Journal of Tropical Ecology (2006) **22**:289–302. Copyright © 2006 Cambridge University Press
doi:10.1017/S0266467406003178 Printed in the United Kingdom

Fire history along environmental gradients in the subtropical pine forests of the Cordillera Central, Dominican Republic

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(*Accepted 27 November 2005*)

Abstract: Fire history was reconstructed from fire-scarred individuals of the endemic pine (*Pinus occidentalis*) along climatic gradients in the Cordillera Central, Dominican Republic. We analysed variation in fire frequency by climate, elevation and aspect (windward and leeward of the central massif). A high correspondence between known fires and fire-scar chronologies indicates that the primary rings of this species are annual. Evidence was found for 41 fire years since 1727 A.D.; 28 were landscape-scale fires, nine of which were exceptionally large and linked to El Niño-triggered droughts. Mean fire return interval (FRI; the mean of individual samples) and mean fire interval (MFI; the composite mean of a group of samples) were used to estimate the upper and lower range in fire frequency. Mean FRI of the entire study area was 31.5 y (± 24.9 y SD) and MFI for landscape-scale fires was 5.6 y (± 4.1 y SD). The fire regime varied significantly with elevation and aspect. Mean FRI was 42.1 y (± 27.6 y SD) and MFI was 9.8 y (± 16.7 y SD) on moister windward zones, and mean FRI was 16.7 y (± 7.8 y SD) and MFI 4.2 y (± 1.9 y SD) in drier leeward zones. On windward slopes, high-elevation mean FRI (26.4 y) was significantly shorter than at middle (44.5 y) and low elevations (58.4 y). On leeward slopes, mean FRI did not vary significantly with elevation. The strong windward elevational patterning of the fire regime is driven by the trade wind inversion which traps moist air below 2000–2300 m. Such elevational patterns may be characteristic of montane fire regimes throughout the tropical trade wind belt.

Key Words cloud forest, dendrochronology, Dominican Republic, El Niño, fire history, fire regimes, fire scars, *Pinus occidentalis*, trade wind inversion, tropical montane forest

INTRODUCTION

Dendrochronological reconstructions of fire history have played a pivotal role in our understanding of fire's critical function in many temperate ecosystems (Agee 1974, Barton 1993, Brown *et al.* 2001, Swetnam & Baisan 1996a, 2003). A similar appreciation of fire's historical importance in tropical ecosystems has lagged despite the common occurrence of natural fires (Cochrane 2003), particularly in tropical montane systems (Smith & Young 1987). Fire history studies in the tropics have been hampered by a lack of long-term fire records and a shortage of tropical tree species suitable for dendrochronology (Speer *et al.* 2004, Worbes 2002). The paucity of long-term tropical fire history studies limits our understanding of fire's role in shaping vegetation structure and composition, and hinders our ability to make fire regime comparisons over broad scales (e.g. links between fires and interregional climate synchronicities such as El Niño; Speer *et al.* 2004). In this light, tree species that form annual rings in fire-prone tropical systems provide a valuable opportunity to improve our understanding of fire's long-term role in tropical ecosystems.

Tropical fire regimes may be distinctive from those in other latitudes given the unique climatic patterns found in the tropics. Subtropical montane mesoclimates, in particular, are strongly shaped by a synoptic subsidence inversion, known as the trade wind inversion (TWI). The TWI traps moist air and clouds on windward slopes below a roughly constant elevation (Orvis *et al.* 1997, Riehl 1954, 1979), above which pronounced decreases in humidity and precipitation occur. Orographic effects on moisture patterns also influence tropical montane fire regimes, as is common in temperate systems (Baisan & Swetnam 1990, Barton 1993, Brown *et al.* 2001, Peet 1981).

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The opportunity to study fire history in the subtropics exists in the Cordillera Central mountains in the Dominican Republic, where fires are common. To date, studies of fire history in this region have been limited to short-term vegetation recovery (Horn *et al.* 2001) and radiocarbon-dated sediments (Horn *et al.* 2000). The latter study provided evidence of frequent fire activity over the last 40 000 y (Horn *et al.* 2000), well before first human settlement of the island (7000 BP at earliest; Wilson 1990). Nevertheless, fundamental aspects of fire regimes in the Dominican highlands – sources of ignition, frequency, extent and severity – are unknown. Fortunately, a species with dendrochronological potential has recently been identified, the endemic West Indian pine (*Pinus occidentalis* Swartz) (Speer *et al.* 2004). This species is widespread in fire-prone areas and numerous individuals display multiple fire scars. Stand structure and evidence of fire damage in the Cordillera Central point to a mixed fire regime of moderately frequent surface fires punctuated with patchy fires intense enough to kill mature trees (Martin 2005, Myers *et al*. 2004).

Our objectives were: (1) to provide further verification of the suitability of *P. occidentalis* for dendrochronological studies, (2) to quantify the fire regime of the highland pine forests of the Cordillera Central and (3) to determine how the fire regime varies across mesoclimatic gradients. Given the likely sharp drop in moisture above the TWI and in the leeward rain-shadow, we expected a marked increase in fire frequency with elevation and leeward aspect. Below the TWI, we expected fire frequency to be constant with increasing elevation on windward slopes. We expected that less frequent, but more intense fires would predominate in transitional areas along the TWI boundary where fuel loads should be higher.

METHODS

Study area and study species

The Cordillera Central mountain range is located in the interior of the Dominican Republic (Figure 1). Two national parks, Armando Bermúdez (766 km^2) and José del Carmen Ramírez (679 km^2), form a continuous protected area of virgin forest in this region. This area ranges from 1100–3087 m in elevation, which includes the highest point in the Caribbean basin, Pico Duarte. The majority of our study area is dominated by monospecific stands of *P. occidentalis*, with mixed pine-cloud forest and pure cloud forest stands limited to the north-eastern, windward one-third of the study area (Sherman *et al.* 2005). *Pinus occidentalis* is endemic to Hispaniola, found from 200–3100 m in elevation (Darrow & Zanoni 1990). It is a moderately fast-growing tree, typically reaching 30–40 m in height and attaining diameters at breast height of 100–120 cm. *Pinus occidentalis* does not have serotinous cones, but its thick bark and self-pruning habit provide protection from surface fires (Darrow & Zanoni 1990).

Archaeological evidence indicates that Amerindians rarely visited the region in the pre-Columbian era (Bolay 1997), and Dominicans did not begin to use the highlands for timber or grazing until the early 20th century (Bolay 1997, Kustudia 1998). Permanent settlements near our study area were established in the same period. In response to rapid deforestation of the lower areas of the Cordillera Central, most of the remaining unlogged forest above ~1000 m was put under conservation protection in 1923 (Dirección Nacional de Parques 1997). To further protect the region, the Dominican Forest Service began aggressively enforcing a policy of fire suppression – including the outlawing of igniting fires – when it was placed under the aegis of the Dominican military in 1967 (Kustudia 1998). The principal effect of this policy has been to change attitudes in rural communities about the desirability of starting fires in the parks (Schelhas *et al.* 2002). Fire-fighting focuses on containing large fires, as days are still required for fire-fighting crews to reach remote fires (pers. obs.). The creation of the national parks in the mid-1950s was probably the most important event in reducing anthropogenic sources of ignition in the study area, as the small settlements that existed inside the present park boundaries were gone by the early 1960s. Riparian areas at the park's eastern boundary provide an effective buffer to fires entering the study area's interior, as fires rarely enter these riparian forests (Martin *et al.* 2004).

