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Insights into Holocene vegetation and climate changes at the southeast of the Andes: *Nothofagus* forest and Patagonian steppe fire records

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Abstract

Ecosystem fire regimes are a consequence of interactions among fuels and climate. The reconstruction of past fire regimes is of great importance for studying past climate changes and controls. The aim of this study is to compare two charcoal and pollen records from the *Nothofagus* forest-grass steppe ecotone (50°S) and the grass steppe (49°). We compare fire regime responses to local vegetation changes, and inferred variation on climate conditions between 49° and 52°S during the Holocene. Cerro Frías and La Tercera charcoal records seem to be sensitive to centennial and millennial timescales of vegetation and climate variability inferred for southern Patagonia. During the Pleistocene–Holocene transition and during the middle Holocene, forest patchiness provided fuel vertical and horizontal continuity favoring fire activity. In contrast, in steppe environments high cover of shrubs favored grass patchiness, impeding fire spread. Higher pollen richness and variability through time seem to be related to higher vegetation patchiness. Past fire regime variability at the eastern side of the Andes has been closely related to westerly moisture influence between 52° and 48°S. Southern latitudes have been influenced by polar air mass intrusions to the continent during the last 5000 cal. yr BP.

Keywords

fire regime, grass steppe, Holocene, *Nothofagus forest*, palynological richness, Patagonia

Introduction

The latitudinal location of southern South America, and the north–southward extension of Cordillera de los Andes determine different vegetation units that have been modelled principally by climate factors and topographic conditions. The climate evolution of this region during the Pleistocene–Holocene offers a unique opportunity to study and learn about its forcing mechanisms and possible interactions. The areas surrounding the southern Patagonian ice field have been major witnesses of landscape change over the Holocene. During these periods changes in glacier extent, temperature and precipitation have been determined for southern Patagonia and the Antarctic Peninsula through the analysis of different proxies from peat and lakes records (e.g. Bentley et al., 2009; Gilli et al., 2005; Heusser, 1995; Huber et al., 2004; Mancini, 2009; Markgraf et al., 2003; McCulloch and Davies, 2001; Mercer and Ager, 1983; Moreno et al., 2009; Tonello et al., 2009; Wille and Schabitz, 2009; Wille et al., 2007). Holocene climatic variations have been attributed to phenomena associated with different timescale fluctuations. Some of them take place at millennial timescales, such as those linked to solar insolation patterns (Renssen et al., 2005), while others are related to shorter timescale phenomena, such as westerlies north-poleward migration and strengthening, or long-term variations on intensity and frequency of ENSO (Moy et al., 2002, 2009). Recent research has warned about some discrepancy about western and eastern southern Patagonian paleoenvironmental and paleoclimatic interpretations. Therefore more high-resolution multiproxy studies should be carried out on the eastern side of the Andes to solve this puzzle.

Ecosystem fire regimes are a consequence of interactions among fuel accumulation, fuel moisture content and ignition sources. All these factors are directly or indirectly influenced by climate (Whitlock and Larsen, 2001). Climatic variations influence fire regimes across a broad range of temporal scales. Thus, the reconstruction of past fire regimes are of great importance for studying past climate changes and controls. The fire regime in a particular region is registered in sedimentary charcoal records through total charcoal abundance (charcoal accumulation rates), which is proportional to total biomass burned in a given depositional environment (Power et al., 2008). Charcoal particles, found in sedimentary samples from Patagonia in Argentina and Chile

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southward to Tierra del Fuego, indicate that fire has been an important source of disturbance in cool temperate *Nothofagus* forest, and Patagonian grass steppe for at least several thousand years (Moreno et al., 2009; Whitlock et al., 2007). Differences in the sensitivity and nature of the response of fire regimes to climate variation have to be considered when comparing different vegetation communities (e.g. evergreen forest versus deciduous forest; or forest versus grass steppe). Indeed, factors related to either local or landscape vegetation distribution, as well as fuel horizontal and vertical continuity and quality may be forcing differences in fire regime sensitivity and responses to environmental changes (Kitzberger, 2003; Kitzberger et al., 1997). Thus, comparing fire variations and its response to climate change under different spatial vegetation distribution is important to interpret regional patterns of climate change.

The aim of this study is to compare two fire and pollen records from the *Nothofagus* forest-grass steppe ecotone and the grass steppe at high southern latitudes. The comparison is focused on two aspects. The first emphasizes studying fire regime responses to local vegetation changes and inferred variation on climate conditions during the Holocene. The second is to compare the charcoal and pollen records between 49° and 52°S and discuss regional patterns of climate variability during the Holocene.

Study area

Cerro Frías peatland (50°24'S, 72°42'W) is located in the southern coast of Lago Argentino, 2.8 km east to the *Nothofagus* forest-grass steppe ecotone (Figure 1). The Sub-Antarctic forest that receives annual precipitation (Pann) between 800 and 400 mm is composed of two deciduous species of *Nothofagus*: *N. pumilio* and *N. antarctica*. The *N. pumilio* forest is present at higher elevations on the mountain slopes. *N. antarctica* is a typical pioneer plant that forms the timberline in Patagonia and Tierra del Fuego but also tolerates wet conditions close to mires at any elevation. Evergreen forest of *N. betuloides* is present in the southwestern sector of the Lago Argentino area where precipitation is higher (600–850 mm) than in the deciduous forest. The *Festuca pallescens* grass steppe extends between 250 and 500 mm of annual precipitation. Ecotone areas are dominated by patches of *Nothofagus* trees mixed with shrublands represented by *Maytenus magellanica*, *Embothrium coccineum*, *Ribes magellanicum*, *Gaultheria mucronata*, *Empetrum rubrum* and *Escallonia rubra*. *Baccharis patagonica*, *Berberis heterophylla* and *Mulinum spinosum* grow in drier sectors. The mean annual temperature for the area is 10°C (Puerto Banderas, 50.18°S, 72.47°W; Pisano and Dimitri, 1973). La Tercera peatland (49°11'S, 72°22'W) is located in the south shore of San Martín Lake (Figure 1) in the *Festuca pallescens* grass steppe as well. However, this site is located more than 15 km east from the *Nothofagus* forest and it neighbours the grass steppe-dwarf shrub steppe ecotone located 8 km eastward. Tussock grasses ('Coirones') dominate the area, mainly *Festuca pallescens*, *Stipa speciosa*, *Stipa humilis* and other subordinated species such as *Poa ligularis* and *Stipa chrysiphylla*, *Festuca pyrogea* and *Festuca argentina* (Movia et al., 1987). The dwarf-shrub steppe is characterised by woody plants such as *Nassauvia*, *Chuquiraga*, *Acantholippia* and *Brachyclados* and scarce cover of *Stipa*, *Poa* and *Festuca pallescens*. The shrub steppe is better represented in the Lago San Martin area (mainly on the eastern coast) than in Lago Argentino. This unit has a dense shrub and grass cover and is associated with particular edaphic and topographic conditions. Its main woody species are *Berberis heterophylla*, *Senecio filaginoides*, *Mulinum spinosum*, *Lycium chilense*, *Junellia tridens* and *Schinus polygamus*. There is larger vegetation heterogeneity at a landscape scale in Lago San Martin than in Lago Argentino (Figure 1, Movia et al., 1987). Another distinctive feature of La Tercera vegetation is that the grass steppe presents several subordinated shrubby species such as *Baccharis patagonica*, *Senecio filaginoides*, *Berberis heterophylla*, *Nassauvia* and *Mulinum spinosum* (Bamonte and Mancini, 2011; Movia et al., 1987) (Figure 1).

Methods

Chronology

Age determinations were based on accelerator mass spectrometry (AMS) ^{14}C dates from different levels of peat (plant remains) for each site (Figure 2). Ages are expressed as calibrated ^{14}C age before present (cal. yr BP) using CALIB 5.0.1 software (Stuiver et al., 2005) and calibrated with the Southern Hemisphere (SHCal04) calibration curve (McCormac et al., 2004). The basal age of Cerro (Table 1) Frias core was calibrated with the Northern Hemisphere curve (IntCal04) (Reimer et al., 2004). The age–depth models were obtained by MCAge software using a cubic smoothing spline and a bootstrap approach (Monte Carlo sampling) (Higuera et al., 2009). The confidence intervals for the age–depth models, reflecting the combined uncertainty of all age estimates, were derived from 1000 bootstrapped chronologies. For each bootstrapped chronology, each age used to develop the chronology was selected randomly based on the probable distribution of calibrated ^{14}C dates (Table 1). The final chronology represents the median age at each depth from all the runs.

