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150 Years of Tree Establishment, Land Use and Climate Change in Montane Grasslands, Northwest Argentina

Julieta Carilla[1] and **H. Ricardo Grau**

Laboratorio de Investigaciones Ecológicas de las Yungas (LIEY), Universidad Nacional de Tucumán (UNT), Cc 34 (4107), Yerba Buena, Tucumán, Argentina

ABSTRACT

Degraded grasslands resulting from intensive land use appear to be highly resistant to tree invasion due to interactions between land use, climate, grazing and fire. We describe long-term patterns of tropical montane forest regeneration into degraded grasslands and analyze their relationships with historical changes in rainfall, grazing and fire in Los Toldos valley (Northwest Argentina), cloud forest life zone (1600 m asl). We used dendrochronological techniques to reconstruct spatial and temporal patterns of *Podocarpus parlatorei* establishment (the dominant tree species in secondary forests) and grassland fires for the last 150 yr. We assessed current livestock spatial distribution along the valley through feces sampling. Inferred tree establishment patterns (*i.e.*, considering age structure and mortality) were analyzed in relation to temporal and spatial patterns of grazing and fire derived from our own analyses and from government statistics, and to rainfall patterns derived from previous dendrochronological reconstructions. Current grazing intensity was higher close to the local township. Fire occurrence increased with periods of above-average rainfall (higher fuel productivity), and tended to increase with distance to township (less grazing). Tree establishment in grasslands was spatially associated with high grazing intensity and low fire frequency, and temporally associated with periods of high grazing intensity and below-average rainfall. Despite climatic and land-use changes leading to conditions potentially favorable for trees (*i.e.*, more rainfall, less grazing), grasslands persist in this study area, likely due to the direct (saplings burning) and indirect (soil degradation and desiccation) effects of recurrent fires, enhanced by decreasing grazing and increasing rainfall.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp

Key words: cloud forest; dendrochronology; disturbance; fire; forest transition; grazing; *Podocarpus parlatorei*; vegetation switches.

Forests and grasslands represent the two most important broad land-cover types in tropical mountains. The dynamics of forests–grasslands ecotones is regulated by the interaction between climatic and anthropogenic factors (Sarmiento 1984, 1997, 2002; Archer *et al.* 1995; Scholes & Archer 1997; Cavelier *et al.* 1998; Veblen *et al.* 1999; Sternberg 2001). The most widespread land use of anthropogenic grasslands is grazing, often associated with fire as a management tool (Cavelier *et al.* 1998, Geist & Lambin 2002). Fire is controlled by ignition sources (Flannigan & Wotton 1991, Pyne 1993) and fuel availability, which in turn is affected by biomass removal through grazing (Scott 1977, Savage & Swetnam 1990, Cochrane & Laurance 2002), and by climatic factors that influence fuel production and desiccation (Swetnam 1993, Kitzberger *et al.* 1997, Grau & Veblen 2000). Fire often plays a main role in tree regeneration dynamics through its effect on both tree mortality and recruitment opportunities after the fire (Kellman & Tackaberry 1993, Grau & Veblen 2000, Gould *et al.* 2002, Hille & Ouden 2004). Hence, to understand the dynamics of forest–grassland ecotones, it is important to account for the interplay of grazing, fire and climate (Archer *et al.* 1995, Veblen *et al.* 1999).

Livestock ranching has been a major historical cause of tropical deforestation, both in lowlands and montane areas of South America (Geist & Lambin 2002, Grau & Aide 2008). In Andean montane ecosystems, grasslands and savannas cover extensive areas, and in many cases their climatic and topographic conditions suggest an anthropogenic origin: *e.g.*, abrupt forest–grassland ecotones, coexistence of both systems at the same altitude in the slope, no differences in geological formation or soil water content (Ellenberg 1979, Lægard 1992, Young 1993, Cavelier *et al.* 1998, Young & Leon 2007). Today, however, several montane regions that are marginal for modern agriculture are experiencing land-use disintensification due to socioeconomic changes that promote rural–urban migration and disfavor traditional production systems such as livestock ranching (Preston *et al.* 1997, Aide & Grau 2004, Grau & Aide 2007). The resulting decreases in livestock density could represent an opportunity for spontaneous forest recovery into degraded grasslands (Perez *et al.* 2003, Renison *et al.* 2005, Aide *et al.* 2010), and this process could potentially lead to large-scale 'forest transition' processes (Rudel *et al.* 2005), likely reducing biodiversity losses and improving environmental services (Aide & Grau 2004, Wright & Muller-Landau 2006, Grau & Aide 2008).

