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Above-ground biomass and carbon and nitrogen content of woody species in a subtropical thornscrub parkland

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Abstract

Regression equations were developed to predict above-ground biomass, carbon and nitrogen content from stem and canopy dimensions for 10 shrub species common to subtropical thorn parklands of southern Texas. Projected canopy area yielded slightly more precise estimates of biomass and nutrient concentrations than the sum of stem basal diameters at the soil surface. All such equations were significant ($p<0.05$) and had r^2 values $\geqslant 0.70$, except dead wood and large stems of one species. These equations are potentially useful for estimating woody biomass and nutrient content from remotely sensed or field survey data, and in evaluating models of ecosystem biogeochemistry.

Keywords: Allometry; Canopy area; Linear regression; Stem basal diameter; Thorn woodland; Tamaulipan Biotic Province

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1. Introduction

Biomass production and accumulation integrate plant responses to biotic and abiotic features of their environment. Plant biomass is therefore a metric fundamental to understanding and managing ecosystems, whether it be to estimate primary production, nutrient pools, species dominance, responses to experimental manipulation, or fuel loads for fire. In recognition of its central importance, models of ecosystem processes often include plant biomass or biomass-related variables as inputs and outputs.

Direct assessment of plant biomass requires destructive harvest, drying and weighing. This is a tedious, labor-intensive approach, and a significant disturbance to study sites. As such, direct assessments are often not feasible—especially in remote areas, or in systems where plants are large (e.g. shrublands, woodlands, forests). An alternate approach is to collect non-destructive measurements of plant attributes (e.g. height, canopy dimensions, stem diameters) and relate these metrics to biomass with allometric equations developed from destructive sampling of plants from a range of size classes. These allometric approaches are quick, reasonably accurate, and allow non-destructive estimations of biomass over larger areas than possible with harvest methods. Recent examples of this widely used approach include Coomes and Grubb (1998), White (2001), Navar et al. (2002) and Paton et al. (2002).

Generalized (multi-species) allometric regression models are moderately efficient for making non-destructive estimates of above-ground plant biomass. However, species-specific equations that describe relationships between plant attributes and biomass are more accurate and flexible (Buech and Rugg, 1989). Furthermore, it is preferable to use region or site-specific relationships where possible. Species size–biomass relationships could differ as plants alter allocation patterns in response to soils, climate and disturbance.

Changes in structure and composition of vegetation are often accompanied by changes in biomass. In many arid ecosystems, woody plants have increased in stature and density over the past century, particularly in grasslands and savannas (see Archer et al., 2001). Although this phenomenon has been widely observed, there is little quantitative information regarding the magnitude of biomass change accompanying this structural shift. In recent assessments of the USA carbon budget, 'thickening' of woody vegetation in arid and montane forest ecosystems was a potentially significant, but uncertain, carbon sink (Schimel et al., 2000; Pacala et al., 2001; Houghton, 2003a, b). Reducing uncertainty in these estimates requires quantification of change in ecosystem biomass that accompanies shifts towards woody plant domination within many arid plant communities.

We have studied encroachment of woody plants into grasslands in north-eastern portions of the Tamaulipan Biotic Province and have documented rates and patterns of vegetation change (Archer, 1995). How these changes in woody plant cover translate into changes in plant biomass, carbon and nitrogen pools are not known. Recent modeling exercises have generated predictions (Hibbard et al., 2003), but their validity must be tested against field data. As a first step toward quantifying existing plant above-ground biomass, carbon, and nitrogen pools on landscapes

undergoing succession from grass to woody plant domination, we developed size–biomass relationships for key species and determined tissue carbon and nitrogen concentrations.

2. Methods

2.1. Site description

Plant biomass–allometry relationships were assessed during the 1994–1995 growing seasons on the Texas Agricultural Experiment Station, La Copita Research Area (LCRA) near Alice, Texas (27°40′N, 98°12′W). The LCRA (1093 ha) is located in the eastern portion of the central Rio Grande Plains within the Tamaulipan Biotic Province (Blair, 1950). The climate is subtropical with hot, humid summers and mild winters, with a mean annual temperature of 22.4 °C and an average growing season of 289 days (Scifres and Koerth, 1987). Long-term annual precipitation (1951–1996 mean = 680 mm) had a bimodal distribution with maxima in April–May and September–October. Annual precipitation in 1993 was 729 mm, and precipitation in 1994 and 1995 was 642 and 655 mm, respectively. Thus, our studies were conducted in years of near-average annual precipitation.

Vegetative communities of sandy loam uplands at the LCRA consist of thornscrub parklands with a well-defined mosaic pattern of shrub clusters scattered throughout low-succession grasslands. These areas are bisected by intermittent clay loam drainages characterized by closed-canopy woodlands (Archer, 1995). Assemblages of woody plants are organized around dominant honey mesquite (*Prosopis glandulosa* var. *glandulosa* Torr.) trees with mixtures of sclerophyllous and coriaceous evergreens and malacophyllous summer and winter deciduous shrubs in the understory (Archer et al., 1988). Vegetation in herbaceous zones is dominated by early succession short and midgrasses, and annual and perennial forbs (Scifres and Koerth, 1987). Additional details on vegetation and soils are given in Boutton et al. (1998).

2.2. Data collection

Data were obtained in May–August of 1994 and 1995. Plants of seven dominant woody species were collected from 14 distinct locations on the study site, and included four upland (sandy loam, tight sandy loam, shallow sandy loam, gray sandy loam) and three lowland (lakebed, clay loam, claypan prairie) range sites (Scifres and Koerth, 1987). Species included: *Condalia hookeri* (M.C. Johnst.), *Diospyros texana* (Scheele), *P. glandulosa*, *Acacia rigidula* (Benth.), *Celtis pallida* (Torr.), *Mahonia trifoliolata* (Moric.), and *Zanthoxylum fagara* (L.). See Nelson et al. (2002) for details on leaf demography of these species and Hatch et al. (1990) for nomenclature.

Approximately 35 plants of each species, covering a range of sizes, were targeted for physical measurement of canopy dimensions and destructive harvest. Basal diameters of all stems originating from the soil surface and canopy dimensions

(longest axis and its perpendicular bisector) were measured. Canopy area (m^{-2}) was computed as: ([longest axis/2] × [perpendicular axis/2]) × π. Measured plants were cut at the soil surface and biomass was separated into leaf (foliar), live woody stem, and standing dead wood fractions. Live stems were further divided into size classes consistent with those used in other studies on woody biomass (e.g. Lugo et al., 1990) and in models that simulate ecosystem biogeochemistry (Parton et al., 1992): <2.5 cm diameter (small stems) and >2.5 cm diameter (large stems). Immediately after harvest, materials were weighed in the field to determine fresh weight. Subsamples collected from each fraction of each plant were oven-dried at 70°C to a constant weight and used to convert fresh mass of each fraction to dry mass (Mannetje, 2000).

In follow-up studies during 1998–2002, stem basal diameter and biomass fractions of three additional species were quantified: *Aloysia gratissima* (Gill.&Hook.) Troncoso ($n = 15$ stems), *Karwinskia humboltiana* (R.&S.) Zucc. ($n = 17$ stems) and *Schaefferia cuneifolia* (Gray) ($n = 30$ stems). All stems of *A. gratissima* plants that originated from the soil surface were measured, while individual stems originating from the soil surface were quantified for *K. humboltiana* and *S. cuneifolia*. These species lacked stems >2.5 cm, so stem mass was not partitioned into size classes.

