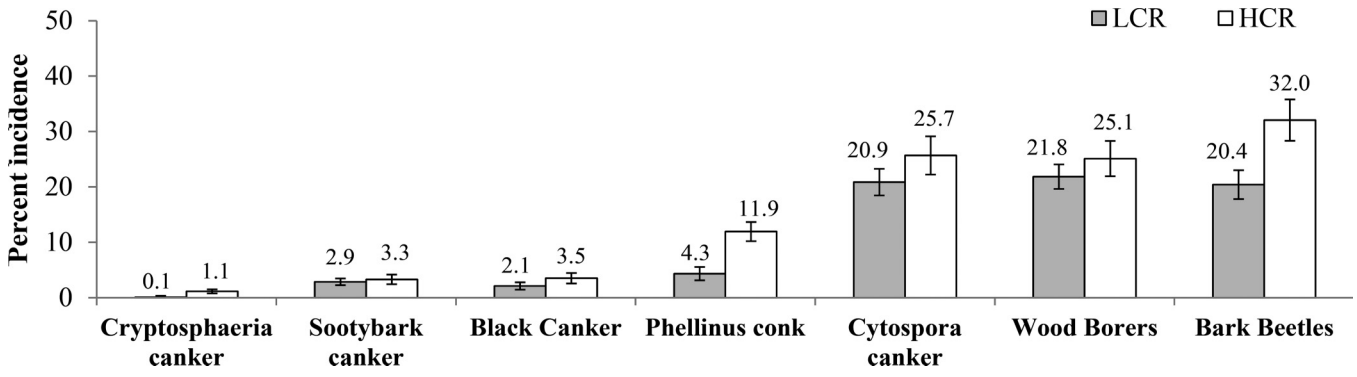


Fig. 4. (A) Annual average precipitation (mm) for four national forests, 1900–2008. (B) Average annual ring width index (RWI, mm) of HCR trees from three national forests, 1900–2008.

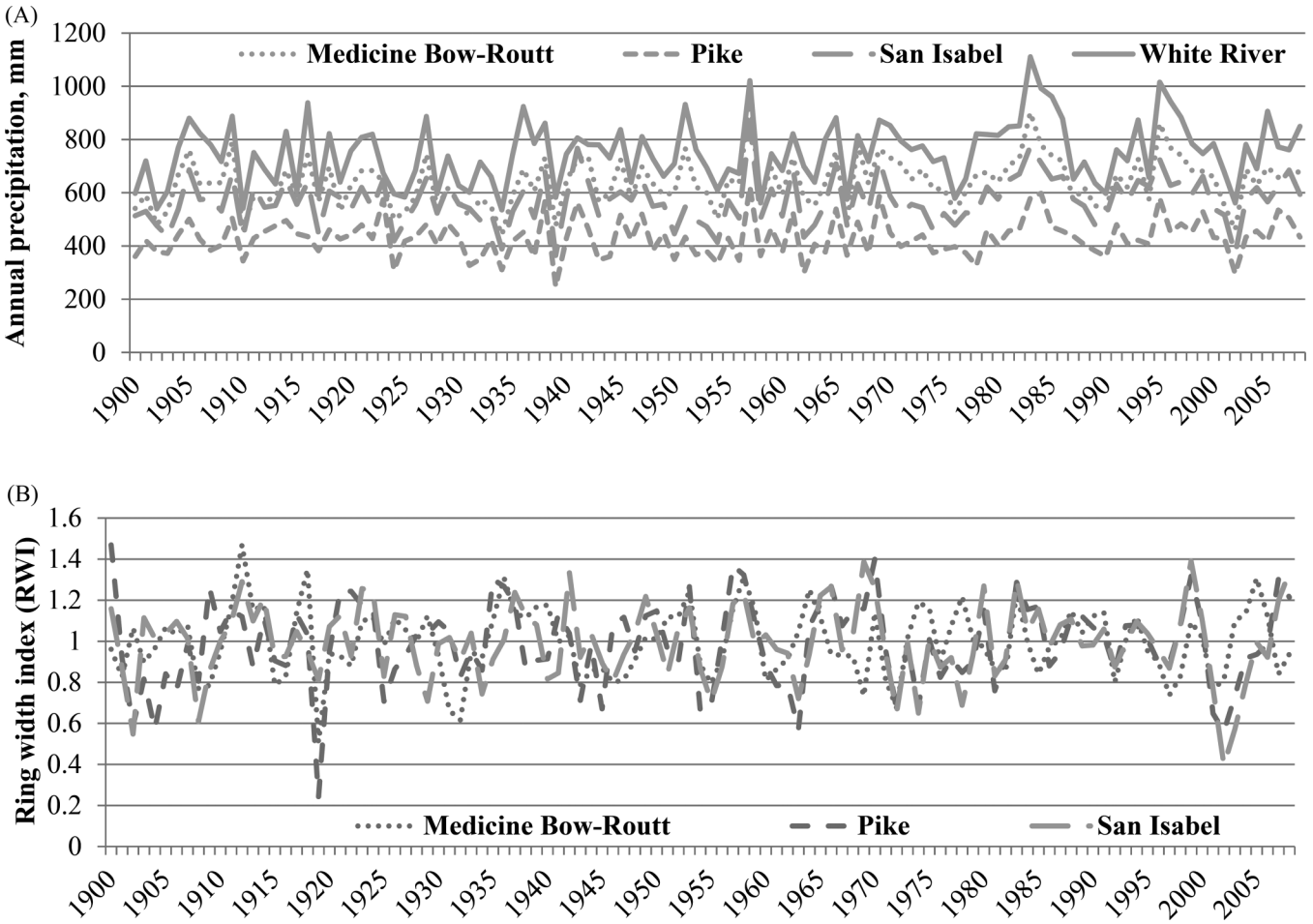


Table 2. Spearman correlation coefficients and *P* values of associations between ring width indices and maximum monthly temperatures from 1950–2008.

	May	June	July	August
Medicine Bow and Routt National Forests				
Spearman	–0.1540	**–0.2142**	–0.1828	0.1054
P value	0.2442	**0.1034**	0.1659	0.4267
Pike National Forest				
Spearman	**–0.2795**	–0.2022	–0.1725	0.1284
P value	**0.032**	0.1247	0.1915	0.3325
San Isabel National Forest				
Spearman	–0.1047	0.0145	–0.0112	–0.1856
P value	0.4299	0.9132	0.9328	0.1594

Note: Values in bold indicate significant relationships at $P = 0.10$; $n = 59$ years.