In addition to land use, climate also plays a key role in the maintenance of savannas and grasslands (Scott 1977) and affects forest–grassland dynamics (Sarmiento 1984, Scholes & Archer 1997, Sternberg 2001). Increases in rainfall are likely to favor forest expansion as trees generally need more soil water than grasses (Woodward 1987, Villalba & Veblen 1997, Sankaran *et al.* 2004, Renison *et al.* 2005). However, even under favorable climatic conditions, decreasing land-use intensity in grasslands and savannas may not lead to forest recovery (Sarmiento 1997, Cavelier *et al.* 1998). Degraded grasslands may behave as a disturbance-dependent alternative state when frequent disturbances interact with environmental factors creating feedbacks that make the system resist forest invasion (Wilson & Agnew 1992, Hobbs & Norton 1996, Suding *et al.* 2004; Fig. S1). Grazing and fire suppression may shift forest and grasslands boundaries to new equilibrium states (Pillar & Quadros 1997). Historical use of fire can cause permanent damage

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[1]Corresponding author; e-mail: julietacarilla@yahoo.com.ar

to soil fertility limiting forest recovery after land abandonment (Scott 1977, Medina & Silva 1990, Aide & Cavelier 1994, Cavelier *et al.* 1998, Viña & Cavelier 1999). Forest–grassland ecotones could be potentially controlled by variables such as landscape fragmentation, lack of seed sources, predation, interspecific competition and other variables that control tree recruitment (Aide & Cavelier 1994, Nepstad *et al.* 1996, Holl 1999, Holl *et al.* 2000, Zimmerman *et al.* 2000).

Studies analyzing several decades of tree regeneration are needed to describe the dynamics of forest–grassland ecotone. Unfortunately, in tropical environments these studies are limited by the lack of long-term historical records of land use and climate. The absence of strong seasonality to produce annual tree rings limits the ability to derive dendroecological studies. In consequence, most empirical studies are limited to the combination of spatial analyses of vegetation patterns and controlled experiments of the underlying causal factors (*e.g.*, Aide & Cavelier 1994, Aide *et al.* 1996, Biddulph & Kellman 1998, Cavelier *et al.* 1998). In contrast, Northwest (NW) Argentina mountains present a noticeable climatic seasonality, which has allowed us to develop dendroecological methods to assess multidecadal patterns of climate and tree regeneration (Villalba *et al.* 1998, Grau *et al.* 2003), providing the opportunity to assess the interactions of climate and land-use change in defining long-term trends of forest regeneration into degraded grasslands. *Podocarpus parlatorei* Pilg., the most abundant species in postgrazing secondary forests at the elevational range of this study, presents well-defined annual tree ring that can be used for dendrochronology (Villalba *et al.* 1985, Villalba 1995). During the 20th century, subtropical mountains of northwestern Argentina have experienced socioeconomic and climatic changes intensified during the last 3–5 decades. Human regional demography is characterized by a trend of rural to urban migration (Reboratti 1996, Bolsi & Pucci 1997, Izquierdo & Grau 2008). Regional climate change is characterized by an increase in rainfall since the late 1950s (Minetti & Vargas 1997, Villalba *et al.* 1998). Despite these trends (less grazing, more rainfall), potentially favorable to forest recovery, a clear forest transition is not observed in the study site (Grau *et al.* 2010). Based on these observations, we hypothesized that the dynamic of forest–grassland ecotone is controlled by the complex interactions among grazing, fire, climate and vegetation dynamics, and that due to the effects of recurrent fires, degraded grasslands persist as an alternative degraded state which resists tree invasion despite improving conditions of land use and climate.

To assess this hypothesis, we derived a series of predictions regarding patterns of establishment (P1), fire (P2) and grazing intensity (P3), to be tested by the detailed analysis of spatial and temporal patterns of disturbance and establishment of *P. parlatorei*. According to our hypothesis, tree recruitment is largely limited by fire; therefore, tree establishment should be positively related to factors that reduce fuel availability. Since grazing has decreased in the region (Grau *et al.* 2010), tree establishment should be decreasing through time during the 20th century (P1.1), and in recent times tree establishment should be more intense near the township (P1.2), where higher grazing intensity reduces fire frequency. Since rainfall is likely to increase fuel availability and fire probability, tree establishment should be negatively related to rainfall (P1.3). Because in the region fire is fuel-limited rather than desiccation limited (Grau & Veblen 2000), fire frequency should be positively correlated with distance to the township where less fuel is removed by grazing (P2.1). Through time, fires should be positively associated with rainfall (P2.2), which increases fuel production. Grazing intensity increases toward the main township of the valley (P3) where human population is concentrated (Fig. S1).

METHODS

STUDY AREA.—The study was conducted in the valley of Los Toldos (22° S, 64° W) Department of Santa Victoria, Salta, Argentina (Fig. 1). The valley is located at *ca* 1600 m elevation, in the subtropical montane forest of northwestern Argentina (phytogeographic province of *Las Yungas*; Cabrera 1976). Mean annual temperature is 15°C and average annual rainfall is 1300 mm. Rainfall is highly seasonal (Fig. 2A), concentrated in the summer (November–March); winters are dry with frequent frosts and occasional snowfall. The valley area is *ca* 6000 ha and encompasses a gradient of land-use intensity, which increases toward the northern part of the valley (near Los Toldos Township, main town of the municipality) and decreases southward into the area known as 'Vallecito' with small isolated houses and low human population density (Fig. 1A).

