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Article

Predicción de biomasa radicular en especies de pastizales semiáridos en el sur del Desierto Chihuahuense

Predicting root biomass for semiarid grassland species of the southern Chihuahuan Desert

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Resumen:

La mayor parte del carbono en los pastizales proviene de la biomasa subterránea, particularmente en pastizales áridos. A pesar de ello, la estimación de la biomasa radicular en esos ecosistemas ha sido poco abordada. En el presente estudio se analizó la correlación entre variables aéreas de la planta y su biomasa radicular para desarrollar modelos estadísticos que permitan la estimación confiable de esta última. Se recolectaron 26 especies vegetales dentro de pastizales sin pastoreo. Se diseñaron modelos de regresión lineal, exponencial y logarítmica para cada taxon y para todos en su conjunto con el fin de determinar las variables que mejor predijeran la biomasa radicular. Solo *Frankenia gypsophila* y *Dalea gypsophila* mostraron relación raíz/tallo (RBR) >1. *Enneapogon desvauxii* y *Atriplex acantocarpha* tuvieron una RBR cercana a 1. Ocho especies mostraron significancia estadística en al menos un análisis de correlación, pero solo *Tiquilia canescens*, *Bouteloua gracilis*, *Machaerantera pinnatifida*, *Lesquerella fendleri*, y *Atriplex acanthocarpa* registraron tanto significancia estadística como un coeficiente de determinación r^2 ≥0.50. Mediante el método Marquardt en la regresión exponencial, 14 de las 15 especies de interés alcanzaron coeficiente de determinación alto y significancia estadística; este método fue el adecuado (r^2=0.853) para estimar la biomasa radicular de las especies analizadas en su conjunto, a partir de la altura de la planta y el diámetro de la copa.

Palabras clave: Biomasa vegetal, ecosistemas áridos, ecuaciones alométricas, método *Marquardt*, modelo de regresión, noreste de México.

Abstract:

Most of carbon in grasslands comes from underground biomass, particularly in arid grassland ecosystems. However, estimation of root biomass in these ecosystems has been poorly studied. In this study was analyzed the correlation between above ground plant variables and root biomass to develop statistical models for reliable root biomass estimations. Twenty-six plant species were collected within grazing-excluded grasslands. Linear, exponential and logarithmic regression models were performed for each species and for the whole data set to determine the variables that best predicted root biomass. Only *Frankenia gypsophila* and *Dalea gypsophila* showed root/shoot ratio (RSR) higher than one. *Enneapogon desvauxii* and *Atriplex acantocarpha* had a RSR close to one. Eight species showed statistical significance in at least one of the correlation analyses but only *Tiquilia canescens*, *Bouteloua gracilis*, *Machaerantera pinnatifida*, *Lesquerella fendleri*, and *Atriplex acanthocarpa* had both statistical significance and acceptable coefficient of determination (r^2 ≥0.50). Using the Marquardt exponential method, 14 out of 15 studied species showed a high determination coefficient and statistical significance. This method was adequate (r^2=0.853) to estimate root biomass for the whole set of plants from plant height and crown diameter.

Key words: Plant biomass, arid ecosystems, allometric equations, Marquardt method, regression model, northeastern Mexico

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Introduction

A substantial proportion of the carbon (C) assimilated by plants through photosynthesis is transferred to roots, usually exceeding the amount allocated in the above ground components. This flux of C has a strong impact on the regulation of major soil processes that affect productivity and bio-chemical cycles of ecosystems (Jansson *et al*., 2010).

Estimation of carbon (C) stocks and emissions of greenhouse gases have received increasing attention in the last decade (Maniatis and Mollicone, 2010; Asner, 2011). However, temperate and tropical forests have been studied more thoroughly (Saatchi *et al*., 2011; Asner *et al*., 2012) and other ecosystems that might contain substantial amounts of C have been neglected (Scurlock *et al.*, 2002; Gibbon *et al.*, 2010).

Covering almost 39 million km^2 (about 25 % of the continental surface of the Earth), grasslands represent one of the most extensive ecosystems in the world and provide numerous environmental services (D'Atri, 2007).

