COMPARISON OF TREE SPECIES SENSITIVITY TO HIGH- AND LOW-EXTREME HYDROCLIMATIC EVENTS

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Abstract: We present here a six-species comparison of tree-ring growth response to extremes (below the 30th and above the 70th percentile) in temperature, precipitation, and corresponding streamflow. The species compared are Pinus edulis (PIED), Pseudotsuga menziesii (PSME), Pinus ponderosa (PIPO), Pinus flexilis (PIFL), Pinus aristata (PIAR), and Picea engelmannii (PCEN). Sensitivity was determined using contingency scores obtained by comparing tree-ring growth at different lags with hydroclimatic observations from the Upper Colorado River Basin in the southwestern United States. The scores were computed using dual scaling methods in which the higher scores are assigned to stronger relationships between tree-ring growth and severe hydroclimatic occurrences. At lag 0, PIED and PSME present the greatest sensitivity to severe streamflow events. For precipitation and temperature the most sensitive species at lag 0 are PIED and PIPO. PIAR and PCEN show no significant relationship with extreme hydroclimatic events. PIFL shows more uniform lag-to-lag scores, suggesting a higher year-to-year persistence for this species. In general, tree-ring growth for all sensitive species is more responsive to hot-dry than to cool-moist extreme conditions. The scoring method proposed in this study for the analysis of tree-ring records proved to be a useful tool for evaluating ring-width sensitivity to extreme climatic forcing.

INTRODUCTION

This study compares the relative response of several tree species to high and low extremes of temperature, precipitation, and corresponding streamflow. The four...
hydroclimatically sensitive species examined are: Pinus edulis (PIED), Pseudotsuga menziesii (PSME), Pinus ponderosa (PIPO), and Pinus flexilis (PIFL). For comparison purposes, the analysis includes two more complacent species: Pinus aristata (PIAR) and Picea engelmannii (PCEN). The objective is to determine which species are more sensitive to extreme hydroclimatic conditions and the characteristics of this sensitivity.

Understanding the relative sensitivities of different species is especially important if subsets of tree-ring chronologies (or individual trees) are being evaluated in the development of climate reconstruction models (Meko, 1997; Hidalgo et al., 2000). Tree-ring data sets used in large-scale dendroclimatologic studies often contain chronologies from multiple species to provide better spatial coverage of the study area and to include varying climatic signals captured by each species (Fritts et al., 1971; Fritts, 1974). However, a tradeoff exists between the need to use more predictors and a subsequent decrease in the real skill of the reconstruction model resulting from predictor overrepresentation (Loftgren and Hunt, 1982; Belsley, 1991, Garen, 1992; Hidalgo et al., 2000). A discussion about predictor overrepresentation in transfer models can be found in Garen (1992), Belsley (1991), and McCuen (1985). Loftgren and Hunt (1982) mentioned some of the drawbacks of overfitting tree-ring climate transfer functions. A balance can be achieved by producing models with fewer predictors that result in better validation statistics—i.e., $r$-square ($r^2$), root mean standard error (RMSE), cross-validation standard error (CVSE), reduction-of-error statistic (RE)—(Garen, 1992; Hidalgo et al., 2000). By testing different subsets of tree-ring networks, those chronologies that are the most responsive to climate can be determined, reducing the number of predictors and avoiding overfitting of the model.

As with more predictor-abundant models, parsimonious models also depend on a dataset composed of predictors from multiple tree species, but with fewer chronologies for each species, and some subsets may exclude certain species from the model. Using fewer variables in the interests of parsimony increases the importance of the chronologies chosen by the model. Thus, it is important to provide the model initially with the possibility of using all the species available for a site, but especially those which are more responsive. Ultimately, chronology or variable selection will be related to the subset that produces the best model (lowest CVSE or other verification/validation criteria). It should be noticed that variables with a modest correlation with the dependent variable may contain additional information not contained in other variables with better correlations. Variable selection is determined by a balance between correlation with the dependent variable and intercorrelation among the independent variables (Hidalgo et al., 2000).