The valley landscape is a mosaic of secondary forests dominated by *P. parlatorei* (*ca* 50–500 individuals/ha, in old and young *Podocarpus* forest, respectively) and, to a lesser extent, by *Alnus acuminata* H. B. K. (*ca* 40–400 individuals/ha, in old and young Alnus forest, respectively); anthropogenic grasslands dominated by *Elionurus muticus* (Spreng.) Kuntze and *Paspalum notatum* Flüngeé; and shrublands, usually an intermediate successional stage between grasses and trees, are dominated by *Baccharis* spp. and *Stevia* spp. (Aragón *et al.* 2006). Shrublands appear to favor tree recruitment by facilitating bird-dispersed seed input and creating a less harsh microenvironment (Ramadori 1997). Grasslands cover *ca* 1600 ha in the valley bottom, creating a matrix in which small secondary forest patches are located. Larger forest patches, including mature forests, occur in the slopes bordering the valley and along watercourses. Mature forests are dominated by *Cedrela lilloi* C. D. C., *Juglans australis* Griseb., *Ilex argentina* Lillo and several Myrtaceae species (Malizia 2003, Pinazo & Gasparri 2003).

The study area is located in the Upper Bermejo River Basin and is part of *Las Yungas* Biosphere Reserve. Original native inhabitants of the area were the *Chiriguanos* Indians. Since the end of 18th century Spanish influence became important. Human population has increased in the last 20 yr, by 40 percent for the department (Fig. S2A) and by 700 percent for Los Toldos township (Instituto Nacional de Estadísticas y Censos [INDEC] 2001). This high population growth in Los Toldos township cannot be explained even by the high birth rate (28.5‰) and decreasing mortality rate (from 30‰ to 5.3‰ between 1970 and 2001; Gil Montero 2005); therefore, it implies a concentration of the scattered rural population in Los Toldos township (Grau *et al.* 2010).

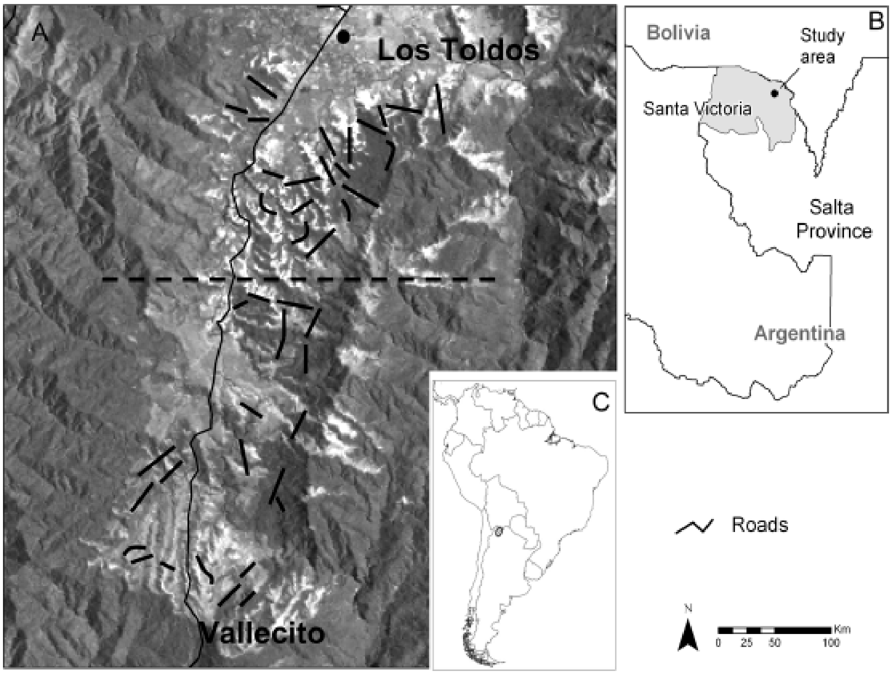

FIGURE 1. Study area. (A) Landsat TM satellite image of valley of Los Toldos, Department of Santa Victoria, Province of Salta. Forests appear as dark gray, shrublands and grasslands as pale gray, and bare soil and highly degraded grasslands as very light gray or white. The valley encompasses a gradient of land-use intensity that increases from Vallecito to Los Toldos township. In the image, a dashed horizontal line divides the valley in the northern (Los Toldos; higher density of houses) and southern (Vallecito; scattered houses) sectors. Sampling transects are represented by thick black lines. (B) Location in NW Argentina and (C) in South America.