Grasslands are potential C sinks to reduce atmospheric CO_2 (Jones and Donnelly, 2004; Acharya *et al.*, 2012). Studies on C storage suggest that most of the C in grasslands originates from below ground biomass (Jackson *et al.*, 2002) and total allocated C increases with plant species richness (Adair *et al.*, 2009), particularly in arid systems where grass root growth can be much higher than grass shoot growth (Evans *et al.*, 2013).

Also, it is common that under adverse environmental conditions such as water or nutrient deficit in the root zone, the relationship between root biomass and shoot biomass (RSR= Root/Shoot ratio) tends to increase (Wan *et al.*, 1993; Mata *et al.*, 2002; Mata and Meléndez, 2005; Sainju *et al.,* 2017). However, root biomass in arid grasslands has been poorly investigated and it has frequently been underestimated in determining C pools in different ecosystems, even though roots can be the main biomass source in some species (Evans *et al.*, 2013; Hernández-Gómez *et al.,* 2013).

Several studies have reported results for the quantification of above ground biomass through allometric equations in arid systems (Navar *et al.*, 2004; Flombaum and Sala, 2007; McClaran *et al.*, 2013). Some other studies have estimated root biomass in cultivated temperate pastures (Vinther, 2006; Rasmussen *et al.*, 2010; Acharya *et al*., 2012; Eriksen *et al.*, 2012) although most of them have assessed biomass by sampling soil at a standardized depth and without differentiating species.

Also, it has been worked on determining the proportion of root biomass that is produced or that dies annually (root turnover coefficients) using environmental and above ground plant characteristics to determine below ground net primary productivity of grasslands (Gill *et al.*, 2002). None of these studies has attempted to develop a statistical model that allows a quick estimation of root biomass from easy measurable plant variables. There is a definite lack of experiences to document allometric equations for the estimation of root biomass in arid and semiarid natural grasslands, perhaps because of the difficulty involved in quantifying below-ground production.

Allometric equations require an initial extensive destructive biomass sampling, but they can be used later as a consistent and non-destructive method for estimating below-ground root biomass. Species differences in biomass allocation should be considered in land management and conservation practices. Species-particular information on root and shoot biomass is also important in parameterizing ecological models that are used to support land and environmental management (Mata *et al.*, 2008). In this case, it was hypothesized that root biomass can be reliably estimated from above ground plant parameters. Hence, specific species-allometric equations were developed for 26 native taxa of the Chihuahuan desert as well as multispecies equations for all them as a whole.

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Materials and Methods

Study area

The study was carried out in two cattle-excluded semiarid grasslands of the southern part of the Chihuahuan Desert in northeastern Mexico. Mean annual temperature for the region is 17.2 °C with a minimum of -1.8 °C in January and maximum of 35.1 °C in May. Average annual rainfall is 386.43 mm. March and July are considered the driest (8.43 mm) and wettest (58.06 mm) months, respectively (SMN, 2012). Sampling areas were between 1 800 and 2 000 masl at the localities of *La Soledad* in the state of *Nuevo León* and *El Salado* in the state of *San Luis Potosí*.

Vegetation is conformed by communities of short halophytic/gypsophyllus grasslands (between 0.05 and 0.2 m height) associated with microphyllous and rosetophyllous desert scrub (Estrada *et al.*, 2010) where the most abundant species are *Muhlenbergia villiflora* Hitchc., *Scleropogon brevifolius* Phil., *Zinnia acerosa* (DC.) A. Gray, *Dasyochloa pulchella* (Kunth) Willd. ex Rydb., *Bouteloua chasei* Swall., *Frankenia gypsophila* I. M. Johnst., *Calylophus hartwegii* (Benth.) P.H. Raven, *Dalea gypsophila* Barneby and *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths. These grasslands embrace several endemic plants (*Dalea gypsophila*, *D. radicans* S. Watson, *Frankenia gypsophila*, *Machaeranthera heterophylla* R. L. Hartm. and *M. crutchfieldii* B.L. Turner) (Estrada *et al.*, 2010) and animals such as the Mexican prairie dog (*Cynomys mexicanus* Merriam, 1892) that is a regionally endemic species with a status of globally endangered (Baillie and Groombridge, 1996). This ecosystem also provides an important refuge for resident and migratory animals (Day and Ludeke, 1993).