Carbon and nitrogen concentrations in foliar and woody tissues were determined on samples collected from subsets of harvested plants. Total number of plants sampled ranged from 8 to 15 per species and spanned the size range within each species. Samples of dead wood were collected only from *D. texana* ($n = 5$) and *P. glandulosa* ($n = 7$) plants. Leaf and live wood samples were also collected from an additional 10 woody species present on the study site. Included were: *Acacia farnesiana* [L. (Willd.)], *Acacia greggii* (Gray), *Colubrina texensis* [T&G (Gray)], *Ephedra antisyphylitica* (C.A. Mey), *Eysenhardtia texana* (Scheele), *Guaiacum angustifolium* (Engelm.), *Lycium berlandieri* (Dun.), *Opuntia leptocaulis* (DC), *Opuntia lindheimeri* (Engelm.), and *Ziziphus obtusifolia* [(T&G.) Gray]. Samples were oven-dried at 70 °C, ground to pass a 40-mesh screen, and C and N concentrations determined by combustion gas chromatography (Carlo Erba Model NA-1500, Fison Instruments, Inc., Danvers, MA).

2.3. Statistical analyses

Relationships between plant architecture (stem basal diameter and projected canopy area) and biomass fractions of the different species were examined by regression analyses (Statsoft Inc., 1995) of logarithmically (Ln) transformed dependent and independent variables (Steel and Torrie, 1980). For relationships between stem basal diameter and biomass fractions, the sums of basal diameter of all stems originating from the soil surface were used. The exceptions were *K. humboltiana* and *S. cuneifolia* where single stem biomass was estimated from the diameter of individual stems. Correction factors (*CF*) for the different relationships were calculated as described by Sprugel (1983), and can be multiplied by predicted values (prior to back-transformation to original scale) to correct for bias caused by

logarithmic transformations (Whittaker and Marks, 1975). Final equations have the form: $\mathrm{Ln}(y) = [b_0 + b_1(\mathrm{Ln}(x)) \pm \varepsilon]^* CF$ with x as the predictor, b_0 and b_1 the y-intercept and slope coefficient, and ε the standard error or uncertainty in estimates. While logarithmic regressions are biologically and mathematically appropriate for relating plant dimensions to biomass, such transformations result in systematic errors in estimates. Ln transformations functioned by converting values to a scale where variance in the relationship was more homogeneous, allowing effective use of least-squares regression (Steel and Torrie, 1980). Such transformations reduce effects of large dependant values (y) relative to that of small values on the prediction equation. In effect, this fits the regression to geometric means of y for ranges of the predictor (x) rather than arithmetic means (Whittaker and Marks, 1975). As geometric means are smaller than arithmetic means, predicted values are underestimated (10–20%) across some range of the predictor, hence the need for *CF*.

Species differences in carbon and nitrogen concentrations within tissue types were determined by general linear model procedures (SAS, 2002). Simple linear regressions tested for relationships between leaf and stem C and N concentrations. Previous studies at this site indicated strong relationships between basal area and stem age of *P. glandulosa* (Stoker and Archer, 1996). Tissue C and N concentrations were therefore regressed against *P. glandulosa* age estimated from basal diameter of the largest (and dominant) stems originating from the soil surface, to determine if values changed with plant development.

We were also interested in determining if nutrient mass of plants in this subtropical thorn woodland could be reasonably predicted from canopy area or stem basal diameter, regardless of species. To test for potential relationships, C and N concentrations of analysed samples of the seven dominant species were multiplied by biomass in the different above-ground fractions to estimate total C and N within plants. Best-fit relationships between canopy area and total (all components), foliar, stem and dead wood C and N contents were described by non-linear regressions across species (Statsoft Inc., 1995). Significance levels were set at $p = 0.05$ for all statistical tests.

3. Results

3.1. Descriptive characteristics

Mean sum of stem basal diameters for whole plants included in our analyses ranged from a minimum of 7.68 cm in *D. texana* to a maximum of 16.83 cm for *A. rigidula* (Table 1). The mean number of basal stems per plant ranged from 1.4 in *P. glandulosa* to a maximum of 10.7 in *M. trifoliolata*. Mean canopy area ranged from a minimum of 1.06 m^2 (*Z. fagara*) to a maximum of 16.98 m^{-2} (*P. glandulosa*), while total biomass ranged from a minimum of 1.71 kg (*Z. fagara*) to a maximum of 108.51 kg (*P. glandulosa*). Based on numbers of basal stems, these woody species could be placed into three groups, with *C. hookeri*, *D. texana* and *P. glandulosa* averaging 1–2 stems/plant, *A. rigidula*, *A. gratissima* and *C. pallida* averaging 5–7

Table 1
Metrics of plants of 10 woody species common to thornscrub parklands and woodlands of southern Texas collected during 1994–1995

Species		Basal stems (no.)[a]	Basal diameter (cm)[b]	Canopy area (m^2)	Total biomass (kg)[c]	Leaf (% biomass)[c]	Live stems (% biomass)[c]	Dead wood (% biomass)[c]
A. rigidula	Mean	6.8	16.83	5.06	11.70	13.7	83.6	1.9
$n = 35$	S.E.	1.0	3.09	1.17	3.78	1.4	1.3	0.7
A. gratissima	Mean	5.7	0.63	—	0.068	12.8	87.2	—
$n = 15$	S.E.	1.9	0.10	—	0.002	1.2	1.2	—
C. pallida	Mean	6.2	12.0	3.41	5.81	9.9	88.1	2.0
$n = 36$	S.E.	0.7	2.11	0.94	1.64	0.9	0.8	0.5
C. hookeri	Mean	2.0	8.52	3.88	11.20	11.7	82.3	6.0
$n = 35$	S.E.	0.2	1.21	0.73	2.14	1.5	1.4	0.7
D. texana	Mean	1.5	7.68	6.23	24.15	15.9	82.9	1.1
$n = 36$	S.E.	0.1	1.29	1.84	7.87	1.6	1.5	0.4
K. humboltiana[b]	Mean	—	1.12	—	0.209	15.2	84.8	—
$n = 17$	S.E.	—	0.24	—	0.106	2.4	2.4	—
M. trifoliolata	Mean	10.7	16.05	1.96	3.42	21.3	77.3	1.0
$n = 35$	S.E.	1.1	2.36	0.38	0.84	1.7	1.6	0.7
P. glandulosa	Mean	1.4	15.5	16.98	108.51	10.1	80.4	9.4
$n = 37$	S.E.	0.1	2.37	3.87	31.28	1.4	1.2	1.1
S. cuneifolia[b]	Mean	—	0.54	—	0.029	22.0	78.0	—
$n = 30$	S.E.	—	0.08	—	0.011	3.3	3.2	—
Z. fagara	Mean	9.6	8.51	1.06	1.71	18.0	76.0	6.0
$n = 34$	S.E.	2.2	1.14	0.16	0.34	1.9	2.1	1.4

[a]Number of basal stems per plant originating from the soil surface.
[b]Values for *K. humboltiana* and *S. cuneifolia* were individual basal stems; values for the remaining species were sums of all basal stems originating from the soil surface.
[c]Total biomasss is reported on an oven-dry basis. Biomass fractions are percent of total oven-dry biomass of plants.

stems/plant and *M. trifoliolata* and *Z. fagara* averaging 9–11 stems/plant. Mean allocation of biomass to leaves ranged from a low of 9.9% of total (live and dead) in *C. pallida* to a maximum of 22.0% for *S. cuneifolia*. Mean canopy area and total biomass of *P. glandulosa* was considerably greater than that of the other species. Of the three species in which only individual stems were measured, *K. humboltiana* had the largest basal diameter and total biomass. Percent of biomass as leaves and stems were within the same range as noted for entire plants in the other seven species.

