Journal of Arid Environments 75 (2011) 29–37

Contents lists available at ScienceDirect

Journal of Arid Environments

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

Carbon pools in an arid shrubland in Chile under natural and afforested conditions

J.F. Perez-Quezada [a,b,*], C.A. Delpiano [a], K.A. Snyder [c], D.A. Johnson [d], N. Franck [b,e]

[a] Departamento de Ciencias Ambientales y Recursos Naturales Renovables, Universidad de Chile, Casilla 1004, Santiago, Chile
[b] Centro de Estudios de Zonas Áridas, Universidad de Chile, Casilla 36-B, La Serena, Chile
[c] USDA-ARS, Exotic and Invasive Weeds Research Unit, 920 Valley Road, Reno, NV 89512, USA
[d] USDA-ARS, Forage and Range Research Lab, Utah State University, Logan, UT 84322-6300, USA
[e] Departamento de Producción Agrícola, Universidad de Chile, Casilla 1004, Santiago, Chile

ARTICLE INFO

Article history:
Received 19 December 2009
Received in revised form
3 August 2010
Accepted 11 August 2010
Available online 15 September 2010

Keywords:
Aboveground biomass
Acacia saligna
Afforestation
Belowground biomass
Carbon stocks
Plant allometry

ABSTRACT

The pattern of carbon (C) allocation among the different pools is an important ecosystem structural feature, which can be modified as a result of changes in environmental conditions that can occur gradually (e.g., climatic change) or abruptly (e.g., management practices). This study quantified the C pools of plant biomass, litter and soil in an arid shrubland in Chile, comparing the natural condition (moderately disturbed by grazing) vs. the afforested condition (two-year-old plantation with *Acacia saligna* (Labill.) H.L. Wendl.), each represented by a 60 ha plot. To estimate plant biomass, allometric functions were constructed for the four dominant woody species, based on the volume according to their shape, which showed high correlation ($R^2 > 0.73$). The soil was the largest C pool in both natural and afforested conditions (89% and 94%, respectively) and was significantly lower in the afforested than natural condition at all five soil depths. The natural condition had in total 36.5 ton (t) C ha^{-1} compared to 21.1 t C ha^{-1} in the afforested condition, mainly due to C loss during soil preparation, prior to plantation of *A. saligna*. These measurements serve as an important baseline to assess long-term effects of afforestation on ecosystem C pools.

1. Introduction

Terrestrial and marine ecosystems are estimated to absorb about half of the CO_2 emissions from fossil fuel combustion (Schimel et al., 2001). In terrestrial ecosystems, carbon (C) absorbed via photosynthesis is stored in the biomass of living vegetation (leaves, branches, trunks and roots), litter and soil (Vande Walle et al., 2001). Among these components, soil is the largest pool of organic C in the biosphere, storing more C than plants and the atmosphere combined, and also containing inorganic C forms such as calcite and dolomite (Allison, 1965; Jobbagy and Jackson, 2000; Vande Walle et al., 2001). Most studies that have examined C storage have been conducted in ecosystems with a high biomass content such as tropical and temperate forests; considerably less is known about C storage in arid and semiarid ecosystems (Bonino, 2006). Although arid and semiarid ecosystems have less vegetation cover and hence have a lower C accumulation per unit land area than tropical or temperate forests, they cover more than 30% of the global continental area (Bechtold and Inouye, 2007) and are estimated to contain 20% of the global soil C pool (organic plus inorganic) (Rasmussen, 2006). Recent studies have provided estimates of C pools in arid and semiarid ecosystems of the United States (Bechtold and Inouye, 2007; Rasmussen, 2006; Vourlitis et al., 2007), Africa (Glenday, 2008; Takimoto et al., 2008; Woomer et al., 2004), China (He et al., 2008) and Argentina (Bonino, 2006). In Chile, C pools have been estimated for native deciduous forests (Doll et al., 2008) and central native sclerophyllous forests (Muñoz et al., 2007), but no estimates of C pools have been reported for semiarid or arid regions. Arid and semiarid regions comprise 41% of the continental area of Chile, covering 31.3 Mha (Benites et al., 1994). In the Coquimbo Region of Chile, which has an arid Mediterranean climate, 25% of the territory is covered by natural shrubland (INE, 1998); however, large areas of this natural shrubland have been degraded by over-grazing due to intensive goat husbandry, resulting in soil erosion (Armesto et al., 2007). One of the strategies for recovering these degraded lands has been active afforestation with drought-tolerant woody species such as saltbush (*Atriplex* spp.) and *Acacia saligna* (Labill.) H.L. Wendl. Recent afforestation efforts have used *A. saligna* mainly because it has demonstrated excellent forage quality and resprouting capacity and rapid recovery after grazing (Mora et al., 2002);

* Corresponding author at: Departamento de Ciencias Ambientales y Recursos Naturales Renovables, Universidad de Chile, Casilla 1004, Santa Rosa 11315, Santiago, Chile. Tel.: +56 2 978 5840; fax: +56 2 978 5929.
E-mail address: jorgepq@uchile.cl (J.F. Perez-Quezada).

0140-1963/$ – see front matter © 2010 Elsevier Ltd. All rights reserved.
doi:10.1016/j.jaridenv.2010.08.003

therefore, it has been planted on over 12 900 ha in the region (Avila et al., 2007). Although afforestation with exotic species such as *A. saligna* helps to mitigate soil degradation, the effects of this ecosystem management practice on C storage compared to C storage in native shrubland ecosystems remain unknown.

Estimates of C pools in the vegetation component of ecosystems can be obtained by using allometric functions (Navar et al., 2002). Such functions allow the estimation of plant biomass from variables that are easily and non-destructively measured, such as maximum plant height and trunk diameter at chest height (Gayoso et al., 2002; Prado et al., 1987). For many plant species, especially those of economic importance, allometric functions have been determined and can be readily used to estimate their biomass (Azocar et al., 1998, 2001). However, for many native species with low economic value, but high ecological importance, allometric functions are not available in the literature so they must be developed to estimate their contribution to ecosystem biomass and C pools. For shrubs, most allometric equations for estimating aboveground biomass use volume in single- or multiple-variable analyses (Huenneke et al., 2001; Murray and Jacobson, 1982; Uresk et al., 1977; Vora, 1988). Soil C content is generally measured through chemical analyses from soil samples obtained at representative soil depths (Jobbagy and Jackson, 2000).

This study was conducted in a Mediterranean shrubland in the arid Chilean Region of Coquimbo, under two conditions: natural (moderately disturbed by grazing) and afforested with a two-year-old planting of *A. saligna*. Our objectives were to: (1) construct allometric functions to estimate aboveground and belowground biomass of predominant plant species and (2) quantify and compare the C pools of biomass, litter and soil for both the natural and afforested conditions. We hypothesized that the natural shrubland condition would contain greater C pools than the afforested condition.

2. Materials and methods

2.1. Site description

The study area is located in the Coquimbo Region of Chile (30°15′S; 71°17′W), 45 km south of La Serena, in the central depression between the Coastal Ranges and the Andes Mountains. The sampling sites were located at the Las Cardas Experimental Station of the University of Chile. The climate is arid Mediterranean, with an average annual precipitation of 153 mm, concentrated between June and September (local records from 1977 to 2008). The average air temperature in January is normally lower than 26 °C, and the average for July has never been lower than 5 °C in recorded history. The vegetation of the study area is an open, low-statured shrubland, which is an ecotone dominated by *Gutierrezia resinosa* (S.F. Blacke) and *Flourensia thurifera* (Molina) D.C., with sporadic occurrences of trees, mainly *Acacia caven* (Molina) and *Lithraea caustica* (Hook. & Arn.) and succulents, and an ephemeral grass component dominated by therophytes (Lailhacar and Aylwin, 1988). Shrublands dominated by *F. thurifera* are an earlier successional stage of a vegetation type, which in its climax stage is an arboreal shrubland dominated by *Cordia decandra* (Hook. & Arn.); shrublands with a high abundance of *G. resinosa* typically are a result of anthropogenic perturbation (Luebert and Pliscoff, 2005).