Soils in the area are mainly Solonchack and calcaric Phaeozem, and smaller areas of chromic Vertisol and luvic Chernozem (INEGI, 1981).

Sampling and data analysis

26 plant species were sampled for the analysis of biomass estimation. Sampling was done during July, August, and September 2011-2013, about a month after the even scarce rainy season. Plants were collected from 240 randomly established plots (1 m^2 each); out of which 144 were located in *El Salado* and 96 in *La Soledad.* The number of plant samples per species varied between 8 and 18 according to the availability in the field and covered a broad range of heights and diameters for each species.

Samples were extracted from wet soil (during the rainy season), either immediately after a rain or after manual watering the soil to allow root extraction as complete as possible. Roots were washed out with distilled water and plants measured for shoot height, mean crown diameter and root length. Roots were separated from the aerial part of the plant and both were dried at 70 °C with a *Riossa* HCF-102-D digital drying oven until dry weight remained constant. The stems and roots were measured with an Urrea graduated plastic measuring tape. These values were used to assess the relationship between shoot and root biomass (RSR) and to develop a non-destructive model to determine root biomass.

Data complied with statistical assumptions (multivariate normality, no multicollinearity, no auto-correlation and homoscedasticity). Then, linear, exponential and logarithmic regression models were performed for each species (Table 1) and individual plant traits such as plant height (H), mean crown diameter (D) or a combination of them (H*HD, H+HD and H,D) were used as independent variables that best estimate root biomass, which was the dependent variable. Linear regression analysis was carried out by the least-square method while the exponential model was performed using the Marquardt (non-linear minimum square) procedure (Marquardt, 1963). Analyses were performed by using SPSS and PROC NLIN SAS/STAT (SAS Institute, 2004).

Table 1. Regression analyses models to estimate root biomass (RB) as a function of plant crown diameter (D) and plant height (H) in 26 plant species from the southern Chihuahuan desert.

Model	**Variable**	**Mathematical expression**
Linear	Diameter (D)	$RB = B_0 + B_1 D$
	Height (H)	$RB = B_0 + B_1 H$
	Height*Diameter (H*D)	$RB = B_0 + B_1 HD$
	Height + Diameter (H+D)	$RB = B_0 + B_1 H + B_2 D$
Logarithmic	Diameter (D)	$RB = \beta_0 + \beta_1 \, ln(D)$
	Height (H)	$RB = \beta_0 + \beta_1 ln(H)$
	Height*Diameter (H*D)	$RB = \beta_0 + \beta_1 \, ln(HD)$
	Height + Diameter (H+D)	$RB = \beta_0 + \beta_1 ln\,(H) + \beta_2 ln\,(D)$
Exponential	Diameter (D)	$BR = B_0 e^{B_1 D}$
	Height (H)	$BR = B_0 e^{B_1 H}$
	Height*Diameter (H*D)	$BR = B_0 e^{B_1 HD}$
	Height, Diameter	$BR = B_0 e^{B_1 H + B_Z D}$
	Height + Diameter (H+D)	$BR = B_0 e^{B_1 H + D}$

B_0 = Y-axis intercept of the regression model; B_1 and B_2 = The slopes of the regression models; Log and *e* = The base 10 logarithmic and the exponential function value.

Results

Root-shoot biomass relation

Only two out of 26 plant species showed a higher root to shoot value higher than one.

The two species are *Frankenia gypsophila* (2.27) and *Dalea gypsophila* (1.95). *Enneapogon desvauxii* and *Atriplex acantocarpha* had a root/shoot relation close to one, which means that they have a similar production of above and below-ground biomass (Table 2).

Table 2. Shoot and root biomass and RSR (Root/Shoot Relation) for 26 native plant species of the southern Chihuahuan Desert.