Cerro Frías and La Tercera records experienced less than 10% compression after core extrusion. Previous pollen studies (Bamonte and Mancini, 2009; Mancini, 2009; Tonello et al., 2009) did not include this factor in the age–depth construction, assuming that the timing of pollen long trend patterns would have not been affected. In this high-resolution study involving charcoal analysis, depths were adjusted with field measurement information and used to construct a new age–depth model (Table 1, Figure 2).

Pollen records (Figure 6)

Pollen sampling, processing and results from both records have been previously discussed in Mancini (2009) and Bamonte and Mancini (2009, 2011). Frequencies (%) of the main taxa were calculated from pollen sums of 300–1500 grains. Pollen of *Cyperaceae*, *Podocarpus*, *Gunnera*, *Myriophyllum* and spores of Bryophyta, Pterydophytes, *Pediastrum* and *Bothryococcus* were calculated separately and related to the sum of terrestrial pollen. Pollen diagrams present the main pollen types and some of them were summed as herbs (Rubiaceae, Scrophulariaceae, Monocotyledoneae, Caryophyllaceae, Asteraceae subf. Cichorioideae, Lamiaceae, Apiaceae, Ranunculaceae, *Polemonium*, *Plumbago*, Malvaceae, Asteraceae subf. Mutisieae, *Valeriana*, Rosaceae, Chenopodiaceae, Brassicaceae, Convolvulaceae and Euphorbiaceae); shrubs and dwarf shrubs (*Berberis*, *Empetrum*, *Mulinum*, Verbenaceae, Ericaceae, Solanaceae, Fabaceae and *Nassauvia*) and dwarf shrub steppe (*Plantago*, *Azorella* and *Ephedra*). Pollen zones were established following similar physiognomic types inferred in Mancini (2009) and Bamonte and Mancini (2011).

Rarefaction analysis has frequently been used in paleoecology to estimate palynological richness, which has been interpreted in terms of plant diversity on a landscape scale (Birks and Line,

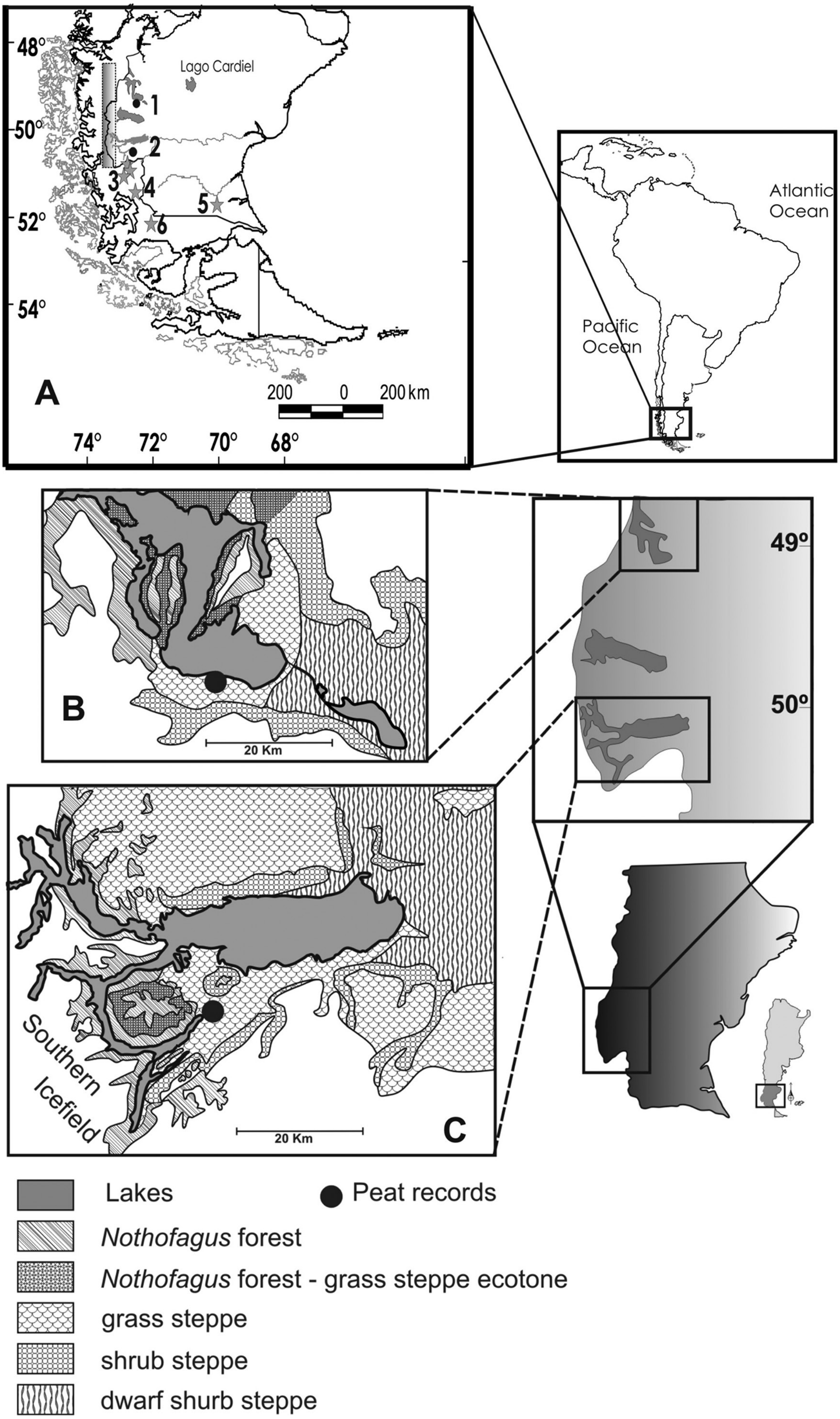

Figure 1. Geographic location of the study area. (A) Charcoal records in southern Patagonia: 1, La Tercera; 2, Cerro Frías; 3, Lago Guanaco; Vega Ñandú, Torres del Paine; 4, Meseta Latorre; 5, Potrok Aike; 6, Río Rubens. (B) Lago San Martín vegetation units and La Tercera record location. (C) Lago Argentino vegetation units and Cerro Frías record location. Different textures indicate vegetation units distribution modified from Movia et al (1987)

Table 1. Radiocarbon ages from Cerro Frías and La Tercera peat sequences.

Site	Depth(cm)	^{14}C yr BP	Cal yr BP (median probability)	References
Cerro Frías	17	280±35	296	Mancini 2009; Tonello et al. 2009
	73	990±40	852	
	306*	5590±40	6336	
	460*	8480±50	9452	
	547	11607±92	13459	–
La Tercera	53–54	1570±37	1398	–
	111–113*	5715±45	6440	Bamonte y Mancini 2009
	142–144*	7540±160	8284	
	173–174	8439±52	9407	–

*Adjusted depth estimated from field measurements

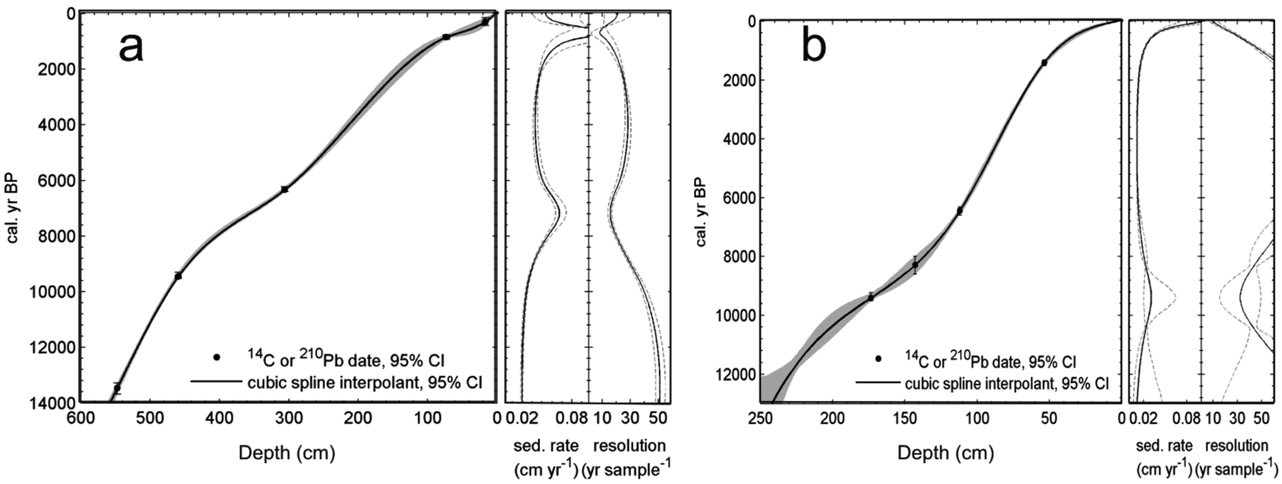

Figure 2. Age–depth curve based on five calibrated AMS radiocarbon dates from Cerro Frías (a) and four calibrated AMS radiocarbon dates from La Tercera (b). Error bars represent two standard deviations and the grey zone the 95% confidence intervals

