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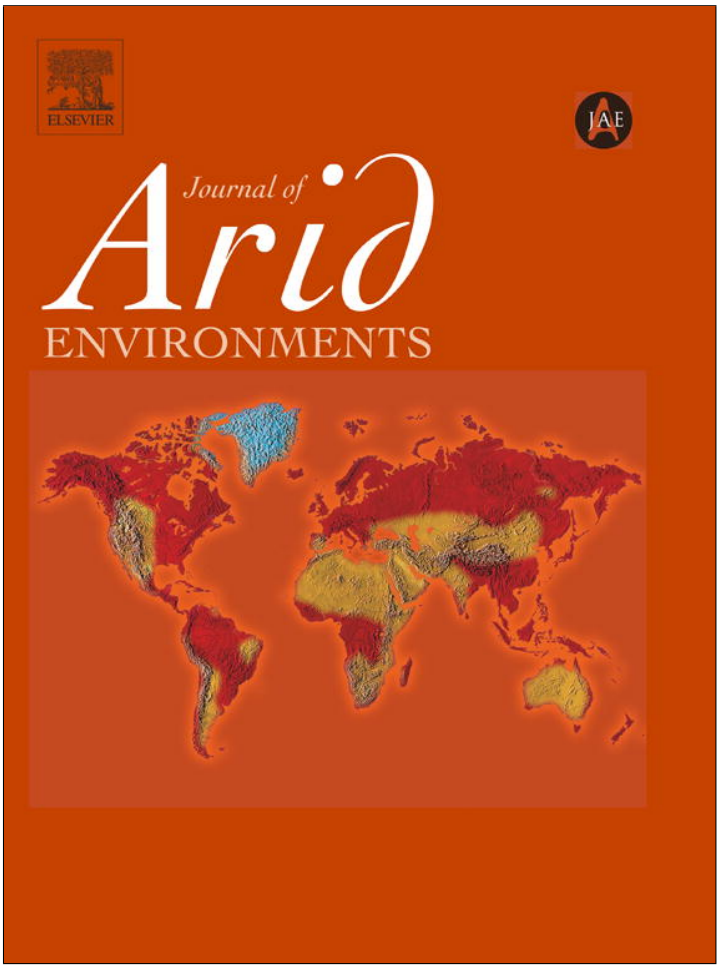

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Short communication

A tool for estimating impacts of woody encroachment in arid grasslands: Allometric equations for biomass, carbon and nitrogen content in *Prosopis velutina*

M.P. McClaran [a,*], C.R. McMurtry [a,b], S.R. Archer [a]

[a] School of Natural Resources and the Environment, University of Arizona, Tucson, AZ 8721, USA
[b] P.O. Box 194, Trimont, MN 56176, USA

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ABSTRACT

Regression equations were developed to estimate above ground biomass and carbon and nitrogen mass of foliage and stem size fractions from plant size dimensions (basal diameter, canopy area, height, canopy volume) for a tall shrub species (*Prosopis velutina*) that has increased in abundance in arid and semi-arid grasslands in the southwestern United States and northwestern Mexico. Regression equations were also developed to describe relationships among the dimensions of plant size. All equations were significant ($p < 0.001$); and all but two had r^2 values >0.72. In addition to species-specific information, we found support for the global patterns of foliar biomass increasing to the $^3/_4$ power of stem biomass and height increasing to the ½ power of stem diameter. We provide a comprehensive report of all equations, which can support a variety of *in situ* (ground-based), modeling, and remote-sensing objectives related to quantifying changes in ecosystem function and carbon sequestration accompanying changes in woody plant abundance. We advocate that comprehensive reporting should become more common for arid and semi-arid woody species in order to support a broad spectrum of users while laying the foundation for the development of global generalizations similar to those available for forest trees.

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1. Introduction

The widespread encroachment of woody plants into arid and semi-arid landscapes in recent decades has important implications for water and nutrient dynamics, energy balance, and greenhouse gas contributions to climate change, fire regimes, livestock production, and wildlife habitat (Eldridge et al., 2011). Allometric equations are an important tool for quantifying changes in above ground biomass and ecosystem carbon (C) and nitrogen (N) pools associated with this encroachment (e.g. Browning et al., 2008).

