Amount and Distribution of Dry Matter, Nitrogen, and Organic Carbon in Soil-Plant Systems of Mesquite and Palo Verde

R.C. BARTH AND J.O. KLEMMEDSON

Abstract

Over a 3-year period, soil-plant systems of velvet mesquite and palo verde from the Sonoran Desert were sampled by standing crop, litter, and soil components and analyzed to describe the amount and distribution of dry matter, nitrogen, and carbon in the systems. Honey mesquite was sampled on a limited basis in southern New Mexico. Velvet mesquite averaged about one-third larger in crown area and weight than palo verde, but the two shrubs were similar in the distribution of dry matter, N, and C. Honey mesquite was much smaller and differed in distribution of dry matter, N, and C. Regression analysis showed that dry matter, N, and C in components of shrub systems of velvet mesquite and palo verde varied in a predictable manner and can be estimated with good precision using height, average crown diameter, or crown area of shrubs as the independent variable. Functional analysis showed that soil under palo verde did not accumulate N or C with increase in shrub size, whereas that under velvet mesquite accumulated N at the rate of 11.2 g/m² per meter of height and C at the rate of 0.11 kg/m² per meter of height.

Shrubs dominate the vegetation on over 200 million hectares of land in the conterminous United States, mostly in the Southwest and the Intermountain Basin. Many authorities consider shrubs the climax vegetation on about one-half this area, while on the remaining 100 million hectares shrubs now dominate where grasses were once the climax dominants. Man has been using shrublands since prehistoric times, but until recently little management has been applied. When used, management usually has been directed at eliminating shrubs. Because shrubs play an important role in terrestrial ecosystems, we should understand their ecological role. This is especially important in arid areas where shrubs are an important component of the vegetation. This paper reports on a study to determine how dry matter, nitrogen, and carbon were accumulated and distributed in soil-plant systems of two desert shrubs: velvet mesquite *(Prosopis juliflora)* and palo verde (*Cerdicium floridum).* Limited data on honey mesquite *(Prosopis juliflora* var. *glandulosa)* are included as an adjunct to the main study.

Methods

Study Locations

The study area was located in the Upper Sonoran Desert approximately 32 km south of Tucson, Arizona, at the Santa Rita Experimental Range. The study site was on an alluvial plain with a slope of less than 5% and an elevation of 975 m. Numerous arroyos and small shallow washes dissect the upland areas. Sampling was conducted on the upland sites on the Sonoita soil series, a coarse, loamy, mixed, thermic family of Typic Haplargids derived from moderately coarse-textured alluvium of mixed origin. The study site has been grazed lightly for the past 60 years.

The limited adjunct study of honey mesquite was conducted at the Jornada Experimental Range in the Chihuahuan Desert northeast of Las Cruces, N.M. Honey mesquite shrubs, which dominate this area, were less than 2 m high at maturity and multi-stemmed. These scrubs were growing on small dunes, a result of accumulating aeolian material that partially covered the plant base. Although rodents are commonly associated with the *Prosopis* dunes, evidence indicates the rodents are merely occupying a favorable habitat and play no role in dune formation (Campbell. 1929; C.H. Herbel, Las Cruces, N.M., personal communication). Soils, which were loamy sand and structureless with little vertical differentiation throughout the profile, appeared to be Torrifluvents. Climate of the Chihuahuan Desert is somewhat cooler, drier, and more windy than that of the Sonoran Desert.

Field Sampling

A total of 58 randomly selected soil-plant systems (34 velvet mesquite and 24 palo verde) covering the range of size classes were sampled at Santa Rita during spring, early fall, and winter from 1971 to 1973 (Barth and Klemmedson 1978). For both species these seasons coincided with full bloom, cessation of shrub growth, and maximum herbaceous understory development, and dormancy, respectively. As used here, a soil-plant system is a small ecosystem that includes the entire shrub, its understory, litter, and soil to a depth of 60 cm within the crown area of the shrub. The area and depth of sampling were selected to correspond to the zone of maximum shrub influence.