1992). Rarefaction analysis was calculated using standardized pollen and spore counts of 118 grains for the Cerro Frías record and 213 grains for the La Tercera record. The units of rarefaction analysis represent the estimated number of pollen taxa reduced to a certain pollen sum (the lowest sum of the group of samples being compared) (Birks and Line, 1992). Palynological richness was calculated using Psimpoll 4.27 software (Bennett, 2003).

Charcoal records

Macroscopic charcoal analysis was undertaken to reconstruct local fire history. Sediment samples of 2.5 cm^3 were taken at contiguous 1 cm intervals and soaked in 10% potassium hydroxide (KOH) and 6% bleach for 24 h. They were washed through 250 and 125 µm mesh screens, and residues were counted in gridded Petri dishes (Whitlock and Larsen, 2001). Charcoal particles were counted under a stereomicroscope at 50–100× magnification. Charcoal particles were classified in grass and wood particles. In order to infer the severity of fire events a grass/total charcoal index was calculated (Whitlock et al., 2006): (total grass charcoal particles/cm^3)/(total charcoal particles/cm^3 + 1). This index ranges from 0 (indicating crown or woody fires, high severity) to 1 (indicating surface fires, low severity). Charcoal particles >250 µm and between 250 µm and 125 µm were summed together as they show the same patterns (see Figure 7). Charcoal concentrations (number of particles/cm^3) were multiplied by estimated sedimentation rate (cm/yr) to obtain the charcoal accumulation rate (CHAR; particles/cm^2 per yr) of each sample. Charcoal data were interpolated to constant 23 years in Cerro Frías record and 46 years in La Tercera record, corresponding approximately to the median temporal resolution of each record (http://CharAnalysis.googlepages.com; Higuera et al., 2007).

Low-frequency variations in a charcoal record, $C_{background}$, represent changes in charcoal production, sedimentation, mixing, and sampling, and were subtracted to obtain a residual series, C_{peak}. It is assumed that C_{peak} is composed of two subpopulations (Higuera et al., 2008, 2009): C_{noise}, representing variability in sediment mixing, sampling, and analytical and naturally occurring noise; and C_{fire}, representing charcoal input from local fires. A Gaussian mixture model was used for each sample to identify the C_{noise} distribution. The 90th, 95th and the 99th percentiles of the C_{noise} distribution were considered as possible thresholds separating samples into 'fire' and 'non-fire' events, but the 90th percentile was chosen for simplicity and between-record differences were similar based on all three threshold criteria. $C_{background}$ was estimated with a locally weighted regression using a 500- or 700-yr window in Cerro Frías and La Tercera, respectively, in order to maximize the signal-to-noise index and the goodness-of-fit between the empirical and the modelled C_{noise} distributions (Higuera et al., 2009). All statistical treatments were done using the program CharAnalysis, written by Philip E. Higuera (http://CharAnalysis.googlepages.com).

Characterization of fire regimes

Past fire regimes characteristics were inferred based on the magnitude and temporal pattern of identified charcoal peaks. Peak magnitude, the number of charcoal pieces from all samples

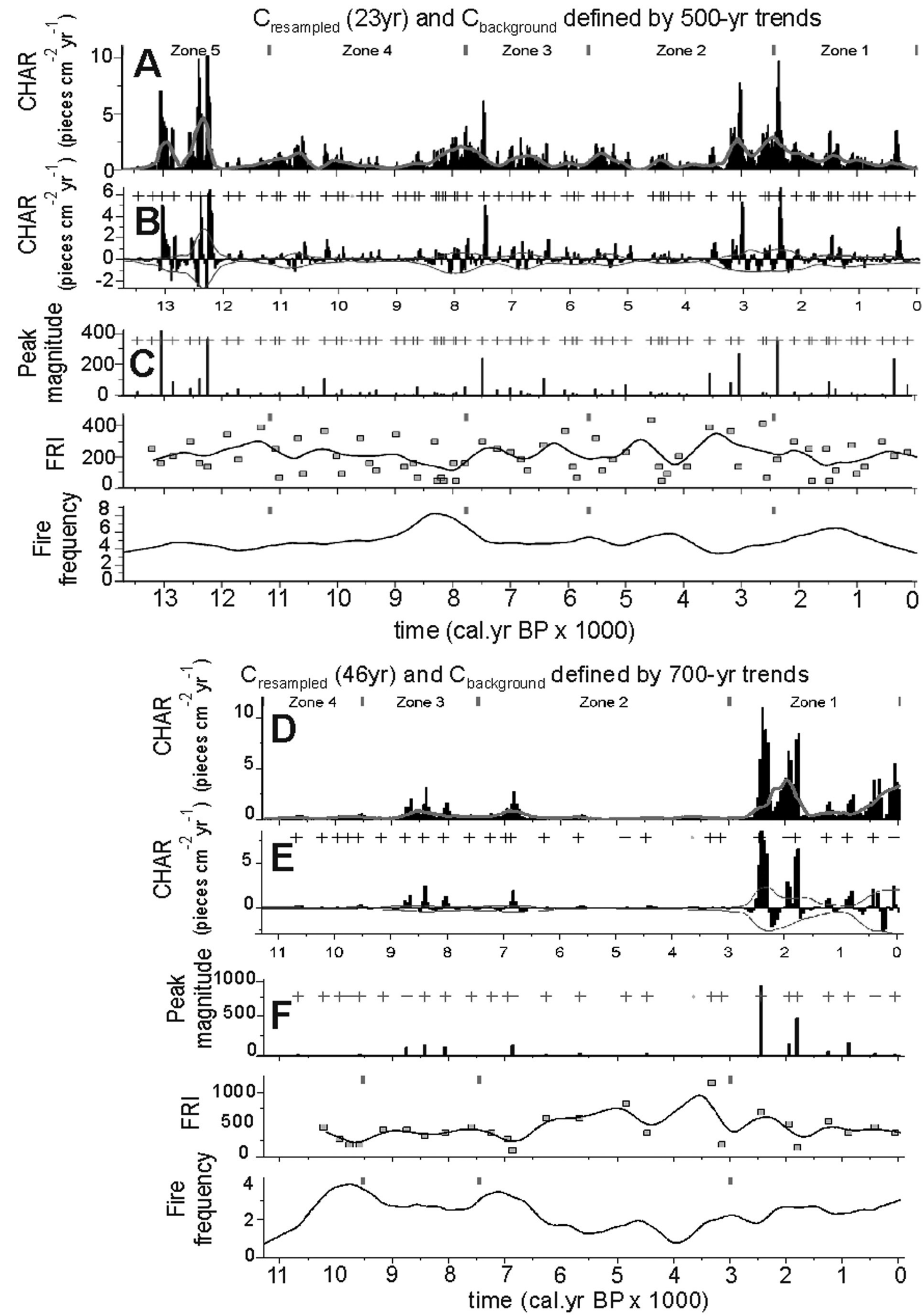

Figure 3. Charcoal records for Cerro Frías peatland (A,B,C) and La Tercera peatland (D,E,F). (A) and (D) $C_{resampled}$ (black), interpolated charcoal accumulation rates (CHAR); C_{back} (grey), background CHAR. (B) and (E) C_{peak}, peak CHAR, with the values identifying noise-related variability (positive and negative red lines). The 90th percentile criterion used for interpretation is represented with +. (C) and (F) Peak magnitude for all charcoal accumulation rate (CHAR) values exceeding the positive threshold value in panel (B); FRI, fire return interval (years per fire) and fire frequency smoothed with a 1000 year window

