Fire History of the Sierra de Manantlán Biosphere Reserve in Western México

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DEDICATION

To Jesse

For countless hours in the field, hundreds of meals cooked,
late nights and endless encouragement, I thank you.

INTRODUCTION

Fire is a natural process involved in the development of many ecosystems (Agee, 1993). It is a disturbance factor that influences ecosystem structure and function by affecting biotic and physical characteristics. Fire can both maintain and alter ecosystems and microenvironments by selecting for extant species, by allowing the invasion of new species and by changing the physical characteristics of soil (Agee, 1993; Whelan, 1995). In order to understand the role of fire in various ecosystems and to design scientifically informed ecosystem management, we must know how often those fires have occurred through a historical period and what the variability of this period has been.

Fire regimes differ in frequency, intensity, severity, extent and effect to vegetation communities (Agee, 1993; Whelan, 1995). Low-intensity fires in dry conifer forest usually have low mortality rates and impact on vegetation while similar intensity fires in montane cloud forest can have high mortality rates and create lasting changes to vegetation communities (Jardel-Peláez, personal communication). Fire history studies have been a valuable way to understand the frequency and effects of fires in varied ecosystems for many years (Grissino-Mayer, 2010). In fire-adapted ecosystems with high-frequency, low-severity fire regimes, tree-ring studies are frequently employed to reconstruct fire history and to use these disturbance-based reconstructions to determine the historical range of variation (Agee, 2003; Cissel et al., 1999).

I conducted a dendropyrochronological study of the pine and pine-oak forests of the Las Joyas Research Station in the Sierra de Manantlán Biosphere Reserve (referred to as “Biosphere Reserve” hereafter), located in the Sierra Madre del Sur mountain range in the states of Jalisco and Colima, México. This study was undertaken to expand our understanding of historical fire frequency in that region and to inform future fire and land management decisions. In the

Biosphere Reserve, as in a range of Mexican ecosystems, fire is recognized to be an influential factor in vegetation composition, structure and succession (Jardel, 1991; Jardel P. et al., 2003), however, studies of fire history in the region are scarce. This study fulfills a research need, as previous understanding of historical fire frequency in this area is limited to fire-fighting records dating back to 1995 (Jardel P. et al., 2003; Castillo-Navarro et al., 2003), inspection of satellite imagery (Balcázar-Medina, 2011), oral interviews with residents and preliminary dendrochronology studies (Jardel, 1991).

This study complements recent research conducted by Balcázar-Medina (2011) that investigated the geoecological patterns of wildfire across the reserve from 1995 – 2008 as well as fire history studies currently being undertaken by students at the University of Guadalajara. Additional fire-related research in the Sierra de Manantlán has focused on ecological effects of different fire regimes (Castillo, 2007), the role of fire in successional dynamics (Jardel, 1991), wildfire incidence (Castillo-Navarro et al., 2003), fire management and restoration (Jardel P. et al., 2003) and characterization of forest fuel beds (Alvarado-Celestino et al., 2008). This fire history study reconstructs fire frequency in the pine-dominated portions of the Biosphere Reserve, which will serve both as a foundation for development of scientifically informed restoration and fire management plans and as valuable background for future fire ecology studies.

BACKGROUND

Dendrochronology

Dendrochronology, the study of assigning accurate dates to historical events using tree rings, dates back to the early 1900s and the pioneering work of Andrew E. Douglass (Fritts, 1976). Trees in seasonal climates form annual rings as they grow radially in size. These rings are variable in width depending on limiting growth factors such as temperature, water availability or between-tree competition. Crossdating, a technique developed by Douglass, is used to match patterns of wide and narrow rings among trees and sites. Using this technique, we can assign the correct calendar year to events such as drought, insect outbreak and fire in samples of both living and dead wood (Speer, 2010).

Very little dendrochronological work has been undertaken in tropical conifers. The first crossdated and standardized tree-ring chronology in the North American Tropics was completed in *Abies religiosa* by Huante et al. (1991), demonstrating that Mexican tropical conifers can be used in dendrochronological studies. However, *A. religiosa* is a high elevation species and therefore may have similar growth behavior to northern conifers. More recent dendrochronological studies were conducted at the western end of the Trans-Mexican Neovolcanic Belt in *Pinus hartwegii*, but these trees were also in a seasonal climate at high-elevation sites above 3,500 meters above sea level (Biondi, 2001; Biondi et al., 2003)

False Rings

Annual rings are divided into earlywood, which contains relatively large tracheid cells with thin walls, and latewood, which contains smaller tracheid cells with thicker walls (Fritts, 1976; Stokes and Smiley, 1968). Earlywood is formed during the growing season, which in the

Sierra Madre del Sur is the rainy season from approximately mid-May to mid-December. Latewood forms as cambial activity slows before dormancy during the winter dry season. In many climates, the transition from early to latewood is gradual, while the transition from late to earlywood in the next growing season is sharply defined (Fritts, 1976; Speer, 2010; Stokes and Smiley, 1968). However, when seasonal changes are mild, annual growth deviates from this pattern. For instance, conifer growth in the Biosphere Reserve is water-limited, but during years when water is not limiting, trees may not become dormant at all causing diffuse ring boundaries (Speer, 2010). Additionally, when a limiting factor affects growth several times over one year, trees may put on double or false rings (Speer, 2010; Stokes and Smiley, 1968). Causes can be climatic such as droughts or monsoons (Hoffer and Tardif, 2009; Marchand and Filion, 2012; Priya and Bhat, 1998; Wimmer et al., 2000), environmental such as pollution (Copenheaver et al., 2006; Priya and Bhat, 1998) or phenological (Edmondson, 2010), but the causes of false rings in many species are still poorly understood.

Fire Scars

Trees that survive surface fires but experience sufficient heat to penetrate the bark and kill cambium form scars with distinctive post-fire curled ring patterns (Dieterich and Swetnam, 1984). Once scarred, trees are likely to scar again along the same bole radius resulting in a series of scars (Agee, 1993; Speer, 2010; Wright, 1996) as pictured in Figure 1. Fire-scarred trees often form what is commonly called a “catface”, an upside-down V-shaped injury, which is often, but not always, on the uphill side of the tree.

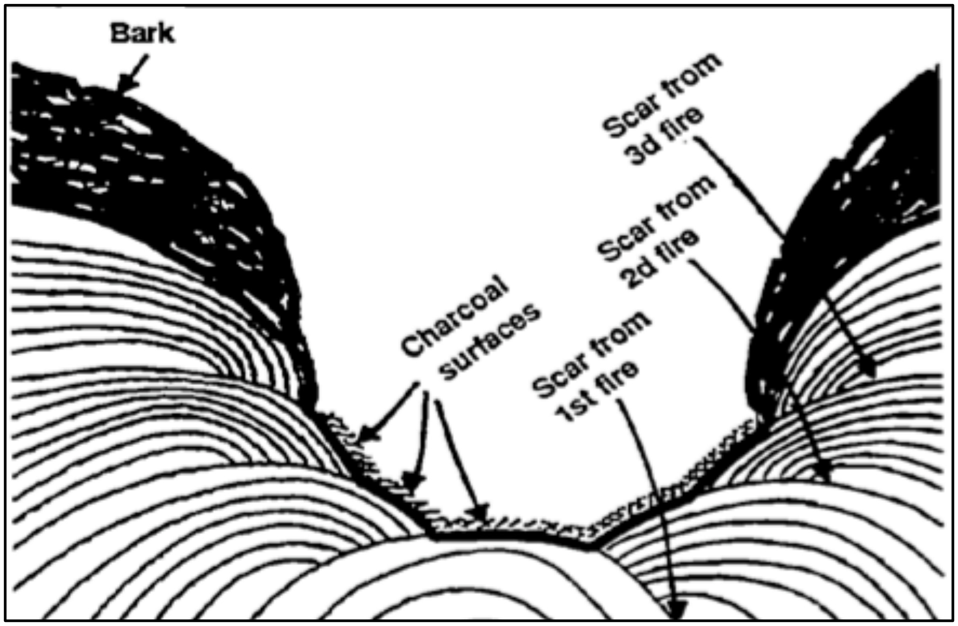


Figure 1. An illustration of multiple fire scars along the same bole radius of a tree (from Morrison and Swanson, 1990).

By taking partial cross sections from living or dead trees and crossdating the annual rings, calendar years can be assigned to historical fires by observing the date of the annual ring in which they occur. Crossdating of fire scars is the best method of dating historical fires in low-severity, frequent fire regimes such as pine and oak ecosystems in Western México (Swetnam and Dieterich, 1983). In many cases, the seasonality of fires can be inferred from the scar's location in the annual ring combined with information on the cambial phenology of the species in which they occur (Deiterich and Swetnam, 1984; Heyerdahl et al., 2007). It is important to note that fires do not always scar every tree (Arno and Sneck, 1977; Dieterich, 1980), so even a composite fire history from multiple trees at a site might be a conservative record.

Fire Regimes and Fire Frequency

The term *fire regime* is used to describe a suite of features that characterize fire occurrence within a given geographic location. These include frequency, intensity, severity, extent, predictability, seasonality and synergism (Agee, 1993; White and Pickett, 1985). A thorough description of all components of a fire regime is desirable to inform conservation and management decisions, following the premise that species within an ecosystem have adapted to such regimes. However, it is not always possible to address all elements of a fire regime in a single study. In this study I concentrate on the frequency, intensity and severity aspects of fire within pine-dominated forests in the Sierra de Manantlán Biosphere Reserve.

Frequency

Understanding how often fire has historically occurred in ecosystems, and the variation during those timeframes, is important in understanding the ecological effects of fire (Agee, 1993; Whelan, 1995). There are several methods of expressing the time intervals related to fire that are commonly used for different fire regimes. Natural fire rotation is defined as the length of time necessary for an area equal in size to the study area to burn, and is typically used to analyze infrequent, stand-replacing fire regimes. Fire interval, or fire-return interval, is the number of years between fires that occurred over a given area. Mean fire-return interval (MFI) is the arithmetic mean of all fire-return intervals that occurred over a given time and area, and it is typically used to analyze frequent, low-severity fire regimes (Agee, 1993) such as the fire regime in the study area. The MFI is frequently calculated from fire scar dates composited from multiple trees in a site to capture a more complete record of fires.

Fire return intervals are not always normally distributed, so the flexible Weibull distribution is often fit to the fire return interval distribution, and moments of the Weibull distribution are used to describe fire frequency. The Weibull distribution is a cumulative distribution function that allows analysis of the probability of non-normally distributed events such as fire intervals (Grissino-Mayer, 1999). The Weibull Median Interval (WME) is often reported in fire history studies along with the MFI.

Intensity

The intensity with which a fire burns is also a key part of defining fire regimes. Intensity is frequently measured in energy release per unit length of fireline, which is a function of flame length (Keeley, 2009; Rothermel and Deeming, 1980). Low-intensity surface fires have flame lengths <1 meter; intermediate-intensity understory fires have flame lengths 1-3 meters; and high-intensity crown fires and stand-replacing fires have flame lengths >3 meters (Agee, 1993).

Severity

Fire severity in forests is a measure of fire-caused damage to both aboveground and belowground organisms and disturbance to ecosystem processes (Runkle, 1985). Severity is determined by fire intensity as well as fire behavior, duration and fuel amounts and conditions (Agee, 1993; Whelan, 1995). In its simplest, most generalizable form it is divided into three categories:

1. Low Severity: frequent, low-intensity fire with low rates of mortality and ecological impact.
2. Mixed Severity: intermediate frequency of fire with a mix of low, medium and high-intensity fire resulting in patches of low, medium and high mortality and ecological impact.
3. High Severity: infrequent, high-intensity or low-intensity fire that causes high mortality rates and ecological impact. (Agee, 1993; Agee, 1998; Agee, 2003)

Although fire intensity and severity are related, fires of a given intensity may have very different severity levels in different ecosystems, therefore highly specific classification systems, such as the Composite Burn Index (CBI) have been developed for fire severity in specific vegetation communities and at different scales (Agee, 1993; Keeley, 2009; Key and Benson, 1999; Wright, 1996).

Fire and Climate

Studies have shown that there is a close link between variation in climate and fire occurrence (Swetnam and Betancourt, 1990). One example is drought conditions, which can result in vulnerability to fire by reducing fuel moisture and making wildfire more likely to spread. The El Niño-Southern Oscillation (ENSO) is a commonly used term to refer to atmospheric and oceanic climate cycling as measured over particular regions in the Pacific Ocean. It has warm phase (El Niño) and cool phase (La Niña) components that are designated for periods of time when average temperature anomalies exceed either a positive or negative threshold for a designated period of time. Definitions for these specific conditions have changed throughout time, but in general, phases are defined as periods of at least six months when averaged sea surface temperature (SST) anomalies exceed 4-5°C (El Niño) or remain below 4-5°C (La Niña; Trenberth, 1997).

Studies have linked ENSO phases to fire occurrence at the regional scale (Fulé et al., 2005; Heyerdahl and Alvarado, 2003; Heyerdahl et al., 2002; Swetnam and Betancourt, 1990). While in Northern México, as in the Southwestern United States, La Niña years (cool phase) have been linked to increased likelihood of fire (Fulé et al., 2005; Heyerdahl and Alvarado, 2003), El Niño winters have been linked to increased likelihood of fire in Southern México (Román-Cuesta et al., 2003; Román-Cuesta et al., 2004; Seager et al., 2009). Less is known about the influence of ENSO on fire in Western México, and it is unknown whether climate or other factors, such as variation in human ignitions, are stronger drivers of fire.

ENSO climate patterns have been shown to influence weather in Western México. Specifically, it has been shown that interannual variability in tropical storm rainfall is apparently linked to ENSO and North Pacific SST conditions (Englehart and Douglas, 2001). Therefore, it is desirable to investigate whether ENSO patterns are a driver of fire in Western México.

Fire Regimes in México

México is a megabiodiverse country (Rodríguez-Trejo, 2008), as of 2010 ranking fourth in the world in species richness (Sarukhán et al., 2010). There are three major mountain ranges, the Sierra Madre Occidental, the Sierra Madre Oriental and the Sierra Madre del Sur, which run roughly north to south and one major mountain range, the Trans-Mexican Neovolcanic Belt, which runs west to east. Ecosystems range from coniferous forest, deciduous forest and cloud forest to grasslands and desert with 66-million forested hectares, or about 47% of México's territory. An average of 221,000 hectares are annually burned by wildfire (Sarukhán et al., 2010). Anthropogenic ignition sources initiate 90% of fires in México, of which 50% are related to cattle-raising and agriculture (Rodríguez-Trejo, 2008).

México's fire regimes are as diverse as its heterogeneous landscape, and they have been defined in terms of ecosystem type (Rodríguez-Trejo, 2008) and most recently in terms of climate zones (Table 1; Jardel-Peláez et al., in press).

Table 1. Fire regimes in México in terms of climate zones. (Adapted from Jardel-Peláez et al., in press). The sites in this study fall into the humid category.

Climate Zone	**Climate's influence on fuels and the likelihood of fire**	**Fire Frequency**
Cold/moist (alpine and subalpine)	Low temperatures limit primary productivity (PP), and humidity reduces the likelihood of fire spread.	Moisture and fuel-limited infrequent fires
Wet and cool summers, short dry season (<3 months)	Moisture (high PP), and low temperatures (slow decomposition of organic matter) favor the accumulation of fuels. Persistent moisture and cool temperatures reduce the likelihood of fires.	Moisture-limited infrequent fires
Humid climate with warm summers and long dry season (3-6 months)	Favorable conditions for the spread of fire: PP relatively high and long dry period	Frequent fires
Warm-moist or semi-hot with short dry season (<3 months)	High PP but with fast decay rates: short but warm dry season with available fuels but low fuel loads	Moisture and fuel-limited infrequent fires
Very warm and moist with very short or no dry season	Very high PP with rapid decomposition: low surface fuel loads, persistent moisture except in abnormally dry years	Moisture-limited infrequent or rare fires
Sub-humid or semi-arid with long dry season (6-9 months)	PP relatively low: slow fuelbed build-up following fire	Fuel-limited infrequent fires
Warm semi-arid and arid	Low PP: discontinuous and low fuelbeds, long dry season	Fuel-limited infrequent or rare fires

Understanding of fire ecology in México is still in the beginning stages. Since the late 1800s, fire management has primarily focused on fire prevention and suppression, while studies in fire ecology and the synergistic role that fire plays in Mexican ecosystems only began in the 1960s (Rodríguez-Trejo et al., 2011).

Fire history studies in México have primarily been conducted in pine, pine-oak and mixed-conifer forest in the Sierra San Pedro Martir National Park on the Baja California (Evett et al., 2007; Stephens et al., 2003), the Sierra Madre Oriental in the northeast of México

(González-Tagle et al., 2007; Yocom, 2011), the Sierra Madre Occidental in the northwest (Fulé and Covington, 1997; Fulé et al., 2005; Heyerdahl and Alvarado, 2003) and one study on the Pico de Orizaba in the southeast (Yocom, 2011). This is the first dendrochronological fire history study south of the Tropic of Cancer in western México.

Sierra de Manantlán Biosphere Reserve

Location and History

The Sierra de Manantlán Biosphere Reserve is a 139,577 ha area of heterogeneous landscape located at the intersection of the Sierra Madre del Sur mountain range and the Trans-Mexican Neovolcanic Belt in the states of Jalisco and Colima, México at N19°20’ – 19°43’ latitude and W103°49’ – 104°27’ longitude (Figure 2; UNESCO – MAB Biosphere Reserves Directory, 2011). It has high biodiversity, including over 560 vertebrate species and 2,900 species of vascular plants (Jardel P. et al., 2003; Jardel P. et al., 2004). Many of these species are endemic to the state of Jalisco, and some, including a subspecies of the Mexican vole (*Microtus mexicanus* Saussure) and a subspecies of the Llano pocket gopher (*Pappogeomys gymnurus* Merriam) are endemic to the Sierra de Manantlán. The reserve is also home to several threatened, endangered and rare species including the near-threatened jaguar (*Puma onca*), endangered thick-billed parrot (*Rhynchopsitta pachyrhyncha*), and threatened Guatemalan fir (*Abies guatemalensis*) (INE, 2000).

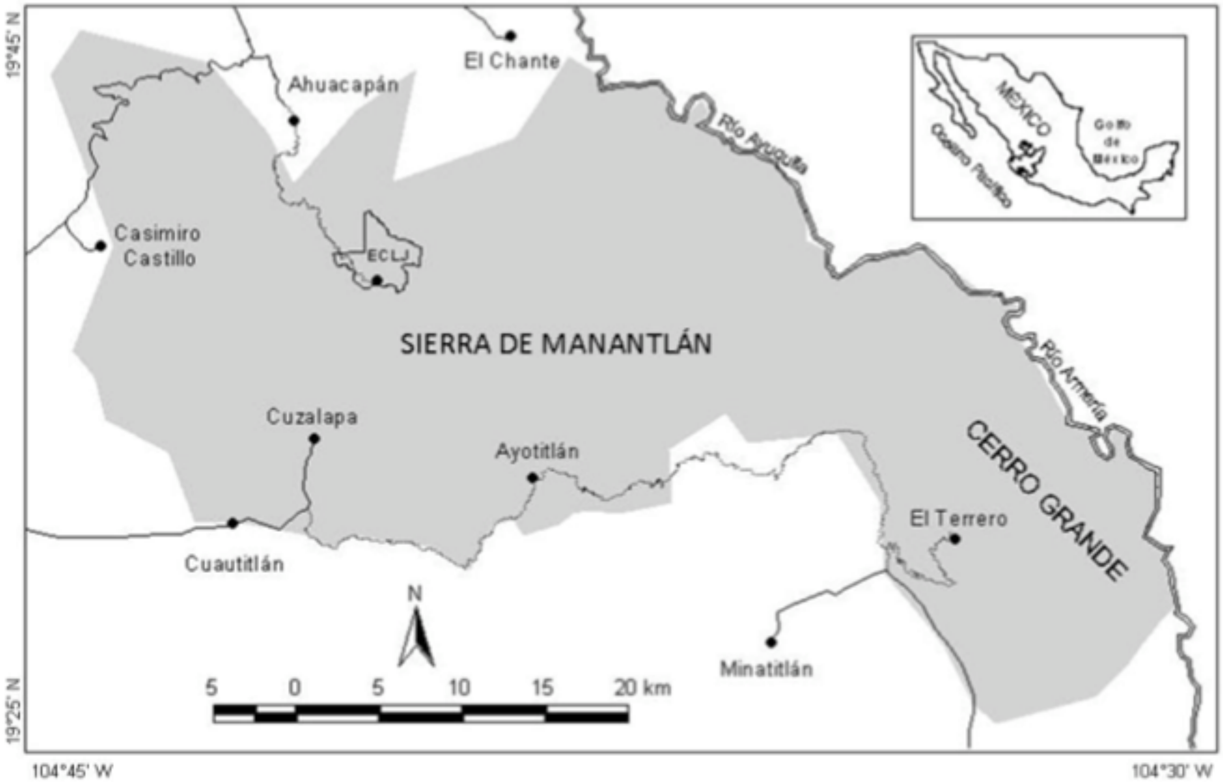


Figure 2. Location of the Sierra de Manantlán Biosphere Reserve and the Las Joyas Research Station (ECLJ) (from Balcázar-Medina, 2011)

The reserve was established following the discovery of *Zea diploperennis*, an endemic, diploid maize previously thought extinct (Iltis et al., 1979), which is culturally and biologically significant (Jardel, 1991; Jardel P. et al., 2003; Jardel P. et al., 2004). This discovery brought attention to the rich biodiversity in the Sierra, which led to the establishment of the Las Joyas Research Station (ECLJ) in 1984, followed in 1985 by the creation of the Manantlán Institute of Ecology and Conservation of Biodiversity (Instituto Manantlán de la Ecología y Conservación de la Biodiversidad – IMECBIO) at the University of Guadalajara (INE, 2000). In 1987 a federal decree officially designated the land as a protected area (Jardel P. et al., 2003).

Approximately 32,000 people live within or partially within the reserve, and land tenure remains divided as it was prior to establishment of the reserve. Indigenous communities and ejidos communally own about 67% of the land, while about 33% is privately owned (Balcázar-

Medina, 2011). A federal directorate co-manages with reserve councils made up of state and local representatives, ensuring that communities affected by decisions also have a voice in the decision-making process (Jardel P. et al., 2004). The reserve has three core zones equaling 41,901 ha within which strict protection is enforced. The remaining 97,676 ha are a buffer zone where timber harvest and agriculture are practiced (Jardel P. et al., 2004; UNESCO, 2011).

Logging has been part of the landscape since the early 1900s. Environmental degradation and deforestation was most damaging from the 1940s to 1980s due to intensive unsustainable timber extraction (Jardel P. et al., 2004). Logging is now prohibited in the core zones and practiced more sustainably in the buffer zones.