The final model of RWI and climatic influences included both maximum temperature and precipitation ($P = 0.0002$) (Table 3). Maximum May and July temperatures, combined with both annual precipitation (of the same calendar year) and the annual precipitation of the previous year, were selected based on the AIC_c score (Table 3). When maximum monthly temperature was removed from both of the precipitation models, differences in RWI were predicted by forest and the current or previous year's annual precipitation (Figs. 5 and 6; Appendix Figs. A5–A7). Trees on the Pike and San Isabel National Forests produced larger annual rings when either the current or previous year's annual precipitation was above average than during periods of normal or below-average precipitation. This pattern was not observed among cores taken from the Medicine Bow and Routt National Forests; average increment did not vary among the three precipitation classes (Figs. 5 and 6; Appendix Figs. A5–A7). We further noted that the standard error of annual growth for years with normal precipitation and monthly temperature was very small relative to error values for growth under other conditions (Appendix Figs. A8–A10). This pattern persisted across all three national forests and ranged from 0.018 to 0.019 relative to the standard errors of other temperature and precipitation combinations (0.076–0.174).

Analysis of 10-year averaged annual precipitation by tree sensitivity (HCR or LCR), stand type (healthy or damaged), and national forest indicated pronounced differences (Appendix Figs. A11–A15). We detected differences between LCR and HCR sites located within heavily damaged stands but not between LCR and HCR sites located within lightly damaged stands (Appendix Figs. A11–A12). There were marked differences between HCR and LCR sites on the Medicine Bow and Routt and San Isabel National Forests but not between HCR and LCR sites on the Pike National Forest (Appendix Figs. A13 and A14). HCR sites on the Medicine Bow and Routt National Forests consistently received significantly more annual precipitation for every decade since 1900 (Appendix Fig. A13). This pattern was reversed on the San Isabel National Forest, where HCR sites received less annual precipitation for every decade since 1900, except for 1910–1919 (Appendix Fig. A15).

Table 3. Model selection of effects for the prediction of annual ring width indices of quaking aspen.

Step	Effect entered	Number	Model R^2	Adjusted R^2	AIC	AIC_c	*F* value	Pr > *F*
0	Intercept	1	0	0	–799.00	–798.97	0	1
1	Maximum July temperature	2	0.0322	0.0292	–807.61	–807.54	10.72	0.0012
2	Annual precipitation	3	0.0629	0.057	–816.04	–815.92	10.5	0.0013
3	Maximum May temperature	4	0.0699	0.0612	–816.48	–816.29	2.42	0.1207
4	Lagged annual precipitation	5	0.0767	0.0651*	–816.85*	–816.58*	2.34	0.1272
	Final model	1–5	0.0767	0.0651	816.85	–816.58	6.62	**0.0002**

Note: Numbers 2 and 3 are included in the final model, which includes steps 1–4. Climate data are from 1950–2008. Asterisk (*) indicates optimal criterion value. No effects were removed in this model selection. Final model *P* value was calculated using the *F* statistic (6.62); numerator degrees of freedom, *k*–1 (3); denominator degrees of freedom, *N*–*k* (320).

Fig. 5. Average annual ring width index (RWI, mm) of adult aspen among three national forests and three moisture classes,* as modeled with the corresponding year's total precipitation (by plot, averaged to national forest), 1900–2008. All means are least-square means. Error bars represent LSD; bars that do not overlap are significantly different at $P = 0.10$. *Moisture classes are based on a 90% CI of annual precipitation data (1900–2008), where "normal" includes years with precipitation amount within the 90% range, and "dry" and "wet" years are those above or below range cutoff. RWI is represented based on 69 tree cores (18, Medicine Bow and Routt National Forests; 21, Pike National Forest; 30, San Isabel National Forest).

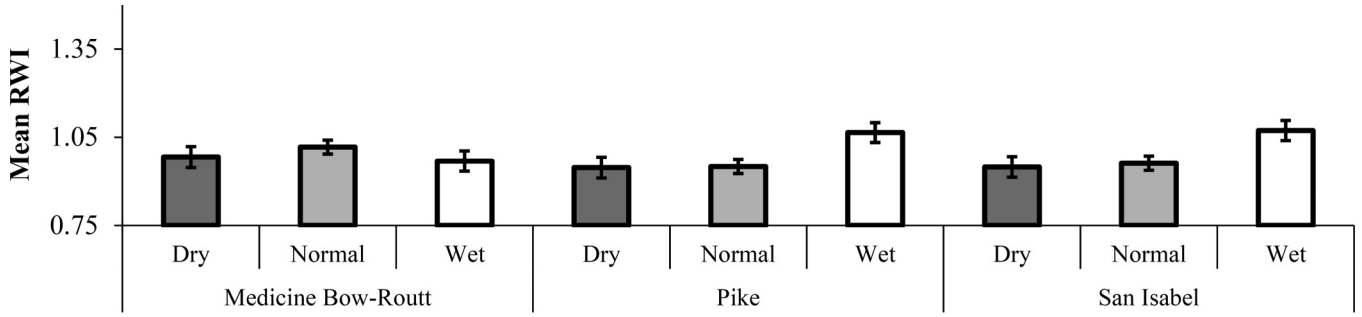
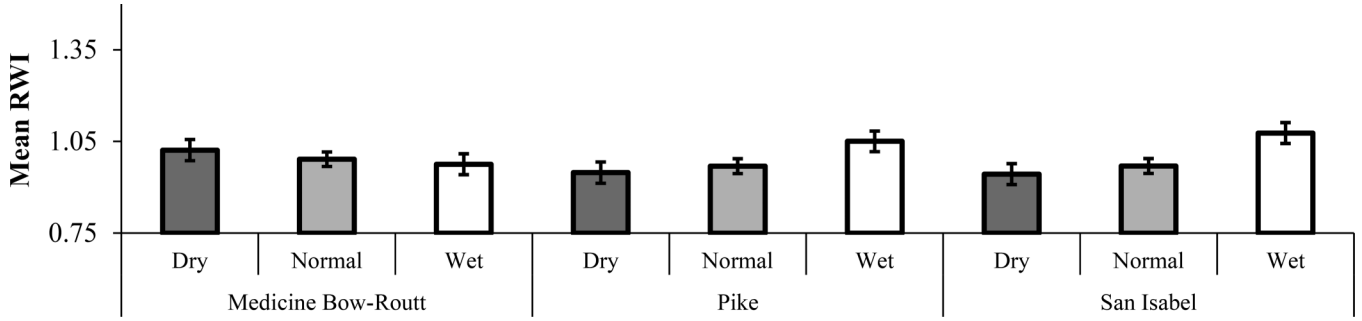


Fig. 6. Average annual ring width index (RWI, mm) of adult aspen among three national forests and three moisture classes,* as modeled with one year lagged annual precipitation (by plot, averaged to national forest), 1900–2008. All means are least-square means. Error bars represent LSD; bars that do not overlap are significantly different at $P = 0.10$. *For explanation of moisture classes, see Fig. 5 caption.



