

## *Prosopis* L. woody growth in relation to hydrology in South America: A review

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### ABSTRACT

Arboreal species of the genus *Prosopis* L. have played an important role in the development of tree-ring research in arid and semi-arid ecoregions of South America. Given the distribution of *Prosopis* across a broad precipitation gradient from 0 to 2000 mm y<sup>-1</sup> and its unique role as a phreatophyte, the relationship between *Prosopis* species growth and water has been a recurring theme over the past century. We conducted a systematic review of the literature addressing *Prosopis* and water research in South America, and combined site coordinates with GIS data of mean annual precipitation (MAP), elevation, biome, and soil moisture from online databases to understand the spatial distribution of research to date. We compiled 40 publications from 1931 to 2022, including results from 11 species of *Prosopis* among four countries, on the relationship between *Prosopis* spp and precipitation, groundwater levels, soil humidity, among other hydrological parameters. The spatial distribution of research sites spans tropical-subtropical and temperate latitudes from 4° to 35°S, excluding regions where the genus is present in Patagonia and northeastern South America. Studies covered a broad range of elevations from 30 to 3500 m a.s.l. but was limited to 1–730 mm y<sup>-1</sup> MAP, excluding more humid climates where *Prosopis* occurs. Results obtained from 32 dendrochronological studies and eight studies relating to *Prosopis* and hydrology, were grouped into sub-disciplines of tree-ring formation and the hydrosystem, dendroclimatology, dendrohydrology, and dendroecology. The review highlights the unique affinities of *Prosopis* to arid conditions, and the use of tree rings as a proxy for historical droughts and variability in water tables. Nonetheless, there are opportunities to expand the geographical-climatological extent of *Prosopis* growth research to humid climates, as well as to incorporate novel techniques such as stable isotopes and vessel size chronologies to understand how this genus records hydrological change throughout South America.

### 1. Introduction

Advancing tree-ring research in the tropics and subtropics involves the analysis of a diversity of angiosperm woods. The genus *Prosopis* L. has played an important role in the development of dendrochronology in

tropical and subtropical latitudes of the Americas for almost a century (Krebs and Fischer, 1931; Bogino, 2014). In addition to tree-ring dating, the abundance and distribution of the genus in arid and semi-arid regions has facilitated historical records of climate variability in tree rings, and of events such as fire, insect outbreaks, and changes in belowground

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water resources. A global review of 10 species of *Prosopis* from over 50 studies highlights the differential growth-climate relationships depending upon distance to ground water resources and other regional climatic and geographic differences (Cangiano et al., 2020). For example, Cangiano et al. (2020) notes the sensitivity of *Prosopis* growth to rainfall in the high-elevation regions of the Andes, but sensitivity to temperature at lower elevations of the Pampas, where access to the water table likely plays a key role. In the past two decades, literature reviews have highlighted the uniqueness of *Prosopis* for developing relatively long-term (>100 yr) chronologies as paleoclimate proxies in their distribution range (Villalba et al., 2000). In particular, the morphological and physiological adaptations of *Prosopis* to water stress makes these species a valuable proxy for water availability (Villagra et al., 2010). Given the present context, *Prosopis* tree-ring chronologies become a tool to evaluate and compare historical hydroclimatological trends in the Americas.

Climate change and water resource management is a central focus in South America. Within its wide range of climates and ecosystems, water availability mediates spatial trends in biodiversity (Alcaraz-Segura et al., 2013), forest structure (Klein et al., 2015) agriculture, and human populations over the past millennia (Morales et al., 2009). Among the examples of major hydro-climatological change with ecological and socio-economic implications is the megadrought in central Chile (Garreaud et al., 2017, 2020), drought and deforestation in the Amazon basin (Nepstad et al., 2004; Staal et al., 2020), and extreme flooding events in Southeastern South America (Cavalcanti et al., 2015). These phenomena represent challenges for water management within the context of land-use and climate change. An increasing focus on freshwater resources and relationships between forests and hydrology have resulted in studies on the local, regional and global drivers of rainfall and water availability in different regions of South America (Davidson et al., 2012; Jones et al., 2017; Alvarez-Garretón et al., 2019). South America encompasses a diversity of hydroclimate regions, from the driest nonpolar desert in the Atacama region of northern Chile (Bull et al., 2018), to the humid tropical rainforests of the northwestern Amazon basin (Coe et al., 2016). Scarce historical data for hydroclimate variables limits information to understand long-term trends in water availability and to inform decision-making regarding water use (Rice et al., 2009). Proxy data for hydrological variables is valuable for reconstructing historical variability in water availability or streamflow in many watersheds throughout the Americas (Woodhouse and Lukas, 2006; Margolis et al., 2011; Ferrero et al., 2015; Sauchyn et al., 2015; Muñoz et al., 2016; Fernández et al., 2018; Lucas et al., 2022).

Research in dendroclimatology and dendrohydrology are making a critical contribution towards understanding historical variability in precipitation, streamflow and drought indices as a context for long-term conservation and management planning (Barría et al., 2019; Morales et al., 2020; Muñoz et al., 2020). Given that seasonality in the tropics and subtropics depends on rainfall, hydrology is a major driver for the growth patterns and tree-ring attributes. Tree-ring chronologies are used in the tropics and subtropics to reconstruct historical hydroclimatic variations and provide evidence for the frequency and severity of drought conditions, as well as extreme flooding over centuries (Boninsegna et al., 2009; Ferrero et al., 2015; Humanes-Fuente et al., 2020). Long-term averages for discharge spanning over 100 years demonstrate the pitfalls of water management based on relatively limited time series (Fernández et al., 2018; Muñoz et al., 2020). Given the influence that hydrological variability has on ring growth and molecular composition of photosynthates that make up wood, tree-ring isotope data has also contributed to understanding how tree water use efficiency and carbon sequestration are influenced by drought (Brienen et al., 2011). In tropical and subtropical ecosystems, angiosperm species such as those from the genus *Prosopis* L. (Villalba et al., 2000; Piraino et al., 2015; Piraino and Roig, 2016) and *Mimosa* L. (Brienen et al., 2011), among others, have played a key role in providing proxy data regarding annual variations in water availability at these latitudes.

Dendrochronological research using the genus *Prosopis* has been conducted in South America since the 1930s. Among the earliest studies using tree-ring dating in the continent, growth rings of a 159-year-old *Prosopis caldenia* Burkart tree from the Argentinean Pampas recorded historical variability in rainfall, suggesting the occurrence of seasonal droughts in the early 1800s (Krebs and Fischer, 1931; Bogino, 2014). This pioneer study showed a relationship between growth and rainfall, an early antecedent to the now extensive network of 286 tree-ring chronologies comprising the Drought Atlas for Southern South America (Morales et al., 2020). The second dendrochronological study with the genus *Prosopis* was published in the 1980s, by the IANIGLA Dendrochronology Laboratory in Mendoza, Argentina (Villalba, 1985; Villalba and Boninsegna, 1989), and during the 2000s onwards (Giantomasi et al., 2009, 2012, 2013; Piraino et al., 2015; Piraino and Roig, 2016). The past four decades of research on *Prosopis* tree rings emphasize the influence of hydrological variables on *Prosopis* growth and wood anatomy (Villalba et al., 2000; Villagra et al., 2010; Piraino et al., 2015; Nogueira et al., 2019; Cangiano et al., 2020). Nonetheless, they also suggest that the relationship between *Prosopis* tree rings and hydroclimate variables such as rainfall and streamflow is complex, influenced or masked by groundwater table oscillations and human activity (Decuyper et al., 2016; Cangiano et al., 2020).