The dominant land use in the valley is grazing. Fire is human ignited to promote pastures' resprout during spring (September–October). Traditional grazing practices (*i.e.*, since the 18th century) involve altitudinal displacements of cattle (transhumance), between high grasslands in summer (wet season) and forests at lower elevations in winter (Reboratti 1996). During the 19th century records based on oral accounts suggest a high cattle load (likely associated with extensive grasslands), particularly during the independence and Paraguay wars (1810–1822 and 1865–1870, respectively; Reboratti 1996). Since the turn of the 20th century, there are quantitative records of livestock at department level (Santa Victoria), for 1906 (Registro de las Fincas Rústicas del Vicecantón de Toldos 1906), 1952, 1964, 1974, 1977, 1988 and 2002. Given the strong socioeconomic and ecological similarities with the rest of the department of Santa Victoria, we assumed that the local temporal patterns of livestock of Los Toldos followed the same pattern as the complete department in 1906 and from 1952 to 2002. Currently, almost 50 percent of the cattle of the department occur in Los Toldos municipality; and cattle represent 73 percent of the total livestock in Los Toldos. Historical records showed two periods with high livestock density, in 1900 and in 1960, followed by a general decrease during the second half of the 20th century (Fig. S2B).

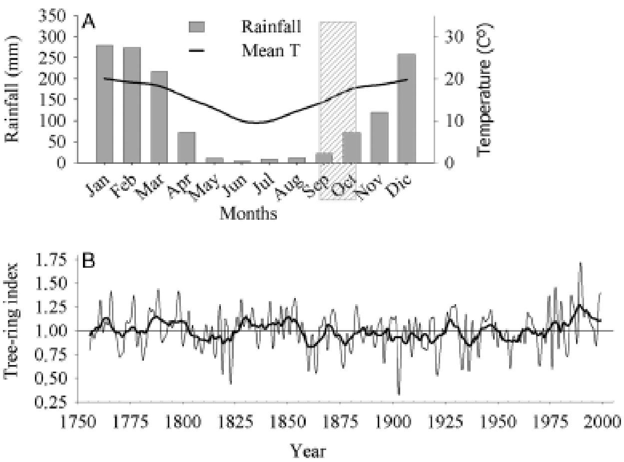

FIGURE 2. Climatic patterns in the study area. (A) Average monthly rainfall and temperature in Los Toldos valley based on instrumental data from 1970 to 1990. The shaded zone in the graph indicates the peak in the fire season. (B) Tree ring index (TRI, an index of rainfall) calculated from *Juglans australis* Griseb. series chronology for Los Toldos (1750–1999) (based on Grau *et al.* 2010); thick line shows 5-yr moving average.

CLIMATIC DATA.—Climatic data availability in Argentinean subtropical montane forest is limited because most meteorological stations are in lowland plains and the few stations in the mountains present short and incomplete records. Los Toldos rainfall instrumental record only extends from 1972 to 1990 (Bianchi & Yañez 1998). Hence, to analyze long-term climatic trends we used the tree ring index (TRI; Fig. 2B; Grau *et al.* 2010), based on tree ring chronologies of *J. australis*, the most reliable species for rainfall reconstructions (Villalba *et al.* 1998). TRI is defined as a chronological series of standardized tree ring width measure, with mean = 1. TRI used in this study covers the period from 1750 to 1999, and was derived from *J. australis* ring width chronologies collected nearby Los Toldos in areas of northern slope aspect, where forests where growth is sensitive to rainfall. TRI explains a large proportion of the regional rainfall and temperature and is useful to reconstruct climate patterns at multidecadal and century scales. We used TRI to explore rainfall long-term influence on fire and tree establishment, since TRI is well correlated with instrumental records of rainfall (Villalba *et al.* 1998), is a local climatic proxy and extends for a temporal scale appropriated for this study. TRI was significantly correlated to the average of the annual precipitation from the three closest weather stations with longer term records (Pozo Sarmiento, Aguas Blancas and Oran, 1945–2005; *source*: Red Hidrólogica Nacional 2006; $r = 0.6$, $P = 0.008$).

SAMPLING.—Fire event and tree age structure were obtained from *P. parlatorei*, which presents well-defined growth rings that can yield reliable dating of tree establishment with a temporal resolution of 5 yr, and with a temporal span of > 200 yr, making this species useful for dendroecological studies (Grau *et al.* 2003). However, due to the presence of false and missing rings, tree ring series cannot be crossdated limiting the accuracy of dating, for example, for dendroclimatological studies (Villalba *et al.* 1985, Villalba 1995).

Fire events and tree age structure were sampled in secondary forest patches located throughout the valley, between October 2003 and October 2005. We established 42 transects, of 200–1000 m long depending on forest patch size, distributed along a gradient of land-use intensity from Los Toldos township southward; 21 transects were located in the northernmost part of the valley, in Los Toldos sector (with a higher density of houses), and 21 transects located in the southernmost part of the valley, in Vallecito sector, where houses are more scattered (Fig. 1A). Every 50 m along each transect, we established a sampling site, where we sampled the four closest living individuals of *P. parlatorei* (P1: tree establishment decrease with time), including a wide range of sizes, from the smallest tree with lignified stems to the largest ones (until *ca* 1 m diam.). Trees were sampled with an increment borer at *ca* 20 cm of height (basal diameter) from ground, seedlings and saplings (< 5 cm basal diam.) were cut, and dating was based on cross sections. When core samples did not reach the pith in the increment borer sample, we estimated missing rings based in the geometry of the ring (Duncan 1989). Samples with more than five estimated missing rings ($N = 74$) were discarded for the analysis.

