

L.R. Peach EDI Metadata

Northern Arizona University: 2020 – 2021

Advisors: Dr. Pete Fulé and Dr. Kristen Waring

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Dataset Title

Tree Ring, Dendrophenotype, and Climate Data from *Pinus strobiformis* / *Pinus flexilis* Hybrid Zone, Southwestern U.S. 2016/2020

Abstract

Southwestern white pine provides valuable forest resources and limber pine is an ecosystem pioneer, but both species are threatened by increased frequency of intense drought. Both species are also vulnerable to white pine blister rust but may stand an adaptive advantage due to their hybridization. To understand the tree-level response of hybrids to extreme drought events across the hybrid zone, we crossdated cores from nine hybrid populations and calculated their resilience to extreme drought events from 1950 - 2015. We constructed statistical models to understand the relationship between hybrid ancestry, drought response, growing conditions, and climate across the hybrid zone. In the context of recent genetic evidence that drought recovery and resistance diverge more sharply along the extreme boundaries of the hybrid zone due to reduced capacity for gene flow, we hypothesize that hybrids differ in drought response across a drought gradient in the southwestern U.S. We predict that there will be a positive relationship between resilience and southwestern white pine ancestry expressed by an individual hybrid.

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License

Selected license: CCO

Keywords

dendroecology; resilience; forestry; genomics; dendrophenotype; *strobiformis*; *flexilis*; SWWP; NAU Ecology Lab; NAU Silviculture and Applied Forest Health Lab

Funding of this work

PI First Name	PI Middle Initial	PI Last Name	PI ORCID ID (optional)	Title of Grant	Funding Agency	Funding Identification Number
Kristen	M	Waring	0000-0001-9935-9432	NSF Grant 1 NSF Grant 2	NSF – National Science Foundation	1: EF-1442597 2: EF-1442486
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Angelina Joseph	Ellis	Palumbo Miller	n/a	Graduate Assistantship – Northern Arizona University	NAU Center for International Education	n/a

Timeframe

- Project beginning: May 2020
- Project end: August 2021
- Data collection completed May 2020 – September 2020

Geographic location

- **DESCRIPTION**
 - All trees collected came from the southwestern U.S. (Texas, New Mexico, Arizona, and Colorado), specifically the Sky Islands, or Madrean Archipelago.
- **BOUNDING COORDINATES**
 - North: 40.0°
 - South: 30.0°

- East: -102.5°
- West: -112.5°

Taxonomic Species or Groups

- *Pinus flexilis* E. James
- *Pinus strobiformis* Engelm.
- *Pinus reflexa* Engelm.

Methods

From the “Materials and Methods” section of L.R. Peach’s M.S. thesis, completed summer 2021:

MATERIALS AND METHODS

FIELD SAMPLING

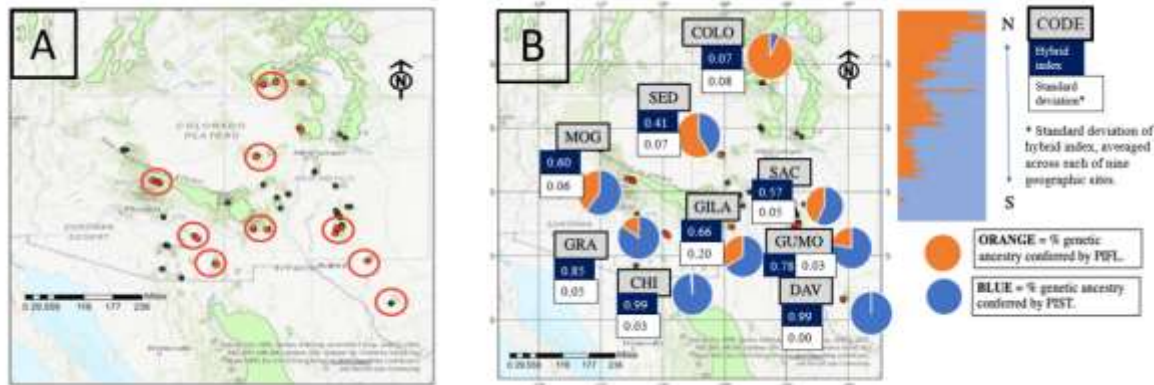
Menon et. al. (2021) sampled 22 populations of pure PIST, 12 populations of pure PIFL and 98 populations from the PIST / PIFL hybrid zone. Foliage was sampled at each population for destructive genetic analysis, which provided hybrid index data for sampled trees (Menon et. al. 2021). Collection trees were separated by at least 30 – 60m and 6-10 trees were sampled within each population. A gridded design of latitude and longitude with paired high-low elevation populations dictated core and foliage collections within the hybrid zone (Menon et. al. 2021).

