
Volume 261, issue 1, 1 January 2011
ISSN 0378-1127
ELSEVIER
Forest Ecology and Management

Forest Ecology and Management 265 (2011) 218–229

Contents lists available at SciVerse ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Carbon storage, community structure and canopy cover: A comparison along a precipitation gradient

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ARTICLE INFO

Article history:
Received 6 May 2011
Received in revised form 26 October 2011
Accepted 27 October 2011
Available online xxxx

Keywords:
Aboveground biomass
Carbon storage
Arid Chaco and Monte
Nature reserves
Community structure
Plant functional types

ABSTRACT

Protected areas play a significant role in carbon storage in arid and semi-arid land. In the central region of Argentina, there are three nature reserves located along a West to East rainfall gradient between two different phytogeographical provinces: the Monte and the Arid Chaco. The aims of this work were: (1) to quantify carbon storage in the three nature reserves and (2) to compare the different vegetation communities in the internal structure, expressed as canopy cover, diversity and relative abundance of woody plant functional types in each of the nature reserves. The combination of remote sensing data with a detailed inventory and local biomass allometric equations models were found to be appropriate tools for the estimation of carbon storage in each nature reserve. In general, canopy cover and carbon storage tends to increase from west to east and, within each nature reserve, from shrubland into mature forest community. Total carbon storage in mature woodlands ranged from 48 to 95 Mg ha^{-1}, in open and mixed woodlands from 21 to 36 Mg ha^{-1}, and in shrublands from 8 to 19 Mg ha^{-1}. On the other hand, many similarities were observed between the mixed woodlands of the wetter Reserve and the mature forest of the more arid Reserve of the Arid Chaco, based on the organization of plant functional types, canopy cover and carbon storage. This knowledge of carbon storage would thus be a useful input for the development of strategies for reducing CO_2 emissions caused by deforestation and forest degradation and, in particular, it is significant for planning policies to mitigate desertification in arid and semiarid lands.

1. Introduction

Forests account for a large fraction of the carbon (C) stored in soils and vegetation globally (Dixon et al., 1994; Woomer et al., 2004; Keith et al., 2009). During recent decades, the amount of C stored in the biomass has gained special attention as a result of the UN Framework Convention on Climate Change (UNFCCC) as well as its Kyoto Protocol. Knowledge of the C storage function of protected areas would therefore be a useful input into the development of strategies for reducing CO_2 emissions caused by deforestation and forest degradation (REDD) (Campbell et al., 2008) and, in particular, it is significant for planning policies to mitigate desertification in arid and semiarid lands. Although the need is great, little is known about the C storage potential of the protected areas, especially in arid and semiarid lands of Argentina with different water availability (Bonino and Araujo, 2005; Gasparri et al., 2007).

Arid zones cover 40% of the Earth's surface (Dregne, 1991; Verón et al., 2006), and forest covers 6% of these zones (i.e. 230,000,000 hectares) (Malagnoux, 2007). In Argentina, arid and semiarid regions represent 70% of the territory (Roig et al., 1991; Fernandez and Busso, 1997), and more than 75% of this area is affected by desertification processes (SRNyDS, 2002). In these areas, native forests provide most of their economic productivity, so it is very important to have detailed information on their extent and on the role of these forests in C storage (Abraham, 2002). These regions are functionally dependent on hydro-ecological systems, showing a strong feedback at different scales, spatial and temporal (Noy-Meir, 1973; Ludwig et al., 2005; Iglesias et al., 2010), in which water controls primary productivity and therefore the potential accumulation of C of the whole system (Wiegand and Jeltsch, 2000; Verstraeten et al., 2006). Studies on the relationship between vegetation and climate show a positive association between water availability and the increase of C storage (Steffen et al., 1999; Woomer et al., 2004; Dauber et al., 2008; Cifuentes Jara et al., 2008) represented by soil coverage and functional plant types (Cabido et al., 1993; Ni and Zhang, 2000; Caylor et al., 2003; Ni, 2003).

It is known that vegetation is a good indicator of climate variation and desertification (Tongway, 1995; Wu et al., 2000; Hanson

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doi:10.1016/j.foreco.2011.10.036

and Weltzin, 2000; Verón et al., 2006; Maestre and Escudero, 2009), which makes nature reserves ideal places to obtain reference values for desertification and climate change studies (Reynolds and Stafford Smith, 2002; Reynolds et al., 2005; Paruelo et al., 2005; Verón et al., 2006), since these mature systems keep their structure and function with no anthropogenic disturbance (Illera et al., 1998; Alcaraz-Segura et al., 2008). Nevertheless, many nature reserves in central Argentina have received anthropogenic and natural disturbances in the past such as fire, over-grazing and excessive logging (Carranza et al., 1992; Cabido and Pachá, 2002; Bonino and Araujo, 2005; Villagra et al., 2009; Pelegrin and Buche, 2010) and clearly show a loss of biodiversity, canopy cover and biomass (Gandía and Meliá, 1993; Reynolds et al., 2005).

In recent years, there is an increase interest in the global distribution of vegetation types and their implication in global change research (IGBP, 1990; Townshend et al., 1991; Loveland et al., 2000; Pan et al., 2003; Song et al., 2005; Weng and Zhou, 2006; Xu and Yaping, 2009). Plant communities in dry lands have exhibited widespread and fast changes in response to changes in climate and/or disturbance in the past (Archer et al., 1988; Keeley and Mooney, 1993; Shugart, 1998; Ni, 2003; Pausas et al., 2004). A main approach for assessing the complex responses of these communities is to identify plant functional types (PFTs) and characterize the functional response of each type to a suite of environmental conditions (Golluscio and Sala, 1993; Epstein et al., 1997; Steffen et al., 1999; Smith et al., 1997). Reliable, georeferenced data on arid vegetation cover is a basic requirement to the modeling of the earth system (IGBP, 1992). The conjunction of field information as vegetation types distribution and the percentage of cover with satellite sensor data can provide a truly synoptic view of these systems. As an example we can mention Woomer et al. study (2004) who combined satellite imagery information from different years of Africa's Sahel ecological regions with field-based carbon measurements adjusted for generated estimates of total terrestrial carbon stocks in Senegal. This methodology allows to study diverse areas with different climatic conditions as a different scenarios of climatic global change.

In the central region of Argentina, there is a clear rainfall gradient in the area between the Monte Phytogeographical Province and the Arid Chaco. There are three nature reserves with different mean annual precipitation, and there are reported changes in plant functional types with increasing gradients of aridity (Cabido et al., 1993). Based on these, it was hypothesized that as the mean annual precipitation in the environmental gradient increases, the vegetation canopy cover, diversity and C storage of woody species will increase too. Moreover, the PFTs vary in abundance responding to the change in the precipitation gradient and in the different vegetation communities present in each nature reserve. The aims of this work are (1) to analyze the contribution of woody vegetation in C storage and the variation of its accumulation in three nature reserves located in areas with a range of 150 to 500 mm of mean annual precipitation; and (2) to compare the internal structure of vegetation communities in each of the nature reserves.

2. Materials and methods

2.1. Study area

The study was carried out in three provincially managed nature reserves in the centre of Argentina with different mean annual precipitation values (Fig. 1) varying from 150 mm to 513 mm. The distance between the eastern and western nature reserve was 280 km. The central Nature Reserve was located 116 km east of the western Reserve.