The relationship between hydroclimatic variations (especially temperature and precipitation) has been well documented (Fritts, 1976; 1991, Cook and Kairiukstis, 1990). There are fewer studies comparing the relative sensitivity to hydroclimatic variation (especially streamflow) grouped by tree species. A detailed study by Schuman (1956) for the semi-arid United States shows statistical characteristics for individual trees and chronologies from different species, including correlations with seasonal precipitation and streamflow. Fritts (1974) evaluated the relationship between tree-ring width and climate using principal component and cluster analy-
The resulting clusters had different climatic response, and the percentage of sites tabulated by species (PSME, PIED, PIPO, PIAR, PIFL and other species) suggested a relationship between species type and variations of precipitation and temperature for different seasons. A study by Fritts and Shatz (1975) on the western United States is a common reference for comparison of species' sensitivity to climate. This study used the averaged intercorrelations between nearby chronologies as an indication of the hydroclimatic signal contained in the chronologies. In a 1982 study, Fritts et al. analyzed response functions that represent the correlation with hydroclimatic forcing by month with ring-widths for five tree species in North America. The study included PSME, PIPO, *Pinus longaeva*, *Quercus alba*, and *Picea rubens* chronologies from different locations. Landwehr and Matalas's (1986) study concerning the presence of persistence in tree-ring records includes statistical comparison of five species. In a 1987 study, Kienast et al. identified tree-ring parameters and site types most suitable for reconstruction of temperature and precipitation records using chronologies from different species for four regions of the world. One of the study regions was the Front Range of Colorado; in which two PCEN, two PIPO, one PSME and one *Picea pungens* chronologies were compared. Schweingruber (1993) presents some general physiological and morphological comparisons of a number of tree species. Villalba et al. (1994) compared ring-width variation from 25 tree-ring chronologies (11 PCEN, 1 PIFL, 9 *Abies lasiocarpa* and 4 *Pinus contorta* var. *latifolia*) using correlation and response function analysis in the Colorado Front Range. Garfin (1998) compared severe growth anomalies in the Sierra Nevada for *Sequoiadendron* and *Pinus* species and their relation to atmospheric circulation patterns.

In a recent study of the Colorado River Basin, Hidalgo et al. (2000) found that species differences could play a role, more important than some statistical characteristics, in the determination of the potential suitability of a chronology as a predictor in reconstruction models. The study recommended chronology-selection procedures based on the minimization of the cross-validation standard error (CVSE). Meko (1997) previously used a CVSE selection process to select the best subset among many single-tree predictors (instead of chronologies). The best models (lowest CVSE) are usually composed of few chronologies (parsimonious model) from multiple species. However, in some regions (in Colorado and Utah), chronologies from many species were available, but the better models consistently selected only certain species. This suggests that species type may be an important characteristic for defining the potential suitability for a chronology to be part of a reconstruction model.

Our goal is to directly compare the ring-width records from different tree species to hydroclimatic time series. In addition to direct comparisons, we also study the effect of lagging chronologies. We focus our study on tree growth response to extreme hydroclimatic events below the 30th percentile and above the 70th percentile and the coincidence of these events with extreme tree-ring growth. We compared these coincidences by species, by hydroclimatic parameter, and by lag time.
STUDY AREA AND DATA SOURCES

The study area is in the Upper Colorado River basin (UCRB), the principal source of water for the southwestern United States. The total area of the UCRB comprises approximately 283,100 km². Except for areas of high precipitation in the mountainous areas, much of the region is arid to semi-arid (Stockton and Jacoby, 1976).

The streamflow record most commonly used in hydrologic studies in the UCRB is the record at Lee’s Ferry, Arizona, which was obtained from the United States Bureau of Reclamation (USBR, 1998). It consists of adjusted total monthly streamflow measured at the Colorado River compact point one mile downstream of the confluence of the Colorado and the Paria rivers. Water-year totals were computed from the monthly streamflow values from 1896 to 1995. However, only streamflow data from 1914 to 1960 were used for three reasons. First, the majority of the available chronologies around the basin end around 1960. As a result, the hydrological and climate records were truncated to have a common ending with the tree-ring records. Second, data after 1963 are adjusted by the U.S. Bureau of Reclamation to account for upstream water diversion, especially from Lake Powell. Third, the streamflow data from 1896 to 1913 were extrapolated from distant stations and are not as reliable as the data after 1913 (Stockton and Jacoby, 1976).

Annual water-year precipitation totals and water-year temperature averages from 1914 to 1960 were computed from monthly values obtained from the National Climate Data Center (NCDC, 1999) for the following climate divisions: Wyoming (zone 3), Utah (zones 2 to 7), and Colorado (zone 2). Climate division boundaries do not exactly match the hydrologic basin boundaries, but the differences were considered small compared to the total common area.

Tree-ring index chronologies from six different species from the UCRB were obtained from the International Tree-Ring Data Bank (NOAA, 1997). A tree-ring index chronology is a standardized record of tree growth. Standardization removes the inherent growth trend in the raw tree-ring data resulting from normal physiological aging processes. There were 82 chronologies available for the basin: 25 are PSME, 16 are PIPO, 9 are PIFL, 16 are PIED, 7 are PIAR, and 9 are PCEN. Location of the chronologies by species can be found in Figure 1 and average species characteristics are listed in Table 1. It would be difficult to create a superior and/or uniform density of chronologies because of the lack of available chronologies in the NOAA (1997) database for some species, especially on the northern and western parts of the basin. For both the climate and tree-ring records, the main common signals were extracted using principal components analysis (PCA). To take advantage of the length and similarities in the variation of the chronologies at low and high frequencies, the tree-ring components were extracted from the period common to all chronologies, 1574–1960. The use of principal components (PCs) extracted from tree-ring records has been widely practiced and documented in dendroclimatic analyses (Fritts et al., 1971; Fritts, 1976; Guiot et al., 1982; Kutzbach and Guetter, 1982; Fritts, 1991).