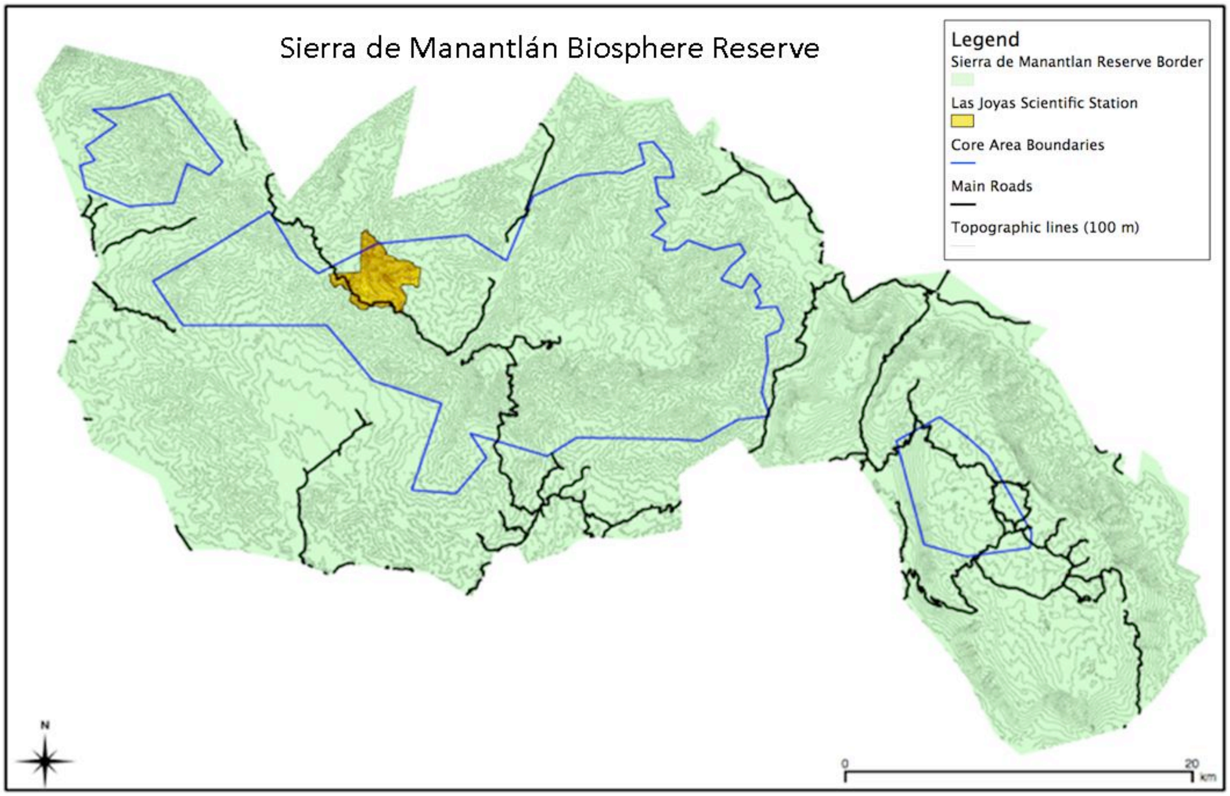


Figure 3. The Sierra de Manantlán Biosphere Reserve with core area boundaries and the boundary of the Las Joyas Scientific Research Station.

Climate and Ecosystems

The elevation gradient in the reserve spans 350 – 2,860 meters above sea level. Vegetation communities vary with elevation, landform and aspect, with dense vegetation in mesic concave landforms and open-structured stands on convex landforms, which are more xeric and exposed (Castillo, 2007). Annual precipitation also varies by elevation and aspect: 600 mm in low-elevation sites in the northeast of the reserve to 1,500 mm in the southwest with monsoon rains during summer months. A rainshadow causes south Pacific-facing slopes to be more mesic and north and east-facing slopes to be more xeric (Jardel P. et al., 2003). Likewise, annual average temperatures vary from warm (30°C) to temperate (5°C; INE, 2000). There is a 5.5 month dry season, generally from the end of December until the beginning of June, and most fires occur during this season (Jardel P. et al., 2003). Winter temperature ranges from -1°C to +10°C (Dvorak et al., 2007).

Forest comprises 76% of the reserve with the remaining 24% divided among shrubland, agriculture, pasture and areas that are disturbed to the point of having no vegetation. There is a mosaic of forest types across elevations and concave/convex landforms, as illustrated in Figure 4, including tropical sub-humid forest, tropical dry forest, deciduous oak forest, montane cloud forest, pine-oak forest and fir-pine-oak forest.

These varied forest types have equally varied fire regimes. Montane cloud forest is not fire-adapted, and infrequent, low-intensity fires can cause high mortality in part due to slow smoldering in the mesic organic soils (Jardel P., personal communication). High elevation fir forests are thought to have a fire regime characterized by infrequent, high-severity fires with fire return intervals of 50-100 years and high rates of mortality similar to boreal forest described by Agee (1993) and Johnson (1992), albeit in smaller patch sizes (Jardel P. et al., 2003).

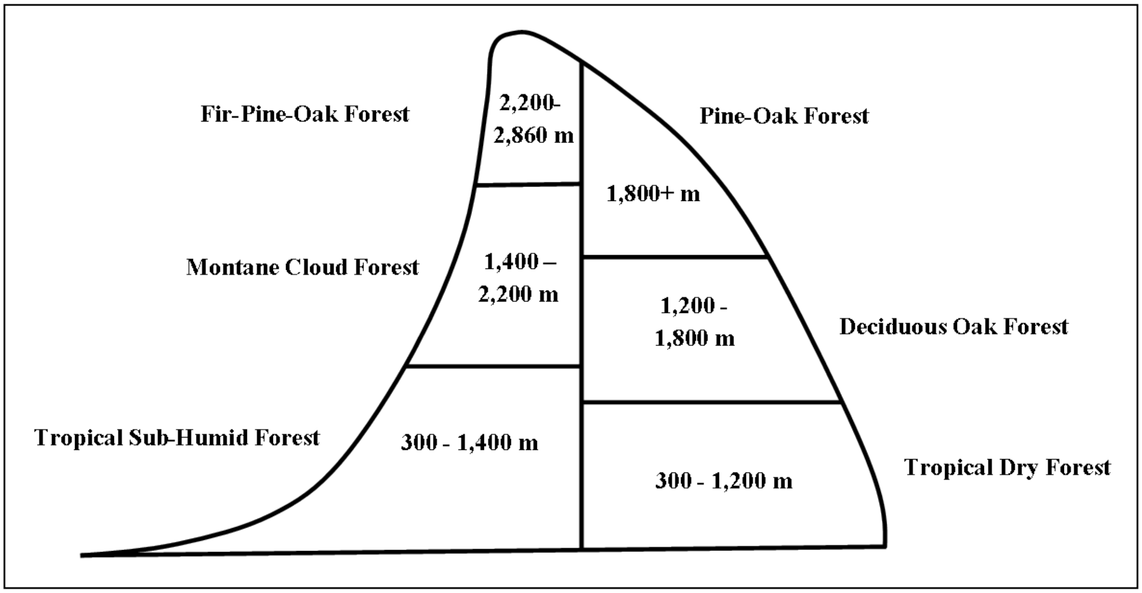


Figure 4. Forest types in the Sierra de Manantlán as distributed by elevation and convex or concave landform (adapted from Jardel P. et al., 2003). Most sites in this study were in pine-dominated forest with one site in deciduous oak forest.

Most fires in the Biosphere Reserve, 64%, occur in pine, oak and pine-oak forests. These ecosystems are apparently adapted to frequent, low-severity fires, and previous studies based on interviews with local inhabitants, fire fighting records and tentatively dated fire scars have shown fire return intervals of 5 to 15 years within stands (Jardel, 1991; Jardel P. et al., 2003). México is home to 47 pine species (Perry, 1991), of which 4 species occur in the study site: *Pinus douglasiana, P. herrerae, P. oocarpa,* and *P. maximinoi*. See Appendix C, Dominant Tree Species Descriptions, for descriptions of pine and oak fire adaptations.

Fire Management

Approximately 65% of wildfires in the Biosphere Reserve result from anthropogenic ignitions including escaped agricultural fires, illegal crop cultivation, arson and accidental ignitions, while approximately 30% of fires are ignited by unknown sources (Jardel P. et al., 2003). Although lightning strikes are common during monsoon season, lightning ignition is rare due to its concurrence with high levels of precipitation (Castillo, 2007). Fire has been used as a tool to clear land for agriculture for the last 3,000 years and to maintain patches of cattle pasture

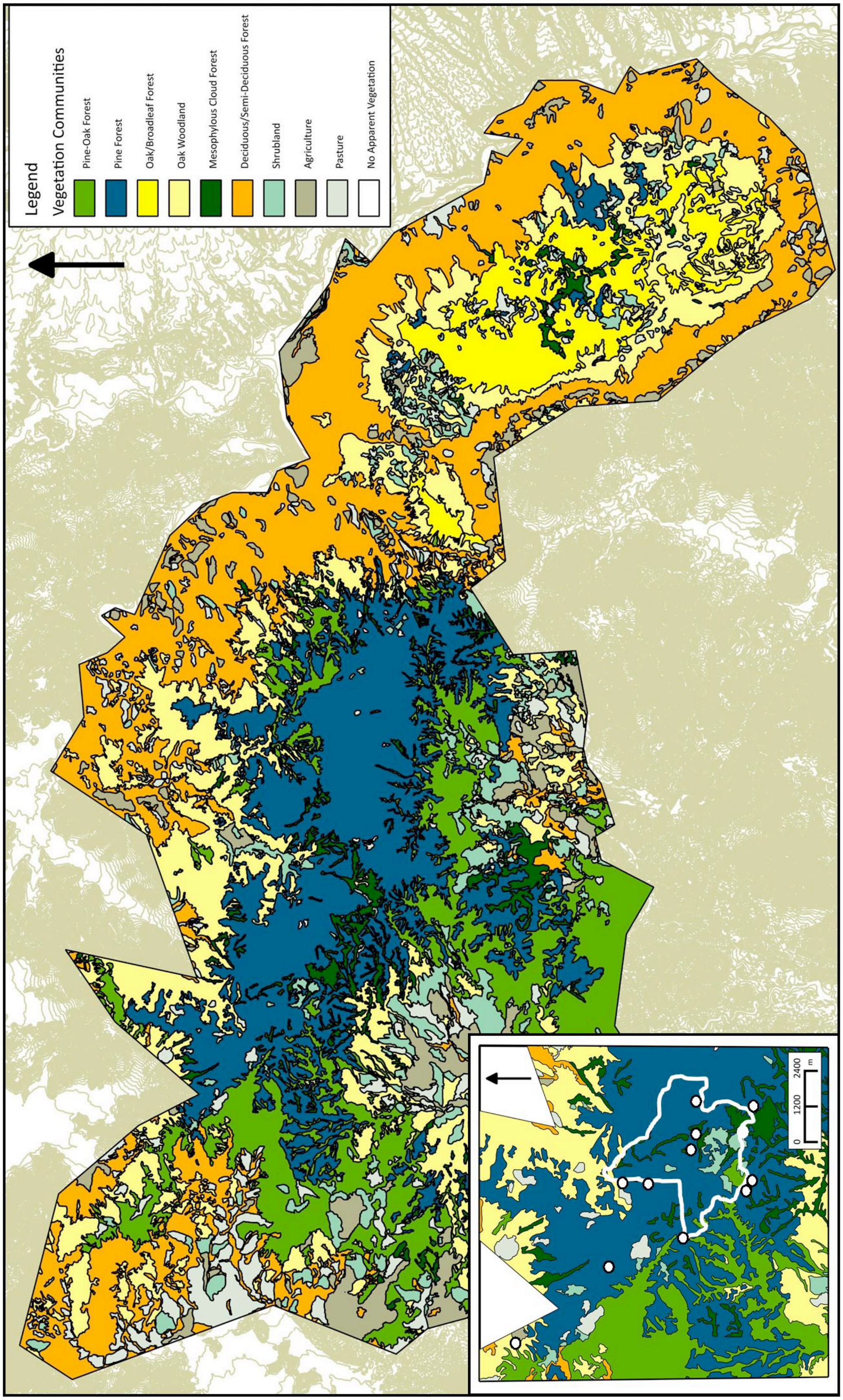


Figure 5. Vegetation map of the Sierra de Manantlán Biosphere Reserve and the study area (inset).

since the 17th century (Jardel P. et al., 2003; Jardel P. et al., 2004). Fire also maintains open areas where *Zea diploperennis* flourishes.

Modern fire management, especially since 1987, has focused on fire suppression, which has led to ecosystem alterations. Frequent fire favors pine and oak over shade-tolerant broadleaf species and kills understory trees, promoting large, widely-spaced pines. Very frequent fire, however, has been observed to repeatedly kill pine regeneration, leading to the replacement of pine forest by oak and/or scrubland (Jardel P. et al., 2003). The exclusion of fire can also cause changes in vegetation composition by favoring fire-sensitive, shade-tolerant species. Previous studies in the Biosphere Reserve have shown that exclusion of disturbance factors such as fire and cattle grazing results in the establishment of broadleaf species and succession to cloud forest, especially in mesic, concave landforms (Jardel, 1991; Jardel P. et al., 2004; Figure 6). Jardel-Paláez (2008) reported a 1,500% increase in pine-broadleaf mixed forest in the Biosphere Reserve from 1990 – 2000 and an 80% decrease in pine-oak forest during the same period, likely due to exclusion of disturbances including fire.

This change in vegetation toward a homogeneous landscape may lead to a reduction in biodiversity and loss of plant and animal species. For example, the rufous hummingbird (*Selasphorus rufus*) migrates from Alaska, Canada and the United States (Ridgely et al., 2011) to overwinter in fire-maintained, non-forested areas of the Sierra de Manantlán Biosphere Reserve (del Coro-Arizmendi, 2001). Fire exclusion-forced succession to broad-leaf forest may push this species out of the reserve. Similarly, *Zea diploperennis* does not flourish in densely forested areas, and elimination of disturbance-maintained open areas could lead to its extinction.

Figure 6. The border between the Manantlán-Las Joyas core, where grazing is not allowed (left side of fence), and the buffer zone, where grazing is allowed (right side of fence) (photo by the author).

Fire exclusion also results in increased fuel loads in pine-dominated forest (Agee and Skinner, 2005; Jardel-Peláez et al., 2006), which, given conducive climate conditions, can result in high-severity fires, deviating from the historical range of variation and resulting in ecosystem modifications. Fire management, including fuel treatments and prescribed fire, are possible methods of forest restoration to emulate historical conditions. Instead of focusing solely on fire suppression, reserve management has begun to incorporate fire as a tool for conservation of biodiversity of ecosystem structure across the landscape. Recent developments in geographic information systems (GIS) databases and detailed modern records are being incorporated in ecosystem restoration-driven land management plans, which include the use of prescribed fire (Castillo-Navarro et al., 2003). However, fire fighting is still an important aspect of fire management, as large areas, an average of 5% of the total area of the reserve from 1995-2008, burn annually (Balcázar-Medina, 2011).

STUDY OBJECTIVES AND HYPOTHESIS

The primary purpose of this study is to infer historical fire frequency in pine-dominated forests of the Sierra Madre del Sur mountains to enable land managers to make informed decisions about fire management in protected and unprotected areas. To achieve this, four consecutive and successive objectives were addressed:

1. To develop a master tree-ring width chronology for the Sierra de Manantlán Biosphere Reserve;
2. To determine whether tree rings are a viable source of information about fires in this ecosystem;
3. To reconstruct historical fire frequency in pine-dominated forests in and around the Las Joyas Research Station for supporting development of sound fire management strategies; and
4. To investigate seasonality of fires and to determine whether fires are climate driven.

In addition to these outcome-driven objectives, the following hypothesis was tested:

> Fire frequency prior to the Biosphere Reserve establishment in 1987 was significantly different from fire frequency after 1987.

METHODS

First Field Season

I conducted the first field season from July 1 through July 9, 2010. Prior to the establishment of plots, I interviewed local experts about the location of pine-dominated sites including pine, pine-oak and pine-mixed broadleaf forest where sensitive (i.e. not complacent, sensu Stokes and Smiley, 1968), large pines could grow. These sites would ideally include conditions conducive to climate responses in annual ring increment such as steep slopes, ridge tops and thin, rocky soils. I established eleven variable-sized plots (see Table 2 for plot names), each with its center at a large pine, defined as having a diameter at 1.3 meters above the ground (DBH) of at least 50 cm, followed by identifying five additional large pines nearest plot center. Trees with DBH < 50 cm were only sampled when larger trees were not present in the plot. I measured DBH and cored each tree at approximately 1.3 meters above the ground. I took a maximum of three cores from each tree to minimize staining, pitch soaking, decay and disease (Maeglin, 1979), and I kept one core from each side of the bole, perpendicular to the slope.

Table 2. Plot names, acronyms and chronology and/or fire plot designations.

Plot Name	**Acronym**	**Chronology or Fire Plot**
Puerto del Belloteadero	BEL	Chronology and Fire
Charco de los Perros	CLP	Chronology
Charco de los Perros II	CL2	Chronology
Escarbadero de los Toros	ELT	Chronology
Las Mantequillas	LMA	Chronology and Fire
Picacho del Sol y la Luna	PSL	Chronology and Fire
Picacho San Campús	PSC	Chronology and Fire
Plaza de Gallos	PLG	Chronology and Fire
Plaza de Gallos II	PL2	Chronology and Fire
Puerto del Escobedo	PUA	Chronology and Fire
Puerto del Escobedo II	PU2	Chronology
Puerto de Tecatas	PUT	Chronology and Fire
Tepehuaje	TEP	Chronology
Tierritas Blancas	TBL	Chronology and Fire

In the first two plots, TEP and ELT, I took cores from only three trees because I originally intended to use these plots to test coring tropical pines and because there were not many accessible pines with a DBH of ≥ 50 cm in these plots. Four cores from two of the three trees sampled at TEP are included in the final master chronology, but no cores from ELT are included.

I recorded visual observations of approximate density, species composition and qualitative descriptions of terrain characteristics at each plot (see Plot Descriptions). Fog prevented GPS satellite recordings for some plots and individual trees (See Table 4 in Plot Descriptions).

Second Field Season

Between January 22 and February 2, 2011, all plots that had been previously established within the boundary of the Las Joyas Research Station, and where fire-scarred pines were present, were revisited and fire-scarred trees were sampled. The plots revisited were: PLG, PL2, PSC, PSL and PUA. I established four additional variable-density plots for a total of nine plots. All plots sampled in 2011 were located in, or within approximately 300 meters of, the Las Joyas Research Station boundary. Plot centers were established at a large pine with a visible catface, and the five to six nearest additional large fire-scarred trees, snags, logs and stumps were identified. I measured DBH for each tree, and calculated each plot's tree density by establishing a 1/20-hectare circular sub-plot at plot center and counting the number of live trees, snags, stumps and logs of at least 2 cm DBH within that sub-plot. I measured elevation using a GPS unit, slope using a clinometer and aspect using a compass and recorded visual observations of species composition and other descriptions of terrain and plot characteristics (see Plot Descriptions).

Each fire-scarred tree was sampled with a chainsaw to remove a partial cross section (Arno and Sneck, 1977). Most snags, logs and stumps were too decayed to sample, so most of the 56 fire-scarred trees (88%) were from live trees with the rest from snags (five trees), logs (one tree) and stumps (one tree).

In new plots that were not previously sampled, I cored trees as described above to obtain additional cores to create a master tree-ring width chronology. Cores were also taken from each live fire-scarred tree. Where possible, these cores were taken at 1.3 meters above the ground on the uphill side of the tree. Where the catface prevented coring at this location, the core was either taken from above the catface or to one side or the other of the catface.

The Laboratorio de Ecologia del Manejo de Recursos Forestales in the Centro de Investigaciones en Ecosistemas, Universidad Nacional Autonoma de México in Morelia, Michoacan, México provided a plant-dehydrating oven where samples were dried at temperatures of 20 - 27°C for four days to prevent cracking, insects and fungi.

Preparation and Analysis of Wood Cores and Fire-Scarred Sections

A total of 236 cores were sampled, including 175 from trees without fire scars and 61 from trees with fire scars; 56 fire-scarred sections were collected. *Pinus douglasiana* comprised 95% of all samples, *P. herrerae* 4%, *P. maximinoi* 1% (cores only) and one fire-scarred sample was from a stump that could not be identified to species. Fire-scarred sections were glued as necessary and cut into thinner sections using a bandsaw, and cores were mounted on wooden holders. I then sanded all cores and sections with progressively finer grit sandpaper using a belt sander and by hand using up to 1000-grit sandpaper until the cell structure was visible under a binocular microscope to allow accurate crossdating and ring-width measurements. I then crossdated the cores and measured annual rings to .001 mm accuracy using a stereoscope, VelMex Unislide and Measure J2X Version 4.2 software (VoorTech Consulting, Holderness, NH, USA). I crossdated the cores and sections using a combination of skeleton plotting (Speer, 2010) and the list method (Speer, 2010; Stokes and Smiley, 1968), and I used the computer program COFECHA (Holmes, 1983) to statistically verify the crossdating. I also used a master tree-ring chronology that was developed in high-elevation *Pinus hartwegii* in the Nevado de Colima region, about 70 kilometers away from this site (Biondi, 2001) as well as a skeleton plot created from *P. douglasiana* increment cores taken from within the Biosphere Reserve (Villanueva-Diaz, unpublished data) to aid in crossdating.

Detection of false rings is vital in crossdating, and several methods have been proposed to identify them, such as following a ring around its entire circumference to determine whether it is continuous (Stokes and Smiley, 1968), observing the abruptness of the transition from late to earlywood (Speer, 2010; Stokes and Smiley, 1968), checking for radial files that contain a row of earlywood cells extending through the latewood as an indicator that the ring is false (Speer, 2010), and observing whether resin ducts are contained within the latewood, as false latewood in some species will terminate at the duct (Stokes and Smiley, 1968). However, false rings in *P. douglasiana* and *P. herrerae* in the Biosphere Reserve do not consistently follow these patterns, making detection very challenging. Boundary transitions vacillate between abrupt and diffuse within single rings. Early earlywood often leads into one or two false rings that either terminate at or encompass a row of resin ducts. Early latewood is often divided into several false rings that separate and merge around the circumference of sections. I suggest that additional research needs to be undertaken into the causes of false rings in *P. douglasiana* and *P. herrerae* as well as other tropical pines.

I created a master chronology and identified years in which false and missing rings tended to occur. Some cores (77%) and sections (16%) were not measured because I could not identify all of their ring boundaries. For sections where the year of fire could not be identified, fire dates were bracketed with minimum and maximum years based on conservative and liberal interpretations of which rings were false.