Species	**Family**	**Life cycle**	**N**	**Shoot biomass (g)**	**Root biomass (g)**	**RSR**
Frankenia gypsophila I.M. Johnst.	Frankeniaceae	Perenne	15	19.43±4.12	44.19±10.32	2.27
Dalea gypsophila Barneby	Fabaceae	Perenne	12	0.69±0.15	1.35±0.27	1.95
Enneapogon desvauxii P. Beauv.	Poaceae	Perenne	4	2.04±0.08	2.02±0.36	0.99
Atriplex acanthocarpa (Torr.) S. Watson	Chenopodiacea	Perenne	10	8.25±2.46	8.02±2.01	0.97
Scleropogon brevifolius Phil.	Poaceae	Perenne	4	1.34±0.18	1.01±0.37	0.76
Muhlenbergia arenicola Buckley	Poaceae	Perenne	5	0.87±0.13	0.52±0.11	0.60
Dieteria canescens (Pursh) A. Gray *(Syn.: Machaeranthera canescens)*	Asteraceae	Anual o Perenne breve	4	7.48±1.87	3.90±0.77	0.52
Bouteloua gracilis (Willd. ex Kunth) Lag. ex Griffiths	Poaceae	Perenne	10	11.37±2.51	5.82±1.12	0.51
Rumex crispus L.	Polygonaceae	Perenne	5	0.88±0.33	0.43±0.13	0.49
Aristida havardii Vasey	Poaceae	Perenne	10	1.28±0.15	0.63±0.09	0.49
Zinnia acerosa (DC.) A. Gray	Asteraceae	Perenne	18	3.77±0.69	1.71±0.48	0.45
Muhlenbergia repens (J. Presl) Hitchc.	Poaceae	Perenne	10	8.50±0.65	2.92±0.45	0.34
Machaeranthera pinnatifida (Hook.) Shinners	Asteraceae	Perenne	10	4.79±1.18	1.38±0.35	0.29
Muhlenbergia villiflora Hitchc.	Poaceae	Perenne	13	1.37±0.18	0.36±0.07	0.26
Dasyochloa pulchella (Kunth) Willd. ex Rydb.	Poaceae	Perenne	15	2.25±0.21	0.56±0.19	0.25
Bouteloua chasei Swall.	Poaceae	Perenne	10	1.42±0.21	0.35±0.05	0.25
Lepidium virginicum L.	Brassicaceae	Anual Bienal	13	9.30±1.90	2.19±0.55	0.24
Atriplex canescens (Pursh) Nutt.	Chenopodiaceae	Perenne	4	29.30±10.37	10.92±5.06	0.20
Croton dioicus Cav.	Euphorbiaceae	Perenne	5	22.58±2.53	2.87±0.31	0.13
Hoffmanseggia glauca (Ort.) Eifert	Caesalpiniaceae	Perenne	5	0.50±0.10	0.06±0.03	0.11
Euphorbia prostrata Aiton	Euphorbiaceae	Perenne	5	2.00±0.50	0.20±0.12	0.10
Gaura coccinea Pursh	Onagraceae	Perenne	13	11.53±3.21	1.06±0.13	0.09
Lesquerella fendleri (A. Gray) S. Watson	Brassicaceae	Perenne	15	3.40±0.57	0.27±0.02	0.08
Tribulus terrestris L.	Zygophyllaceae	Anual	5	1.01±0.27	0.07±0.03	0.07

Tiquilia canescens (DC.) A. Richardson	Boraginaceae	Perenne	8	63.20±9.20	4.45±0.58	0.07
Aristida adscencionis L.	Poaceae	Anual	5	2.75±0.39	0.08±0.02	0.03

Values represent the mean ± standard error.

Estimation of root biomass from above ground plant parameters

Linear, exponential, quadratic and logarithmic regression analyses among above ground plant traits and root biomass were carried out for those species with a sample size larger or equal to 8 (15 species; Table 3). Eight species showed significance ($P \leq 0.05$) in at least one of the analyses but only five species (*Tiquilia canescens*, *Bouteloua gracilis*, *Machaerantera pinnatifida*, *Lesquerella fendleri*, and *Atriplex acanthocarpa*) had both significance and acceptable coefficient of determination (r^2 adjusted ≥0.50). *A. acanthocarpa* was the species that showed acceptable coefficient of determination for a higher number of variables (H, D and D+H) and types of regression analyses (linear, exponential, quadratic and logarithmic). A quadratic polynomial regression analysis was the most adequate model with a higher r^2 value for most of the species. The plant parameter that best explained root biomass was plant crown diameter.