3.2. Size–biomass relationships

Leaf biomass of all species was significantly ($p < 0.05$) and highly correlated with stem basal diameter and canopy area (Table 2). Relationships between stem basal diameter and leaf biomass generated r^2 values > 0.80 for all species and in many cases exceeded 0.90. The relationship between leaf mass and stem basal diameter was weakest ($0.79 < r^2 < 0.86$) for the species included in the follow-up studies, as noted in

Table 2
Equations predicting foliar biomass (*FB*, g) from stem basal diameter (*BD*, cm) and canopy area (*CA*, m^{-2}) for 10 common woody species of southern Texas thorn woodland

Species	d.f.	Equation[a]	r^2	*CV*	Standard errors			*CF*
					b_0	b_1	$s_{y,x}$	
Stem basal diameter (cm)[b]								
A. rigidula	34	$\text{Ln}(FB) = 2.086 + 1.375(\text{Ln}\, BD)$	0.90	12	0.18	0.07	0.139	1.010
A. gratissima	14	$\text{Ln}(FB) = 0.761 + 1.013(\text{Ln}\, BD)$	0.80	46	0.16	0.14	0.581	1.184
C. pallida	35	$\text{Ln}(FB) = 1.384 + 1.648(\text{Ln}\, BD)$	0.86	17	0.25	0.11	0.174	1.053
C. hookeri	34	$\text{Ln}(FB) = 2.428 + 1.835(\text{Ln}\, BD)$	0.92	11	0.18	0.09	0.138	1.009
D. texana	35	$\text{Ln}(FB) = 2.646 + 2.081(\text{Ln}\, BD)$	0.92	10	0.15	0.07	0.136	1.009
K. humboltiana[b]	16	$\text{Ln}(FB) = 1.807 + 1.714(\text{Ln}\, BD)$	0.84	42	0.16	0.19	0.620	1.212
M. trifoliolata	34	$\text{Ln}(FB) = 1.948 + 1.387(\text{Ln}\, BD)$	0.90	10	0.19	0.07	0.116	1.007
P. glandulosa	36	$\text{Ln}(FB) = 2.496 + 1.938(\text{Ln}\, BD)$	0.95	9	0.17	0.06	0.134	1.009
S. cuneifolia[b]	29	$\text{Ln}(FB) = 2.323 + 2.468(\text{Ln}\, BD)$	0.85	193	0.19	0.19	0.661	1.244
Z. fagara	33	$\text{Ln}(FB) = 2.220 + 1.280(\text{Ln}\, BD)$	0.86	6	0.18	0.08	0.179	1.016
Canopy area (m^{-2})								
A. rigidula	34	$\text{Ln}(FB) = 4.334 + 1.125(\text{Ln}\, CA)$	0.97	7	0.06	0.03	0.079	1.003
C. pallida	35	$\text{Ln}(FB) = 4.386 + 1.176(\text{Ln}\, CA)$	0.82	19	0.14	0.09	0.198	1.019
C. hookeri	34	$\text{Ln}(FB) = 4.951 + 1.198(\text{Ln}\, CA)$	0.96	8	0.07	0.04	0.099	1.005
D. texana	35	$\text{Ln}(FB) = 5.392 + 1.189(\text{Ln}\, CA)$	0.94	11	0.10	0.04	0.146	1.011
M. trifoliolata	34	$\text{Ln}(FB) = 5.338 + 0.956(\text{Ln}\, CA)$	0.93	8	0.07	0.04	0.101	1.005
P. glandulosa	36	$\text{Ln}(FB) = 4.787 + 1.218(\text{Ln}\, CA)$	0.98	7	0.08	0.03	0.105	1.006
Z. fagara	33	$\text{Ln}(FB) = 5.065 + 1.022(\text{Ln}\, CA)$	0.92	14	0.10	0.05	0.134	1.009

CV = coefficient of variation; b_0, b_1, and $s_{y,x}$ = standard errors of intercept, slope and error term, respectively; *CF* = correction factor.

[a]All relationships were significant, $p < 0.05$.

[b]Equations for *K. humboltiana* and *S. cuneifolia* were for individual basal stems. Equations for the remaining species were for sums of all basal stems per plant originating from the soil surface.

standard errors of estimates ($s_{y,x}$). Canopy area typically produced slightly more precise estimates of leaf biomass than stem basal diameter in the seven other species.

Stem basal diameter and canopy area were also good predictors of small stem (<2.5 cm diameter) biomass ($p < 0.05$) for all species (Table 3); the weakest relationships noted were for *M. trifoliolata* ($r^2 = 0.83$ and 0.80). As with the leaf fraction, canopy area was a slightly more precise predictor of small stem biomass than stem basal diameter. Equations developed for the three species from the follow-up studies were variable. *A. gratissima* produced the weakest equation ($r^2 = 0.77$), while equations for *K. humboltiana* and *S. cuneifolia* had higher co-efficients of determination ($r^2 = 0.96$). Prediction of biomass contained in large stems was less precise than noted for small stems (Table 4). For example predicting large stem (>2.5 cm) biomass for *Z. fagara* from basal diameter resulted in one of the few non-significant relationships ($r^2 = 0.32$) of the study. Large stems were recorded in only nine of 34 *Z. fagara* plants sampled in the study. As with small stem and leaf fractions, canopy area generally produced more precise equations for estimating large stem fractions than basal diameter, regardless of species.

Table 3
Equations predicting small stem (<2.5 cm diameter) biomass (*SS*, g) from stem basal diameter (*BD*, cm) and canopy area (*CA*, m^{-2}) for 10 common woody species of southern Texas thorn woodland

Species	d.f.	Equation[a]	r^2	*CV*	Standard errors			*CF*
					b_0	b_1	$s_{y,x}$	
Stem basal diameter (cm)[b]								
A. rigidula	34	$\text{Ln}(SS) = 3.338 + 1.606(\text{Ln}\, BD)$	0.88	12	0.25	0.10	0.189	1.018
A. gratissima	14	$\text{Ln}(SS) = 2.636 + 1.219(\text{Ln}\, BD)$	0.77	23	0.22	0.18	0.760	1.019
C. pallida	35	$\text{Ln}(SS) = 3.207 + 1.785(\text{Ln}\, BD)$	0.85	13	0.29	0.12	0.198	1.019
C. hookeri	34	$\text{Ln}(SS) = 3.621 + 2.090(\text{Ln}\, BD)$	0.93	9	0.19	0.09	0.148	1.011
D. texana	35	$\text{Ln}(SS) = 3.675 + 2.283(\text{Ln}\, BD)$	0.95	10	0.17	0.08	0.153	1.012
K. humboltiana[b]	16	$\text{Ln}(SS) = 3.899 + 2.573(\text{Ln}\, BD)$	0.96	13	0.13	0.13	0.428	1.096
M. trifoliolata	34	$\text{Ln}(SS) = 2.805 + 1.435(\text{Ln}\, BD)$	0.83	12	0.28	0.11	0.171	1.015
P. glandulosa	36	$\text{Ln}(SS) = 3.719 + 2.038(\text{Ln}\, BD)$	0.96	7	0.17	0.06	0.133	1.009
S. cuneifolia[b]	29	$\text{Ln}(SS) = 4.412 + 3.330\ (\text{Ln}\, BD)$	0.96	25	0.13	0.12	0.431	1.097
Z. fagara	33	$\text{Ln}(SS) = 3.245 + 1.496(\text{Ln}\, BD)$	0.88	15	0.20	0.09	0.182	1.017
Canopy area (m^{-2})								
A. rigidula	34	$\text{Ln}(SS) = 5.949 + 1.341(\text{Ln}\, CA)$	0.98	5	0.06	0.03	0.082	1.003
C. pallida	35	$\text{Ln}(SS) = 6.451 + 1.307(\text{Ln}\, CA)$	0.85	13	0.14	0.09	0.195	1.019
C. hookeri	34	$\text{Ln}(SS) = 6.496 + 1.364(\text{Ln}\, CA)$	0.96	6	0.07	0.04	0.104	1.005
D. texana	35	$\text{Ln}(SS) = 6.687 + 1.310(\text{Ln}\, CA)$	0.95	9	0.11	0.05	.152	1.012
M. trifoliolata	34	$\text{Ln}(SS) = 6.306 + 0.957(\text{Ln}\, CA)$	0.80	13	0.13	0.08	0.187	1.018
P. glandulosa	36	$\text{Ln}(SS) = 6.132 + 1.277(\text{Ln}\, CA)$	0.98	6	0.09	0.03	0.107	1.006
Z. fagara	33	$\text{Ln}(SS) = 6.550 + 1.171(\text{Ln}\, CA)$	0.91	13	0.13	0.06	0.168	1.014