Climate and fire ignition

The Cordillera Central has a marked wet-dry elevation gradient common to subtropical montane systems. The orographic influence of the central massif, whose elevation exceeds 3000 m, creates a windward-leeward PPT gradient, and the TWI augments this pattern by trapping most moisture on windward slopes. The base of the TWI is frequently observed between 2000–2300 m in the Caribbean (Schubert *et al.* 1995). Precipitation (PPT) throughout the central Dominican Republic is seasonal, with a dry season in January–March, and two rainfall peaks, in May and August–September (Horst 1992). The higher elevations of the Cordillera Central are unique in the Caribbean in experiencing regular below freezing temperatures (Pedersen 1953). However, detailed climate records in the study area are lacking. We measured selected climatic parameters across the study area to compare with the spatial pattern of fire frequency and to seek evidence of any distinct seasonality. Temperature and moisture were sampled at a series of stations distributed along the elevation gradient (Figure 1). PPT

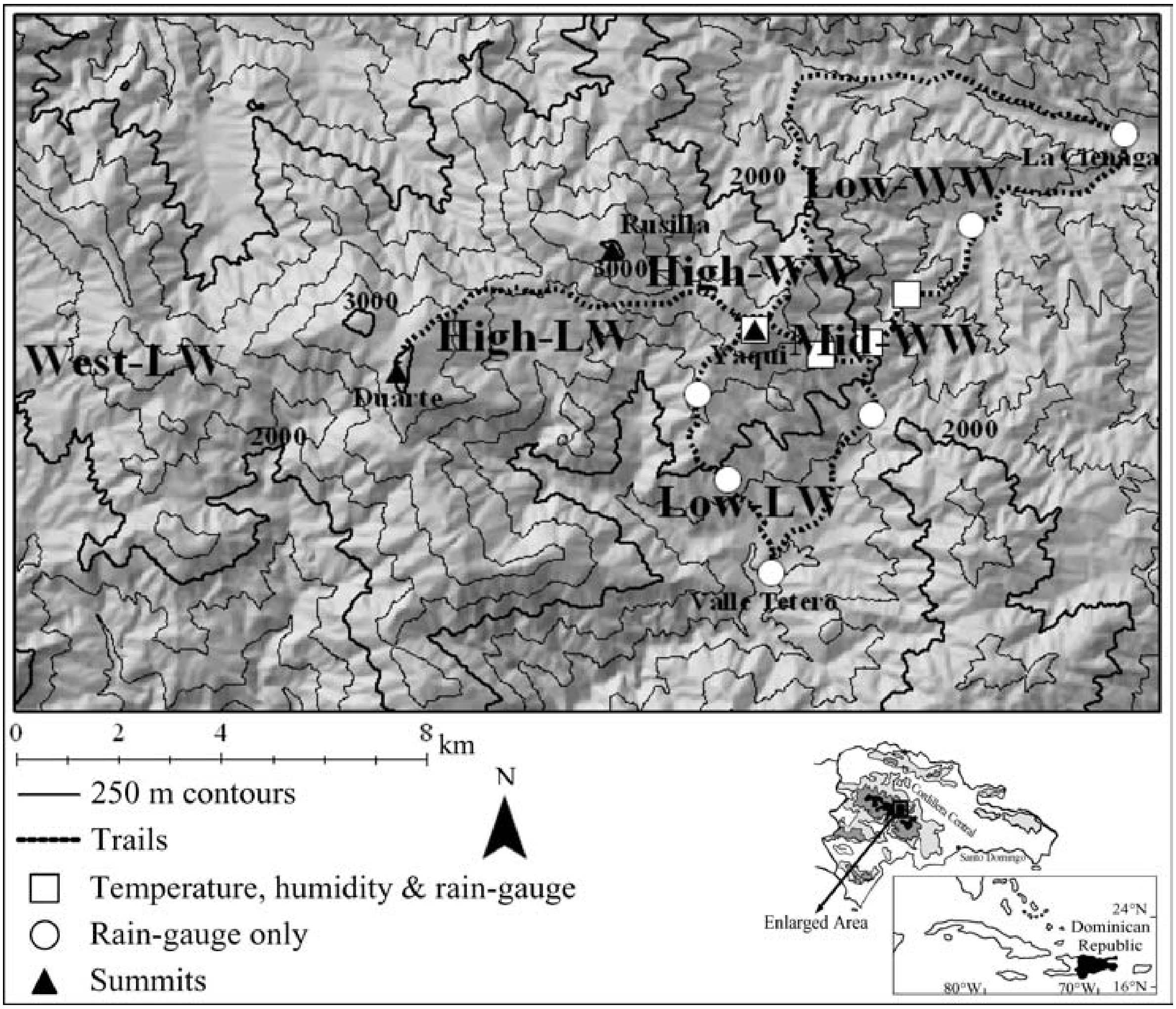

Figure 1. Map of sampling zones and climate stations in the National Parks Armando Bermúdez and José del Carmen Ramírez, Cordillera Central, Dominican Republic. Sampling zones were partitioned by elevation and aspect. Zones are abbreviated: Low, Mid and High correspond to elevation ranges; WW indicates windward; LW indicates leeward.

was measured over a 3-y period (1999–2001) at seven locations using recording rain gauges (Rainew Tipping Bucket Rain Gauge, RainWise Inc., Bar Harbor, ME, USA) positioned in openings $\geq$ 30 m in radius. Rain gauges had to be located near enough to the park entrance to allow bi-weekly servicing; hence, we lack climate data for the western end of the study area. Air temperature and relative humidity were measured every 30 min 1 m above the ground at four stations for 2 y (June 2001–May 2003) using HOBO H8 Pro RH/Temperature data loggers (Onset Computer Corp., Bourne, MA, USA). Estimates of cloud-base elevation on the windward, north-eastern slopes of the massif were made twice a day (10h00 and 16h00) over a 1.5-y period (April 1999–September 2000) by visual reconnaissance from a viewpoint at the park entrance.

We used monthly PPT records from La Vega, Constanza, and San Juan meteorological stations to examine correlations between patterns in PPT (annual PPT, dry season PPT, wet season PPT) and El Niño intensity, the warm phase of the El Niño–Southern Oscillation. These rainfall records span 1931–1989 and 1994–present. The La Vega, Constanza, and San Juan stations are at 100 m, 1160 m and 415 m in elevation, respectively, and form a windward and leeward transect spanning the Cordillera Central. We also used the Constanza records to examine connections between PPT patterns and the fire regime, including indicators of fire extent (defined below), as this station is within ~20 km of our study area.