Previous reviews describe the advances of dendrochronology in South America, valuing tree-ring research as a proxy to obtain ecological and climatic data (Villalba et al., 2000; Boninsegna et al., 2009; Villagra et al., 2010; Cangiano et al., 2020). The recent review by Cangiano et al. (2020) highlights the global importance of *Prosopis* value for dendroecological research. We add to this discussion in two ways, one, by focusing solely on the relationship between *Prosopis* woody growth and hydrological parameters in South America, adding a deeper understanding as to how this genus responds to variability in climate and water resources specifically in South America; two, we also add a spatial analysis of the location, climate, soil humidity and topography of tree-ring research to understand geographical gaps in the study of this growth-water relationship. This review provides an analysis of the dendrochronological capacity of the genus *Prosopis* focusing on the tree growth - water relationship and the spatial distribution of this research with respect to hydrological and topographical gradients. This paper reviews the literature on dendrochronological research using *Prosopis* in relation to hydrological variables and uses GIS tools to overlay study locations with geographical and hydroclimate data in South America. We aim to 1) Analyze the frequency and spatial distribution of research studies and tree-ring chronologies addressing *Prosopis* spp. growth and hydrology in South America with respect to geographic, hydroclimate, soil moisture and elevational gradients; and 2) further the understanding of the relationship between *Prosopis* spp growth and hydrological variables via the recompilation of the literature from South America. Due to the distribution of the genus, the studies revised are largely restricted to tropical and subtropical latitudes but span a diversity of climates and biomes within the Americas to which this genus is native.

## 2. Materials and methods

### 2.1. *Prosopis* genus

*Prosopis* L. is a genus of the Fabaceae family with 44 species distributed in arid and semi-arid areas (Burkart, 1976; Pasiecznik et al., 2004) in Southeastern Asia (three native species), tropical Africa (one native species) and the Americas, from the Southwestern USA to Patagonia in Chile and Argentina (40 species), from which 31 species are exclusive to South America (Burkart, 1976). The genus *Prosopis* L. currently occurs in 129 countries worldwide and is an exotic invasive species in 112 countries (Shackleton et al., 2014), including in northeastern Brazil where *Prosopis juliflora* is considered an exotic invasive in the Caatinga region (Nogueira et al., 2019). Within the genus, many species are known to form hybrids with intermediate traits (Pasiecznik

et al., 2004). Arboreal species are distributed throughout arid and semi-arid climates of Argentina, Northern and Central Chile, Southern Bolivia and Western Paraguay and along subtropical humid climates of Southeastern South America, including Uruguay, northwestern Argentina, Southern Brazil and Eastern Paraguay. *Prosopis* species also occur at high-elevation semi-arid environments in the tropical latitudes of Perú, Ecuador, Colombia, and Venezuela (Pasiecznik et al., 2004). In the colder temperate climates of Southern Argentina, arbustive species occur, including *P. denudans*, *P. alpataco*, and other woody species with low, shrub-like architecture, reaching the southern provinces of Chubut and Santa Cruz in Patagonia (Fig. 1). The ability of many species within the genus to tolerate drought, salinity and alkalinity, and the impressive extent of its root system, reaching 30 m horizontally and 17 m vertically within this phreatophyte group (Villagra et al., 2010), make it a

dominant genus among woody flora of these areas, largely within the tropical and subtropical (35°N–35°S) latitudes of the Americas (Roig, 1993; Villalba et al., 2000).

## 2.2. Literature review and meta-analysis

A systematic review of the literature in *Prosopis* tree-ring research in the Americas was conducted for the period 1930–2021 using Google Scholar search engine. We used as keywords various combinations of the following English and Spanish keywords: “Dendro”; “*Prosopis*”; “South America” to select a pool of eligible papers. We then searched within those obtained papers for the keywords, “Water”, “Precipitation”, “Rainfall”, and “Phreatic” to assess if the article addressed these topics. Three review papers, Villalba et al. (2000), Villagra et al. (2010) and

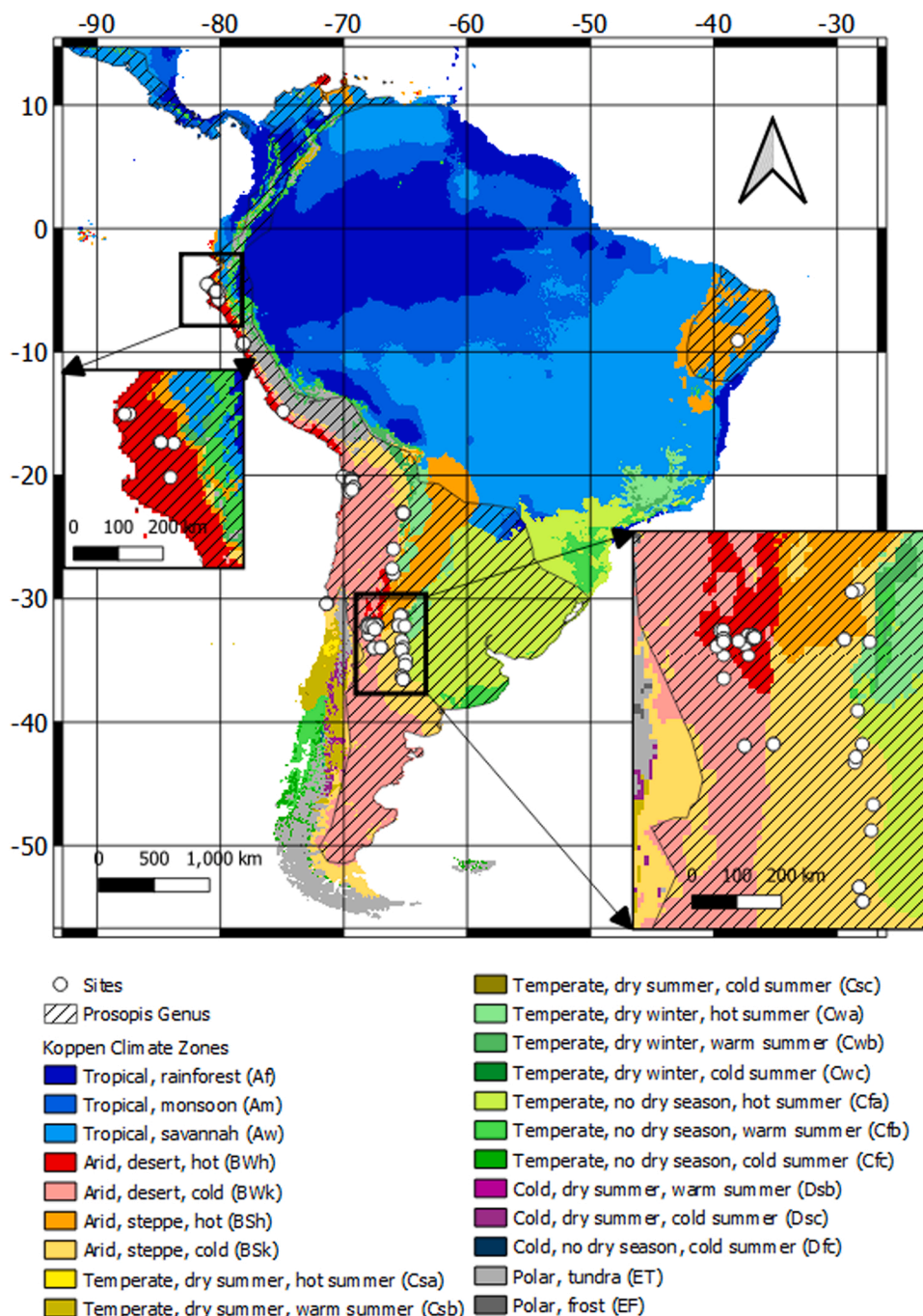


Fig. 1. Map of the distribution of 83 study sites reviewed for *Prosopis* in the tropical Americas, laid over Köppen Climate regions. Studies were in Arid desert, hot (BWh); Arid, desert, cold (BWk); Arid, steppe, hot (BSh); Arid, steppe, cold (BSk); Temperate, dry Winter, hot summer (Cwa); Temperate, no dry season, hot summer (Cfa). Hashed polygon shows the approximate present-day distribution of arboreal species, sensu Pasiecznik et al. (2004), extended to Southern Argentina to include shrub species, sensu Palacios & Brizuela 2005, of the genus *Prosopis* in South America.



Cangiano et al. (2020), and the obtained peer-reviewed articles were used to find further literature that addressed the *Prosopis* – water relationship. We also referred to the International Tree Ring Database (ITRDB) for *Prosopis* chronologies (N = 4). We exclusively compiled field studies, excluding those based on greenhouse or laboratory experiments. We limited the search to peer-reviewed scientific articles, book chapters, and published academic theses, excluding conference papers/abstracts and other gray literature.