For our study, we used two enclosures of about 60 ha each, one covered by the natural shrubland (moderately disturbed by grazing) and the other afforested with *A. saligna*, planted between 2005 and 2006 (1200 trees ha^{-1}). We subdivided each 60 ha enclosure into five smaller areas of equal surface, which were drawn around five points selected randomly using a Geographic Information System tool. From these five smaller areas, three were selected to sample the ecosystem carbon pools. This pseudo-replication sampling scheme was used in order to capture the spatial variability of each vegetation condition. Percentage cover of woody species (trees and shrubs) was estimated along three 50-m transects for each management condition, which were positioned in representative areas within each of the three sub-plots. The dominant species were *F. thurifera*, *G. resinosa* (both Compositae family) and *Heliotropium stenophyllum* (Hook. & Arn.) (Boraginaceae family) (Table 1).

The soil at the study sites is an Aridisol derived from granitic and andesitic alluvium. The soil textural class is sandy loam in the surface horizons and loamy sand at depth. The drainage class is moderate with low sodium content and no carbonates (Casanova and Luzio, 2008). The soil depth is variable from 50 to 100 cm over a duripan.

Prior to afforestation with *A. saligna*, a bulldozer was used in 2005 to build 40-cm berms and infiltration ditches to increase water availability for the planted species. This resulted in removal of many shrub individuals, although an effort was made to leave the few existing trees in place. Moderate grazing occurred in both natural and afforested conditions prior to sampling during the winter months (June–August 2007). Precipitation was low in 2006 (99 mm) and 2007 (32 mm) compared to the average annual precipitation.

2.2. Estimation of biomass from allometric variables of shrubs

Biomass for the three dominant woody species of the natural shrubland and *A. saligna* was estimated using regression models based on allometric variables: maximum height (H_{MAX}); relative height (H_{REL}), which is the height where the maximum concentration of plant biomass occurs (Paton et al., 2002); and north–south (D_{NS}) and east–west (D_{ES}) diameters of canopy projection (Murray and Jacobson, 1982). The diameter of the basal trunk (D_{BT}) or group of trunks was also estimated (from the measured perimeter of the trunk base, P_{BT}), because of its potential relationship to belowground biomass. The range and distribution of each allometric variable in the shrub species were determined using the moving transect method (Kent and Coker, 1992). This method started with the measurement of one randomly chosen individual. At the point of the first individual sampled, an imaginary 90° angle was drawn, where the bisector pointed to the north. The closest individual of the species being sampled, which was rooted within the 90° angle, was chosen and measured. This procedure was repeated until 30 individuals were sampled in the natural condition site, for each of the four sampled species. The statistical distribution of maximum height for the four species sampled is depicted in Fig. 1. From the 30 plants originally measured, the distribution classes were used to choose the minimum number of individuals for destructive measurement of aboveground and belowground biomass, so

Table 1
Percentage cover of woody species and bare ground along three transects (T) and the mean cover for natural and afforested conditions of a Mediterranean arid shrubland in Chile.

Species	Natural				Afforested			
	T1	T2	T3	Mean (SD)	T1	T2	T3	Mean (SD)
F. thurifera	26.4	14.7	0.6	13.9 (7.0)		2.2	13.3	5.2 (7.1)
G. resinosa	2.3	4.5	20.9	9.2 (3.5)	2.4	11.1	1.2	4.9 (5.4)
H. stenophyllum		22.8		7.6 (11.6)	0.8			0.3 (0.5)
L. caustica			0.7	0.2 (0.1)				
S. cumingii			0.2	0.1 (0.1)				
A. saligna						0.7	0.5	0.4 (0.4)
A. caven					3.9			1.3 (2.3)
Bare ground	71.2	58.0	77.7	69.0 (7.1)	92.9	85.9	85.1	88.0 (4.3)
Total	100	100	100	100	100	100	100	100

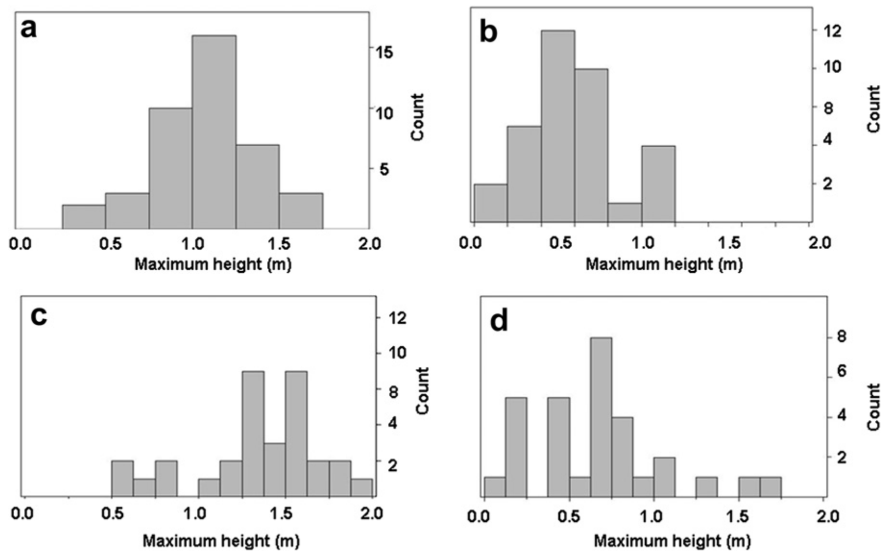

Fig. 1. Distribution of maximum height for *F. thurifera* (a), *G. resinosa* (b), *H. stenophyllum* (c) and *A. saligna* (d).

that each one of the distribution classes in the histogram (Fig. 1) was represented by at least one individual. This was done for all the allometric variables sampled. This way of choosing the individuals to harvest minimized the sampling effort and assisted in fitting regression models to the data (Cochran, 1971). Using this procedure, a total of 13 individuals were harvested for *F. thurifera*, 7 for *H. stenophyllum*, 9 for *G. resinosa* and 11 for *A. saligna*.

Plants were excavated during three field campaigns between May and July 2007, separating aboveground biomass (B_A, leaves and shoots) and belowground biomass (B_B), the latter representing only roots with a diameter >5 mm for *F. thurifera* and *H. stenophyllum* and >2 mm for *G. resinosa* and *A. saligna*. The total biomass fresh weights were measured for each harvested individual, separating by plant component (roots, shoots and leaves). Five subsamples (between 100 and 500 g) were taken from each plant component and dried at 60 °C for 48 h to estimate the percentage of water content, which was used to calculate dry biomass weight. Carbon concentration was determined from these same five subsamples using an Elementar Vario-El (Germany), which produces a dry combustion at 1150 °C in an oxygen flow and separates gases that are produced in chromatographic columns, which are detected through thermal conductivity.

By the time of sampling (May–July), shrubs usually have no green leaves, except for a few plants of *G. resinosa*. Because 2007 was an extremely dry year, the herbaceous component did not grow at all, although during the sampling period it is normally beginning to emerge.

Simple linear regression models (forward stepwise) were fit to the data sets of B_A, B_B and total biomass ($B_T = B_A + B_B$) for *F. thurifera*, *H. stenophyllum* and *G. resinosa*. Predictor variables were the measured allometric variables, their squared values and their cross multiplication (e.g., H_{MAX}, H^2_{MAX}, $H_{MAX} \times H_{REL}$). Additional predictor variables were obtained by calculating the volumes that resembled the species architecture (semi-sphere, cone and cylinder); these volumes were calculated using the combination of allometric variables. For example, five semi-sphere volumes were calculated from the various diameter measurements (north–south, east–west, mean, minimum, maximum). Similarly, cylinder volumes were calculated from the various measurements of diameter and height (maximum, relative, average). Statistical analyses were conducted using JMP 5.1 (SAS Institute Inc., Cary, NC, USA). The criteria to select a model were the following:

- The sign of model components had to be positive (i.e. the greater the diameter, the greater the biomass).
- Models with higher coefficients of determination corrected by the number of variables (adjusted R^2) were selected.
- Residuals of the model had to be normally distributed, which was verified with the Shapiro–Wilk test.
- Models had to be as simple as possible in terms of the number of variables included.
- Volume formulas were preferred and selected according to the shape of each species.