Similar to a previous study in the UCRB (Stockton and Jacoby, 1976), chronologies outside the boundaries of the basin were also included. Since the total signal
of the basin was considered to be contained in the first PC, those chronologies with ring-width variations uncorrelated with this main mode of variability will have small loadings (Figure 1). In this way, the PCA excludes those sites unrelated to the major mode of variability by assigning them to later PCs.

Fig. 1. Spatial distribution of the chronologies used in this study. The values correspond to the loadings for PC1 at lag 0. Abbreviations: PIED = Pinus edulis; PSME = Pseudotsuga menziesii; PIPO = Pinus ponderosa; PIFL = Pinus flexilis; PIAR = Pinus aristata; PCEN = Picea engelmannii.
### Table 1. Averaged statistics for different tree species around the Upper Colorado River Basin

<table>
<thead>
<tr>
<th>Species</th>
<th>NAT STRW</th>
<th>PC1 PREC</th>
<th>PC1 TEMP</th>
<th>( r_{ib} )</th>
<th>Mean</th>
<th>S.D.</th>
<th>( \eta_{lag} )</th>
<th>M.S.</th>
</tr>
</thead>
<tbody>
<tr>
<td>PIED</td>
<td>0.56</td>
<td>0.40</td>
<td>-0.44</td>
<td>0.40</td>
<td>0.99</td>
<td>0.395</td>
<td>0.30</td>
<td>0.45</td>
</tr>
<tr>
<td>PSME</td>
<td>0.47</td>
<td>0.28</td>
<td>-0.37</td>
<td>0.39</td>
<td>0.98</td>
<td>0.388</td>
<td>0.40</td>
<td>0.38</td>
</tr>
<tr>
<td>PIPO</td>
<td>0.40</td>
<td>0.31</td>
<td>-0.31</td>
<td>0.36</td>
<td>1.00</td>
<td>0.378</td>
<td>0.42</td>
<td>0.38</td>
</tr>
<tr>
<td>PIFL</td>
<td>0.30</td>
<td>0.24</td>
<td>-0.16</td>
<td>0.21</td>
<td>0.99</td>
<td>0.263</td>
<td>0.46</td>
<td>0.23</td>
</tr>
<tr>
<td>PIAR</td>
<td>-0.14</td>
<td>-0.05</td>
<td>0.12</td>
<td>0.08</td>
<td>0.99</td>
<td>0.239</td>
<td>0.73</td>
<td>0.14</td>
</tr>
<tr>
<td>PCEN</td>
<td>-0.03</td>
<td>-0.02</td>
<td>0.01</td>
<td>0.09</td>
<td>1.00</td>
<td>0.184</td>
<td>0.60</td>
<td>0.13</td>
</tr>
</tbody>
</table>

**Notes:**
- NAT STRW is the annual natural streamflow record at Lee’s Ferry. PC1 PREC and PC1 TEMP are the first principal component of the total precipitation and temperature records, respectively. The averaged correlation between species is denoted by \( r_{ib} \). S.D. is the standard deviation, \( \eta_{lag} \) is the lag 1 autocorrelation coefficient, and M.S. is the mean sensitivity coefficient. All correlations are computed for the period 1914–1960. Statistics are computed for the period 1574–1960 (in parentheses). Insignificant correlations at the 95% confidence level are italicized. Abbreviations: PIED = *Pinus edulis*; PSME = *Pseudotsuga menziesii*; PIPO = *Pinus ponderosa*; PIFL = *Pinus flexilis*; PIAR = *Pinus aristata*; PCEN = *Picea engelmannii*. 
This study looks at the response of different tree species to hydroclimatic extremes for an entire basin. In order to obtain a single-basin response, it is necessary to integrate spatial variation of climate and tree response into single records for each species and for each hydroclimatic variable.

Precipitation and temperature data were integrated using PCA. Spatial PCs were extracted from the annual temperature averages and precipitation totals from the climate divisions listed in Table 2. The first principal component (PC1) of temperature and precipitation represents the major mode of variability of each variable in the UCRB and it is used in this study as a representation of a common underlying signal of hydroclimatic variation in a single record. Temperature PC1 accounted for 86.61% and precipitation PC1 for 68.17% of the total variability of the climate division data (Table 2). The streamflow record from Lee’s Ferry already integrates spatial variation of the basin through normal physical hydrologic processes.

We are investigating the factors of tree growth that are associated with a common major mode of hydroclimatic variability in the UCRB, which results in a stronger driving signal in the growth of sensitive species. This variability is represented by the temperature and precipitation PC1 extracted from the basin sub-regions.