Since the tested models only allowed prediction of root biomass for five species, an exponential regression using the Marquardt method was also tested. The Marquardt procedure is a maximum neighborhood method that performs an optimum interpolation between linearization and the steepest-descent or gradient method (Marquardt, 1963). This method uses an iterative process of non-linear equations by a minimum square method that minimize the square sum of residuals of the model, allowing the maximum possible value for the likelihood function according to the required precision (Aguirre, 1994).

Table 3. Equations derived from the regression analyses.

Species	Variable	n	r^2Aj	Sig.	Regression model	Equation
Atriplex acanthocarpa	H	10	0.563	0.012	Lineal	$BR = 2.324 + 0.729X$
Atriplex acanthocarpa	H	10	0.562	0.013	Exponencial	$BR = 3.179\, e^{(0.084H)}$
Atriplex acanthocarpa	D	10	0.832	0.000	Lineal	$BR = 1.019 + 0.038D$
Atriplex acanthocarpa	D	10	0.577	0.011	Logarítmico	$BR = -16.197 + 4.972\, lnD$
Atriplex acanthocarpa	D	10	0.838	0.002	Cuadrático	$BR = 1.900 + 0.028D + 1.782E - 5D^2$
Atriplex acanthocarpa	D	10	0.735	0.002	Exponencial	$BR = 2.94\, e^{(0.004DH)}$
Atriplex acanthocarpa	D+H	10	0.797	0.001	Lineal	$BR = -19.713 + 0.873(D + H)$
Atriplex acanthocarpa	D+H	10	0.740	0.001	Logarítmico	$BR = -92.470 + 29.200\, ln(D + H)$
Atriplex acanthocarpa	D+H	10	0.841	0.002	Cuadrático	$BR = 14.375 - 1.108\,(D + H) + 0.028(D + H)^2$
Atriplex acanthocarpa	D+H	10	0.598	0.009	Exponencial	$BR = 0.396\, e^{(0.087D+H)}$
Bouteloua gracilis	D	10	0.620	0.007	Lineal	$BR = -0.975 + 0.763D$
Bouteloua gracilis	D	10	0.794	0.004	Cuadrático	$BR = 7.322 - 1.213D + 0.102D^2$
Bouteloua gracilis	D	10	0.573	0.011	Exponencial	$BR = 2.095\, e^{(0.101D)}$
Bouteloua gracilis	DH	10	0.603	0.008	Lineal	$BR = 1.134 + 0.016DH$
Bouteloua gracilis	DH	10	0.683	0.018	Cuadrático	$BR = 5.227 - 0.014DH + 4.147E - 5DH^2$
Bouteloua gracilis	DH	10	0.558	0.013	Exponencial	$BR = 2.767\, e^{(0.002DH)}$
Lesquerella fendleri	D	15	0.723	0.000	Cuadrático	$BR = -0.647 + 0.175D - 0.008D^2$
Machaerantera pinnatifida	D	10	0.514	0.020	Exponencial	$BR = 0.155\, e^{(0.129D)}$
Machaerantera pinnatifida	DH	10	0.689	0.017	Cuadrático	$BR = -3.238 + 0.047DH - 9.457E - 5DH^2$
Machaerantera pinnatifida	D+H	10	0.672	0.020	Cuadrático	$BR = 10.932 + 1.135(D + H) - 0.019(D + H)^2$
Tiquilia canescens	H	8	0.730	0.038	Cuadrático	$BR = 37.516 - 3.583H + 0.092H^2$
Tiquilia canescens	D	8	0.512	0.046	Lineal	$BR = -2.244 + 0.208D$
Zinnia acerosa	H	18	0.509	0.005	Cuadrático	$BR = 8.717 - 0.743H + 0.016H^2$
Zinnia acerosa	DH	18	0.533	0.003	Cuadrático	$BR = 7.032 - 0.043DH + 6.349E - 5DH^2$

Zinnia acerosa	D+H	18	0.502	0.001	Logarítmico	$BR = 18.572 - 5.150\ ln(D + H)$
Zinnia acerosa	D+H	18	0.536	0.003	Cuadrático	$BR = 13.171 - 0.661(D + H) + 0.008\ (D + H)^2$

Only those plant species that meet the significance criterion (P≤0.05) and determination coefficient (adjusted r^2 ≥0.50) are shown in the Table. D = Plant crown diameter; H = Plant height.