Although velvet mesquite and palo verde both tend to be multistemmed at the base, this tendency was somewhat greater for velvet mesquite (91%) than for palo verde (78%) at the study site. Number of stems per shrub averaged 2.8 for mesquite and 1.9 for palo verde. Both species averaged 3.3 m in height. Velvet mesquite is more squat-shaped than palo verde, as reflected in a crown area that averages one-third larger (Table 1). For each system sampled, six 0.093 m² plots were located on a north-south line running through the center of the shrub. Plots were located under the shrub canopy at points equivalent to 1/3, 2/3, and 3/3 the north and the south canopy radius (CR). In each plot standing understory live and dead vegetation was harvested at ground level. Litter from the overstory shrub (shrub litter) and from understory species (understory litter) also were collected in each plot. Material collected from north and south plots at the same canopy position for a given shrub was combined into one sample, thus making the plot for each CR location 0.186m² in size. The shrub was then cut at ground level and separated into leaves, flowers, fruit, current twigs (woody growth less than 1 year old), small branches (<1 cm in diameter), large branches (>1 cm in diameter), and deadwood. All shrub components were weighed in the field and sampled randomly for moisture content and laboratory analyses.

The authors are senior research ecologist, Colorado School of Mines Research Institute, Golden, Colo. 80401, and professor, School of Renewable Natural Resources, University of Arizona, Tucson. 85721.

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Soil columns were collected from each of the six 0.093 m² plots and at an additional plot located at the center of the shrub. Surface dimensions of soil columns were 8 by 10 cm; columns were separated into four depths: 0-5 cm, 5-15 cm, 15-30 cm, and 30-60 cm. All soil, rock, and shrub roots in soil columns were recovered and those from the same depth and canopy position on north and south sides of each shrub were combined for weighing and analysis.

At the Jornada Experimental Range, we sampled three soil-plant systems of honey mesquite in mid-August, 1972, using field sampling and laboratory methods identical to those described above. This sampling was conducted as an adjunct to the main study for purpose of relative comparison only. Comparisons of honey mesquite, with the other species are limited (and slightly biased) more by the single season of sampling than the number of samples.

As indicated by measures of variance presented in this paper (Tables 1,2,4,5,6) and elsewhere for other phases of study (Barth and Klemmedson 1978), sampling procedures were adequate for all components except roots. The size and depth of soil columns lead to higher variance in the root data and conservative estimates were obtained.

Laboratory Methods

Vegetal and litter samples were oven-dried at 70°C, weighed, and ground to pass a 40-mesh (0.42 mm openings) sieve. Soil samples were passed through a 9-mesh (2mm openings) sieve; the resulting fine earth fraction was then ground to pass a 100-mesh (0.15 mm openings) sieve. Roots were separated from soil during the initial laboratory sieving, added to those recovered in the field, and then processed in the same manner as other vegetal samples. Total N was determined by the macro-Kjeldahl method (Bremner 1965). Organic C was determined by analysis of total C by dry combustion (Allison et al. 1965) and corrected for carbonate C (Bundy and Bremner 1972). All C data reported are for organic C.

Results

Average Size Shrubs

Dry Matter

Total dry matter of the soil-plant systems for velvet mesquite, palo verde and honey mesquite averaged 147.6, 103.1, and 13.4 kg/shrub and the crown areas were 20.9, 15.2 and 3.9 m², respectively (Table 1). Thus, velvet mesquite shrub systems were about 43% larger by weight than palo verde, while honey mesquite were comparatively small. Because of these size differences, we will resort to weight per unit crown area and percentage distribution among components for comparisons among species.

Shrub standing crop represented about 88% of total dry matter in the system for both velvet mesquite and palo verde, but only 75% for honey mesquite. The remaining dry matter was in understory (2.0 to 4.5%) and litter (7.5 to 22.5%). Of total shrub dry matter, about 79% was allocated to shoots in velvet mesquite and palo verde; shoots accounted for about 67% of the dry matter for honey mesquite. Percentage of dry matter in roots was similar among all species (Table 1). Distribution of dry matter among shoot components differed markedly among the three shrubs, thus reflecting differing growth habits. In particular, the proportions of dry matter in leaves, large and small branches, and deadwood differed among the three species (Table 1). Velvet mesquite had a very low proportion of small branches and palo verde characteristically had practically no leaves. Percentage dry matter in leaves of honey mesquite was deceivingly high because honey mesquite was collected only in the full leaf stage; the other shrub systems were collected in leafless as well as full leaf stages.