We reviewed more than 97 articles, from which 57 were set aside for lack of mention of hydrology, precipitation, or water. Among the 40 remaining articles, we compiled a database containing country, province or state, site name, latitude, longitude, altitude (m a.s.l.), annual precipitation, species, publication year, authors, and study focus; georeferencing the articles according to provided geographic coordinates of the study site or study area (Fig. 1). When not available, coordinates of the approximate location of the study were obtained from Google Earth. We used as the unit of analysis the studies and chronologies when available, given that some publications included multiple chronologies and others none (Table 1). Each study was assigned a “focus” as one of four categories, dendrochronology, dendrohydrology, dendroclimatology and wood anatomy (including tree-ring formation and hydrosystem), based on the outlined objectives of each study.

To map the distribution of these chronologies, we obtained a global network of rivers and watersheds from the WWF HYDROSheds (Lehner and Grill, 2013). The location of each chronology was mapped in QGIS v. 3.14 (GIS Development Team, 2020). Gridded data for mean annual precipitation (MAP) from 1970 to 2020 over the continent of South America was calculated from monthly time series of the Climatic Research Unit (University of East Anglia) CRU TS 4.05 and Met Office (Harris et al., 2020) at a spatial resolution of 0.5°. Similarly, mean annual soil moisture at 0–10 cm depth from 1982 to 2020 in South America was calculated using the gridded time series for monthly soil moisture from FLDAS (McNally, 2018) at a spatial resolution of 0.1°. MAP and mean annual soil moisture at the location of each site shown in Table 1 were obtained from the closest grid point in each database to each site. Elevation was obtained from the intersection of points with a Digital Elevation Map (DEM) for South America at a spatial resolution of 0.018° longitude and 0.015° latitude. We used the Xarray package (Hoyer and Hamman, 2017) in the Python 3.8 language (Van Rossum and Drake, 2009) to map locations of research sites across gradients of elevation, MAP, and mean annual soil moisture. GIS shapefiles for Köppen climate zones (Fig. 1) were downloaded from <http://www.gloh2o.org/koppen/>.

To evaluate the spatial distribution of research across environmental and geographical gradients, we developed histograms for the frequency of sites – including tree-ring chronologies and other growth-related study locations – across latitude, longitude, mean annual precipitation (MAP), elevation (m a.s.l.), soil moisture, species and countries.

### 3. Results and discussion

We reviewed the literature on the relationship between *Prosopis* and hydrology in South America. The 40 articles reviewed covered 11 species from six Köppen climate zones (Fig. 1) and four countries (Fig. 2), including 56 tree-ring chronologies and 27 sites with other analysis (isotopes, water potential, growth, anatomy, etc.). Given multiple tree-ring chronologies per research article, we used site (n = 83) as the unit of analysis to explore spatial patterns of research to date. Sites comprised latitudes from 4.5° S to 35.4°S, comprising largely tropical and subtropical latitudes (Fig. 1). Nonetheless, there was a lack of published studies from Patagonia in southern Argentina, where *Prosopis* is present as shrub species, as well as in Northwestern South America, in Ecuador, Colombia and Venezuela where the genus occurs at high elevations (Figs. 1, 3). Study sites spanned a rainfall gradient from 1 to 730 mm y<sup>-1</sup>, according to rainfall data reported by the studies, with an even distribution of sites across mapped MAP from 0 to 700 mm y<sup>-1</sup>

(Fig. 3A). One study of *P. burkartii* was conducted in northern Chile where mean annual precipitation was 1 mm y<sup>-1</sup> (Fig. 2). There was a lack of published research in subhumid and humid regions where *Prosopis* occurs with precipitation from 731 to over 1500 mm y<sup>-1</sup>, and where soil humidity is above 0.22 m<sup>3</sup> m<sup>-3</sup>, including in Southeastern South America (Fig. 3A,B). Such regions are climatically distinct from the desert, arid and semi-arid steppe regions where *Prosopis* spp. research was more prevalent. Studies also spanned a broad elevational gradient between 30 and 3500 m a.s.l. (Figs. 4,5), with 65% of sites occurring between 200 and 600 m. High elevation sites above 2800 m were exclusively studies of *P. ferox* in the intermontane valleys of northern Argentina (Fig. 2; Table 1). Low elevation studies were exclusively based on *P. pallida* and growth-climate relationships in the arid environments of coastal Peru (Figs. 2, 4). Research covered at least 11 species of *Prosopis* (Fig. 2), dominated in number of sites by *P. flexuosa* (43%), *P. pallida* (14%), *P. ferox* (10%) and *P. caldenia* (10%; Fig. 2). We begin the literature review with a summary of the formation of growth rings and anatomy of *Prosopis* species, as a basis for understanding their unique and complex relationship with water and hydrology.

#### 3.1. Formation of growth rings and anatomy of the hydrosystem

In *Prosopis*, the identification of annual growth rings is challenging given the variability among species and among individuals of the same species (Villalba et al., 2000) and require an exhaustive analysis to become familiar with annual growth patterns of each species. In an analysis of ring formation among 25 species of *Prosopis* in South America, three main anatomical parameters are described in order to identify the growth-ring limits: vessels, parenchyma and fibers (Villalba et al., 2000). Early wood is typically characterized by the presence of large vessels, while late wood usually has smaller vessels and a higher percentage of fibers. In many species the annual growth ring is delimited by a band of terminal parenchymal tissue. According to Villalba et al. (2000), the cambial activity in *Prosopis flexuosa* DC. indicates that these bands are formed annually.

Among the wood characteristics associated with hydrology and hydrological variability over time is the size and distribution of the conducting elements within the annual ring. As water conductivity is reflected in water-conducting cell (e.g. vessel) size and density, the analysis of cell structure and function allows for the study of the physiological mechanisms behind tree growth and growth sensitivity to water availability (Fonti et al., 2010; De Micco et al., 2016). The intra-annual variability in cell structure provides additional information regarding the hydrological effect on growth processes rather than tree-ring width alone (e.g., Giantomasi et al., 2013). For instance, *Prosopis flexuosa* DC. presents semi- to diffuse ring porosity, where, depending on water availability, vessels can be larger (humid periods) or smaller (dry periods) within the annual ring, a typical pattern among phreatophyte species (Villalba, 1985; Giantomasi et al., 2013). The *Prosopis* hydrosystem – the network of tubular cells for water transport (Eckstein, 2004) – suggests adaptation to limited rainfall and prolonged droughts, with small and short vessel elements, simple perforation plates and thick walls; characteristics that allow for high metabolic activity during periods of short and infrequent rains in arid zones (see figures of ring anatomy in Villalba et al., 2000). *P. flexuosa* presents large vessels concentrated in the earlywood, permitting physiological adjustment to large demands for water transport through the xylem at the onset of the growth season, coinciding with Nov-Dec rainfall in central Argentina (Villalba and Boninsegna, 1989; Giantomasi et al., 2009).

Growth ring formation in *Prosopis* can respond to seasonal changes in water availability, as was observed in regions of seasonal rainfall concentrated in austral spring and summer, as in central-western Argentina (Karlin and Díaz, 1984; Piraino et al., 2015). For example, cambial activity in *Prosopis flexuosa* DC. in Argentina presented differentiation of vessels in the early wood during the first week of November,

**Table 1**

Reviewed papers, indicating country, province, site, latitude, longitude, species, year published, authors, focal sub-area (Dendroclimatology, Dendroecology, Dendrohydrology, Wood Anatomy), mean annual precipitation (MAP), soil moisture at 0–10 cm depth (SM), and elevation (m a.s.l.) data were obtained from GIS databases over the same time period and may differ from that reported within each study.