Table 2. Loadings of the First Principal Component (PC1) Extracted from Total Precipitation (PREC) and Temperature (TEMP) Records

<table>
<thead>
<tr>
<th>Climate division</th>
<th>Area, km²</th>
<th>PREC</th>
<th>TEMP</th>
</tr>
</thead>
<tbody>
<tr>
<td>Colorado 02</td>
<td>99,721</td>
<td>0.88</td>
<td>0.94</td>
</tr>
<tr>
<td>Utah 02</td>
<td>3,562</td>
<td>0.55</td>
<td>0.87</td>
</tr>
<tr>
<td>Utah 03</td>
<td>14,508</td>
<td>0.90</td>
<td>0.96</td>
</tr>
<tr>
<td>Utah 04</td>
<td>45,375</td>
<td>0.94</td>
<td>0.97</td>
</tr>
<tr>
<td>Utah 05</td>
<td>29,151</td>
<td>0.77</td>
<td>0.97</td>
</tr>
<tr>
<td>Utah 06</td>
<td>14,816</td>
<td>0.91</td>
<td>0.90</td>
</tr>
<tr>
<td>Utah 07</td>
<td>55,752</td>
<td>0.82</td>
<td>0.87</td>
</tr>
<tr>
<td>Wyoming 03</td>
<td>52,676</td>
<td>0.77</td>
<td>0.95</td>
</tr>
<tr>
<td>Total area</td>
<td>315,561</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Variance explained by PC1, pct.

|                |          | 68.17 | 86.61 |

For climate divisions that cover approximately the Upper Colorado River Basin. Climate division areas as well as the percentage variance explained by the first principal component also are also shown.

METHODS

Spatial Integration of Hydroclimatic and Tree-Ring Data

This study looks at the response of different tree species to hydroclimatic extremes for an entire basin. In order to obtain a single-basin response, it is necessary to integrate spatial variation of climate and tree response into single records for each species and for each hydroclimatic variable.

Precipitation and temperature data were integrated using PCA. Spatial PCs were extracted from the annual temperature averages and precipitation totals from the climate divisions listed in Table 2. The first principal component (PC1) of temperature and precipitation represents the major mode of variability of each variable in the UCRB and it is used in this study as a representation of a common underlying signal of hydroclimatic variation in a single record. Temperature PC1 accounted for 86.61% and precipitation PC1 for 68.17% of the total variability of the climate division data (Table 2). The streamflow record from Lee’s Ferry already integrates spatial variation of the basin through normal physical hydrologic processes.

We are investigating the factors of tree growth that are associated with a common major mode of hydroclimatic variability in the UCRB, which results in a stronger driving signal in the growth of sensitive species. This variability is represented by the temperature and precipitation PC1 extracted from the basin sub-regions.
Therefore, this study will not account for the extra hydroclimatic variability seen in subsequent PCs that may affect tree-growth at a more local scale.

Tree-ring growth chronologies are not directly spatially integrated; along with a more general hydroclimatic forcing signal, their growth is usually dependent on other circumstances (such as stand conditions) unrelated to climate (Schulman, 1956; Fritts, 1974; Villalba et al., 1994). PCA was used in this study to extract a common signal from the tree-ring chronology network. Studies of large regions have shown that for chronologies growing in the most stressful conditions, the larger-scale signal represents the major portion of the hydroclimatic signal contained in the trees (Pittock, 1982; Fritts, 1976).

Even after detrending, many climate-sensitive tree-ring chronologies have relatively high autocorrelation coefficients, caused by the biological carryover effects from year to year. Proper accounting of autocorrelation is necessary for most dendrochronology statistical analysis (Fritts, 1976; 1991; Monserud, 1986; Riitters, 1990). One way to account for autocorrelation is to include lagged chronologies of standardized tree-ring widths in the reconstruction model (Fritts, 1976; 1991; Cook and Kairiukstis, 1990). Therefore, PC1s were computed for standardized chronologies lagged −1, 0, +1, and +2 years, to analyze the response of trees at common lags used in dendroclimatological analyses. Statistical characteristics by species, PCA loadings, and correlation coefficients between tree-ring components and hydroclimatic variables at different lags are shown in Tables 1–3.

Graphic Representation of Contingency Tables

The tree-ring growth response to each hydroclimatic condition is investigated by creating contingency tables (Stockton and Fritts, 1971) represented as graphs. The objective is to express this relationship quantitatively in the form of scores that can be used for comparison between different species and lags. The main advantage of categorizing data into contingency tables is that the form of the relation between the two variables of the table does not have to be linear. Tree rings are often biased toward hot-dry conditions, indicating limited linearity between tree-ring growth and hydroclimatic variability. More information about categorized data analysis and contingency tables can be found in Reynolds (1977), Nishisato (1980), and Stockton and Fritts (1971).