Using the master chronology, I crossdated sections from dead stumps, snags and logs. I dated each fire on fire-scarred sections from living and dead trees by identifying the year, and where possible, the intra-ring position (Dieterich and Swetnam, 1984): ring-boundary scars (D), early earlywood (E), middle earlywood (M), late earlywood (L) or unknown (U). There were no fire scars positioned in the latewood. In the absence of cambial phenology for this region's *P. douglasiana* and *P. herrerae*, the seasonality of fires cannot be inferred, however the timing of dry and wet seasons likely controls the growing season. Because the dry season occurs from mid-December to late-May of each year, ring-boundary scars, which signify a fire occurring after the cessation of growth and prior to the next growing season, were assigned dates in the following year. Seasonality of fires was analyzed by assessing the frequency of early (D and E) and mid-season (M and L) fires.

Statistical Analysis

Master Chronology

COFECHA was used to compute Pearson's correlation coefficient for each core with the master chronology as well as the overall chronology correlation (Grissino-Mayer, 2001a; Holmes, 1983). Only cores with a correlation of ≥ 0.3 were kept in the chronology. First-order autocorrelation was also computed, which reflects the degree to which ring-width is correlated with the previous year's ring-width. The dplR package (Bunn, 2008) within the statistical software program RStudio version 0.95.258 was used to prewhiten, or to fit an autoregressive model to remove the first-order autocorrelation. DplR was also used to detrend the chronology by fitting a spline that is 67% the length of each series, which removes the growth trend of younger trees generally growing larger annual increments than older trees (Fritts, 1976) and to apply a 20-year spline to the resulting detrended series to highlight high-frequency variation (Bunn, 2008; Holmes, 1983). This process yielded a time series by taking the arithmetic mean of each year's ring-width index.

Fire History Reconstruction

Fire history was analyzed for each plot, as well as a composite of all plots, to determine the central tendency and variation of historical fire frequency. The year and intra-ring position, where determined, of each fire scar were entered into the software FHX2 version 3.2 (Grissino-Mayer, 2001b). This software was used to calculate mean fire return interval (MFI) and median fire return interval (MEI), as well as to test for the fit of the Weibull distribution to the data (Johnson and VanWagner, 1985) and obtain the Weibull median fire return interval (WEI; Grissino-Mayer, 1999). Standard deviation and the Weibull Lower Exceedence Interval (LEI) and Upper Exceedence Interval (UEI) were also calculated for each plot and a composite of all plots using FHX2. See Table 3 for descriptions of these parameters.

MFI was compared among all plots with a one-way analysis of variance (ANOVA). If the F-test indicated a difference among plots, post-hoc analysis would be completed to investigate differences in fire frequency among north and south aspect, degree of slope, forest type and tree density, but the F-test was not significant, indicating similar fire frequency among plots. To test the hypothesis that fire frequency was different prior to and after establishment of the reserve, FHX2 was used to test equality of normalized fire interval means prior to 1987 and from 1987 to 2010. Fire return interval data is limited to the time period of 1938 – 2009, and within plots there is a range of one to seven intervals. This is not sufficient to analyze temporal differences within plots. However, because fire data was sampled from a small geographic area of only 740 hectares within ecologically similar forest types, and because the non-significant F-test comparing MFI among plots is evidence that fire history among plots is similar, it was appropriate to analyze temporal differences within the entire study area. An F-test was conducted to determine equality of variances between the two time periods, followed by a Student's t-test to test equality of means (Grissino-Mayer, 2001b).

Table 3. Statistical parameters used in fire history analysis.

Parameter	**Definition**	**Reference**
Mean Fire Return Interval (MFI)	The arithmetic average of all fire intervals	(Agee, 1993)
Median Fire Return Interval (MEI)	The 50th percentile of the interval data	(Agee, 1993)
Weibull Median Fire Return Interval (WEI)	The 50th percentile of the fitted distribution	(Grissino-Mayer, 1999; Johnson and VanWagner, 1985)
Standard Deviation (SD)	A measure of variability about the mean	(Zar, 1984)
Weibull Lower Exceedence Interval (LEI)	The 87.5 percentile of the fitted distribution, which cuts off the lower 12.5%. Any value lower than this parameter is an unusually short interval at a 0.25 level of significance.	(Grissino-Mayer, 1999)
Weibull Upper Exceedence Interval (UEI)	The 12.5 percentile of the fitted distribution, which cuts off the upper 12.5%. Any value higher than this parameter is an unusually long interval at a 0.25 level of significance.	(Grissino-Mayer, 1999)

To infer information about seasonality of fires, I compiled intra-ring position of fire scars, where identified, and determined the proportion of fires that occurred early and later in the growing season. The data were not sufficient to analyze climate-fire interaction. It was my intention to use FHX2 to conduct Superposed Epoch Analysis (SEA), an analysis tool that “superposes” or stacks fire years and compares averaged climate conditions during years prior to, during and after fire years, then performs bootstrapping to provide confidence intervals (Baisan and Swetnam, 1990; Grissino-Mayer, 2001b), to examine the relationship between fire years and ENSO. This was not possible because of the relatively few identified fire years, but SEA analysis should be a component of future research.

PLOT DESCRIPTIONS

Plots included pine, pine-oak and pine-mixed broadleaf forest types as well as one plot each of deciduous oak and montane cloud forest (chronology-only plots). The pine-dominated stands are ecologically similar with dominant pines and some levels of oak and other understory broadleaf species. They were all were on generally convex landforms allowing for small variations within plots. Plots within the same stand may have different plot centers due to sampling schemes with different purposes. Plots established for the development of the master chronology required large trees. Plots established for collection of fire-scarred samples required fire-scarred trees. Therefore, some stands have two separate plots, and their locations and characteristics are designated in Table 4 (chronology plots) and Table 5 (fire plots). See Figures 7 and 8 for locations of chronology and fire plots, and see Appendix A for individual plot maps.

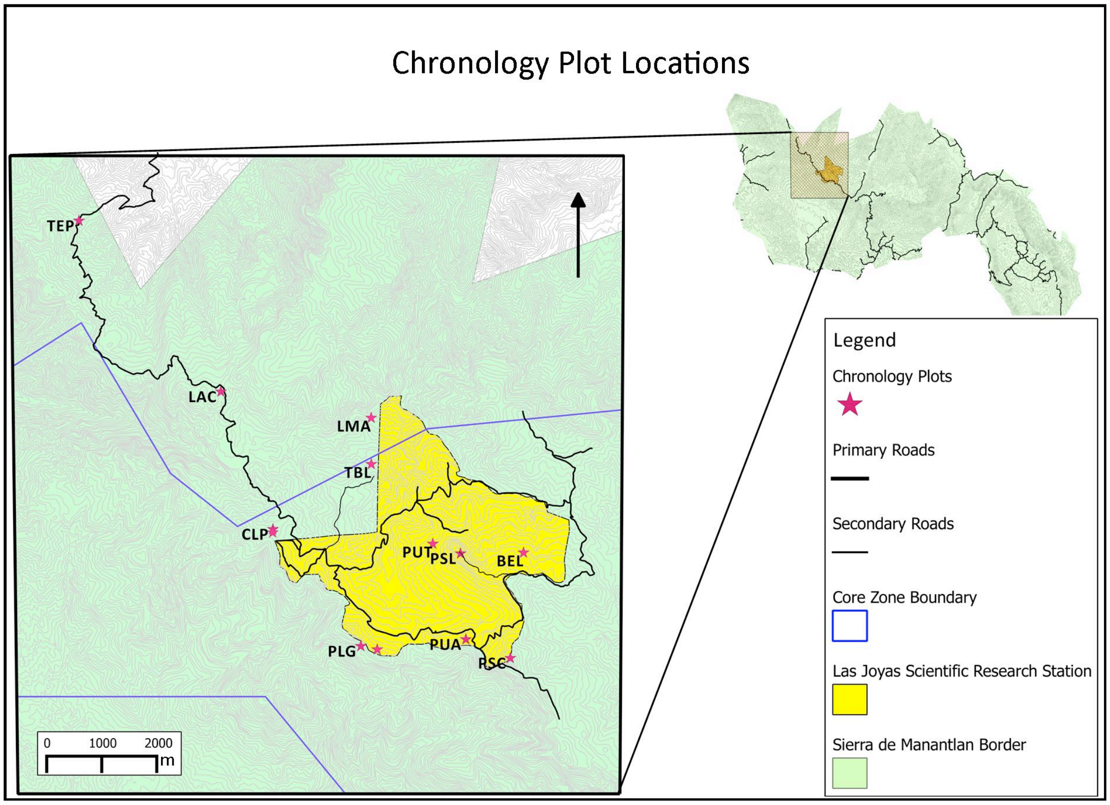


Figure 7. Map of chronology plot locations. PLG denotes both PLG and PL2; CLP denotes both CLP and CL2. Sampling occurred across an area of 2,140 hectares.

Table 4. Chronology plot characteristics listed in ascending order of elevation. *Null entries indicate where fog prevented GPS readings.

Site	Latitude	Longitude	Elevation (m)	Forest Type
TEP	N19°39.803’	W104°20.627’	1505	Deciduous Oak
LMA	N19°37.087’	W104°17.081’	1755	Pine-Mixed Broadleaf
CL2	N19°36.097’	W104°18.130’	1892	Pine-Oak
CLP	N19°36.129’	W104°18.172’	1990	Pine-Oak
LAC	N19°37.502’	W104°18.656’	1990	Pine-Oak
TBL	N19°36.645’	W104°17.088’	1932	Pine-Oak
PLG	N19°34.989’	W104°17.232’	1962	Pine-Oak
PUT	N19°35.884’	W104°16.464’	2002	Pine/Pine-Mixed Broadleaf
PUA	N19°35.051’	W104°16.154’	2060	Pine-Mixed Broadleaf
PU2	*null	*null	*null	Pine-Mixed Broadleaf
ELT	*null	*null	*null	Montane Cloud
PL2	N19°34.956	W104°17.064	2063	Pine-Oak
BEL	N19°35.757’	W104°15.565’	2164	Pine
PSL	N19°35.925’	W104°16.238’	2174	Pine
PSC	N19°34.867’	W104°15.699’	2204	Pine-Mixed Broadleaf

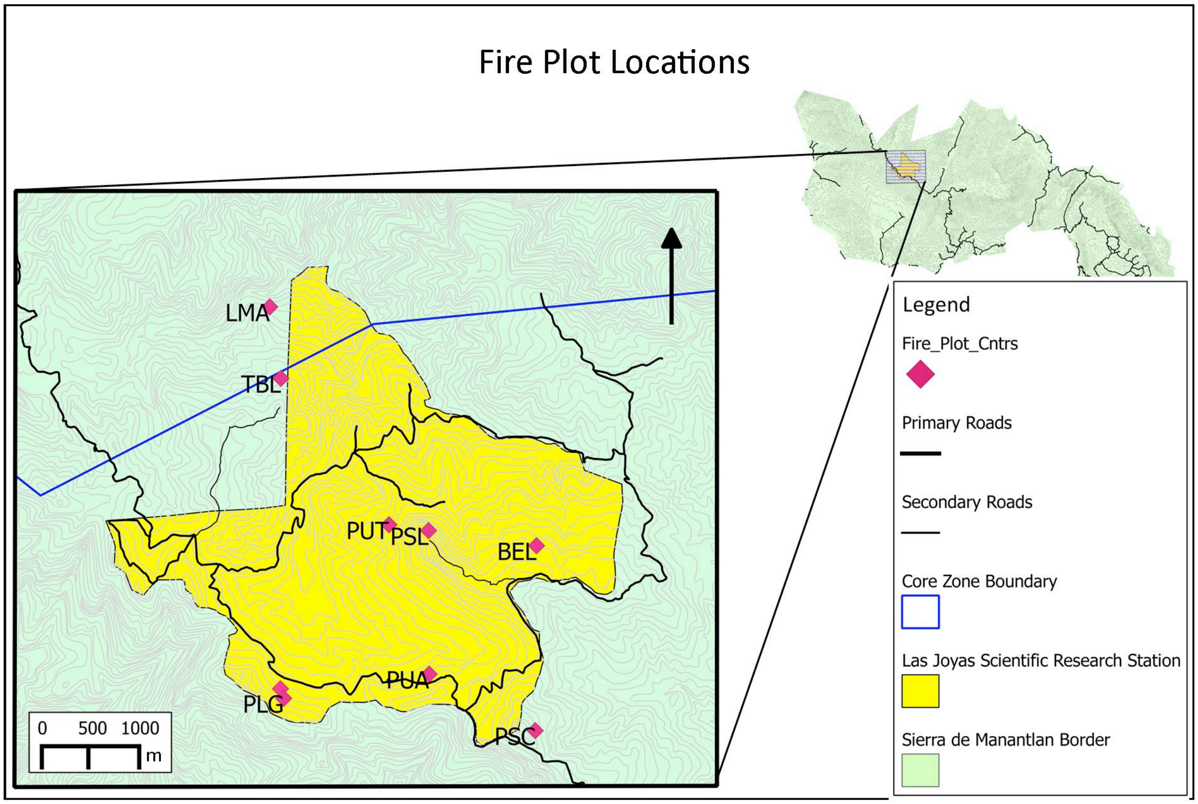


Figure 8. Map of fire plot locations. PLG denotes both PLG and PL2. Sampling occurred across an area of 740 hectares.

Table 5. Fire plot characteristics listed in ascending order of elevation. TPH = Trees per hectare.

Site	**Latitude**	**Longitude**	**Elevation (m)**	**Area (ha)**	**Aspect (°)**	**Slope (%)**	**Forest Type**	**TPH**
LMA	N19°37.085’	W104°17.118’	1755	1	42	52	Pine-Mixed Broadleaf	120
TBL	N19°36.689’	W104°17.054’	1916	1	2	61	Pine-Oak	260
PUA	N19°35.048’	W104°16.196’	1994	1	340	62	Pine-Mixed Broadleaf	560
PUT	N19°35.876’	W104°16.426’	2016	1	162	42	Pine-Mixed Broadleaf	240
PL2	N19°34.971’	W104°17.065’	2039	2	22	53	Pine-Oak	460
PLG	N19°34.918’	W104°17.046’	2053	2	230	60	Pine-Oak	320
BEL	N19°35.757’	W104°15.565’	2164	2	314	63	Pine	460
PSC	N19°34.733’	W104°15.576’	2176	0.5	209	66	Pine-Mixed Broadleaf	660
PSL	N19°35.843’	W104°16.195’	2185	4	278	166	Pine	180

Tepehuaje – (TEP) – *Deciduous Oak Forest*

Figure 9. Tepehuaje (photo by the author)

Xeric site with shallow, rocky Eutric Regosol soils is dominated by oaks (*Quercus resinosa* and *Quercus magnoliifolia*) with a small number of *Pinus oocarpa* and *P. maximinoi* also present. Open stand-structure with sporadic *Agave sp.* and unidentified cactus sp. in the understory as well as mosses and grasses. *P. maximinoi* are the dominant pines, and cores were extracted from three of them, two on a steep north-facing slope and one on a more gentle south-facing slope. No other large pines were located at the site, and no fire scars were visible.

Las Mantequillas – (LMA) – *Pine-Mixed Broadleaf Forest*

Figure 10. Las Mantequillas (photo by the author)

Located on the lower portion of a long northeast-facing slope and downslope from TBL, this stand has dense, 1.5–2 m tall herbaceous understory vegetation and widely spaced *P. douglasiana*. Soils are Ferric Cambisol. There are also scattered *Quercus sp., Arbutus sp.* and mixed young broadleaf trees and shrubs. The larger pines are located on a convex portion of the slope, downslope from an overgrown logging road. Further, the slope descends into a joya, or bowl-shaped valley, and the broadleaf and herbaceous vegetation increases. At 120 trees per hectare, this stand is one of the least dense stands in the study in terms of trees, but this may be due in part to dense herbaceous invader species following fire that are preventing pine regeneration, of which there were none observed. Ratio of species is 2 pine (mature): 1 broadleaf (young). Six pines were cored and seven were sampled for fire scars.

Charco de los Perros (CLP) - *Pine-Oak Forest*

Figure 11. Charco los Perros (photo by the author)

This stand has an open structure with thick duff (approximately 15 – 20 cm) of pine needles over Ferric Cambisol soils but very little understory vegetation or coarse woody debris. *P. douglasiana* is the dominant species, several with catface scars, with some *Quercus sp*., *Arbutus xalapensis* and other small forbs. *Quercus sp.* and other broadleaf species have many ferns and epiphytes growing on their branches. Six trees were cored on the steepest parts of the slope.

Charco de los Perros II (CL2) – *Pine-Oak Forest*

Figure 12. Charco de los Perros II (photo by the author)

Similar to CLP, this plot is in an open-structured stand with very little understory vegetation or coarse woody debris. The dominant tree species is *P. douglasiana* with fewer numbers of *Quercus sp*., *Arbutus xalapensis* and other small understory broadleaf trees. Pine-needle duff is thick (approximately 15 – 20 cm) over Ferric Cambisol soil, and there are scattered bunch grasses and other herbaceous species. The *P. douglasiana* sampled in this site were chosen because of their large diameters (62.7 – 85.8 cm DBH), but they were not on a slope. All six trees were within 20 meters of each other, so they share one GPS point. There was only one fire-scarred tree in this plot.

La Cumbre – (LAC) – *Pine-Oak Forest*

Figure 13 and 14. Mature stand and post-fire regeneration at La Cumbre (photos by the author)

This site is known to have been logged until the 1980s (J. Morfín-Ríos, personal communication), and the *P. douglasiana* are mostly small-diameter (<50 cm) with occasional larger remnant trees in an open, park-like structure. Most trees are scorched 1-3 meters up the bole and some have catfaces with 1-3 visible scars. There is coarse woody debris and some scarred logs and snags, but they are highly decayed. Pine-needle duff is 7-10 cm deep and covers Eutric Regosol soils, and the understory has *Quercus scitophylla* as well as scattered shrubs, herbaceous species, and dense pine regeneration in some areas. Cores were taken from six pines, three of which had fire scars.

Tierritas Blancas – (TBL) – *Pine-Oak Forest*

Figure 15. Tierritas Blancas (photo by the author)

This stand's multiple fires are evidenced by its pattern of even-aged patches of regeneration and mortality. The predominant landform of the stand is a north-facing convex slope, although there are rolling hills and valleys that break up the slope. A 2009 crown-fire killed most trees along its western border, which is also the border of the Las Joyas Research Station. Mortality did not extend outside of Las Joyas, where cattle grazing may have reduced fuel continuity sufficiently to decrease the fire's spread. A new even-aged cohort of *P. douglasiana* and *P. oocarpa* is becoming established, and another even-aged cohort that was missed by the fire is growing south of the plot and over the crest of the slope. Along the eastern slope, the fire appears to have lessoned in intensity, leaving fire scars but not killing the pines. However, most mature *Quercus sp.* were killed. Tree density is 260 trees per hectare with a ratio of 12 pine: 1 oak, but it should be noted that the plot-centered 1/20-hectare subplot fell outside of any of the patches of regeneration, so this figure is representative of patches of mature trees that survived the fire. The soil is Ferric Cambisol and xeric. There are few large diameter trees here, so one of the chronology trees and two of the fire scarred trees are under 50 cm DBH.

Puerto de Tecatas – (PUT) – *Pine / Pine–Mixed Broadleaf Forest*

Figure 16 and 17. South-facing and east-facing slopes at Puerto de Tecatas (photos by the author)

This stand is heterogeneous, both in vegetation structure and landform. It generally faces south/southeast and includes a rounded convex slope with scattered mature *P. douglasiana*, very little understory and dense pine regeneration in the northwest portion of the stand. There is another slope to the south, and between these lies a gulley with dense broadleaf trees and shrubs as well as scattered pines, logs and coarse woody debris. Many of these pines have fire scars indicating that fires may tend to funnel through this gulley as they burn up the slope. The plot extends across a grown-over logging road and down a steep slope with thick pine-needle duff and widely spaced *P. douglasiana*. Tree density is 240 trees per hectare with a ratio of: 3 pine: 1 oak. Three live trees with fire scars were sampled as well as one log, one stump and one snag. Six trees were cored for the master chronology.

Puerto del Escobedo – (PUA) - *Pine-Mixed Broadleaf Forest*

Figure 18. Puerto del Escobedo (photo by the author)

This stand covers a convex landform with a gently sloping peak, a south/southeast slope that ends at the main road through ECLJ and a north/northwest slope that descends into a joya, a bowl-shaped depression, with a pocket of montane cloud forest vegetation. The plot was established on the upper-portion of the north/northwest slope where two cohorts of *P. douglasiana* are dominant. There are a small number of *Quercus sp.* and many, though widely-spaced, other small broadleaf trees including *Arbutus xalapensis* as well as minimal bunch-grasses and a thick duff of pine-needles over Ferric Cambisol soil. Tree density is 560 trees per hectare with a ratio of 4 pine: 1 oak: 22 broadleaf (mainly small diameter). Some large woody debris is present but is highly decayed. Fire scars are present in the upper portion of the slope but were not observed lower into the joya. Six trees were cored and six fire-scarred trees were sampled.

Puerto del Escobedo II – (PU2) – *Pine-Mixed Broadleaf Forest*

This plot was established on the south/southeast slope, and although there were fire scars, none were sampled because of their potential visibility due to proximity to the road. Six trees were cored, however, for use in creating the master chronology. This plot is similar in species composition to PUA, with *P. douglasiana* dominating and a mix of broadleaf species in the understory and Ferric Cambisol soils.

Escarbadero de los Toros – (ELT) – *Montane Cloud Forest*

Mesic site with thick duff and moist soils dominated by *P. douglasiana*, *Quercus sp.* and *Arbutus xalapensis.* Fewer numbers of *Abies guatemalensis* were identified. Very dense, thick understory consists of shrub and herb species. Three cores were extracted from *P. douglasiana*, but no fire scars were observed. The fog was too thick for our GPS unit, so no GPS markers were set and elevation was not obtained.

Plaza de Gallos – (PLG) – *Pine-Oak Forest*

Figure 19. Plaza de Gallos (photo by the author)

The plot was established in the upper part of a south/southwest-facing slope in open pine-oak forest with widely spaced trees, predominantly *P. douglasiana* in the overstory and *Quercus scitophylla* and *Quercus sp.,* both large and small diameter, in the understory along with grasses and other herbaceous species. Tree density is 320 trees per hectare, and only pines fell within the 1/20-hectare subplot. Pines are in three cohorts: Mature/large (≥ 30 cm DBH), sub-dominant/suppressed (5-30 cm DBH) and young (2-5 cm DBH), with many fire scars on the mature trees. The duff of pine needles and decaying plant matter is thick (10-20 cm), and soils are Ferric Cambisol and Eutric Regosol. As the slope descends, broadleaf and herbaceous species density increases and there is little to no evidence of fire scars.