To assess if fire frequency is correlated with distance to the township (P2), fire scar wedges of *P. parlatorei* and of *A. acuminata*, another useful species for dendroecological studies (Grau *et al.* 2003), were collected with a chainsaw (Arno & Sneck 1977) in an opportunistic way along the same transects used for tree age structure sampling. Increment-borer samples, cross sections and fire wedges were processed in laboratory, and mounted, sanded to a fine polish, and visually dated, assigning a calendar year to each ring and identifying narrow rings (*i.e.*, dry years such as 1977, 1982, 1987, 1991, 1997) to make visually dating more reliable. Samples with problematic tree ring identification were discarded if they were too difficult to solve. In most observed samples, no more than five rings per sample were identified as dubious rings; therefore, we assume that a 5-yr window is conservative way to eliminate most errors. For dating purposes, we followed Schulman's (1956) convention for the southern hemisphere, which assigns each ring date (year) to the year when radial grow started (October–November).

To explore the spatial distribution of livestock along the valley (P3), in November 2005, we set up a grid based on satellite images over an area of *ca* 3500 ha including forests and grasslands across the valley of Los Toldos. The area was divided in rectangles of 700 m in north–south direction and 500 m in east–west direction. At each intersection point ($N = 83$), characterized in terms of elevation and distance to Los Toldos township using a Geographic Positioning System, we recorded presence of livestock feces in forty 1 m^2 squared plots and we calculated an index of feces abundance as the frequency of squares in which feces were present. Feces density as an index of grazers' density has been reliably used in similar environments of subtropical Argentina (Cingolani *et al.* 2003). Plots were distributed in two transects located at random around the intersection point, and at least 15 m distant from each other, with 20 squares per transect separated 2 m from each other.

For botanical nomenclature we followed Zuloaga and Morrone (1999a, b).

DATA ANALYSIS.—Present age structure reflects both past establishment and mortality patterns (Kelly & Larson 1997). Therefore, to examine establishment patterns based on present age distributions of living trees, we need to consider mortality. In this study, establishment patterns of *P. parlatorei* were inferred by assuming a constant reconstruction rate of 0.012 (from a mortality rate of 1.2% dead trees/yr), based on secondary forest permanents plots from NW Argentina (Carilla *et al.* 2006). Calculation of the reconstruction rate was done over a population of *ca* 300 individuals of *P. parlatorei* > 10 cm dbh present (alive) in 1991 when permanent plots were established and a population of 265 individuals present in the last remeasurement date (2001), *i.e.*, 35 dead trees in 10 yr of monitoring *P. parlatorei* forest. The sample size did not allow the estimation of mortality rates of different size classes, but showed a trend toward higher mortality in trees > 50 cm dbh. Using a constant mortality rate, therefore, possibly underestimated the number of older trees, being therefore a conservative assumption to test our hypotheses referring to temporal patterns of establishment (see 'Results' and 'Discussion'). Inferred establishments were derived from the following formulas:

$$\mathrm{IE} = \mathrm{OE}(1 + \mathrm{RR})^{a} \tag{1}$$

$$\mathrm{MR} = (n_{2001}/n_{1991})^{1/10} - 1 \tag{2}$$

$$\mathrm{RR} = (n_{1991}/n_{2001})^{1/10} - 1 \tag{3}$$

where IE is the inferred establishments, OE the observed establishments (from the age structure derived from our dendroecological sampling), *a* the tree age (year of sampling collection − year of establishment), MR the mortality rate, RR the reconstruction rate, n_{1991} the number of trees recorded in 1991 in Carilla *et al.* (2006) and n_{2001} the number of trees recorded in 2001 in Carilla *et al.* (2006).

We analyzed the relationship between tree establishment and livestock density across the period of analysis (P1.1: tree establishment decrease with time) using correlation analysis between these inferred establishments and livestock density. To analyze the relationship between distance to the local township and patterns of tree establishment (P1.2: tree establishment is more intense near township), we used correlations between distance to Los Toldos and year of establishment of the oldest tree recorded at each site. To analyze the long-term relationship between rainfall and tree establishment (P1.3: tree establishment is negatively correlated to rainfall) we correlated inferred establishment with TRI values. In all cases, we tested for distribution assumptions (normality and homogeneity of variance) and used Pearson's correlation coefficient for TRI, fire and tree establishment variables at a 5-yr scale, and Kendall's τ nonparametric correlation coefficient for variables related to distance from town: fire and tree establishment at annual scale of resolution.

To assess spatial patterns of fire frequency in relation to distance to township (P2.1: fire frequency is positively correlated with distance to town) we used Kendall's τ correlation coefficient between distance to township and number of fires recorded at each sample site along transect, considering only the sampling sites where at least one fire was recorded. This index must be interpreted with caution because the number of fire dates recorded is not only affected by the fire frequency but also by the 'sample depth' (age of the oldest tree potentially recording fires), a factor for which we could not control and could potentially lead to spurious correlations. However, since most fires occurred during the second half of the 20th century, a period when all transects did have recording trees; we considered it a useful *proxy* for fire frequency.