Three woody species were found in the transects with low cover values (Table 1), therefore no allometric functions were created for them. Only *Senna cumingii* (Hook. & Arn.) H.S. Irwin & Barneby had a published equation to estimate B_A (Prado et al., 1987), which we used:

$$0.3712 + 1.8087\left(D^2_{MIN} \times H_{MAX}\right) - 0.6463D_{MIN}, \quad (1)$$

where D_{MIN} is the minimum diameter of the canopy and H_{MAX}, the maximum height. Equations for *A. caven* and *L. caustica* were not available from the literature. In addition, because their cover was relatively low (Table 1), biomass was not harvested or included for these two tree species.

2.3. Estimation of carbon pools

Three 100-m^2 plots (2 × 50 m) were established in each management condition to estimate ecosystem carbon pools. Plots were drawn around the transects used for estimating the percentage cover of woody species. All the woody plants that were rooted inside the plots were identified, and their allometric variables measured. The B_A and B_B of shrub species were estimated by using the allometric models that were fitted as described in 2.2.

Four samples of litter were taken using a quadrat of 50 × 50 cm on each plot (4 quadrats × 3 plots × 2 conditions = 24 samples). The location of the quadrats was decided according to the percentage cover of each management condition, i.e. the proportion of quadrats located below the canopy of shrubs and in open spaces was as close as possible to the observed proportion of vegetation and bare ground cover (Table 1). On the afforested site, the distribution of plots was decided considering that about 60% of the area was undisturbed soil and the other 40% was bermed. From each plot, one composite sample of 50 g of litter was taken, dried and analyzed for water and C content.

Soil samples were taken to analyze C content from excavations of 30 × 30 cm (within the quadrats used to sample litter), separating the soil strata at 0–5, 5–10, 10–20, 20–30 and 30–50 cm depth intervals. Fine roots (<5 mm diameter for *F. thurifera* and *H. stenophyllum*, and <2 mm for *G. resinosa* and *A. saligna*) were separated from each soil sample. From the total of fine roots, 5 samples of 2 g were dried and analyzed for C content. The four soil samples of each plot were mixed by stratum, dried for 48 h at 60 °C and sieved with a 2-mm mesh screen, from which a homogenized subsample was taken for C content analysis. At each soil stratum, percentage of stones was determined visually, the bulk density was measured using the kerosene method for aggregates (Blake, 1965), and where it was not possible to obtain an aggregate, the gravimetric method was used. The measurement of physical properties of the soil was done by depth strata and not by edaphic strata to obtain a more accurate estimate of soil C stock, because the latter usually involves fewer samples.

Soil C content at each soil stratum *i* was calculated using the following equation:

$$C_i = V_i(1 - P_i) \times BD_i \times Cc_i, \quad (2)$$

where C_i is C content in the *i* stratum, V_i is soil volume, P_i is percentage of stones, BD_i is bulk density, and Cc_i is the *C* concentration. Twelve composite samples were obtained, three from bare ground and three below plants in each management condition, to determine the relation between the type of cover and soil C content, using a Student's *t*-test. Distribution of C stocks in the ecosystem pools (B_A, B_B, litter and soil) was estimated and compared between management conditions at the two sites. Statistical analyses to compare C content in the ecosystem C pools were performed using the average of the three plots for each management condition, using Student's *t*-tests.

3. Results

3.1. Above and belowground plant biomass

The natural shrubland condition was dominated by *F. thurifera*, *G. resinosa* and *H. stenophyllum*, which comprised 99.1% of the total vegetation cover; bare ground at this site represented about 70% of the total area (Table 1). The afforested site was dominated by *F. thurifera* and *G. resinosa*, which comprised 83.7% of the total vegetation cover, with *A. saligna* and *H. stenophyllum* exhibiting less than 1% cover; bare ground represented about 88% of the total area (Table 1).

Of the three dominant woody species, *F. thurifera* had the greatest H_{MAX}, although *H. stenophyllum* individuals were definitely the largest plants in terms of H_{REL} and diameter in both directions (Table 2). The single largest individual of *H. stenophyllum* reached 3.5 m on the D_{NS} dimension. In general, allometric variables exhibited high variability, with coefficients of variation (CV) greater than 33%. The parameter with the lowest CV for *F. thurifera*, *G. resinosa* and *A. saligna* was H_{MAX}, whereas H_{REL} was least variable for *H. stenophyllum*. The parameters with the highest variability were P_{BT} for *F. thurifera* and *G. resinosa*, and D_{NS} for *H. stenophyllum* and *A. saligna*. The other species present at the study site (Table 1) were not sampled because they represented only one or two small individuals, and no allometric relationships were reported in the literature for these species.

Table 2
Population characteristics of allometric variables measured for 30 individual plants of the four dominant woody species occurring in natural and afforested conditions of a Mediterranean arid shrubland in Chile.

Species	Variables	Min (m)	Max (m)	Mean (m)	SD (m)	CV (%)
F. thurifera	H_{MAX}[a]	0.21	2.03	1.26	0.50	39.7
	H_{REL}	0.18	1.40	0.83	0.38	46.1
	D_{NS}	0.25	2.63	1.49	0.81	54.5
	D_{EW}	0.22	2.87	1.44	0.85	59.3
	P_{BT}	0.08	2.16	0.74	0.63	85.8
G. resinosa	H_{MAX}	0.21	1.19	0.67	0.34	50.4
	H_{REL}	0.10	0.85	0.47	0.24	50.7
	D_{NS}	0.05	1.65	0.75	0.62	82.5
	D_{EW}	0.04	1.46	0.70	0.52	74.5
	P_{BT}	0.03	0.73	0.35	0.34	97.1
H. stenophyllum	H_{MAX}	0.58	1.78	1.21	0.44	36.1
	H_{REL}	0.50	1.35	0.89	0.29	33.0
	D_{NS}	0.54	3.52	2.15	0.99	45.8
	D_{EW}	0.47	2.80	1.92	0.77	40.3
A. saligna	H_{MAX}	0.02	1.35	0.76	0.45	59.1
	D_{NS}	0.02	1.21	0.37	0.37	99.3
	D_{EW}	0.01	0.48	0.37	0.32	85.0
	P_{BT}	0.02	0.14	0.05	0.04	67.0

[a] H_{MAX}, maximum height; H_{REL}, relative height; D_{NS}, north–south diameter; D_{EW}, east–west diameter; P_{BT}, perimeter of trunk at the base.

H. stenophyllum had higher relative water content for all plant components compared to other species (Table 3), particularly for leaves (45.9%), whereas *G. resinosa* had lower values of water content for stems and roots. Carbon content was quite consistent among various plant components and species (about 45–47%), except for leaves of *H. stenophyllum* (38%). This species also had the highest values of B_S and B_A, whereas *F. thurifera* exhibited the highest value of B_B. Biomass components varied considerably for all species with high standard deviations compared to the mean values. For *A. saligna*, values of SD were higher than the means. B_A represented a higher proportion of B_T compared to B_B for all species; Values of the root:shoot (B_B/B_A) ratio ranged from 0.22 for *H. stenophyllum* to 0.55 for *A. saligna* (Table 3).

All allometric models had adjusted R^2 values greater than 0.7, with equations for *A. saligna* having the highest values ($R^2 = 0.99$), followed by *H. stenophyllum*, *F. thurifera* and *G. resinosa* (Table 4). For all species, models for B_A had a higher adjusted R^2 (0.75–0.99) compared to B_B (0.56–0.97) (Table 4). When the allometric models

Table 3
Mean and standard deviation (in parentheses) of water and C content of plant components of sampled species and the percentage that aboveground and belowground biomass represented of total biomass, as measured from harvested individual plants in natural and afforested conditions of a Mediterranean arid shrubland in Chile.