CV = coefficient of variation; b_0, b_1, and $s_{y,x}$ = standard errors of intercept, slope and error term, respectively; *CF* = correction factor.

[a]All relationships were significant, $p < 0.05$.

[b]Equations for *K. humboltiana* and *S. cuneifolia* were for individual basal stems. Equations for the remaining species were for sums of all basal stems per plant originating from the soil surface.

Equations developed to predict standing dead wood were the weakest and least precise of those developed (Table 5). Canopy area was generally a better predictor of dead biomass than basal diameter, with the exception of *M. trifoliolata* ($r^2 \leqslant 0.43$, $p > 0.05$), which had dead wood recorded in only five plants. Compared to leaf and stem fractions, standard errors of the *y*-intercept (b_0), slope (b_1), error estimates ($s_{y,x}$), and *CF* for dead wood were considerably larger.

Equations developed to predict total above-ground live biomass were relatively strong ($r^2 > 0.90$) and precise ($CV < 10\%$) in most cases (Table 6). As with the different live components, canopy area predicted total live biomass of all species with slightly more precision than stem basal diameter. Equations developed for the three species in the follow-up studies were variable. *A. gratissima* produced the weakest equation ($r^2 = 0.78$), while equations for *K. humboltiana* and *S. cuneifolia* produced coefficients of determination ($r^2 = 0.95$) similar to the whole-plant equations, though uncertainty in estimates ($s_{y,x}$) were large. *S. cuneifolia* had the largest slope coefficient ($b_1 = 3.111$) for accumulation of total live biomass among the single-stem

Table 4
Equations predicting large stem (>2.5 cm diameter) biomass (*LS*, g) from stem basal diameter (*BD*, cm) and canopy area (*CA*, m^{-2}) for seven common woody species of southern Texas thorn woodland

Species	d.f.	Equation	r^2	*CV*	Standard errors			*CF*
					b_0	b_1	$s_{y,x}$	
Stem basal diameter (cm)								
A. rigidula	13	$\text{Ln}(LS) = 3.041 + 1.713(\text{Ln}\, BD)$	0.72	8	1.06	0.30	0.245	1.031
C. pallida	16	$\text{Ln}(LS) = 2.888 + 1.731(\text{Ln}\, BD)$	0.69	11	0.83	0.30	0.265	1.036
C. hookeri	26	$\text{Ln}(LS) = 3.614 + 2.065(\text{Ln}\, BD)$	0.84	7	0.40	0.17	0.156	1.012
D. texana	25	$\text{Ln}(LS) = 3.314 + 2.469(\text{Ln}\, BD)$	0.89	7	0.40	0.18	0.152	1.012
M. trifoliolata	11	$\text{Ln}(LS) = 2.055 + 1.825(\text{Ln}\, BD)$	0.70	11	1.20	0.37	0.331	1.056
P. glandulosa	27	$\text{Ln}(LS) = 3.350 + 2.463(\text{Ln}\, BD)$	0.92	6	0.39	0.13	0.149	1.011
Z. fagara	9	$\text{Ln}(LS) = 3.780 + 1.276(\text{Ln}\, BD)$	0.32[a]	13	1.59	0.65	0.361	1.067
Canopy area (m^{-2})								
A. rigidula	13	$\text{Ln}(LS) = 5.257 + 1.654(\text{Ln}\, CA)$	0.84	6	0.48	0.21	0.194	1.019
C. pallida	16	$\text{Ln}(LS) = 6.305 + 1.036(\text{Ln}\, CA)$	0.83	8	0.20	0.12	0.192	1.019
C. hookeri	26	$\text{Ln}(LS) = 6.063 + 1.604(\text{Ln}\, CA)$	0.88	7	0.18	0.11	0.138	1.010
D. texana	25	$\text{Ln}(LS) = 6.766 + 1.298(\text{Ln}\, CA)$	0.94	5	0.12	0.06	0.113	1.006
M. trifoliolata	11	$\text{Ln}(LS) = 5.840 + 1.668(\text{Ln}\, CA)$	0.89	7	0.26	0.18	0.202	1.021
P. glandulosa	27	$\text{Ln}(LS) = 6.256 + 1.547(\text{Ln}\, CA)$	0.94	5	0.20	0.07	0.127	1.008
Z. fagara	9	$\text{Ln}(LS) = 5.768 + 1.976(\text{Ln}\, CA)$	0.76	8	0.26	0.39	0.223	1.025

CV = coefficient of variation; b_0, b_1, and $s_{y,x}$ = standard errors of intercept, slope and error term, respectively; *CF* = correction factor.
[a]Non-significant relationship, $p > 0.05$.

data set. Best-fit equations predicting total (live and dead components) above-ground standing biomass (Table 7) using whole-plant measurements performed comparably to equations estimating live biomass.

3.3. C and N concentrations and mass

Concentrations of C and N in leaves differed significantly among species (Table 8). Leaf N was highest in *C. pallida* (3.64%, $p < 0.05$), followed by a group including *A. farnesiana, P. glandulosa*, *C. texensis* and *Z. obtusifolia*. The lowest leaf N concentrations were noted in *M. trifoliolata* (1.28%), while the second lowest were *S. cuneifolia* and *D. texana* (1.90% and 2.05%, respectively). All other species had leaf N concentrations between 2.05% and 2.75%. Leaf C was highest in *A. rigidula* (50.0%); *P. glandulosa*, *A. greggii*, *M. trifoliolata*, and *A. farnesiana* comprised a group with the second-highest levels (45.8–47.3%). The lowest C concentrations were noted in *L. berlandieri*. Leaf C/N ratios ranged from 36.6 in *M. trifoliolata*, an evergreen sclerophyllous shrub, to 10.4 in *C. pallida*, a deciduous shrub. Carbon/nitrogen ratios for Leguminous and Rhamnaceous (families with species potentially capable of N_2 fixation) species ranged from 14.3 to 21.5.