These allometric tools are of greatest value when they 1) report mass–size relationships for a variety of size metrics and a plant tissue fractions, 2) quantify a variety of size–size and mass–mass relationships, and 3) include the power function $y = ax^b$ for these relationships (Kerkhoff and Enquist, 2009). Mass-size equations using a variety of size dimensions are useful for *in situ* ground-based biomass assessment where plant size (e.g. stem diameter, height, and canopy dimensions) is measured directly, as well as for top-down remote-sensing approaches where the size metrics are limited to canopy area (e.g. Asner et al., 2003; Browning et al., 2008) or canopy area and height (in the case of LiDAR – Light Detection And Ranging; e.g. Drake et al., 2003). Relationships that quantify biomass partitioning among tissue fractions are needed to support ecosystem models that estimate primary production, nutrient storage and turnover, and decomposition (e.g. Hibbard et al., 2003). Knowledge of size–size relationships can be used to estimate total mass when only leaf mass can be detected (e.g. Zhang and Kondragunta, 2006); and mass–mass relationships enable comparisons of resource allocation within plants (e.g. Enquist and Niklas, 2002). To this end, we report allometric equations based on the power function for estimating above ground biomass, carbon (C) mass and nitrogen (N) mass from a variety of plant size metrics, and other mass–mass and size–size relationships for an encroaching shrub (*Prosopis velutina* Woot. velvet mesquite), common to the North American Southwest.

Encroachment of *P. velutina*, a shrub- to small tree-sized plant (≤7 m tall), since the early 1900s has transformed semi-arid grasslands into shrublands and woodlands and has altered herbaceous species composition and production (McClaran et al., 2010), the amount and spatial distribution of soil C and N (McClaran et al., 2008), erosion and sediment yield (Polyakov et al., 2010), and water flux and energy budgets (Scott et al., 2009). These changes in ecosystem attributes and processes are closely tied to and

* Corresponding author. Tel.: +1 520 621 1673; fax: +1 520 621 8801.
E-mail addresses: mcclaran@u.arizona.edu (M.P. McClaran), chad.mcmurtry@iberdrolaren.com (C.R. McMurtry), sarcher@ag.arizona.edu (S.R. Archer).

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influenced by changes in *P. velutina* biomass. Therefore, the quantification of *P. velutina* biomass is central to assessing and predicting ecosystem dynamics in the context of changes in vegetation structure. Earlier work used a small subset of these allometric equations in remote-sensing assessments of biomass and carbon at the landscape scale (Browning et al., 2008; Huang et al., 2007). Here, we report the full complement of allometric equations that are needed to support ground-based assessments and ecosystem modeling applications.

2. Study site and methods

The study site was centered at 31° 48.41′N and 110° 52.46′W on a Baboquivari soil series (fine-loamy, mixed, superactive, thermic Ustic Haplagid; Breckenfeld and Robinett, 2003), at 1113 m elevation within the Santa Rita Experimental Range (http://ag.arizona.edu/srer/), 40 km south of Tucson, Arizona, USA (MAP = 375 mm; MAT = 19.5 °C). The site has not burned in >100 y, and has been grazed by livestock since the 1880s (see Browning et al., 2008 for additional details on climate, soils, vegetation, and grazing history). *P. velutina* plants ($n = 31$) were targeted for sampling to capture the range of sizes present within a 2 ha area in June 2004. Hence, these data do not constitute a statistical representation of the *P. velutina* population.