Ignition sources for fires in the region include lightning strikes and human activities (Bolay 1997, Darrow & Zanoni 1990). Anecdotal reports indicate that most fires occur towards the end of the dry season, in late February and early March. The former director of fire fighting in the Dominican Forest Service attributes most fire ignitions in recent decades to human activities, especially hunting (D. Fernandez, pers. comm.). Unfortunately, no regular records of fires in the region were kept until the last 15–20 y. Fires, however, were documented in 1965, 1975, 1983 and 1997 within our study area (Dirección General Forestal 2002, Dirección Nacional de Parques 1997). In particular, 1965 was noted as a severe fire year, as damaging fires were set to protest against a new logging ban in the region and as a part of a general rebellion against the new government (Dirección Nacional de Parques 1997, Kustudia 1998).

Growth periodicity in *Pinus occidentalis*

When using a subtropical species for dendrochronology, the reliability of the annual resolution in basal increment growth (i.e. tree rings) must be established. Dendrometer evidence suggested that above 1200 m in elevation, radial growth ceases completely in *P. occidentalis* from January–March (FAO 1973). Recent research has found that the primary rings of this species are annual at high elevations; temperature lows in January and February and the coincident dry season may cause regular annual dormancy in radial growth in this species (Speer *et al.* 2004). Nevertheless, further confirmation was necessary to demonstrate reliable annual ring formation in our study area. We also sought a 'known' date as a clear calibration of cell structure between primary and secondary rings as this species is reported to form both primary rings and false intra-annual rings (Speer *et al.* 2004). To accomplish this, we sampled 18 fire-scarred pines in two locations which experienced fires with known dates, 1975 and 1997 (Dirección Nacional de Parques 1997). These two sites are in the western portion of our study area and are both over 2100 m in elevation. We also looked for a correspondence between fire-scar chronologies and known fire dates for the entire study area.

Site selection and dendrochronology

Samples were collected in a $\sim$20-km^2 area from fire-scarred individuals of *P. occidentalis* on both windward (wet) and leeward (dry) sides of the central massif (hereafter, termed aspect). This approach was used to enable sampling across a wide range of conditions, including variation in PPT and temperature, and because access was largely limited to areas near established trails due to the extreme terrain. Sampling was stratified by elevation every 100 m along the trails (Figure 1). We collected samples from trees with a maximum number of fire scars in that elevational interval to maximize the length of the fire chronology. While it is a standard practice in fire history studies, targeting trees with multiple fire-scars can overestimate fire frequency (Baker & Ehle 2001). In this study, however, bias should be small given our fine-scale sampling design unless very small fires were common.

We designated six zones partitioned by aspect and elevation (Table 1; Figure 1). On the windward slopes (WW), zones were partitioned by three elevation zones (low, mid, high): (1) Low-WW, below the expected influence of the TWI (< 2000 m; Orvis *et al.* 1997, Sherman *et al.* 2005); (2) High-WW, where we observed a marked decline in humidity (> 2400 m, see below); and (3) Mid-WW, an intermediate zone (2000–2400 m). On leeward (LW) slopes, Low-LW and High-LW were

Table 1. Measures of historical fire frequency in the pine forests of the Cordillera Central, Dominican Republic. Zones (windward and leeward) were designated in respect to the central massif whose orographic influences result in a marked precipitation gradient. Landscape-scale fires occurred in two or more zones in the same year.

Site	Elevation (m)	Size (ha)	Trees[1]	Period of analysis	Fire intervals (y)	MFI ± SD (y)	Mean FRI ± SE (y)	WMPI[2] (y)	5%–95% probability interval[3]	Range of intervals (y)	Fire freq.[4]
All zones											
Landscape-scale Fires	1530–3050	2050	72	1846–2002	29	5.6 ± 4.1	–	4.6	0.9–11.9	1–17	0.186
Windward zones											
Low	1530–2000	500	15	1834–2002	10	18.7 ± 19.2	58.4 ± 9.4	12.1	0.9–53.7	2–59	0.054
Mid	2000–2400	200	10	1771–2002	15	16.5 ± 20.2	44.5 ± 5.4	10.9	0.9–45.4	2–85	0.061
High	2400–3000	300	17	1727–2002	27	10.5 ± 17.0	26.4 ± 2.5	6.8	0.4–31.2	2–92	0.095
Leeward zones											
Low	1530–2200	250	5	1876–2002	15	9.0 ± 9.5	17.9 ± 0.9	7.3	0.9–24.1	3–38	0.111
High	2280–3050	600	13	1846–2002	29	5.4 ± 3.7	18.9 ± 2.4	4.9	0.9–11.9	1–17	0.186
West	1900–2100	200	12	1856–2002	22	6.6 ± 5.8	13.8 ± 2.2	5.8	0.9–16.2	2–29	0.151

[1] Number of individual samples in each fire chronology.
[2] Weibull median (50% exceedance) probability interval.
[3] Weibull 5% and 95% exceedance probability interval in years.
[4] Fires y $^{-1}$.

delineated at 2200 m where a marked change in topography occurs, and samples from the western end of the study area were grouped as West-LW. In each zone, fire chronologies were based on a minimum of five trees. Zone areas were similar, except for Low-WW and High-LW, which were about twice as large as the other zones (Table 1).

To facilitate dating, only living pines were sampled as these have a known 'bark' date. All samples were partial or full cross-sections cut from the face of the fire scar. A series of progressively finer abrasive belts (up to ANSI 400-grit) were used to prepare the surface so that cell structure was clearly visible. A dissecting microscope (× 7–30 variable power) was used to examine the samples.

As did Speer *et al.* (2004), we approached dendrochronology as if in a temperate location, and classified rings as primary or secondary based on our calibration of ring structure from known fire dates. In a subtropical site, however, this process involves some subjectivity since some primary rings may be diffuse rather than 'sincere' (i.e. having a sharp boundary that indicates complete shutdown), which makes them less distinguishable from false rings. Such diffuse primary rings were noted separately in the chronology. We also relied on individual-tree fire return intervals (FRI) (described below) for most comparisons, as FRI is much less sensitive to dating errors than a mean fire interval (MFI) compiled from a group of trees.

Measures of fire frequency

We used two measures to describe fire frequency. First, MFI was calculated for each zone as the average number of years between fire dates during each period of analysis. MFI has been widely used to describe fire frequency in fire history studies (Baisan & Swetnam 1990, Bekker & Taylor 2001, Brown *et al.* 2001, Romme 1980). MFI and FRI were calculated with the pith date when available (59% of samples) as a more conservative measure of fire frequency (Baker & Ehle 2001). Weibull median probability intervals (WMPI; Grissino-Mayer 1999) were also calculated as the fire associated with the 50% exceedance probability of a modelled two-parameter Weibull distribution of fire intervals. Variability with the Weibull model is described by the 5% and 95% exceedance intervals. WMPI is considered to be a better estimator of central tendency in fire interval data because of potential skew in interval distributions (Grissino-Mayer 1999). Only landscape-scale fires (a fire recorded in more than one zone in the same year; Baisan & Swetnam 1990) were used when calculating the MFI for the entire study area. Despite limitations (e.g. multiple fires could burn in the same year), this is a useful metric of the conditions which promote a widespread fire or fires in the same year. Second, we compared FRI of individual trees to obtain smaller-scale estimates of fire patterns. FRI was calculated on an individual tree basis and included all fires recorded by that tree (Romme 1980), and thus, is a point estimate of fire frequency.