Species	*N*[a]	W_L (%)	W_S (%)	W_R (%)	C_L (%)	C_S (%)	C_R (%)	B_A (%)	B_B (%)	B_B/B_A[c]
F. thurifera	13	6.6 (2.9)	23.7 (0.8)	28.3 (1.1)	45.2 (0.1)	47.1 (1.1)	47.7 (0.2)	74.6 (7.2)	25.4 (7.2)	0.34
G. resinosa	9	18.9 (2.6)	10.8 (1.5)	11.1 (2.7)	46.6 (0.7)	46.2 (0.1)	46.0 (1.0)	72.0 (12.1)	28.0 (12.1)	0.39
H. stenophyllum	7	45.9 (1.8)	24.1 (2.7)	33.6 (3.2)	38.4 (3.2)	46.2 (0.2)	47.4 (1.7)	82.1 (11.5)	17.9 (11.5)	0.22
A. saligna	11	–	30.0 (1.3)	30.4 (2.7)	–	47.5 (0.3)	45.8 (0.2)	64.5 (15.5)	35.5 (15.5)	0.55
Mean[b]					43.4 (4.4)	46.5 (0.5)	47.0 (0.9)			0.32 (0.09)

[a] *N*, number of individuals; *W*, water content; *C*, carbon content; *B*, biomass. Subindices are: L, leaf; S, stem; R, root; A, aboveground biomass (L + S); B, belowground.
[b] Average of native species (*F. thurifera*, *G. resinosa* and *H. stenophyllum*).
[c] Root:shoot ratio.

Table 4
Allometric functions used to estimate aboveground (B_A), belowground (B_B) and total biomass (B_T) of dominant woody species in natural and afforested conditions of a Mediterranean arid shrubland in Chile.

Species	B_A	R^2	B_B	R^{2b}	B_T R^2
F. thurifera	1.693 ($D_{NS} \times D_{EW}$)[a]	0.89	0.935 (S-Sph D_{AV})	0.70	0.86
G. resinosa	3.98 (Cone $H_{MAX} - D_{AV}$)	0.75	0.372 (S-Sph D_{EW})	0.56	0.73
H. stenophyllum	2.02 (Cyl $H_{REL} - D_{EW}$)	0.94	0.273 (S-Sph D_{NS})	0.77	0.94
A. saligna	472.3 (Cyl $H_{MAX} - D_{BT}$)	0.99	6118.5 (Cone $H_{MAX} - D_{BT}$)	0.97	0.99

[a] One dimension variables: D_{NS}, north–south diameter; D_{EW}, east–west diameter; D_{AV}, average diameter; D_{BT}, base-of-trunk diameter; H_{MAX}, maximum height; H_{REL}, relative height. Volumes: S-Sph, semi-sphere; Cyl, cylinder; Cone.
[b] Values of R^2 were adjusted by the number of variables that each model included.

were applied to the plant individuals present in each plot, the average dry weight for *F. thurifera* individuals was 1.09 kg plant^{-1} in the natural condition and 0.45 kg plant^{-1} in the afforested condition (Table 5). B_T values for *G. resinosa* were more consistent between the sites and had values about 0.1 kg plant^{-1} under both management conditions. Only one large individual of *H. stenophyllum* (14.7 kg plant^{-1}) was found in one plot in the natural condition.

Under both shrubland conditions, *F. thurifera* had the highest proportion of B_A and B_S with a total of 3.90 ton (t) ha^{-1} and 1.34 t ha^{-1}, respectively (Table 5). These values represented 49 and 76% of total ecosystem plant biomass, which for the natural condition was 7.89 and 1.77 t ha^{-1} for the afforested condition, respectively. Although only one individual of *H. stenophyllum* was found, it was so large that when its weight was averaged across three plots, it contributed 3.43 t ha^{-1} in the natural condition.

3.2. Carbon content of ecosystem pools

The contribution of each species to the vegetation C pool in the ecosystem was calculated by multiplying the percentage of C in biomass components (Table 3) by the biomass of all species found in the plots (Table 5). Because C content of the various plant components was so similar (Table 3), the contribution of each species to the total ecosystem C reflected the species rankings for B_T. The total C from plant biomass in the natural condition was 3.69 t C ha^{-1}, which was comprised of *F. thurifera* with 1.84 t C ha^{-1}, *G. resinosa* with 0.22 t C ha^{-1}, *H. stenophyllum* with 1.59 t C ha^{-1}and *S. cumingii* with 0.04 t C ha^{-1}. For the afforested condition, the total C from biomass was much lower (0.82 t C ha^{-1}) with *F. thurifera* contributing the greatest with 0.63 t C ha^{-1}, followed by *G. resinosa* with 0.18 t C ha^{-1}and *A. saligna* with 0.01 t C ha^{-1}. The natural and afforested conditions did not differ in C content for B_A ($t = 1.57$, $P = 0.19$), B_B ($t = 1.71$, $P = 0.16$) and B_T ($t = 1.59$, $P = 0.19$). Percentage carbon in litter was 39.7 ± 1.1% (mean ± SD) for the natural condition and 41.9 ± 2.4% for the afforested condition, which were not statistically different ($t = -1.51$, $P = 0.21$) (data not shown). These litter C contents (about 40%) were about 15% lower than the average C content of the stems of the native species (about 47%, Table 3). Total carbon contained in litter in the natural condition was 0.36 ± 0.26 vs. 0.43 ± 0.39 t ha^{-1} for the afforested condition, which were not significantly different ($t = -0.23$, $P = 0.83$) (data not shown).

Soil C content decreased with increasing depth, which was due to an increase in percentage of stones and a decrease in C concentration (%) (Table 6). Bulk density and percentage of stones of soils varied widely depending on the shrubland condition, but generally increased with depth, except for bulk density in the 10–20 and 20–30 cm increments in the afforested condition. Soil in the natural condition in the 0–50 cm depth contained 32.5 ± 7.1 t C ha^{-1}, while in the afforested condition had 19.8 ± 4.8 t C ha^{-1} (Table 6). When the differences in carbon content were analyzed by depth strata as paired *t*-tests, we observed significant differences in percentage C ($t = 5.28$, $P = 0.006$) and C content (t ha^{-1}) ($t = 7.73$, $P = 0.02$). However, when the C content was estimated for the whole soil profile (0–50 cm), this difference was only marginally significant ($t = 2.56$, $P = 0.062$) (Table 6). Considering the 0–20 cm depth increment, the soil C content represented 57.7% (18.7 t C ha^{-1}) and 53.8% (10.7 t C ha^{-1}) of total C in the soil profile in the natural and afforested conditions, respectively (Table 6). The shrubland in the natural condition had higher soil C content at all depth increments (Fig. 2). Fine roots were very scarce, with a total of 2.3 kg C ha^{-1} in the natural condition and 2.5 kg C ha^{-1} in the afforested condition. The percentages of C content in the soil under vegetation cover were compared with those in soils under bare ground, and they were not significantly different ($t = 1.26$, $P = 0.23$) (data not shown).

4. Discussion and conclusions

The calculated volumes were highly correlated with plant biomass components (B_A and B_B) for the dominant woody species in our study (Table 4). Allometric functions for estimating coarse root biomass have not been widely reported in the literature, but we found they were useful for the species in our study ($R^2 = 0.56–0.97$) and were similar to results reported by Cleary et al. (2008) ($R^2 = 0.87$) for *Artemisia tridentata* Nutt. Although log–log models typically give higher coefficients of determination, we preferred to follow the selection criteria described in Section 2.2 because log–log models sometimes provided negative values of plant biomass for our species. The equation selected for estimating B_A for *A. saligna* will probably not be useful when trees have leaves because our sampling occurred after plants had been defoliated by goat grazing. This is probably not of major concern given that moderate goat grazing is planned for the future at this site.

The natural condition of the arid Mediterranean shrubland had a greater percentage of woody vegetation cover (31%) compared to the afforested condition (12%). The greater percentage of bare ground in the afforested condition (Table 1) was likely due to the disturbance that occurred during soil preparation prior to planting of *A. saligna*.