Methods of measuring plant dimensions, conversions from live- to dry-weight, and determination of C and N concentrations follow Northup et al. (2005), except as noted below. Basal diameter of primary stems was measured at ca. 5 cm and 10 cm above ground surface for small stems (<20 cm diameter) and larger stems, respectively. Basal diameters were summed for plants with multiple stems originating at ground level. Measured plants were felled with a chain saw and partitioned into leaf, live stem and dead stem fractions. Live stems were further separated into four diameter-based size classes: Fine (≤1 cm), Small (1–2.5 cm), Mid (2.5–10 cm), and Large (>10 cm). Five fresh leaves (including petiole) per tree were collected, scanned (Epson 836XL flatbed scanner) to determine one-sided area (ImageJ 1.38×, National Institutes of Health, USA), dried and weighed to quantify specific leaf area (cm^2/g). For reference, the mean ($\bar{x}$), standard error (SE), and range (R) of physical traits for the 31 plants were: number of primary stems ($\bar{x} = 1.9$, SE = 0.03, $R = 1$–4), basal stem diameter (cm; $\bar{x} = 23.2$, SE = 0.7, $R = 0.7$–80.3), height (m; $\bar{x} = 2.9$, SE = 0.06, $R = 0.5$–6.9), canopy area (m^2; $\bar{x} = 18.4$, SE = 0.6, $R = 0.1$–77.0), total leaf area (m^2; $\bar{x} = 15.2$, SE = 3.0, $R = 0.03$–56.1), specific leaf area (cm^2/g; $\bar{x} = 81.2$, SE = 1.4, $R = 70.7$–104.2), and individual leaf area (cm^2; $\bar{x} = 16.6$, SE = 0.8, $R = 2.9$–55.5).

C and N concentrations ([C] and [N]; % by mass) in foliage and stem fractions were determined on samples from subsets of the harvested plants. Dead stem samples were predominantly in the Mid class. Material was oven-dried at 60 °C to constant weight. Analysis of variance and Bonferroni tests for multiple comparisons were used to describe differences in [C] and [N] among biomass fractions. The products of concentration ([C] or [N]) and mass in each tissue fraction and size class were summed to determine the mass of above ground C and N per plant.

Following Northup et al. (2005), natural log (ln) transformations and a correction factor (CF) for transformation bias were applied to describe relationships between response variables (mass, [C] and [N]) and explanatory variables (size attributes) in a linear regression model: $\ln(y) = (a + b[\ln(x)]) + CF$. The equation back-transforms to $y = e^a x^b$ which is a variation of the power function $y = ax^b$, where b represents a scaling function between the variables. These models were not validated on an independent set of plants.

3. Results and discussion

Means, SEs and ranges for biomass and [C] and [N] of the 31 sampled *P. velutina* plants and their various tissue classes are summarized in Table 1. Plant dimension variables were positively and strongly correlated with each other ($r^2 \geq 0.90$, Table 2). All plant size metrics were strong predictors of *P. velutina* leaf area, total above ground biomass and the biomass of foliar and stem classes ($r^2 = 0.64$ for height and Large stem mass; $r^2 \geq 0.72$ for all others, Table 3).

Our results for the mass–diameter relationship ($b = 2.19$, Table 3) are at the low end of values for other *Prosopis* species ($b = 2.10$–2.37; Alvarez et al., 2011; Northup et al., 2005; Padron and Navarro, 2004). These values are generally consistent with the global mean for trees ($b = 2.37$), and with the pattern of low values being associated with drier growing conditions (Zianis and Menucuccini, 2004). Our results for the mass-canopy area relationships are similar to *Prosopis glandulosa* (Northup et al., 2005) for foliar mass ($b = 1.22$ and 1.23), but slightly lower for total mass ($b = 1.49$ and 1.60, respectively), which likely reflects our drier setting. We encourage more complete and consistent reporting of allometric relationships using the power function in order to lay the foundation for a broader comparison for aridland shrubs and trees in a manner similar to the global generalizations available for forest trees (Zianis and Menucuccini, 2004).

Our results from the size–size and mass–mass relationships (Table 2) support comparisons with global scaling patterns. For example, scaling of height with basal diameter ($b = 0.52$) and foliar biomass with live above ground biomass ($b = 0.77$) are consistent with the global patterns of $b = 0.54$ (Niklas, 1994) and $b = 0.75$, respectively (Enquist and Niklas, 2002). These mass–mass relationships have implications for biogeochemical cycling and fuel accumulations over time. For example, foliar and smaller stem size classes are more flammable and decompose more quickly than larger size classes. Our results show that biomass in foliar and smaller stem size classes increased with plant size, but the increase

Table 1
Mean, standard error (SE) and range of above ground biomass and concentrations of carbon [C] and nitrogen [N] in foliage and stem classes within *Prosopis velutina* plants. Parenthetical values are number of trees sampled for the [C] and [N]. Mean values for [C] or [N] followed by different letters differed at $p < 0.001$.