Data from the hydroclimatic variables and tree-ring PCs for each species were divided into three categories—low, normal, and high—corresponding respectively to conditions below the 30th percentile, between the 30th percentile and the 70th percentile, and above the 70th percentile. For each hydroclimatic variable, two graphs were prepared showing the frequencies of having high, normal, and low hydroclimatic conditions corresponding to high, normal, and low growth on the trees, for each species and lag. This allows us to determine, for example, what percentages of the high or low streamflow events were recorded in the tree-ring record as high, normal, or low growth. This procedure was done for all hydroclimatic variables, but only the streamflow graphs are shown (Figure 2).

In Table 3, species that showed significant (5% level) correlations with hydroclimatic variables (PIED, PSME, PIFL, and PILO) showed positive correlations with soil
moisture, which is a function of water availability represented by streamflow and precipitation. Conversely, tree rings are negatively correlated with temperature. Following these assumptions, narrower tree rings should be expected for hot-dry years and vice versa (Fritts, 1991). However, for species occupying high-elevation sites

Table 3. Characteristics of the First Principal Component (PC1) Extracted from Chronologies from Different Species and Lags

<table>
<thead>
<tr>
<th>Species</th>
<th>Lag</th>
<th>Var. exp. PC1, pct.</th>
<th>STRW</th>
<th>PREC</th>
<th>TEMP</th>
</tr>
</thead>
<tbody>
<tr>
<td>PIED</td>
<td>–1</td>
<td>59.58</td>
<td>0.28</td>
<td>–0.02</td>
<td>–0.26</td>
</tr>
<tr>
<td>PSME</td>
<td>–1</td>
<td>44.23</td>
<td>0.39</td>
<td>0.20</td>
<td>–0.32</td>
</tr>
<tr>
<td>PIPO</td>
<td>–1</td>
<td>45.66</td>
<td>0.29</td>
<td>0.07</td>
<td>–0.32</td>
</tr>
<tr>
<td>PIFL</td>
<td>–1</td>
<td>37.22</td>
<td>0.30</td>
<td>0.00</td>
<td>–0.34</td>
</tr>
<tr>
<td>PIAR</td>
<td>–1</td>
<td>58.59</td>
<td>–0.09</td>
<td>–0.02</td>
<td>0.15</td>
</tr>
<tr>
<td>PCEN</td>
<td>–1</td>
<td>29.78</td>
<td>–0.31</td>
<td>–0.20</td>
<td>0.13</td>
</tr>
<tr>
<td>PIED</td>
<td>0</td>
<td>59.51</td>
<td>0.72</td>
<td>0.51</td>
<td>–0.58</td>
</tr>
<tr>
<td>PSME</td>
<td>0</td>
<td>44.17</td>
<td>0.70</td>
<td>0.43</td>
<td>–0.57</td>
</tr>
<tr>
<td>PIPO</td>
<td>0</td>
<td>45.64</td>
<td>0.60</td>
<td>0.46</td>
<td>–0.47</td>
</tr>
<tr>
<td>PIFL</td>
<td>0</td>
<td>37.35</td>
<td>0.49</td>
<td>0.40</td>
<td>–0.25</td>
</tr>
<tr>
<td>PIAR</td>
<td>0</td>
<td>58.89</td>
<td>–0.17</td>
<td>–0.07</td>
<td>0.16</td>
</tr>
<tr>
<td>PCEN</td>
<td>0</td>
<td>29.88</td>
<td>–0.06</td>
<td>–0.06</td>
<td>0.02</td>
</tr>
<tr>
<td>PIED</td>
<td>1</td>
<td>59.42</td>
<td>0.16</td>
<td>0.11</td>
<td>0.04</td>
</tr>
<tr>
<td>PSME</td>
<td>1</td>
<td>44.25</td>
<td>0.28</td>
<td>0.32</td>
<td>–0.05</td>
</tr>
<tr>
<td>PIPO</td>
<td>1</td>
<td>45.78</td>
<td>0.23</td>
<td>0.20</td>
<td>–0.04</td>
</tr>
<tr>
<td>PIFL</td>
<td>1</td>
<td>37.37</td>
<td>0.34</td>
<td>0.23</td>
<td>–0.19</td>
</tr>
<tr>
<td>PIAR</td>
<td>1</td>
<td>58.96</td>
<td>0.09</td>
<td>0.13</td>
<td>0.23</td>
</tr>
<tr>
<td>PCEN</td>
<td>1</td>
<td>29.80</td>
<td>0.12</td>
<td>0.14</td>
<td>0.13</td>
</tr>
<tr>
<td>PIED</td>
<td>2</td>
<td>59.37</td>
<td>0.11</td>
<td>0.02</td>
<td>–0.12</td>
</tr>
<tr>
<td>PSME</td>
<td>2</td>
<td>44.22</td>
<td>0.10</td>
<td>0.03</td>
<td>–0.09</td>
</tr>
<tr>
<td>PIPO</td>
<td>2</td>
<td>45.84</td>
<td>0.19</td>
<td>0.09</td>
<td>–0.11</td>
</tr>
<tr>
<td>PIFL</td>
<td>2</td>
<td>37.33</td>
<td>0.32</td>
<td>0.26</td>
<td>–0.18</td>
</tr>
<tr>
<td>PIAR</td>
<td>2</td>
<td>59.17</td>
<td>–0.30</td>
<td>–0.20</td>
<td>0.21</td>
</tr>
<tr>
<td>PCEN</td>
<td>2</td>
<td>29.90</td>
<td>–0.15</td>
<td>–0.05</td>
<td>0.10</td>
</tr>
</tbody>
</table>