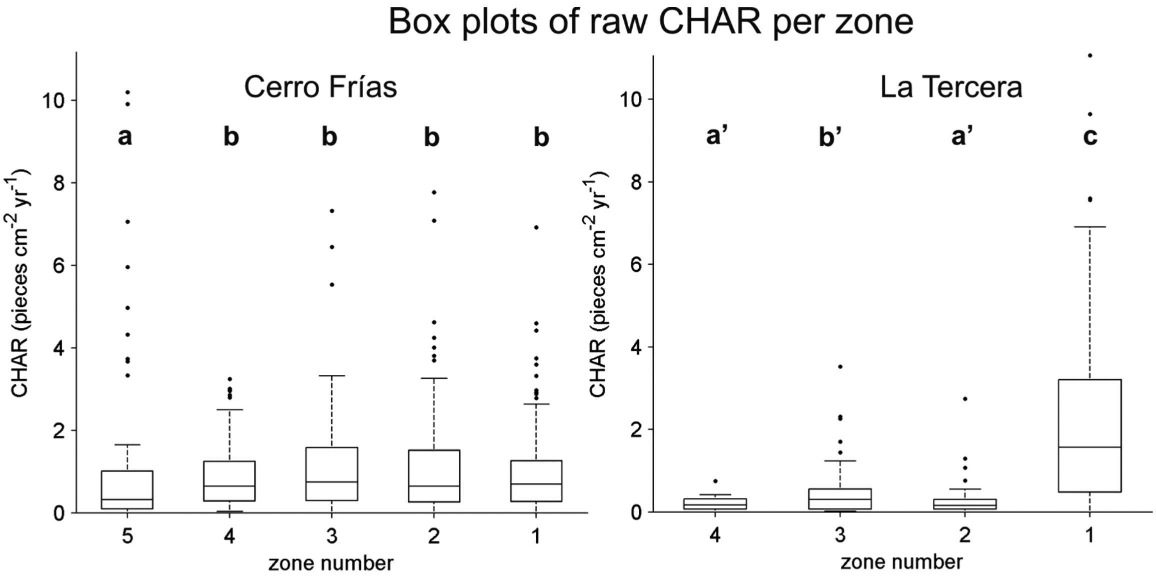

Figure 4. Variation in raw charcoal accumulation rates (CHAR) for each vegetation zone at Cerro Frías and La Tercera. Boxes bound the lower and upper quartiles, with a horizontal line at the median. Whisker bound the central 10th and 90th percentile, and dots represent outliers. Different letters indicate statistically differences between pollen zones (p>0.05)

defining a given peak, is a measure of total charcoal deposition per fire event (Whitlock et al., 2006). Changes in peak magnitude at millennial scales were used as a qualitative proxy for average fuel consumption per fire. The distribution of fire return intervals (years per fire; FRIs) within each pollen zone was used to characterize the temporal characteristics of fire regimes for each vegetation zone. FRI distributions were described by the mean FRI (FRImean). If a pollen zone had >5 FRIs (>6 fires), a two-parameter Weibull model was fit to FRIs using maximum-likelihood techniques. Goodness of fit for each Weibull models were not reported unless $P > 0.10$. Confidence intervals (95%) for Weibull parameters and FRI mean were estimated based on 1000 bootstrapped samples from each distribution. The fire return intervals pattern was smoothered with a 1000 year window in both records and compared with pollen zones. To assess whether CHAR varies statistically between past vegetation communities, we compared CHAR distributions between pollen zones using a two-sample Kolmogorov-Smirnov (K-S) test (Higuera et al., 2009).

Results

Cerro Frías charcoal and pollen records

Grass steppe dominance (zone 5) 13 700–11 100 cal. yr BP. This zone is characterized by high values of Poaceae (50–80%) accompanied by values lower than 5% of herbs, shrubs and Asteraceae subf. Asteroideae. Palynological richness has high values (16) at the beginning of the record and decreases towards 11 100 cal. yr BP (see Figure 6). CHAR values peak between 13 000 and 12 000 cal. yr BP around values of 5 and 10 pieces/cm^2 per yr (Figure 3A). Fire frequency shows no variation around 4 fires/1000 yr and peak magnitude shows the highest values of the record (50–450 pieces/cm^2 per peak, Figure 3C). Fire regime is characterized by a FRImean (95% CI) of 238 (189–296) yr (Figure 3C). Grass charcoal particles are poorly represented (see Figure 5).

Nothofagus colonization of the western slopes and open forest establishment (Zone 4) 11 100–7770 cal. yr BP. During this period *Nothofagus* percentages are higher than 30% and continue rising up to the middle Holocene. Woody plants also slightly increase while Poaceae experiences some decline. Palynological richness oscillates around 10 pollen types up to the edge of zone 3 (see Figure 6). Fire frequency shows a rising trend up to 8500 cal. yr BP representing the highest values of the record. Peak magnitude shows low values (<100 pieces/cm^2 per peak, Figure 3C). Fire regime is characterized by a FRImean (95% CI) of 164 (120–215) yr (Figure 3C). Grass charcoal/total charcoal index ranges between 0.15 and 0.3 (see Figure 5).

Open and dense forest landscape mosaic (Zone 3) 7770–5700 cal. yr BP. *Nothofagus* reaches high values (30–70%); Poaceae (50%) and herb values peak at the beginning of this period, slowing toward 5700 cal. yr BP (see Figure 6). CHAR values decline sharply and show a slight increase around 11 000 cal. yr BP (Figure 3A, B). Fire frequency remains stable around similar values to those registered previous to 11 500 cal. yr BP (Figure 3C). Peak magnitude shows moderate values between 7500 and 6500 cal. yr BP, decreasing to values lower than 100 pieces/cm^2 per peak (Figure 3C).There is a FRImean (95%CI) of 204 (141–267) yr (Figure 3C). Higher palynological richness values (10 pollen types) coincide with the highest fire frequency period (see Figure 6). A rising trend on grass charcoal particles representation is recorded towards Zone 3–2 transition (see Figure 5).

Dense forest landscape configuration (Zone 2) 5700–2400 cal. yr BP. *Nothofagus* is frequently present with values up to 50% and peaking at 80%, *Misodendrum* appears in low values and persists, Poaceae decreases indicating that the forest became denser (see Figure 6). High palynological richness (15 pollen types) is found neighbouring zone 3 and became constantly low after 4500 cal. yr BP (~ 5 pollen types) (see Figure 6). CHAR values reaches values higher than 7.5 pieces/cm^2 per peak between 3500 and 2000 cal. yr BP (Figure 3A, B). Fire frequency minimum values are recorded around 3500 cal. yr BP and then begin to increase up to 1400 cal. yr BP (Figure 3C). Peak magnitude reaches values higher than those of Zones 3 and 4. High FRI and low fire