Discussion

In our analyses of site and stand characteristics of stands producing HCR or LCR trees, four tested variables stood out as predictors of tree sensitivity. The four main predictors of whether a site produces HCR or LCR trees were site elevation, site slope, site aspect, and stand structure, all of which suggest the influence of water availability. We have previously described the differences between cores from the White River National Forest and the four other forests surveyed. The conclusions reached by Hogg et al. (2013), based on a soil moisture index (SMI) model, accurately predicted lags in tree growth occurring on sites with deeper soils. We suspect that a "hydrologic lag" (Hogg et al. 2013) may be occurring on at least some of the sites with LCR trees. Sites on the White River National Forest occurred on soils with a mean epipedon depth of 65.8 cm relative to 13–19 cm on the other four national forests (data not shown). Increment cores from HCR trees clearly indicate key drought years and years of moisture surplus (e.g., 1924, 1939, 1957, and 1982) (Fig. 4), but these patterns were largely absent among LCR cores across all national forests.

Table 4. Mild, severe, and normal annual precipitation values for three national forests from 1900–2008.

	Precipitation (mm)				
National forests	Very wet	Mildly wet	Normal	Mildly dry	Very dry
Medicine Bow and Routt	>827	796–827	486–796	456–486	<456
Pike	>573	549–573	314–549	291–314	<291
San Isabel	>746	717–746	424–717	395–424	<395

Note: Mild and severe categories represent 1.67 and 2 standard errors from the mean, respectively.

The dramatic difference in responses of proximal trees to widespread drought events could also represent phenotypic differences in drought tolerance from one clone to another, as has been documented by Griffin et al. (1991). Mounting genetic evidence suggests

Table 5. Mild, severe, and normal maximum temperature values by month (May, June, July, and August) for three national forests from 1900–2008.

	Temperature (°C)				
National forests	Very cool	Mildly cool	Normal	Mildly warm	Very warm
May					
Medicine Bow and Routt	<9.8	9.8–10.4	10.4–17.0	17.0–17.6	>17.0
Pike	<7.8	7.8–8.5	8.5–15.5	15.5–16.2	>16.2
San Isabel	<9.8	9.8–10.5	10.5–17.0	17.0–17.6	>17.6
June					
Medicine Bow and Routt	<16.0	16.0–16.5	16.5–22.1	22.1–22.7	>22.7
Pike	<14.5	14.5–15.1	15.1–21.0	21.0–21.6	>21.6
San Isabel	<16.3	16.3–16.9	16.9–22.4	22.4–22.9	>22.9
July					
Medicine Bow and Routt	<20.2	20.2–20.6	20.6–24.9	24.9–25.3	>25.3
Pike	<19.0	19.0–19.4	19.4–23.9	23.9–24.3	>24.3
San Isabel	<19.9	19.9–20.3	20.3–24.6	24.6–25.0	>25.0
August					
Medicine Bow and Routt	<19.4	19.4–19.8	19.8–23.4	23.4–23.8	>23.8
Pike	<18.4	18.4–18.7	18.7–22.5	22.5–22.9	>22.9
San Isabel	<18.7	18.7–19.1	19.1–23.0	23.0–23.4	>23.4

Note: Mild and severe categories represent 1.67 and 2 standard errors from the mean, respectively.

that aspen stands are often not comprised of a single clone, but of many distinct individuals (DeWoody et al. 2009; Long and Mock 2012). Based on this, some of the variability in drought response among trees growing near each other (i.e., within 100 m) may be a reflection of varying drought tolerance among genotypes. This explanation is likewise applicable when examining the range of growth responses under conditions other than average maximum monthly temperature and precipitation. Although sampled trees responded similarly to normal moisture and temperature, tree responses to weather conditions outside of the average range varied considerably, although it is uncertain whether the apparent variability in drought tolerance present in these populations is sufficient to protect them from an increasingly warmer and drier habitat. Recently, a study of genetic variability of quaking aspen stands throughout North America indicated that in comparison to stands in the northern and eastern portions of its range, aspen stands in the southwestern US have lower within-population diversity (Callahan et al. 2013). Such decreased allelic richness, as postulated by Callahan et al. (2013), does not bode well for these populations, perhaps making them more vulnerable to the prolonged episodes of drought predicted for the southwestern US under climate change.

We note that aspen stands on the White River National Forest (WRNF), which were sampled and measured but the increment data were not used in RWI analyses, differed from stands on other national forests. Of the more than 40 increment cores collected from the WRNF, only about a dozen had sufficiently high correlation coefficients (in COFECHA). These were later excluded from the final chronologies due to their low EPS values (from ARSTAN). Key site differences are likely the reason that stands on the WRNF did not respond to climatic influence with the same consistent and standwide variations in growth. We suspect that the aspen stands on the WRNF are less likely to experience drought events than those on the other national forests that we surveyed. This is likely due, in part, to the dramatically deeper surface soils that occur in the area and, in part, to phenotypic differences in drought tolerance (discussed above). Measured frequency of Cytospora canker is a reasonable proxy for assessing drought stress in a stand, as the causal organism, *Cytospora* spp., successfully colonizes healthy tissue when the host tree is experiencing some environmental stressor, usually drought (Guyon et al. 1996; Christensen, 1940). Surveyed adult aspen on the WRNF had very low levels of Cytospora canker relative to the other national forests; in 2009–2010, we observed Cytospora canker on about 2% of adult live aspen stems relative to 13%–51% of adult live aspen elsewhere (data not shown) (Dudley et al. 2015).

Our analyses of RWI and annual precipitation (Figs. 5 and 6), which includes the current and previous years' annual precipitation, appears to be more applicable to the southerly locations of the study area. Trees on the Pike and San Isabel National Forests clearly responded favorably to years of above-average precipitation, but those on the Medicine Bow and Routt National Forests did not. It is important to note that the average annual precipitation range for the Medicine Bow and Routt National Forests is over 30% higher than for the Pike National Forest (Table 4; Fig. 4). This may be one reason that the trees on these northern forests do not respond as strongly to years of low precipitation. A dry year in the northern portion of the study area could represent twice as much precipitation as is received in a dry year in the southern portion of the study area (Table 4).

The timing of precipitation over the course of a year also differs dramatically between forests in the north (White River and Medicine Bow and Routt National Forests) and the central and southern portions of Colorado (Pike and San Isabel National Forests) (Appendix Fig. A16). Both forests in the southern portion of the study area receive much of their annual precipitation between April and September, whereas the forests in the north receive most of their precipitation from September to April mainly as snowfall (Fig. A16). In addition to moisture content, snowpack also reduces environmental stress on aspen because it insulates the roots during freeze events, as was shown by Hogg et al. (2002) in the aspen parklands of Alberta, Canada. A recent study of aspen decline and climate factors (Worrall et al. 2013) indicated that a major driver of aspen mortality is precipitation received between April and September paired with maximum summer temperatures, a result similar to the model produced from this study.