*Var. exp. represents the percentage variance explained by PC1. Correlations of these components with Lee’s Ferry streamflow record (STRW), as well as the first component from annual precipitation totals (PREC) and annual averaged temperature (TEMP), also are shown. Italic font indicates insignificant correlations at the 95% confidence. Abbreviations: PIED = Pinus edulis; PSME = Pseudotsuga menziesii; PIPO = Pinus ponderosa; PIFL = Pinus flexilis; PIAR = Pinus aristata; PCEN = Picea engelmannii.
(PIAR and PCEN), the correlation coefficients in Table 3 showed opposite signs. This is consistent with the results found by Fritts (1976) for these species.

The three frequencies for each species at a particular lag can be converted to a single score based on the physical relationship between tree-ring growth and climate delineated in the previous paragraph. The score at each particular lag indicates how well each species’ PC1 follows this physical relationship for severe events.

The graphs in Figure 2 are graphical representations of contingency tables in which the columns represent each species and the rows represent the three frequency conditions of high, normal, and low. The row categories exhibit a natural (or partial) order since they are ordered from low to high growth. A method developed by Rao and Caligiuri (1993) allows the extraction of parameter scores from ordered contingency tables by a concept known as dual scaling. Historical accounts of dual scaling can be found in Nishisato (1980) and Nishisato and Nish-
The scores match the natural order of the categories, making interpretation of the results easier. The procedure requires maximizing the correlation ratio of the column attribute on the row attribute, subject to certain constraints.

Since the objective function is nonlinear (is a ratio of linear equations), it is necessary to solve a non-linear optimization problem in order to obtain the column scores. Lingo 6.0, a computer software program for non-linear optimization, was used to compute the scores (Fig. 3). Since scores were computed with the objective of optimizing the correlation ratio, their individual values do not contain inherent meaning; only their relative differences are important, as this allows comparison between the species’ type (column category). Consequently, it is necessary to include in the optimization routine for all lags and conditions the perfect and the worst possible scores to further re-scale them to vary from 0 (no match) to 1 (perfect score). Re-scaling allows the comparison of scores obtained for different hydroclimatic variables (Fig. 4). For example, for the four most sensitive species (PIED, PSME, PIFL, and PIPO), a perfect score for high (low) streamflow condition is the
A no-match score is the case in which all years of high (low) streamflow coincide with low (high) tree growth for a certain species and lag. Based on the expected sign of the correlation between each hydroclimatic variable and tree-ring growth of the most sensitive species, better scores for high streamflow, high precipitation, and low temperature conditions should correspond to greater frequencies in the first growth category (high). Conversely, having higher

Fig. 3. Scores representing the relative sensitivity of tree species to different extremes of climatic variables at different lags. STRW is annual total streamflow, PREC is total precipitation and TEMP is temperature. High and Low correspond to the upper and lower 30% of each climatic variable. It is assumed that tree-ring growth is positively correlated with both precipitation and streamflow, and negatively correlated with temperature. Abbreviations: PIED = Pinus edulis; PSME = Pseudotsuga menziesii; PIPO = Pinus ponderosa; PIFL = Pinus flexilis; PIAR = Pinus aristata; PCEN = Picea engelmannii.
Fig. 4. Averaged high and low hydroclimatic condition scores from Figure 3. The scores represent the relative sensitivity of tree species to different climatic variables at different lags. STRW is annual total streamflow, PREC is total precipitation, and TEMP is temperature. High and Low correspond to the upper and lower 30% of each climatic variable. It is assumed that tree-ring growth is positively correlated with both precipitation and streamflow, and negatively correlated with temperature. Abbreviations: PIED = Pinus edulis; PSME = Pseudotsuga menziesii; PIPO = Pinus ponderosa; PIFL = Pinus flexilis; PIAR = Pinus aristata; PCEN = Picea engelmannii.

frequencies in the last row category (low) for low streamflow, low precipitation, and high temperature conditions should correspond to better scores. Consequently, the row order for these last three hydroclimatic conditions was reversed before includ-
ing them in the optimizing program. Exceptions were PIAR and PCEN, which have different correlation signs (Table 3).