Because C content in biomass was very stable (around 46%), contribution of ecosystem C by species closely resembled that of total biomass, with *F. thurifera* having the highest total biomass in both management conditions (Table 5). *H. stenophyllum* contained almost as much C as *F. thurifera* even though it only covered about half of the area compared to *F. thurifera* (Table 1) because *H. stenophyllum* individuals were larger (Table 2) and had greater wood density.

Xerophytic plants have various adaptive mechanisms to survive in arid climates. One of these mechanisms involves a greater allocation of plant resources to root growth compared to stem and shoot growth (Donoso, 1997). For example, xerophytic plants typically have root:shoot ratios (B_B/B_A) that are greater than 1, similar to those for plants in the cold deserts of Asia where

Table 5
Mean and standard deviation (in parentheses) of aboveground (B_A), belowground (B_B) and total biomass (B_T) of individuals and per hectare, and C for dominant species in natural and afforested conditions in an arid Mediterranean shrubland in Chile, as estimated from allometric functions for three plots in each shrubland condition.

Species	Natural[a]									Afforested								
	Biomass individuals (kg plant^{-1})			Biomass ecosystem (t ha^{-1})			Carbon ecosystem (t ha^{-1})			Biomass individuals (kg plant^{-1})			Biomass ecosystem (t ha^{-1})			Carbon ecosystem (t ha^{-1})		
	B_A	B_B	B_T	B_A	B_B	B_T	B_A	B_B	B_T	B_A	B_B	B_T	B_A	B_B	B_T	B_A	B_B	B_T
F. thurifera	1.41 (1.10)	0.24 (0.15)	1.65 (1.33)	3.35 (3.43)	0.55 (0.59)	3.90 (4.02)	1.58 (1.61)	0.26 (0.28)	1.84 (1.90)	0.45 (0.43)	0.05 (0.07)	0.50 (0.50)	1.21 (1.10)	0.12 (0.11)	1.34 (1.20)	0.57 (0.52)	0.06 (0.05)	0.63 (0.57)
G. resinosa	0.053 (0.08)	0.017 (0.04)	0.070 (0.11)	0.36 (0.31)	0.12 (0.11)	0.48 (0.42)	0.17 (0.14)	0.05 (0.05)	0.22 (0.19)	0.063 (0.19)	0.033 (0.11)	0.096 (0.29)	0.26 (0.27)	0.14 (0.12)	0.40 (0.39)	0.12 (0.13)	0.06 (0.06)	0.18 (0.18)
H. stenophyllum	12.9 (10.9)	1.8 (1.7)	14.7 (12.5)	3.02 (5.22)	0.42 (0.72)	3.43 (5.94)	1.39 (2.41)	0.20 (0.34)	1.59 (2.75)	–	–	–	–	–	–	–	–	–
S. cumingii[b]	0.28 (0.08)	0.09	0.37	0.06 (0.07)	0.02	0.08	0.04 (0.06)	0.00 (0.00)	0.04 (0.06)	–	–	–	–	–	–	–	–	–
A. saligna	–	–	–	–	–	–	–	–	–	0.02 (0.03)	0.03 (0.04)	0.05 (0.07)	0.01 (0.01)	0.02 (0.01)	0.03 (0.02)	0.01 (0.00)	0.01 (0.00)	0.01 (0.01)
Total						7.89 (6.56)			3.69 (3.04)						1.77 (1.33)			0.82 (0.63)

[a] Statistical comparisons performed for biomass C content showed no significant differences for B_A ($t = 1.57$, $P = 0.19$), B_B ($t = 1.71$, $P = 0.16$) and B_T ($t = 1.59$, $P = 0.19$).
[b] B_A for *S. cumingii* was calculated using the equation from Prado et al. (1987); estimates of B_B and B_T assume that B_S is 23.8% of B_T, which is the average C content (%) for three native species in Table 3.

root:shoot ratios range between 6 and 12, and in shrublands where values range between 1 and 3 (Noy-Meir, 1973). The root:shoot ratios of native shrub species in our study, however, ranged from 0.22 for *H. stenophyllum* to 0.39 for *G. resinosa* (Table 3). These ratios are low compared to the values obtained by He et al. (2008) for grasslands of Mongolia (11–25) and by Fan et al. (2008) for the desert-steppe of China (4.8 and 6.8). Zerihun et al. (2006) reported a root:shoot ratio of 0.58 for the xeric portion of a rainfall gradient of *Eucalyptus populnea* F. Muell. communities in northern Australia, which receives 367 mm of annual precipitation. This value is similar to that of *A. saligna* in our study (0.55), which is also native to Australia. Values lower than 1 were also found in warm deserts (Jackson et al., 1996), semiarid zones of Australia (Fan et al., 2008) and California chaparral, with values between 0.37 for *Arctostaphylos pungens* A. Gray and 0.7 for *Adenostoma fasciculatum* Hook. & Arn. (Kummerow et al., 1977). The low root:shoot ratio values in our study suggest that the species we studied may use different adaptive mechanisms such as entering a dormancy state by shedding their leaves during dry periods (Donoso, 1997). Alternatively, our sampling may have missed some roots, particularly in the deeper soil layers.

The movement of soil during site preparation prior to planting *A. saligna* resulted in the afforested site having values of soil bulk density and percentage of stones that did not follow the typical increase with depth, as observed in the natural condition (Table 6). Soil bulk density was higher in the two top soil depth intervals in the afforested condition than compared to lower soil depth intervals. Increases in soil bulk density, mainly due to the loss of soil structure, have been observed in other natural ecosystems that were converted to agricultural lands, resulting in less water infiltration and a decreased capacity to retain water and air in the soil profile (Celik, 2005; Li et al., 2007). Although afforestation with *A. saligna* does not exactly correspond to agricultural land conversion, site preparation for afforestation apparently had a similar effect on the top soil layers.

The general decrease in soil C stock with depth in both conditions was associated with a lower soil C content and also an increase in the percentage of stones (Table 6). The afforested condition had a lower soil C stock but a higher percentage of stones in the soil than the natural condition (Table 6). The difference in percentage of stones explained 17.2% of the difference in total soil C content between both conditions, and when this difference was removed, the afforested condition represented 32% lower soil C than that in the natural condition.

The soil C content beneath bare ground and under vegetation did not differ in our study. However, only two years had elapsed since afforestation, so this difference may increase in the future, given that less vegetation cover to protect the soil generally increases the C loss due to mineralization and to a lesser extent increases erosion (Martínez-Mena et al., 2002). In addition, because *A. saligna* trees would be expected to develop more extensive canopies in the future, C stocks should increase in the afforested condition with enhanced C fixation. Correspondingly, soil C content in the natural condition may decrease due to increased mineralization and soil erosion losses (Martínez-Mena et al., 2002).

Several studies have measured C pools in arid environments (Table 7). The C content in B_T in the natural condition in our study (3.7 t C ha^{-1}) was similar to the C values reported by Woomer et al. (2004) in a Sahel Desert site dominated by grasses with scattered shrubs (3.1 t C ha^{-1}). Woomer et al. (2004) found in the same study that the C pool in a degraded grassland was 0.4 t C ha^{-1}, which is similar to the value that we observed in the afforested condition (0.8 t C ha^{-1}). In general, the values of C content in B_T for grasslands and shrublands are much lower than the values reported by Glenday (2008) for arid forests in Kenya dominated by *Cynometra webberi*

Table 6
Soil characteristics with mean and standard deviation (in parentheses) for five soil depth intervals in a Mediterranean arid shrubland in Chile under natural and afforested conditions.