When using the Marquardt method, 14 out of the 15 studied species showed a high coefficient of determination (r^2≥0.60) and significance (P≤0.05) (Table 4).

Table 4. Equations derived from the Marquardt method of exponential model analysis to estimate root biomass (RB) as a function of plant crown diameter (D) and plant height (H) by species.

Sspecies	Variable	n	r^2Aj	Sig.	Equation
Aristida havardii	D	10	0.861	0.0004	$RB = 0.561e^{-0.0092D}$
	H	10	0.885	0.0002	$RB = 2.6465e^{0.0589H}$
	H+D	10	0.891	0.0009	$RB = 2.4733e^{(-0.0134H)+(-0.0628D)}$
	H*D	10	0.858	0.0004	$RB = 0.6256e^{-0.00001HD}$
Atriplex acanthocarpha	D	10	0.661	0.0133	$RB = 1.4789e^{-0.07D}$
	H	10	0.847	0.0006	$RB = 3.7664e^{-0.077H}$
	H+D	10	0.937	0.0001	$RB = 0.5382e^{(-0.0822H)+(0.077D)}$
	H*D	10	0.931	<0.0001	$RB = 3.9404e^{-0.00322HD}$
Bouteloua chasei	D	10	0.864	0.0003	$RB = 0.4416e^{0.0228D}$
	H	10	0.858	0.0004	$RB = 0.3616e^{0.00245H}$
	H+D	10	0.862	0.0004	$RB = 0.3973e^{(0.0253H)+(0.00905D)}$
	H*D	10	0.862	0.002	$RB = 0.4091e^{(0.00105HD)}$
Bouteloua gracilis	D	10	0.938	<0.0001	$RB = 1.4998e^{-0.1374D}$
	H	10	0.816	0.0012	$RB = 1.4682e^{-0.0433H}$
	H+D	10	0.940	0.0001	$RB = 1.8543e^{(-0.1519H)+(-0.0111D)}$
	H*D	10	0.917	<0.0001	$RB = 2.4597e^{-0.0026HD}$
Dalea gipsofila	D	12	0.743	0.0011	$RB = 0.5671e^{-0.1097D}$
	H	12	0.751	0.001	$RB = 0.2705e^{-0.2538H}$
	H+D	12	0.778	0.0027	$RB = 0.1994e^{(-0.0837H)+(0.196D)}$
	H*D	12	0.783	0.0005	$RB = 0.5556e^{-0.0171HD}$