	Biomass per tree (kg)			Carbon concentration (%)			Nitrogen concentration (%)		
	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range	$\bar{x}$	SE	Range
Total	95.9	23.9	0.1–435	48.0	0.1	46.9–49.0	0.8	0.05	0.5–1.5
Live	75.1	18.7	0.1–352	48.6	0.2	47.4–49.8	0.8	0.06	0.4–1.5
Foliar (31)	1.9	0.4	0.1–6.5	50.3a	0.1	48.3–51.7	2.8a	0.05	2.0–3.4
Fine (25)	6.5	1.4	0.1–30.6	47.2b	0.2	44.9–48.5	1.2b	0.04	0.8–1.5
Small (12)	8.8	2.5	0.0–70.2	47.4b	0.5	44.6–51.1	0.6cd	0.06	0.3–1.0
Mid (5)	18.6	4.1	0.0–74.2	49.4a	0.3	48.3–50.2	0.4d	0.03	0.3–0.4
Large (10)	39.3	11.6	0.0–93.3	50.3a	0.7	49.3–51.4	0.3d	0.03	0.3–0.4
Dead (5)	20.8	5.5	0.0–113.5	45.1c	1.0	41.2–47.4	0.8bc	0.10	0.6–1.2

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Table 2
Regression parameters for relationships among plant size metrics and among tissue classes and live above ground biomass. The equation form is $\ln(Y) = (a + b(\ln(X)))$ *CF, where CF is correction factor. Parenthetical values denote 95% confidence interval for a and b, respectively. All p-values are ≤0.001; r^2 = adjusted r^2; $n = 31$; BD = basal diameter (cm), CA = canopy area (m^2), HT = height (m), and HT*CA = height × canopy area (m^3), Foliar = foliar biomass (kg), Fine, Small, Mid and Large are stem size-class (see Table 3) biomass (kg), and Live = live above ground biomass (kg).

Y	X	a	b	r^2	CF
CA	BD	−1.46 (0.28)	1.34 (0.10)	0.96	1.01
HT	BD	−0.47 (0.18)	0.52 (0.06)	0.90	1.00
HT*CA	BD	−1.92 (0.39)	1.86 (0.13)	0.96	1.03
HT	CA	0.11 (0.10)	0.38 (0.04)	0.91	1.00
Foliar	Live	−2.38 (0.18)	0.77 (0.05)	0.97	1.01
Fine	Live	−0.96 (0.15)	0.71 (0.04)	0.97	1.01
Small	Live	−0.86 (0.30)	0.72 (0.08)	0.93	1.01
Mid	Live	−1.79 (0.62)	1.09 (0.15)	0.91	1.07
Large	Live	−2.01 (0.67)	1.25 (0.15)	0.95	1.00

was proportionally greater for the larger stem classes (Table 2). The relative contributions of Foliar and Fine stems components to total biomass declined with increasing ln basal diameter ($b = -0.03$ and -0.19, $r^2 = 0.7$ and 0.8, and $p < 0.001$, respectively), whereas relative contributions from Mid and Large stems increased ($b = 0.06$ and 0.12, $r^2 = 0.4$ and 0.7, and $p < 0.001$, respectively). Small stems contributions to total biomass did not vary with ln basal diameter ($b = -0.02$, $r^2 = 0.0$, and $p < 0.4$). This trend of proportionally greater contributions by larger stems with increasing plant size is also evident in the scaling function values (b) for the size-class biomass and total biomass relationships (Table 2), where b was <1.0 for Foliar and Small stems and >1.0 for Mid and Large stems.

Differences in [C] and [N] were significant among plant tissue fractions (Table 1). This is consistent with other reports for live biomass of *P. velutina* (Barth and Klemmedson, 1982) and for *P. glandulosa* from the Southern Great Plains (Northup et al., 2005). [C] was lowest in Dead stems, and greatest in Foliar, Mid and Large stems. [N] was greatest in foliage and declined with increasing stem diameter; and [N] in Dead stems was statistically comparable to that in Fine and Small stems (Table 1). The relatively low [C] of Dead stems ostensibly reflects rapid decomposition of the most labile carbon constituents, while greater [N] relative to equivalent-sized Mid stems may reflect a combination of declines in C as well as N contributions from decomposer organisms or lichens (Harmon et al., 2004). Scaling (b values) relationships between size and total above ground C were steeper than those for N likely because total mass increased faster with plant size than foliar mass, the latter having [N] twice that of other biomass fractions (Tables 2 and 3).