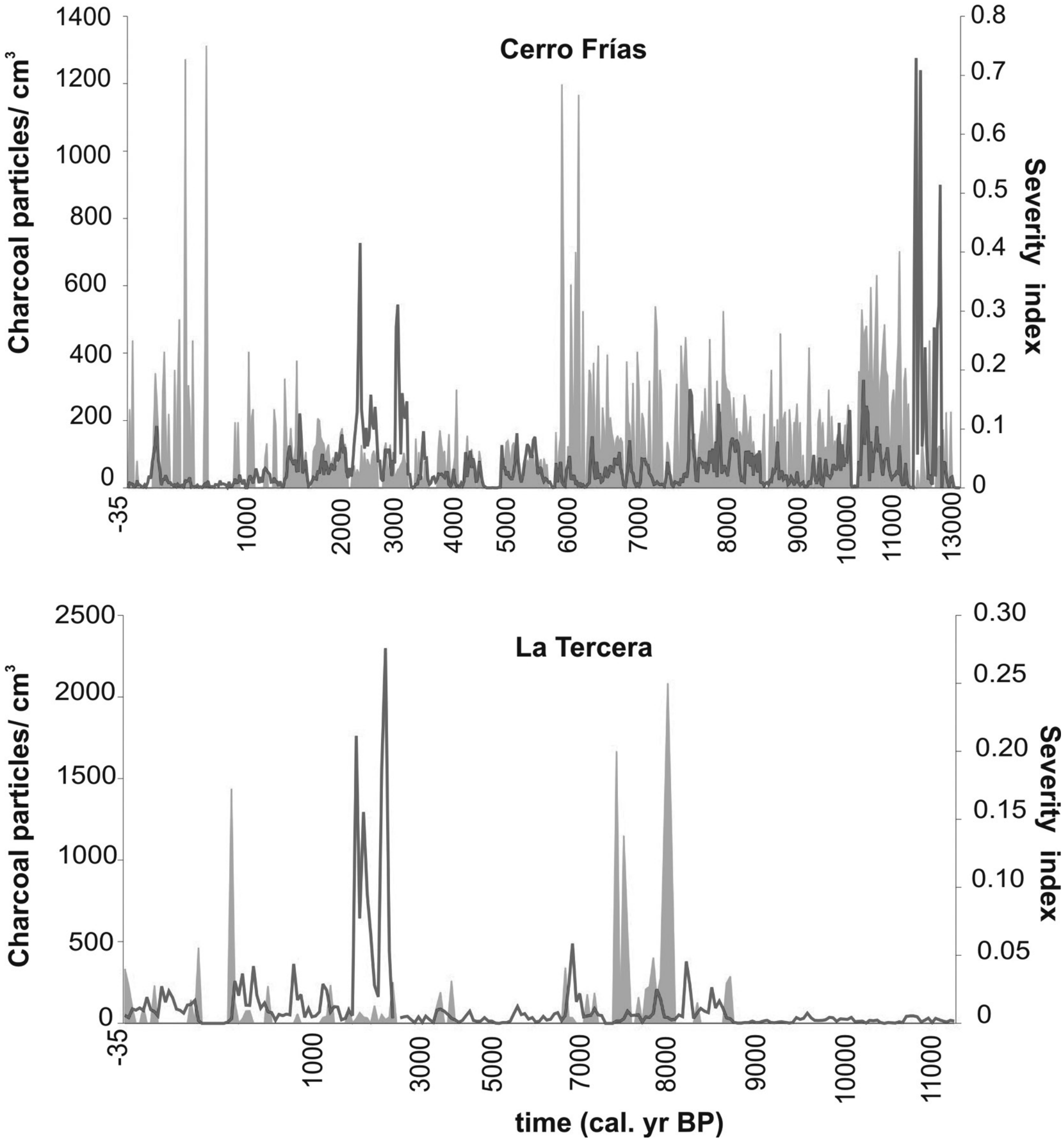

Figure 5. Fire severity index of Cerro Frías and La Tercera records. Continuous line represents total charcoal particles/cm^3. Shadow area represents values of fire severity index (grass/total charcoal index)

frequency are also registered. There is a FRImean (95%CI) of 212 (143–274) (Figure 3C). The lowest grass charcoal/total charcoal index values are registered in this period (see Figure 5).

Open and dense forest landscape mosaic reestablishment (Zone 1) 2400 cal. yr BP–present. *Nothofagus* values (40–25%) decrease and Asteraceae Subf. Asteroideae taxa increase up to 15% indicating open forest conditions. Poaceae values increase during the last centuries up to 70% (see Figure 6). Palynological richness values become significantly fluctuating and higher (see Figure 6). CHAR values show four increasing peaks reaching higher than 5 pieces/cm^2 per peak values (Figure 3A, B). Fire frequency peaks around 1400 cal. yr BP and then decreases up to the present (Figure 3C). Peak magnitude shows high values especially during the last 500 years (Figure 3C). Fire regime is characterized by a FRImean (95%CI) of 188 (134–236) (Figure 3C).

The mean global signal-to-noise index (SNI) for charcoal analysis was 0.77. This indicates a good separation between peak and non-peak values. CHAR distributions between pollen zones indicates that Zone 5 differs in CHAR values from Zones 1, 2, 3 and 4 ($p<0.05$, Figure 4). Grass charcoal/total charcoal index presents the highest values of the record (Figure 5).

La Tercera charcoal and pollen records

Dwarf shrub steppe dominance (Zone 4) 11 300–9500 cal. yr BP. Pollen percentages are dominated by Poaceae (40–60%) and dwarf shrub steppe pollen types. This zone shows an increasing trend in palynological richness towards the transition to Zone 3 (15 pollen types, Figure 6). CHAR values are extremely low (below 1.5 pieces/cm^2 per yr, Figure 3D, E). Fire frequency increases from 1 to 4 fires/1000 yr. Peak magnitude (<20 pieces/cm^2 per peak, Figure 3F) and FRI (around 250) are represented by low values. Grass charcoal/total charcoal index presents values below 0.025 (Figure 5).

Grass steppe establishment (Zone 3) 9500–7500 cal. yr BP. Poaceae values dominate (50–0%) and *Nothofagus* values are significant (10–25%). This grass steppe is characterized by the lowest values of palynological richness (10 pollen types) (Figure 6). Fire frequency decreases and peaks magnitude are represented by higher values than in the previous zone (100 pieces/cm^2 per peak). FRImean ranges around 375 years (Figure 3F). Mean grass charcoal/total charcoal index exhibits the highest values of the record (0.25) (Figure 5).

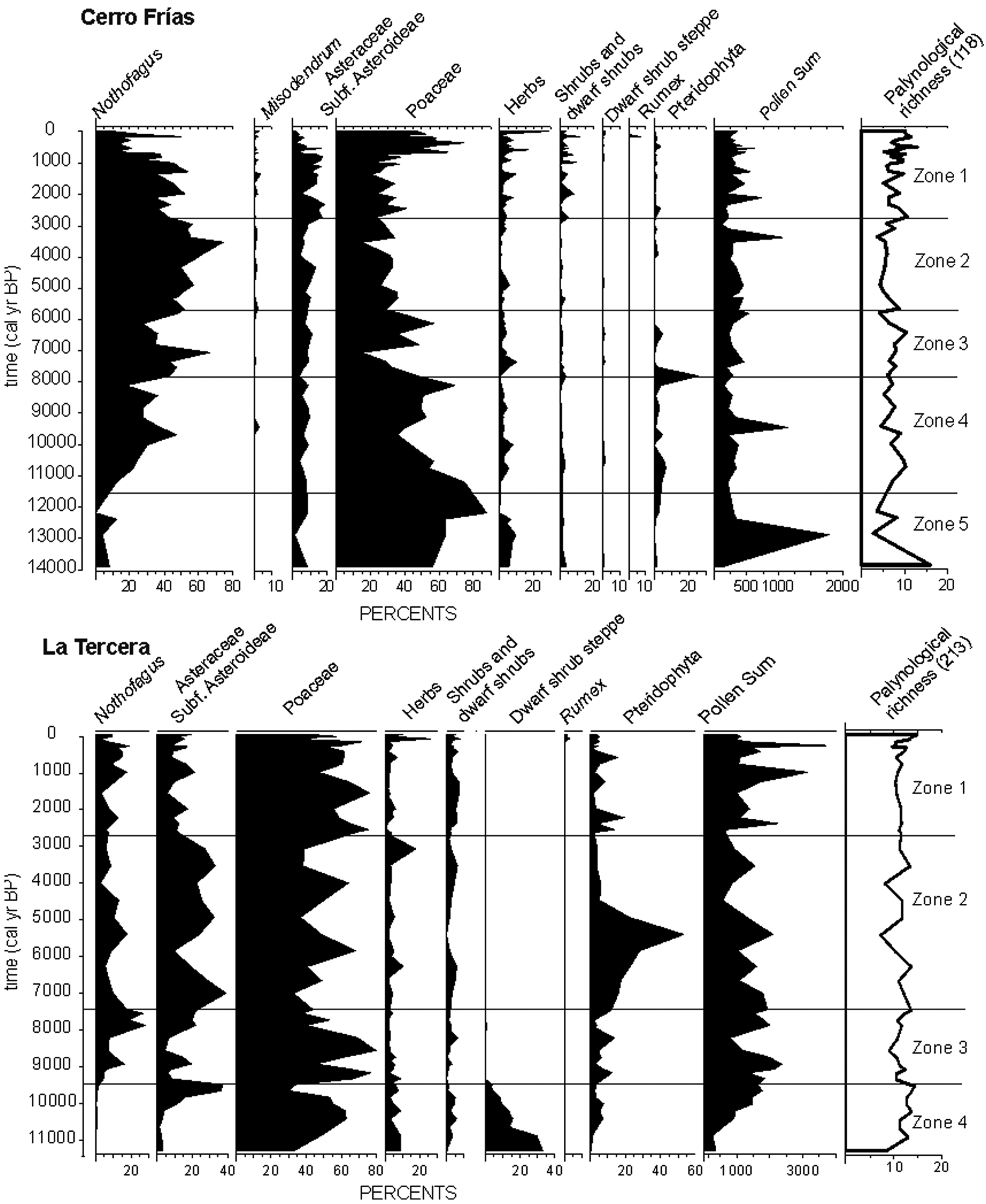

Figure 6. Pollen percentages, palynological richness and pollen zones

Grass steppe with shrub components highly represented (Zone 2) 7500–3000 cal. yr BP. There is an increase in Asteraceae subf. Asteroideae values up to 40% and Poaceae presents some variability through this zone (<25 to >50%) (Figure 6). Fire frequency and palynological richness peak at the beginning and the end of this zone but remains with low values along this time period. Peak magnitude presents values lower than 100 pieces/cm^2 per peak (Figure 3F). This zone presents a FRImean (95%CI) of 512 (299–742). Grass charcoal/total charcoal index shows values below 0.05 (Figure 5).