Depth (cm)	Natural				Afforested			
	Bulk density (g cm^{-3})	Stone (%)	Carbon content[a] (%)	Carbon stock[b] (t ha^{-1})	Bulk density (g cm^{-3})	Stone (%)	Carbon content (%)	Carbon stock (t ha^{-1})
0–5	1.71 (0.16)	5.5 (3.5)	0.85 (0.18)	6.87 (1.50)	1.82 (0.09)	24.6 (16.7)	0.61 (0.24)	3.98 (1.67)
5–10	1.73 (0.07)	14.6 (14.7)	0.59 (0.14)	4.44 (1.51)	1.76 (0.08)	31.7 (22.7)	0.47 (0.14)	2.80 (0.99)
10–20	1.77 (0.05)	21.7 (11.7)	0.53 (0.14)	7.42 (2.32)	1.58 (0.28)	45.0 (16.8)	0.40 (0.11)	3.86 (1.09)
20–30	1.87 (0.06)	32.9 (13.7)	0.45 (0.16)	5.63 (2.13)	1.46 (0.05)	46.7 (15.0)	0.35 (0.09)	3.50 (0.80)
30–50	1.83 (0.07)	43.8 (12.5)	0.39 (0.06)	8.10 (1.07)	1.96 (0.04)	46.7 (7.8)	0.29 (0.06)	5.65 (1.27)
Total [c] 0–50				32.45 (7.09)				19.80 (4.78)

[a] Student's *t*-test showed significant differences ($t = 5.28$, $P = 0.006$).
[b] Student's *t*-test showed significant differences ($t = 7.73$, $P = 0.002$).
[c] Student's *t*-test showed no significant differences ($t = 2.56$, $P = 0.062$).

Baker f. and *Brachystegia spiciformis* Benth. (36–54 t C ha^{-1}), although they estimated B_B as a fixed value of 50% of B_A.

The studies listed in Table 7 considered soil organic carbon (SOC) within the soil C pool, whereas we estimated total soil C (both organic and inorganic carbon) in our study. The soil C pool was an important component of total C in both our natural and afforested conditions (Fig. 3). The soil C content values in our study (19.8 and 32.5 t C ha^{-1}) were similar to those reported by Rasmussen (2006) in the Sonoran Desert (28 t C ha^{-1}) and by Singh et al. (2007) in an Aridisol soil in India (49 t C ha^{-1}). A 32% greater amount of soil C in the natural condition compared to the afforested condition in our study may be attributable to site soil preparation prior to afforestation. Similar changes in SOC were found by Muñoz et al. (2007), who found a 40% loss in SOC on a site of well-preserved espinal (thorny shrubland) compared to a degraded site in the Cauquenes Province of Chile. Martínez-Mena et al. (2002) also reported a significant loss of SOC in a semiarid zone in Spain (vegetation cover consisted of planted *Pinus halepensis* Miller and a native shrub), after nine years of complete vegetation removal, which was attributed to mainly soil mineralization. A total of 0.023 t ha^{-1} y^{-1} of SOC was lost through erosion and another 4.30 t ha^{-1} y^{-1} was lost through mineralization, resulting in a 31% reduction in SOC. In our study, we found a small amount of fine roots with 48% of C concentrated in the first 5 cm soil depth increment, which accounted for only about 2.5 kg C ha^{-1} in both conditions. These values are extremely low compared to those reported by Jackson et al. (1996), who found that fine roots in desert ecosystems can be as high as 2.7 t C ha^{-1}, with 60% of that amount occurring in the 0–30 cm depth increment. The small amount of fine roots observed in our study may have been due to the extremely dry conditions during the sampling year.

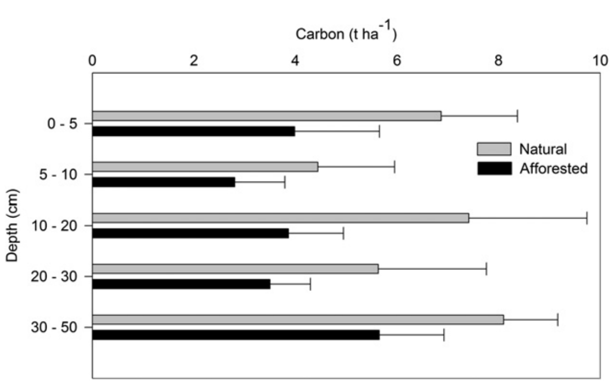

Fig. 2. Soil carbon content (t ha^{-1}) in natural and afforested conditions of an arid Mediterranean shrubland in Chile at five soil depth intervals. Error bars represent standard deviations.

In our study, the soil was the largest C pool in both natural and afforested conditions, followed by B_A, B_B and the litter pools (Fig. 3). The higher percentage that soil C represented in the afforested condition (94%) compared to the natural condition (84%), implies that the C loss was proportionally higher in the B_T pool. Total ecosystem C in the afforested condition was 36% lower than in the natural condition. The distribution of C in the different pools in the natural condition is similar to values reported for a grassland with scattered shrubs (Woomer et al., 2004), where soil C content represented 84% of ecosystem C, 60% of which was concentrated in the first 20-cm soil depth.

We found in B_T a 2.9 t C ha^{-1} lower C level in the afforested compared to natural condition in our study. This is similar to a 2.7 t C ha^{-1} difference in C reported by Woomer et al. (2004) in a grassland with scattered shrubs compared to a degraded grassland in Senegal. In the Sahel of West Africa, Takimoto et al. (2008) found values of total ecosystem C of 35.6 t C ha^{-1} in a fodder bank and 37.1 t C ha^{-1} in a parkland dominated by *Vitellaria paradoxa* C.F. Gaertn., which was similar to the value of 36.5 t C ha^{-1} found in the natural condition in our study. The afforested condition in our study had a total ecosystem C of 21.1 t C ha^{-1}, which was between the values for abandoned land (24.7 t C ha^{-1}) and live fence (17.7 t C ha^{-1}) found by Takimoto et al. (2008). The values reported by Bonino (2006) for a secondary forest in the dry Chaco in Argentina (36.4 t C ha^{-1}) were similar to the value that we found for the natural condition shrubland, although their estimate did not include B_B and litter and used a unique allometric function to estimate B_A in arid forests.

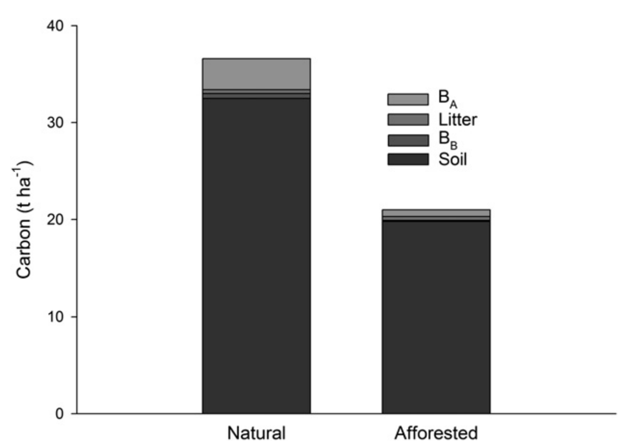

Fig. 3. Carbon content of ecosystem pools in a Mediterranean arid shrubland in Chile under natural and afforested conditions. Because of extremely low values, C content of fine roots was not included in the figure.

Table 7
Carbon content and root:shoot ratios of various ecosystem pools in arid and semiarid ecosystems.