The driest study area is Telteca Nature Reserve, located in the central plains of northeastern Mendoza, Argentina, (32°20′S; 68°00′W, 500–550 m elevation), on the alluvial plain of Mendoza river in the eastern foothills of the Andes in Mendoza province. This nature reserve, within the phytogeographical Province of Monte, was created in 1986 and covers an area of 38,507 ha. Geomorphologically, it is undulated lowland with transverse dunes oriented NNW–SSE. The water table in the lowlands is located 6–15 m below the surface and no permanent surface water is present in the dune territory. Soils are poorly developed Entisols with 95% sand (Jobbagy et al., 2011). The climate is hyper-arid (Torres Guevara, 2007), with mean annual precipitation around 159 mm (Villagra et al., 2005) concentrated in summer. Mean annual temperature is 18.5 °C with high daily and annual thermal amplitudes, with absolute maximum and minimum values that range from 48 °C in summer to −10 °C in winter (Álvarez, 2008). Annual potential evapotranspiration exceeds 900 mm. Because of this limitation, it was widely known that underground water is the most important source of water for tree growth in this Reserve (Morello, 1958; Roig et al., 1991; González Loyarte et al., 1990, Villagra, 2000; Álvarez et al., 2006; Villagra et al., 2009). The vegetation is part of the Central Monte Desert, and several landscape units support the different plant communities: (1) Open Shrubland on dunes (with dominance of *Bulnesia retama*), (2) shrubland of Zygophyllaceae (*Larrea divaricata and L. cuneifolia*), (3) open woodland of *Prosopis flexuosa*, (4) mixed woodland of *P. flexuosa* and *Geoffroea decorticans* and (5) mature woodland of *P. flexuosa* with density of adult trees, height and coverage of *Prosopis* higher than the other three woodlands.

The other two nature reserves belong to the phytogeographical Province of Chaco (Cabrera, 1976) in the south-western portion of the arid Chaco. Both include a mosaic of plant communities, such as forest of *Aspidosperma quebracho-blanco* ('quebrachal'), dominated by 'quebracho blanco' (*A. quebracho-blanco*) and *P. flexuosa*. In the shrub layer (up to 4 m high), the principal species are *Prosopis torquata, Mimozyganthus carinatus* ("lata"), *Parkinsonia praecox* ("brea"), *Geoffroea decorticans* ("chañar"), *Bulnesia retama* ("retamo"), *Celtis ehrenbergiana* ("tala"), *Larrea divaricata* ("jarilla"), *Capparis atamisquea* ("atamisqui"), *Condalia microphylla* ("piquillín") and other shrubs (Luti et al., 1979; Morello et al., 1985; Carranza et al., 1992; Chebez, 2007). Quebracho de la Legua Nature Reserve, is located in the piedmont plain (32°21′S and 66°55′O, 500–550 m elevation) in Ayacucho Department, western Province of San Luis. Was created in 1979, with an area of 2243 ha, it is considered an "ecotone" between Chaco forest of *A. quebracho-blanco* and *Prosopis flexuosa* woodlands typical of Monte desert (Del Vito et al., 1994). The climate is arid (Torres Guevara, 2007) with mean annual precipitation around 308 mm (1980–1990, National Weather Service for the study area), concentrated in summer. Mean annual temperature is 18 °C (Del Vito et al., 1994). There is no surface water and groundwater is deep and is of poor quality. The soils are sandy loam in texture, with occasional areas of bare soil associated with high water erosion and low organic material content (Chebez, 2007). In Quebracho de la Legua, several landscape units support the different plant communities: (1) Shrubland, (2) Open forest of *A. quebracho-blanco* and, (3) Mature forest of *A. quebracho-blanco.* Finally, Chancaní Provincial Park and Nature Forest Reserve is located at 30°22′S and 65°26′W (450–500 m elevation) in Pocho Department, on the western slope of the "Sierras de Pocho-Guasapampa", in the west of Córdoba province, Argentina. This Reserve has an area of 4960 ha and was created in 1986. The climate is arid–semiarid (Torres Guevara, 2007), with mean annual precipitation around 513 mm (1973–2003, internal records of the Reserve) concentrated in summer, and mean annual temperature is 20 °C (Capitanelli et al., 1979). The soils are sandy loam in texture and there is no data on the deep groundwater in the Reserve. In Chancaní, the different plant communities present in the Reserve are: (1) Shrubland, (2)

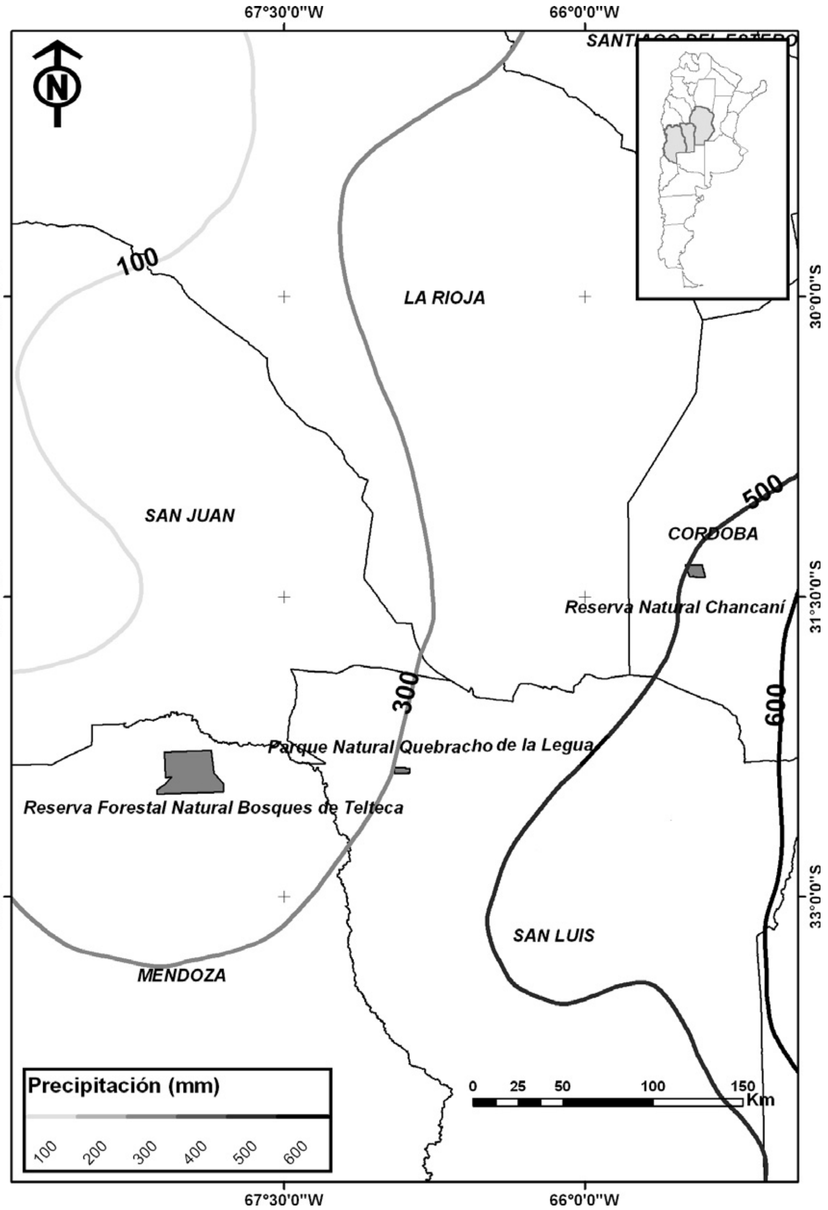

Fig. 1. Location of the three nature reserves and isohyets of annual rainfall average based on national weather service.

Open forest of *A. quebracho-blanco*, (3) Mixed forest of *A. quebracho-blanco* and *P. flexuosa*, and (4) Mature forest of *A. quebracho-blanco.*

The three nature reserves have a heterogeneous landscape. Before they were created as reserves, some sectors were affected by factors that generated forest fragmentation and the formation of new regressive states of vegetation, such as logging, grazing and, in some cases, fire. In particular in the Chancaní and Telteca Reserves, the extensive logging of species such as *A. quebracho-blanco* and *P. flexuosa* is very well documented, generating the transition of mature woodlands to other vegetation formations (Bonino and Araujo, 2005; Bonino, 2006; Villagra et al., 2009).