Grass steppe dominance (Zone 1) 3000 cal. yr BP–present. Poaceae percentages are significantly increased (>50%, Figure 6). Palynological richness remains stable around 10 pollen types. However, palynological richness increases toward 15 pollen types during the last 500 years. Fire frequency is characterized by an increasing trend towards the present. The inverse pattern is observed for FRI (FRImean (95%CI) of 399 (284–498) and Peak magnitude (from 1000 pieces/cm^2 per peak to <100 pieces/cm^2 per peak), that show a decreasing trend towards the present (Figure 3F).

The mean global signal-to- noise index (SNI) for charcoal analysis was 0.79. This indicates a good separation between peak and non-peak values. CHAR distributions between pollen zones indicate that Zone 5 differs in CHAR values from Zones 1, 2, 3 and 4 (p>0.05, Figure 4).

Discussion

Methodological issues of the charcoal record

Fire history from peat has been shown to be less powerful than that from lake sediments; however peat sequences provide very helpful insights where lacustrine sequences are lacking (Conedera et al., 2009). Several charcoal-dispersal and other taphonomic processes affecting charcoal records have been discussed specially for lake deposits and small-hollow sediments (e.g. Clark, 1988; Higuera et al., 2005, 2007; Lynch et al., 2004; Whitlock and Larsen, 2001). Some of the analytical tools and theoretical models developed for these types of depositional basins have been also applied successfully for peatland charcoal record interpretation (Olsson et al., 2010). The macroscopic charcoal record from peat sequences may be biased towards peat fires. Therefore these records may document the frequency of extreme fire years, in which drought conditions led to a lowering of the water-table and fire could have spread onto the dry peatland surface (Huber and Markgraf, 2003). Theoretical models suggest that higher amounts of charcoal particles of the higher size-classes (>200 μm) may be deposited in the basin during these peatland surface fires (Whitlock and Larsen, 2001). La Tercera and Cerro Frías charcoal records are mainly characterized by higher amounts of the 125–250 μm charcoal size fraction than the > 250 μm charcoal size fraction (Figure 7). This pattern indicates that the source area of primary charcoal may be located at a distance > 6 km from these sites (Whitlock and Larsen, 2001).

There are no models of charcoal dispersal based on these types of *Nothofagus* forests or Patagonian steppe vegetation. Therefore, it was necessary to validate inferred fire events with field evidence and historical records. Historic clearance forest fires occurred at European settlements in the 1900s in the Lago Argentino area (Perez Moreau, 1959; Pisano and Dimitri, 1973). After the foundation of the 'Los Glaciares' National Park (AD 1935/−15 cal. yr BP) there has been no record of forest fire occurrence in the Lago Argentino area. Sottile (2008) characterized the understorey vegetation and canopy of the *Nothofagus* forest at Península de Magallanes southern slopes. In this work the author inferred the occurrence of a forest fire at Peninsula de Magallanes previous to the National Park foundation. Cerro Frías charcoal analysis has recorded the last charcoal peak around AD 1850 ± 20 yr (100 cal. yr BP). The charcoal influx involved in the AD 1850 peak may have originated in Península de Magallanes forest fire. Cerro Frías charcoal record shows no peaks after AD 1850. This may suggest a good response of the statistical sensitivity of Cerro Frías peatland macroscopic charcoal record. However this hypothesis should be tested by dendrocronological studies in Peninsula de Magallanes *Nothofagus* forest.

Unfortunately, there are no historical fire records for the southern coast of Lago San Martin. During January 2010 we studied a 40 000 m^2 forest fire stand that occurred around AD 1980 (Estancia La Maipú, personal communication, 2010) at 16 km westward of La Tercera site (data not shown). This crown fire is not recorded in La Tercera charcoal peak component and the most recent one was detected around AD 1893 ± 11 yr (57 cal. yr BP). This feature may reinforce the fact that La Tercera charcoal record may be illustrating the fire history of a closer source area, specially related to the grass steppe dynamic.

The forest-grass steppe ecotone is located at present within 2.8 km westward from the Cerro Frías site at Península de Magallanes, while it is located 15 km westward from La Tercera site. Both sites are surrounded by grass communities. However, the annual prevalence of westerly winds favors the western location of the charcoal source area. According to charcoal-dispersal models, macroscopic charcoal particles (>125 μm in diameter) are abundant within a 10 km radius of a recent fire but are scarce at greater distances (Whitlock and Millspaugh, 1996). Therefore, extra-local Holocene fire reconstruction on centennial to millennial timescales at Cerro Frías may be related mainly to spread and retreat of the forest-steppe ecotone and the variable configuration of forest communities at a landscape scale over Península de Magallanes (e.g. homogeneous dense forest covering the Península versus patches of open forests mixed with steppe patches). On the contrary, La Tercera fire record may be mostly influenced by grass steppe dynamics after 9500 cal. yr BP and dwarf-shrub steppe previous to that date.

Fire regime inferences and paleoecological interpretation

Charcoal records and CHAR values have significant variability during the Holocene in both records. Variations in raw charcoal accumulation rates show rough correlations between different pollen zones. High CHAR values are associated with high values of Poaceae percentages in both records (Figures 4 and 6). At a landscape scale, open forest and grass steppe mosaics seem to favor major fire activity in forest-steppe ecotone areas (Clark et al., 2002; Kitzberger, 2003). Grass abundance favors horizontal fuel continuity, allowing surface fires to take place on these environments. Thus the presence of shrubs or/and tree patches renewal allows vertical fuel continuity favoring crown fires.

The grass charcoal/total charcoal index values are higher in Cerro Frías than in La Tercera (Figure 5). Surface temperatures during fires depend on the type and physical and chemical features of fuels. Woody fires (including forest and shrubs communities) reach higher temperatures than grasslands surface fires. The absence of grass charcoal particles in the La Tercera record during intervals of >25% of Asteraceae subf. Asteroideae, may indicate high combustion levels of fuels due to high local temperatures during fire occurrence. Wooller et al. (2000) showed that grassland produces very little charcoal. This might explain the absence of charcoal in the La Tercera record in spite of the high Poaceae contributions in the pollen record. These features should be taken into account for the interpretation of fire regimes in grassland environments. In fact, the statistical analysis of macroscopic charcoal particles of peatlands surrounded by grass steppe communities probably shows the strongest fire events giving a general picture of the fire history over the Holocene in this region.