Plaza de Gallos II – (PL2) – *Pine-Oak Forest*

Open-structured pine-oak stand on a north/northeast-facing slope with widely spaced trees. The plot was established on the upper and middle slope. Below the plot, the slope descends steeply into dense broadleaf and herbaceous vegetation. Soils are Ferric Cambisol and Eutric Regosol. *P. douglasiana* is the dominant species and appears to be of a single cohort with a number of suppressed trees and remaining legacy trees. The understory is composed of *Quercus scitophylla, Quercus sp*., *Arbutus xalapensis,* other broadleaf trees, grasses, ferns and other small forbs. Tree density is 360 trees per hectare with a ratio of 8 pine: 3 oak: 7 unidentified broadleaf species. Six trees were cored and seven fire-scarred sections were sampled.

Puerto del Belloteadero – (BEL) – *Pine Forest*

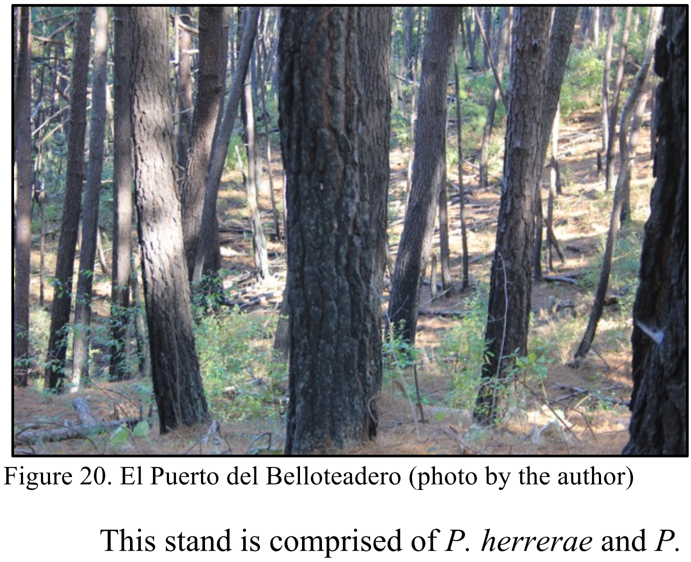


Figure 20. El Puerto del Belloteadero (photo by the author)

This stand is comprised of *P. herrerae* and *P. douglasiana* with small numbers of mature *Quercus sp.* and scattered shrub and herbaceous species. The stand is open and park-like with some clumping of pines and evidence of past logging (decayed stumps) and fires (scorch, fire scars, coarse woody debris and pockets of regeneration). The soil is Ortic Acrisol. Tree density is 460 trees per hectare, with a ratio of 20 pine: 3 oak. To locate fire scars and large trees, we walked a zig-zag pattern from the top of the ridge and along both west/northwest-facing and north/northeast-facing slopes.

Picacho del Sol y la Luna – (PSL) – *Pine Forest*

Figure 21. Picacho del Sol y la Luna (photo by the author)

This peak, considered to be "La Corazon de las Joyas" ("The Heart of Las Joyas"), is surrounded by very steep slopes and has some of the largest pines observed in the reserve. This site is classified as Pine Forest, however there are *Quercus sp., Arbutus xalapensis* and other broadleaf trees in addition to two cohorts of *P. douglasiana*. Tree density is 180 trees per hectare with a ratio of 7 pine: 2 broadleaf. The pine-needle duff is thinner than at other plots (5-10 cm) over Ferric Cambisol soil, and there are bunch grasses and herbaceous species present. Cores were taken from six trees on the east slope, as that was the location of the largest trees, while six fire-scarred sections were sampled on the west slope. Most pines were charred, but there were not many fire scars.

Picacho San Campús (PSC) – *Pine-Mixed Broadleaf Forest*

Figure 22. Picacho San Campús

Densely stocked stand with a mix of *P. douglasiana*, *Quercus sp.* (both tree and shrub forms)*, Arbutus xalapensis,* and unidentified broadleaf tree species as well as understory herbaceous and shrub species. Tree density is 660 trees per hectare with a ratio of 4 pine: 29 oak. Canopy is closed and the pines, which are smaller than in other plots, retain lower live and dead branches. There is no evidence of pine regeneration, likely due to the lack of sunlight under the canopy. Mesic site with a thick duff layer of pine needles and decaying plant matter over the Ferric Cambisol soil. Six trees were cored and six fire-scarred sections sampled.

RESULTS

Forest types sampled were pine, pine-oak, pine/mixed broadleaf, and one plot each in deciduous oak and montane cloud forest, which varied with elevation as shown in Figure 23. All trees sampled for chronology and fire scars were of similar diameter at breast height, with an overall mean of 68 cm and a range of 43-114 cm. At least three tree heights were measured at each of ten plots (BEL, LMA, PL2, PLG, PSC, PSL, PUA, PUT, TBL and TEP), and tree heights averaged 24 m with a range of 9 m (PSC) to 35 m (PL2).

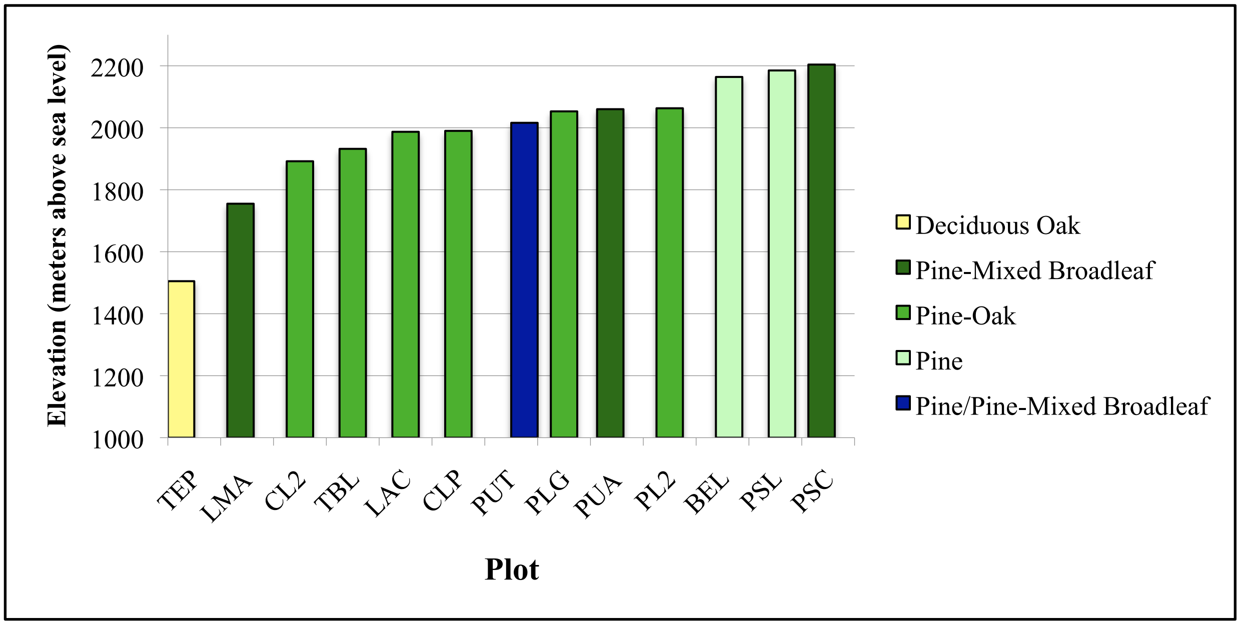


Figure 23. Forest types by elevation. Montane cloud forest is not shown, as elevation was not recorded at ELT.

Tree Ring Chronology

A master tree-ring width chronology was compiled from 78 total samples consisting of 24 fire-scarred sections, each from an individual tree, and 54 cores from 33 individual trees representing all 13 plots. The chronology spans 1881 – 2009, 129 years, while the portion of the chronology with ≥ 5 trees spans 1904 – 2009, 105 years. Pearson's correlation for the master chronology is 0.445, a fairly strong correlation, with a first-order autocorrelation of 0.629, confirming that the data's need to be prewhitened.

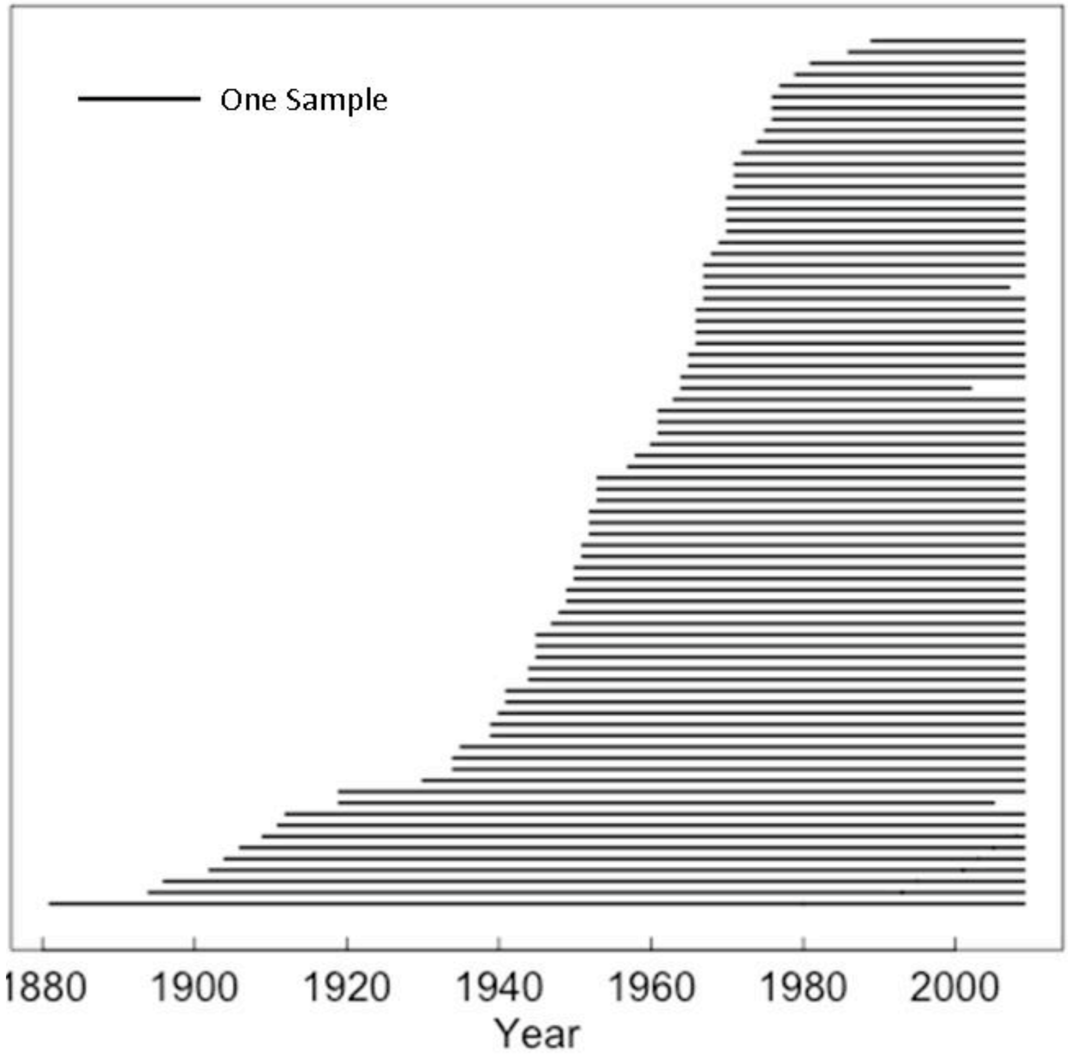


Figure 24. Time span of each sample in the master chronology. Lines that do not extend all the way to the right indicate samples that were from stumps, logs or snags that died prior to 2009.

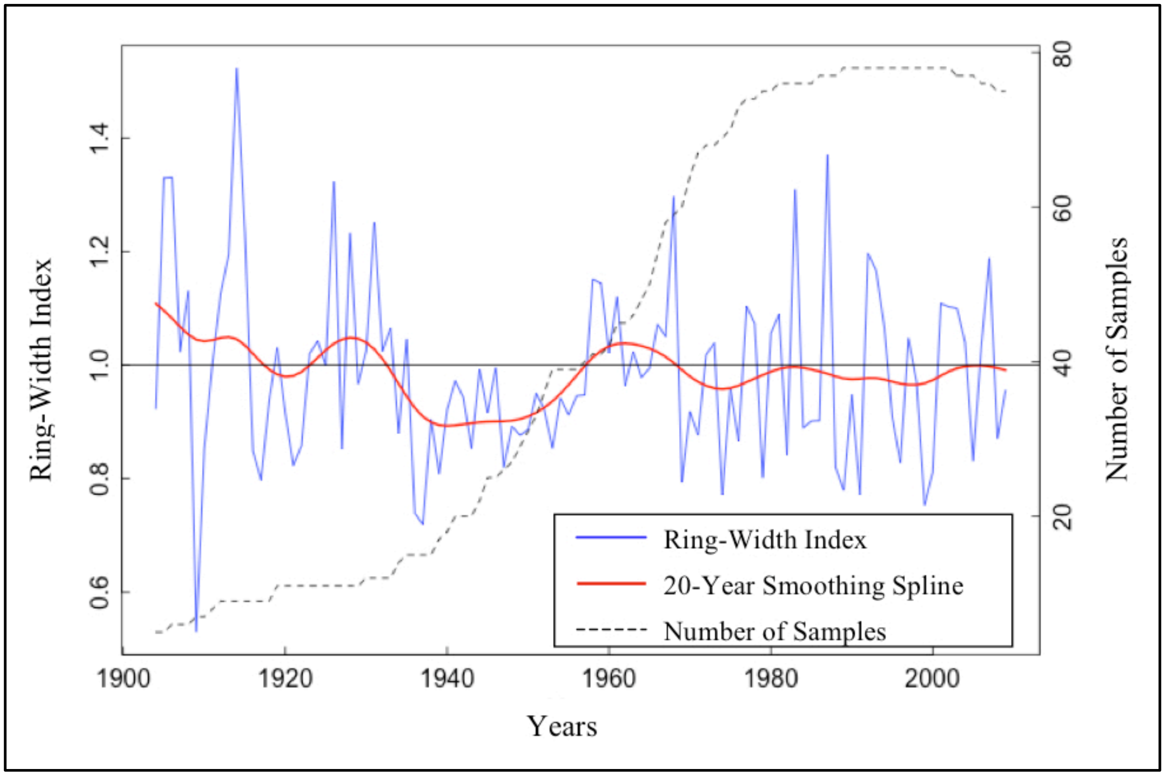


Figure 25. Ring-width index for those portions of the chronology that include ≥ 5 samples. The blue line indicates the prewhitened and detrended mean ring widths, the red line indicates a 20-year smoothing spline and the dotted line indicates the number of trees included for each year.

Microscopic identification of false rings was sometimes not possible due to the diffuse and inconsistent nature of the *Pinus douglasiana* rings (Figure 26). Crossdating was the only reliable method of identifying false rings in this study, and out of 292 total samples, only 97 could be confidently crossdated. Ten of these could be crossdated for only a portion of their rings.

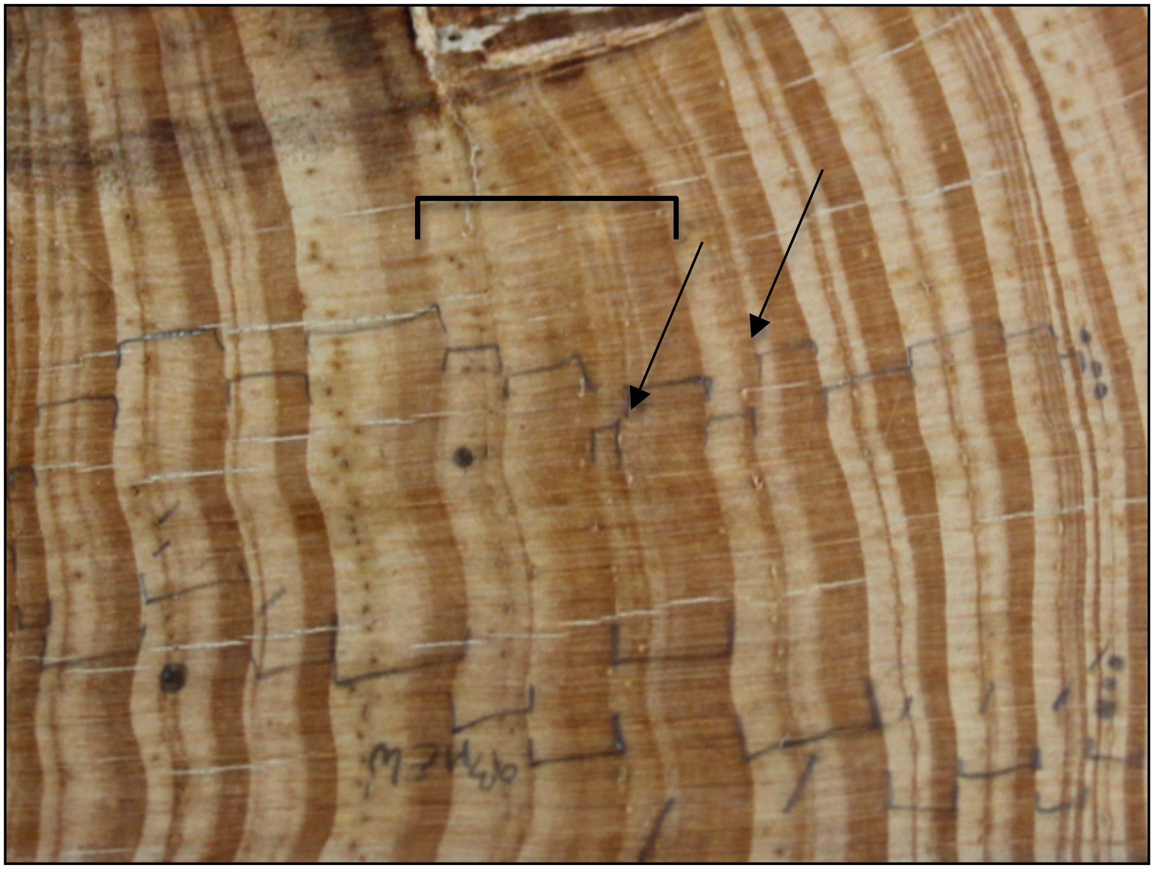


Figure 26. A partial cross section of *Pinus douglasiana* with false and diffuse rings. Arrows indicate rings that are indistinguishable between real and false, and the bracket shows diffuse rings that could encompass from one to four annual rings. Pencil markings indicate two possible dating alternatives: slashes indicate possible false rings, brackets indicate possible annual-ring boundaries and dots indicate possible decades. Crossdating is the most reliable method for differentiating real and false rings (photo by the author).

Fire History Reconstruction

There are 17 unique fire years between 1938 – 2009. Years with fires recorded on at least two non-adjacent plots occurred during 1969, 1974, 1979, 1983 and 2003. Mean fire return interval (MFI) for a composite of all fires across the 740-hectare study area is 4 years with a range of 1 to 14 years. A Kolmogorov-Smirnov goodness-of-fit test shows that the Weibull distribution is appropriate for the composite fire interval data ($P > 0.1$), which gives a Weibull median interval (WEI) of 4 years. Figure 27 shows fire history composited across all sites.

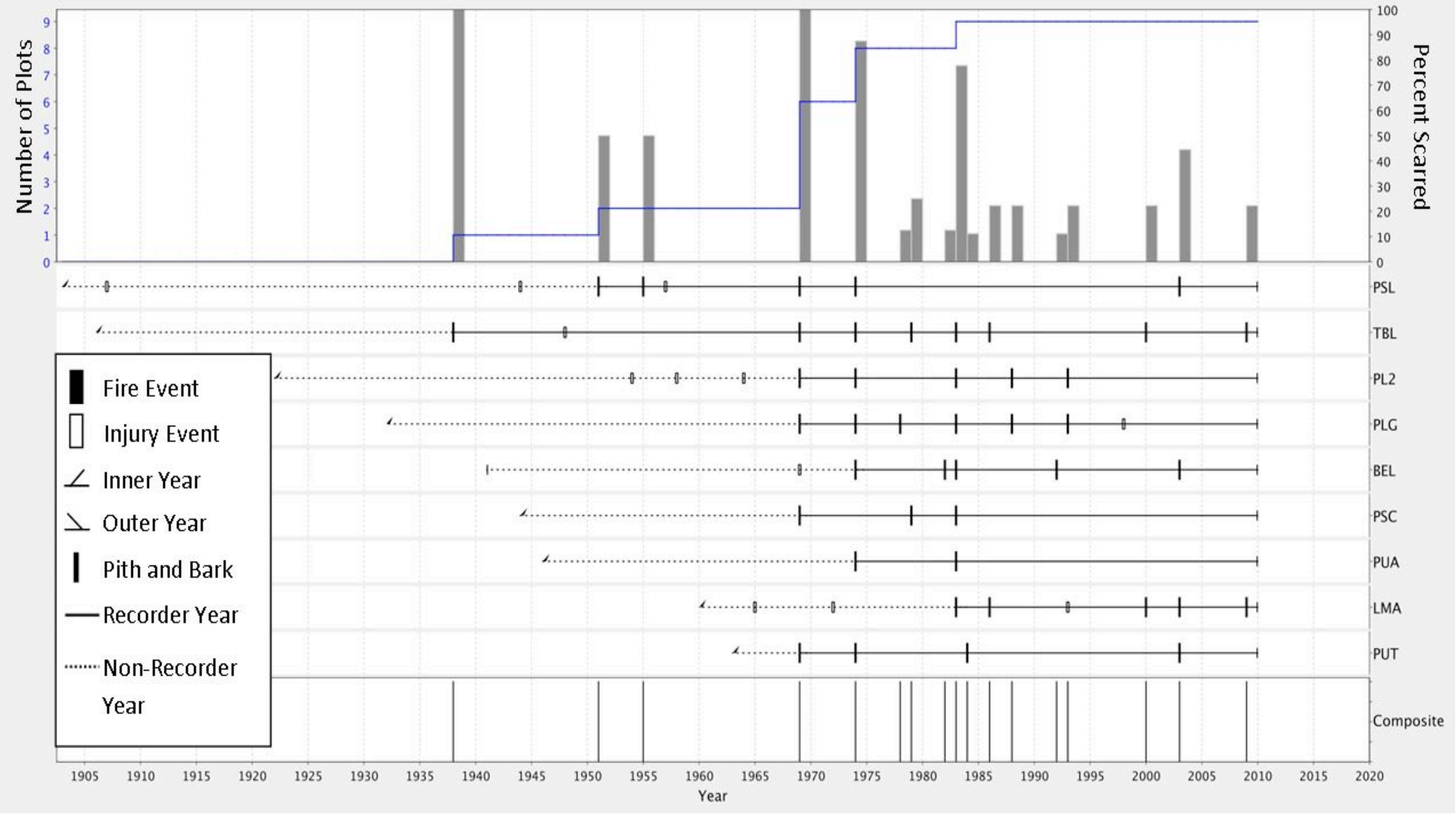


Figure 27. Composite fire history across all plots. The top third of the graph, Number of Plots and Percent Scarred, shows the number of plots represented in each fire year and the percentage of recording trees, i.e. trees that have a fire scar at or prior to that year. The middle portion of the graph shows composites of fire years at each plot, and the lower portion is the composite of fire years over all plots.