Averages for both hydroclimatic conditions (high and low) for each hydroclimatic variable were computed as an indicator of sensitivity to severe hydroclimatic events by tree species and lag (Figs. 3 and 4). Those species and lags presenting a more consistent response to hydroclimatic extremes are given higher scores.

For each species, goodness of fit chi-square and likelihood-ratio chi-square statistics (Reynolds, 1977) were computed to test the null hypothesis that tree-ring growth is independent of hydroclimatic condition. All statistics showed an evident statistical significance, rejecting the hypothesis of independence even for the lowest correlated species. Important limitations have been attributed to the chi-square statistic (Mosteller, 1968; Reynolds, 1977), so its failure to provide additional usefulness in this case prompted us to find a better measure of significance.

To provide indication of the significance of a particular score, 2500 red noise (RN) time series were used to model an autoregressive (AR) background tree-ring growth noise. Based on Meko et al. (1993), the model used to generate the RN was an univariate lag 2 autoregressive model. It is assumed that significant scores should be above those computed for this normal “background” tree-growth variation. The autocorrelation coefficient chosen to generate the RN time series was 0.29, obtained from averaging the second-order autocorrelation coefficients for the species PIED, PSME, PIPO, and PIFL. Exceedence probabilities from the RN scores were assigned using the Weibull probability distribution. The 95% confidence level was found to correspond approximately to a score of 0.53.

RESULTS

Loadings of the PC1 of climate division data can be found in Table 2. These loadings represent the correlation between the data from each particular climate division and the resulting PC1 extracted from the data. Lower loadings for precipitation compared to temperature indicate the increased spatial variability of precipitation, which is more influenced by local hydroclimatic effects in the UCRB. This variability in precipitation is related to the fact that water availability is dependent on more basic parameters (including temperature itself), suggesting that moisture-carrying mechanisms around the basin are more heterogeneous than heat-transference processes through atmospheric circulation. Nevertheless, the loadings for precipitation are significantly high to lead us to conclude that our basic assumption of integrating the hydroclimatic signal by using principal components is suitable for our purposes. That is, when the annual precipitation total and temperature averages are used, synoptic (large-scale) climatological driving patterns affect the majority of the UCRB with similar intensity and this signal is chiefly contained in the first mode of variability. Additionally, this assumption can be partially relaxed for water availability, since analysis of streamflow measurements indicates that almost 85% of the runoff from the UCRB originates from orographic precipitation in 15% of the basin’s area (Stockton and Jacoby, 1976). These areas are located in high-mountain regions and capture most of the snowpack during winter. Cayan et al. (1992) found that snowpack accumulation in the western United States exhibits a high degree of regional
This finding was confirmed by McCabe (1994) for the Gunnison River, one of the tributaries of the Colorado River.

PC1 loadings from tree rings (Fig. 1) are generally not as high as the loadings extracted from climate data (Table 2). Close inspection of the loadings shows that from the total of 25 PSME chronologies used, one is not significantly (Panofsky and Brier, 1968) correlated with PC1. Non-significant correlations were also found for 3 of 16 PIPO chronologies, 4 of 9 PIFL, and 1 of 9 PCEN. PIED and PIAR were the only species in which all the chronologies were significantly correlated with the first principal component extracted from the same chronologies. In some cases, chronologies having non-significant loadings were geographically isolated from the rest. Local growing conditions may play some role in explaining the low correlation in these cases.

Percentage variance explained by each species’ PC1 is presented in Table 3. In addition, Table 3 also contains correlation coefficients between species and hydroclimatic variables for different lags. The correlation coefficient in this Table is shown as a guideline for comparison with the results from the scores defined in Section 2.3. The correlation coefficient assumes linearity, and cannot describe differences between high and low conditions. A fixed correlation coefficient can correspond to different scores. However, low correlation coefficients are probably also an indication of non-significant scores. From Table 3 it can be inferred that, in general, the growth of PIAR and PCEN is not significantly dependent on the general hydroclimatic variation measured by the PC1 axes.

From an analysis of Figure 2A it can be inferred that in some cases the same correlation coefficient can correspond to different frequency distributions and consequently different scores. The results for PIFL chronologies for lags –1 and +1 are an example. Both time series have a correlation coefficient of 0.38 with streamflow; however, it is apparent that the lag +1 chronologies capture high streamflow years more consistently than the lag –1 chronologies.

In other cases, the difference in the correlation coefficient may be attributed to the stronger response of certain species to one of the hydroclimatic conditions. For example, it is apparent that for lag 0, PSME and PIPO chronologies have very similar sensitivity to low streamflow conditions (Fig. 2B), but better results from PSME compared to PIPO for high streamflow conditions (Fig. 2A) could partially explain the better correlation coefficient of the former species.