Prov.	Site name	lat	lon	Species	Year	Authors	Sub-area	MAP	SM	Elev
PERU										
MOR	Rinconada	-4.54	-81	<i>P. pallida</i>	2017	Ancajima EA	Dendroclim	107	0.167	403
PIU	Ignacio Távora	-5.8	-80.18	<i>P. pallida</i>	2017	Ancajima EA	Dendroclim	131	0.158	93
SAP	Piura	-5.1	-80.38	<i>P. pallida</i>	2017	Ancajima EA	Dendroclim	199	0.163	211
MOR	Rinconada	-4.54	-81.1	<i>P. pallida</i>	2018	Salazar et al.	Dendroclim	81	0.159	158
PIU	Piura	-5.1	-80.38	<i>P. pallida</i>	2018	Salazar et al.	Dendroclim	199	0.163	211
SAP	Ignacio Távora	-5.12	-80.11	<i>P. pallida</i>	2018	Salazar et al.	Dendroclim	295	0.188	98
PIU	Piura	-5.1	-80.38	<i>P. pallida</i>	2005	López et al.	Dendroclim	199	0.163	211
PIU	Piura	-5.1	-80.38	<i>P. pallida</i>	2006	López et al.	Dendroclim	199	0.163	211
CAS	Casma	-9.51	-78.22	<i>P. pallida</i>	2006	López et al.	Dendroclim	179	0.182	152
NAZ	Nazca	-14.83	-74.93	<i>P. pallida</i>	2006	López et al.	Dendroclim	66	0.204	597
PI	Piura	-5.1	-80.37	<i>P. pallida</i>	2006	Holmgren	Dendroclim	202	0.164	213
CAS	Áncash	-9.33	-78.14	<i>P. spp</i>	2015	Ghezzi et al.	Dendroclim.	299	0.195	791
CAS	Áncash	-9.33	-78.14	<i>P. pallida</i>	2005	Rodríguez et al.	Dendroclim	299	0.195	791
BRAZIL										
BAH	Paulo Alfonso	-9.1	-38.09	<i>P. juliflora</i>	2019	Carvalho et al.	Dendroclim	544	0.225	489
CHILE										
TAR	Caserones	-20.9	-69.61	<i>P. spp</i>	2019	Olson et al.	Dendroclim	26	0.174	934
TAR	Ramaditas	-20.99	-69.2	<i>P. spp</i>	2019	Olson et al.	Dendroclim	49	0.163	1687
TAR	Guatacondo	-21.03	-69.46	<i>P. spp</i>	2019	Olson et al.	Dendroclim	37	0.151	914
TAR	Salar de Llamara	-21.36	-69.59	<i>P. spp</i>	2019	Olson et al.	Dendroclim	30	0.162	766
TAR	Iquique	-20.14	-70.08	<i>P. burkartii</i>	2017	Carevic et al.	Dendrohidro	5		860
TAR	Tamarugal	-20.28	-69.38	<i>P. tamarugo</i>	2016	Decuyper et al.	Dendrohidro	28	0.182	1629
TAR	Salar de Pintados	-20.32	-69.43	<i>P. tamarugo</i>	2016	Chavez et al.	Dendrohidro	27	0.180	1249
TAR	Salar de Bellavista	-20.43	-69.37	<i>P. tamarugo</i>	2016	Chavez et al.	Dendrohidro	31	0.176	1250
TAR	Q. Guatacondo	-21.01	-69.22	<i>P. alba</i>	2010	Rivera et al.	Dendroclim	50	0.161	1588
				<i>P. tamarugo</i>						
COC	Fray Jorge	-30.41	-71.37	<i>P. chilensis</i>	2006	Holmgren	Dendroclim	126	0.185	213
TAR	Iquique	-21.21	-69.35	<i>P. tamarugo</i>	2016	Garrido et al.	Dendrohidro	48	0.149	1048
COC	Limarí	-30.43	-71.43	<i>P. chilensis</i>	2006	López et al.	Dendroclim	130	0.183	158
ARGENTINA										
JUJ	Q. Humahuaca	-23.1	-65.2	<i>P. ferox</i>	2012	Morales & Villalba	Dendroclim	513	0.291	3990
JUJ	Q. Humahuaca	-23.1	-65.2	<i>P. ferox</i>	2005	Morales et al.	Dendroclim	513	0.291	3990
JUJ	Q. Humahuaca	-23.1	-65.2	<i>P. ferox</i>	2004	Morales et al.	Dendroclim	513	0.291	3990
JUJ	Q. Humahuaca	-23.1	-65.2	<i>P. ferox</i>	2002	Villagra et al.	Wood A.	513	0.291	3990
SAL	Valles Calchaquies	-26	-66	<i>P. flexuosa</i>	2002	Villagra et al.	Wood A.	622	0.268	1895
CAT	Pipano	-28	-66	<i>P. flexuosa</i>	2002	Villagra et al.	Wood A.	541	0.252	2500
MEN	Telteca	-32.5	-68	<i>P. flexuosa</i>	2002	Villagra et al.	Wood A.	220	0.197	565
MEN	Nacuñán	-34	-67	<i>P. flexuosa</i>	2002	Villagra et al.	Wood A.	429	0.228	425
JUJ	Churquiaguada	-23.11	-65.19	<i>P. ferox</i>	2001	Morales et al.	Dendroclim	521	0.292	3970
JUJ	Q. Sapagua	-23.08	-65.21	<i>P. ferox</i>	2001	Morales et al.	Dendroclim	504	0.290	4124
CAT	Pipano	-27.58	-66.1	<i>P. flexuosa</i>	2005	Villagra et al.	Dendroeco	577	0.252	1854
MEN	Telteca	-32.2	-67.52	<i>P. flexuosa</i>	2005	Villagra et al.	Dendroeco	282	0.200	505
MEN	Nacuñán	-34.03	-67.58	<i>P. flexuosa</i>	2005	Villagra et al.	Dendroeco	345	0.220	482
COR	El Álamo	-31.36	-65.3	<i>P. flexuosa</i>	2013	Giantomasi et al.	Dendrohidro	561	0.235	1100
SL	Luján	-32.21	-65.58	<i>P. flexuosa</i>	2013	Giantomasi et al.	Dendrohidro	582	0.252	460
MEN	Santa Luisa	-32.3	-67.57	<i>P. flexuosa</i>	2013	Giantomasi et al.	Dendrohidro	277	0.201	507
COR	Chancaní	-31.4	-65.43	<i>P. flexuosa</i>	1989	Villalba et al.	Dendroclim	551	0.229	395
MEN	Telteca	-32.9	-68	<i>P. flexuosa</i>	1989	Villalba et al.	Dendroclim	240	0.203	591
MEN	Pozo Verde	-32.06	-68.07	<i>P. flexuosa</i>	2015	Piraino et al.	Dendroclim	185	0.193	541
MEN	La Juana	-32.14	-67.51	<i>P. flexuosa</i>	2015	Piraino et al.	Dendroclim	281	0.200	510
MEN	El Mateo	-32.14	-67.41	<i>P. flexuosa</i>	2015	Piraino et al.	Dendroclim	299	0.201	508
MEN	Puesto Viejo	-32.18	-67.38	<i>P. flexuosa</i>	2015	Piraino et al.	Dendroclim	307	0.203	504
MEN	Río Viejo	-32.18	-67.38	<i>P. flexuosa</i>	2015	Piraino et al.	Dendroclim	307	0.203	504
MEN	Caferino	-32.19	-67.42	<i>P. flexuosa</i>	2015	Piraino et al.	Dendroclim	300	0.202	505
MEN	Puesto Viejo	-32.18	-67.38	<i>P. flexuosa</i>	2015	Piraino et al.	Dendroclim	307	0.203	504
MEN	Telteca	-32.2	-68	<i>P. flexuosa</i>	2005b	Villagra et al.	Dendroeco	204	0.195	539
MEN	Nacuñán	-34.03	-67.58	<i>P. flexuosa</i>	2005b	Villagra et al.	Dendroeco	345	0.220	482
MEN	El Mateo	-32.14	-67.41	<i>P. flexuosa</i>	2016	Piraino et al.	Dendrohidro	299	0.201	508
MEN	Telteca	-32.2	-68	<i>P. flexuosa</i>	2009	Guevara et al.	Dendrohidro	204	0.195	539
MEN	Pozo Verde	-32.06	-68.01	<i>P. flexuosa</i>	2017	Piraino et al.	Dendrohidro	194	0.193	536
MEN	La Juana	-32.14	-67.51	<i>P. flexuosa</i>	2017	Piraino et al.	Dendrohidro	281	0.200	510
MEN	El Mateo	-32.14	-67.41	<i>P. flexuosa</i>	2017	Piraino et al.	Dendrohidro	299	0.201	508
MEN	Puesto Viejo	-32.18	-67.38	<i>P. flexuosa</i>	2017	Piraino et al.	Dendrohidro	307	0.203	504
MEN	Río Viejo	-32.18	-67.38	<i>P. flexuosa</i>	2017	Piraino et al.	Dendrohidro	307	0.203	504
MEN	Caferino	-32.19	-67.42	<i>P. flexuosa</i>	2017	Piraino et al.	Dendrohidro	300	0.202	505
MEN	Puesto Viejo	-32.18	-67.38	<i>P. flexuosa</i>	2017b	Piraino et al.	Dendrohidro	307	0.203	504
MEN	Puesto Viejo	-32.18	-67.38	<i>P. flexuosa</i>	2011	Jóbbágy et al.	Dendrohidro	307	0.203	504
MEN	Telteca	-32.2	-68	<i>P. alpataco</i>	2011	Jóbbágy et al.	Dendrohidro	204	0.195	539
MEN	Asunción	-32.22	-68.14	<i>P. alpataco</i>	1997	Villagra et al.	Dendroclim	192	0.197	560
MEN	Telteca	-32.2	-68	<i>P. argentina</i>	1997	Villagra et al.	Dendroclim	204	0.195	539
MEN	Puesto La Penca	-32.25	-68	<i>P. flexuosa</i>	2011	Giordano et al.	Dendrohidro	207	0.195	542