2.2. Field measurement

In each nature reserve, the different types of vegetation cover, such as different kind of plant communities as woodland, forest and shrubland were discriminated by field observation. The field survey was carried out from 2007–2008 to map out the three nature reserve vegetation. All species were recorded in belt transects of 250 m^2 (50 $\times$ 5 m) to describe the different vegetation cover present in each Reserve. A total of 31, 18 and 22 belt transects were taken for Telteca, Quebracho de la Legua and Chancaní, respectively. In each belt transect we sampled the relative abundance of the woody species, the richness and canopy cover (percentage), recorded in a line 50 m long. Also, the height and diameter at the base (DAB) of each individual woody tree or shrub was recorded. To determine the heights, we use tape measure for tree >3 m, and for tree <3 m we used the Height of Person Method (http://www.ontariowoodlot.com/pdf_older/simple_tools_measuring.pdf.) and to record the DAB we employed a tape measurement. The canopy cover can be defined as the percent of vegetation area occupied by the vertical projection of tree and shrub crowns (Avery and Burkart, 1994; Korhonen et al., 2006) in a line 50 m long. Finally a global positioning system (GPS) reading was taken at the beginning and finish of each transects using a Garmin TM GPS system to identify each transect with an accuracy of 10 m. GPS readings were also collected for different vegetation communities through an extensive observation in the field (around 120 point in Telteca and 100 in Quebracho de la Legua and Chancaní).

2.3. Land cover classification

To obtain maps of C storage of each Reserve, we used high resolution satellite imagery from the Landsat TM 5 platform, level five (231–083, 231–082 and 230–082 for the month of March 2002, December 2002 and February 2001, respectively). We employed summer images as summer is the rainy season in the area. The study areas have cloud-free conditions. Pre-processing of satellite data, includeed radiometric and geometric correction. For radiometric correction we employed the gain and offset data provided for each image band. Later the Landsat TM images were georeferenced in Idrisi Taiga (Eastman, 2009) with approximately 30 ground control points (GCP's), collected in quadrangles distributed throughout each study area. Using these points, linear geometric transformations were computed. Then, each image was classified using a maximum-likelihood classifier under supervised. Six classes were extracted in Telteca Reserve (Open Shrubland on dunes, Shrubland of Zygophyllaceae, Open woodland of *P. flexuosa*, mixed woodland of *P. flexuosa* and *Geoffroea decorticans,* Mature woodland of *P. flexuosa* and bair soil), four in Quebracho de la Legua (Shrubland, Open forest of A. Quebracho-blanco, Mature forest of *A. quebracho-blanco* and bair soil) and five classes in Chancaní Reserve (Shrubland, Open forest of *A. quebracho-blanco*, Mixed forest of *A. quebracho-blanco* and *P. flexuosa*, Mature forest of *A. quebracho-blanco* and bair soil).

2.4. Data analysis

First, we generated PFTs for the woody species of the area. We compile data on both physiological and ecological traits of the principal species found in the three nature reserve. The dataset was analyzed using Principal Component Analysis (PCA) and a simple numerical hierarchical agglomerative clustering method with Gower's General Similarity Coefficient in the statistical package InfoStat (2007, 2008). The Gower metric was chosen for this study as it can measure the association between mixed data types, whether these are a combination of ordinal, continuous or binary data types. The main ecological traits surveyed were the following:

- Average values of DAB and height of the samples recorded in the field.
- Life form, considered as continuous categories: (1) monopodial trees, (2) species with both life forms: small monopodial trees or shrubs with multistem structures, (3) shrubs with multistem structures.
- Wood density, obtained in previous studies (Vendramini, 2004; Zanne et al., 2009; Iglesias, 2010).
- Specific Leaf Area (SLA) based on published information of species of the region under Arid Chaco studies (Vendramini et al., 2002; Vendramini, 2004; Giorgis, 2004). As a way to synthesized the available information, four ranges of SLA were considered: (1) from 0 to 4 mm^2/mg; (2) from 4 to 8 mm^2/mg; (3) from 8 to 12 mm^2/mg; (4) greater than 12 mm^2/mg. There were no SLA values for *Aloysia grattissima*, *Larrea cuneifolia*, *Atriplex emarginatum*, *Prosopis torquata*, *Cercidium praecox* and *Mimozyganthus carinatus*, and therefore a rank value was assigned based on morphological similarity to other species.

From this analysis, PFTs were generated. Then, the PFTs richness (number of PTFs per unit area, relative abundance (the proportion of each PTFs per area) and the diversity index (Simpsońs and Shannon-Wiener, Magurran, 1989) were analyzed.

Second, we estimate the biomass of the PTFs. These estimations were based on allometric equations that were previously developed on the basis of direct measurement, using destructive methods for species in the study area (Álvarez et al., 2011; Iglesias and Barchuk, 2010; Iglesias, 2010). For those species that did have an allometric equation, the biomass was estimated by applying the corresponding regression equation for the functional type. The total biomass was obtained by applying these allometric equations to each individual present in each belt transect. Biomass can be converted to total C content by assuming that biomass is approximately 50% C (Gaillard de Benítez et al., 2000; Vidal et al., 2003; Menéndez et al., 2005; Vande Walle et al., 2005). Finally, these values were averaged to obtain biomass per hectare and the contribution (in percentage) of tree and shrub for each plant communities.

Third, the different plant communities were characterized and compared on the basis of the results of the censuses. The variables analyzed were: mean values of floristic composition of functional types of plants, amounts of C and percentage of canopy cover. Then a conglomerate analysis was made to group plant communities according to their similarities.

Fourth, we estimate the C storage, in metric Mg of C per hectare, for each Nature Reserve. These values were obtained by multiplying average values of C of each particular vegetation community (obtained from the biomass inventories) and the area of each vegetation community. Finally, the total stock of C for each Nature Reserve was obtained by adding the contributions of C of each vegetation community present in each nature reserve.

3. Results

3.1. Canopy cover and height

The canopy of mature forest in Arid Chaco Reserves was almost exclusively composed of *A. quebracho-blanco,* with a maximum height of 9 and 12 m in Quebracho de la Legua and Chancaní, respectively. In Telteca, the canopy of mature woodland was exclusively composed of *P. flexuosa*, with a height of 7 m.

As we expected, the percentage of canopy cover tends to increase from west (Telteca) to east (Chancaní) with increasing the mean annual precipitation. In each Nature Reserve, the mature forest presented the greater coverage in each site, with values of 54%, 84% and 82% for Telteca, Quebracho de la Legua and Chancaní. In telteca, the open and mixed woodland presented values of 34% and 52%. In Quebracho de la Legua the open forest arise 60% of canopy cover. In Chancaní open and mixed forest showed values of 63% and 68%. The canopy covers of shrubland in Telteca were between 28% and 33% (shrubland in dune and shrubland of *Larrea sp.*). In the arid Chaco, shrubland canopy cover presented values of 51% and 54% in Quebracho de la Legua and Chancaní.