We adopted a number of recent suggestions for minimizing bias in estimating parameters of the fire regime. As recent studies have outlined (Baker & Ehle 2001, Reed & Johnson 2004), MFI can result in a biased overestimate of fire frequency, particularly when comparing between study areas of different sizes (MFI typically declines with increasing sample size) or between time periods (sample sizes of older fires are usually smaller). To address this bias, we calculated mean FRIs, also called mean-individual tree fire intervals (Baker & Ehle 2001). Mean FRI reduces bias, as it is not sensitive to scale, sample size or small fires. However, mean FRI can substantially underestimate fire frequency; thus we used MFI to estimate the lower end of fire return intervals. If no fires went unrecorded by sample trees, mean FRI is equal to actual zone-scale fire frequency; if unrecorded fires were common, then MFI may be a better estimate (Baker & Ehle 2001). In this study, MFI signifies the frequency with which fire returns to any part of a given zone; it is not an estimate of a zone's fire rotation. Landscape-scale fires, however, do not have a scale bias as all samples and areas are compiled together, though it may still overestimate fire frequency.

To explore the influence of human activities on fire frequency, mean FRI was calculated for periods of analysis corresponding to major shifts in human activity: (1) pre-1900, when human settlement in the region was light; (2) 1900–1965, when local settlements became permanent; and (3) post-1965, when the park was placed under active protection and fire suppression policies were implemented (Dirección Nacional de Parques 1997). To minimize bias (Baker & Ehle 2001), only samples which spanned all three periods of analysis were used to calculate fire frequency.

Differences in mean FRI were assessed using one-way analysis of variance (ANOVA) and linear regression with JMP software (SAS Institute Inc., Cary, NC, USA). All post-hoc comparisons were made with Tukey–Kramer HSD.

RESULTS

Climate, precipitation patterns and El Niño

Climate varied markedly across the study area. Windward annual PPT remained fairly uniform with elevation, but declined sharply on leeward slopes (Figure 2a). Across the entire 8-km transect, PPT dropped by ~35% from the north-east to the south-west; from atop the central massif, it dropped by 26% in only 3 km. PPT is reported to be even

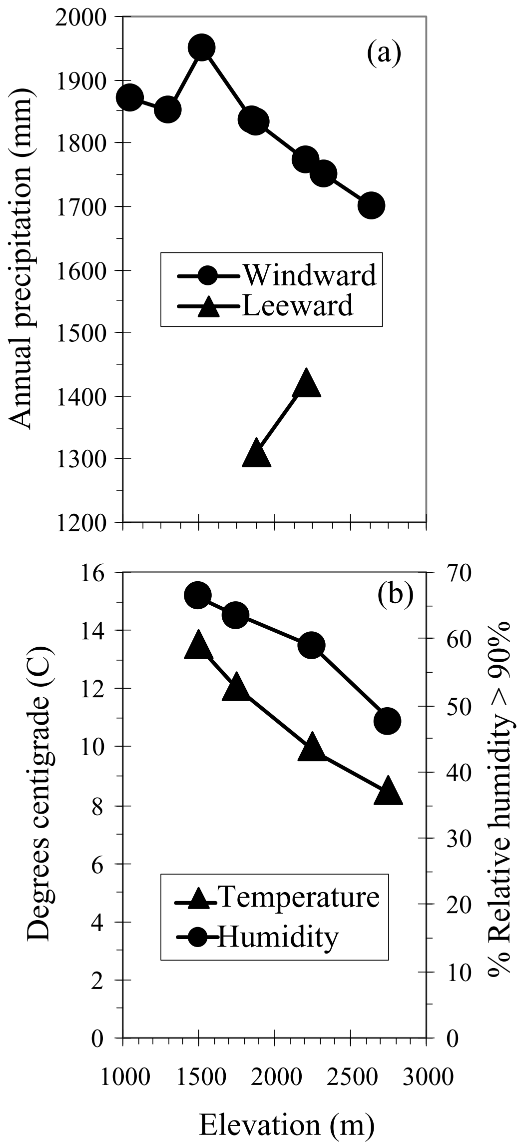

Figure 2. Climate data collected along an elevational gradient in the Cordillera Central, Dominican Republic. (a) Annual precipitation on the windward and leeward slopes; and (b) mean annual night temperature and high relative humidity on windward slopes (percentage of measurements ≥ 90% relative humidity).

lower in the western portion of the study area (Dirección Nacional de Parques 1997). Annual PPT distribution was bimodal with a marked 3-mo dry season from January–March when monthly rainfall averaged 80 mm on the windward slopes and 31 mm on leeward slopes.

Relative humidity (RH) declined gradually on the windward slopes from 1500–2300 m and then more abruptly above 2300 m (Figure 2b). On windward slopes below 2300 m, relative humidity rarely dropped below 65%, a threshold considered critical for the ignition of sustained fires (Uhl *et al.* 1988). The elevation of the

Table 2. Per cent decrease from mean dry-season rainfall (January–March) during El Niño episodes from 1931–2000 in the Cordillera Central, Dominican Republic. In this period, there were 19 El Niño episodes – three were categorized as very strong, seven as strong, four as moderate plus, and five as moderate. El Niño categories follow Quinn *et al.* (1987). Rainfall data are from meteorological stations in La Vega (100 m), Constanza (1160 m) and San Juan (415 m), which respectively form a windward and leeward transect spanning the Cordillera Central. WW indicates windward; LW indicates leeward. Positive values are shown in bold face.

	Dry-season PPT during El Niño years		
El Niño Category	La Vega (WW)	Constanza (WW)	San Juan (LW)
Very strong	−36	−52	−28
Strong	−18	−35	−53
Moderate plus	−19	−40	**9**
Moderate	**8**	−52	−10
Overall mean	−16	−43	−27

cloud base, which developed most afternoons, showed a substantial peak in frequency (53%) between 1800 m and 2300 m in elevation, dropping off sharply at higher elevations (18%). Combined with RH, these data indicate that the cloud zone generally formed between 1800–2300 m.

We witnessed repeated ground-frosts, lows of 0 °C were recorded frequently, and mean temperatures in December into March were low enough to cause dormancy in basal growth (Jacoby 1989). These data depict a marked cold season at elevations as low as 1500 m, coincident with the lowest PPT and RH of the year.