We are uncertain how robust these allometric relationships may be or the degree to which they may vary with soil type, geomorphology, land use, or disturbance history. General predictive equations have been developed across sites and species in woodland ecosystems (e.g. Williams et al., 2005), but significant within-species variation in architecture has also been documented along hill-slope (bajada) landform gradients (Martinez and Lopez-Portillo, 2003). It is also important to recognize that these equations are based on plant-scale relationships. As such, they should not be applied to area-based measures like percent canopy cover. Such extensions are inappropriate because different arrangements and combinations of plant numbers and sizes can occur for a given percent canopy cover. Therefore, remote-sensing approaches that cannot confidently distinguish between individual plant canopies in vegetation patches should not use plant canopy area–biomass relationships such as those presented here. This constraint also

Table 3
Regression parameters for per plant leaf area, carbon and nitrogen mass, and biomass components related to basal diameter, canopy area, height and volume in *Prosopis velutina*. The equation form is $\ln(Y) = (a + b(\ln(X)))$*CF, where CF is a correction factor. All p-values are ≤0.001; r^2 = adjusted r^2. Parenthetical values denote ±95% confidence interval for a and b, respectively. Live stem categories are as follows: Fine stem = <1 cm, Small stem = 1–2.5 cm, Mid stem = >2.5–10 cm, Large stem = >10 cm. For all categories, $n = 31$, except Small stem $n = 26$, Mid stem $n = 23$, Large stem $n = 18$, and Dead $n = 25$. Volume = Canopy area × Height.

	Basal diameter (cm)				Canopy area (m^2)				Height (m)				Volume (m^3)			
	a	b	r^2	CF	a	b	r^2	CF	a	b	r^2	CF	a	b	r^2	CF
Leaf area (m^2)	−2.72 (0.34)	1.64 (0.12)	0.96	1.02	−0.90 (0.31)	1.21 (0.08)	0.97	1.01	−1.05 (0.37)	2.94 (0.33)	0.92	1.10	−0.99 (0.20)	0.87 (0.05)	0.97	1.01
Carbon (kg)	−3.77 (0.45)	2.19 (0.16)	0.96	1.06	−1.32 (0.31)	1.60 (0.12)	0.96	1.06	−1.58 (0.45)	3.94 (0.40)	0.93	1.23	−1.45 (0.28)	1.16 (0.08)	0.97	1.04
Nitrogen (g)	−0.41 (0.37)	1.96 (0.13)	0.97	1.02	1.77 (0.26)	1.44 (0.10)	0.97	1.03	1.56 (0.41)	3.51 (0.36)	0.93	1.15	1.67 (0.24)	1.03 (0.06)	0.97	1.02
Total biomass (kg)	−3.02 (0.45)	2.19 (0.16)	0.96	1.06	−0.59 (0.31)	1.60 (0.12)	0.96	1.06	−0.83 (0.45)	3.93 (0.40)	0.93	1.24	−0.71 (0.28)	1.16 (0.08)	0.97	1.04
Live biomass (kg)	−3.02 (0.45)	2.12 (0.16)	0.96	1.06	−0.67 (0.31)	1.55 (0.12)	0.96	1.06	−0.92 (0.41)	3.82 (0.37)	0.94	1.16	−0.79 (0.27)	1.12 (0.07)	0.97	1.03
Foliar (kg)	−4.88 (0.36)	1.67 (0.13)	0.96	1.02	−3.03 (0.20)	1.23 (0.07)	0.97	1.01	−3.20 (0.36)	3.00 (0.32)	0.92	1.09	−3.12 (0.19)	0.89 (0.05)	0.98	1.01
Fine stem (kg)	−3.15 (0.26)	1.52 (0.09)	0.98	1.01	−1.45 (0.21)	1.11 (0.08)	0.97	1.01	−1.61 (0.33)	2.70 (0.30)	0.92	1.07	−1.54 (0.20)	0.80 (0.05)	0.97	1.01
Small stem (kg)	−2.79 (0.82)	1.45 (0.26)	0.84	1.07	−1.50 (0.54)	1.18 (0.19)	0.86	1.05	−1.38 (0.67)	2.65 (0.56)	0.79	1.12	−1.56 (0.54)	0.84 (0.13)	0.87	1.05
Mid stem (kg)	−4.93 (1.68)	2.27 (0.52)	0.79	1.44	−2.77 (1.02)	1.79 (0.34)	0.84	1.23	−2.54 (0.98)	4.04 (0.77)	0.84	1.23	−2.93 (0.88)	1.30 (0.21)	0.88	1.12
Large stem (kg)	−4.30 (2.07)	2.27 (0.59)	0.79	1.07	−2.01 (1.54)	1.74 (0.50)	0.76	1.10	−1.54 (1.79)	3.36 (1.28)	0.64	1.23	−2.32 (1.52)	1.29 (0.33)	0.80	1.06
Dead biomass (kg)	−6.80 (1.36)	2.81 (0.43)	0.88	1.41	−4.09 (1.07)	2.20 (0.37)	0.86	1.62	−3.54 (1.50)	4.68 (1.23)	0.72	7.26	−4.14 (1.12)	1.56 (0.56)	0.85	1.77