Carbon and N concentrations in stems were also significantly different (Table 8). Eight species had C contents between 44.3% and 46.1%; eight other species had

Table 5
Equations predicting standing dead wood mass (*DB*, g) from stem basal diameter (*BD*, cm) and canopy area (*CA*, m^{-2}) for seven common woody species of southern Texas thorn woodland

Species	d.f.	Equation	r^2	*CV*	Standard errors			*CF*
					b_0	b_1	$s_{y,x}$	
Stem basal diameter (cm)								
A. rigidula	12	$\text{Ln}(DB) = 1.517 + 1.428(\text{Ln}\, BD)$	0.50	20	1.46	0.42	0.454	1.109
C. pallida	18	$\text{Ln}(DB) = 1.040 + 1.436(\text{Ln}\, BD)$	0.51	27	0.91	0.34	0.390	1.079
C. hookeri	30	$\text{Ln}(DB) = 1.980 + 1.902(\text{Ln}\, BD)$	0.75	17	0.43	0.20	0.237	1.028
D. texana	24	$\text{Ln}(DB) = 0.539 + 1.916(\text{Ln}\, BD)$	0.61	26	0.70	0.31	0.313	1.050
M. trifoliolata	5	$\text{Ln}(DB) = -1.485 + 2.115(\text{Ln}\, BD)$	0.43[a]	42	3.46	1.21	1.032	1.703
P. glandulosa	30	$\text{Ln}(DB) = 1.107 + 2.286(\text{Ln}\, BD)$	0.90	11	0.39	0.14	0.203	1.021
Z. fagara	20	$\text{Ln}(DB) = 1.389 + 1.403(\text{Ln}\, BD)$	0.33	33	1.02	0.44	0.434	1.099
Canopy area (m^{-2})								
A. rigidula	12	$\text{Ln}(DB) = 2.615 + 1.665(\text{Ln}\, CA)$	0.59	18	0.98	0.41	0.427	1.095
C. pallida	18	$\text{Ln}(DB) = 3.756 + 0.967(\text{Ln}\, CA)$	0.57	25	0.33	0.20	0.369	1.070
C. hookeri	30	$\text{Ln}(DB) = 4.465 + 1.341(\text{Ln}\, CA)$	0.80	15	0.19	0.12	0.208	1.022
D. texana	24	$\text{Ln}(DB) = 3.102 + 1.081(\text{Ln}\, CA)$	0.68	23	0.28	0.15	0.285	1.041
M. trifoliolata	5	$\text{Ln}(DB) = 2.746 + 1.819(\text{Ln}\, CA)$	0.39[a]	43	1.27	1.12	1.060	1.754
P. glandulosa	30	$\text{Ln}(DB) = 4.854 + 1.421(\text{Ln}\, CA)$	0.90	10	0.23	0.08	0.193	1.019
Z. fagara	20	$\text{Ln}(DB) = 4.461 + 1.275(\text{Ln}\, CA)$	0.51	28	0.27	0.28	0.373	1.072

CV = coefficient of variation; b_0, b_1, and $s_{y,x}$ = standard errors of intercept, slope and error term, respectively; *CF* = correction factor.
[a]Non-significant relationship, $p > 0.05$.

values between 40.5% and 43.4%. The *Opuntia* species differed markedly in C content within pads or stem joints. *O. leptocaulis* was similar to *G. angustifolium* (41.4%), while *O. lindheimerii* had the lowest C of the species examined (30.5%). Stem N was highest in *G. angustifolium*, and slightly exceeded leaf N (2.7% vs. 2.5%). The lowest N values for stems or cladophylls were noted for *O. lindheimeri* and *A. farnesiana* (0.70% and 0.82%, respectively). When pooled across species, there was no correlation between leaf and stem N concentration.

C/N ratios for woody tissues ranged from 58.7 (*A. farnesiana*) to 15.8 (*G. angustifolium*). Of the 17 species sampled (Table 8), C/N ratios of stem tissues in nine species fell within the range noted for leaves (10.3–35.9). C/N ratios for dead *P. glandulosa* wood did not differ from dead *D. texana* wood, and both were similar to live wood for most of the 17 species. Regressing C/N ratios against C and N in leaves and stems (pooled across species) produced non-significant correlations for C [foliage ($p = 0.18$), stems ($p = 0.81$)], and significant correlations with tissue N ($p = 0.01$, data not shown).

Regressing tissue C and N concentrations against *P. glandulosa* age estimated from stem basal diameter did not produce useful results. Stems of *P. glandulosa* plants ranged from 10 to 85 years in age, but no significant relationship was detected between stem age and C or N in live tissues (leaf, small stems, large stems). Concentrations of C in dead wood decreased with plant age ($r = -0.81$, $n = 7$,

Table 6
Equations predicting total (leaf + stem) live biomass (*LB*, g) from stem basal diameter (*BD*, cm) and canopy area (*CA*, m^{-2}) for 10 common woody species of southern Texas thorn woodland

Species	d.f.	Equation[a]	r^2	*CV*	Standard errors			*CF*
					b_0	b_1	$s_{y,x}$	
Stem basal diameter (cm)[b]								
A. rigidula	34	$\text{Ln}(LB) = 3.420 + 1.775(\text{Ln}\, BD)$	0.89	12	0.26	0.10	0.193	1.019
A. gratissima	14	$\text{Ln}(LB) = 2.787 + 1.192(\text{Ln}\, BD)$	0.78	22	0.21	0.17	0.731	1.306
C. pallida	35	$\text{Ln}(LB) = 3.321 + 1.905(\text{Ln}\, BD)$	0.86	13	0.29	0.13	0.202	1.021
C. hookeri	34	$\text{Ln}(LB) = 3.943 + 2.286(\text{Ln}\, BD)$	0.94	8	0.19	0.09	0.142	1.010
D. texana	35	$\text{Ln}(LB) = 4.043 + 2.502(\text{Ln}\, BD)$	0.96	8	0.16	0.08	0.146	1.011
K. humboltiana[b]	16	$\text{Ln}(LB) = 4.045 + 2.448(\text{Ln}\, BD)$	0.95	13	0.11	0.14	0.452	1.107
M. trifoliolata	34	$\text{Ln}(LB) = 2.865 + 1.705(\text{Ln}\, BD)$	0.90	9	0.24	0.09	0.147	1.011
P. glandulosa	36	$\text{Ln}(LB) = 4.064 + 2.369(\text{Ln}\, BD)$	0.97	6	0.16	0.06	0.129	1.008
S. cuneifolia[b]	29	$\text{Ln}(LB) = 4.498 + 3.111(\text{Ln}\, BD)$	0.95	23	0.13	0.13	0.455	1.109
Z. fagara	33	$\text{Ln}(LB) = 3.648 + 1.533(\text{Ln}\, BD)$	0.90	13	0.18	0.08	0.178	1.016
Canopy area (m^{-2})								
A. rigidula	34	$\text{Ln}(LB) = 6.316 + 1.465(\text{Ln}\, CA)$	0.97	6	0.07	0.04	0.102	1.005
C. pallida	35	$\text{Ln}(LB) = 6.782 + 1.406(\text{Ln}\, CA)$	0.88	12	0.13	0.08	0.188	1.018
C. hookeri	34	$\text{Ln}(LB) = 7.088 + 1.488(\text{Ln}\, CA)$	0.98	5	0.07	0.03	0.092	1.004
D. texana	35	$\text{Ln}(LB) = 7.343 + 1.439(\text{Ln}\, CA)$	0.97	8	0.09	0.04	0.134	1.009
M. trifoliolata	34	$\text{Ln}(LB) = 7.033 + 1.174(\text{Ln}\, CA)$	0.92	8	0.09	0.05	0.131	1.009
P. glandulosa	36	$\text{Ln}(LB) = 6.873 + 1.482(\text{Ln}\, CA)$	0.98	5	0.08	0.03	0.104	1.005
Z. fagara	33	$\text{Ln}(LB) = 7.049 + 1.213(\text{Ln}\, CA)$	0.95	9	0.10	0.04	0.126	1.008

CV = coefficient of variation; b_0, b_1, and $s_{y,x}$ = standard errors of intercept, slope and error term, respectively; *CF* = correction factor.