The negative correlation between RWI and the three-month precipitation average from August to October for sites on the San Isabel National Forest could be a reflection of the dependency of these stands on monsoonal moisture. The monsoon season, which typically begins mid-July in Colorado, is often preceded by periods of hot, dry weather (Doeskin et al. 2003). Late monsoonal moisture could, therefore, account for the negative correlation of August–October precipitation with RWI; the later the arrival of the summer storms, the more pronounced the drought is in areas dependent on these weather patterns.

We note that maximum temperatures during the spring (May) and midsummer (July) have a significantly negative impact on the growth of trees on the Pike and Medicine Bow and Routt National Forests (Table 5), independent of precipitation. This finding is similar to that of Hanna and Kulakowski (2012) and Spond et al. (2014), who

observed negative relationships between RWI of aspen and seasonal maximum temperatures. It is therefore likely that as the incidence of extreme heat events increases (as predicted by the most recent Intergovernmental Panel on Climate Change (IPCC) report for the coming century; IPCC 2013), aspen will continue to experience conditions that are not conducive to optimal growth, also supported by the findings of Rehfeldt et al. (2009). It should also be noted, however, that this relationship between drought and stem mortality is not always clear; a recent large-scale study of aspen stands throughout the western US have shown that although aspen mortality is influenced by drought, these impacts can be obscured by stand dynamics and stand age (Bell et al. 2014).

It has been well documented that aspen stands experiencing environmental stress are highly prone to certain insects and diseases such as wood borers, bark beetles, and (as noted above) Cytospora canker (Hogg et al. 2008; Marchetti et al. 2011; Worrall et al. 2008, 2010; Guyon et al. 1996; Christensen 1940). Drought, as well as secondary disease and damage agents and excessive browsing by ungulates, can result in stands with high levels of mortality and low levels of regeneration (Rogers et al. 2013; Worrall et al. 2008, 2010).

Maintaining aspen stands on western landscapes, especially under prolonged drought conditions, may require proactive management actions such as overstory removal (through mechanical or prescribed fire treatments) and ungulate exclusion (Rogers et al. 2013). We observed that stands that responded to drought conditions (i.e., HCR stands) were spatially distinctly located and not randomly found across the aspen forest types. The series examined in this study also indicate that quaking aspen in Colorado and southern Wyoming have varying degrees of tolerance to drought, and this tolerance is likely the result of a complex of genotype and site conditions. Based on the variation in spatial pattern and degree of drought tolerance, proactive management will need to be tailored to the stand or district level.

Acknowledgements

We would like to acknowledge and thank J. ZumBrunnen for consultation on statistical analyses, P. Brown and L. Huckaby for lending their expertise on all things dendrochronological, M. Hallowed for field assistance, K. Jacobi for cross-dating assistance, and S. Nilson for technical expertise and assistance with sample preparation.

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Appendix A

Table A1. Descriptive statistics of the residual chronologies used in ring width indices (RWI) analyses from the output of two software programs (ARSTAN and COFECHA) from tree cores collected from adult quaking aspen on five national forests in Colorado and southern Wyoming in 2009–2010.

	Residual chronologies (ARSTAN)							Raw chronologies (COFECHA)	
	Running *r*-bar								
National forest	Year interval	No. of series	$\bar{r}$	EPS	Years	Total no. of series	Mean, mm (SE)	Mean sensitivity	SIC
Medicine Bow and Routt	1890–1940	15	0.253	0.832	1883–2008	21	1.00 (0.158)	0.318	0.428
	1915–1960	20	0.208	0.838					
Pike	1860–1910	14	0.307	0.856	1857–2008	18	1.00 (0.205)	0.373	0.45
	1885–1935	17	0.300	0.878					
	1910–1960	18	0.311	0.888					
San Isabel	1860–1910	19	0.390	0.922	1856–2008	30	0.992 (0.177)	0.365	0.467
	1885–1935	25	0.260	0.898					
	1910–1960	29	0.302	0.925					
White River*	1910–1960	7	0.353	0.801	1906–2008	8	0.99 (0.344)	0.326	0.362

Note: EPS, expressed population signal; SE, standard error; SIC, series intercorrelation coefficient.
*Series not used in RWI analysis.

Table A2. Site and stand characteristics of healthy and damaged aspen stands on 11 ranger districts and five national forests.

Stand type	Site type	Elevation (m)	Aspect (degrees)	% Slope	% Conifer encroachment	Depth of "A" horizon	No. of stems·ha^{-1} (adults)	No. of stems·ha^{-1} (understory)	Basal area·ha^{-1} (m^2) (adults)	QMD (cm) (adults)	% Live stems (adults)	% Live stems (understory)	% Dead crown (adults)
Medicine Bow and Routt National Forests													
Healthy	LCR	2559a	155bc	11.8a	10.5b	16.4a	2446b	10612b	108.2c	23.8bc	85.4bc	93.0cd	22.3ab
	HCR	2641a	112ab	14.3a	7.8ab	19.9a	2178b	9750b	89.5bc	24.5bc	82.5bc	91.1cd	25.9b
Damaged	LCR	2580a	162c	12.6a	5.2a	19.8a	2103b	9689b	79.4bc	23.1bc	61.3a	92.9cd	47.7c
	HCR	2712b	204c	23bc	0.5a	21.3a	1792ab	6854bc	81.9bc	24.4bc	63.3a	91.6bcd	48.6c
Pike National Forest													
Healthy	LCR	2921bc	175bc	6a	5.5ab	14a	1200ab	3854a	19.9a	17.2ab	50.0a	95.0bcd	50.6c
	HCR	3069c	187bc	12.3ab	0.4a	14.5a	1800ab	4625abc	80.2b	21.4ab	79.5bc	64.2a	7.9a
Damaged	LCR	3077c	185bc	23bc	4.7a	13.6a	1864ab	4083ab	50.0ab	17.0a	63.6a	75.1abc	39.4c
	HCR	3040c	43a	8a	4.7a	13a	2425ab	4035ab	75.1abc	20.1ab	62.8ab	92.9bcd	44.6bc
San Isabel National Forest													
Healthy	LCR	2678ab	162bc	30.2c	7.0ab	15.3a	2042ab	5166ab	63.6ab	20.7ab	81.7bc	77.1abc	18.6a
	HCR	2941c	181c	18.8ab	7.8ab	13.7a	2025ab	4725abc	61.4ab	20.1ab	82.0bc	73.5abc	23.8ab
Damaged	LCR	—	—	—	—	—	—	—	—	—	—	—	—
	HCR	2914c	133b	18.1ab	10.6b	15a	2036b	6172abc	52.4a	18.1ab	65.2a	76.3abc	44.0c
White River National Forest													
Healthy	LCR	2693ab	228c	26.6bc	6.9ab	65.6b	2121b	4350ab	82.8b	22.2b	89.1bc	74.3abc	13.9a
	HCR	—	—	—	—	—	—	—	—	—	—	—	—
Damaged	LCR	2660ab	229c	31.6c	1.5a	66b	1233a	4883ab	62.8ab	26.0c	67.6a	96.0d	45.7c
	HCR	—	—	—	—	—	—	—	—	—	—	—	—

Note: Estimates are least-squares means. Lowercase letters following values indicate significant differences between the means at $P \leq 0.10$. Means in the same column with the same letter are not significantly different from each other. Site types: LCR, low cohesive response; HCR, high cohesive response. QMD, quadratic mean diameter: QMD = $\sqrt{\left(\frac{\text{BA} \times \text{Frequency}}{k \times \text{tpha}}\right)}$, where BA is basal area (m^2), tpha is trees per hectare, and k is a constant, 0.0000785.