Vegetation/soil type	Location	Carbon content[a] (t ha^{-1})								Root:shoot	Reference
		B_A	B_B	B_T	Litter	SOC	SIC	STC	TEC		
Temperate desert-steppe[b]	China	0.5 (0.4)	3.4 (2.0)	3.9 (2.1)						6.8	Fan et al. (2008)
Temperate steppe-desert		0.5 (0.2)	2.4 (2.0)	2.9 (1.9)						4.8	
Degraded grassland	Sahel Desert, Senegal			0.4		11.6			12		Woomer et al. (2004)
Shrubby grassland				1.9		25.3			27.2		
Grassland w/scattered shrubs				3.1		16.3			19.4		
Severe degraded grassland	Mongolia Grassland Ecosystem Research Station, China	0.2	5	2.5	0.02	5.5			13.2	25	He et al. (2008)
Light degraded grassland		0.3	7	7.3	0.2	10			24.8	23.3	
Grazing exclusion		0.7	8	8.7	0.7	14			32.1	11.4	
Mixed grassland	Arizona, USA					16	12	28			Rasmussen (2006)
Creosotebush-bursage/Aridisol						14	127	141			
Natural shrubland	Coquimbo Region, Chile	3.2 (2.7)	0.5 (0.4)	3.7 (3.1)	0.4 (0.3)			32.5 (7.1)	36.5 (9.5)	0.16	This study
Afforested shrubland		0.7 (0.5)	0.1 (0.1)	0.8 (0.6)	0.4 (0.4)			19.8 (4.8)	21.1 (5.7)	0.14	
Very degraded espinal	Cauquenes, Chile					42.0					Muñoz et al. (2007)
Degraded espinal						36.0					
Good espinal						67.9					
Well-preserved espinal						70.2					
Native forest						135.5					
Aridisol	Rajasthan, India	–				24.2	20.7	44.9			Singh et al. (2007)
Primary forest	Dry Chaco, Argentina	30.3				34.6			64.9		Bonino (2006)
Secondary forest		8.4				28.0			36.4		
Shrubby grassland		1.4				23.0			24.4		
Cynometra forest	Arabuko-Sokoke Forest, Kenya	42 (6)	12 (2)	54	1.5 (0.2)	25 (2)			83 (8)	0.29	Glenday (2008)
Cynometra thicket		28 (5)	8 (1)	36	2.3 (0.5)	22 (3)			65 (7)	0.28	
Faidherbia albida parkland	Ségou Region, Mali			54		16.8			70.8		Takimoto et al. (2008)
Vitellaria paradoxa parkland				21		16.1			37.1		
Fodder bank				1.5		12.5			14.0		
Abandoned land				0.7		24			24.7		
Livefence				3.2		14.5			17.7		
Calcaric fluvisols	Guadix–Baza Basin, Southeast Spain					52	310[c]	362			Diaz-Hernandez et al. (2003)
Calcisols						52	390	442			

[a] B_A, aboveground biomass; B_B, belowground biomass; B_T, total biomass; SOC, soil organic carbon; SIC, soil inorganic carbon; STC, soil total carbon; TEC, total ecosystem carbon.
[b] Desert-steppe is dominated by grasses, whereas steppe-desert is dominated by shrubs.
[c] Inorganic C is composed of dolomite and calcite with the high C amount due mainly to calcite.

In general, conversion of ecosystems from natural conditions to agricultural use results in decreased stocks of ecosystem C (Abule et al., 2005; Girmay et al., 2008; Steffens et al., 2008; Woldeamlak and Stroosnijder, 2003). This decrease was also found in our study, mainly due to the loss of C from the soil C pool and reductions in B_A and B_B, which likely occurred during site preparation for afforestation. The planting of *A. saligna* in berms with infiltration ditches, as used in our study, was recommended by Perret and Valdebenito (1997) as a soil conservation technique that results in greater shrub height and diameter with reduced soil erosion from runoff. They did not specifically address the potential loss of C during site preparation prior to afforestation. According to Perret et al. (2001), management practices that maximize the yield of fodder would have a negative impact on increases in stem diameter and plant height. Residue management during site preparation was recognized as an important way to maintain or increase soil and ecosystem C content (FAO, 2002; Lal, 2003). For afforestation, Serra (1997) recommended establishment of three strata: herbaceous layer consisting of annual plants, a low-statured shrub stratum of *Atriplex nummularia* Lindl. with high forage value, and a tree layer consisting of a low to medium density of *A. saligna*.

In summary, our initial evaluation of C stocks is an important baseline to assess the long-term effects of afforestation on ecosystem C pools in *A. saligna* plantations in Chile. Fluxes of CO_2 are also being monitored on our sites with Bowen ratio energy balance instrumentation to determine shorter-term trends of carbon fixation and efflux.

Acknowledgements

Funding for J. Perez-Quezada came from Vicerrectoría de Investigación, Universidad de Chile, research fund (DI I2 06/01-2) and from FONDECYT 11070101. The authors want to thank Claudia Torres, the field workers at Las Cardas Experimental Station, Carolina Bravo and Nicolás Fuentes, for their help with the fieldwork. Thanks also to Dr. Oscar Seguel for use of his field equipment for soil sampling and physical analyses in his laboratory. Finally, we thank one anonymous reviewer who helped us to improve this manuscript.

References

Abule, E., Smit, G., Snyman, H., 2005. The influence of woody plants and livestock grazing on grass species composition, yield and soil nutrients in the Middle Awash Valley of Ethiopia. Journal of Arid Environments 60, 343–358.

Allison, L.E., 1965. Total carbon. In: Black, C.A. (Ed.), Methods of Soil Analysis Part 2: Chemical and Microbiological Properties. American Society of Agronomy, Madison, WI, pp. 1346–1365.

Armesto, J.J., Arroyo, M.T.K., Hinojosa, L.F., 2007. The Mediterranean environment of Central Chile. In: Veblen, T.T., Young, K.R., Orme, A.R. (Eds.), The Physical Geography of South America. Oxford University Press, New York, pp. 184–199.

Avila, A., Muñoz, J., Peña, O., Uribe, M., 2007. Superficie de plantaciones forestales. Regiones de Coquimbo a Aysén. Actualización a diciembre de 2006. In: Informe Técnico 174. INFOR, Santiago, Chile.

Azocar, P., Paton, D., Matas, A., Rojo, H., 1998. Utilización de modelos de regresión múltiple logarítmica en el análisis de la información de fitomasa forrajera de arbustos. Caso con cuatro especies arbustivas del secano mediterráneo árido de Chile. Avances en Producción Animal, 17–33.

Azocar, P., Paton, D., Santibañez, F., Torres, C., 2001. Modelo para estimar fitomasa en repanda (*Atriplex repanda*) en función de parámetros alométricos, precipitación y densidad. Avances en Producción Animal, 107–118.

Bechtold, H.A., Inouye, R.S., 2007. Distribution of carbon and nitrogen in sagebrush steppe after six years of nitrogen addition and shrub removal. Journal of Arid Environments 71, 122–132.

Benites, J., Saintraint, D., Morimoto, Y.K., 1994. Degradación de tierras y producción agrícola en Argentina, Bolivia, Brasil, Chile y Paraguay. Erosión de suelos en América Latina. FAO, Santiago, Chile, pp. 83–116.

Blake, G.R., 1965. Bulk density. In: Black, C.A. (Ed.), Methods of Soil Analysis, Physical and Mineralogical Properties, Including Statistics of Measurement and Sampling. American Society of Agronomy, Madison, WI, pp. 374–390.

Bonino, E.E., 2006. Changes in carbon pools associated with a land-use gradient in the Dry Chaco, Argentina. Forest Ecology and Management 223, 183–189.

Casanova, M., Luzio, W., 2008. The International Conference and Field Workshops on Soil Classification. Northern Field-guide between 30° S and 33° 30′ S. Universidad de Chile, Santiago, pp. 48–49.

Celik, I., 2005. Land-use effects on organic matter and physical properties of soil in a southern Mediterranean highland of Turkey. Soil & Tillage Research, 270–277.

Cleary, M.B., Pendall, E., Ewers, B.E., 2008. Testing sagebrush allometric relationships across three fire chronosequences in Wyoming, USA. Journal of Arid Environments 72, 285–301.

Cochran, W.G., 1971. Técnicas de muestreo, Tercera. Compañía Editorial Continental, S.A., Ciudad de Mexico.

Diaz-Hernandez, J.L., Fernandez, E.B., Gonzalez, J.L., 2003. Organic and inorganic carbon in soils of semiarid regions: a case study from the Guadix-Baza basin (Southeast Spain). Geoderma 114, 65–80.

Doll, U., Vallejos, O., Bilbao, N., Jara, C., 2008. Estimación preliminar de la retención de carbono en raíces finas y mantillo de un renoval de Nothofagus glauca de la precordillera andina de la Región del Maule, Chile. Bosque 29, 91–96.

Donoso, C., 1997. Ecología forestal, el bosque y su medio ambiente. Editorial Universitaria, Santiago, Chile.

FAO, 2002. Captura de Carbono en los Suelos para un Mejor Manejo de la Tierra. Informe Sobre los Recursos Mundiales de Suelos. FAO, Rome.