To assess P2.2 (fire is limited by fuel production, which is expected to be higher during periods of above-average rainfall) we explored the relationship between TRI and fire at two temporal scales: annual and 5-yr periods. The 5-yr scale analysis is more consistent with the dating errors of *P. parlatorei* whereas the annual scale provides a statistically more robust analysis of the relationships between fire and climatic factors potentially leading to the production and desiccation of fine fuels. We present a comparison between the histogram of the number of fires along the time series and the curve of TRI, including Pearson's correlation coefficients to quantify the relationship. Given the lack of independence between 'samples' (*e.g.*, the number of fires during 1 yr influences fuels and fires during subsequent periods); this analysis should be considered for descriptive purposes rather than as a strict statistical test. For a more rigorous statistical analysis of the relationship between fire events and TRI at the annual scale, we used superposed epoch analysis (SEA), performed with the program FHX2 (Grissino-Mayer 1995), which analyzed mean annual values of TRI calculated for 5-yr windows including the fire year and the four previous years for each 'fire year', defined as those years during which > 5 percent of the trees across the whole study area recorded fires. SEA compares the values of TRI of these years with the complete time series by performing Monte Carlo simulations that randomly selects years, calculates expected means and provides 95% CI, and hence identifies the statistical significance of the associations between 5 yr and climatic conditions of the years included in the time window.

To explore the effects of distance to the township on grazing intensity (P3: grazing intensity increases toward township), we used Kendall's τ nonparametric correlation coefficient between distance to Los Toldos township and the index of grazing intensity based on feces abundance.

RESULTS

Tree establishment patterns.—We cored a total of 1808 *P. parlatorei* trees, 1194 individuals in Los Toldos and 614 in Vallecito, which yielded 3585 inferred tree establishments, 2027 in Los Toldos and 1558 in Vallecito, due to the inclusion of estimated dead individuals based on the species' mortality rate (Table 1).

Considering the complete study area, the age structure (*i.e.*, without correcting for mortality) showed a pattern of a comparative low number of young individuals (*i.e.*, < 10–15 yr, indicating a decreasing number of establishments toward the present). Inferred establishments (3585 trees) showed more clearly an overall decreasing trend during the last 50 yr with a marked decrease during the last 20 yr (supporting P1.1, tree establishment decrease with time). In the histogram of inferred establishments, two establishment peaks can be observed, corresponding to peaks in the two sectors of the valley: in Los Toldos inferred establishments peaked between 1950 and 1970 (Fig. S2C), 50–70 yr later than in Vallecito (farther away from the township), where establishment peaked between 1890 and 1900, with a high also in 1915 (Fig. S2D). Inferred tree establishments in the whole study area were associated with livestock density across the time series and the two peaks of maximum livestock load (Fig. S2B) coincided with periods of the high tree establishment in the entire area. This pattern is consistent with P1.2, which is also reflected in the trend of younger trees close to the township (Fig. 3A). In support of P1.3 (tree establishment is

TABLE 1. Podocarpus parlatorei *size categories based on basal diameter (diam. 20 cm from ground), number of individuals and range of tree ring counted (tree age estimated) by size category. It corresponds to a subsample of 1170 individuals (772 of Los Toldos [LT] and 378 of Vallecito [V]).*

Basal diam. categories (cm)	No. of individuals		Range of tree ring	
	LT	V	LT	V
1–10	106	73	5–70	4–40
10.1–20	349	42	12–102	8–91
20.1–30	198	100	8–119	19–117
30.1–40	75	112	14–130	31–116
40.1–50	32	48	32–130	45–169
> 50	12	39	37–129	37–156

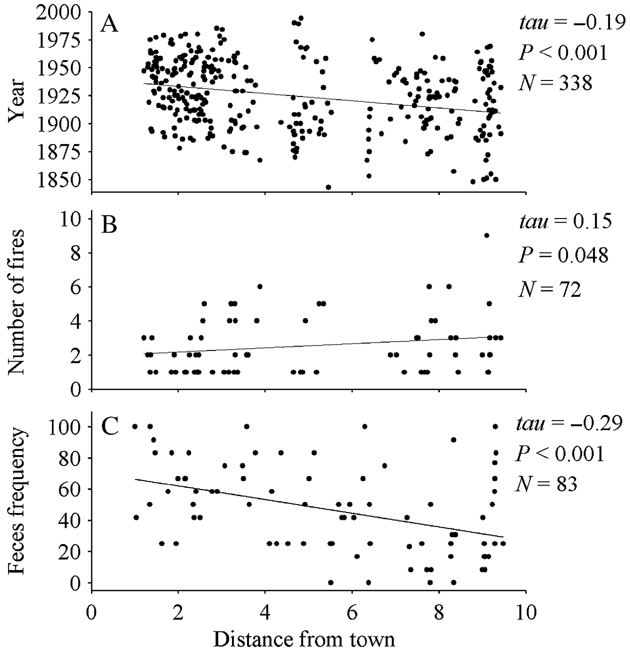

FIGURE 3. Scatterplots in relation to distance from township of (A) year of tree establishment in each sampling site; (B) number of fires; (C) index of grazing intensity based on feces.