(continued on next page)

Table 1 (continued)

Prov.	Site name	lat	lon	Species	Year	Authors	Sub-area	MAP	SM	Elev
MEN	Telteca	-32.24	-67.7	<i>P. flexuosa</i>	2021	Meglioli et al.	Dendrohidro	250	0.198	516
SL	Puesto El Águila	-34.3	-65.37	<i>P. caldenia</i>	2011	Bogino et al.	Dendroclim	639	0.264	389
SL	Luján	-32.21	-65.58	<i>P. flexuosa</i>	2009	Giantomasi et al.	Wood A.	582	0.252	460
MEN	Telteca	-32.5	-67.5	<i>P. flexuosa</i>	2015	Giantomasi et al.	Dendroeco	299	0.205	497
SL	Las Isletas	-33.44	-65.31	<i>P. caldenia</i>	2008	Bogino et al.	Dendrohidro	662	0.253	670
SL	Don Roberto	-34	-65.22	<i>P. caldenia</i>	2008	Bogino et al.	Dendrohidro	675	0.252	404
SL	Las Taguas	-34.21	-65.35	<i>P. caldenia</i>	2008	Bogino et al.	Dendrohidro	646	0.268	398
SL	El Liberal	-32.25	-65.07	<i>P. caldenia</i>	2008	Bogino et al.	Dendrohidro	636	0.264	701
MEN	Nacuán	-34	-67	<i>P. flexuosa</i>	1985	Villalba	Dendroclim	429	0.228	425
COR		-35	-65	<i>P. caldenia</i>	2018	Risio et al.	Dendroclim	654	0.263	265
LP	Ingeniero Foster	-35.42	-65.04	<i>P. caldenia</i>	2014	Bogino	Wood A.	655	0.246	302
LP	Las Vertientes	-36.34	-65.28	<i>P. caldenia</i>	2019	Bogino	Dendroclim	628	0.262	296
				<i>P. ferox</i>						
LP	Naicó	-36.57	-65.21	<i>P. caldenia</i>	2019	Bogino	Wood A.	595	0.262	279
				<i>P. ferox</i>						

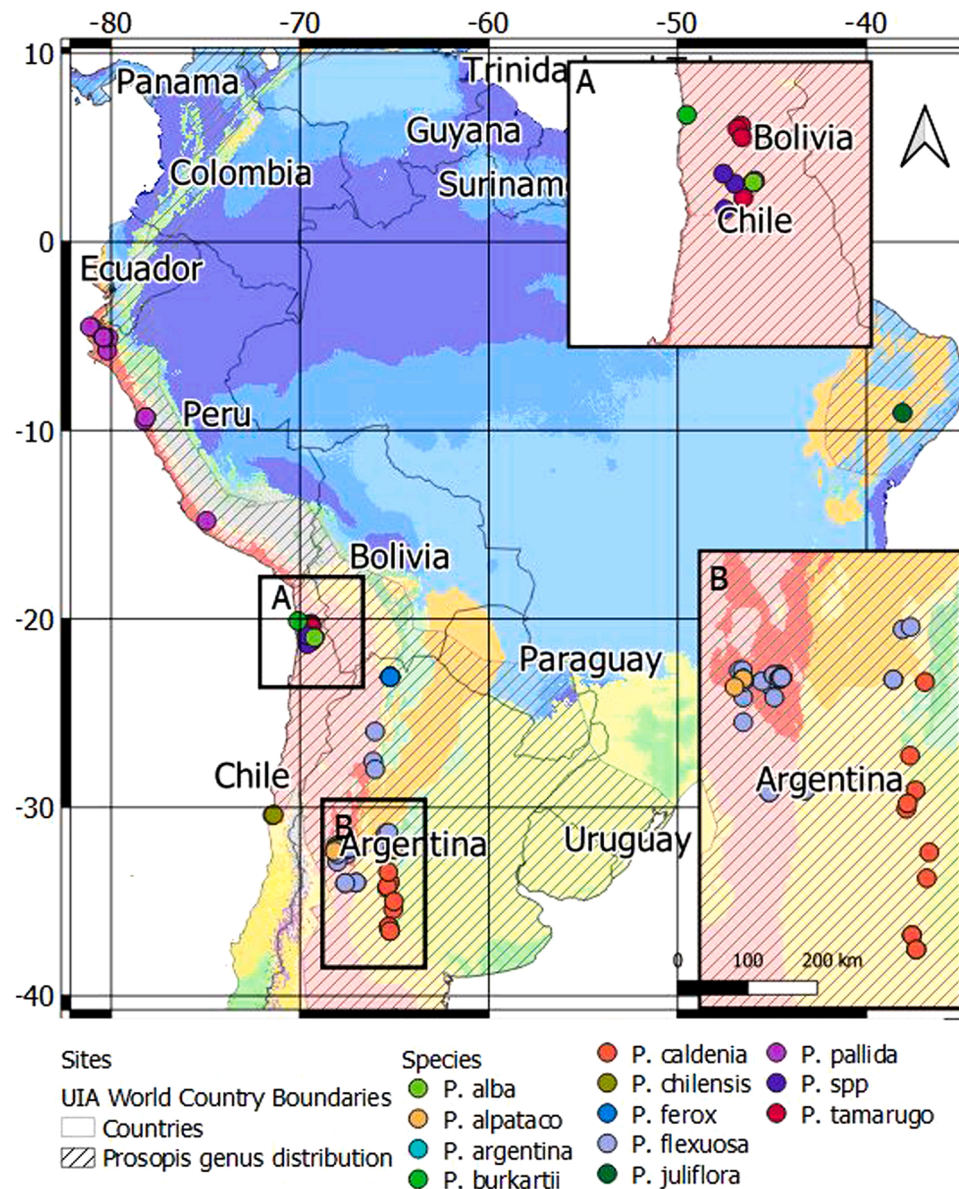
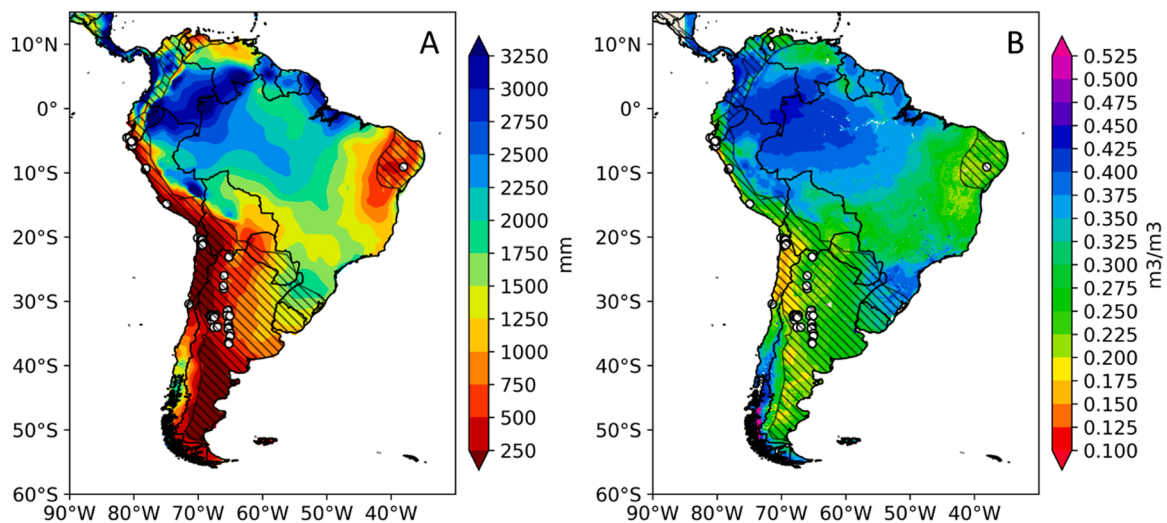
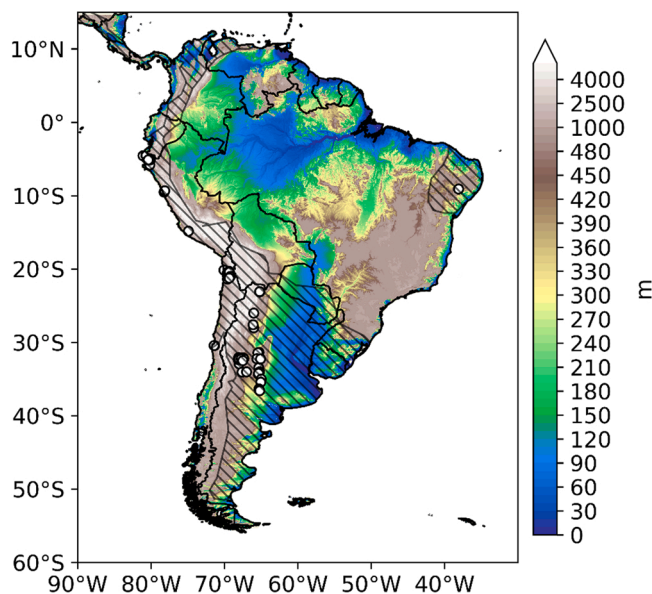