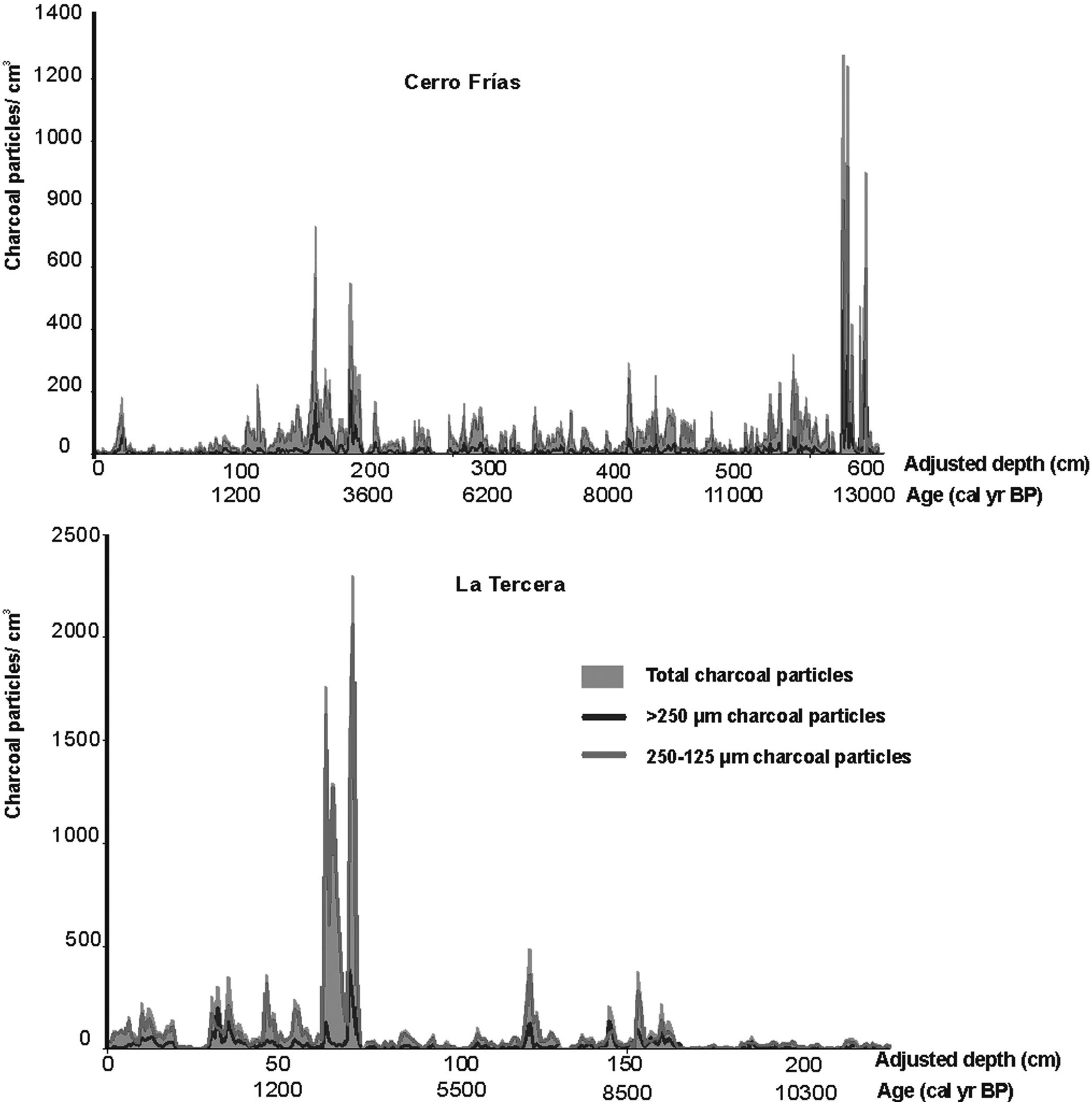

Figure 7. Cerro Frías and La Tercera charcoal particles size classes (>250 µm; 250–125 µm) and total charcoal particles/cm^3

Fire regimes model a wide variety of landscape features such as physiognomy, species replacement and heterogeneity. At a landscape scale, pollen and plant diversity are roughly correlated (Peros and Gajewski, 2008). These relationships have only been studied on coastal sand dune areas of the South Atlantic coast by Fontana (2004). Bianchi and Ariztegui (2011, this Issue) have discussed variation of palynological richness in northern Sub-Antarctic forest modern environments and Holocene fluctuations. Thus there is little known about palynological richness on Patagonian forests and steppe communities. The lowest palynological richness values in Cerro Frías are recorded between 5000 and 3000 cal. yr BP coinciding with the highest *Nothofagus* percentages. Closed *Nothofagus* forest patches would not favor understorey non-anemophilous pollen type dispersal such as *Berberis*, Apiaceae (possibly *Osmorhiza chilensis*) and Rubiaceae (possibly *Galium* spp); see Mancini (2009, 2002). On the other hand, open forest patches are colonized by a mixture of xerophytes and hydrophytes understorey species (Sottile, 2008). These understorey pollen types could be easily transported by the western air masses blowing through this open landscape. The possible relationsip between forest landscape heterogeneity and fire frequency should be carefully studied to test fire frequency–palynological richness relationships.

Patterns of fire regime, pollen percentage variation and pollen richness reconstructed during the Holocene from Cerro Frías and La Tercera showed empirical evidence of non-steady-state shifting-mosaic landscape behaviors for both areas (Perry, 2002). In landscapes dominated by *Nothofagus* forest at a stand scale, fluctuations in grass and herb biomass or tree age classes have been naturally caused by different kinds of disturbance and succession processes. At the landscape scale, fluctuation in biomass arises from the cumulative stand-level dynamics. Conversely, climate acts as top-down driver of fire disturbance regimes (Whitlock et al., 2010). These processes are illustrated in the Cerro Frías record by high correlations between high fire frequencies and CHAR during inferred open forest landscape and intermediate modeled Pann values (~ 400 mm, Tonello et al., 2009). High values of FRI and peak magnitude coincide with high values of Poaceae during the early Holocene or high values of *Nothofagus* during the middle (~7500 cal. yr BP) and late Holocene (4000–3000 and last 500 cal. yr BP). These periods may have been characterized by adverse conditions for fire activity. Then biomass would have accumulated during long time periods until a quick environmental change may have favored fire ignition and large biomass burning (brief periods of wetter conditions during the early Holocene and brief drier condition periods during high *Nothofagus* values periods).

Steppe fires in the La Tercera record may be illustrating some relationship with tussock grasses intra-community distribution. In Patagonia, steppe environments depend on precipitation amounts and interactions with tall shrubs species (Armas et al., 2008). Shrub patches are often encircled by a dense ring of tussock grasses and surrounded by scattered tussocks in a bare-soil matrix. Aguiar and Sala (1994) developed a model in which mature shrubs facilitate grasses establishment under their canopies via amelioration of microclimatic conditions and an increase in water availability compared with bare soil. The model suggests that when the shrub dies and begins to collapse, the density of grasses becomes higher than the current carrying capacity of the grass ring, which results in the death of some tussocks leading to a thinning of the grass ring. The high levels of shrubs recorded in La Tercera during the middle Holocene would have favored tussock grass biomass patchiness avoiding fire to spread to neighboring stands. During this period, the variability of Poaceae, Asteraceae subf. Asteroideae shrub values, the low fire frequency and the CHAR values may be a result of a long trend of cyclical succession during periods of fuel patchiness and low fire activity during periods of sparse grasses distribution.

Comparison with other charcoal records

Macroscopic charcoal analysis has widely been undertaken to reconstruct local and extra-local Holocene fire history in northern Patagonia, northward to 45°S (Bianchi, 2000; Markgraf et al., 2007, 2009; Whitlock et al., 2006, 2007). Holocene regional fire history reconstructions in southern Patagonia are mainly based on microcharcoal series obtained by analyzing pollen slides. Macroscopic charcoal data are available only from Rio Rubens (Huber and Markgraf, 2003; Huber et al., 2004; Markgraf and Huber, 2010) and Potrok Aike (Haberzettl et al., 2006) encompassing the entire Holocene and the last five centuries, respectively. Therefore, Cerro Frías and La Tercera records provide essential macroscopic charcoal data for southern Patagonia covering the entire Holocene, where charcoal series are decomposed in background and peak components.