El Niño years were coincident with a marked drop in dry-season PPT throughout the Cordillera Central (Table 2). On average, dry-season PPT was lower in all 'very strong' El Niño years and in 80% of all El Niño years combined (El Niño categories follow Quinn *et al.* 1987). From 1931–2003, the four worst dry-season droughts on record occurred in El Niño years. Overall, dry-season PPT decreased significantly (Linear regressions) with increased El Niño intensity (viz. Nino3 index, Mann *et al.* 2000) in Constanza ($F_{1,49} = 10.3$, $P < 0.007$, $R^2 = 0.18$) and La Vega ($F_{1,48} = 7.95$, $P < 0.007$, $R^2 = 0.15$), but not San Juan ($F_{1,45} = 1.3$, $P < 0.26$, $R^2 = 0.029$).

Annual growth periodicity

Evidence of annual growth periodicity was strong. Of the 26 fire-scarred cross-sections collected from stands known to have burned in 1975 and 1997, 25 showed annual rings while the 26th sample had one false ring. By itself, this cannot be taken a priori as evidence of annual periodicity in a subtropical location (Speer *et al.* 2004). However, the excellent correspondence of recent fire years in the Cordillera Central (1965, 1975, 1983, 1990, 1993 and 1997; Dirección General Forestal 2002) with the fire-scar dates in our chronologies (Figure 3) substantially

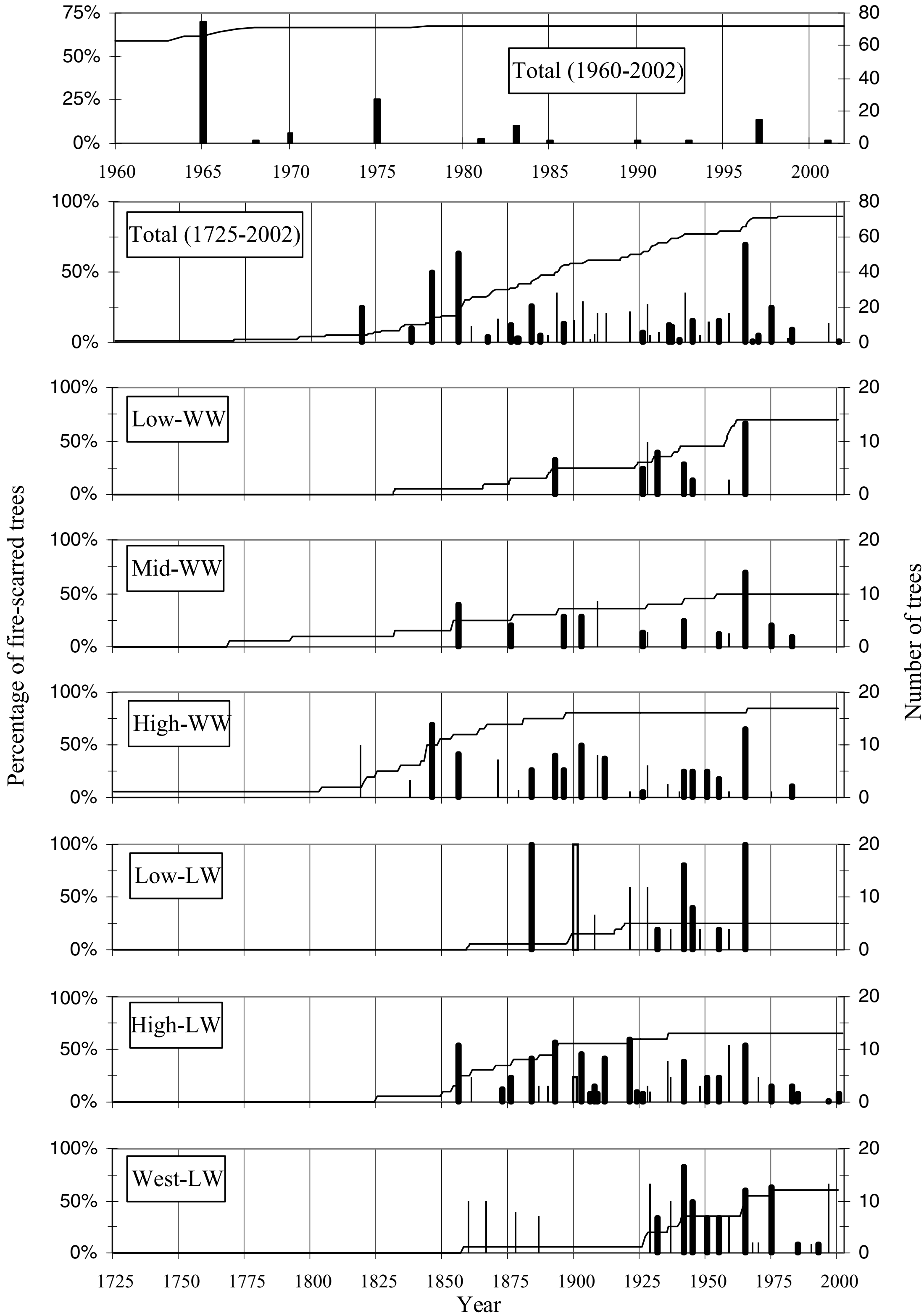

Figure 3. Fire chronologies in zones of *Pinus occidentalis* forest in the Cordillera Central, Dominican Republic. Lines are cumulative number of trees in the chronology by year. Histograms are percentages of fire-scarred trees for a fire year relative to the number of trees in the chronology that year. The number of sampled trees is lowest at the start of each chronology, as older fire-scarred pines are less common. Total (1960–2002) is an enlargement of Total (1725–2002), which is a composite of all fires from all zones. Dominican Park and Forest Service records documented fires in the study area in 1965, 1975, 1983, 1990, 1993 and 1997. For each zone: Low, Mid and High correspond to elevation ranges; WW indicates windward; LW indicates leeward.