Fig. 2. Map of the distribution of 83 studies by *Prosopis* species (locations associated with more than one species are indicated as *Prosopis* spp.), showing country and Köppen climate regions as in Fig. 1. Hashed polygon shows the approximate present-day distribution of arboreal species, *sensu* Pasiecznik et al. (2004), extended to Southern Argentina to include shrub species, *sensu* Palacios & Brizuela 2005, of the genus *Prosopis* in South America.





**Fig. 3.** Map of study locations by A) Mean annual precipitation – MAP (mm), B) Mean annual soil moisture at 0–10 cm depth ( $\text{m}^3/\text{m}^3$ ). Hashed polygon shows the approximate present-day distribution of arboreal species, *sensu* Pasiiecznik et al. (2004), extended to Southern Argentina to include shrub species, *sensu* Palacios & Brizuela 2005, of the genus *Prosopis* in South America.



**Fig. 4.** Map of study locations by Elevation (m a.s.l.). Hashed polygon shows the approximate present-day distribution of arboreal species, *sensu* Pasiiecznik et al. (2004), extended to Southern Argentina to include shrub species, *sensu* Palacios & Brizuela 2005, of the genus *Prosopis* in South America.

coinciding with the beginning of the rainy season. Cambium activity peaks during December and January and ceases at the end of the rainy period (April) and remains completely inactive during the dry season, an adaptation to the rigorous environmental conditions where the species occurs (Villalba, 1985). The monthly and seasonal patterns of cambial activity and ring formation in climates with no dry season (see Fig. 1) is poorly known in South America.

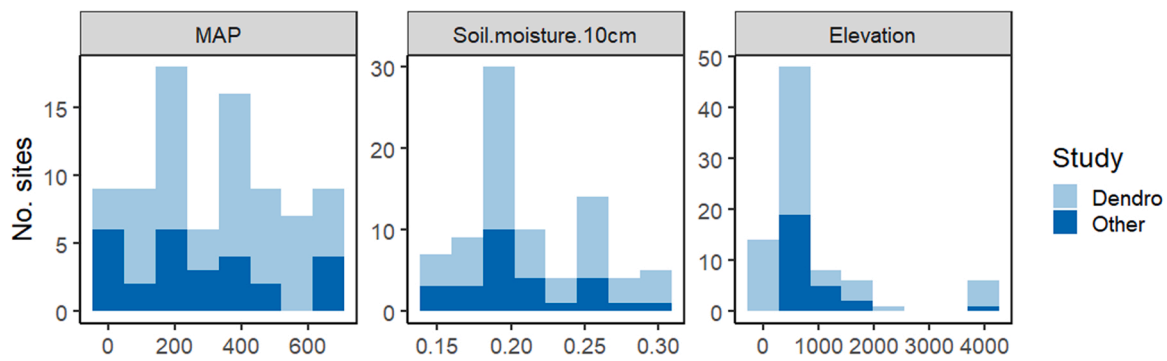
Variability among species in cell structure within the hydrosystem are indicative of its growth and survival strategy in arid and semi-arid environments with different sources and seasonality in water availability. In the species *Prosopis alata* Phil. and *Prosopis argentina* Burkart of central-western Argentina, the wood is semi-ring porous (Villagra and Roig, 1997). *P. argentina* has greater variability in vessel diameter than *P. alata*, suggesting that it behaves as a xeromorphic species, maximizing resistance against water stress in the sand dunes where it

grows without access to groundwater (Villagra and Roig, 1997). Alternatively, *P. alata* has mesomorphic features, including a hydrosystem that prioritizes efficiency in water conduction, coinciding with moderately humid environments. This species tends to grow in areas with access to groundwater and minimal dependence on pluvial sources, especially in dry regions (Villagra and Roig, 1997). These interspecific differences in the structure characteristics of the hydrosystem show that *Prosopis* is a highly plastic genus, adapting growth strategies to different environmental conditions, especially the availability of water. Groundwater accessibility can explain unusual or unexpected variability in growth rates and woody density of *Prosopis*, due to its phreatic capacity. Based on isotopic signals and fluctuations in groundwater levels in interdune areas of a desert ecosystem in Argentina, Jobbágy et al. (2011) determined that phreatic water was accessible to *P. flexuosa* at a depth of up to 6–10 m. *P. flexuosa* is a facultative phreatic species that grows in dunes without access to groundwater, while *Prosopis alata*, another characteristic species of the Monte desert, only grows in the low inter-dune zones, entirely dependent upon access to groundwater as an obligate phreatophyte species (Jobbágy et al., 2011).

The architecture of the hydrosystem as a whole – including rooting depth – is also indicative of how *Prosopis* species growth is linked to water resources in different environments. *Prosopis flexuosa* is a phreatophyte species that grows in the central-west of Argentina with a rainfall less than  $500 \text{ mm y}^{-1}$ , and accesses both underground and pluvial water sources, through horizontal (30 m) and vertical (17 m depth) stratification of its root system (Villagra et al., 2010), guaranteeing a more stable water source than solely rainfall and allowing it to grow in soils where other woody species struggle. *P. flexuosa* roots in different soil environments, where it showed a great phenotypic plasticity when growing with differential access to the water table (Guevara et al., 2010).