Fan, J.W., Zhong, H.P., Harris, W., Yu, G.R., Wang, S.Q., Hu, Z.M., Yue, Y.Z., 2008. Carbon storage in the grasslands of China based on field measurements of above- and below-ground biomass. Climatic Change 86, 375–396.

Gayoso, J., Guerra, J., Alarcón, D., 2002. Contenido de carbono y funciones de biomasa en especies nativas y exóticas. Universidad Austral de Chile, Valdivia, Chile, 157 pp.

Girmay, G., Singh, B.R., Mitiku, H., Borresen, T., Lal, R., 2008. Carbon stocks in Ethiopian soils in relation to land use and soil management. Land Degradation & Development 19, 351–367.

Glenday, J., 2008. Carbon storage and emissions offset potential in an African dry forest, the Arabuko-Sokoke Forest, Kenya. Environmental Monitoring and Assessment 142, 85–95.

He, N.P., Yu, Q., Wu, L., Wang, Y.S., Han, X.G., 2008. Carbon and nitrogen store and storage potential as affected by land-use in a *Leymus chinensis* grassland of northern China. Soil Biology & Biochemistry 40, 2952–2959.

Huenneke, L.F., Clason, D., Muldavin, E., 2001. Spatial heterogeneity in Chihuahuan Desert vegetation: implications for sampling methods in semi-arid ecosystems. Journal of Arid Environments 47, 257–270.

INE, 1998. VI Censo nacional agropecuario: total nacional, año 1997. Instituto Nacional de Estadísticas, Santiago, Chile.

Jackson, R., Canadell, J., Ehleringer, J., Mooney, H., Sala, O., Schulze, E., 1996. A global analysis of root distribution for terrestrial biomes. Oecologia 108, 108.

Jobbagy, E.G., Jackson, R.B., 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecological Applications 10, 423–436.

Kent, M., Coker, P., 1992. Vegetation Description and Analysis. A Practical Approach, 1. John Wiley & Sons Ltd., London.

Kummerow, J., Kraus, D., Jow, W., 1977. Root systems of chaparral shrubs. Oecologia 29, 163–177.

Lailhacar, S., Aylwin, M., 1988. Efecto de tres especies leñosas en algunas variables del suelo y del estrato herbáceo en la pradera de clima mediterráneo árido. Simiente 58, 51–61.

Lal, R., 2003. Carbon sequestration in dryland ecosystems. Environmental Management 33, 528–544.

Li, X.G., Rengel, F.M., Zhan, Z., Singh, B., 2007. Soil physical properties and their relations to organic carbon pools as affected by land use in an alpine pastureland. Geoderma 139, 98–105.

Luebert, F., Pliscoff, P., 2005. Sinopsis bioclimática y vegetacional de Chile. Editorial Universitaria, Santiago, Chile.

Martínez-Mena, M., Alvarez, J., Castillo, V., Albaladejo, J., 2002. Organic carbon and nitrogen losses influenced by vegetation removal in a semiarid Mediterranean soil. Biogochemistry, 309–321.

Mora, F., Meneses, R., Perret, S., 2002. Potencialidades y limitaciones de Acacia saligna en la Región de Coquimbo, Chile; y su relación con los ecosistemas de clima mediterráneo. Avances en Producción Animal 27, 9–20.

Murray, R.B., Jacobson, M.Q., 1982. An evaluation of dimension analysis for predicting shrub biomass. Journal of Range Management 35, 451–454.

Muñoz, C., Ovalle, C., Zagal, E., 2007. Distribution of soil organic carbon stock in an Alfisol profile in Mediterranean Chilean ecosystems. Revista de la Ciencia del Suelo y Nutrición Vegetal 7, 15–27.

Navar, J., Najera, J., Jurado, E., 2002. Biomass estimation equations in the Tamaulipan thornscrub of north-eastern Mexico. Journal of Arid Environments 52, 167–179.

Noy-Meir, I., 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4, 25–49.

Paton, D., Nuñez, J., Bao, D., Muñoz, A., 2002. Forage biomass of 22 shrub species from Monfragüe Natural Park (SW Spain) assessed by log–log regression models. Journal of Arid Environments 52, 223–231.

Perret, S., Valdebenito, G., 1997. Evaluación de pérdidas de suelo y escorrentía bajo diferentes esquemas productivos en la provincia de Choapa, IV Región. In: Valdebenito, G., Benedetti, S. (Eds.), Forestación y silvicultura en zonas áridas y semiáridas de Chile. INFOR-CORFO, Santiago, Chile, pp. 60–71.

Perret, S., Delard, C., Mora, F., Jara, R., 2001. Monografía de *Acacia saligna* (Labill) H.L. Wendl. INFOR-CORFO, Santiago, Chile.

Prado, J., Infante, P., Arraigada, M., Aguirre, S., 1987. Funciones de biomasa para seis especies arbustivas de la zona árida chilena. Ciencia e Investigación Forestal 1, 11–19.

Rasmussen, C., 2006. Distribution of soil organic and inorganic carbon pools by biome and soil taxa in Arizona. Soil Science Society of America Journal 70, 256–265.

Schimel, D.S., House, J.I., Hibbard, K.A., Bousquet, P., Ciais, P., Peylin, P., Braswell, B.H., Apps, M.J., Baker, D., Bondeau, A., Canadell, J., Churkina, G., Cramer, W., Denning, A.S., Field, C.B., Friedlingstein, P., Goodale, C., Heimann, M., Houghton, R.A., Melillo, J.M., Moore, B., Murdiyarso, D., Noble, I., Pacala, S.W., Prentice, I.C., Raupach, M.R., Rayner, P.J., Scholes, R.J., Steffen, W.L., Wirth, C., 2001. Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. Nature 414, 169–172.

Serra, M.T., 1997. *Acacia saligna*. Especies árboreas y arbustivas para las zonas áridas y semiáridas de América Latina. FAO, Santiago, Chile, pp. 171–176.

Singh, S.K., Singh, A.K., Sharma, B.K., Tarafdar, J.C., 2007. Carbon stock and organic carbon dynamics in soils of Rajasthan, India. Journal of Arid Environments 68, 408–421.

Steffens, M., Kolbl, A., Totsche, K.U., Kogel-Knabner, I., 2008. Grazing effects on soil chemical and physical properties in a semiarid steppe of Inner Mongolia (PR China). Geoderma 143, 63–72.

Takimoto, A., Nair, P.K.R., Nair, V.D., 2008. Carbon stock and sequestration potential of traditional and improved agroforestry systems in the West African Sahel. Agriculture, Ecosystems & Environment 125, 159–166.

Uresk, D.W., Gilbert, R.O., Rickard, W.H., 1977. Sampling big sagebrush for phytomass. Journal of Range Management 30, 311–314.

Vande Walle, I., Mussche, S., Samson, R., Lust, N., Lemeur, R., 2001. The above- and belowground carbon pools of two mixed deciduous forest stands located in East-Flanders (Belgium). Annals of Forest Science 58, 507–517.

Vora, R.S., 1988. Predicting biomass of 5 shrub species in Northeastern California. Journal of Range Management 41, 63–65.

Vourlitis, G.L., Zorba, G., Pasquini, S.C., Mustard, R., 2007. Carbon and nitrogen storage in soil and litter of southern Californian semi-arid shrublands. Journal of Arid Environments 70, 164–173.

Woldeamlak, B., Stroosnijder, L., 2003. Effects of agroecological land use succession on soil properties in Chemoga watershed, Blue Nile basin, Ethiopia. Geoderma 111, 85–98.

Woomer, P.L., Toure, A., Sall, M., 2004. Carbon stocks in Senegal's Sahel transition zone. Journal of Arid Environments 59, 499–510.

Zerihun, A., Montagu, K.D., Hoffmann, M.B., Bray, S.G., 2006. Patterns of below- and aboveground biomass in *Eucalyptus populnea* woodland communities of northeast Australia along a rainfall gradient. Ecosystems 9, 501–515.