The scores and the 95% confidence level (dotted line) presented in Figure 3 were computed following the procedure described in Section 2.3 using the data from Figure 2 and from similar analyses for precipitation and temperature (not shown). Consistent with Tarboton (1994) and Fritts (1976), it can be inferred from Figure 3 that tree rings are generally more sensitive to dry-hot than to wet-cold conditions. Excluding PIAR and PCEN chronologies and averaging all lags, high streamflow condition scores are 89% to 95% of the scores for low streamflow conditions, depending on the species. For precipitation, the fraction is between 85% and 90%. For temperature, low-condition scores are 80% to 85% of the high-condition values.

Low-temperature-condition scores were the lowest overall. Except for PIED and PIPO chronologies, years of low temperature do not usually produce a wider
growth ring. It is reasonable that lower evapotranspiration stress caused by low temperatures, rather than increased soil moisture, does not induce strong positive growth responses. This would particularly be true at higher sites where low temperatures could inhibit photosynthesis.

The score averages for high and low conditions from Figure 3 are presented in Figure 4. Results showed that PIED is the most sensitive species at lag 0, with the highest overall scores for all climate variables. It is important to notice that PIED chronologies have the lowest lag-1 autocorrelation coefficient (Table 1), concentrating the sensitivity at lag 0. In contrast, for other species with a higher autocorrelation coefficient, the sensitivity is diluted over one or two lagged years. The score used in this study favors tree species with a quick response, which is especially important when switching between opposite conditions. Quick response is partially related to lower autocorrelation coefficients.

Considering the highest score for each species (at any lag), PSME is more sensitive to streamflow variation than PIPO. However, PIPO chronologies are slightly better than PSME for reflecting extreme precipitation and temperature conditions. PIFL chronologies are less sensitive to hydroclimatic variation than PSME, PIPO, and PIED. More uniform lag-to-lag scores suggest higher year-to-year persistence for PIFL, also an indication of higher biological carryover effect on the trees. The higher persistence of PIFL species is also consistent with higher averaged Hurst's coefficients for this species (Landwehr and Matalas, 1986). PIAR and PCEN chronologies were not responsive to hydroclimatic variation in the UCRB.

In general, lower scores for lags other than zero suggest that extreme hydroclimatic events are captured mostly in the same growing season of the tree (lag 0). However, particular chronologies can present significant scores at lags other than zero when considered individually.

Fritts and Shatz (1975) and Fritts (1991) suggested that the best chronologies for dendroclimatology are those with the highest standard deviation, highest mean sensitivity, highest percentage of variance in common, and lowest first-order autocorrelation. The results of our study confirmed the importance of having low first-order correlation as an indication of potential for a chronology to be a good hydroclimatic predictor (Table 1 and Fig. 4). Having a high mean sensitivity coefficient and standard deviation were not as decisive as having low autocorrelation coefficients.

CONCLUSIONS

The contingency table scores used in this study are a good indicator of the association between hydroclimatic forcing and tree-ring growth. The scores are particularly useful for determining differences in the sensitivity of tree-ring growth to extreme hydroclimatic conditions. Additionally, the scores have the advantage of not assuming any specific functional form (e.g., linearity). Having different scores for high- and low-growth conditions is an intrinsic indication of limited range of linearity caused by growth-limiting factors not related to climate.

Differences between the species can be attributed to a number of factors. Owing to physiology and growth characteristics, some species may be less sensitive to precipitation stress. In addition, the growth environment typical of each species can
affect potential dendroclimatological usefulness. For example, *Pinus edulis* is typically found in open stands on relatively dry low-elevation sites with thin soils. Such characteristics are ideal for climatological sensitivity. The trees are in moisture-limited settings and are not affected by canopy and root competition with other trees. In contrast, *Picea englemanni* grows in dense stands at higher elevations. At these sites moisture is not as limiting, and canopy interactions can cause tree-ring variations that mask climate.

Consistent with other studies (Meko et al., 1995; Schulman, 1956), ring-width sensitivity to precipitation is lower than to streamflow. Higher streamflow scores can be attributed to better integration and persistence of the total basin hydroclimatic variation by way of normal hydrological processes (Loaiciga et al., 1993). Precipitation is inherently more spatially variable than streamflow, which is modulated through the basin’s antecedent moisture conditions.

The objective of this research was to study differences in the sensitivity to climate forcing in several species. Consistent with results in Hidalgo et al. (2000), this study found PIED and PSME to be the species most sensitive to hydrologic variability in the UCRB at lag 0. For precipitation and temperature, the most sensitive species at lag 0 are PIED and PIPO. For dendroclimatic reconstructions, other factors such as tree availability, the need to use the oldest species at a site, or the requirement for an increase of spatial coverage density will also play a role in selecting chronologies. However, an understanding of species’ relative responses presented in this study can be useful in future research in interpreting results in reconstruction models calibrated using alternative subsets of chronologies.

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