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applies to *in situ* ground-based efforts that only report canopy cover (e.g. line-intercept transects), and do not measure the size of each plant encountered.

Our results will support many different objectives and approaches related to quantifying the impacts of woody encroachment. For example, estimates of the amount and quality of annual Foliar and Fine stem production and litter inputs will serve models estimating primary production and biogeochemical cycling (e.g. Hibbard et al., 2003). Our inclusion of mass-canopy area equations (Table 3) will support estimates of large-scale C sequestration and biomass allocation from remotely-sensed measures of canopy area (e.g. Asner et al., 2003; Browning et al., 2008). Size–size relationships (Table 2) can be used to derive broad-scale estimates of total mass from remotely-sensed foliar mass (Zhang and Kondragunta, 2006). Despite the potential to support diverse purposes, comprehensive descriptions of allometric relationships for separate size fractions are uncommon. Most reports provide only the best equations (e.g. Barth and Klemmedson, 1982; Navar et al., 2004) or equations for a single size metric such as basal diameter (Padron and Navarro, 2004; but see Alvarez et al., 2011, and Northup et al., 2005 for exceptions). We therefore encourage comprehensive reporting of allometric relationships to support the greatest possible range of ground, remote-sensing, and modeling applications.

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References

Alvarez, J.A., Villagra, P.E., Villalba, R., Cony, M.A., Alberto, M., 2011. Wood productivity of *Prosopis flexuosa* D.C. woodlands in the central Monte: influence of population structure and tree-growth habit. Journal of Arid Environments 75, 7–13.

Asner, G.P., Archer, S.R., Hughes, R.F., Ansley, R.J., Wessman, C.A., 2003. Net changes in regional woody vegetation cover and carbon storage in Texas Drylands, 1937–1999. Global Change Biology 9, 316–335.

Barth, R.C., Klemmedson, J.O., 1982. Amount and distribution of dry matter, nitrogen, and organic carbon in soil-plant system of mesquite and palo verde. Journal of Range Management 35, 412–418.

Breckenfeld, D.J., Robinett, D., 2003. Soil and ecological sites on the Santa Rita Experimental Range. In: McClaran, M.P., Ffolliott, P.F., Edminster, C.B. (Eds.), Santa Rita Experimental Range: 100 Years (1903 to 2003) of Accomplishments and Contributions. USDA Forest Service Proceedings RMRS-P-30. Rocky Mountain Research Station, Fort Collins, Colorado, pp. 157–165.

Browning, D.M., Archer, S.R., Asner, G.P., McClaran, M.P., Wessman, C.A., 2008. Woody plants in grasslands: post-encroachment stand dynamics. Ecological Applications 18, 928–944.