However, as the area of the study becomes larger, the fire-return interval becomes smaller (Agee, 1993), so it is important to look at fire frequency for individual sites. Plot area ranged from 0.5 – 4 hectares, and fire-return intervals ranged from 1 to 31 years within individual plots. The MFI within plots ranged from 5 – 13 years; and again the Weibull distribution was tested for each plot with a Kolomorov-Smirnov goodness-of-fit test (P > 0.1) giving Weibull median intervals ranging from 5 – 11 years. The most common interval within plots was 5 years. See Appendix B for fire chronologies for all plots. There was no difference in MFI among plots (P=0.85, F=0.494, d.f.=8), which indicates that there were also no differences in MFI among north and south aspect, degree of slope, forest type or tree density.

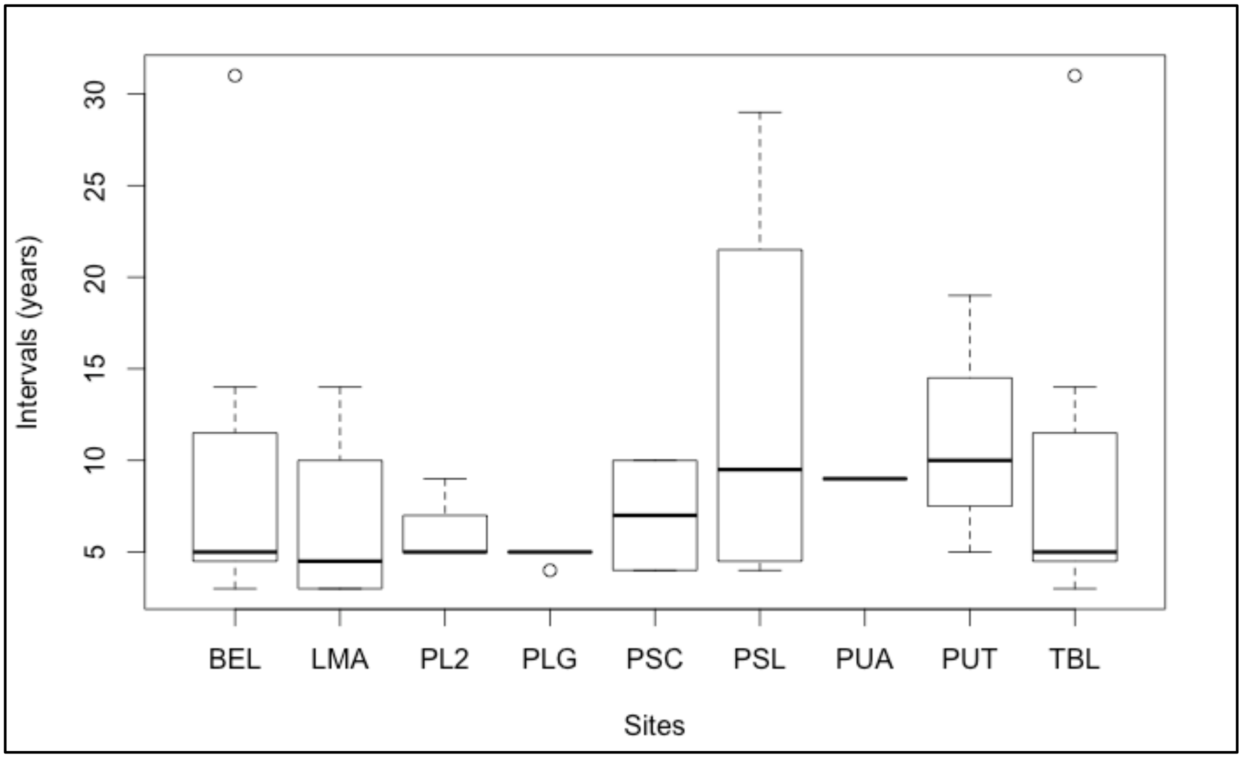


Figure 28. Fire Return Intervals (MEI) within each site. Boxes enclose the 25th and 75th percentiles, dark line indicates the median, whiskers enclose the 10th and 90th percentiles, and the circles indicate outlier values.

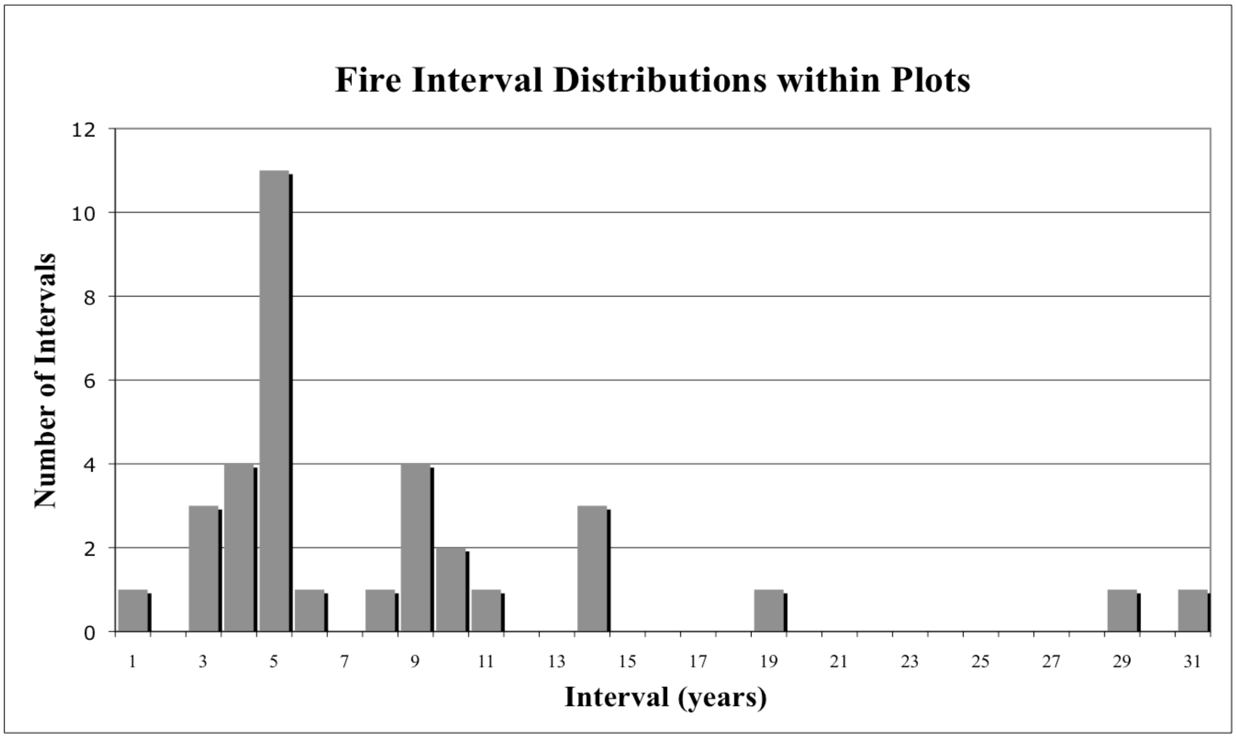


Figure 29. Fire interval distributions within plots over 740 hectares for the years 1938 - 2009.

Table 6. Descriptive statistics of fire intervals. MFI = Mean Fire Interval; MEI = Median Fire Interval; WEI = Weibull Median Interval; SD = Standard Deviation; CV = Coefficient of Variation; LEI = Weibull Lower Exceedence Interval; UEI = Upper Exceedence Interval. A dash indicates too few intervals for analysis. COMP = composite interval statistics across all plots.

Site	Number of intervals	Min. Interval	Max. Interval	MFI	MEI	WEI	SD	LEI	UEI
BEL	4	1	11	7.25	8.5	6.49	4.35	2.53	12.16
LMA	4	3	14	6.5	4.5	5.79	5.2	2.03	11.66
PLG	5	4	5	4.8	5	4.86	0.45	4.47	5.13
PL2	4	5	9	6	5	6.01	2	3.78	8.18
PSC	2	4	10	-	-	-	-	-	-
PSL	4	4	29	13	9.5	10.86	11.58	3.2	24.57
PUA	1	9	9	-	-	-	-	-	-
PUT	3	5	19	11.33	10	10.82	7.09	4.96	18.2
TBL	7	3	31	10.14	5	8.19	9.94	2.19	19.79
COMP	16	1	14	4.44	3.5	3.57	3.98	.95	8.63

Undated Fire Scars

Twenty-two fires from nine samples were identified that could not be crossdated. Possible fire return intervals ranged from 0 – 60 years (see Table 7), but these intervals were excluded from analysis. These samples were from six out of the nine plots and were from all three pine-dominated forest types (pine, pine-oak and pine-mixed broadleaf), sampled on both north and south-facing slopes, and from plots with tree densities ranging from 180 to 660 trees per hectare. Seven samples were from *P. douglasiana* and two samples were from *P. herrerae*.

Table 7. Bracketed fire years and intervals for undateable fire-scarred sections.

Plot	**Sample #**	**Range of Fire Year**	**Year of Next Sequential Fire at Plot**	**Range of Interval (years)**
BEL	S6	1966-1972	1974	2 - 4
		1992-1993	1992 - 2003	0 - 10
PLG	S1	1954-1958	1959 - 1963	1-9
		1959-1963	1966 - 1969	3-10
		1966-1969	1969	0-3
		1975-1978	1978	0-3
PL2	S2	1958-1961	1969	8-11
PL2	S7	1967-1969	1969	0-2
		1972-1974	1974	0-2
PSC	S2	1902-1950	1921 - 1962	12-60
		1921-1962	1969	7-48
		1964-1983	1969 - 1983	0-19
PSC	S6	1919-1941	1921 - 1962	2-43
		1952-1958	1969	11-17
PSL	S3	1942-1973	1949 - 1976	3-34
		1949-1976	1951 - 1984	2-35
		1961-1984	1969 - 2003	9-19
		1997-2004	2003	0-6
PSL	S6	1930-1954	1938 - 1959	5-29
		1938-1959	1964 - 1969	5-31
		1964-1973	1969 - 1974	1-10
TBL	S6	1909-1910	1938	28-29

Temporal Analysis

The hypothesis that fire frequency has changed since the reserve was established was not supported by analysis. The null hypothesis of equal variance between fire intervals prior to and after 1987 was not rejected (P=0.65, F=1.68, d.f. = 9, 4), so a Student's t-test assuming equal variances was conducted. The null hypothesis of equal mean fire intervals was not rejected (P=0.85, t=-0.19, d.f.=13), and these results do not show that the fire frequency across the study area is different following establishment of the reserve. However, this result may be due to the small sample size of the study and the short period of time from 1987 – 2009.

Intra-Ring Position of Fire Scars

Where intra-ring position of scars was identifiable, it was most often early in the growing season or mid-growing season. Fire scars were rare in the later third of the earlywood, and there were no fire scars in the latewood. There was variation in position of fire scars on individual trees during single fire years both within and among plots. Intra-ring position was tallied for each fire, and the most common position was determined except where positions were evenly distributed. The years with most widespread fire, 1969, 1974 and 1983, were evenly represented in the early part of the growing season and mid-season and are designated as Early/Middle in Figure 35. This could indicate that there were more than one fire during these years. The fourth large fire year, 2003, was early in the season, as were 1951, 1979, 1986, 2000 and 2009. Nearly a quarter of fire years' intra-ring position could not be identified due to very narrow rings and unclear ring boundaries.

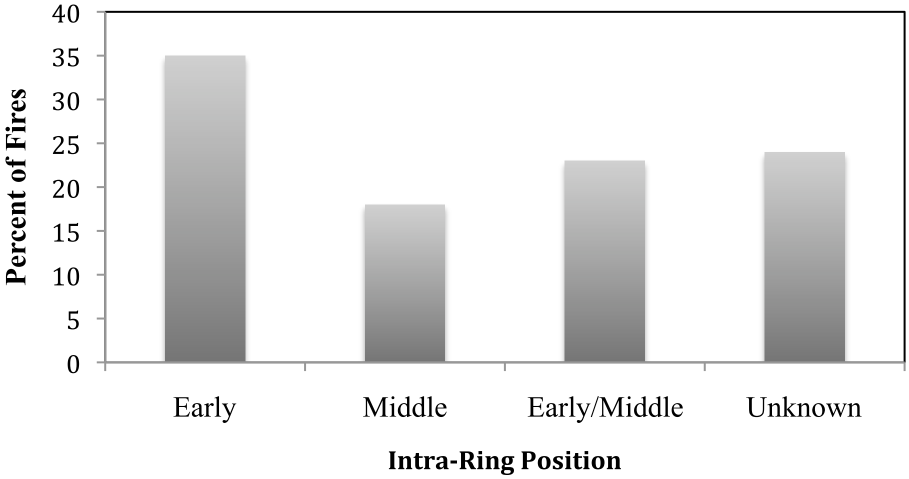


Figure 30. Intra-ring position of fire scars for the 17 fire years from 1938 - 2009. Early includes both ring-boundary and early earlywood scars.

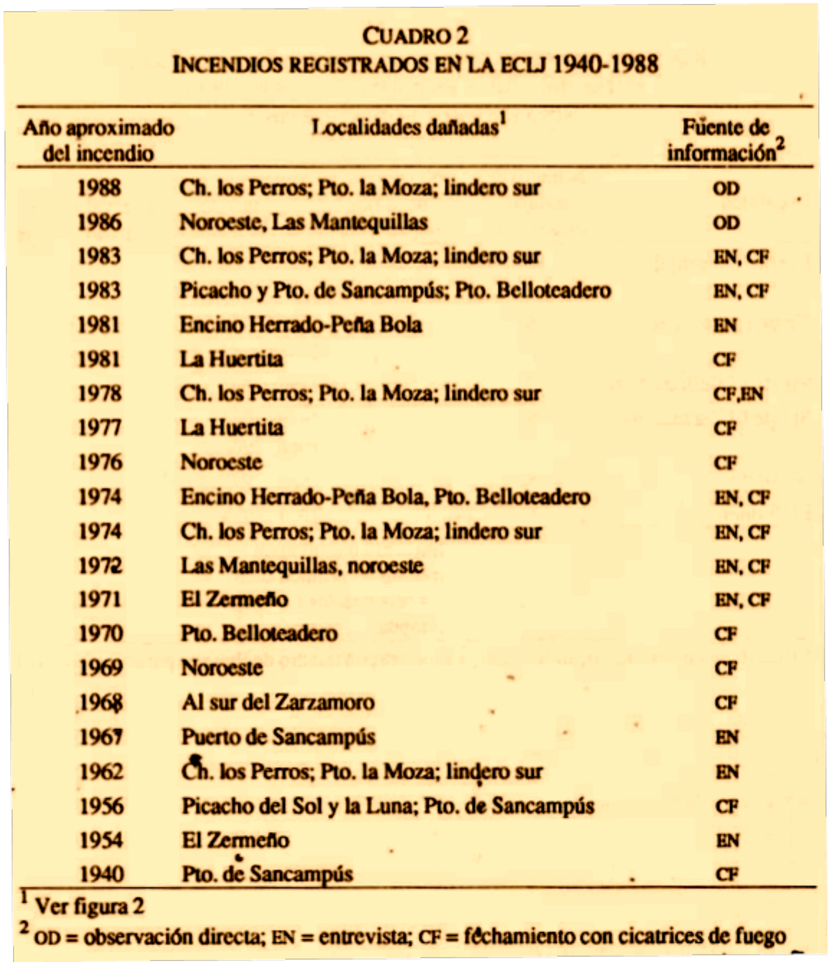
DISCUSSION AND CONCLUSION

By constructing a ring-width index and dating historical fires in the Biosphere Reserve, this study shows that tree rings are a viable source of information about past fires in these pine-dominated forests. The central tendency of fire intervals across the study area is four years, and it is unusual to have a fire-return interval across the study area greater than nine years. The data show that in individual stands it is not unusual to have a fire-return interval up to 25 years but is unusual to burn every year. Also, of 17 unique fire years, only five were large fire years in which at least two non-adjacent plots burned, which indicates that the majority of fires were likely of small extent.

Fire-return intervals prior to 1950 in the Sierra de Manantlán should be interpreted conservatively. Not only did logging until the 1980s remove many available old trees, the stumps that were left decayed quickly and removed much of the historical record. Additionally, many trees that were small enough to be left behind during logging operations and are still alive in the present would likely have had their older fire scars burned away in subsequent fires, as demonstrated by the number of injuries prior to 1950 that could not be shown to be true fire-scars and therefore cannot be included in analysis. Large trees that were not logged due to their position on hard-to-reach slopes may retain identifiable fire-scar records, but those sparse records may skew results to indicate a longer fire-return interval because of their nature as individual point samples (Agee 1993).

Jardel P. et al. (2003) proposed a forest restoration plan that includes recommendations for the use of prescribed fire and fuel treatments in the fire-adapted ecosystems in the Biosphere Reserve. The results of this research support that plan. I recommend that fire management plans include prescribed fire in pine-dominated stands on a random or semi-random rotation throughout the reserve with some stands receiving treatment more often than others, but no stand having a fire-free interval of >24 years or <2 years. When prescribed fire is not desirable, management of fuels by thinning from below is recommended to decrease the continuity of fuels and raise canopy height in order to minimize risk of low-severity fires spreading to high-conservation priority areas, such as pockets of cloud forest, and becoming high-severity fires. In buffer zones, commercial logging operations can be combined with thinning efforts. If neither of these treatment options is feasible due to logistical or economic constraints, it may be desirable to deemphasize fire-fighting efforts when fires occur in pine-dominated stands and allow them to burn while preventing fire spread into fire-sensitive cloud and fir forests.

Another result of this study is to serve as scientific documentation of historical fires where records have been incomplete or unverifiable. Jardel (1991) compiled a list of fires in the Biosphere Reserve and their locations dating back to 1940. The list was comprised of information from interviews with community members, fires he personally observed and tentatively dated fire scars. This study has scientifically confirmed many of those fires, adjusted the dates of others and added new fires to the historical records as shown in Figure 31 and Table 8.



CUADRO 2
INCENDIOS REGISTRADOS EN LA ECLJ 1940-1988

Año aproximado del incendio	Localidades dañadas[1]	Fuente de información[2]
1988	Ch. los Perros; Pto. la Moza; lindero sur	OD
1986	Noroeste, Las Mantequillas	OD
1983	Ch. los Perros; Pto. la Moza; lindero sur	EN, CF
1983	Picacho y Pto. de Sancampús; Pto. Belloteadero	EN, CF
1981	Encino Herrado-Peña Bola	EN
1981	La Huertita	CF
1978	Ch. los Perros; Pto. la Moza; lindero sur	CF,EN
1977	La Huertita	CF
1976	Noroeste	CF
1974	Encino Herrado-Peña Bola, Pto. Belloteadero	EN, CF
1974	Ch. los Perros; Pto. la Moza; lindero sur	EN, CF
1972	Las Mantequillas, noroeste	EN, CF
1971	El Zermeño	EN, CF
1970	Pto. Belloteadero	CF
1969	Noroeste	CF
1968	Al sur del Zarzamoro	CF
1967	Puerto de Sancampús	EN
1962	Ch. los Perros; Pto. la Moza; lindero sur	EN
1956	Picacho del Sol y la Luna; Pto. de Sancampús	CF
1954	El Zermeño	EN
1940	Pto. de Sancampús	CF

[1] Ver figura 2
[2] OD = observación directa; EN = entrevista; CF = fechamiento con cicatrices de fuego

Figure 31. Fires between 1940 – 1988 at sites in and around the Las Joyas Research Station by "OD" (direct observation by the author), "EN" (interview) and "CF" (dating via fire scars). (from Jardel, 1991)

Table 8. Crossdated fire years across the study site and their locations

Fire Year	Locations
1938	Tierritas Blancas
1951	Picacho del Sol y la Luna
1955	Picacho del Sol y la Luna
1969	Puerto de Tecatas, Picacho del Sol y la Luna, Picacho San Campús, Tierritas Blancas, Plaza de Gallos I and II,
1974	Puerto del Belloteadero, Picacho del Sol y la Luna, Puerto de Tecatas, Tierritas Blancas, Plaza de Gallos I and II, Puerto del Escobedo
1978	Plaza de Gallos
1979	Picacho San Campús
1982	Puerto del Belloteadero
1983	Puerto del Belloteadero, Picacho del Sol y la Luna, Puerto de Tecatas, Tierritas Blancas, Plaza de Gallos, Las Mantequillas, Tierritas Blancas, Puerto del Escobedo
1984	Puerto de Tecatas
1986	Las Mantequillas, Tierritas Blancas
1988	Plaza de Gallos
1992	Puerto del Belloteadero

Table 8 cont.

1993	Plaza de Gallos
2000	Las Mantequillas, Tierritas Blancas
2003	Las Mantequillas, Puerto de Tecatas, Picacho del Sol y la Luna, Puerto del Belloteadero
2009	Las Mantequillas, Tierritas Blancas

The objective of determining whether climate in fire years was different from climate in non-fire years was not analyzable due to the small number of identified fire years. However, this is an important topic for further research. Balcázar-Medina (2011) found that weather explained 40% of variation in fire occurrence from 1995 – 2008, and patterns in fire synchrony among plots in this study could indicate that climate is a driver of fire. For example, fires in 1969, 1974 and 1983 were identified in the tree-ring record in six to seven plots. The heterogeneity of the Biosphere Reserve's terrain and the network of firebreaks makes it unlikely that these were large single fires across the entire study site. Likewise, fire scars from these years are located in both early and middle intra-ring positions. It is likely, therefore, that there were multiple fires during the same years. Since the use of agricultural fires does not likely vary to a great degree each year, and fire in the Biosphere Reserve is almost solely anthropogenic, this could indicate that climate conditions in these years were more conducive to the spread of fire than years where fewer plots experienced fire.

Analysis of intra-ring position also showed that more than a third of fires occurred early in the growing season after cool, dry winters dried out available fuels, making wildfire more likely, and coinciding with the timing of agriculture fires, which are often lit by ejido and community members prior to the start of the summer rains (Jardel-Peláez et al., in press). It is important, however, to consider that the study area is small, and although large-scale climate patterns such as ENSO have been shown to be regional drivers of fire occurrence, human or other factors may be stronger drivers of fire in this location. Expanding our understanding of historical climate-fire interaction will be vital for long-term management goals in a changing climate.