Figs. A1–A4. The characteristics of adult aspen (≥12.0 cm DBH) by national forest, stand type, and tree response type, as recorded during a 2009–2010 aspen health survey. Data are averaged to the plot level and designated high cohesive response (HCR) if at least one of the three cores was HCR. All means are least-square means. Error bars represent LSD; bars that do not overlap are significantly different at $P = 0.05$. MB & RT, Medicine Bow and Routt National Forests; LCR, low cohesive response; HCR, high cohesive response.

Fig. A1. Basal area (m^2) of adult aspen per hectare in Colorado and southern Wyoming surveyed in 2009–2010.

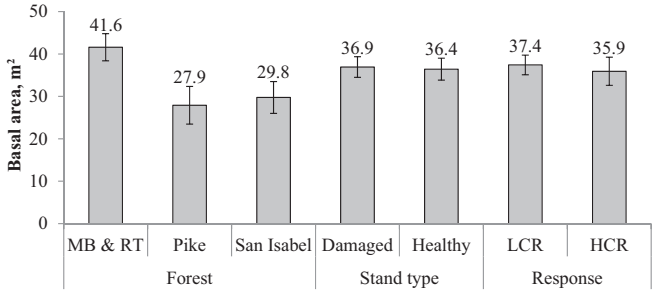

Fig. A2. Live adult aspen stems in Colorado and southern Wyoming surveyed in 2009–2010.

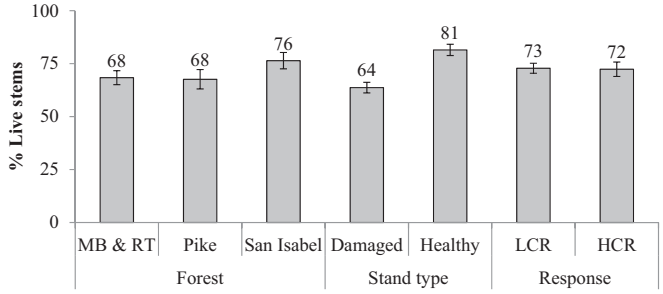

Fig. A3. Average dead crown of adult aspen in Colorado and southern Wyoming surveyed in 2009–2010.

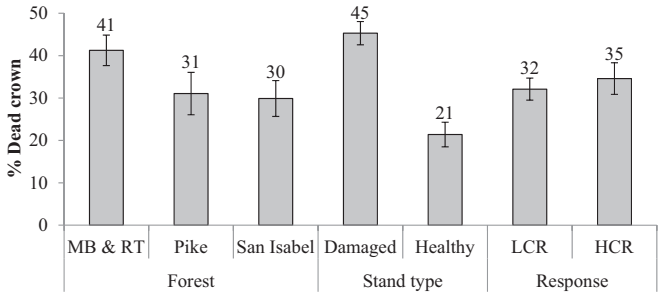

Fig. A4. Average health index score (1–3; 1 = very healthy, 2 = marginal, 3 = dying) of adult live aspen in Colorado and southern Wyoming surveyed in 2009–2010.

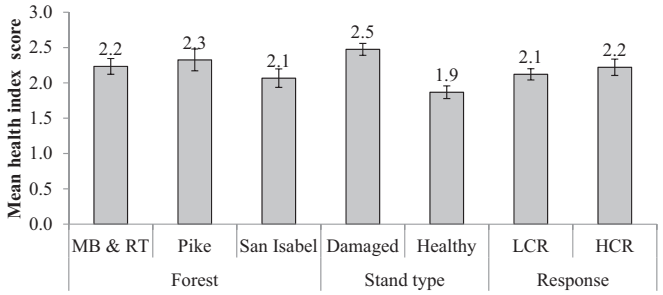

Fig. A5. All four (stacked) chronologies of adult aspen from increment cores collected from the Medicine Bow and Routt National Forests, 2009–2010.

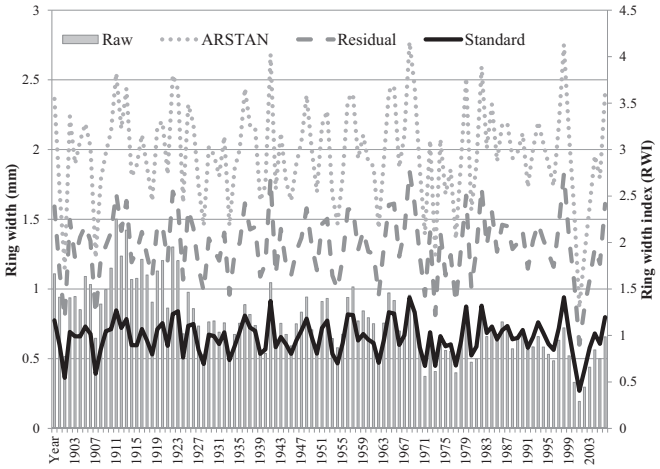

Fig. A6. All four chronologies of adult aspen from increment cores collected from the Pike National Forest, 2009–2010.

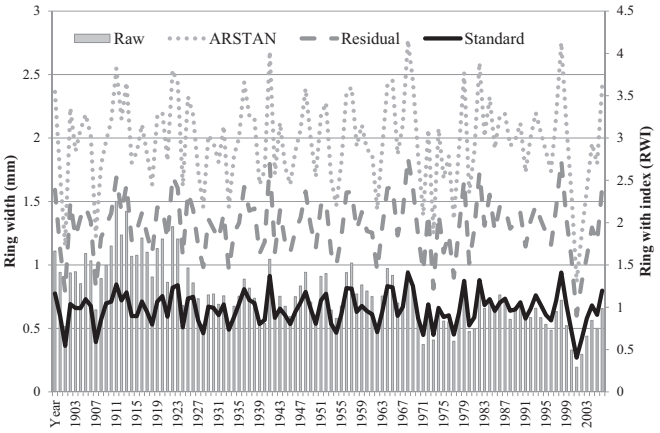

Fig. A7. Three chronologies and the raw ring width values of adult aspen from increment cores collected from the San Isabel National Forest, 2009–2010.