Although velvet mesquite systems contained the largest weight of litter (15 g), honey mesquite contained the most litter per unit area as a percentage of total dry matter (22.5%). This is attributed to the low stature of honey mesquite and demonstrates an ability to collect and hold litter. Distribution of shrub litter and understory litter differed greatly among the three shrub systems (Table 1). Honey mesquite had nearly four times as much understory litter as shrub litter. The converse was found for velvet mesquite whereas shrub and understory litter did not differ greatly for palo verde.

Nitrogen

Although differences occurred among shoot components, velvet mesquite and palo verde are remarkably similar in how they distributed N among the principal components of the soil-plant system, both in g/m² and percentage distribution among components (Table 2). This is attributed to similarity in growth form (described above) and N composition of components (Table 3) between velvet

Table 1. Amount and distribution of dry matter in soil-plant systems of average size for three species of desert shrubs.

	Velvet Mesquite			Palo Verde			Honey Mesquite		
Component	kg/shrub	kg/m²	%	kg/shrub	kg/m²	%	kg/shrub	kg/m²	%
Standing Crop									
Shrub									
Shoot									
Leaves	3.24 ± 0.54	0.148	2.2	0.18 ± 0.08	0.012	0.2	0.70 ± 0.12	0.180	5.2
Flowers	0.04 ± 0.02	0.002	<0.1	0.10 ± 0.06	0.007	0.1	0.00	0.000	0.0
Fruit	0.07 ± 0.04	0.003	<0.1	0.05 ± 0.04		<0.1	0.18	0.047	1.3
Current twigs	0.26 ± 0.05	0.012	0.2	1.65 ± 0.46	0.108	1.6	0.24 ± 0.12	0.062	1.8
Small branches	8.25 ± 1.05	0.379	5.6	17.08 ± 2.43	1.122	16.6	1.86 ± 1.10	0.479	13.9
Large branches	75.92 ± 12.93	3.483	51.4	54.35 ± 9.86	3.571	52.7	3.04 ± 2.70	0.784	22.6
Deadwood	26.36 ± 3.97	1.209	17.9	9.44 ± 1.98	0.620	9.1	3.05 ± 3.11	0.786	22.7
Subtotal	114.14 ± 17.19	5.236	77.3	82.85 ± 13.92	5.443	80.3	9.07 ± 7.04	2.338	67.5
Roots	15.44 ± 3.63	0.709	10.5	7.96 ± 3.63	0.523	7.7	1.04 ± 0.75	0.268	7.8
Shrub total	129.58 ± 18.95	5.945	87.8	90.81 ± 16.42	5.966	88.0	10.11 ± 6.76	2.606	75.3
Understory	2.98 ± 0.54	0.137	2.0	4.60 ± 1.51	0.302	4.5	0.30 ± 0.22	0.077	2.2
Litter									
Shrub	11.76 ± 2.84	0.539	8.0	4.36 ± 1.45	0.286	4.2	0.61 ± 0.31	0.157	4.5
Understory	3.26 ± 0.55	0.149	2.2	3.36 ± 0.86	0.221	3.3	2.41 ± 2.20	0.621	18.0
Subtotal	15.02 ± 3.24	0.689	10.2	7.72 ± 1.92	0.507	7.5	3.02 ± 2.32	0.778	22.5
Soil	—	—	—	—	—	—	—	—	—
Soil-plant system	147.58 ± 21.66	6.771	100.0	103.13 ± 18.42	6.775	100.0	13.43 ± 9.29	3.461	100.0
Mean crown area (m²)	20.90			15.22			3.88		

[1]Sample mean ± standard error

Table 2. Amount and distribution of nitrogen in soil-plant systems of average size for three desert shrubs.