Dasyochloa pulchella	D	15	0.419	0.0292	$RB = 0.1203e^{-0.1513D}$
	H	15	0.623	0.0018	$RB = 0.0124e^{-0.4223H}$
	H+D	15	0.678	0.0028	$RB = 0.0127e^{(-0.2369H)+(0.6708D)}$
	H*D	15	0.505	0.0103	$RB = 0.1708e^{-0.0133HD}$
Frankenia gipsofila	D	15	0.612	0.0021	$RB = 25.5739e^{0.0338D}$
	H	15	0.605	0.0024	$RB = 30.4454e^{-0.0376H}$
	H+D	15	0.615	0.0079	$RB = 25.3009e^{(-0.0248H)+(0.0159D)}$
Lepidium virginicum	D	13	0.585	0.0079	$RB = 1.3999e^{-0.0149D}$
	H	13	0.612	0.0055	$RB = 1.1626e^{-0.0276H}$
	H+D	13	0.621	0.0175	$RB = 1.216e^{(0.0191H)+(0.0191D)}$
	H*D	13	0.588	0.0076	$RB = 1.7525e^{-0.0003HD}$
Lesquerella fendleri	D	15	0.941	<0.0001	$RB = 0.1593e^{-0.0553D}$
	H	15	0.937	<0.0001	$RB = 0.1633e^{-0.0428H}$
	H+D	15	0.944	<0.0001	$RB = 0.136e^{(-0.0405H)+(0.0254D)}$
	H*D	15	0.943	<0.0001	$RB = 0.1927e^{-0.00292HD}$
Machaeranthera pinnatifida	D	10	0.724	0.0058	$RB = 0.4364e^{-0.0766D}$
	H	10	0.635	0.0177	$RB = 1.4201e^{0.00241H}$
	H+D	10	0.738	0.0192	$RB = 0.5581e^{(-0.0876H)+(-0.0354D)}$
	H*D	10	0.656	0.014	$RB = 1.0422e^{-0.00158HD}$
Muhlenbergia repens	D	10	0.863	0.0004	$RB = 0.1317e^{-0.1864D}$
	H	10	0.875	0.0002	$RB = 0.1386e^{-0.1908H}$
	H+D	10	0.875	0.0015	$RB = 0.1423e^{(0.0119H)+(0.2015D)}$
Muhlenbergia villiflora	H	13	0.031	0.0002	$RB = 0.1345e^{-0.0769H}$
	H+D	13	0.805	0.0007	$RB = 0.1024e^{(-0.0705H)+(0.0504D)}$
	H*D	13	0.804	0.0001	$RB = 0.1847e^{-0.00553HD}$
Tiquilia canescens	D	8	0.951	0.0001	$RB = 1.1298e^{-0.0418D}$
	H	8	0.917	0.0006	$RB = 2.0123e^{-0.0402H}$
	H+D	8	0.952	0.001	$RB = 1.1462e^{(-0.0461H)+(-0.00795D)}$
	H*D	8	0.944	0.0002	$RB = 2.3945e^{-0.00093HD}$
Zinnia acerosa	D	18	0.631	0.0003	$RB = 31.5865e^{0.2417D}$
	H	18	0.693	<0.0001	$RB = 11.7601e^{0.1492H}$
	H+D	18	0.720	0.0002	$RB = 24.3341e^{(0.099H)+(-0.1114D)}$
	H*D	18	0.723	<0.0001	$RB = 8.6773e^{0.0101HD}$

Some species such as *Tiquilia canescens* and *Lesquerella fendleri* showed a highly significant ($P<0.001$) coefficient of determination ($r^2>0.90$) for all included variables. The only species which showed a low coefficient of determination ($r^2\leq 0.319$) and non-significance ($P=0.275$; not shown in Table 3) was *Gaura coccinea*.

Several regression analyses pursuing to estimate root biomass from above ground plant traits were run for data of all the species as a whole. The exponential regression models showed (Table 5) to be statistically significant in the estimation of root biomass as a function of plant variables, although with very low determination coefficient values ($r^2\leq 0.122$). Only the exponential regression with the Marquardt method showed a high coefficient of determination and significance using the variable H, D ($r^2=0.853$; $P<0.001$).

Table 5. Results and equations derived from linear, exponential and logarithmic analyses for all the species as a whole to estimate root biomass (RB) as a function of plant crown diameter (D) and plant height (H).

Regression model	Variable	n	r^2	Sig.	Equation
Exponential	D	182	0.122	0.000 *	$RB = 0.445e^{(0.64D)}$
	DH	182	0.037	0.009 *	$RB = -0.894e^{(0.001DH)}$
	D+H	182	0.067	0.000 *	$RB = 0.506e^{(0.028D+H)}$
Exponential using the Marquardt method	H	182	0.004	<0.0001 *	$RB = 6.2293e^{-0.0178H}$
	D	182	0.006	<0.0001 *	$RB = 3.1317e^{0.0266D}$
	D,H	182	0.8529	<0.0001 *	$RB = 7.7889e^{0.0145D+0.0298H}$

Equations are shown only for statistically significant results.

Discussion

Most species displayed low RSR values. Only *Frankenia gypsophila* (2.27) and *Dalea gypsophila* (1.95) showed RSR > 1. These two are endemic presumably highly adapted to the gypsophyllous characteristics of the local soil conditions. However, these values are considerably lower than that reported by Evans *et al.* (2013) for *Sporobolus airoides* (Torr.) Torr. whose RSR value was 5.5, thus denoting a much greater root production proportion. These authors found higher RSR values in grasses than in desert shrubs, where the last ones exhibited RSR numbers between 0.25 and 0.50.