### 3.2. Dendroclimatology

The durability of *Prosopis* wood and weather resistance, together with its historical use in ancient constructions of arid sites, has facilitated the development of century-long tree-ring chronologies. This has enabled the development of ring-width chronologies, such as those from the wood of *Prosopis caldenia* Burkart and *Prosopis flexuosa*, both used as posts to build water wells over 250 years ago in the Argentinean Pampas (Bogino et al., 2019). Similarly, *Prosopis tamarugo* Phil. and *Prosopis alba* Griseb. wood samples over 2600 year old were recovered at the



**Fig. 5.** Number of sites ( $N = 83$ ), according to A) Mean annual precipitation (MAP,  $\text{mm y}^{-1}$ ), B) Mean annual soil moisture at 0–10 cm depth ( $\text{m}^3/\text{m}^3$ ) and C) Elevation (m a.s.l.). Bars are stacked for studies with tree-ring chronologies (Dendro) and those regarding other aspects of *Prosopis* spp. (Other).

archeological site “Las Ramaditas” in Atacama Desert in Chile (Rivera et al., 2010); and *Prosopis* sp. 2300 year old from the archeological astronomical observatory of Chankillo in the coastal desert of Peru (Ghezzi and Rodríguez, 2015). Similarly, it has been possible to study the Atacama Desert climate system in the Holocene, where annually and sub-annually resolved tree-ring  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values from *Prosopis* sp. trees were collected from surface deposits and archaeological sites in the Pampa del Tamarugal basin of northern Chile (Olson et al., 2020). This record of ancient trees was compared to modern records of *Prosopis* sp. trees, showing that *Prosopis* sp. records of wet and dry events during the Holocene in the Pampa del Tamarugal are sub-decadal and likely regulated by El Niño Southern Oscillation (ENSO) variability (Olson et al., 2020). In the case of living trees, some individuals of *Prosopis flexuosa* reach up to 200 years old, while *Prosopis caldenia* trees age over 300 years old (Villalba et al., 2000) and individuals from *Prosopis ferox* Griseb. can reach more than 500 years old (Morales et al., 2001). In these papers, *Prosopis* is presented as a key proxy for historical environmental variability in arid and semi-arid ecosystems in South America.

The relationship between *Prosopis* ring-width and regional climate variables such as rainfall and temperature vary among regions and sites. Both rainfall and temperature can mediate growth, as temperature—particularly early summer or dry season temperatures in tropical and subtropical climates— influences rates of evaporation, evapotranspiration, and thus water availability and hydric stress in the typically arid or semiarid conditions of the *Prosopis* genus distribution (Morales et al., 2004; Morales and Villalba, 2012; Salazar et al., 2018). For example, the relationship between climate variability and wood anatomy was evaluated among *Prosopis flexuosa* DC. in the Chaco and Monte phytogeographic regions of Córdoba and Mendoza provinces of Argentina (Villalba and Boninsegna, 1989). Results showed that below-average temperatures and above-average rainfall in spring (Oct-Dec) favored increased growth. In spring, rainfall before and during the growth season are positively correlated with tree growth, while high spring temperatures in the same growth season reduced annual growth. *Prosopis juliflora* DC., a native species of North America introduced in the semi-arid region of northeast Brazil (Caatinga), also shows a correlation between tree-ring and climate, where wider growth rings were related to increased rainfall during the dry periods, showing that this species is highly sensitive to rainfall variability (Nogueira et al., 2019). Studies of the climate-growth relationship in *Prosopis* have contributed to a broader understanding of limiting factors in high-elevation tropical latitudes. In contrast to research in temperate montane climates where temperature is often a major limiting factor for growth, among populations of *Prosopis ferox* Griseb. in Quebrada de Humahuaca (Argentina) at 3450 m a.s.l., precipitation limits the growth (Morales et al., 2004). The study demonstrated a strong positive correlation with below-average temperatures and above-average rainfall during the previous growth season. The correlation of annual growth with

abundant rainfall and high levels of humidity suggest that water is a main limiting factor for woody growth in subtropical latitudes, even at high elevations.

The sensitivity of *Prosopis* growth to local rainfall and temperature variability is also tied to global climate forces that influence regional climate. In some regions within South America, seasonal increases in rainfall are associated with the El Niño phase of the El Niño Southern Oscillation (ENSO). The record of ENSO events was evaluated in tree-ring chronologies of *Prosopis pallida* (Humb. & Bonpl.) Kunth, a dominant arboreal species in the dry forests of Northern Peru (López et al., 2005). Annual growth anomalies were correlated with annual rainfall, where increases in growth coincided with years of abundant rainfall during El Niño events in 1983, 1987, 1992, 1998. Other studies on the relationship between ENSO and the growth of *P. pallida* suggests that trees allocate resources to growth during El Niño events (Ancajima More, 2017) increasing up to 4 times its average growth rates during El Niño years (Salazar et al., 2018). These results concur with other studies of *P. pallida* (Rodríguez et al., 2005) and demonstrate that ENSO events are detectable in the growth rings of *P. pallida* and *Prosopis chilensis* (Molina) Stuntz (Lopez et al., 2006), and likely among other species in regions with climates linked to ENSO phenomena.

### 3.3. Dendrohydrology and groundwater

*Prosopis* can contribute to the understanding of interannual variability in streamflow of rivers in arid environments, a critical aspect of water management in water-limited systems. Tree-ring chronologies from *Prosopis flexuosa* in gallery forests of the del Monte desert in central-western Argentina, showed that tree growth in individuals near the river had a positive correlation with streamflow variability in spring and summer, coinciding with the growth season, while the individuals removed from the river's margin had growth correlated with winter and spring discharges, which recharge groundwater levels with rainfall in late summer (Piraino and Roig, 2016). Similarly, *P. flexuosa* tree-ring growth was highly correlated with rainfall in lowland sites with permeable soils far from rivers, and less correlated with rainfall near rivers, due to the presence of a stable water source (Piraino et al., 2015). The high correlation between streamflow and annual growth of individuals near the river reflects the value of *P. flexuosa*, and possibly other species of the genus, as a candidate for streamflow reconstruction.

The availability of water – including from underground sources – is a main limiting factor for the growth of woody species in arid and semi-arid climates of South America, such that tree-ring chronologies in xeric environments can provide a proxy for annual fluctuations in water table levels accessible to phreatophyte species (Villagra et al., 2005a; Bogino and Jobbágy, 2011). Accessible groundwater can have variable effects on vegetation, and mask tree-growth correlation with precipitation and streamflow. In Arid Chaco and Monte ecosystems, tree-ring growth in stands with access to groundwater was unrelated to climate, while those



without accessible groundwater sources were correlated with temperature and precipitation (Giantomasi et al., 2013). Similarly, micro-topographic heterogeneity in desert landscapes modulate the frequency and intensity of water stress experienced by *P. flexuosa* populations, due to differences in root system architecture and access to rainwater vs. groundwater (Giordano et al., 2011). Variations in groundwater levels are also associated with phenological changes among *Prosopis*, with decreasing groundwater levels during rainy periods when *Prosopis* peaks metabolic activity, and groundwater level recovery during leaf drop and low metabolic activity at the onset of winter, despite a seasonal lack of rain (Jobbágy et al., 2011). Grazing in arid and semi-arid systems can also combine with other factors to influence groundwater levels and ultimately tree growth. *P. flexuosa* populations showed a decline in groundwater levels in wooded areas compared to grazed areas, due to the lower cover of phreatophyte plants (Meglioli et al., 2021). Isotopic studies showed that grazing affects the chemistry of groundwater, increasing the concentrations of chlorides, nitrates and salts (Meglioli et al., 2021), increasing soil salinity and compromising plant establishment and growth.

*Prosopis* trees can be indicative of the presence of accessible groundwater sources in arid climates (Roig, 1993; González Loyarte et al., 2000), and ontogenic changes in annual growth can suggest changes in the access to ground water as trees develop root systems to access deep water (Villagra et al., 2005a). This phenomenon is demonstrated by the presence of *Prosopis flexuosa* trees with higher growth rates, height and basal area in the Telteca reserve with groundwater accessible at 5–20 m, and a mean annual rainfall of 159 mm y<sup>-1</sup>; and lower rates of growth in the Ñacuñán reserve, despite a rainfall of 329 mm y<sup>-1</sup>, and groundwater at 70–80 m depth (Villagra et al., 2005a). Tree growth during establishment was greater in Ñacuñán, favored by increased rainfall, while annual growth increased in Telteca when tree root systems reached groundwater (Villagra et al., 2005a). Similar results were found for *Prosopis caldenia* in San Luis, Argentina (Bogino and Villalba, 2008).