[a]All relationships were significant, $p < 0.05$.

[b]Equations for *K. humboltiana* and *S. cuneifolia* were for individual basal stems. Equations for the remaining species were for sums of all basal stems per plant originating from the soil surface.

$p < 0.05$). Regression of whole-plant nutrient mass (obtained by multiplying biomass values for components of harvested plants by average nutrient concentrations in Table 8) against canopy area produced significant exponential (simple model) relationships for all fractions when data were pooled across species (Fig. 1). Equations predicting C and N mass in leaf, small stem, large stem and total plant components all had r^2 values >0.87. Equations developed to predict C and N mass in dead wood were also significant, but less effective ($r^2 = 0.63$ and 0.66, respectively). Relationships between summed stem basal diameters and total nutrient contents, pooled across species, produced equations with reasonable coefficients of determination (kg $\text{C} = 0.0198(BD)^{1.933}$, $r^2 = 0.72$, $p < 0.05$; kg $\text{N} = 0.001(BD)^{1.881}$, $r^2 = 0.74$, $p < 0.05$). However, variance in the relationship was extreme across the upper half of the range of predictors and resulted in unreliable estimates. For example plants ($n = 3$) with 54–55 cm stem basal diameter had between 8.2 and 376 kg C in above-ground tissues. Equations predicting total C and N with stem basal diameter, when data were pooled according to growth form (basal stems per plant), were comparable to results of the canopy area analyses (Table 9).

Table 7
Equations predicting total (live + dead) biomass (*TB*, g) from stem basal diameter (*BD*, cm) and canopy area (*CA*, m^{-2}) for seven common woody species of southern Texas thorn woodland

Species	d.f.	Equation[a]	r^2	*CV*	Standard errors			*CF*
					b_0	b_1	$s_{y,x}$	
Stem basal diameter (cm)								
A. rigidula	34	$\text{Ln}(TB) = 3.409 + 1.790(\text{Ln}\, BD)$	0.89	12	0.26	0.10	0.212	1.023
C. pallida	35	$\text{Ln}(TB) = 3.323 + 1.914(\text{Ln}\, BD)$	0.86	13	0.29	0.13	0.203	1.021
C. hookeri	34	$\text{Ln}(TB) = 3.989 + 2.296(\text{Ln}\, BD)$	0.94	8	0.19	0.09	0.145	1.011
D. texana	35	$\text{Ln}(TB) = 4.053 + 2.502(\text{Ln}\, BD)$	0.96	8	0.16	0.08	0.146	1.011
M. trifoliolata	34	$\text{Ln}(TB) = 2.854 + 1.715(\text{Ln}\, BD)$	0.90	10	0.25	0.09	0.149	1.012
P. glandulosa	36	$\text{Ln}(TB) = 4.129 + 2.387(\text{Ln}\, BD)$	0.97	6	0.16	0.06	0.130	1.009
Z. fagara	33	$\text{Ln}(TB) = 3.690 + 1.549(\text{Ln}\, BD)$	0.90	13	0.19	0.09	0.186	1.017
Canopy area (m^{-2})								
A. rigidula	34	$\text{Ln}(TB) = 6.330 + 1.477(\text{Ln}\, CA)$	0.97	6	0.08	0.04	0.103	1.005
C. pallida	35	$\text{Ln}(TB) = 6.802 + 1.412(\text{Ln}\, CA)$	0.88	12	0.14	0.09	0.189	1.018
C. hookeri	34	$\text{Ln}(TB) = 7.148 + 1.496(\text{Ln}\, CA)$	0.98	5	0.07	0.04	0.096	1.005
D. texana	35	$\text{Ln}(TB) = 7.354 + 1.440(\text{Ln}\, CA)$	0.97	8	0.09	0.04	0.133	1.009
M. trifoliolata	34	$\text{Ln}(TB) = 7.046 + 1.181(\text{Ln}\, CA)$	0.92	9	0.09	0.06	0.132	1.009
P. glandulosa	36	$\text{Ln}(TB) = 6.960 + 1.492(\text{Ln}\, CA)$	0.98	5	0.09	0.03	0.108	1.006
Z. fagara	33	$\text{Ln}(TB) = 7.127 + 1.229(\text{Ln}\, CA)$	0.95	9	0.10	0.04	0.127	1.008

CV = coefficient of variation; b_0, b_1, and $s_{y,x}$ = standard errors of intercept, slope and error term, respectively; *CF* = correction factor.
[a]All relationships were significant, $p < 0.05$.

4. Discussion

Equations developed from projected canopy area consistently produced more precise estimates of above-ground biomass of the different shrub species than stem basal diameter. However, this improvement was slight and either metric could be used to develop predictions from survey data. Metrics based on stem basal diameter may be more robust since they will likely be less sensitive to short-term environmental fluctuations. Seasonal changes in leaf area and current year stems may affect measurements of dimensions used in calculating canopy area. However, measuring basal diameter can require more time per plant, particularly for multi-stemmed species, thus extending the time required for field surveys and limiting the number of plants assayed. The metric used may partly depend on level of comfort users have with uncertainty in the predictions. While basal area has advantages relative to reduced seasonal fluctuations in measurements, some accuracy (and confidence) in estimates was sacrificed. For example errors in estimates ($s_{y,x}$) of total mass for the seven key species ranged 13–21% and 10–19% using basal diameter and canopy area, respectively, as predictors.

One useful advantage of canopy dimensions is that canopy area of identifiable individual plants could be quantified over large areas and through time from aerial photographs or satellite images to estimate biomass (e.g. Asner et al., 2003). Such an

Table 8
Mean (±1 S.E.) leaf and wood nitrogen and carbon concentration (percent dry mass) of woody plant species from a southern Texas thorn woodland