Drake, J.B., Knox, R.G., Dubayah, R.O., Clark, D.B., Condit, R., Blair, J.B., Hofton, M., 2003. Above-ground biomass estimation in closed canopy Neotropical forests using lidar remote sensing: factors affecting the generality of relationships. Global Ecology and Biogeography 12, 147–159.

Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F., Whitford, W.G., 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecology Letters 14 (7), 709–722.

Enquist, B.J., Niklas, K.J., 2002. Global allocation rules for patterns of biomass partitioning in seed plants. Science 295, 1517–1520.

Harmon, M.E., Fanklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Augmen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack Jr., K., Dummins, K.W., 2004. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 34, 60–203.

Hibbard, K.A., Schimel, D.S., Archer, S.R., Ojima, D.S., Parton, W., 2003. Grassland to woodland transitions: integrating changes in landscape structure and biogeochemistry. Ecological Applications 13, 911–926.

Huang, C., Marsh, S.M., McClaran, M.P., Archer, S.R., 2007. Post-fire stand structure in a semi-arid savanna: cross-scale challenges estimating biomass. Ecological Applications 17, 1899–1910.

Kerkhoff, A.J., Enquist, B.J., 2009. Multiplicative by nature: why logarithmic transformation is necessary in allometry. Journal of Theoretical Biology 257, 519–521.

Martinez, A.J., Lopez-Portillo, J., 2003. Allometry of *Prosopis glandulosa* var. *torreyana* along a topographic gradient in the Chihuahuan desert. Journal of Vegetation Science 14, 111–120.

McClaran, M.P., Moore-Kucera, J., Martens, D.A., van Haren, J., Marsh, S.E., 2008. Soil carbon and nitrogen in relation to shrub size and death in a semi-arid grassland. Geoderma 145, 60–68.

McClaran, M.P., Browning, D.M., Huang, C., 2010. Temporal dynamics and spatial variability in desert grassland vegetation. In: Webb, R.H., Boyer, D.E., Turner, R.M. (Eds.), Repeat Photography: Methods and Applications in the Natural Sciences. Island Press, Covelo, CA, pp. 145–166.

Navar, J., Mendez, E., Najera, A., Graciano, J., Dale, V., Parresol, B., 2004. Biomass equations for shrub species of Tamaulipan thornscrub of North-east Mexico. Journal of Arid Environments 59, 657–674.

Niklas, K.J., 1994. Plant Allometry: the Scaling of Form and Process. University of Chicago Press, Chicago, 412 pp.

Northup, B.K., Zitzer, S.F., Archer, S.R., McMurtry, C.R., Boutton, T.W., 2005. Above-ground biomass and carbon and nitrogen content of woody species in a subtropical thornscrub parkland. Journal of Arid Environments 62, 23–43.

Padron, E., Navarro, R.M., 2004. Estimation of above-ground biomass in naturally occurring populations of *Prosopis pallida* (H. & B. ex. Willd.) H.B.K. in the north of Peru. Journal of Arid Environments 56, 283–292.

Polyakov, V.O., Nearing, M.A., Nichols, M.H., Scott, R.L., Stone, J.J., McClaran, M.P., 2010. Long-term runoff and sediment yields from small semi-arid watersheds in southern Arizona. Water Resources Research 46. http://dx.doi.org/10.1029/2009WR009001.

Scott, R.L., Jenerette, G.D., Potts, D.L., Huxman, T.E., 2009. Effects of seasonal drought on net carbon dioxide exchange from a woody-plant-encroached semiarid grassland. Journal of Geophysical Research – Biogeosciences 114, G04004. http://dx.doi.org/10.1029/2008JG000900.

Williams, R.J., Zerihun, A., Montagu, K.D., Hoffman, M., Hutley, L.B., Chen, X., 2005. Allometry for estimating aboveground tree biomass in tropical and subtropical eucalypt woodlands: towards general predictive equations. Australian Journal of Botany 53, 607–619.

Zhang, X., Kondragunta, S., 2006. Estimating forest biomass in the USA using generalized allometric models and MODIS land products. Geophysical Research Letters 33, L09402. http://dx.doi.org/10.1029/2006GL025879.

Zianis, D., Menucuccini, M., 2004. On simplifying allometric analyses of forest biomass. Forest Ecology and Management 187, 311–332.