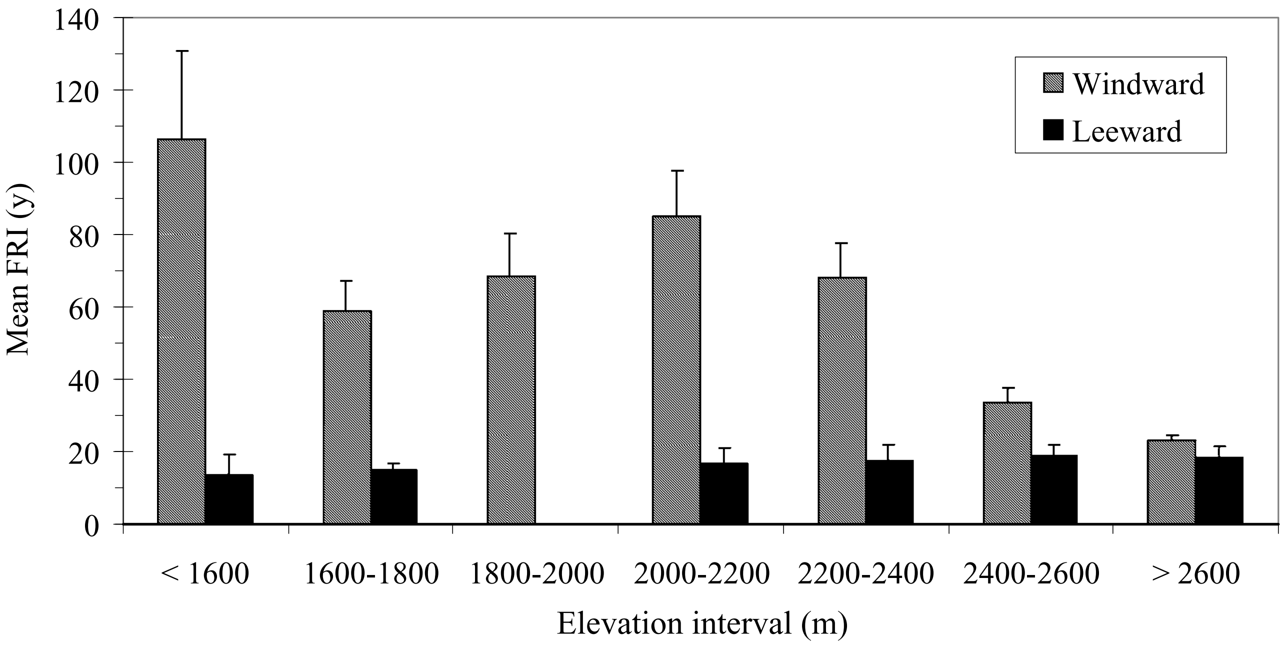

Figure 4. Fire return intervals (FRI) averaged by 200-m elevation intervals and aspect in the Cordillera Central, Dominican Republic. FRIs are individual tree (point) estimates of fire frequency. Bars are one SE. There is no FRI for leeward areas 1800–2000 m, as this elevation interval was not sampled.

increased our confidence in the annual periodicity of ring growth. Moreover, the strong internal consistency of fire scar patterns within stands (i.e. fire scars on different trees within a stand usually dated to the same year) also provided strong evidence that a large majority of our samples had annual rings, even in lower elevation areas. The widespread fire year in 1965 facilitated dating fire scars as it occurred in all zones (see below), and as no notable fires have occurred since in the lower elevation zones, Low-WW and Low-LW (Dirección Nacional de Parques 1997).

Cross-sections that could not be reliably dated, usually with an excess of diffuse secondary rings and pinched rings, were discarded, representing 8% of the samples. In general, most cross-sections (76%) were sampled from elevations above 2000 m. A diffuse secondary ring was the portion of an increment where dark late wood becomes light again before the formation of a primary ring. The use of full or partial cross-sections was critical in this regard: when present, diffuse secondary rings were generally localized to a small portion of the ring, making the correct interpretation of rings straightforward when examining cross-sections. Diffuse rings were common in some samples, but using cross-sections and calibrations from 'known' ring ages, we felt confident in distinguishing between primary and false rings. Likewise, pinched rings were highly localized in most cross-sections. Based on these findings, the use of cross-sections rather than increment cores is essential for a reliable dendrochronological reconstruction of *P. occidentalis*, especially for samples from below 2000 m. Overall, these results indicate that in cross-section, individual trees can provide reliable annual growth rings from 1530 m to 3100 m elevation.

Fire history and regime

We counted 339 individual fire scars representing 41 separate fire years. Individual trees had as many as 13 fire scars (median = 4). Fire chronologies for the entire study area and the six zones are shown in Figure 3. For the entire study area, fire frequency was between 9.8 y ($\pm$ 24.6 y SD) to 31.5 y ($\pm$ 24.9 y SD). This range is bracketed on the lower end by the MFI of landscape-scale fires (a fire recorded in $\geq$ two zones) and on the upper end by the mean FRI of all samples. Landscape-scale MFI shortens to 5.6 y ($\pm$ 4.1 y SD) when the period of analysis is set to coincide with the beginning of most chronologies (1846–2002).

Fire frequency had strong spatial patterns (Figure 4). Mean FRI declined significantly (ANOVA, $F_{1,71} = 24.0$, $P < 0.000$) along the path of the trade winds (NE to SW): when pooled by aspect, mean FRI was 42.1 y ($\pm$ 4.3 y SE) on windward slopes and 16.7 y ($\pm$ 1.4 y SE) on leeward slopes. Mean FRI also varied significantly between zones (ANOVA, $F_{5,71} = 10.6$, $P < 0.000$). Mean FRI was significantly longer in Low-WW (58.4 y) and

Mid-WW (44.5 y) than in the other zones (Table 1), the rest of which were statistically equivalent. At finer scales (point FRI), elevation was a significant predictor of increasing fire frequency on windward slopes (Linear regression, $F_{1,41} = 18.9$, $P < 0.000$, $R^2 = 0.40$) and showed little pattern on leeward slopes (Linear regression, $F_{1,29} = 0.73$, $P = 0.646$, $R^2 = 0.01$). When averaged by 200-m elevation intervals, mean FRI on windward slopes was steady at 60–70 y from 1600–2000 m but increased to 90 y from 2000–2200 m (Figure 4). This interval is within the zone of maximum cloudiness. Above this interval, FRI dropped markedly on windward slopes to 34 y between 2400–2600 m and 24 y above 2600 m. With the exception of the > 2600 m interval, mean FRI by 200-m intervals was significantly longer in windward intervals than in the leeward interval of the same elevation.

Spatial patterns in fire frequency held for comparisons of MFIs. MFI was 9.8 y (± 16.8 y SD) on all windward slopes and 4.2 y (± 1.9 y SD) on all leeward slopes. Windward and leeward slopes were comparable in area (1000 vs. 1050 ha) and sample size (42 vs. 30); hence, these comparisons are reasonable. Moreover, the relative change in MFI between zones paralleled mean FRI. Still, the large disparity between MFI and mean FRI indicate that fires which only burned part of a zone were common, particularly in leeward areas. In leeward zones, MFIs were a good estimate of fire frequency as they were similar to WMPIs. In windward zones, however, MFIs were longer than WMPIs as the larger range in fire intervals resulted in skewed MFI estimates of the central tendency (Table 1).

Large fires were less common. We defined large fires as those recorded in ≥ 50% of zones and scarring ≥ 30% of all fire-scar-susceptible trees. A fire-scar-susceptible tree has been previously scarred by at least one fire (Romme 1980). This method may indicate a large fire or a large fire year, as multiple fires may burn within and between zones in a single year. By these criteria, large fires occurred in 1856, 1884, 1893, 1903, 1912, 1921, 1928, 1942 and 1965. Hence, large fires exhibited a MFI of 17.3 y from 1846–2002 and a range of 7–28 y. Only three fires – 1942, 1959 (which did not qualify as large because of insufficient evidence of scarring) and 1965 – occurred in all zones in the same year.