Component	Velvet Mesquite g/shrub	g/m²	%	Palo Verde g/shrub	g/m²	%	Honey Mesquite g/shrub	g/m²	%
Standing Crop									
Shrub									
Shoot									
Leaves	96.6 ± 15.7[1]	4.62	1.3	6.6 ± 2.7	0.43	0.1	22.4 ± 15.3	5.77	1.8
Flowers	1.6 ± 0.6	0.07	<0.1	3.8 ± 2.2	0.25	0.1	0.0	0.00	0.0
Fruit	0.8 ± 0.4	0.04	<0.1	1.4 ± 0.9	0.09	<0.1	5.6	1.44	0.4
Current twigs	4.7 ± 0.9	0.23	0.1	39.1 ± 10.3	2.57	0.8	3.3 ± 1.3	0.85	0.3
Small branches	128.5 ± 17.4	6.15	1.7	285.3 ± 44.9	18.74	5.7	26.0 ± 13.7	6.70	2.1
Large branches	868.9 ± 155.4	41.57	11.7	651.2 ± 126.1	42.78	13.0	34.6 ± 29.6	8.92	2.7
Deadwood	278.1 ± 43.3	13.31	3.8	87.9 ± 16.9	5.78	1.8	39.1 ± 33.2	10.08	3.1
Subtotal	1379.2 ± 212.5	65.99	18.6	1075.4 ± 184.9	70.64	21.5	131.0 ± 97.4	33.76	10.4
Roots	216.5 ± 50.8	10.35	2.9	83.0 ± 37.0	5.45	1.7	17.7 ± 13.1	4.56	1.4
Shrub total	1595.7 ± 240.0	76.34	21.5	1158.3 ± 206.4	76.09	23.2	148.7 ± 93.5	38.32	11.8
Understory	35.3 ± 6.5	1.69	0.5	44.6 ± 12.7	2.93	0.9	6.1 ± 4.6	1.57	0.5
Litter									
Shrub	180.5 ± 42.9	8.63	2.5	54.6 ± 18.6	3.59	1.1	12.6 ± 6.4	3.25	1.0
Understory	47.0 ± 9.0	2.25	0.6	46.5 ± 12.5	3.05	0.9	23.3 ± 20.9	5.98	1.8
Subtotal	227.5 ± 44.5	10.88	3.1	101.1 ± 26.9	6.64	2.0	35.9 ± 24.2	9.25	2.8
Soil	5547.6 ± 246.5	265.42	74.9	3696.0 ± 541.4	242.81	73.9	1073.4 ± 653.2	276.65	84.9
Soil-plant system	7406.0 ± 1002.5	354.33	100.0	5000.0 ± 766.7	328.47	100.0	1264.1 ± 1145.1	325.80	100.0

[1]Sample mean ± standard error

mesquite and palo verde. Higher amounts of root N in velvet mesquite offset slightly higher amounts of N in aboveground components of palo verde (Table 2) so that total shrub N(g/m²) for velvet mesquite and palo verde was similar and about double that for honey mesquite. Garcia- Moya and McKell (1970) observed standing crop N amounts (10.5 and 18.4 g/m²) for *Acacia greggi* and *Larrea divaricata* that were much lower than for the shrubs we studied. About 22% of the N in velvet mesquite and palo verde systems was located in the shrub standing crop, while only about 12% of the N in honey mesquite systems was located in the shrub (Table 2).

Amount of litter N per unit area was 30 to 40% greater in the two mesquite systems (10.9 and 9.2 g/m²) than in the palo verde system (6.6 g/m²). Velvet mesquite litter was mostly leaves that were high in percentage N (Barth and Klemmedson 1978); that for honey mesquite was mostly from understory species and although abundant (Table 1), was low in N. Palo verde litter was high in bark and was neither abundant (Table 1) nor high in N (Barth and Klemmedson 1978).

Although the amount of soil N was similar for each of the three systems (243 to 277 g/m²), its contribution to total system N differed among species. Soil N as a percentage of total N was the same for velvet mesquite and palo verde (about 74.5%) or about 10% less than that for the honey mesquite system (85%). However, honey mesquite shrubs were considerably smaller than the two other shrubs and because soil N as a percentage of total N (Y) declines significantly with shrub size (X), it appears that less N is distributed to soil in honey mesquite systems than in velvet mesquite and palo verde systems. Thus, for the latter shrubs of the same height as the average honey mesquite (1.43 m), we calculate[1] that about 90% of system N would be found in the soil component.