3.2. Supervised classifications

In Telteca Reserve, due to the high heterogeneity of the landscape, there was confusion between some vegetation classes, in particular between the three types of woodland communities, showing an overall kappa coefficient of 0.5. The classification map showed the presence of dunes almost devoid of vegetation (open shrubland on dunes) and close to this, *Prosopis* forests, usually in the lower parts of the dunes (Fig. 2, left). The most degraded part of the Reserve is an old riverbed, with bare ground surrounded by open shrubland dominated by *L. divaricata.*

The kappa coefficient was 0.69 for the Quebracho de la Legua Reserve supervised classification. This suggests a good level of confidence of the estimate. In the southern part of the Reserve, there were large patches of mature forests and around these there are

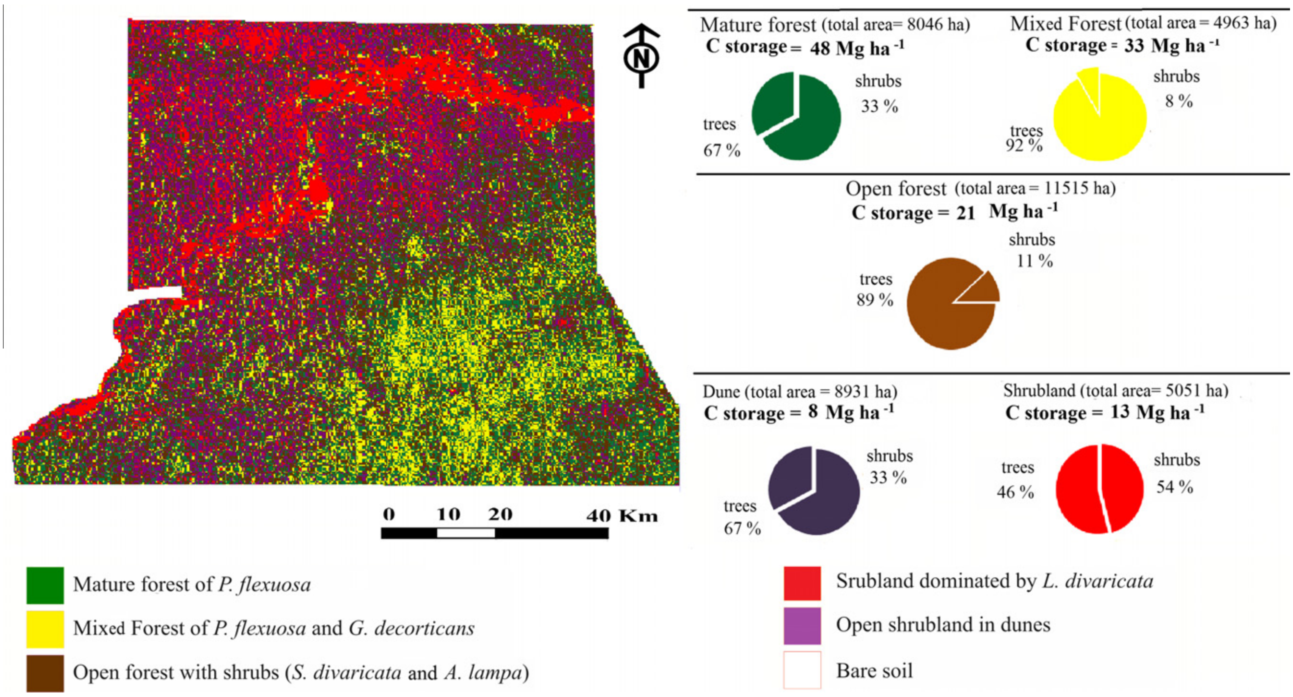

Fig. 2. (A) Principal Components Analysis (PCA) biplot of 20 species representative of Chaco Arid and Monte region. (B) Dendrogram tree of cluster analysis (Gower similarity coefficient), showing the discrimination of twelve plant functional types.

usually patches of secondary forest. The northern part of the Reserve is significantly more disturbed, with large patches of shrubland and open forests (Fig. 3, left).

In Chancaní, the kappa coefficient showed a good level of confidence (value 0.64), although there was confusion between some vegetation classes. The different plant formations in the Reserve are clearly separated into different sectors (Fig. 4, left): there is a continuous strip of shrubland along the west part of the Reserve dominated by *L. divaricata*, *A. gilliessi* and *M. carinatus*; in the north, a large patch of mature forest of *A. quebracho-blanco*, and in the southeast there is open forest of *A. quebracho-blanc*o and *P. flexuosa*.

3.3. Plant functional types

The PCA showed that species were separated by similar combinations of traits. The first two axes included 83% of the variation. The largest amount of variation (Axis 1, 54.4%) was associated with

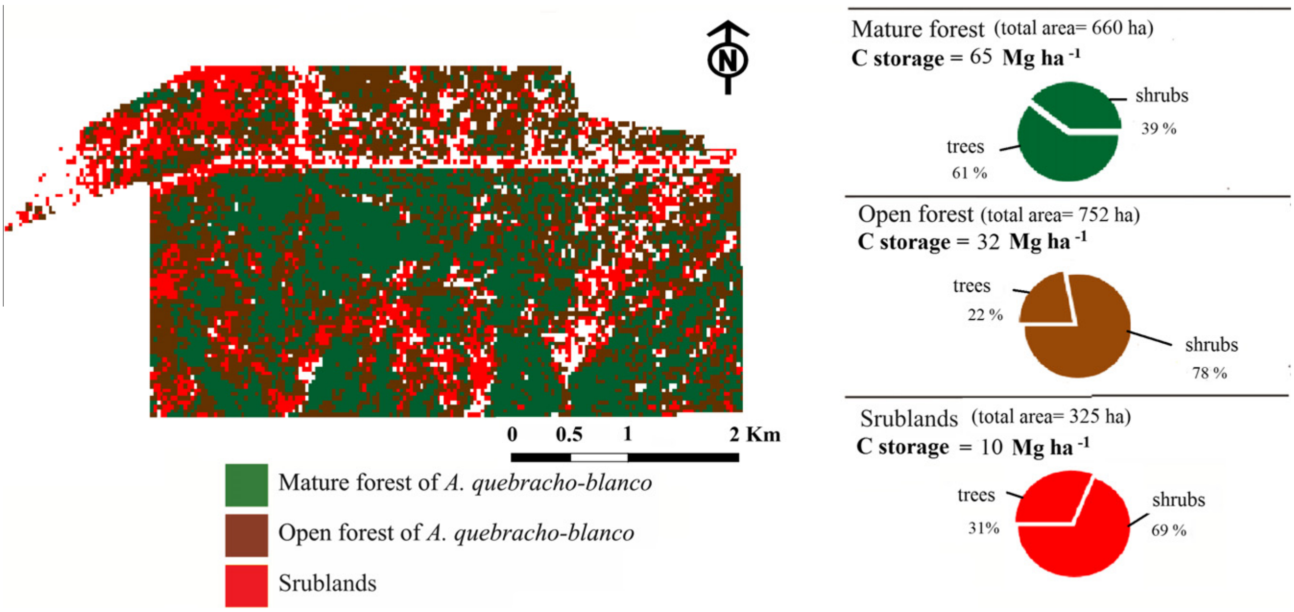

Fig. 3. Dendrogram tree of cluster analysis for the twelve vegetal formation TSh-L (Telteca – shrubland dominated by *Larrea sp.*); TSh-D (Telteca – shrubland in dune); TmxW (Telteca – mixed woodland of *P. flexuosa* and *G. decorticans*); TOW (Telteca – open woodland of *P. flexuosa*); TMW (Telteca – mature woodland of *P. flexuosa*); QM (Quebracho de la Legua-shrubland); QOF (Quebracho de la Legua – open forest of *A. quebracho-blanco*); QBM (Quebracho de la Legua – mature forest of *A. quebracho-blanco*); ChS (Chancaní – shrubland); ChMxF (Chancaní – mixed forest of *A. quebracho-blanco* and *P. flexuosa*);ChOF (Chancaní – open forest of *A. quebracho-blanco*), Ch BM (Chancaní – mature forest of *A. quebracho-blanco*).