Species	Leaf				Stem			
	n	Nitrogen	Carbon	C:N	*n*	Nitrogen	Carbon	C:N
A. farnesiana[a]	2	3.20±0.14b	45.8±0.1b	14.3±0.3de	5	0.82±0.12f	43.9±0.3bc	58.7±8.9a
A. greggii[a]	4	2.75±0.30c	46.6±1.2b	17.1±1.0cd	4	1.50±0.07b	45.4±0.4ab	30.5±1.6de
A. rigidula[a]	3	2.34±0.10cd	50.0±0.1a	21.5±0.8b	0	—	—	—
C. pallida	11	3.64±0.12a	37.6±0.4f	10.4±0.4f	9	1.69±0.12b	44.3±0.2abc	27.3±2.0de
C. texensis[b]	3	2.80±0.30bc	43.2±1.3cd	15.5±0.8cde	3	1.37±0.07bcd	45.4±0.3ab	33.4±1.6bcde
C. hookeri[b]	10	2.57±0.09c	42.0±0.2d	16.6±0.8cde	17	0.96±0.05def	45.0±0.2ab	48.7±2.4abcd
D. texana	12	2.05±0.03de	43.9±.02c	21.4±0.2b	14	0.97±0.05def	44.3±0.2abc	47.2±2.5abcd
E. antisyphylitic	0	—	—	—	4	1.40±0.29bc	40.5±3.0e	32.6±6.6cde
E. texana[a]	2	2.50±0.28c	43.1±0.7cd	17.3±1.2cd	3	1.27±0.03bcde	44.4±0.3abc	35.1±0.9bcde
G. angustifolium	2	2.50±0.00c	44.0±1.9c	17.6±0.5cd	2	2.70±0.40a	41.7±0.2de	15.8±2.3e
L. berlandieri	4	2.75±0.40c	35.3±1.6g	13.0±0.9ef	8	1.60±0.08b	46.1±0.2a	29.3±1.4de
M. trifoliolata	8	1.28±0.06f	46.0±0.1b	36.6±1.6a	11	0.93±0.05ef	45.2±0.1ab	49.9±3.2abcd
O. leptocaulis	0	—	—	—	8	0.90±0.06ef	41.4±1.0e	47.7±4.5abcd
O. lindheimeri	0	—	—	—	3	0.70±0.10f	30.5±1.4f	44.7±4.0abcd
P. glandulosa[a]	15	3.22±0.06b	47.3±0.1b	14.8±0.3de	50	0.93±0.04ef	45.9±0.1a	55.5±3.0ab
S. cuneifolia	9	1.90±0.30e	39.9±0.8e	22.0±1.2b	10	1.62±0.15b	43.0±0.6cd	33.2±8.4bcde
Z. fagara	12	2.36±0.10cd	43.6±0.3c	18.8±0.8bc	19	1.29±0.10cde	45.8±0.2a	40.1±3.5abcd
Z. obtusifolia[b]	6	2.78±0.50bc	42.4±2.5cd	15.7±1.3cde	7	1.50±0.08b	45.6±0.4ab	30.9±1.6de
Dead wood *Diospyros*	0	—	—	—	5	0.92±0.15ef	44.4±0.1abc	53.9±9.4abc
Dead wood *Prosopis*	0	—	—	—	7	1.04±0.10cdef	45.8±0.4a	47.3±5.9abcd
F (pr>*F*)	103	31.6 (<0.01)	77.5 (<0.01)	46.9 (<0.01)	189	11.1 (<0.01)	30.3 (<0.01)	4.3 (<0.01)
Overall mean[c]	15	2.56±0.15	43.4±1.0	18.2±1.6	19	1.27±0.11	43.6±0.8	40.1±2.6

Means in the same column followed with the same letter were not significantly different ($p>0.05$).
[a]Denotes species in the Leguminosae.
[b]Denotes species in the Rhamnaceae.
[c]Based on $n=1$ per species; overall means were not weighted by total biomass or species dominance in the field.

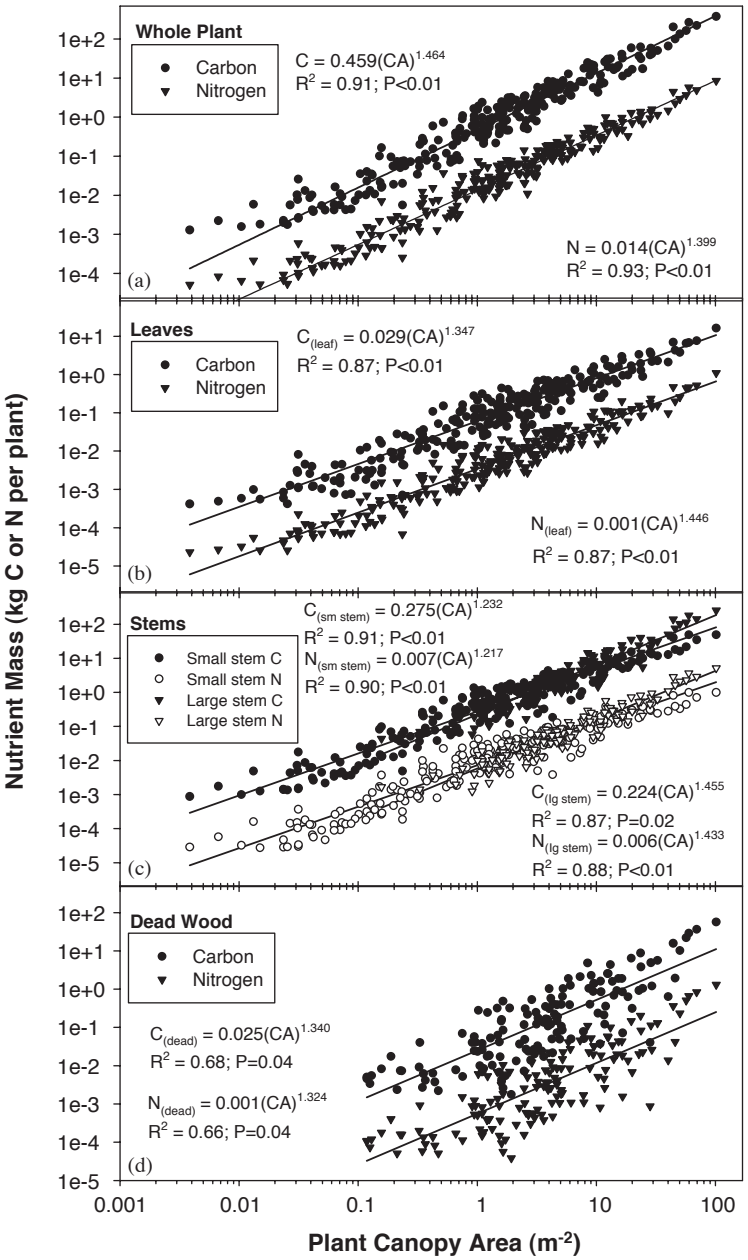

Fig. 1. Non-linear relationships (Log scale) between plant canopy area (m^{-2}) and nutrient mass (kg per plant) of above-ground components. Nutrient mass for plants of the dominant species in Table 1 was computed by multiplying dry weight (kg) of components (leaf, small stem, large stem, dead stem) by mean C and N concentrations in Table 8. Whole-plant nutrient mass (panel a) is the summation of all biomass components. Each point represents a single plant.

Table 9
Carbon (C) and nitrogen (N) mass (kg per plant)of woody plants (by growth form according to numbers of basal stems per plant in Table 1) in a thorn woodland of southern Texas

Growth form grouping[a]	Stems per plant	Equation	n	r^2
Carbon content				
Prgl-Dite-Coho	1–2	$C = 0.0259(BD)^{2.395}$	108	0.96
Cepa	6–7	$C = 0.0121(BD)^{1.919}$	36	0.86
Zafa-Matr	9–11	$C = 0.0141(BD)^{1.559}$	69	0.89
Nitrogen content				
Prgl-Dite-Coho	1–2	$N = 0.0008(BD)^{2.319}$	108	0.95
Cepa	6–7	$N = 0.0006(BD)^{1.883}$	36	0.84
Zafa-Matr	9–11	$N = 0.0005(BD)^{1.481}$	69	0.86

Nutrient mass was predicted from the sum of basal diameters (BD, cm) of stems on a plant arising from the soil surface. All relationships were significant at $p < 0.05$.

[a]Species codes are: Cepa = *C. pallida*, Coho = *C. hookeri*, Dite = *D. texana*, Matr = *M. trifoliolata*, Prgl = *P. glandulosa*, and Zafa = *Z. fagara*.

approach would allow descriptions of both spatial and temporal dynamics in biomass allocation. Further, the relationships in Fig. 1 suggest above-ground C and N pools associated with woody plants in thorn woodlands could be derived from remotely sensed estimates of canopy area, even when communities are comprised of multiple species whose identities are not discernable. Datasets that include stand-level determinations of C and N concentrations in biomass components of plants, and measures of physical dimensions, are required to fully test this approach.