STUDY AREA

In the present study, we selected a subsample of 30 hybrid populations from the original 98 that (a) represented a range of climatic conditions across the hybrid zone and (b) had enough cores for a reliable sample of each selected population (Figure 3.2). We then grouped populations together into nine geographic sites for analyses. These nine sites represent a diverse assortment of locations across the hybrid zone in terms of annual precipitation, temperature, and average hybrid index.

For each tree sampled, we first collected an increment core on the uphill slope and a then collected a second core at a 90-degree angle from the first core to account for potential reaction wood. We froze each core for storage. Individual tree characteristics and environmental conditions at each population were recorded during the time of core collection. These characteristics included presence of white pine blister rust on individual sampled trees, diameter at breast height (DBH; cm), geographical coordinates, elevation (m), aspect, presence or absence of plants of the genus *Ribes* (which act as hosts for white pine blister rust), and white pine regeneration within each population.

Figure 3.2a and 3.2b: In 3.2a, nine geographic sites within the hybrid zone, subsampled from an original 98 populations by (Menon et. al. 2021), are circled in red. In 3.2b, the same nine subsampled sites are



labeled in grey and accompanied by corresponding ancestry pie charts (where blue represents hybrid index, or percent PIST ancestry, and orange represents percent PIFL ancestry).

LABORATORY METHODS

Climate Data

Climate variables marked as potentially relevant to biological growth response in the literature and previous research were downloaded from ClimateWNA (see Supplemental Table 1) (Hamaan et. al. 2013; Goodrich et. al. 2016; Goodrich et. al. 2017; Bucholz et. al. 2020; Menon et. al. 2021). By dividing summer precipitation (PPT_sm) by mean annual precipitation (MAP), we calculated monsoon indices to understand the relationship between hybrid index and regional changes in water availability across the portion of the hybrid zone sampled for this study. Arizona and New Mexico receive up to half of annual rainfall from the summer monsoon season, which is driven by unbalanced heating of the southwestern US and Pacific Ocean (Guido 2008). Warm air in the southwestern US rises, causing moist, cool air to fill the low-pressure space that forms and deliver summer monsoon rain. Available SoilGrids250m data were also extracted at the site-level within each of the nine sites at depths of 0-5cm and 100-200m. (Hengl et. al. 2017). In SoilGrids, prediction models are fitted using more than 230,000 soil profile observations from the World Soil Information Service (WoSIS) and a series of environmental covariates. Soil property maps are generated at 250m spatial resolution at six sampling depths. Five soil properties were taken into consideration across the nine populations: bulk density of fine earth (kg / m^3), cation exchange capacity (cmolc / kg), soil organic carbon content (permille), pH measured in water solution, and pH measured in KCl solution.

Dendrochronology

We thawed cores in 2020, dried them for 24 hours after removal from the freezer, extracted cores from storage straws, and glued them to wooden mounts. We surfaced cores with sandpaper of increasingly fine grit until wood cells were clearly visible under magnification. We visually crossdated cores by comparing particularly narrow rings, or marker years, with existing chronologies from the International Tree Ring Database (Stokes and Smiley 1968). Then we scanned the samples at 1200 dpi resolution and used the program Coo Recorder v. 9.3 (Cybis Elektronik & Data A.B. 2019) to digitally measure the width of each tree ring. We checked the accuracy of crossdating using the program COFECHA (Holmes 1983). We dated a total of $n=104$ trees. We read raw ring widths into R using the dplR library (Bunn et. al. 2021) raw measurements were converted to BAI using the bai.out() function. Prior to calculation of RWI from raw ring data, each chronology must be detrended to remove age-related growth trends and climate-influenced signals. We used the detrend() function, also from the dplR library, to apply a cubic smoothing spline, which removes the age-related growth trend and other unwanted signals from tree-ring data, and converted raw measurements to RWI (Cook & Kairiukstis 1990).