Fire incidence and extent were most strongly connected to the intensity of dry-season droughts. On average, dry-season PPT in Constanza (1931–2003) was 50% lower in fire years than non-fire years (t-test, $F_{1,70} = 7.69$, $P < 0.007$), and the intensity of dry-season droughts was a significant predictor of per cent zones burned (Linear regression, $F_{1,19} = 5.25$, $P < 0.035$, $R^2 = 0.236$). Given the link between El Niño and dry-season PPT (see above), it is not surprising that many large fires were synchronized with El Niño events, as compiled by Quinn *et al.* (1987). Six of nine large fires were synchronized with very strong El Niño events. Of recent fires, the 1965 fire was timed with a moderate El Niño, and the 1983 and 1997 fires were coincident with very strong El Niños. Overall from 1856–1980, there was significant relationship (Linear regressions) between the Nino3 index (Mann *et al.* 2000) and per cent zones burned ($F_{1,25} = 8.42$, $P < 0.008$, $R^2 = 0.252$) and per cent trees scarred ($F_{1,25} = 4.95$, $P < 0.03$, $R^2 = 0.127$).

Fire and settlement history

Notable changes in fire frequency were timed with human activities (Figure 5). As noted above, only samples whose chronology spanned all three periods of analysis were used in these comparisons to minimize bias. Within windward slopes, mean FRI varied significantly by time period (ANOVA, $F_{2,73} = 3.4$, $P < 0.038$): 1900–1965 (24.1 y) was significantly shorter than pre-1900 (37.3 y) and post-1965 (31.9 y). Within leeward slopes, mean FRI also varied significantly by time period (ANOVA, $F_{2,36} = 8.17$, $P < 0.0013$): 1900–1965 (14.9 y) and pre-1900 (19.3 y) were significantly shorter than post-1965 (26.9 y). Only the 1900–1965 period was significantly different (ANOVA, $F_{1,37} = 7.17$, $P < 0.011$) when comparing between aspects, as mean FRI was significantly shorter on leeward slopes (14.9 y) than windward slopes (24.1 y) in this period.

Smaller-scale patterns (within zones) showed similar patterns. To reduce potential bias, we only used the high-elevation zones for zone-scale ANOVA analysis as the other zones had much smaller sample sizes (n ≤ 6). Within High-WW ($F_{2,44} = 4.96$, $P < 0.014$), mean FRI from 1900–1965 (19.9 y) was significantly shorter than pre-1900 (29.2 y) and post–1965 (33.6 y). Within High-LW ($F_{2,26} = 3.76$, $P < 0.037$), mean FRI from 1900–1965 (15.4 y) was significantly shorter than post-1965 (26.1 y), while pre-1900 (19.1 y) was not significantly different from either period.

Overall, this period of higher fire frequency from 1900–1965 culminated with a major fire in 1965. This fire was recorded in 70% of all cross-sections, including portions of Low-WW (as low as 1530 m). Extreme post-fire suppression of radial growth in most cross-sections fire-scarred in 1965 also suggests that this fire was very intense.

DISCUSSION

Landscape-scale fire regimes are set foremost by meso-climate, particularly moisture patterns. The Cordillera Central is no exception, as orographic effects and the elevation of the trade wind inversion (TWI) produce steep

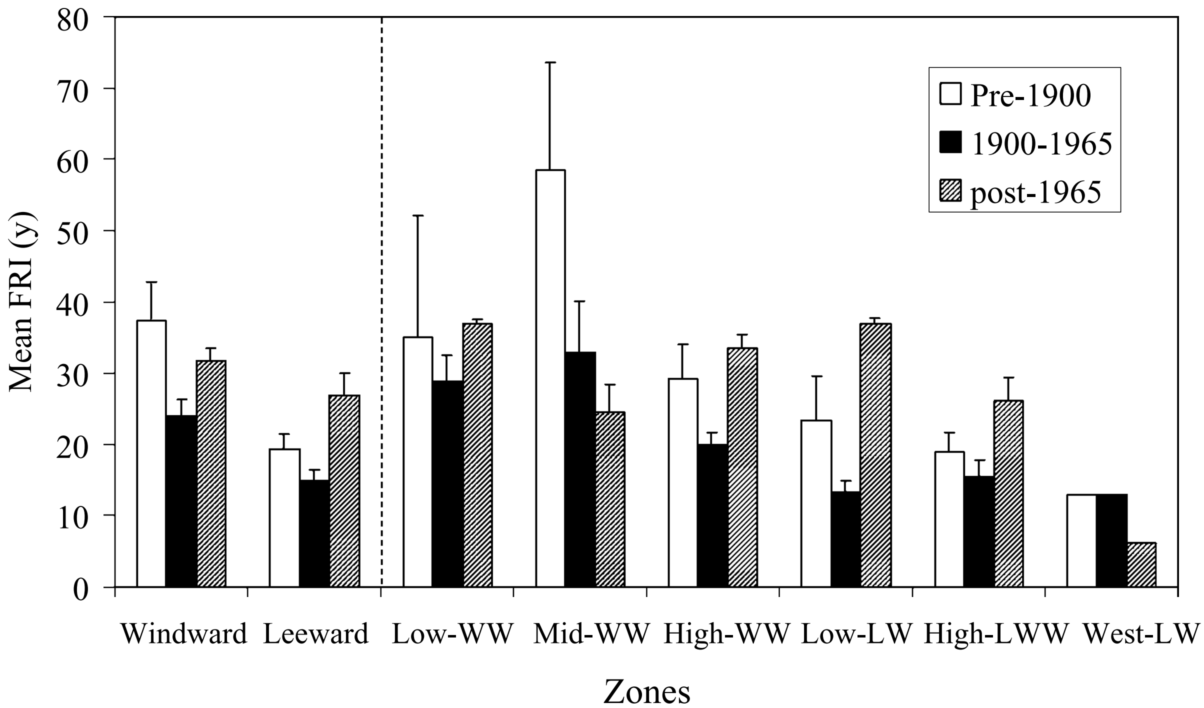

Figure 5. Mean fire return intervals (FRI) for zones by period in the Cordillera Central, Dominican Republic. Periods correspond to human activities in the region: pre-settlement (pre-1900), settlement (1900–1965), and fire suppression (post-1965). Zones are abbreviated: Low, Mid and High correspond to elevation ranges; WW indicates windward; LW indicates leeward. Only samples which covered the entire period of analysis (from 2002 to 1850 or earlier) were used in this analysis. Bars are one SE (West-LW has no SE as n = 1).

gradients in rainfall and cloud-formation patterns, which in turn, drive pronounced spatial patterning in the fire regime. Indeed, fire frequency increased markedly from lower to higher elevations on windward slopes and from windward to leeward slopes overall. The abrupt shift in fire frequency around the elevation of the TWI is especially striking. This sharp spatial patterning differs from many temperate montane fire regimes where meso-scale variation in fire frequency can be modest and where fire frequency typically decreases with elevation (Agee 1993, Bekker & Taylor 2001, Brown *et al.* 2001, McCune & Allen 1985, Swetnam *et al.* 2001). The influence of the TWI on fire regimes is presumably not limited to the Dominican Republic, given its occurrence on oceanic and coastal mountains throughout the tropics (Stadtmüller 1987). Sharp discontinuities in tropical montane vegetation patterns in other areas influenced by the TWI indicate that humid-dry interfaces on windward slopes may be common, particularly in the subtropics (Davis *et al.* 1997, Kitayama & Mueller-Dombois 1994, Rzedowski 1978, Young 1995).