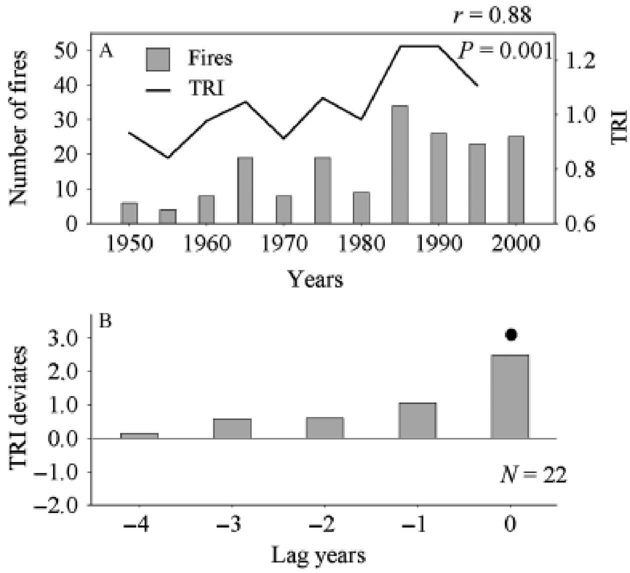

FIGURE 4. Relationship between fires and tree ring index (TRI): (A) fires frequency in the valley compared with TRI at 5-yr scale. Labels correspond to the first year of the 5-yr period (*e.g.*, 1950 indicates the period 1950–1954), (B) relationship between occurrence of 'fire years' in relation to departures from the mean TRI during the 'current' and previous 4 yr. Dots indicate statistical significance ($P < 0.05$) as derived from superposed epoch analysis.

negatively correlated to rainfall), for the same period, inferred tree establishment was negatively correlated with TRI at a 5-yr scale ($r = -0.7$, $P = 0.024$, $N = 11$).

FIRE PATTERNS.—A total of 191 fires were recorded in the entire valley, with the first fire records almost simultaneous in the Los Toldos (1914) and Vallecito (1919) sectors. Ninety-six percent of the recorded fires occurred after 1950 and 62 percent after 1980. Consistent to P2.1, number of fires recorded per site increased with distance from Los Toldos township (Fig. 3B). Consistently with P2.2, fire years were clearly associated with above-average TRI values at both temporal scales analyzed (Fig. 4). At the 5-yr scale the curve of number of fires clearly followed the 5-yr TRI average (Fig. 4A). At the annual scale, SEA showed a statistically significant association between fire years and above-average TRI (Fig. 4B). Fire occurrence and inferred tree establishments showed negative correlations ($r = -0.68$, $P = 0.03$) during the period 1950–2000, when 95 percent of fires occurred.

GRAZING INTENSITY.—Despite a high variability among samples, the index of grazing intensity based on feces abundance showed a significant decreasing trend with distance to town (Fig. 3C), consistently with P3.

DISCUSSION

The persistence of anthropogenic grasslands within montane life zones is a salient biogeographic feature of Andean ecosystems. Historically, the study of this process has been restricted to observational descriptions (*e.g.*, Scott 1977, Ellenberg 1979) and to short-term experimental analyses (Aide & Cavelier 1994, Sarmiento 1997, Cavelier *et al.* 1998). In contrast, we have taken advantage of the methodological opportunities provided by NW Argentina ecosystems (long-term records of land use, climatic seasonality generating annual tree rings) to conduct the first long-term (*i.e.*, more than a century) assessment of the dynamics of forest regeneration in Neotropical montane grasslands within the montane forest life zone.

We have hypothesized that degraded grasslands in our study system, resulting from intensive land use, are resilient to tree invasion due to interactions with climate, grazing and fire, and, more specifically, that fire regime is a main factor controlling this resilience. The different predictions (Fig. S1) derived from this hypothesis were supported by our analysis. Decreasing tree establishment during the 20th century reflected decreasing grazing and increasing fire (P1.1), even when we probably underestimated establishments at the beginning of the study period. Supporting P1.2, in recent times, tree establishment was more active near township where grazing was more intense (P3; Fig. 3A, C). The decrease in grazing pressure far from township (P3), reflected in feces distribution (Fig. 3C), is associated with an increase in fire frequency (P2.1; Fig. 3B), which is consistent with a previous study in the region, showing that fuels (controlled by grazing and climate) rather than ignition sources are the main predictors of fire probability (Grau & Veblen 2000, Grau 2001). This association suggests that fire is fuel limited rather than desiccation limited, probably because winters are generally dry enough to carry fire (Grau & Veblen 2000), and is also reflected in the positive association between fires and periods of above-average rainfall (P2.2; Fig. 4). Previous studies (Ramadori

1997) have shown that *P. parlatorei* seedlings establish vigorously under shrubs canopies (likely due to enhanced seed dispersal and a less harsh environment), and these shrublands are favored by grazing, and disfavored by fire.