Analysis

We implemented two methods for quantifying each individual tree's response to drought stress: a) a calculation of resistance (Rt), recovery (Rc), and resilience (Rs) and b) a Wet:Dry ratio. Resistance is defined as the inverse of the total growth reduction that occurs during a drought period, recovery is defined as the growth increase that occurs after a drought period in relation to growth rate during the drought event, and resilience is defined as a tree's capacity to reach pre-drought growth levels after that drought has subsided (Lloret, Keeling, & Sala 2011). The benefit of using such indices to understand growth response to drought conditions is that patterns of tree growth can account for past and present influences on an individual tree's ability to minimize change during a disturbance, then recover to a pre-disturbance state. A limitation of the Rt/Rc/Rs indices is the temporal proximity of some drought years (for example, 2000 and 2002). We used such indices to capture lagged recovery that may occur due to drought legacy effects, which can lead to imprecise estimation of resilience (Ovenden et. al. 2020). The calculations of Rt/Rc/Rs (Equations 1-3) are ratios based on an absolute measurement (basal area increment; BAI) to identify three aspects of tree response to a stress event (in this case, a drought period).

$$\text{Equation 1: resistance (Rt)} = \frac{\text{during drought BAI}}{\text{BAI averaged over 5 years pre-drought}}$$

$$\text{Equation 2: recovery (Rc)} = \frac{\text{BAI averaged over 5 years post-drought}}{\text{during drought BAI}}$$

$$\text{Equation 3: resilience (Rs)} = \frac{\text{BAI averaged over 5 years post-drought}}{\text{BAI averaged over 5 years pre-drought}}$$

The Wet:Dry ratio (W:D) compares tree growth between major wet years and major dry years using RWI, and is useful because it provides an assessment of growth change in relation to limiting conditions, such as drought (Fekedulegn et. al. 2003; Bickford et. al. 2011; Hess & Fule 2020). Because W:D compares individual years rather than periods, it should be less susceptible to the legacy effects of temporally close droughts such as 2000 and 2002. RWI is a dimensionless unit that compares one year of individual radial growth to average annual radial growth across a tree's lifetime. We calculated W:D by dividing average RWI for the five wettest water years by average RWI for five driest water years at each site (Equation 4).

$$\text{Equation 4: wet: dry (W:D)} = \frac{\text{Average RWI from 5 wettest water years}}{\text{Average RWI from 5 driest water years}}$$

We calculated average sensitivity (average annual percentage change in ring width) of each site to address Q1. We also calculated correlations between all combinations of monsoon index, hybrid index, and sensitivity to address Q1 as well as correlation coefficients and coefficients of determination for hybrid index and (a) monsoon index, (b) relative spring humidity, (c) maximum temperature in autumn, and (d) annual precipitation as snow to identify relationships between hybrid index and regional water availability. To calculate drought indices for addressing Q2 and Q3, we selected drought years around which to calculate Rt, Rc, and Rs. We averaged longitude and latitude for each site and downloaded monthly precipitation and other climate data for those averaged coordinates for the period 1950 – 2015 (ClimateNA; Wang et. al. 2016). Time scale included the current “climate-change-type” drought from the mid-1990s to present (Allen & Breshears 1998) as well as the previous largest recorded southwestern drought, approximately 1951-56 (Swetnam & Betancourt 1998). All the tree-ring chronologies had adequate sample depth (minimum 8 trees) by 1950. Annual precipitation for the period 1950 – 2015 was calculated for each group by water year rather than by calendar year due to the close relationship between tree-ring growth and previous winter / current growing year precipitation (Yang et. al. 2014). A water year is the 12-month period extending from October 1st of year (X) to September 30th of year (X + 1). For each group, we sorted water years and identified the five driest years within the period 1950 – 2015. We calculated indices of resistance, recovery, and resilience using BAI around each population's five driest water years.

For each individual tree, a total of five Rt measurements, five Rc measurements, five Rs measurements, and a single W:D was calculated. Finally, we created single values of each index per tree

by averaging Rt, Rc, and Rs across all five driest water years for each individual tree. To test for a relationship between hybrid index and growth response to drought conditions and address Q2, we graphed each of our four drought indices versus hybrid index and used a Pearson's correlation matrix to identify multicollinearity and significant correlation between hybrid index and covariates from sampled sites (where significant is defined as $p < 0.05$).