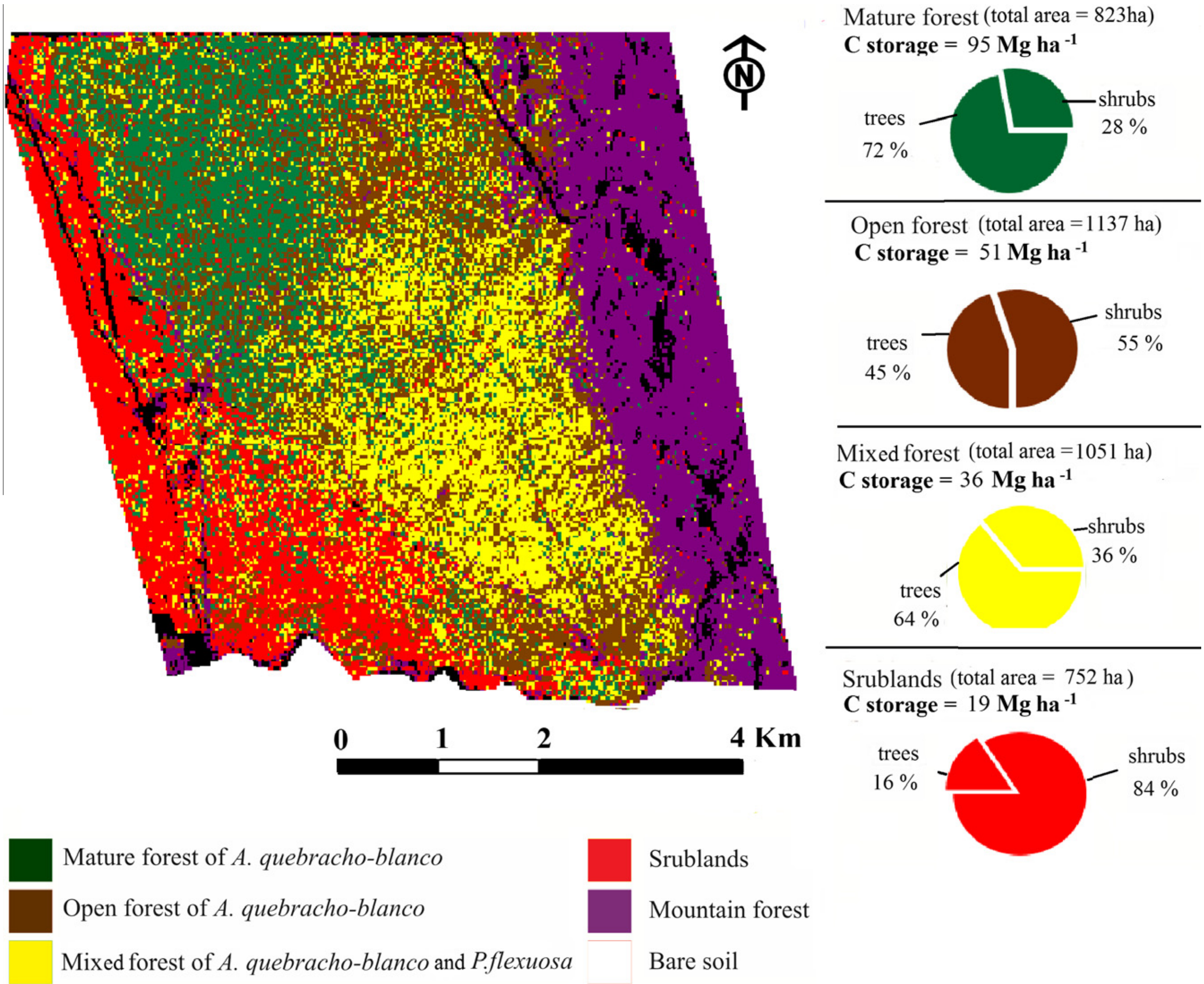

Fig. 4. Supervised classification of Telteca Natural Reserve. Values of area and mean C storage for each vegetable community present.

traits such as DAB, and SLA, separating big trees (e.g. *A. quebracho-blanco*, *P. flexuosa, Zizyphus mistol*) from small shrubs (e.g. *S. aphyla, T. usillo, A. lampa*). The second axis was associated with wood density and DAB and separated the shrubs with high wood density from others (Fig. 5A).

Cluster analysis discriminated 12 different plant functional types within 20 dominant woody species analyzed, with a cophenetic correlation of 0.83 at 50% and with distance of 0.36 (Fig. 5 B). This analysis separated, in the first instance, trees species from shrubs and, within these groups, discriminated according to SLA and wood density (Table 1). The regression models for obtaining C storage for each species or PFTs are displayed in Table 2.

3.4. Vegetation community composition and functional type distribution

The abundance of woody functional types varied in the different locations. Some were absent (PFT 8, PFT 10 and PFT 11) in the most xeric Reserve (Telteca). Others, like PFT 2 (jumes and cachiyuyos), PFT 3 (*Larrea* sp), PFT 12 (*Prosopis flexuosa*) and PFT 9 (sclerophyllous shrubs), were present in all sites. Functional type 1 (*Schinus sp.*) was irrelevant, as well as PFT 11 (*Z. mistol*), which was only found at a low abundance in Chancaní (Table 3). On the other hand, the functional type of *Larrea sp.* (PFT 3), showed an abundance of almost 50% of the bushes in Quebracho de la Legua and Telteca shrubland.

Diversity indices (Simpson's and Shannon-Wiener) indicated the internal variability of each Reserve. The highest diversity values were found in all the forests, while the shrubland formation had the lowest values of diversity indices, especially in Quebracho de la Legua and Telteca. However in Chancaní, this vegetation formation is also represented by *A. gilliessi* and *M. carinatus* (PFT 4), PFT 2 (jumes and cachiyuyos) and other tree species such as *A. quebracho-blanco* (PFT 10) and *P. flexuosa* (PFT 12), which contribute to increasing C storage.

3.5. Variation of C in each nature reserve

The C storage of each vegetation community present in each Reserve and the contribution of each canopy layer (trees or shrubs) in the C storage are showed in right side of Figs. 3–5, respectively. Is observed that the mature forests increase C stocks from west to east as the mean rainfall becomes more abundant. The total aboveground biomass of this kind of forest increased 26% from Telteca to Quebracho de la Legua. This increase corresponds with more than 100% increase of rainfall (150–310 mm from Telteca to Q. de la Legua). However, there is an increase of 31% of woody biomass in the mature forests from Q. de la Legua to Chancaní, with an increase in rainfall of only 65%.