The fire science community in México has been calling for research to improve understanding of fire regimes and espousing the need for research to incorporate fire management and ecological use of fire into fire prevention and fire fighting (Jardel-Peláez et al., in press; Rodríguez-Trejo et al., 2011). Difficulties in conducting fire history studies in tropical ecosystems with low-severity fire regimes include: the inability to delimit fire boundaries through regeneration patterns from satellite imagery because fires primarily affect the understory; rapid rates of decomposition that remove much of the historical record of fire; and challenges in crossdating tree rings from tropical trees with false, diffuse and missing rings. As a result of this study, a master chronology of tree rings will be available for future research and will enable other researchers to crossdate cores and fire scars from *Pinus sp.* in the region. This study will also contribute to ecosystem management in pine-dominated forest in the Biosphere Reserve by offering a more complete understanding of the reserve's fire-return intervals to be incorporated into reserve management and restoration plans.

RESEARCH LIMITATIONS

There were several limitations that impacted the results of this study, and they should be taken into account by future researchers when conducting dendrochronological investigations in tropical pines. Each limitation is outlined below with a corresponding recommendation:

Limitation 1.

This study was originally intended to compare fire history within the core zone and within the buffer zone of the Biosphere Reserve. Due to the presence of illegal crop growers, we were unable to sample in a second core zone, and due to our inability to obtain the necessary permit, we were unable to sample fire-scarred trees in the buffer zone.

Recommendation 1.

There is no method to control for illegal growers, but have a backup plan for alternate sampling sites. In future studies, anticipate a lengthy process for obtaining the necessary permits for all sampling areas, and start the process at least several months ahead of schedule.

Limitation 2.

Dendrochronology and fire history studies attempt to sample for tree rings that extend as far back in history as possible. That was the intention and the expectation of this study, and the presence of large trees, >100 cm DBH in some cases, seemed to indicate that would be possible. However, climate conditions in the Biosphere Reserve are conducive to rapid growth, and almost all trees sampled were < 100 years of age with the majority of trees < 60 years. In addition, most of the large trees were removed by high-grade logging that took place until the 1980s, resulting in a master chronology that only extends back to 1881.

Recommendation 2.

If logging records can be located, it may be helpful to select sites that were not logged in order to locate older trees. Sampling trees located on extremely steep slopes may also yield older trees, as these slopes would have been more difficult to harvest.

Limitation 3.

The climate in much of the Biosphere Reserve is humid with monsoon rains in the summer but with dry winters. These conditions are conducive to rapid rates of wood decomposition. Stumps, logs and snags that would be expected to yield some of the oldest fire scars were too decomposed to analyze.

Recommendation 3.

There are no stumps, logs or snags that are more than one to two years old in sound condition. If there is a current logging operation in the buffer zone, it would be beneficial to obtain a permit to sample stumps from harvested trees.

Limitation 4.

While this study has demonstrated that it is possible to use *Pinus douglasiana* in dendrochronological studies, it has also demonstrated the difficulty of analyzing tree rings from this species. False, diffuse and missing rings make crossdating challenging. Only 27% of my samples were used in the final master chronology, and I was able to crossdate only 75% of my fire-scarred samples.

Recommendation 4.

Sample three to four times the number of samples needed according to your sample size power analysis and/or experimental design. Allow three to four times the amount of time you would normally allot for crossdating your samples.

Limitation 5.

Temporal analysis did not yield significant results in this study, which may be due to small sample size resulting from both the limited historical fire interval information and the number of samples that could not be crossdated. Also, there are few fire-return intervals following the establishment of the reserve in 1987, which does not allow a strong comparison between pre and post-protection fire frequency.

Recommendation 5.

Instead of comparing fire-return intervals before and after the Biosphere Reserve was established, it may be more informative to compare fire-return intervals inside and outside the core zones, as was originally planned for this study.

Limitation 6.

Because of the limited number of identified fire years, climate analysis could not be completed.

Recommendation 6.

Superposed Epoch Analysis (SEA) should be completed to investigate whether there is a significant difference in climate between fire years and non-fire years, and as many fire years as possible should be included in the analysis.

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APPENDIX A

Individual Plot Maps

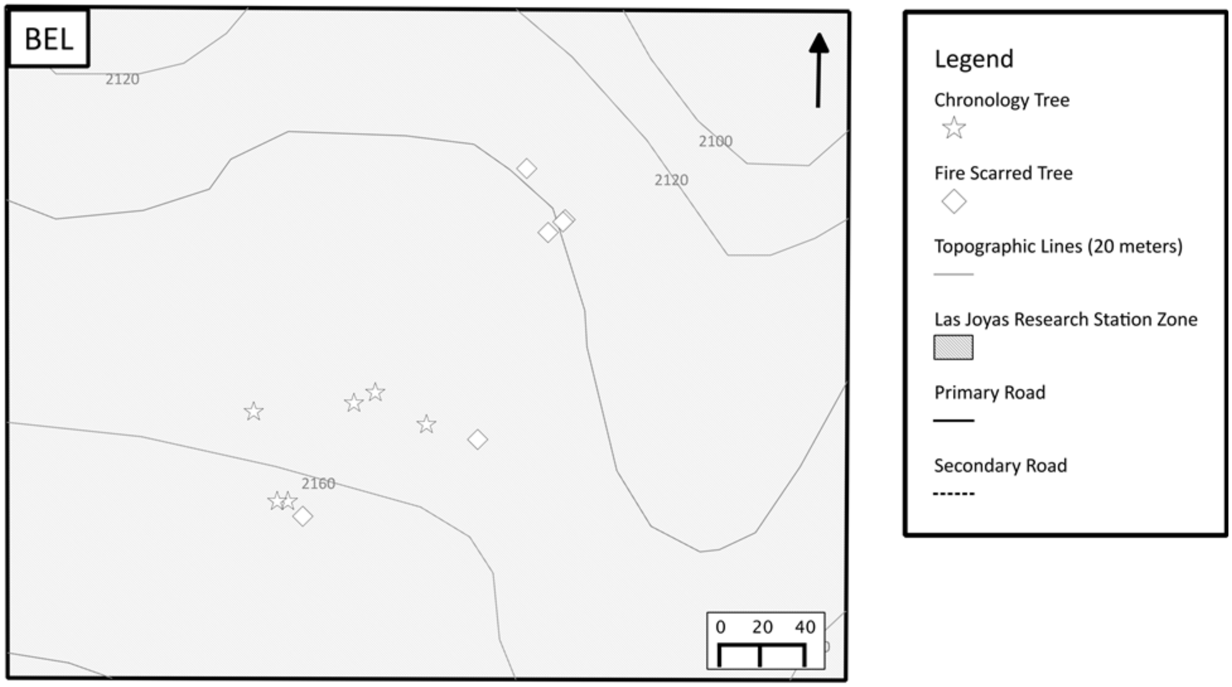

Figure A.1. Map of Puerto del Belloteadero, chronology and fire plot. Scale is in meters.

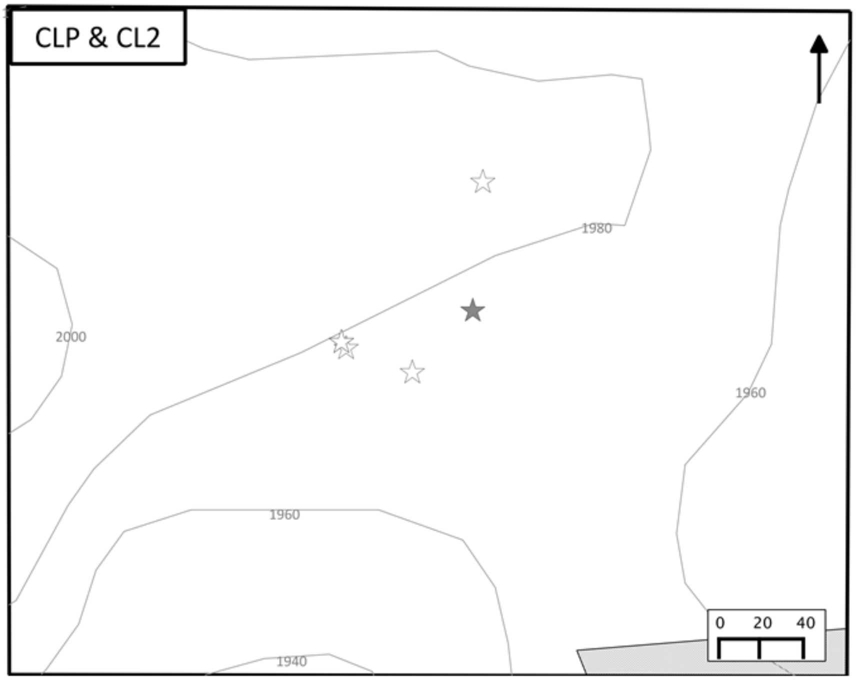

Figure A.2.Map of Charco los Perros I and II, chronology plots. Open symbols denotes CLP and filled symbol denotes CL2. All six sample trees in CL2 were within 20 meters of each other, so one GPS point is used for all. Scale is in meters.

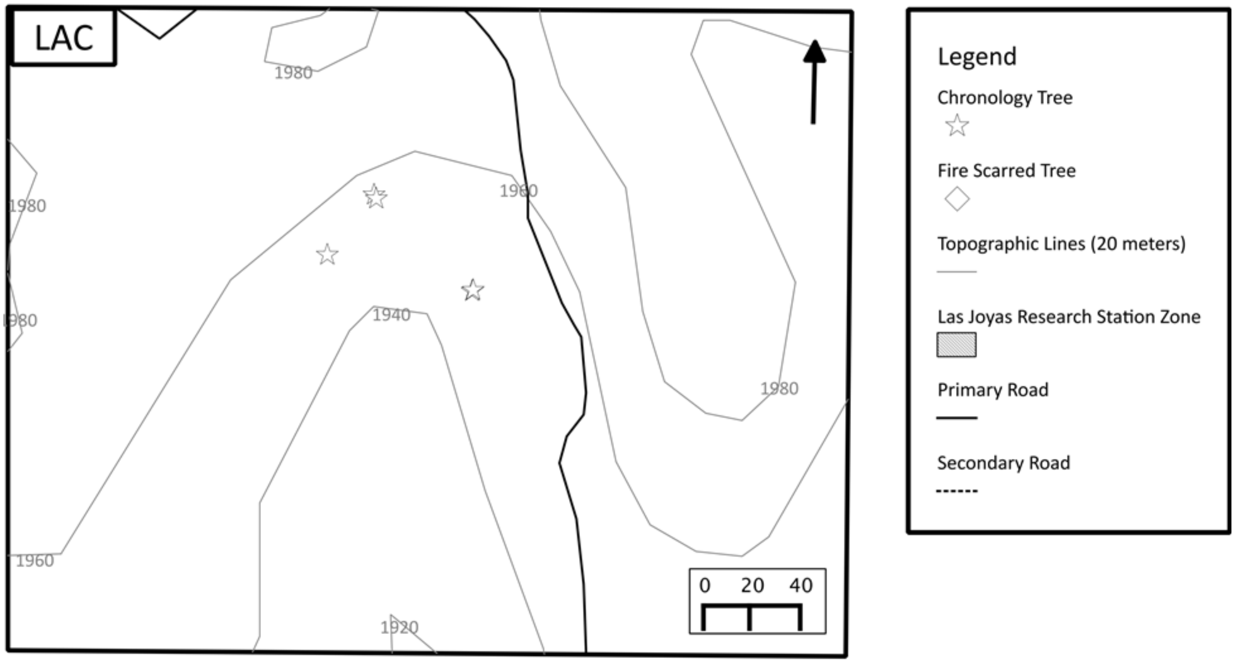

Figure A.3. Map of La Cumbre, chronology plot. Scale is in meters.

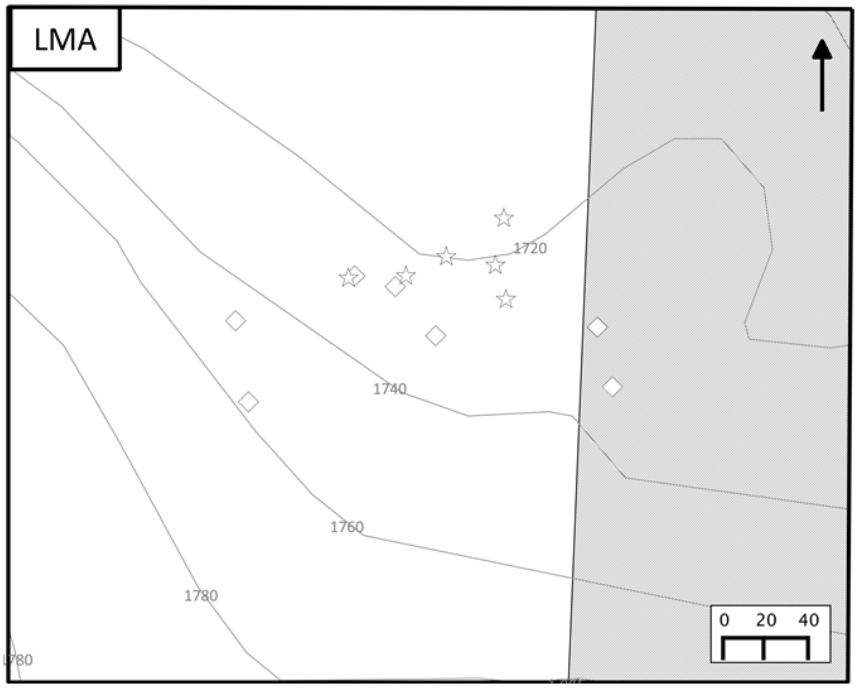

Figure A.4. Map of Las Mantequillas, chronology and fire plot. Scale is in meters.

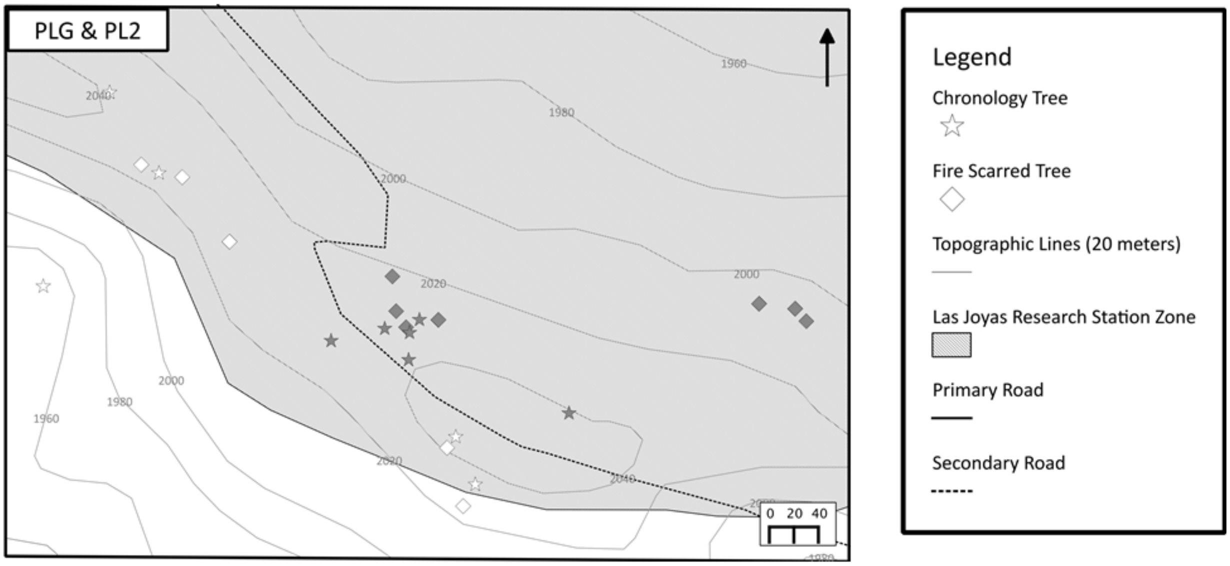

Figure A.5. Map of Plaza de Gallos I and II, chronology and fire plots. Open symbols denote PLG and filled symbols denote PL2. Scale is in meters.

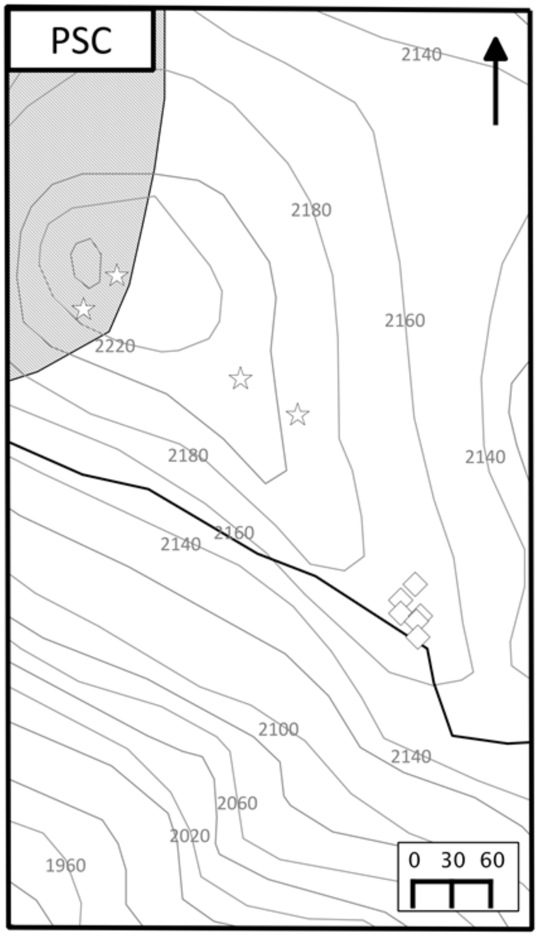

Figure A.6. Map of Picacho San Campús, chronology and fire plot. Scale is in meters.

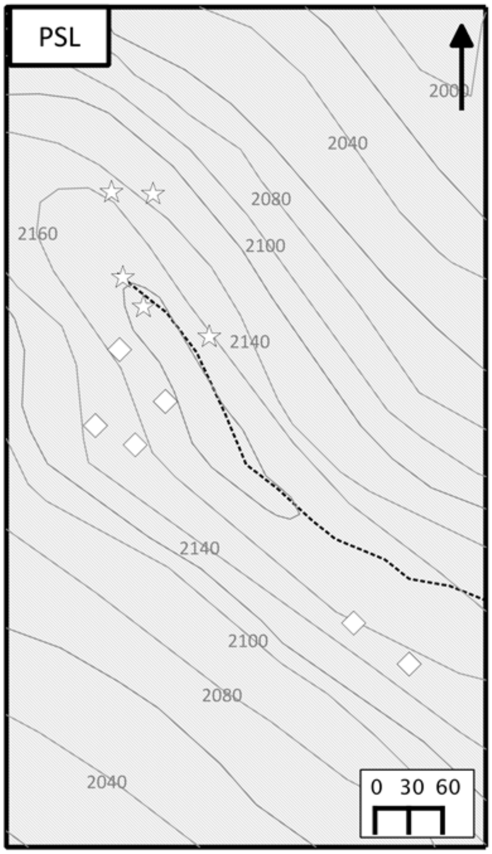

Figure A.7. Map of Picacho del Sol y la Luna, chronology and fire plot. Scale is in meters.

Legend

Chronology Tree
☆

Fire Scarred Tree
◇

Topographic Lines (20 meters)
—

Las Joyas Research Station Zone
▨

Primary Road
—

Secondary Road

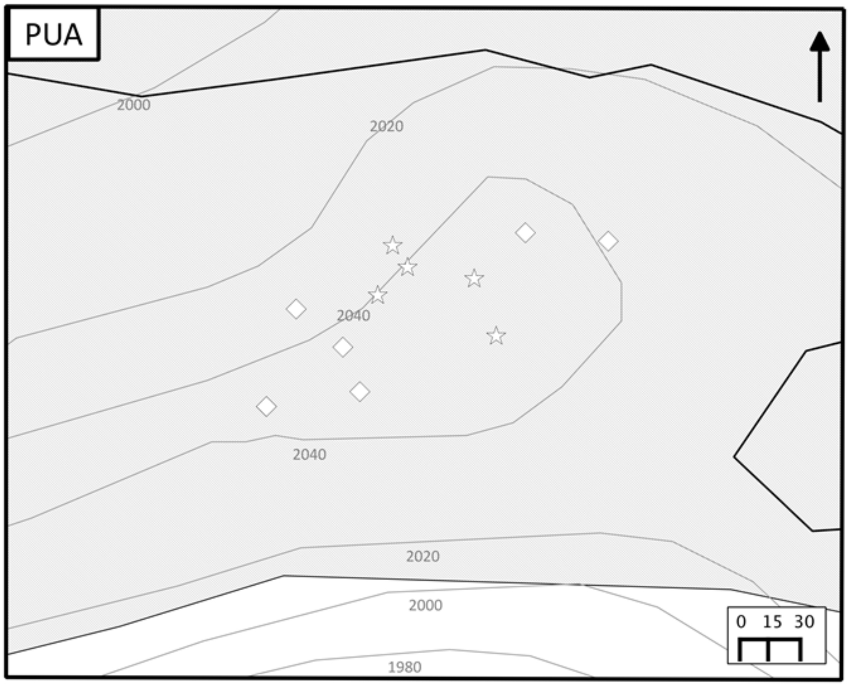

Figure A.8. Map of Puerto del Escobedo, chronology and fire plot. Scale is in meters.

Figure A.9. Map of Puerto de Tecatas, chronology and fire plot. Scale is in meters.

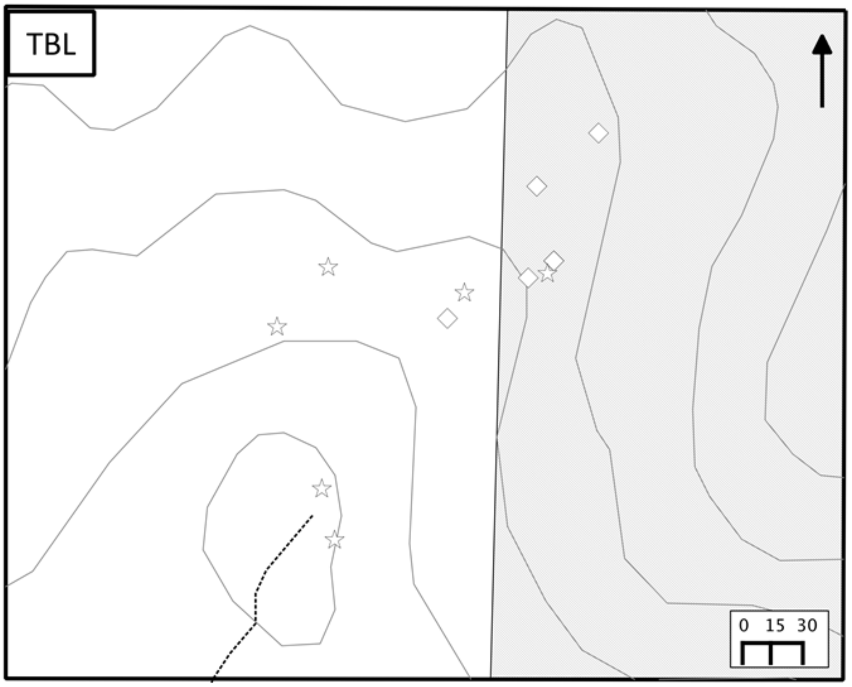

Figure A.10. Map of Tierritas Blancas, chronology and fire plot. Scale is in meters.