Variable Selection and Model Development

We developed four linear a priori models using the `lm()` package in R for each of the four drought indices / dependent variables, Rt, Rc, Rs, and W:D for the purpose of addressing Q3. We included hybrid index values for each individual tree (Menon et. al. 2021), along with aspect, mean annual temperature and presence / absence of white pine blister rust as independent covariates in each a priori model. For our four final models, we initiated the building process with 26 environmental, 5 soils, and 15 tree-level independent variables. We chose to convert our categorical aspect values to numerical values, where $N = 360^\circ$ and $NE = 45^\circ$. Prior to final model development, we used the Pearson's correlation matrix to assess correlation between independent covariates of interest. To develop final models, we used LASSO training in R's `glmnet()` package (Friedman et. al. 2010), which combines backwards and forwards model selection by shrinking the coefficients of significant covariates and setting non-significant covariate coefficients to zero while minimizing the residual sum of squares. We loaded our four model datasets into R before "training" LASSO with `lasso.model()` from the `glmnet()` package (Friedman et. al. 2010). We added a single random effect to the model to account for differences generated by individual hybrid sites before implementing the training procedure. Next, we carried out model selection in LASSO for each of the four response variables, or drought indices, using bootstrapped data and 1000 replicates, which allowed us to obtain coefficients for each independent variable included in the training procedure. We saved these coefficients from the training procedure and converted them to percentage of time included in model selection for the total 1000 replicates. We identified covariates that appeared in the four training models more than 50% of the time, and created final linear mixed-effects models using the `lmer()` package in R. To see the relative fit of each of our four final models for Rt, Rc, Rs, and W:D, we used the `BIC()` function in R to obtain values from the Bayesian Information Criterion, by which low values indicate a better model fit.

Data Provenance

Dataset Title	Dataset DOI or URL	Creator (name & email)	Contact (name & email)
Data from: The role of hybridization during ecological divergence of southwestern white pine (<i>Pinus strobiformis</i>) and limber pine (<i>P. flexilis</i>).	https://doi.org/10.5061/dryad.f6r55	Mitra Menon	mbmenon@ucdavis.edu

Data Table

1. Table Name: Covariate_List_LRP_A.xlsx

Table Description: all data included in final multivariate models produced for four drought calculated drought indices. Most data is from PRISM; hybrid index data is from M. Menon's data cited in the previous section (Data Provenance).

Column Name	Description	Unit / code explanation / date format	Missing value code
Pop_code (A)	This column contains three- or four-letter codes specifying a particular geographic site (9 overall).	No units / each code is three OR four letters / NA	No missing values.
Pop_Ind (B)	This column contains (1) the appropriate geographic code (see A), (2) a number indicating sub-site, (3) an H or L indicating a high (H) or low (L) site, and (4) an underscore and number. The number indicates individual tree number sampled at that sub-site.	No units / see description for labelling info / NA	No missing values.
lat (C)	This column contains the latitudinal coordinates for each individual tree sampled.	Decimal degrees / NA / NA	No missing values.
long (D)	This column contains the longitudinal coordinates for each individual tree sampled.	Decimal degrees / NA / NA	No missing values.
ele (E)	This column contains the elevation, in meters, for each individual tree sampled.	Meters / NA / NA	No missing values.
SWWP (F)	This column contains the percentage of <i>Pinus strobiformis</i> ancestry that each sampled tree exhibited, based on previous work of the SWWP team, specifically Menon et. al. 2020.	Decimal proportion (0 = NO SWWP; 1 = ALL SWWP) / NA / NA	No missing values.
Rt_avg (G)	This column contains calculated resistance values for each individual tree, where resistance = average during-drought BAI for 5 driest water years (1950-2010)/ average pre-drought BAI for the 5 years preceding drought.	No units / NA / NA	No missing values.
Rc_avg (H)	This column contains calculated recovery values for each individual tree, where recovery = average post-drought BAI for the five years following drought / average during –	No units / NA / NA	No missing values.