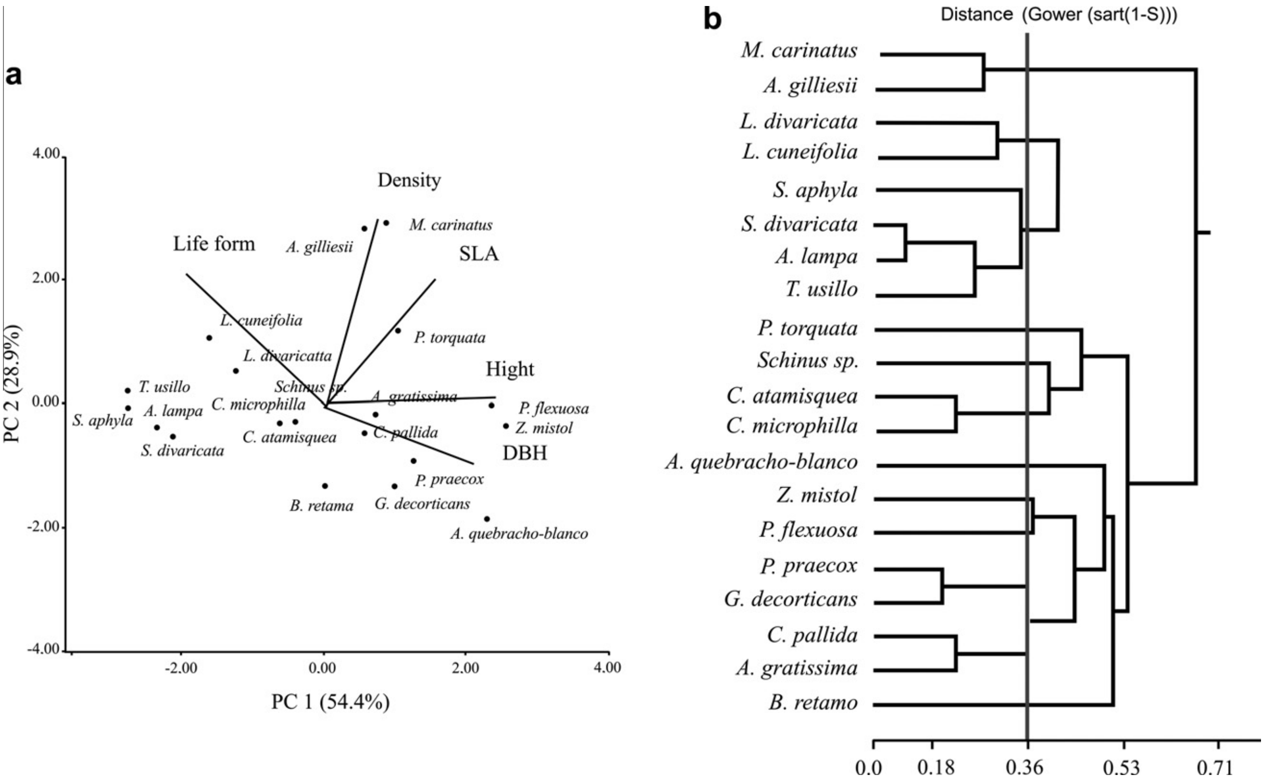

Fig. 5. Supervised classification of Quebracho de la Legua Natural Reserve.

Table 1
Functional traits of twelve 12 plant functional types discriminated by cluster analysis.

Plant functional type	Description	Species
PFT 1	Evergreen multi-stemmed shrub with height between 1.5 and 4 m. Wood density between 0.7 and 0.8 g/cm^3. SLA's values between 8 and 12 mm^2/mg	*Schinus fasciculata*
PFT 2	Short size evergreen or without leaves multi-stemmed shrub. Wood density above 0.7 g/cm^3. SLA's values below 8 mm^2/mg	*T. usillo, A. lampa, S. aphyla* and *S. divaricata*
PFT 3	Sclerophyllous evergreen multi-stemmed belonging to the family Zygophyllaceae, with height between 1.5 and 4 m. Wood density between 0.7 and 0.8 g/cm^3. SLA values between 4 and 8 mm^2/mg.	*L. divaricata* and *L. cuneifolia*
PFT 4	Deciduous shrub multi-stemmed shrub with height between 1.5 and 4 m. Wood density above 0.9 g/cm^3. SLA's values ranging from 5 and 12 mm^2/mg.	*M. carinatus* and *A. gilliessi*
PFT 5	Medium size tree, deciduous. Height between 1.5 and 4 m. Wood density ranging from 0.7 and 0.8 g/cm3. SLA's values below 4 mm^2/mg	*B. retamo*
PFT 6	Medium size tree, deciduous. Height between 1.5 and 4 m. Wood density ranging from 0.7 and 0.8 g/cm^3. SLA's values between 7 and 12 mm^2/mg	*A. gratissima* and *C. pallida*
PFT 7	Medium size tree, deciduous. Height above 4 m. Wood density ranging from 0.7 and 0.8 g/cm^3. SLA's values ranging from 8 to 12 mm^2/mg	*C. praecox* and *G. decorticans*
PFT 8	Deciduos medium size tree or multi-stemmed shrub. Height between 1.5 and 4 m. Wood density ranging from 0.7 and 0.8 g/cm^3. SLA's values ranging from 8 to 12 mm^2/mg	*P. torquata*
PFT 9	Evergreen medium size tree or multi-stemmed shrub with height between 1.5 and 4 m. Wood density ranging from 0.7 and 0.8 g/cm^3. SLA's values ranging from 4 to 8 mm^2/mg	*C. atamisquea* and *C. microphyla*
PFT 10	Evergreen tree Height above 4 m. Wood density ranging from 0.7 and 0.8 g/cm^3. SLA's values ranging from 8 to 12 mm^2/mg	*A. quebracho-blanco*
PFT 11	Deciduos tree. Height above 4 m. Wood density ranging from 0.7 and 0.8 g/cm^3. SLA's values ranging from 8 to 12 mm^2/mg	*Z. mistol*
PFT 12	Deciduos tree. Height above 4 m. Wood density ranging from 0.7 and 0.8 g/cm^3. SLA's values above 12 mm^2/mg	*P. flexuosa*

3.6. Characterization and comparison of vegetation communities in nature reserves

These vegetation communities were compared in terms of their canopy coverage and the biomass contribution of each functional type present in the nature reserves. Cluster analysis showed a cophenetic correlation of 0.87. Cutting at 35%, Fig. 6 shows close similarities of the mixed forest of *A. quebracho-blanco* and *P. flexuosa* from Chancaní with mature forests in Quebracho de la Legua. At 50%, the cluster analysis shows similarities between mature and open forests of Telteca. Finally, with a wide range of 75%, the vegetation communities of the Monte and of the typical Arid Chaco are clearly distinct.

3.7. C Stock in the three nature reserves

Our results showed that, although Telteca Reserve has the biggest C storage because of its extension (889052.8 Mg of C), the

Table 2
Best fit linear equations and power equations (Iglesias, 2010; Iglesias and Barchuk, 2010; Álvarez, 2008) for predicting total aboveground biomass of the twelve plant functional types. PFT: Plant functional type. Regression model. TDW: total dry weight. R^2: coefficient of determination. References.

Plant functional type	Regression model	R^2	References
PFT 1			
S. fasciculata	TDW = 1.15 + 0.22 ∗ (DAB^2)	0.80	Iglesias (2010)
PFT 2			
T. usillo, A. lampa, S. divaricata and *S. aphyla*	TDW = 0.59 + 0.02 ∗ (DAB^2 ∗ height)	0.62	Iglesias (2010)
PFT 3			
L. divaricata and *L. cuneifolia*	TDW (*L. divaricata*) = 0.57 + 0.03 ∗ (DAB^2 ∗ height)	0.83	Iglesias (2010)
	TDW (*L. cuneifolia*) = 0.28 + 0.04 ∗ (DAB^2 ∗ height)	0.82	Iglesias (2010)
PFT 4			
M. carinatus and *A. gilliessi*	TDW (*M. carinatus*) = 3.51 + 0.03 ∗ (DAB^2 ∗ height)	0.92	Iglesias and Barchuk (2010)
	TDW (*A. gilliessi*) = 1.45 + 0.05 ∗ (DAB^2 ∗ height)	0.90	
PFT 5			
B. retama	TDW = 0.40 + 0.02 ∗ (DAB^2 ∗ height)	0.93	Iglesias (2010)
PFT 6			
A. gratísima, C. pallida and *L. ciliatum*	TDW = −2.16 + 0.90 ∗ DAB	0.93	Iglesias (2010)
PFT 7			
P. praecox and *G. decorticans*	TDW (*P. praecox*) = −10.34 + 0.37 ∗ (DAB^2)	0.98	Iglesias and Barchuk (2010)
	TDW (*G. decorticans*) = 1.72 + 0.04 (DAB^2 ∗ height)	0.80	
PFT 8			
P. torquata	TDW = −6.04 + 0.22 ∗ (DAB^2)	0.94	Iglesias and Barchuk (2010)
PFT 9			
A.emarginata and *C. microphyla*	TDW = −1.48 + 0.14 ∗ (DAB^2 ∗ height)	0.91	Iglesias (2010)
PFT 10			
A. quebracho-blanco	TDW = −101.57 + 0.49 ∗ (DAB^2)	0.95	Iglesias (2010)
PFT 11			
Z. mistol	TDW = −10.30 + 0.48 ∗ (DAB)^2	0.98	Iglesias (2010)
PFT 12			
P. flexuosa	TDW = 0.035 ∗ (DAB)$^{2.37}$	0.94	Álvarez et al. (2011)

average contribution per hectare was only 23.80 Mg of C, as canopy cover was more sparse with small patches of *P. flexuosa* woodland. The mature woodland of *P. flexuosa* had an area of 8046 ha and stores 390321.16 Mg of C. Open forest and mixed forest vegetation communities store 124673.07 and 241817.52 Mg of C, respectively. The more open communities of *L. divaricata* shrubland and shrubland on dunes stored only 51772.7 and 80452 Mg of C in areas of 5051 and 8931 ha, respectively. The contribution of tree and shrub for each plant cover its shows in Fig. 3.