On a weight per unit area basis there was little difference in total N in the three soil-plant systems (Table 2); the velvet mesquite system contained about 8% more N/m² than the other two systems, probably a nonsignificant difference.

Organic Carbon

Because C percentage of a given plant part varies little among species, the relative differences in total C per shrub and per unit area (Table 4) among species for any component was similar to that observed for dry matter (Table 1). However, percentage distribution of C among components is distinctly different from that for dry matter and the two parameters are not readily comparable. Organic C is distributed in all components of the soil-plant system whereas dry matter exists only in the standing crop and litter components.

Overall, percentage distribution of C between components was quite similar for velvet mesquite and palo verde: the greatest relative differences between species were for roots (6.5 vs. 4.7%), understory (1.1 vs. 2.4%), and litter (5.2 vs. 3.7%), respectively. The percentage of total C in the standing shrub and in soil was nearly identical for velvet mesquite and palo verde. But, comparison of C in these two systems with that for honey mesquite is striking. Although honey mesquite systems contained only half as much C per unit area in the standing crop plus litter as velvet mesquite and palo verde systems, they contained 173% more C in the soil and 45% more C for the total system on a unit area basis. Thus, whereas C was about equally distributed between the aboveground shrub components and soil in velvet mesquite and palo verde systems (Table 4), 80% of C in honey mesquite systems was soil C with only 14.1% in the aboveground shrub. In a separate paper, Barth and Klemmedson (1978) show that percentage C was high for every soil

Table 3. Percentage nitrogen of the standing crop of velvet mesquite, palo verde, and honey mesquite soil-plant systems.[1]

Component	Velvet mesquite	Palo verde	Honey mesquite
Leaves[2]	2.95	3.89	3.03
Flowers	3.81	3.59	—
Fruit	2.32	2.84	3.08
Current growth	2.01	2.61	1.56
Branches < 1 cm	1.51	1.58	1.40
Branches > 1 cm	1.13	1.12	1.29
Deadwood	1.01	0.93	1.35
Roots	1.55	1.17	1.64

[1]Nitrogen percentages for understory, litter, and soil components are found in Barth and Klemmedson (1978).

[2]Of the components in this table, only leaves differed significantly in N percentage between velvet mesquite and palo verde. Honey mesquite was not included in these tests.

[1]For velvet mesquite and palo verde, respectively: $Y=99.3-6.1X$ and $Y=97.2-6.0X$ ($r = 0.80$ and 0.86).

Table 4. Amount and distribution of carbon in soil-plant systems of average size for three desert shrubs.

	Velvet Mesquite			Palo Verde			Honey Mesquite		
Component	kg/shrub	kg/m²	%	kg/shrub	kg/m²	%	kg/shrub	kg/m²	%
Standing Crop									
Shrub									
Shoot									
Leaves	1.37 ± 0.23[1]	0.066	1.3	0.08 ± 0.03	0.005	0.1	0.33 ± 0.22	0.085	1.2
Flowers	0.2 ± 0.01	0.001	<0.1	0.05 ± 0.03	0.003	0.1	0.00 ± 0.00	0.000	0.0
Fruit	0.02 ± 0.01	0.001	<0.1	0.02 ± 0.02	0.001	<0.1	0.08	0.021	0.3
Current twigs	0.12 ± 0.02	0.005	0.1	0.71 ± 0.20	0.047	1.0	0.11 ± 0.06	0.028	0.4
Small branches	3.56 ± 0.45	0.171	3.3	7.18 ± 1.02	0.472	9.6	0.84 ± 0.47	0.216	2.9
Large branches	32.44 ± 5.48	1.552	29.5	23.35 ± 4.27	1.534	31.2	1.35 ± 1.20	0.348	4.7
Deadwood	10.97 ± 16.50	0.525	10.0	3.82 ± 0.82	0.251	5.1	1.32 ± 1.17	0.340	4.6
Subtotal	48.50 ± 7.23	2.321	44.2	35.21 ± 5.96	2.313	47.1	4.03 ± 3.16	1.039	14.1
Roots	7.15 ± 1.69	0.342	6.5	3.48 ± 1.57	0.229	4.7	0.47 ± 0.34	0.121	1.6
Shrub total	55.65 ± 8.06	2.663	50.7	38.69 ± 7.06	2.542	51.8	4.50 ± 3.04	1.160	15.7
Understory	1.26 ± 2.36	0.060	1.1	1.82 ± 0.58	0.120	2.4	0.11 ± 0.08	0.028	0.4
Litter									
Shrub	4.44 ± 1.07	0.213	4.1	1.52 ± 0.53	0.100	2.0	0.24 ± 0.12	0.062	0.8
Understory	1.24 ± 0.21	0.059	1.1	1.26 ± 0.33	0.083	1.7	0.95 ± 0.87	0.245	3.3
Subtotal	5.68 ± 1.22	0.272	5.2	2.78 ± 0.71	0.183	3.7	1.19 ± 0.92	0.307	4.1
Soil	47.26 6.64	2.261	43.0	31.43 5.12	2.064	42.1	22.90 17.02	5.902	79.8
Soil-plant system	109.85 15.39	5.256	100.0	74.72 12.76	4.909	100.0	28.70 21.04	7.397	100.0