	drought BAI for 5 driest water years (1950 – 2010).		
Rs_avg (I)	This column contains calculated resilience values for each individual tree, where resilience = average post-drought BAI for five years following drought (1950 – 2010) / average pre-drought BAI for five years preceding drought (1950 – 2010).	No units / NA / NA	No missing values.
W_D (J)	This column contains calculated wet:dry ratio values for each individual tree, where W:D (wet:dry) = average RWI for five wettest water years / average RWI for five driest water years.	No units / NOTE: W:D is how this value is reported in the description and in the thesis. W_D was used in this spreadsheet due to inability to include a colon in Excel headings.	Missing values indicated with “NA” .
DBH (K)	This column contains DBH (diameter at breast height) values for each tree sampled.	Inches / DBH stands for diameter at breast height / NA.	No missing values.
aspect (L)	This column contains a categorical aspect value for each individual tree sampled.	No units / 8 categories, where.... NE = northeast N = north E = east SE = southeast S = south SW = southwest W = west NW = northwest / NA	No missing values.
BLDFIE_sl1 (M)	This column contains measurements for bulk density of fine earth (BLDFIE), measured by sub-sites within overall geographic sites, at the 0-5cm resolution.	Units for BLDFIE are kg/m ³ / NA / NA	No missing values.
BLDFIE_sl6 (N)	This column contains measurements for bulk density of fine earth (BLDFIE), measured by sub-sites within overall geographic sites, at the 100-200cm resolution.	Units for BLDFIE are kg/m ³ / NA / NA	No missing values.
CECSOL_sl1 (O)	This column contains measurements for cation exchange capacity of soil, measured by sub-sites within overall geographic sites, at the 0-5cm resolution.	Units for CECSOL are cmolc/kg / NA / NA	No missing values.

CECSOL_sl6 (P)	This column contains measurements for cation exchange capacity of soil, measured by sub-sites within overall geographic sites, at the 100-200cm resolution.	Units for CECSOL are cmolc/kg / NA / NA	No missing values.
ORCDRC_sl1 (Q)	This column contains measurements for soil organic carbon content, measured by sub-sites within overall geographic sites, at the 0-5cm resolution.	Units for ORCDRC are in permilles / NA / NA	No missing values.
ORCDRC_sl6 (R)	This column contains measurements for soil organic carbon content, measured by sub-sites within overall geographic sites, at the 100-200cm resolution.	Units for ORCDRC are in permilles / NA / NA	No missing values.
PHIHOX_sl1 (S)	This column contains measurements for pH index, measured in water solution, measured by sub-sites within overall geographic sites, at the 0-5cm resolution.	NOTE: each pH value listed is multiplied tenfold (for example, if an individual tree has a listed pH value of 65, this would be a 6.5 on the pH scale) / NA / NA	No missing values.
PHIHOX_sl6 (T)	This column contains measurements for pH index, measured in water solution, measured by sub-sites within overall geographic sites, at the 100-200cm resolution.	NOTE: each pH value listed is multiplied tenfold (for example, if an individual tree has a listed pH value of 65, this would be a 6.5 on the pH scale) / NA / NA	No missing values.
PHIKCL_sl1 (U)	This column contains measurements for pH index, measured in KCl solution, measured by sub-sites within overall geographic sites, at the 0-5cm resolution.	NOTE: each pH value listed is multiplied tenfold (for example, if an individual tree has a listed pH value of 65, this would be a 6.5 on the pH scale) / NA / NA	No missing values.
PHIKCL_sl6 (V)	This column contains measurements for pH index, measured in KCl solution, measured by sub-sites within overall geographic sites, at the 100-200cm resolution.	NOTE: each pH value listed is multiplied tenfold (for example, if an individual tree has a listed pH value of 65, this would be a 6.5 on the pH scale) / NA / NA	No missing values.
Tmax_at (W)	This column contains, at the sub-site level, the average maximum autumn temperature (1980-2010).	Units are in degrees C / Tmax_at = average maximum autumn temperature / NA	No missing values.

DD_0_at (X)	This column contains, at the sub-site level, the number of degree days in autumn with a temperature below 0°C.	Units are in # of days / DD_0_at = # degree days in autumn below 0°C / NA	No missing values.
dd5_SP (Y)	This column contains, at the sub-site level, the number of degree days in spring with a temperature below 5°C.	Units are in # of days / dd5_SP = # of degree days in spring below 5°C / NA	No missing values.
DD18_sp (Z)	This column contains, at the sub-site level, the number of degree days in spring with a temperature below 18°C.	Units are in # of days / DD18_sp = # of degree days in spring below 18°C / NA	No missing values.
DD18_at (AA)	This column contains, at the sub-site level, the number of degree days in autumn with a temperature below 18°C.	Units are in # of days / DD18_at = # of degree days in autumn below 18°C / NA	No missing values.
PAS_wt (AB)	This column contains, at the sub-site level, the amount of precipitation received as snow in winter.	Units are in mm / PAS_wt = amount of precip, in mm, received as snow in winter / NA	No missing values.
RH_sp (AC)	This column contains, at the sub-site level, relative spring humidity.	Units = percentages / RH_sp = % relative spring humidity / NA	No missing values.
MAT (AD)	This column contains, at the sub-site level, mean annual temperature.	Units are in °C / MAT = mean annual temperature / NA	No missing values.
MWMT (AE)	This column contains, at the sub-site level, the mean temperature during the warmest month of the year.	Units are in °C / MWMT = mean temperature in the warmest month of the year / NA	No missing values.
TD (AF)	This column contains, at the sub-site level, continentality.	Units are in °C / TD = continentality, or the difference (in °C) between the mean temperature during the warmest month of the year and the mean temperature during the coldest month of the year / NA	No missing values.
MAP (AG)	This column contains, at the sub-site level, mean annual precipitation.	Units are in mm / MAP = mean annual precipitation / NA	No missing values.