Cerro Frías high CHAR and $C_{\text{background}}$ levels around 13 000–11 500 cal. yr BP are synchronous with high microcharcoal levels in Torres del Paine (Heusser, 1995).This may be explained by similar Late Pleistocene–early Holocene vegetation communities arrangements at a landscape scale surrounding the areas of Cerro Frías and Torres del Paine. The Cerro Frías CHAR pattern between 10 000 and 7000 cal. yr BP coincides with Rio Rubens microscopic and macroscopic charcoal levels and with Vega Ñandú (Villa-Martínez and Moreno, 2007) CHAR patterns. During the last 5000 cal. yr BP CHAR patterns from Cerro Frías are similar to major trends of Meseta La Torre, Torres del Paine, Vega Ñandú and particularly match with millennial- to centennial-scale variations in Lago Guanaco (Moreno et al., 2009) microscopic charcoal records patterns. Río Rubens experienced an abrupt decrease in fire frequency after 5500 cal. yr BP accompanied by the establishment of dense *Nothofagus* forests. This vegetation remained until the arrival of European settlers in the early twentieth century. Huber et al. (2004) suggested that the higher fuel moisture levels of woody fuel components may have greatly decreased the probability of fire, even in the presence of ignition sources. Considering the southern location of Rio Rubens, after 5000 cal. yr BP, this area may have been affected by westerlies and polar air moisture allowing dense forest establishment and stability. Rio Rubens fire and vegetation trends during the last 5000 cal. yr BP match those of Tierra del Fuego records (Huber et al., 2004) suggesting similar climatic conditions and forcing factors southward to 52°S. The Cerro Frías charcoal record seems to reflect regional patterns of fire regime northward of 52°S. Differences in centennial charcoal patterns synchronicity of Cerro Frías to other forest-steppe ecotone records during the late Holocene may be partially explained by the necessity of better chronological adjustment.

Huber et al. (2004) suggested that in the grass steppe, low accumulation and discontinuous fuel structure may potentially become limiting factors for the occurrence of fires during the middle Holocene. La Tercera charcoal record allows us to test this hypothesis partially. Macroscopic charcoal from La Tercera suggests that between 11 500 and 9500 cal. yr BP reduced CHAR and $C_{\text{background}}$ values illustrate limited fuel accumulation because of too dry conditions. Since the early Holocene three periods of favorable moisture based on pollen and charcoal records are registered: (1) during 9500–8500 cal. yr BP, (2) during 7000–6500 cal. yr BP and (3) during the last 2500 cal. yr BP. La Tercera charcoal record shows higher variability than Potrok Aike charcoal record. The microscopic charcoal record of Laguna Potrok Aike located in the grass steppe peaks between 13 000 and 11 000 cal. yr BP and remains stable until the last 500 years (Wille et al., 2007). The differences between sites might be explained by differences on the patterns of vegetation communities surrounding the basins. However La Tercera charcoal record seems to be sensitive to regional reconstruction of climate variability during the Holocene in southern Patagonia.

Late-Pleistocene and Holocene fire regime responses to inferred climate change

Glaciological studies have suggested glacier recession since 13 500 cal. yr BP in Lago Argentino area (Strelin and Malagnino, 2000). Poaceae dominance and high charcoal depositional rates in Cerro Frías record during the Late Pleistocene imply dry conditions or the occurrence of successive shifting humid-to-dry periods dealing fuels to support fires. Temperatures must have been high enough to allow grass type fuels to reach the ignition

Table 2. List of charcoal and pollen records of southern Patagonia

Site name	Location	Modern environnment	Type of record	Source
Río Rubens	52.08 S/71.52 W	Deciduous forest	Peat	Huber and Markgraf, 2003
Meseta Latorre I	51.31 S/72.03 W	*Nothofagus antarctica* woodlands	Mire	Huber et al., 2004
Torres del Paine	50.59 S/72.40 W	Scrub steppe(close to steppe-forest ecotone)	Peat	Heusser, 1995
Vega Ñ and ú	51 S/72.75 W	*Nothofagus* forest-Patagonian steppe ecotone	Peat	Villa-Martínez and Moreno, 2007
Lago Guanaco	51.03 S/72.83 W	*Nothofagus* forest-Patagonian steppe ecotone	Lake	Moreno et al., 2009
Launa Potrok Aike	51.97 S/70.38 W	Dwarf shrub steppe	Lake	Wille et al., 2007

temperatures. Ackert et al. (2008) suggested that the ice caps retreated within the Cordillera during the so-called Antarctic Cold Reversal (15 000–11 000 cal. yr BP) coinciding with Cerro Frías pollen and charcoal signals. After 12 000 cal. yr BP CHAR values decreased rapidly suggesting colder and humid conditions (Tonello et al., 2009) suppressing fire activity.

Early-Holocene paleoclimate models (Renssen et al., 2005) describe higher than present mean annual insolation poleward of 45°S due to changes in the Earth's obliquity. This large-scale phenomenon would illustrate a possible mechanism for generating weaker westerlies in the early Holocene and shifting them poleward. Vegetation shifted from a dwarf-shrub steppe to grass steppe dominance in La Tercera (Bamonte and Mancini, 2011) shifting the grass steppe-dwarf shrub steppe ecotone eastward. This vegetation change and high fire frequency during 10 000–9000 cal. yr BP, suggest western precipitation was reaching the area. During weaker westerlies periods, west–east precipitation gradients would be gentler than during intense westerlies (Garreaud et al., 2009; Moy et al., 2009; Whitlock et al., 2007). High CHAR levels during the early Holocene (9000–7000 cal. yr BP) in Cerro Frías and other southern Patagonia forest-steppe ecotone records (Table 2) would also support this hypothesis. An intensification of westerlies at 50°S during the mid Holocene (~5000 cal. yr BP) is suggested by the Pann increase in Cerro Frías (Tonello et al., 2009) and other paleoclimatic records (Villa-Martínez and Moreno, 2007). This intensification may have been associated with a steepening of the pole-to-equator temperature gradient, caused by a cooling trend in the South Pacific Ocean and Antarctica (Bentley et al., 2009). Cerro Frías low fire activity during the middle Holocene and the highest *Nothofagus* pollen values, illustrate the highest Holocene precipitation values in this area. During this period, the increase in shrubs, low grass values, low fire activity and deposition of marl layers in La Tercera (Bamonte and Mancini, 2011) indicate lower moisture availability than in the early Holocene towards the east. An intensification of the westerlies and a steepening in the west–east precipitation gradient can account for these vegetation and fire patterns several kilometers eastward to the Andes.

Four wet pulses and Neoglacial maxima (4400–4100, 2900–1900, 1300–1100 and 570–60 yr cal. BP) have been linked to increased precipitation of westerly origin at centennial–millenial timescales in Lago Guanaco and Pantano Margarita (Moreno et al., 2009; Villalba et al., 2005). Humid conditions inferred at La Tercera and drier conditions inferred at Cerro Frías would suggest an amelioration of westerly winds allowing humid air masses to reach eastward into the steppe next to the Andes (Moy et al., 2009). Wille et al. (2007) suggest an increase of available moisture in Potrok Aike after 2300 cal. yr BP. Air masses from easterly directions reached Potrok Aike during weakened Southern Hemisphere westerlies (Mayr et al., 2007) giving rise to enhanced precipitation. Climatic patterns inferred in Cerro Frías and La Tercera are coincident with this regional circulation picture for the late Holocene. After 2500 cal. yr BP both records present some CHAR peak variability which may be linked to Neoglacial advances driving factors. However, better chronological control is necessary to check these connections. Also, late-Holocene climate variability and consequently fire regime variability may be attributed to the increasing strength of ENSO (Moy et al., 2002).

Conclusion

Cerro Frías and La Tercera charcoal records seems to be sensitive to centennial and millennial timescale vegetation and climate variability inferred for southern Patagonia.

Holocene fire activity increases in steppe environments and decreases on forest-steppe ecotone landscapes as effective moisture increases. Forest patchiness provided vertical and horizontal fuel continuity favoring fire activity. In contrast, in steppe environments high cover of shrubs favored grass patchiness, impeding fire spread. These conditions were recorded in eastern areas during the Pleistocene–Holocene transition and during the middle Holocene.

High and moderate CHAR values have been recorded during three periods in Cerro Frías: (1) between 13 000 and 10 000 cal. yr BP, (2) between 8000 and 6000 cal. yr BP and finally (3) around 2500 cal. yr BP. La Tercera record registered two pulses of moderated CHAR values that occurred between 9000 and 6500 cal. yr BP. The higher CHAR values took place around 2500 cal. yr BP.

Past fire regime variability in southwestern Patagonia at the eastern side of the Andes seems to have been closely related to westerly moisture influence between 52° and 49°S. Southern latitudes seem to be influenced also by other forcing factors probably related to the dynamics of polar air masses intrusions to the continent during the last 5000 cal. yr BP. More lake and peat macroscopic charcoal analyses combined with long-term forest dynamics studies should be undertaken in forest and steppe environments at the east side of the Andes in order to test the influence of western versus eastern air masses during the Holocene.

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