[1]Sample mean ± standard error

layer and canopy position sampled under honey mesquite. Parent materials for this Fluvent soil and biotic effects, including the shrubs influence on aeolian deposition of plant debris and soil, are thought to be the primary contributing causes for the high C in this soil.

Effect of Shrub Size

How do dry matter and amount of nutrients in various shrub components vary with shrub size? The answers to this question are useful in understanding how these constituents accumulate with shrub growth and for estimating dry matter, N or C of particular components, or entire soil-plant systems on an areal basis. For example, we may want to estimate the fuel wood reserves on a tract of desert grassland invaded by mesquite, or estimate the amount of N tied up in shrubby vegetation on such a tract.

Data for the 34 velvet mesquite and 24 palo verde shrubs were graphed and simple linear and multiple regression equations were calculated for all components described in Table 1 (except flowers and fruit) using dry matter, N and C as the dependent variables, and height, average crown diameter and crown area[2] as independent variables. Because of curvilinear functions and a tendency for variance to increase with shrub size, equations with the natural logarithm (ln) of dry matter, N and C also were used as Y variables. Thus, six simple linear equations were calculated for each component.

Dry Matter

For velvet mesquite, each simple regression attempted gave a regression coefficient significant at the $p<0.01$ level for all components except shrub roots. Only the best equations (highest r^2) for selected components are shown in Table 5. Regression coefficients for estimating root dry matter with height or average crown diameter were significant at $p<0.05$, while that estimated with crown area was nonsignificant. Limitations of root sampling were discussed earlier. Equations for leaves, current twigs, and understory accounted for 25 to 60% variation about regression, while those for litter accounted for 40 to 80% of variation. Equations for dry matter of perennial components of the shrub, and for shrub shoot, shrub shoot and root, and standing crop and litter accounted for 50 to 90% of total variation. For velvet mesquite, ln dry matter = f (height) was the best overall simple regression (Table 5). Of the six equations attempted, ln dry matter as a function of height gave the highest r^2 values for all components except understory litter and total litter. Coefficients of variation for regression (CV_b) were all less than 10.0% (Table 5).

Multiple regression improved estimation of dry matter; for ln dry matter equations, coefficients of determination were up to 0.20 units higher than those for the best simple regression equations (Tables 5 and 6).

Choice of the best simple regression equation was less obvious for palo verde and, probably because of leaf scarcity and the difficulty in discerning current growth, no equation gave satisfactory estimates for leaves and current twigs. Otherwise, regression coefficients for all equations and components were significant, mostly at the $p<0.01$ level. Weight of shrub root, understory and litter were estimated with less precision than were perennial shrub components and component categories representing a grouping of other components (i.e. shrub shoot, shrub shoot and root, standing crop and litter). The equation dry matter = f (crown area) was most satisfactory for aboveground shrub components (except deadwood), shrub shoot and root, and standing crop and litter (Table 5) while ln dry matter = f (average crown diameter) was most satisfactory for estimating deadwood, roots, understory, and litter. Multiple regression gave improved estimates of dry matter for palo verde (Tables 5 and 6) and ln dry matter was the best dependent variable based on R^2 values. The best simple regression equations for selected components of palo verde (Table 5) show that average crown diameter, rather than shrub height was the key independent variable.