As in Speer *et al.* (2004), our results indicate that *P. occidentalis* has annual primary rings in the high-elevation regions of the Cordillera Central, and we concur that a yearly cold and coincident dry-season in the mountains most likely drives the reliable annual growth periodicity in this species. Based on analysis of increment cores, Speer *et al.* (2004) advised that primary rings would be most reliably found above 2000 m. We determined using cross-sections that a considerable percentage of samples can be reliably dated over a wider range in elevation. Nevertheless, strict interpretations of the fire regime based on reconstructions from this species must be made with care, as dating individual samples can be problematic even at elevations above 2000 m. In this regard, the use of fire frequency metrics that are less sensitive to minor errors in dating is advisable (e.g. mean FRI). Further efforts to lengthen and augment the resolution of chronologies constructed from this species are warranted.

The synchrony of many fires across the study area was somewhat surprising, given the steep gradient in moisture and the rugged topography. Severe droughts, often linked to El Niño episodes, may override these factors. Although not well studied in the Caribbean, El Niño episodes generally result in atypically dry weather in the region (Ropelewski & Halpert 1987). The very strong El Niño events of 1983 and 1997 created conditions for widespread fires which burned throughout the broader region (Horn *et al.* 2001). More recently, in March 2005 a severe fire burned large areas of the two parks coincident with the El Niño event of 2004–2005. Beyond the Caribbean, El Niño events have been linked to increase fire occurrence in temperate regions (Swetnam & Baisan 1996a, b; Swetnam & Betancourt 1990, 1998; Swetnam *et al.* 2001, Veblen & Kitzberger 2002), and to a lesser degree, in tropical ones (South-East Asia, Goldammer & Price 1998). Overall, the well-established connection between El Niño events and droughts in many subtropical montane forests (e.g. Hawaii, Chu 1989; Sabah, Kitayama 1995; Sri Lanka, Werner 1998) suggests that the pattern in this study may be widespread.

The marked spatial partitioning in fire frequency had a strong influence on vegetation patterns, most notably associated with a discrete vegetation boundary at 2250 m on windward slopes: species-rich cloud forest gives way to monospecific pine forests above this elevation (Sherman *et al.* 2005). Simultaneously, this contrasting vegetation boundary could reinforce spatial patterns by influencing fire likelihood. Pine stands are relatively likely to carry a fire (Horn *et al.* 2001), while the structure of the cloud forest and its abundant epiphytes probably reduce fire likelihood (Martin 2005). Epiphytic plants are well known to 'strip' substantial quantities of moisture from clouds even during the dry season (Bruijnzeel & Proctor 1995), substantially decreasing fire likelihood, particularly along this boundary where cloud occurrence and humidity are highest (Figure 2b). Likewise, in other tropical areas contrasting vegetation composition has been shown to reinforce spatial patterning in fire regimes by altering fuels and microclimates (Biddulph & Kellman 1998, Kalisz & Stone 1984, Kellman & Meave 1997).

Fire frequency increased with the onset of permanent human settlement in the region *c.* 1900 (Figure 5), though our relatively brief fire history record tempers this interpretation. Once settled, human sources of ignition undoubtedly increased, especially when incipient settlements were still within the park's eventual boundaries. Today, human sources of ignition are reported to be largely accidental in the Cordillera Central, started by hunters and tourists (D. Fernandez, pers. comm.). Indeed, the decades-old Dominican policy of forest fire suppression has returned fire frequency in windward zones to levels approximating the pre-settlement fire regime. In the drier leeward areas, however, fire frequency and extent appear lower than pre-1900 levels. This decrease may reflect the higher fire frequency from 1900–1965, which probably reduced fuel loads. Nevertheless, the decades-long drop in fire frequency and extent in leeward zones has probably allowed fuels to accumulate. Further inputs of woody debris after recent hurricanes (1979 and 1998) may have also exacerbated this situation. Management plans should consider a 'let burn' role for natural fires in these areas, requiring a change in the negative perceptions of fire in natural areas held in the Dominican Republic (Bolay 1997).

The importance of climate (TWI and El Niño) detailed here suggests that rising global temperatures will have profound effects on fire regimes in subtropical mountains. Models of climate change under doubled atmospheric CO_2 concentrations forecast a general increase in wildfires in tropical forests as dry-season length, droughts, El Niño and lightning frequency are all predicted to increase (Goldammer & Price 1998, Timmermann *et al.* 1999). Forecasts for the TWI are less clear. The 'lifting cloud-base' hypothesis predicts that the elevation of the TWI will rise (Hamilton *et al.* 1995), while other climate-change models project a high-elevation drought on tropical mountains due to reduced cloud formation and a lower elevation of the TWI (Foster 2001, Loope & Giambelluca 1998). However altered, fire regimes will be strongly influenced by any disruption of the average elevation and magnitude of the TWI. The predicted increase in hurricane frequency and severity in most climate change scenarios could lead to increase fire severity in the subtropics. Hurricane damage can leave high fuel loads and allow fuels to dry more rapidly due to greater light penetration to the understorey (Myers & van Lear 1998). The high fuel loads left by Hurricane Gilbert (1987) in the forests of the Yucatan and a subsequent drought in 1988–89 led to exceptionally severe and large fires in 1989 (Goldammer & Price 1998). Patterns of hurricane-promoted fires have been reported also for tropical rain forests in the cyclone-prone region of Australia (Stocker 1981, West *et al.* 1988). A review by Myers & van Lear (1998) suggests that hurricane-fire interactions may be fairly common in forests which experience regular hurricanes.

Reconstructions of fire history are a crucial step towards understanding the ecological role of fire in a particular system (Brown *et al.* 2001). This reconstruction of fire history in the Cordillera Central illustrates the centuries-long influence fire has had on this ecosystem. Future studies with a longer fire chronology and more within-zone replication would improve our understanding of the fire regime in the area. In general, more study of fire history is needed in the tropics where possible, as climatic conditions and the high frequency of human-ignited fires (Goldammer 1990) are sufficiently dissimilar to make the application of temperate fire regime models inadequate. The influence of the TWI, in particular, has the potential to drive exceptionally strong spatial patterning in some subtropical fire regimes.

ACKNOWLEDGEMENTS

We thank Ruth Sherman, Francisco Peralta, Pedro Martinez, Ekers Raposo, Olivia Duren, Jason Demers, Evan Grant, Jen Cramer, Garret Meigs and Jeannette LeBoyer for their help with field and lab work. We thank Tom Swetnam, Chris Baisan and the Lab of Tree-Ring Research, Univ. Arizona for technical guidance. We gratefully acknowledge the logistical support provided by Dr Radhames Lora and the support of the Dominican Park Service. Comments from Peter Marks, Tom Whitlow, Ken Orvis and three anonymous reviewers substantially improved this manuscript. This research was supported by an Andrew W. Mellon Ecosystem Research Program grant administered by the Nature Conservancy and a Garden Club of America Award in Tropical Ecology.

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