Most of the equations developed to predict biomass components of the listed species were relatively robust and functional. These equations are potentially useful for estimating browse availability, estimating total leaf area where specific leaf areas are known, or developing parameters for models of ecosystem biogeochemistry. However, equations with high levels of uncertainty in estimates ($s_{y,x} > 20\%$) were present, though generally restricted to cases with small sample numbers. In such instances, some caution should be applied when using predictions. Equations predicting standing dead wood, and large stems for some species, were the least precise. Improved estimates for dead wood might have occurred if a division into size classes was utilized, though improvement could not be guaranteed. Stem mortality in this system can be episodic in response to frost (Lonard and Judd, 1985) or drought (Carter, 1964). Persistence of dead wood within canopies may also be variable due to episodic sloughing during intense storms that transit the region. Applying allometric equations developed from such reduced datasets could thus greatly over- or underestimate dead mass.

Differences in the slopes (b_1) of the relationships between predictor and dependent variables for the listed species (Tables 2–5) suggest potential ontogenetic differences in the allocation of resources to canopy components as plants develop. Alternatively, these differences could be related to the influence of habitat on allocation patterns.

In either case, plant allometry and allocation of biomass to organs are highly plastic features of plant development, rather than fixed responses (Niklas, 1995). Factors such as climate, environment, and competition all affect plant development in these communities (Archer, 1995). As such, variance in relationships between plant metrics and mass noted here were not unexpected.

Allocation of biomass to the various canopy components differed with species, growth form (e.g. numbers of basal stems) and plant size. These differences were partially related to physical development of plants as they progressed from relatively simple growth forms for small (young) plants to the complex, more diverse forms of larger (older) plants (Niklas, 1995). Allocation to different components also varied by predictor used. When estimated by stem basal diameter, the predominately single-stemmed species (*P. glandulosa*, *D. texana*, *C. hookeri*) generally had higher allocations to canopy components, per unit predictor, than multi-stemmed species which had two distinct groups (*Z. fagara* and *M. trifoliolata* vs. *A. rigidula* and *C. pallida*). These differences were partly related to the predictor itself. Summation of stem basal diameters for the multi-stemmed plants resulted in partial dilution of biomass (and nutrients) per unit predictor, compared to single-stemmed plants. Alternatively, when considered on a canopy area basis, some multi-stemmed species allocated more mass (to components) per unit canopy area than the dominant *P. glandulosa*.

Questions related to how shrub species apportion mass (and nutrients) as plants develop have many practical considerations. Of particular import are effects on nutrient cycles in thornscrub-dominated ecosystems, and changes that can occur with succession of existing savannas to closed-canopy woodlands (Archer, 1995). In this study, C and N concentrations in stems and leaves were fairly consistent, with leaves having generally higher N than stems, and C concentrations relatively constant across species and canopy component. Further, our analyses indicated species-level differences in C/N ratios mostly resulted from variation in N rather than C. It is noteworthy that, C/N ratios of species in the Leguminous and Rhamnaceous families, which include species potentially capable of N_2 fixation (Boutton et al., 1992), were in the same range as non-fixing species. Such responses indicate factors other than N_2 fixation were involved in accumulation (Zitzer et al., 1996). Minor interspecies variation did exist in allocation of C and N to leaves vs. stems; so changes in species abundance with succession (Archer, 1995) will potentially affect litter quality in these woodlands. In this study, the extent to which among species variation in leaf N reflected differences in allocation to the carboxylation enzyme used in photosynthesis vs. nitrogenous secondary compounds is unknown. The former has implications for primary production, whereas the latter has implications for decomposition and herbivory. For example Windels et al. (2003) showed stems of *Acacia berlandieri*, a species not included in this study, contained 1.8–6.0% of N in stems as amine-based defensive compounds.

Nitrogen concentrations in *G. angustifolium* differed from the other species, with higher levels noted in stems than leaves. However, this result may not hold true for the entire population of this species. Stems from the plants we sampled ($n = 2$) had a greenish color and appeared to be partially photosynthetic, whereas mature stems of

G. angustifolium are thick, stubby, and covered in a gray-black bark (Everitt and Drawe, 1993). If this reversal in N concentrations held true for a large portion of stems within a canopy, such an allocation pattern could have physiological significance for individual plants. However, effects of *G. angustifolium* on ecosystem C and N dynamics would vary in relation to its abundance which ranges from uncommon at our La Copita site, to 13 plants ha^{-1} (Ruthven et al., 1993), and >1000 plants ha^{-1} on other sites in southern Texas (Fulbright and Beasom, 1987).

In this study, leaves comprised 14% (range = 10–21%) of above-ground biomass in the sampled species. This was higher than values reported for woody species in studies on subtropical savannas, in western Africa (3–7%, Meneaut and Cesar, 1979), northern Australia (3–5%, Werner and Murphy, 2001), and South Africa (4%, Huntley and Morris, 1982; Rutherford, 1982). Our study included small plants, which had higher fractions of biomass as leaves than more mature individuals, and contributed to the higher range of values we noted. Alternatively, leaf tissue comprised 29–34% of above-ground biomass in mopane savannas of Zimbabwe (Rutherford, 1982). Live stems comprised 84% (range = 76–88%) of above-ground biomass in our study, which was slightly lower than values recorded in other studies. Regardless of plant size, there is considerable variation in biomass allocated to leaves (or stems) in woody species of tropical and subtropical savannas, perhaps reflecting the range of climatic and edaphic variability present in the world's savannas.

The strong allometric relationships quantified in this study were consistent with results of other studies in the region. Hughes et al. (1987) found significant relationships between total production and canopy width for a variety of species, including one of our site dominants (*A. rigidula*), at a thornscrub site (620 mm MAP) 230 km north-west of our study area. Bryant and Kothmann (1979) reported strong relationships ($r^2>0.85$) between total above-ground biomass and canopy volume for *D. texana*, *Z. fagara*, *M. trifoliolata*, and *P. glandulosa* on drier Cretaceous limestone sites 400 km north-west of our site. Navar et al. (2002) also observed strong multi-variable relationships for subtropical thornwood species in a higher-rainfall zone of north-eastern Mexico. Allometric equations for *P. glandulosa* also exist for agroforestry settings (Felker et al., 1990) and various bioclimatic zones including northern (Asner et al., 2003) and central Texas (Whisenant and Burzlaff, 1978).

A comparison of our results (Table 7) against an equation developed by Ludwig et al. (1975) for relationships between canopy area and above-ground biomass of *P. glandulosa* in south-eastern New Mexico [g total biomass = 287(canopy area, m^{-2})^2] showed our equation predicted ~10% less biomass for the same sized canopies. This difference was likely related to regional differences in soils, climate, and land use that can cause variation in biomass accumulation. However, it is a relatively small difference, so estimates from allometric equations developed for widely distributed species could be useful in predicting biomass (or nutrients) across broad geographic regions. A comparison of species-specific equations from different regions (developed from the same allometric characteristic) that tests for similarities in equation co-efficients might be a useful area of research. Such an approach could help describe regional robustness of biomass–allometry relationships.

Canopy area and stem diameter are commonly measured during inventories of plant communities to quantify relative abundance and dominance. The accumulation of allometric databases for thornscrub vegetation of the south-western US and northern Mexico suggest we may be approaching a point where stem or canopy surveys of plant communities in past studies could be converted to estimates of both biomass and nutrient mass. This approach would offer the opportunity to broadly describe ecosystem-level distribution of above-ground biomass and carbon and nitrogen mass in subtropical thorn woodlands; validate regional predictions of vegetation change (Field et al., 1995; Neilson, 1995; VEMAP, 1995; Daly et al., 2000; Schimel et al., 2001); link remote sensing-biogeochemisty models (DeFries et al., 1999; Hibbard et al., 2003); and verify regional remote sensing classifications (DeFries and Townshend, 1995; DeFries et al., 1995, pp. 867–820).

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