The general hypothesis tested in this paper that frequent fires maintain grasslands in a degraded state has been proposed by several studies based on inferences from spatial patterns (Scott 1977, Cavelier *et al.* 1998, Sarmiento & Frolich 2002, Young & Leon 2007) and local scale experiments (Aide & Cavelier 1994, Cavelier *et al.* 1998). While the later type of study is important to identify the key variables controlling tree recruitment, the authors were unable to quantify the relationships with long-term trends in environmental changes as we did.

As in other Andean ecosystems, decreasing intensity of marginal land uses associated with rural–urban migration may have significant environmental effects. In our study area, the decrease in grazing pressure in the last decades is reflected in the replacement of rural agricultural activities by government employment concentrated in the urban center (Reboratti 1996, INDEC 2001). These current trends of decreasing human pressure over natural resources would favor tree establishment in mountain forests potentially leading to process of forest recovery (Perez *et al.* 2003, Aide & Grau 2004, Sankaran *et al.* 2004, Renison *et al.* 2005, Wright & Muller-Landau 2006, Grau & Aide 2007) and in a broader scale, to forest transition (Rudel *et al.* 2005). Similarly, rainfall increases in the region (Minetti & Vargas 1997, Villalba *et al.* 1998) should also favor forest expansion into degraded grasslands. But our long-term analysis showed a different response; despite these seemingly favorable changes, forests are not invading grasslands likely because fires acted as a barrier against forest invasion. Instead, as other studies have shown, tree establishment was promoted by grazing (Scott 1977, Archer *et al.* 1995) and by low rainfall that decrease fire occurrence.

In the last years tropical dendrochronological studies have gained importance, most of them followed dendrochronologist conventional methods (*e.g.*, Worbes *et al.* 2003), but others, such as the present study, were partially limited by the difficulties of crossdate samples (Brienen & Zuidema 2006). Despite this limitation, this study reveals the potential of a tropical species to study the ecological effects of long-term land use and climatic changes by using tree rings, even when errors in year determination exist (Brienen & Zuidema 2005).

As opposed to manipulative experiments, long-term dendroecological studies such as the present one are largely correlative and are unable to clearly discriminate causal relationships. The present study, however, allows making hypotheses on the dominant mechanisms that can be tested through controlled experiments of tree recruitment and mortality in degraded grasslands. The key processes emerging from this study to be analyzed by experiments include the links between grazing, fire, soil moisture, soil fertility and tree establishment. Complex temporal dynamics between these factors appear to be associated with great resilience of the degraded grasslands to fire, which results in relatively stable alternative conditions despite important environmental changes. The establishment of shrublands as an early successional stage in the limits between grasslands and forest could act as a mechanism weakening the robust interactions between fire and grasslands that maintain them as a stable alternative state of the system. Therefore, the empirical assessment of the rates of shrubland establishment and its flammability should be a priority research objective. The negative correlation between fire and tree recruitment could be explained both by direct effects on seedling and sapling mortality and by indirect effects on soil fertility and soil water availability (Wagle & Kitchen 1972, Ivanauskas *et al.* 2003). In addition, the resilience of degraded grasslands can be further promoted by biological mechanisms such as lack of tree propagules availability, predation, and interspecific competition (Aide & Cavelier 1994, Nepstad *et al.* 1996, Paine *et al.* 1998, Holl 1999, Holl *et al.* 2000, Zimmerman *et al.* 2000, Mazia *et al.* 2001). Compounded perturbations (natural and anthropogenic), in conjunction with climate change, likely lead ecosystems to alternative altered states that can persist in time or not (Paine *et al.* 1998, Platt *et al.* 2002). Dynamic models would be very helpful to understand the complex interactions among land use, climate and fire, and hence merge the results of experimental studies with long-term analysis as the present study.

CONCLUSION

Dendroecological methods allowed the assessment of multidecadal patterns of climate and tree regeneration, for the first time in a cloud forest life zone within the tropics. The resulting 150-yr chronology of tree regeneration patterns into degraded grasslands resulting from intense land use was analyzed in relation to spatial and temporal patterns of land use and climate. Despite decreasing grazing intensity and increasing rainfall, forests are not actively recovering over degraded grasslands, likely because recurrent fires make the ecosystem resistant to change through its direct effects on seedlings mortality and/or its indirect effects on soil and the microclimate. The temporal scale of analysis proved to be a useful complement to experiments and dynamic models to understand the consequences of land use and climatic changes in tropical montane ecosystems.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

FIGURE S1. Diagram summarizing the hypothetical relationships between main variables.

FIGURE S2. (A) Human population in Santa Victoria department (which includes Los Toldos municipality). (B) Livestock in Santa Victoria department expressed in cattle units (GMU) in which data from all domestic grazers have been added using a conversion factor: 1 for horses and cattle, 0.15 for sheep and goat and 0.35 for swine.

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