Finally, as expected, of the two nature reserves of Arid Chaco, Chancaní was the one that showed the highest amount of C, with around 95 Mg ha^{-1} in mature forests of *A. quebracho-blanco*. Here canopy cover is very high, with big trees. The mature forest of *A. quebracho blanco* covered 659.5 ha in Quebracho de la Legua and 822 ha in Chancaní, storing 9233 and 78197.6 Mg of C, respectively. Other vegetation communities, such as open forest, show an area of 752 ha in Q. de la Legua and store 27306 Mg. The contribution of trees and shrubs for each vegetation communities its shows in Fig. 4. In Chancaní, the open forest of *A. quebracho-blanco* and the mixed forest of *A. quebracho-blanco* and *P. flexuosa* had an area of 1136.35 and 1050.5 ha and store 58078.8 and 31525.5 Mg of C each. More open covers, like shrubland of *L. divaricata* had areas of 325 and 832 ha and stored only 21141.25 and 12487.5 Mg of C in Quebracho de la Legua and Chancaní.

4. Discussion

Plant communities have changed as the precipitation increases along the three nature reserves. The native vegetation responds to the increase in precipitation with an increase of C storage, percentage of canopy cover and diversity index. Similar responses were observed in other rainfall gradients around the world (Ni and Zhang, 2000; Woomer et al., 2004; Cifuentes Jara et al., 2008; Dauber et al., 2008). In addition, the PFTs vary in abundance responding to the change in the precipitation gradient and internally in each nature reserve, showing the heterogeneity of the landscape. If the predictions made about climate change for the next century are true (Christensen et al., 2007), the temperature will increase 2 °C and the precipitation is likely to decrease in the western nature reserve (Telteca) and in the wetter end of the gradient, summer precipitation is likely to increase by 5%. Our results show that under this future scenario, the more arid Reserve will be more affected by the effects of the global change. At least three changes will take place in this reserve: a decrease in the percentage of the canopy cover, a change in the plant functional types and ultimately a reduction on carbon storage. Nevertheless these changes cannot be attributed only to the lack of precipitation. There are many other factors involved, such as anthropogenic effects, land use change or other disturbances (Steffen et al., 1999), the topography, the different kinds of soil and underground water, to name a few. For example, in Telteca reserve, underground water appears to be the most important source of water for tree growth (Villagra et al., 2005), which is why we found woodland in such arid land (Morello, 1958; Roig et al., 1991).

Our estimates of C stock in aboveground biomass storage of the Arid Chaco and Monte were the highest values reported from similar forests in other regions (Padrón and Navarro-Cerrillo, 2002; Schulze et al., 1996; Mills et al., 2005; Bonino, 2006; Pérez et al., 2007; Gasparri et al., 2007). There are no previous studies on the Telteca region. In comparison with other similar regions, as in *Prosopis pallida* forests in Peru (annual rainfall average 100 mm), much lower C storage values (9.9 Mg ha^{-1}) were reported, around 80% of our estimates. The biomass of xeric shrub and grassland on arid Patagonian steppe (120–170 mm of precipitation) show values between 0.15 and 0.71 kg/m^2 respectively (Schulze et al., 1996), equal to 7.5 and 35 Mg ha^{-1} and some African xeric shrubland show average values around 12 Mg ha^{-1} (Mills et al., 2005). These values are similar to those we found in *Larrea* shrubland in Telteca. In Chancaní, Bonino and Araujo (2005) estimated values for the primary and secondary forests and shrubland of 30.3, 8.38 and 1.37 Mg ha^{-1} (around 50–80% of our estimates). Gasparri et al.

Table 3
Relative Abundance and diversity index of Plant Functional Types in every plant community present in each nature reserve. Simpson diversity index: I. Simpson, Shannon diversity index and Winner: I. Winner Shannon.

Plant functional type	Telteca					Quebracho de la Legua			Chancaní			
	Open shrubland on dune	Shrubland	Open woodland	Mixed woodland	Mature woodland	Shrubland	Open forest	Mature forest	Shrubland	Mixed forest	Open forest	Mature forest
PFT 1	1.36	0.63	1.05	0.32	1.46	0	0	0	1.08	0.2	0.2	0
PFT 2	48.46	10.57	46.15	29.35	45.25	27.66	12.56	14.04	0.73	1.8	1.58	4.16
PFT 3	7.85	66.4	0	0	0	57.44	25.6	35.18	33.22	21.21	20.8	16.9
PFT 4	0	0	0	0	0	4.25	31.22	29.12	4.7	52.32	51.3	47.6
PFT 5	30.71	11.4	11.53	5.48	12.4	2.12	3.35	0	0	0	0	0
PFT 6	0.34	0	0	0	0	0	0	0.17	0	0.2	0.19	0
PFT 7	0	4.65	21.3	27.74	0	0.42	7.65	7.63	13.72	1.61	1.5	1.82
PFT 8	0	0	0	0	0	0	0.36	0.7	0	0	0.1	0
PFT 9	6.8	1.05	13.63	25.8	22.63	0.42	10.16	7.45	26.36	14.34	16.24	18.6
PFT 10	0	0	0	0	0	0	5.5	3.12	6.86	5.45	5.37	9.23
PFT 11	0	0	0	0	0	0	0	0.35	0.36	0.6	0.6	0.91
PFT 12	4.4	5.28	6.3	11.3	18.25	7.65	3.59	2.25	19	2.22	2.18	0.78
I. Simpson	2.92	2.12	3.4	4.07	3.28	2412	5.6	4.14	4.5	2.91	2.97	3.32
I. Shannon winner	1.31	1.13	2.85	1.49	1.33	1.13	1.76	1.65	1.69	1.38	1.4	1.47

PFT 1: *Schinus fasciculata;* PFT 2: *T. usillo, A. lampa, S. aphyla* y *S. divaricata;*PFT 3 *L. divaricata* and *L. cuneifolia;* PFT 4:*M. carinatus* and *A. gilliessi;* PFT 5: *B. retamo;* PFT 6: *A.gratissima* and *C. pallida;* PFT 7: *P. praecox* and *G.decorticans;* PFT 8: *P. torquata;* PFT 9: *C. atamisquea* and *C. microphyla;* PFT 10: *A. quebracho-blanco;* PFT 11: *Z. mistol* and; PFT 12: *P. flexuosa.*