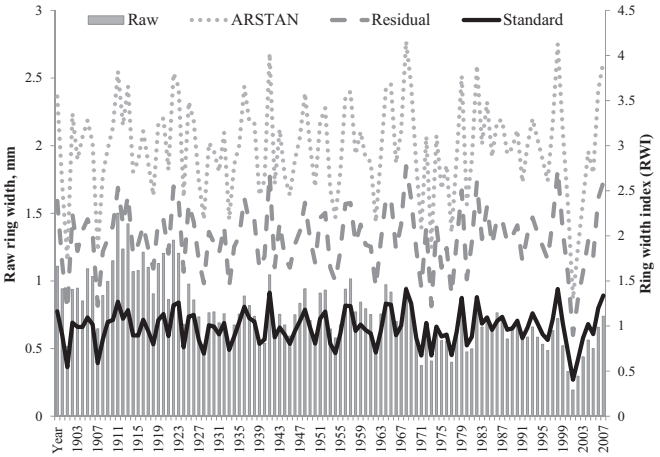

Fig. A8. Modeled ring width index (RWI) among series on the Medicine Bow and Routt National Forests (MBRT), with monthly maximum temperature and either the current or lagged annual precipitation. Precipitation and maximum temperature categories are identical to those listed in Tables 4 and 5. Error bars represent LSD; bars that do not overlap are significantly different at $P = 0.10$.

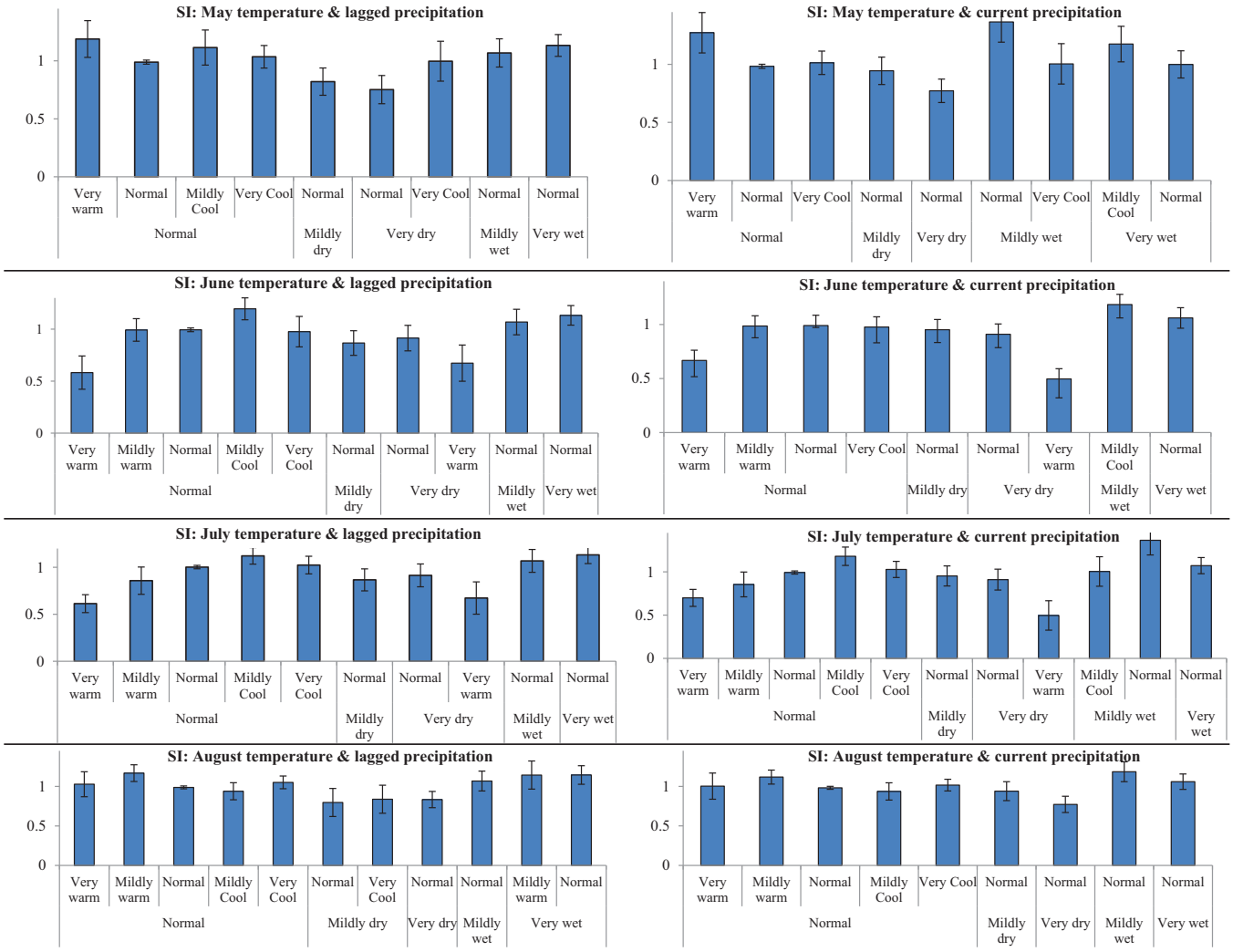

Fig. A9. Modeled ring width index (RWI) among series on the Pike National Forest, with monthly maximum temperature and either the current or lagged annual precipitation. Precipitation and maximum temperature categories are identical to those listed in Tables 4 and 5. Error bars represent LSD; bars that do not overlap are significantly different at $P = 0.10$.