MSP (AH)	This column contains, at the sub-site level, the amount of precipitation received from May-September.	Units are in mm / MSP = mean precipitation received May - Sept / NA	No missing values.
AHM (AI)	This column contains, at the sub-site level, the annual heat-moisture index.	Units are in °C / AHM = annual heat-moisture index / NA	No missing values.
SHM (AJ)	This column contains, at the sub-site level, the summer heat-moisture index.	Units are in °C / SHM = summer heat-moisture index / NA	No missing values.
DD_0 (AK)	This column contains, at the sub-site level, the number of degree days (annually) below 0°C, or “chilling degree-days.”	Units are # of days / DD_0 = number of degree days below 0°C / NA	No missing values.
DD5 (AL)	This column contains, at the sub-site level, the number of degree days (annually) above 5°C, or “growing degree days.”	Units are # of days / DD5 = number of degree days above 5°C / NA	No missing values.
DD18 (AM)	This column contains, at the sub-site level, the number of degree days (annually) below 18°C, or “heating degree days.”	Units are # of days / DD18 = number of degree days below 18°C / NA	No missing values.
NFFD (AN)	This column contains, at the sub-site level, the number of frost-free days annually.	Units are # of days / NFFD = number of frost-free days per year / NA	No missing values.
bFFP (AO)	This column contains, at the sub-site level, the day of the year on which the frost-free period begins.	Units are # of days / bFFP = number day (of a possible 365) on which the frost-free period begins / NA	No missing values.
FFP (AP)	This column contains, at the sub-site level, the length of the annual frost-free period.	Units are # of days / FFP = number of days comprising the annual frost-free period / NA	No missing values.
PAS (AQ)	This column contains, at the sub-site level, the amount of precipitation received as snow between August in the previous year and July of the current year.	Units are in mm / PAS = amount of precipitation received as snow between August of the previous year and July of the current year / NA	No missing values.
EMT (AR)	This column contains, at the sub-site level, the extreme minimum temperature over the past 30 years (1980 – 2010).	Units are in °C / EMT = the minimum temperature over the past 30 years (1980-2010) / NA	No missing values.

EXT (AS)	This column contains, at the sub-site level, the extreme maximum temperature over the past 30 years (1980 – 2010).	Units are in °C / EXT = the extreme maximum temperature over the past 30 years (1980 – 2010) / NA	No missing values.
Eref (AT)	This column contains, at the sub-site level, the Hargreaves reference evaporation.	Units are in mm / Eref = Hargreaves reference evaporation.	No missing values.
CMD (AU)	This column contains, at the sub-site level, the Hargreaves climatic moisture deficit.	Units are in mm / CMD = Hargreaves climatic moisture deficit.	No missing values.

Scripts / Code

File name	Description	Scripting language
LRP_Archival_2021.Rmd	R markdown file containing LASSO covariate selection script and final multivariate models documented in LRP M.S. thesis.	R

Other (miscellaneous) Objects

File name	Description	Data type
LRP_Thesis_08.12.pdf	Final PDF document submitted as a final requirement for LRP's M.S. thesis to NAU ETD and ProQuest.	PDF document
FOLDER: COFECHA outputs	This folder contains a singular text output from COFECHA for final chronologies developed for each of nine geographic sites.	COFECHA output (.OUT; open with Notepad or a comparable text reader)
FOLDER: Updated Text Files	This folder contains the text files used to create the COFECHA outputs listed above.	.txt files