Changes in rainfall and groundwater levels can affect the establishment of phreatophyte species. Groundwater levels of some aquifers can undergo rapid change due to human activities and use, generating modifications in the landscape. The extraction of groundwater for mining and urban use has led to decline in water table in the Pampa del Tamarugal aquifer in Chile. Above this aquifer is the Atacama Desert, considered as the driest place on Earth, where the phreatophyte species *Prosopis tamarugo* Phil. accesses groundwater (Decuyper et al., 2016). A tree-ring study of the effect of groundwater extraction on *P. tamarugo* growth rates showed that the radial growth of trees in the high depletion zone was 48% lower than in the low depletion zones (Decuyper et al., 2016). Many of the trees in the highly depleted zone showed signs of stress to groundwater levels at 12 m deep (Chávez et al., 2016). The decline in groundwater levels is approximately 3–4 m (from 8 to 12 m) in recent decades, causing water stress in the crown and reducing radial growth. Water management mitigation to allow populations to recover are recommended (Decuyper et al., 2016), especially when groundwater levels reach 11 m deep (Garrido et al., 2016). In the same area, *Prosopis bukartii* Muñoz individuals showed greater hydraulic vulnerability during winter (May–Aug) frosts that can produce xylem cavitation leading to decreased xylem water potential (Carevic et al., 2017). During late spring and summer, the Pampa del Tamarugal aquifer has high recharge rates, providing these trees with a continuous water source. Studies like these may provide useful data to manage the coexisting water use and conservation interests.

Deforestation and increasing precipitation have caused the water tables to rise in parts of the flatland forests dominated by caldén (*Prosopis caldenia* Burkart). The effect of different levels of groundwater on *P. caldenia* growth, establishment, and survival was measured in a valley with shallow groundwater (0.5 m depth) and an adjacent plateau with groundwater at 8 m depth (Bogino and Jobbágy, 2011). Increased groundwater levels in the valley were associated with tree mortality,

while in the plateau led to increased establishment and growth. Based on aerial photographs and descriptions of local inhabitants, prior to 1960 the valley was the more favorable environment for the establishment of this species. The study suggests that changes in groundwater levels have varying effects on growth and persistence of *Prosopis*, which are susceptible to waterlogging.

### 3.4. Dendroecology and woodland management

Water availability and hydrological variability not only affect annual growth but also the population dynamics of *Prosopis* species. The influence of water on *Prosopis* interacts with multiple anthropic factors, including pruning, logging and use as shelter for livestock. *Prosopis ferox* is widely used for fuel, construction material, and feed for livestock. *P. ferox* woodlands provide 70% of the energy used by the population of Quebrada de Humahuaca (Jujuy), Argentina (Morales et al., 2005). Increased rainfall during 1950–1990 and a decrease in the intensity of land use benefitted the establishment of local *P. ferox* populations (Morales et al., 2005). A reduction in rainfall in 1990–2000 affected establishment despite decreased grazing pressures since 1950, demonstrating that the future sustainable production of wood in this region depends on rainfall and reduced cattle densities to promote the establishment of *P. ferox* (Morales et al., 2005). Controlled pruning in small trees of *Prosopis flexuosa* promoted radial growth and increased the number of xylem vessels, while decreasing vessel area (Giantomasi et al., 2015). These results suggest the formation of a more efficient and resilient hydrosystem, with a greater number of small vessels responding to conductive demands of the plant and, in turn, anticipating embolisms, usually generated in large diameter vessels (Carlquist, 2013). The increases in main stem basal area not reduce wood density, maintaining quality (Giantomasi et al., 2015). Removal of *P. flexuosa* trees generated resource-rich patches of nutrients and water availability, potentially exploited by the roots of neighboring trees and generating a “growth release” among the remaining individuals (Piraino et al., 2017).

The effect of environmental variability on tree growth and woody production was demonstrated along a latitudinal gradient northeastern Argentina (Villagra et al., 2005b) where mean growth, density, mean basal diameter, mean height, canopy cover and total wood biomass decreased along a north-south gradient. Wood production varied among sites, revealing that the northern mesquite trees had superior quality of wood for construction, while multi-stem forests in the south would provide local firewood and livestock shelter (Villagra et al., 2005b). Although in dendrochronology single-stemmed individuals are preferred for sampling, a study on the sensitivity of tree-ring chronologies with singular vs. multi-stemmed *Prosopis flexuosa* trees, showed that the latter had a higher correlation with climate variability, evidenced by greater sensitivity in the growth response to exceptionally rainy or dry years (Piraino and Roig, 2017). This was explained by the competition for resources between stems of the same tree, promoting water stress, generating greater sensitivity to variations in rainfall. The application of this study to understand the role of dendrochronology in forest management as a tool for sustainable use (Villagra et al., 2005b).

The establishment of trees and shrubs in arid and semiarid ecosystems is also influenced by climate variability and modulated by herbivore pressure. A comparative study on the effects of ENSO and herbivory on *Prosopis pallida* and *Prosopis chilensis* in Chile showed that, in Peru, twice as many individuals were recruited in ENSO years compared to years without ENSO events (Holmgren et al., 2006). Ring width was 2.8 times higher during ENSO years, but herbivory reduced survival to 31% in plots with herbivory. Alternatively in Chile, there was no correlation between tree establishment and annual rainfall. Under strong ENSO events and with protection against herbivory, only 8% of seedlings persisted, showing that other factors such as lower temperature and winter rainfall could affect establishment Chile (Holmgren et al., 2006). Similarly, the establishment of *Prosopis ferox* in Quebrada de Humahuaca, Argentina required at least 4 years with abundant rainfall

(Morales and Villalba, 2012). Although extreme rainfall events induced germination and establishment, without persistent rains and under the effects of high cattle density causing soil compaction, survival of young plants was hampered (Morales and Villalba, 2012).

The phreatophyte species of *Prosopis* play an indispensable role in xeric environments, including for the diversity of species associated with *Prosopis* trees and woodland ecosystems. The establishment of *Prosopis* forests in arid and semi-arid zones is a source of refuge and resources, generating habitat for other flora and fauna as well as resources for human use and consumption (Choge et al., 2007; Beresford-Jones et al., 2009; William and Jafri, 2015).

#### 4. Conclusions

This review compiles dendrochronological and other investigations of the genus *Prosopis* and its relation to water in South America, describing research to date and identifying general spatial distribution of research according to geographic, hydroclimate, and elevational gradients. We highlight:

- 1) The potential to expand the geographic range of *Prosopis*-hydrology studies to humid regions with no dry season; high-elevation regions of northwestern South America; and potentially to the steppe of Patagonia.
- 2) The frequent positive correlation between annual growth and rainfall, but that these relationships can be confounded by the tree's relationship with groundwater resources, including distance to groundwater table.
- 3) As phreatophytes, many *Prosopis* populations have complex relationship with streamflow, whereby underground water recharge and water tables confound seasonal signals for variable flow, making *Prosopis* rings challenging proxies for the reconstruction of streamflow data.
- 4) *Prosopis* trees are a human resource with socio-economic and cultural values throughout the Americas – given their value and historic declines in many regions, data that contributes to the sustainable management and conservation of this species will be important.

*Prosopis* species constitute the principal dendrochronological data source in many arid and semiarid ecosystems in South America. Geographical gaps in research were identified in subhumid and moist humid climates, Patagonian steppes, and high elevation regions of Bolivia, Ecuador, Colombia and Venezuela, where published data is currently scarce. Considering the increasing scarcity of freshwater in some regions where *Prosopis* occurs, its contribution to understanding historical trends in water availability is crucial. Further investigation of *Prosopis* woody growth, integrating new approaches such as vessel size chronologies, density marked rings and stable carbon and oxygen isotopes may help enrich tree-ring databases and further our understanding of how this unique genus provides a tool for water research and long-term management.

#### Note

At the final stages of publication, the genus *Prosopis* L. in South America was changed to *Neltuma* Raf. and *Strombocarpa* (Benth.) A. Gray, following Hughes et al. 2022.

#### Declaration of Competing Interest

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