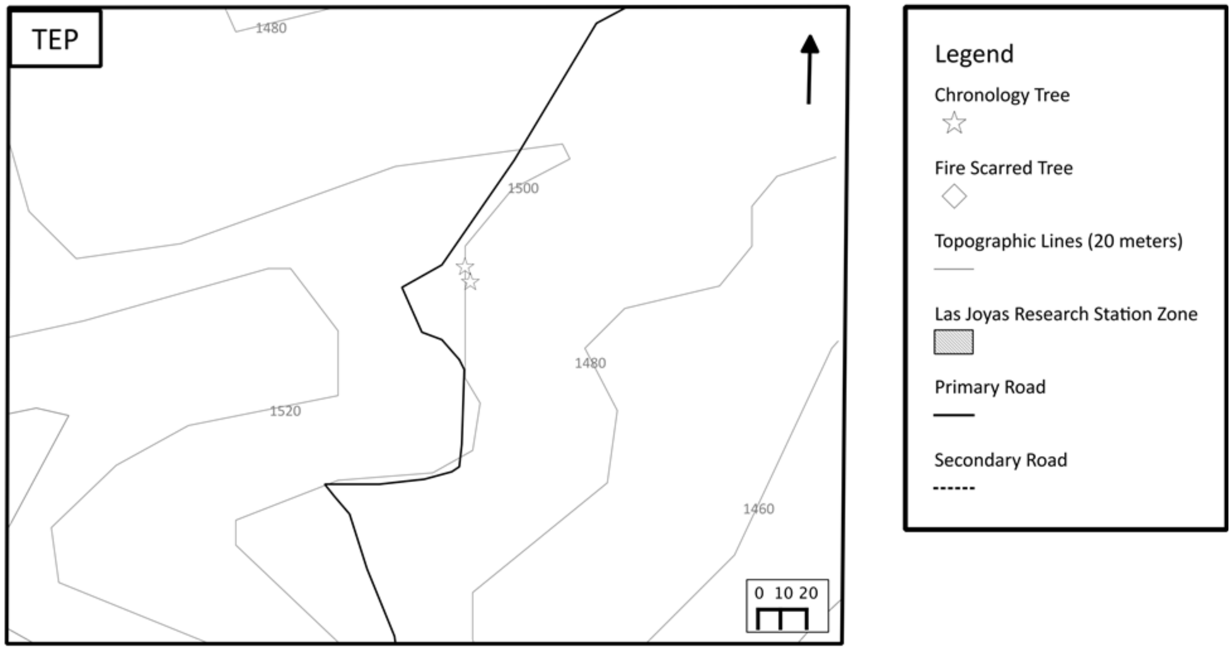

Figure A.11. Map of Tepehuaje, chronology plot. Scale is in meters.

*Note: Because Puerto del Escobedo II (PU2) and Escarbadero de los Toros (ELT) were sampled on foggy days, the GPS unit was unable to register their latitude and longitude. Therefore there are no maps for those two sites. No fire scars were sampled at either plot.

APPENDIX B

Fire Chronologies by Plot

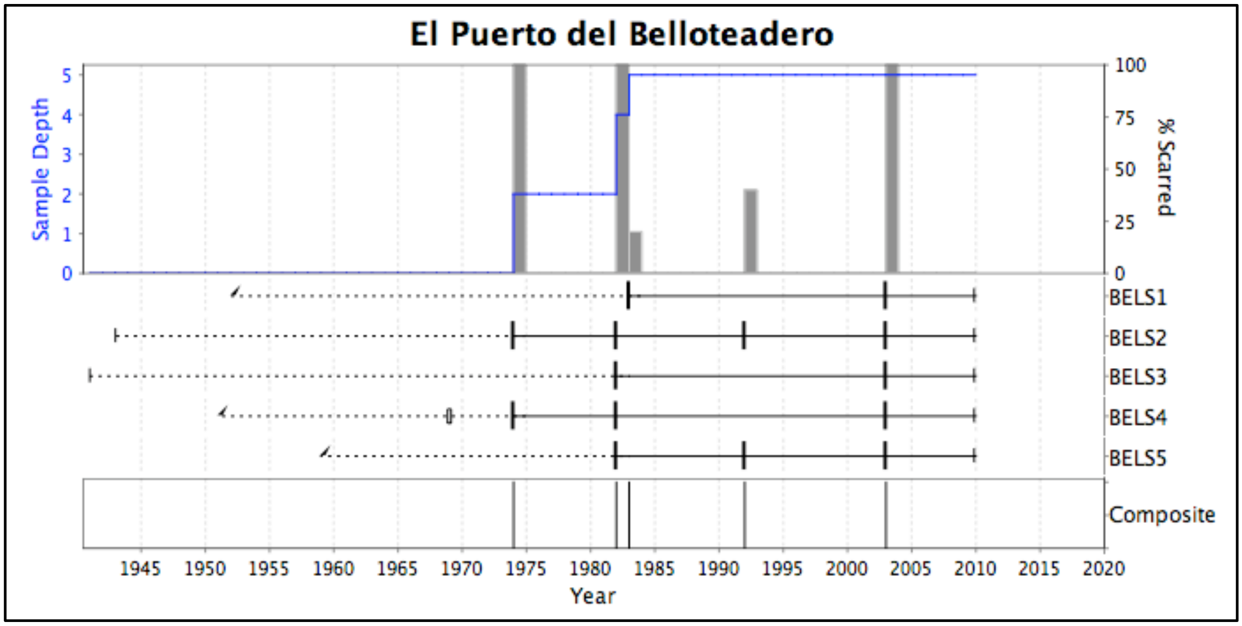

Figure B.1. Fire chronology for El Puerto del Belloteadero (BEL).

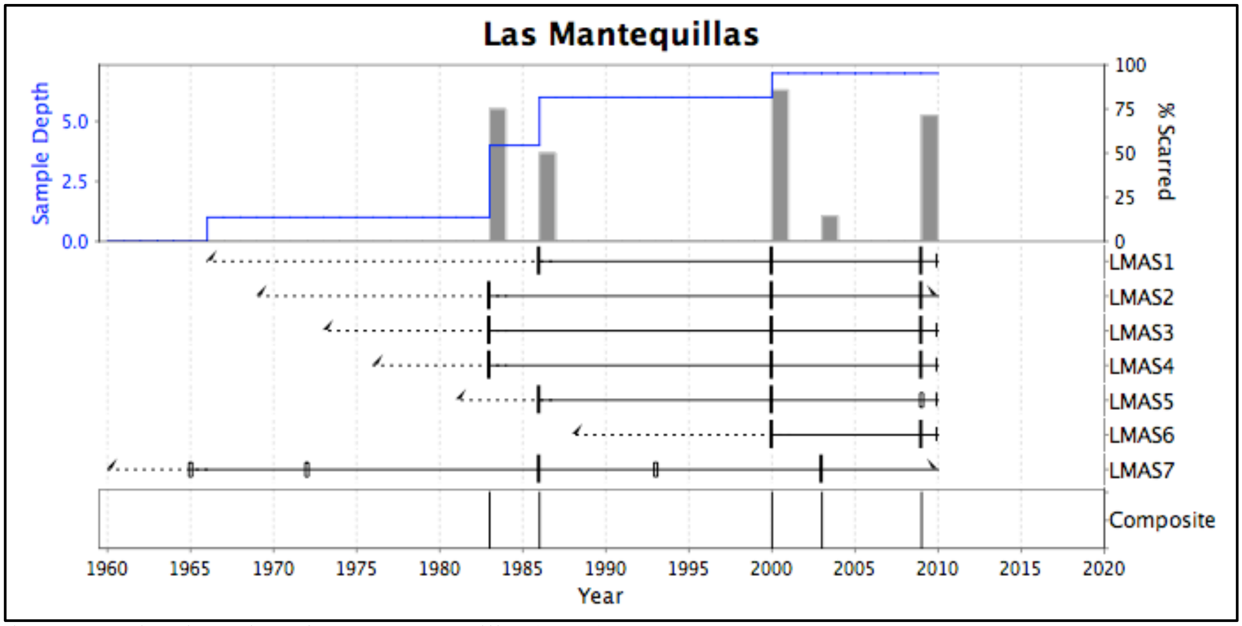

Figure B.2. Fire chronology for Las Mantequillas (LMA).

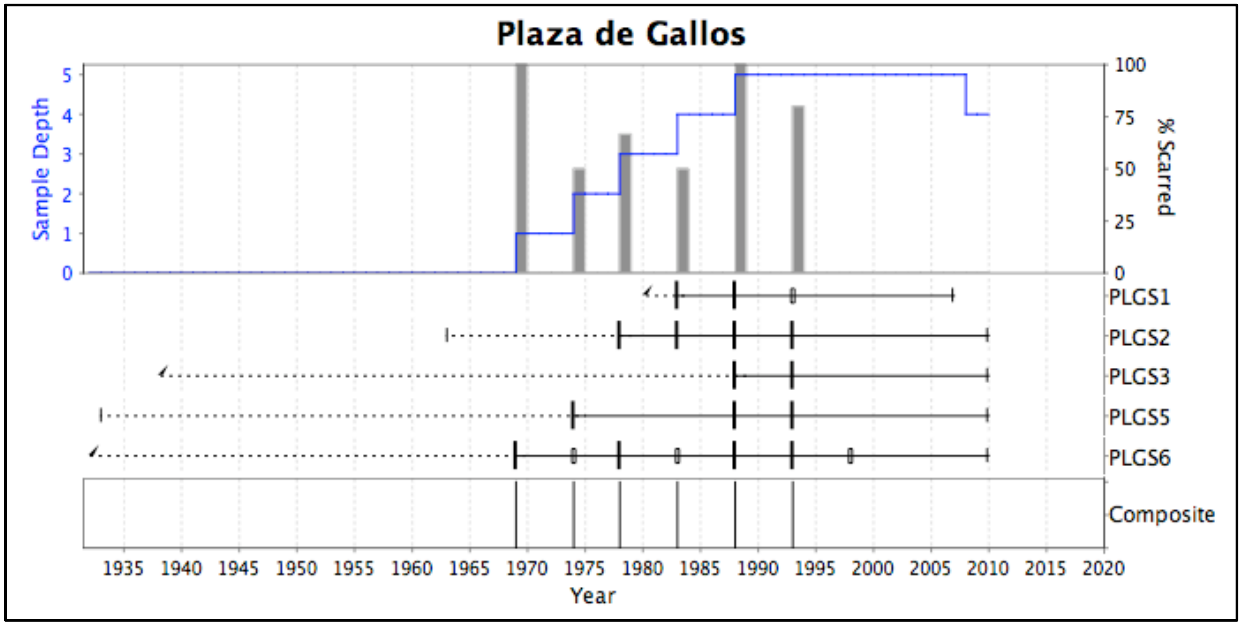

Figure B.3. Fire chronology for Plaza de Gallos (PLG).

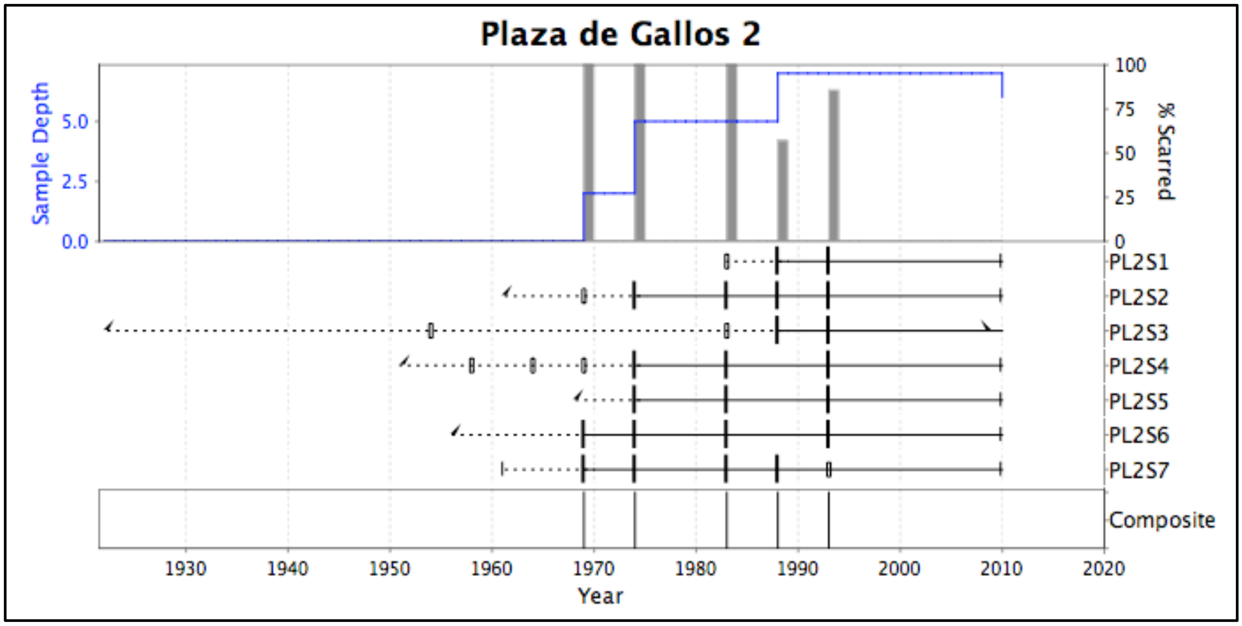

Figure B.4. Fire chronology for Plaza de Gallos II (PL2).

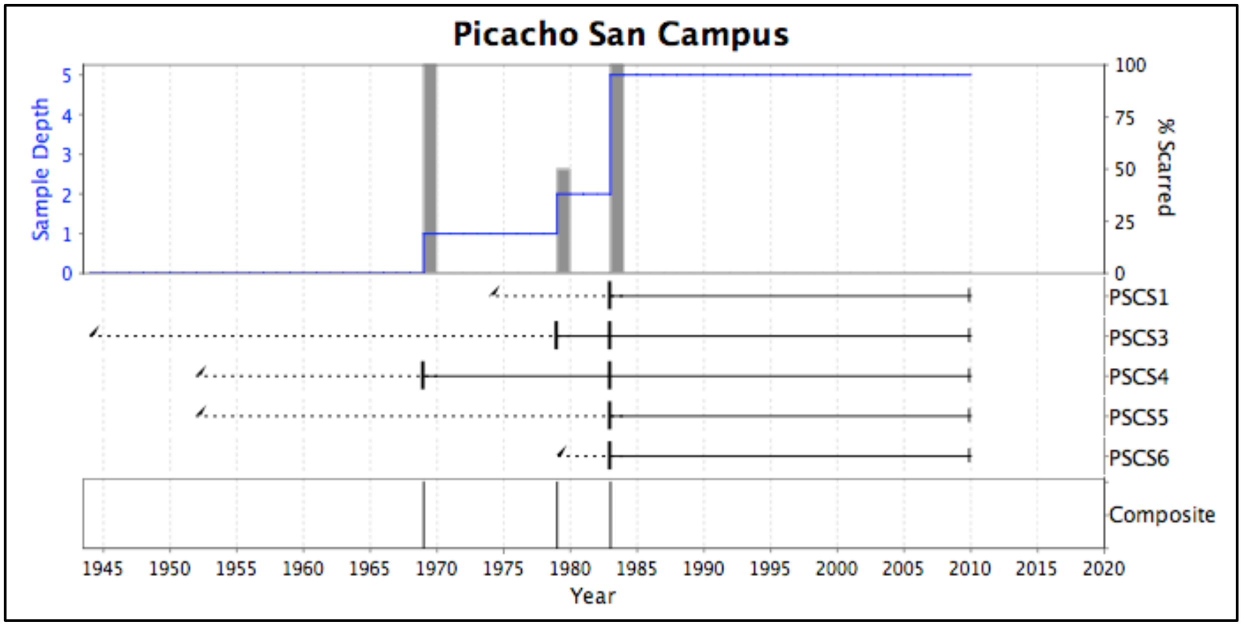

Figure B.5. Fire chronology for Picacho San Campus (PSC).

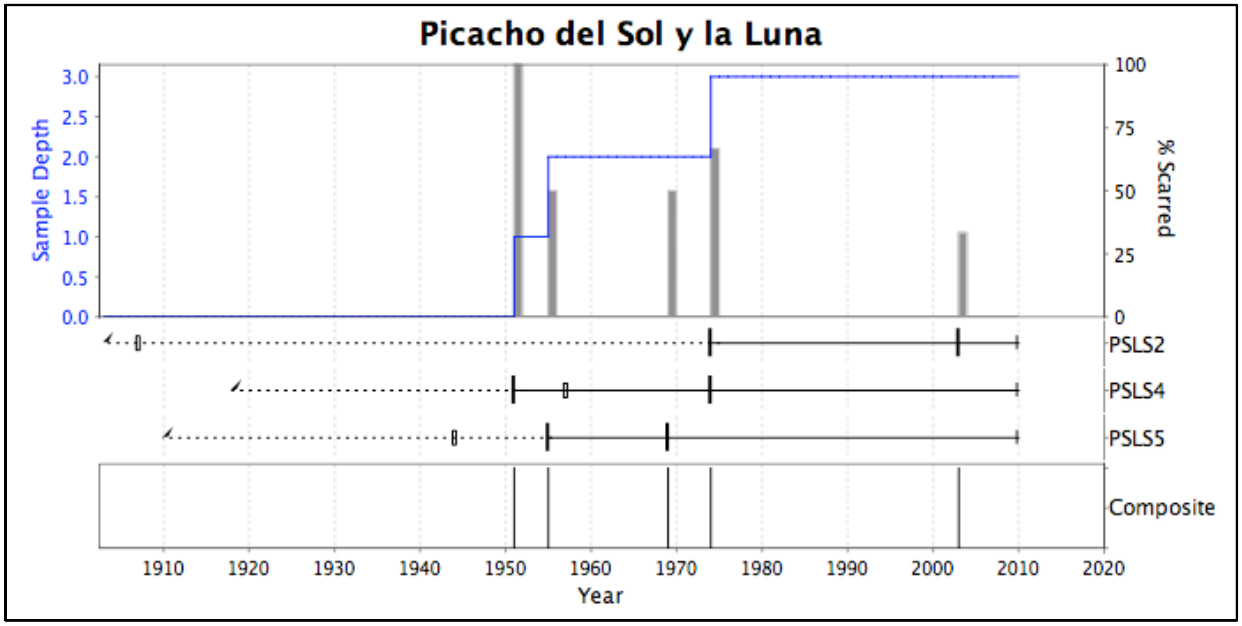

Figure B.6. Fire chronology for Picacho del Sol y la Luna (PSL).

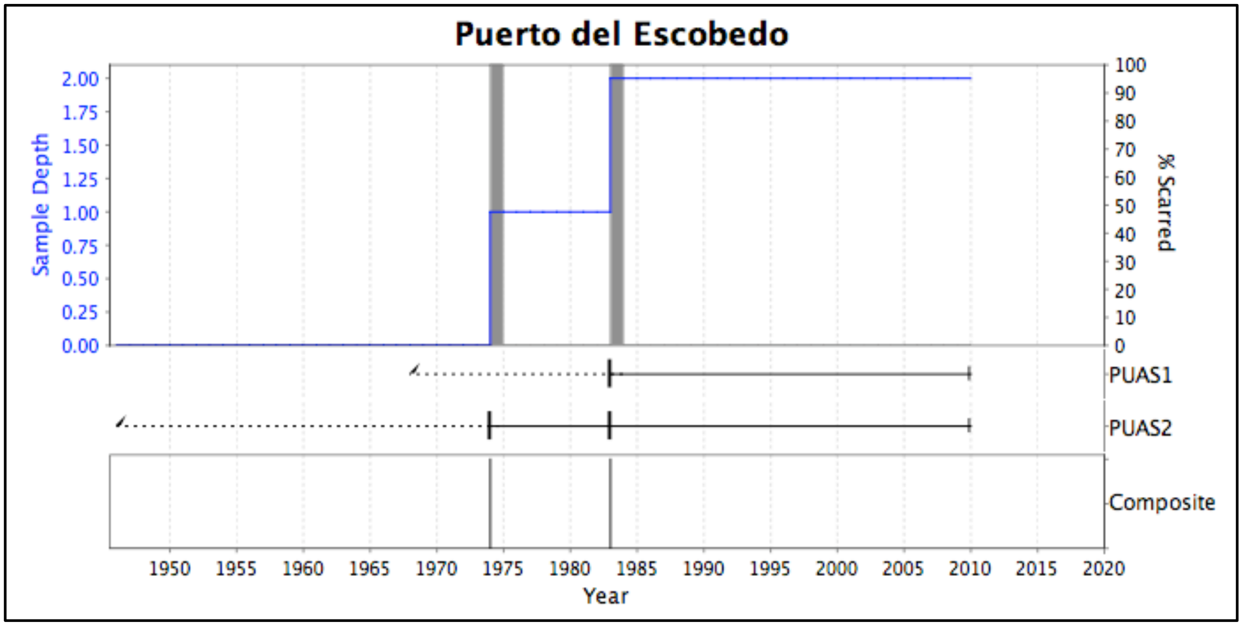

Figure B.7. Fire chronology for Puerto del Escobedo (PUA).