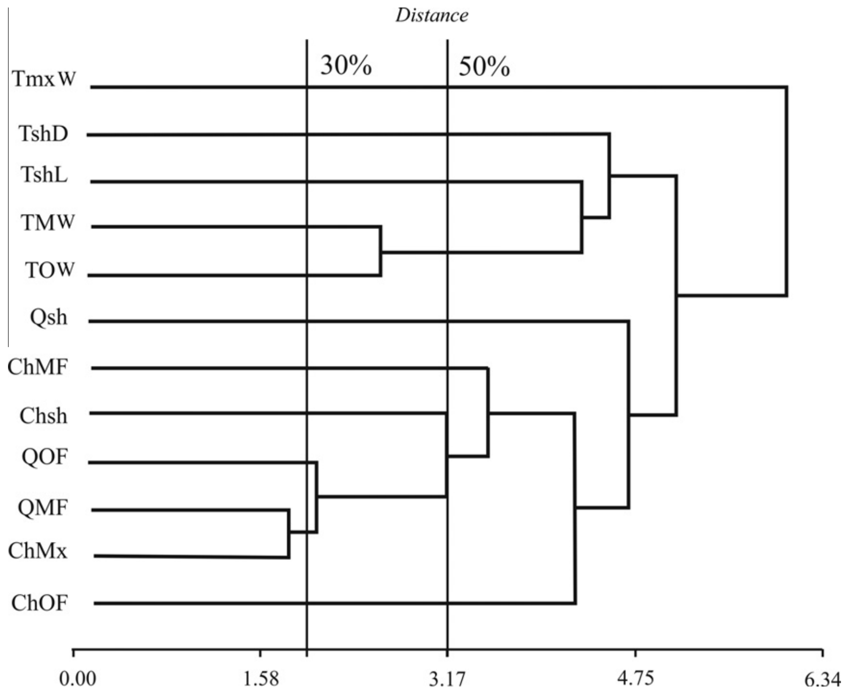

Fig. 6. Supervised classification of Chancaní Natural Reserve.

(2007) found values between 27.3 and 67 Mg ha^{-1}of C in the dry subtropical Chaco forest (with 400–900 mm annual rainfall). On the other hand, forests communities of the sub-humid Chaco in the province of Salta, Argentina (600–800 mm annual rainfall) are dominated by *Schinopsis quebracho-colorado* and *A. quebracho-blanco* and storage around 144.75 Mg ha^{-1}of C (Pérez et al., 2007).

There are various reasons that may explain these differences at local level; (1) Different climatic and edaphic conditions; (2) The absence of an appropriate allometric equation for the study area. Several studies use a general allometric equation or use the wood density as an estimation (Fearnside, 1997). Other studies use, for those individuals with diameter at breast height (DBH) of less than 5 cm, the average weight values of three species at four increasing ranges of height (Bonino, 2006); (3) The use of the National Inventory of Native Forest. Many studies use these data because it is a cheaper and faster way to estimate C storage, but, in general, these inventories considered only those individuals with a DBH greater than 10 cm. In our study, if we considered only the tree canopy (72%) in the Chancaní mature forest, it would give values up to an average of 68. 5 Mg ha^{-1}, very similar to the extreme values found in Gasparri's work. However, it should be noted that the shrub layer in the Chancaní mixed and open forests (trees and shrubs with values of DBH below 10 cm or shrubs below 1.3 m), mainly dominated by functional type 4 (*M. carinatus* and *A. gilliessi*), provides almost the same amount of C as *A. quebracho-blanco*, so we consider it very important not to ignore the shrub layer, especially in secondary forests; (4) Atypical life forms of trees and shrubs: due to land use change, trees and shrubs can vary from monopodial to multi-shoot form, so the equation should be different in each case; and finally; (5) The underestimation or overestimation of large trees (Clark et al., 2001). Generally, exponential equations are the most used. However, when the sampling does not consider a wide range of sizes, the use of an exponential equation can overestimate the biomass of trees.

Another important contribution is the similarities between different vegetation formations in the gradient according to the organization of plant functional types, canopy cover and the C storage; e.g., the cluster analysis shows that Chancani's mixed forests are quite similar to the mature forest of Quebracho de la Legua. This can be an indirect measure of desertification scenarios in terms of rainfall gradient. There is a clear difference between the vegetation formation of the Monte Region (Telteca) and the Arid Chaco region (Quebracho de la Legua and Chancaní). The "Shrubland" vegetation community of Telteca and Quebracho de la Legua are very similar, widely dominated by *L. divaricata* (more than 57% relative abundance). This species is characterized as a riverside species in Monte deserts (Ezcurra et al., 1991). Most of them are found in the proximity of the old riverbed of Telteca and dominate the area near the dry river that crosses Quebracho de la Legua.

We found a clear spatial variability of C storage in biomass at a fine-scale resolution in each Reserve. Our results show that spatial variability in Quebracho de la Legua and Chancaní can be explained by anthropogenic disturbances (logging and fire) rather than deterministic factors (edaphic variability). Chancaní Reserve has a long history of over-logging evidenced by the presence of charcoal production (Alessandria et al., unpublished 1977) and wildfire. The last fire, in 1994, affected 230 ha within the northwest boundaries of this Reserve (Pelegrin and Buche, 2010). On the other hand, in Telteca, abiotic factors such as climate, and geomorphological and edaphic factors as soil particle size, slope angle (Simpson and Solbrig, 1977; Solbrig et al., 1977; Álvarez, 2008) and mainly the presence of the water-table (Rundel et al., 2007; Guevara et al., 2010; Jobbagy et al., 2011) are commonly responsible for the distribution of communities in the landscape (Morello, 1958; Bisigato et al., 2009). Bisigato et al. (2009) suggested that at the bases of Teltecas dunes, where the slope is gentle and the sediments are fine- textured, shrubland *Larrea* are found. We also found *Prosopis* sp. woodland. The *Prosopis* sp. genus is originated from a more humid area, the Chaco phytogeographic regions. Several studies suggest that *P. flexuosa* is a phreatophitic species associated with the occurrence of superficial water-tables in regions with less than 350 mm total annual precipitation (Morello, 1958; Villagra et al., 2005; Bisigato et al., 2009).

The protection of forests from deforestation and degradation helps to reduce significant carbon emissions to the atmosphere and also plays an important role in the mitigation of desertification. Studies of C storage in forest and woodland often concentrate on the role of trees, but in general ignore the importance of the shrub layer. In secondary forests of these areas the shrub layers represent more than 50% of C storage, it is relevant to highlight that these layers not only play an important role in the C storage, but are also essential as protectors of the soil in areas with a high risk of desertification processes (González Loyarte et al., 1990; Maestre et al., 2009).

5. Conclusion

Arid and semiarid nature reserves store considerable amounts of C in aboveground biomass. Total carbon storage ranged from 8 to 95 Mg h^{-1}. Canopy cover percentage and carbon storage increased according to the rainfall and within each natural reserve from shrubland into mature forest.

We found substantial differences between previously published estimates of C for similar areas. These differences are based principally in the use of non-specific allometric equations or the use of the National Inventory of Native Forest which are considered only those individuals with a DBH greater than 10 cm. We found that, from a functional point of view, shrub cover becomes very important in these areas, especially in secondary forest and shrubland, because of the potential in C storage and as soil conservation in areas with high risk of desertification.

We also found, similarities between the degradated forests of the wetter reserve, and the mature forest in the more arid reserve of the Arid Chaco. Based on the organization of plant functional types, land cover and C storage, can be an indirect measure of desertification scenarios in terms of rainfall gradient. This knowledge of carbon storage of arid nature reserves would be a useful input for the development of strategies for reducing CO_2 emissions caused by deforestation and forest degradation.

Acknowledgements

This research was supported by Agencia Nacional de Promoción Científica y Técnica Argentina (FONCYT, proyect "El secuestro de Carbono y el papel ecológico de las especies leñosas en un gradiente de déficit hídrico en la zona árida - semiárida argentina", PICTR 2002-00200). We are grateful for the valuable contribution of M. Boetto, S. Katlirevsky, F. de Rosa, D. Sercovich, J.L. Zamar, E. Alessandria, M.B. Matheu in field sampling and Michelle Malan for her English revision.

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