Graminoids tend to accumulate large quantities of carbon below ground, which make grasslands an attractive biome for carbon sequestration (Sharrow and Ismail, 2004). However, a low below-ground carbon accumulation is typical of annual species, which represents a negative implication if they invade grasslands (Evans *et al.*, 2013). In this regard, the results of this study coincide since the perennial grass *Enneapogon desvauxii* had the highest RSR value (0.99) while *Aristida adscencionis*, which is an annual grass, had the lowest RSR (0.03). It could be said that, more often, perennial species may have greater root biomass than annuals as the they remain a longer time in the field, although phenology, climate, and characteristics of the plant need to be considered. For instance, Snyman (2014), when studying two *Opuntia* species, found that root biomass decreased with water stress, although the opposite occurred with root length.

Eight species showed significance ($P \leq 0.05$) in at least one of the analyses but only five (*Tiquilia canescens*, *Bouteloua gracilis*, *Machaerantera pinnatifida*, *Lesquerella fendleri* and *Atriplex acanthocarpa*) were significant and had an acceptable coefficient of determination ($r^2 \geq 0.50$). *A. acanthocarpa* showed adjusted $r^2 > 0.50$ for a higher number of variables (H, D and D+H) and types of regression analyses (linear, exponential, quadratic and logarithmic).

A quadratic polynomial regression analysis was the most adequate model with a higher r^2 value for most of the species. The plant parameter that best explained root biomass was plant crown diameter. However, when using the Marquardt method, 14 out of the 15 studied species showed a high determination coefficient ($r^2 \geq 0.60$) and significance ($P \leq 0.05$).

The Marquardt exponential model was also adequate to estimate root biomass for the whole set of plants using the variable D, H which resulted in a high coefficient of determination ($r^2 = 0.853$) and significance ($P \leq 0.05$). The equation developed with the exponential model could be very useful for pragmatic purposes (*e.g.,* estimation of C sequestration below ground) since it allows estimation of root biomass avoiding the task of identifying plants at species level.

In a similar way, Gill *et al.* (2002) developed an algorithm using environmental and above ground plant characteristics for estimating below-ground net primary productivity in grasslands and they arrived at an equation that predicted below ground biomass with reasonable confidence (r^2=0.54) although lower than the documented in this paper (r^2= 0.853).

Also, Kuyah *et al*. (2012) analysed the relationship between DBH and root biomass of a mixture of tree species (*Markhamia lutea*, (Benth.) K. Schum., *Mangifera indica* L.*, Eucalyptus* spp., *Cupressus lusitanica* Mill*.* and *Acacia mearnsii* De Wild.) along the Yala river basin in Western Kenya and found that a linear relationship (r^2=0.90) was better to describe the correlation for larger trees (DBH>40 cm) compared to a power function relationship (r^2=0.86). In both cases, coefficients of determination were higher than those reported in this paper for grassland species.

In the semiarid forests of the Argentine pampa, Risio *et al*. (2013) developed a model to estimate above and below-ground biomass of *Prosopis caldenia* Bukart. They found that the most adequate model to predict root biomass for the species with basal area (AB) and total height (h) as the independent variables was:

$$W = (\beta * AB2) + (\lambda * h)$$

And reported an adjusted r^2 value of 0.70, a lower coefficient of determination than the one presented in this paper.

Conclusions

The results of the actual study highlight, to some extent, that measurable above plant variables strong correlate with root biomass, which enabled to propose several reliable models to predict it.

The Marquardt method of the exponential model proved to be suitable to estimate root biomass of 15 species of semiarid grasslands of northern Mexico, both when they were analysed individually and the whole set of plants. The latter is a practical advantage of the method since it could allow estimation of root biomass of similar species without the need of identifying plants at species level.

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Conflict of interests

The authors declare no conflict of interests.

Contribution by author

Miguel Á. Hernández-Gómez: development of the research, fieldwork, capture and analysis of data, drafting of the manuscript; Marisela Pando Moreno: conceptual development of research, structuring of the manuscript and final editing; Ricardo Mata González: support in the understanding of results and drafting of discussion for the manuscript; Humberto González Rodríguez: support in the understanding of results and drafting of discussion for the manuscript; Julio Chacón Hernández: support with the statistical analyses of data; Maritza Gutiérrez: fieldwork, review of the manuscript and final editing.

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