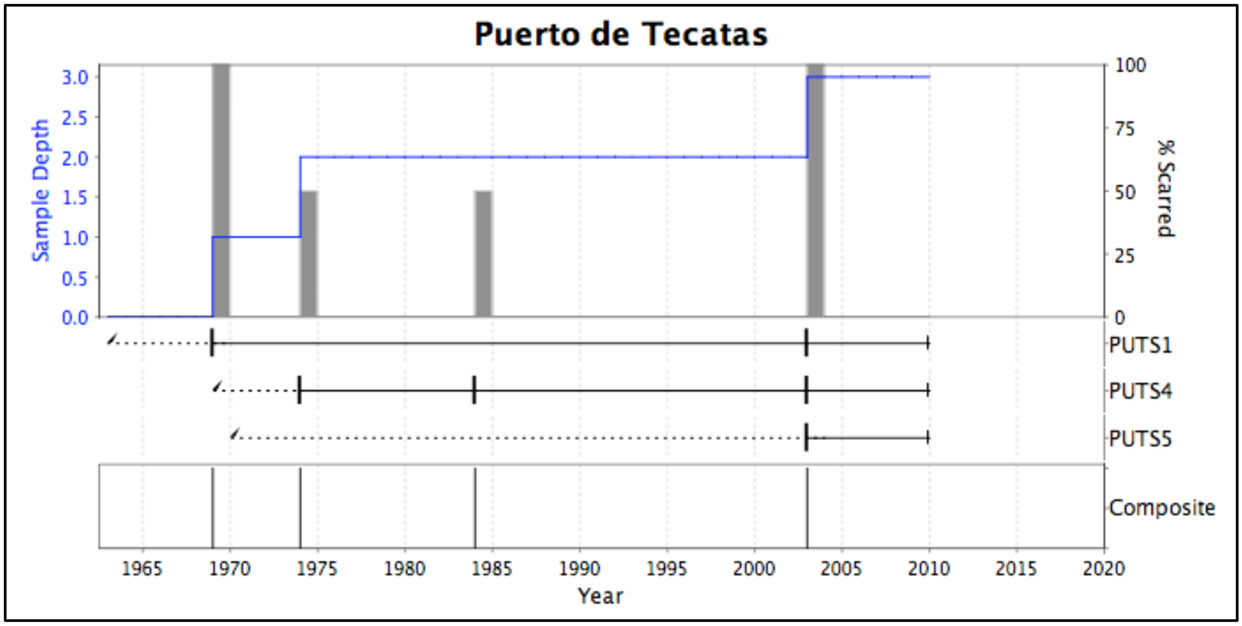

Figure B.8. Fire chronology for Puerto de Tecatas (PUT).

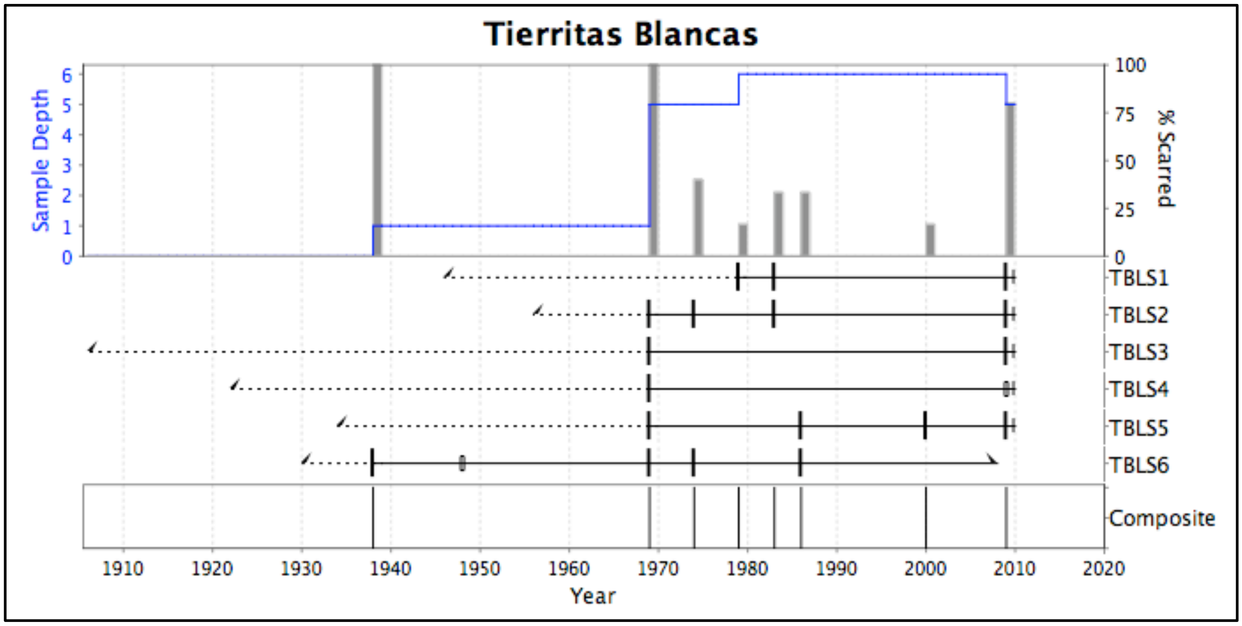

Figure B.9. Fire chronology for Tierritas Blancas (TBL).

APPENDIX C

Dominant Tree Species Descriptions

Abies guatemalensis (ABGU)

Figure C.1. *Abies guatemalensis* (photo by the author)

Common names: Guatemalan fir, pinabete, pashaque, romerillo

This true fir is the southernmost *Abies*, and it ranges along the southern Pacific coast of México (Nayarit, Jalisco, Colima, Michoacán, Guerrero, Oaxaca, Chiapas) as well as the northeastern state of Tamaulipas. It is also found in Guatemala, El Salvador and Honduras. It has been listed as a vulnerable species since 1998 (Conifer Specialist Group, 1998). ABGU grows 35-40 m in height and 1-1.5 m in diameter. Depending on variety, its needles can be 1.2 – 6.5 cm long and emarginated, truncate or bluntly notched. Cones are 6-12 cm long (Andersen et al., 2006). Fire ecology: Little to no research has been conducted on the impacts of fire on ABGU (Andersen et al., 2006), but because the bark is smooth and is not thick, it can be inferred that this species is likely fire sensitive and experiences moderate to high mortality during fire as do other *Abies* species (Agee, 1998; Agee, 1993).

Arbutus xalapensis (ARXA80)

Figure C.2. and C.3. *Arbutus xalapensis* tree and leaves (photos by the author)

Common name: Texas madrone

Evergreen tree-shrub with multiple stems of up to 8 meters and irregularly branching limbs. Bark is reddish-brown and peeling; mature bark turning grey and scaly. Leaves are alternate, simple, elliptic to ovate and leathery-shiny. This species has been identified in the United States in New Mexco and Texas, throughout much of México and into Guatemala, growing at 610-1829 m. in moist, rocky soils ("Lady Bird Johnson", 2010), but is also found in xeric sites (Tirmenstein, 2012). The leaves and bark are astringent and have medicinal value (Tirmenstein, 2012). Fire ecology: Little has been reported about fire effects for this species. Regeneration is very limited, with extensive seed dispersal resulting in very few successful seedlings, and although stump sprouting has been observed following mechanical removal, sprouting has not been observed following fire (Tirmenstein, 2012).

Pinus douglasiana (PIDO)

Figure C.4. and C.5. *Pinus douglasiana* crown and cone (photos by the author)

Subgenus: Diploxylon (Hard Pines) Section: Montezumae, Subsection: Montezumae

Common Name: Gordon’s pine

PIDO is the dominant pine in most of the study area. It grows in a narrow elevation band of 1,500-2,500 m in warm to temperate areas with around 1,000 mm annual precipitation. It grows to heights of 30-35 m and mature trees tend to have a rounded crown while young trees have a pyramidal shape. 20-30 cm-long needles with stomata on dorsal and ventral surfaces grow in fascicles of 5. Cones, non-persistent and non-serotinous, are 7-10 cm long, ovate, and fall with their 1-2 cm-long peduncle attached obliquely. The bark is thick, reddish brown and scaly, breaking into plates as the tree matures (Perry, 1991). Fire ecology: PIDO displays resistor characteristics (Rowe, 1983) with its thick bark that can withstand frequent low intensity fires. It also displays invader characteristics (Rowe, 1983) by quickly regenerating via seed after high severity fire. Up to 8,000 seedlings ha^{-1} have been reported two years after crown fires for this species, as well as *P. herrerae* and *P. oocarpa* (Rodríguez-Trejo, 2008).

Pinus herrerae (PIHE) - née *P. herrerai*

Subgenus: Diploxylon (Hard Pines) Section: Teocote

Common Names: Gordon's pine, pino chino

A thick-barked pine with a rounded and open crown, PIHE grows 25-35 in height at an elevation range of 1,200-2400 m and in moist, well-drained soils. It is known to be distributed through Durango, Guerrero, Jalisco, Michoacán and Sinaloa, but its distribution may extend farther than has been reported. Its needles are 10-20 cm long, in fascicles of 3, and have stomata on both ventral and dorsal surfaces. Identification can be made by its cones, which are quite small in comparison with its associated pine species at only 2-4 centimeters, almond-shaped, and with 5 mm long peduncles (Perry, 1991). Fire ecology: PIHE displays resistor characteristics (Rowe, 1983) with its thick bark that can withstand frequent low intensity fires.

Pinus maximinoi (PIMX)

Figure C.6. *Pinus maximinoi* (photo by the author)

Subgenus: Diploxylon (Hard Pines) Section: Pseudostrobus, Subsection: Pseudostrobus

Common Name: pino canis

This tall, straight pine is found throughout a wide distribution in Méxic*o* including the states of Chiapas, Colima, Guerrero, Hidalgo, Jalisco, México, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, Sinaloa, Tlaxcala and Veracruz. It grows 20-35 m high, at elevations of 600–2,400 m, and has been identified on well-drained soils where annual rainfall is 1,000-2,000 mm. 15-28 cm-long needles are in fascicles of 5 and are 0.7-0.8 mm wide. Cones, non-serotinous and non-persistent, are long-ovate and 10-15 mm long. They fall from the tree with the peduncle still attached (Perry, 1991). Fire ecology: PIMA displays resistor characteristics (Rowe, 1983) with its thick bark that can withstand frequent low intensity fires.

Pinus oocarpa (PIOO2)
Subgenus: Diploxylon (Hard Pines) Section: Serotinae, Subsection: Oocarpa
Common Names: pino prieto, pino colorado, ocote chino

P. oocarpa is found in México in the states of Chihuahua, Durango, Guerrero, Jalisco, México, Michoacán, Morelos, Nayarit, Oaxaca, Sinaloa, Sonora and Zacatecas and can grow in conditions that range from dry-temperate to humid subtropical. Its bole can be tall and straight or spindly and crooked. PIOO2 can grow 15-30 m high and the crown tends to be round-shaped. Stiff needles, 20-25 cm-long, are in fascicles of 3-5. Long-persistent cones are often round or egg-shaped, often serotinous, and the dropped cones maintain their peduncle (Perry, 1991). Fire ecology: PIOO2 displays life history strategies of resistor with its thick bark and self-pruning abilities (Rodríguez-Trejo, 2008), evader with its serotinous cones (Perry, 1991; Rodríguez-Trejo, 2008) and endurer, because it is capable of sprouting after fire (Rowe, 1983; Rodríguez-Trejo, 2008).

Quercus magnoliifolia

This white oak is an intermediate or late seral species with deciduous or briefly-deciduous foliage. Its acorns can be small (<2 cm diameter) or large (>2cm) diameter (Rodríguez-Trejo and Myers, 2010). Fire ecology: Q. magnoliifolia's fire return interval is dependent upon the forest type it is found in, which has been recorded as oak forest, pine-oak forest and deciduous tropical forest (Rodríguez-Trejo and Myers, 2010). Its functional adaptation to fire is that of an endurer, as it sprouts following fire (Rowe, 1983), and at least in the state of Guerrero, *Q. magnoliifolia* has been observed to survive low intensity frequent fires, although regeneration can be reduced by fire (Peña Ramírez and Bonfil, 2003).

Quercus resinosa

Also a white oak, *Q. resinosa* proliferates in clearings and has deciduous foliage and both small and large acorns. Its bark is thick and it is found in both dry and transitional sites in oak forest, pine-oak forest and deciduous tropical forest (Rodríguez-Trejo and Myers, 2010). Fire ecology: Its functional adaptation to fire is that of an endurer as it sprouts following fire (Rowe, 1983; Rodríguez-Trejo and Myers, 2010).

Quercus scytophila

Q. scytophila is an early seral red oak that regenerates in clearings. Its foliage is evergreen, rigid with stiff points, dark green and shiny on top and dull whitish green on the undersides. Its acorns are small (< 2 cm diameter). Fire ecology: In Jalisco, fire return intervals of 5-17 years have been reported (Rodríguez-Trejo and Myers, 2010). Because in general, oaks with small acorns are known to regenerate well after fire (Rodríguez-Trejo, 2008), this species is likely fire-adapted.

APPENDIX D

Tree data from chronology and fire scar plots.

Table D.1. Tree Data. Null in the height field indicates that tree height was not recorded. Species are *Pinus douglasiana* (PIDO), *Pinus herrerae* (PIHE), *Pinus maximinoi* (PIMX) and unidentified *Pinus* species (PISP)

Site	Tree #	Chronology or Fire Scar Plot	Species	Live = 1, Dead = 0	DBH (cm)	Height (m)
BEL	C1	Chronology	PIDO	1	56.7	17.3
BEL	C2	Chronology	PIHE	1	56.1	25.6
BEL	C3	Chronology	PIHE	1	52.5	23.1
BEL	C4	Chronology	PIHE	1	66.0	32.5
BEL	C5	Chronology	PIDO	1	62.0	null
BEL	C6	Chronology	PIDO	1	76.2	null
BEL	S1	Fire Scar	PIHE	1	76.6	30.1
BEL	S2	Fire Scar	PIDO	1	57.8	19.0
BEL	S3	Fire Scar	PIDO	1	55.0	28.5
BEL	S4	Fire Scar	PIDO	1	66.8	29.8
BEL	S5	Fire Scar	PIHE	1	56.2	34.7
BEL	S6	Fire Scar	PIHE	1	57.3	24.7
CL2	C1	Chronology	PIDO	1	85.8	null
CL2	C2	Chronology	PIDO	1	78.2	null
CL2	C3	Chronology	PIDO	1	85.0	null
CL2	C4	Chronology	PIDO	1	62.7	null
CL2	C5	Chronology	PIDO	1	71.2	null
CL2	C6	Chronology	PIDO	1	68.8	null
CLP	C1	Chronology	PIDO	1	64.3	null
CLP	C2	Chronology	PIDO	1	66.5	null
CLP	C3	Chronology	PIDO	1	63.4	null
CLP	C4	Chronology	PIDO	1	88.1	null
CLP	C5	Chronology	PIDO	1	68.1	null
CLP	C6	Chronology	PIDO	1	64.7	null
ELT	C1	Chronology	PIDO	1	76.1	null
ELT	C2	Chronology	PIDO	1	63.0	null
ELT	C3	Chronology	PIDO	1	73.0	null
LAC	C1	Chronology	PIDO	1	87.5	null
LAC	C2	Chronology	PIDO	1	70.5	null
LAC	C3	Chronology	PIDO	1	63.7	null
LAC	C4	Chronology	PIDO	1	65.9	null
LAC	C5	Chronology	PIDO	1	71.1	null
LAC	C6	Chronology	PIDO	1	93.5	null
LMA	C1	Chronology	PIDO	1	56.2	25.5
LMA	C2	Chronology	PIDO	1	66.5	null
LMA	C3	Chronology	PIDO	1	56.8	26.5
LMA	C4	Chronology	PIDO	1	64.8	null
LMA	C5	Chronology	PIDO	1	53.5	27.4

Table D.1. cont.

LMA	C6	Chronology	PIDO	1	58.1	27.3
LMA	S1	Fire Scar	PIDO	1	80.6	25.4
LMA	S2	Fire Scar	PIDO	1	57.9	14.9
LMA	S3	Fire Scar	PIDO	1	68.2	23.0
LMA	S4	Fire Scar	PIDO	1	65.1	11.8
LMA	S5	Fire Scar	PIDO	1	54.7	null
LMA	S6	Fire Scar	PIDO	1	50.4	24.2
LMA	S7	Fire Scar	PIDO	0	91.7	null
PL2	C1	Chronology	PIDO	1	65.9	null
PL2	C2	Chronology	PIDO	1	73.2	null
PL2	C3	Chronology	PIDO	1	60.8	null
PL2	C4	Chronology	PIDO	1	73.2	null
PL2	C5	Chronology	PIDO	1	71.0	null
PL2	C6	Chronology	PIDO	1	71.4	null
PL2	S1	Fire Scar	PIDO	1	72.6	32.3
PL2	S2	Fire Scar	PIDO	1	84.3	27.0
PL2	S3	Fire Scar	PIDO	0	70.7	29.9
PL2	S4	Fire Scar	PIDO	1	78.2	23.7
PL2	S5	Fire Scar	PIDO	1	87.2	41.8
PL2	S6	Fire Scar	PIDO	1	96.7	32.7
PL2	S7	Fire Scar	PIDO	1	45.8	27.7
PLG	C1	Chronology	PIDO	1	54.4	null
PLG	C2	Chronology	PIDO	1	62.1	null
PLG	C3	Chronology	PIDO	1	84.6	null
PLG	C4	Chronology	PIDO	1	62.7	null
PLG	C5	Chronology	PIDO	1	73.6	null
PLG	C6	Chronology	PIDO	1	54.5	null
PLG	S1	Fire Scar	PIDO	0	62.5	28.6
PLG	S2	Fire Scar	PIDO	1	60.0	27.7
PLG	S3	Fire Scar	PIDO	1	81.5	30.1
PLG	S4	Fire Scar	PIDO	1	56.1	17.3
PLG	S5	Fire Scar	PIDO	1	84.1	31.0
PLG	S6	Fire Scar	PIDO	1	74.2	18.7
PSC	C1	Chronology	PIDO	1	56.4	null
PSC	C2	Chronology	PIDO	1	51.9	null
PSC	C3	Chronology	PIDO	1	57.9	null
PSC	C4	Chronology	PIDO	1	56.9	null
PSC	C5	Chronology	PIDO	1	50.3	null
PSC	C6	Chronology	PIDO	1	60.1	null
PSC	S1	Fire Scar	PIDO	1	88.2	28.5
PSC	S2	Fire Scar	PIDO	1	66.5	22.0
PSC	S3	Fire Scar	PIDO	1	43.5	8.5
PSC	S4	Fire Scar	PIDO	1	92.5	23.0
PSC	S5	Fire Scar	PIDO	1	63.4	23.3
PSC	S6	Fire Scar	PIDO	1	72.1	21.0
PSL	C1	Chronology	PIDO	1	114.0	null

Table D.1. cont.

PSL	C2	Chronology	PIDO	1	107.5	Null
PSL	C3	Chronology	PIDO	1	42.6	null
PSL	C4	Chronology	PIDO	1	54.5	null
PSL	C5	Chronology	PIDO	1	54.9	null
PSL	C6	Chronology	PIDO	1	85.0	null
PSL	S1	Fire Scar	PIDO	1	66.0	26.3
PSL	S2	Fire Scar	PIDO	1	83.3	33.3
PSL	S3	Fire Scar	PIDO	1	81.9	20.5
PSL	S4	Fire Scar	PIDO	1	78.1	18.5
PSL	S5	Fire Scar	PIDO	1	82.7	27.7
PSL	S6	Fire Scar	PIHE	1	66.1	29.0
PU2	C1	Chronology	PIDO	1	79.5	null
PU2	C2	Chronology	PIDO	1	66.9	null
PU2	C3	Chronology	PIDO	1	72.0	null
PU2	C4	Chronology	PIDO	1	83.6	null
PU2	C5	Chronology	PIDO	1	86.6	null
PU2	C6	Chronology	PIDO	1	76.0	null
PUA	C1	Chronology	PIDO	1	70.7	null
PUA	C2	Chronology	PIDO	1	65.9	null
PUA	C3	Chronology	PIDO	1	67.6	null
PUA	C4	Chronology	PIDO	1	65.9	null
PUA	C5	Chronology	PIDO	1	60.8	null
PUA	C6	Chronology	PIDO	1	68.0	null
PUA	S1	Fire Scar	PIDO	1	95.5	37.4
PUA	S2	Fire Scar	PIDO	1	83.2	32.5
PUA	S3	Fire Scar	PIDO	1	85.0	21.3
PUA	S4	Fire Scar	PIDO	1	67.8	17.4
PUA	S5	Fire Scar	PIDO	1	86.9	23.4
PUA	S6	Fire Scar	PIDO	1	76.5	24.9
PUT	C1	Chronology	PIDO	1	66.4	23.9
PUT	C2	Chronology	PIDO	1	63.2	26.3
PUT	C3	Chronology	PIDO	1	72.8	null
PUT	C4	Chronology	PIDO	1	76.7	null
PUT	C5	Chronology	PIDO	1	57.8	null
PUT	C6	Chronology	PIDO	1	73.0	null
PUT	S1	Fire Scar	PIDO	1	67.2	22.6
PUT	S2	Fire Scar	PIDO	0	44.0	null
PUT	S3	Fire Scar	PIDO	0	66.7	15.8
PUT	S4	Fire Scar	PIDO	1	61.2	25.5
PUT	S5	Fire Scar	PIDO	1	63.6	24.7
PUT	S6	Fire Scar	PISP	0	70.9	null
TBL	C1	Chronology	PIDO	1	57.0	19.8
TBL	C2	Chronology	PIDO	1	61.3	19.2
TBL	C3	Chronology	PIDO	1	69.3	24.6
TBL	C4	Chronology	PIDO	1	49.5	null
TBL	C5	Chronology	PIDO	1	56.5	null

Table D.1. cont.

TBL	C6	Chronology	PIDO	1	58.4	Null
TBL	S1	Fire Scar	PIDO	1	48.1	19.6
TBL	S2	Fire Scar	PIDO	1	46.4	21.2
TBL	S3	Fire Scar	PIDO	1	50.1	21.7
TBL	S4	Fire Scar	PIDO	1	50.6	19.9
TBL	S5	Fire Scar	PIDO	1	61.3	22.6
TBL	S6	Fire Scar	PIDO	0	65.2	19.9
TEP	C1	Chronology	PIMX	1	55.5	18.4
TEP	C2	Chronology	PIMX	1	63.4	22.5
TEP	C3	Chronology	PIMX	1	49.2	22.1

APPENDIX E

R Code for Statistical Analysis of Tree Ring Width Indices

This analysis was completed in RStudio version 0.95.258 (2007) and R version 2.15.0 (2012) using the dplR package (Bunn, 2008) and the detrendeR package (Compelo, García-González and Nabais, 2011).

```
##Read in raw ring-width file
best <- read.rwl("Best.rwl")
##Plot segments
best.seg.plot <- seg.plot(best, main="Sierra de Manantlán")
##Create table of statistics
best.stats <- rwl.stats(best)
##Create an un-prewhitened and un-detrended chronology
best.crn <- chron(best)
##Plot chronology vs. sample depth
crn.plot(best.crn, col=4)
##Prewhiten with autoregressive model using default settings (this file was then saved to an rwl file using detrendeR in Windows 7 as this plugin is not compatible with RStudio for Mac)##
best.ar <- ar(best)
##Read in the prewhitened rwl file
best.ar <- read.rwl("best.ar.rwl")
##Detrend prewhitened chronology by fitting a smoothing spline of 67% of the length of each series##
```

```
best.ar.spline <- detrend(best.ar, make.plot=F, method='Spline')
##Build a chronology for the spline-detrended series##
best.ar.spline.chron <- chron(best.ar.spline, prefix='SDM')
##Truncate the chronology to have sample depth of at least 5
best.ar.spline.trunc <- subset(best.ar.spline.chron, samp.depth > 4)
##And plot with color and 20-year smoothing spline
crn.plot(best.ar.spline.trunc, add.spline=T, nyrs=20, col=4)
```