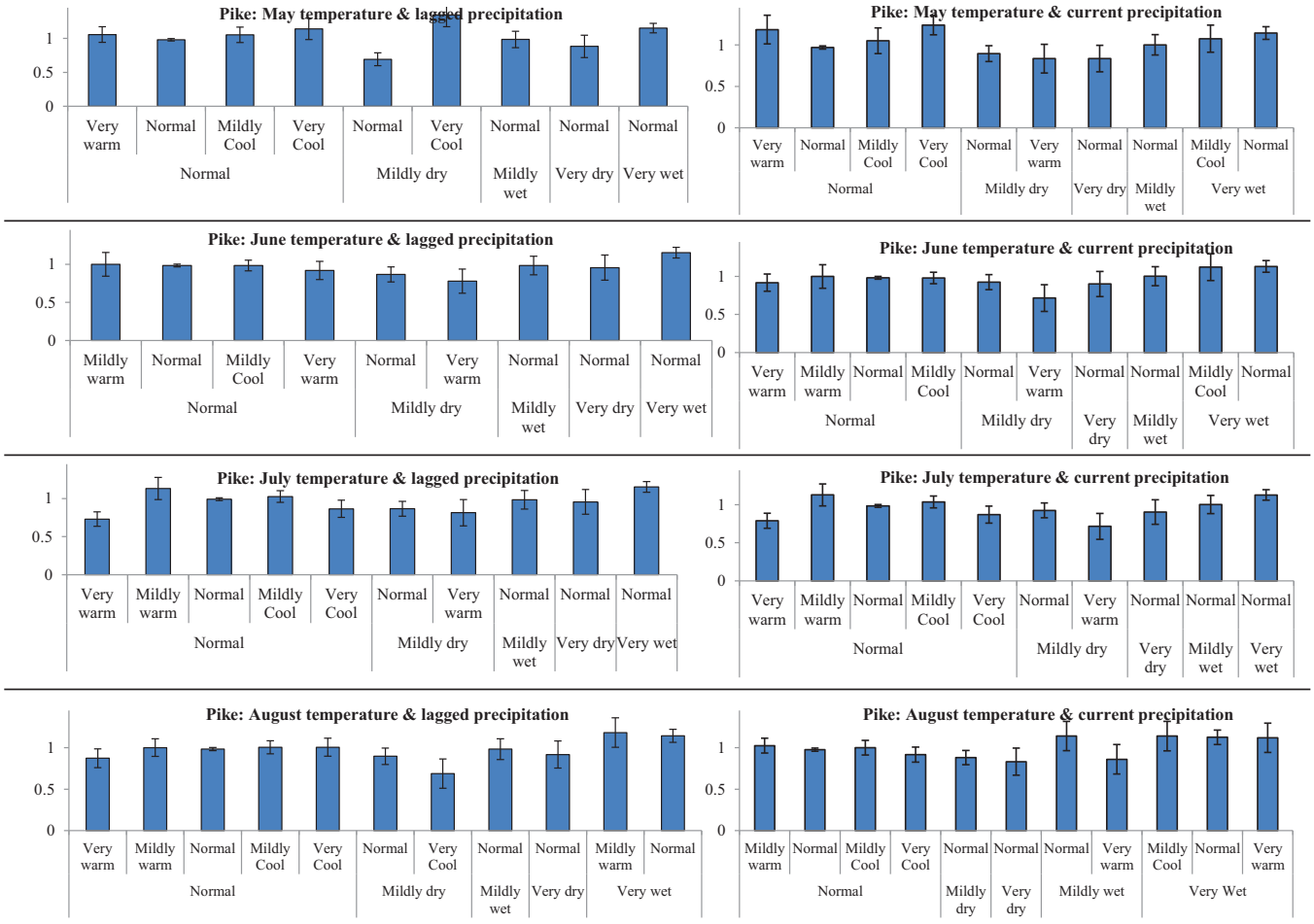

Fig. A10. Modeled ring width index (RWI) among series on the San Isabel National Forest (SI), with monthly maximum temperature and either the current or lagged annual precipitation. Precipitation and maximum temperature categories are identical to those listed in Tables 4 and 5. Error bars represent LSD; bars that do not overlap are significantly different at $P = 0.10$.

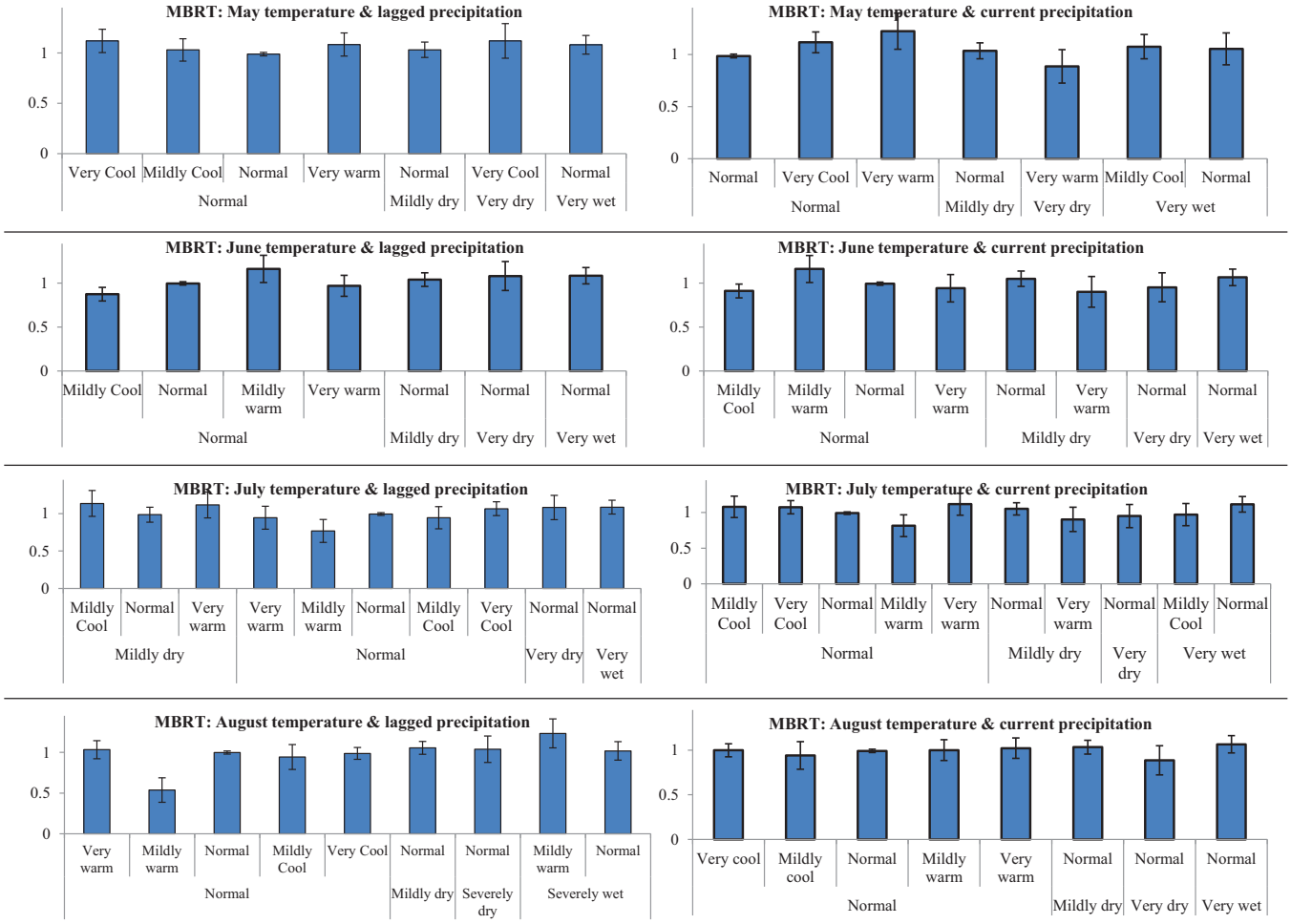

Fig. A11. Average annual precipitation (mm) by decade among low cohesive response (LCR) and high cohesive response (HCR) sites within lightly damaged stands. Means are least-square means. Error bars represent LSD; bars that do not overlap are significantly different at $P = 0.10$.

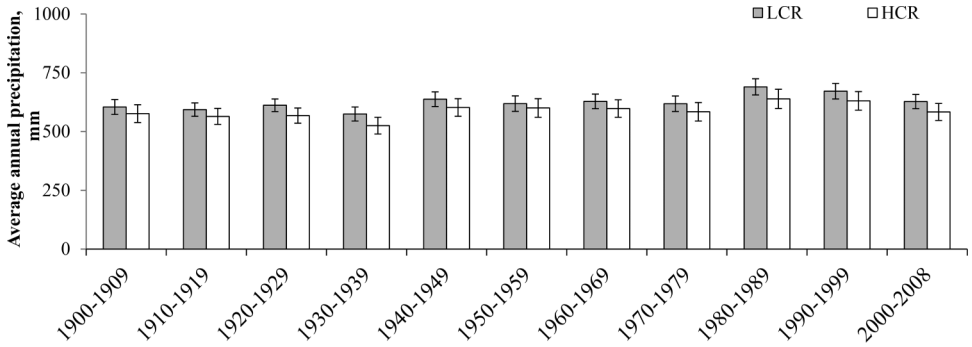

Fig. A12. Average annual precipitation (mm) by decade among low cohesive response (LCR) and high cohesive response (HCR) sites within heavily damaged stands. Means are least-square means. Error bars represent LSD; bars that do not overlap are significantly different at $P = 0.10$.

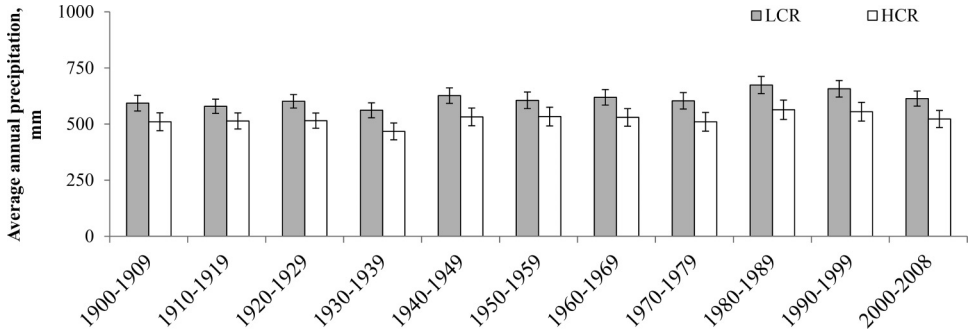

Fig. A13. Average annual precipitation (mm) by decade among among low cohesive response (LCR) and high cohesive response (HCR) sites within the Medicine Bow and Routt National Forests. Means are least-square means. Error bars represent LSD; bars that do not overlap are significantly different at $P = 0.10$.

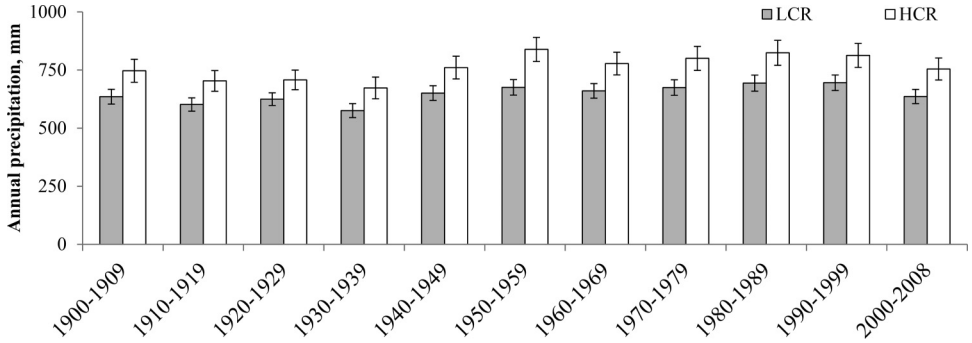

Fig. A14. Average annual precipitation (mm) by decade among low cohesive response (LCR) and high cohesive response (HCR) sites within the Pike National Forest. Means are least-square means. Error bars represent LSD; bars that do not overlap are significantly different at $P = 0.10$.

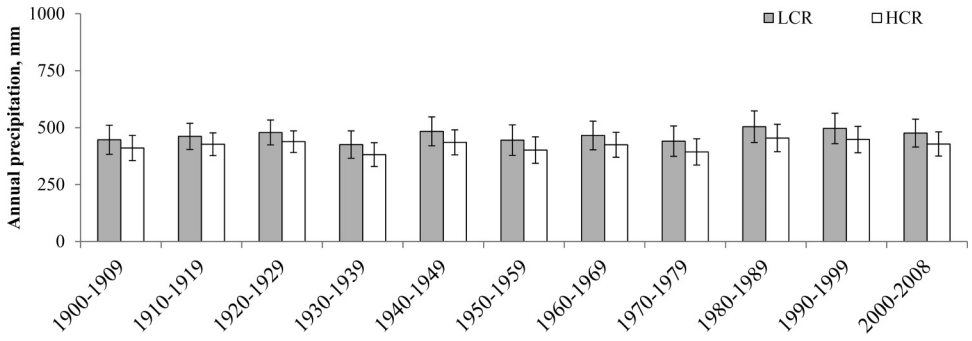

Fig. A15. Average annual precipitation (mm) by decade among low cohesive response (LCR) and high cohesive response (HCR) sites within the San Isabel National Forest. Means are least-square means. Error bars represent LSD; bars that do not overlap are significantly different at $P = 0.10$.

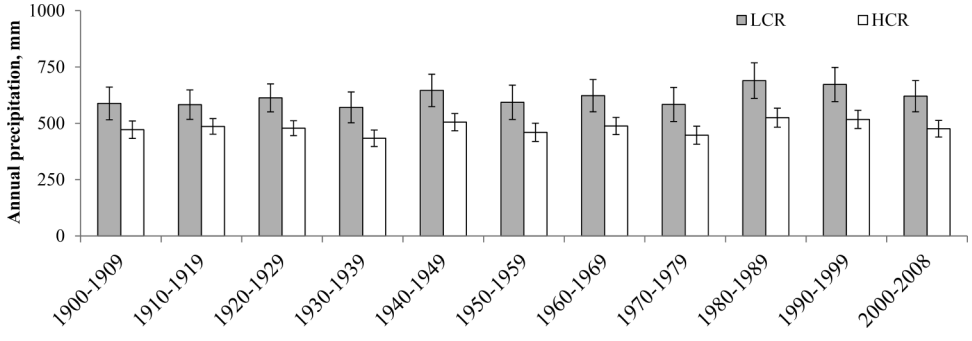

Fig. A16. Three-month running averages of precipitation (mm) by national forest from 1950–2008. Error bars represent LSD; bars that do not overlap are significantly different at $P = 0.10$. MB & RT, Medicine Bow and Routt National Forests.