Nitrogen

For velvet mesquite the equation ln N = f (height) estimated amount of N with a higher r^2 than the other five simple regression equations for 10 of 13 components (Table 5). N = f (crown area) was somewhat better for estimating N in leaves and ln N = f (average crown diameter) was slightly better for N in understory litter and total litter. Except for root N ($r^2 = 0.47$), N in all components was estimated with coefficients significant at $p<0.01$ and $r^2>0.60$.

For palo verde, simple regression equations with highly significant regression coefficients ($p<0.01$) were obtained for every component except leaves and current twigs. Any one form of equation

[1]Calculated as a circle or ellipse, depending on relative magnitude of the two crown diameter measurements.

Table 5. Best simple regression equations, based on r^2 values, for estimating dry matter, nitrogen and carbon for selected components of mesquite and palo verde ecosystems.

Component	Velvet mesquite			Palo verde		
	Equation	r^2	CV_b[1]	Equation	r^2	CV_b
			Dry Matter (kg/shrub)			
Small branches	Ln DM = -2.007 + 1.059 H[2]	0.830	8.0	DM = 0.726 + 1.074 A	0.889	7.5
Large branches	Ln DM = -3.244 + 1.899 H	0.845	7.6	DM = -13.98 + 4.489 A	0.944	5.2
Deadwood	Ln DM = -3.334 + 1.662 H	0.770	9.7	Ln DM = -2.339 + 0.935 D	0.760	12.0
Shrub shoot	Ln DM = -1.494 + 1.577 H	0.868	6.9	DM = -13.66 + 6.341 A	0.944	5.2
Shrub shoot and root	Ln DM = -1.131 + 1.520 H	0.867	6.9	DM = -19.06 + 7.218 A	0.880	7.9
Standing crop and litter	Ln DM = -0.740 + 1.454 H	0.887	6.3	DM = -22.57 + 8.258 A	0.914	6.5
			Nitrogen (g/shrub)			
Small branches	Ln N = 0.526 + 1.107 H	0.837	7.8	N = -8.539 + 19.31 A	0.914	9.3
Large branches	Ln N =-1.884 + 2.166 H	0.788	9.2	N =-214.1 + 56.84 A	0.926	6.0
Deadwood	Ln N =-1.760 + 1.852 H	0.748	10.3	Ln N = - 1.742 + 1.658 H	0.760	12.0
Shrub shoot	Ln N = 1.128 + 1.544 H	0.886	6.3	N = -212.8 + 84.63 A	0.954	4.7
Shrub shoot and root	Ln N = 1.499 + 1.489 H	0.879	6.5	N = -265.2 + 93.52 A	0.935	5.6
Standing crop and litter	Ln N = 1.783 + 1.455 H	0.895	6.1	N = -310.7 = 106.1 A	0.944	5.2
Soil	Ln N = 5.110 + 0.628 D	0.894	6.1	N = -40.90 + 245.5 A	0.936	5.6
Soil-plant system	Ln N = 5.187 = 0.663 D	0.891	6.2	N = -351.6 + 351.6 A	0.957	4.5
			Carbon (g/shrub)			
Small branches	Ln C = 4.012 + 1.071 H	0.828	8.1	C = 293.6 + 452.6 A	0.890	7.5
Large branches	C = -7895 + 1930 A	0.769	9.7	C = -6199 + 1941 A	0.942	5.3
Deadwood	Ln C = 2.073 + 1.820 H	0.735	10.6	Ln C = 2.198 + 1.608 H	0.750	12.3
Shrub shoot	Ln C = 4.557 + 1.578 H	0.866	7.0	C = -6078 + 2713 A	0.941	5.3
Shrub shoot and root	Ln C = 4.938 + 1.518 H	0.864	7.0	C = -8402 + 3094 A	0.875	8.1
Standing crop and litter	Ln C = 5.323 + 1.451 H	0.884	6.4	C = -9458 + 3465 A	0.902	7.0
Soil	Ln C = 7.192 + 0.636 D	0.892	6.1	Ln C = 7.255 + 0.655 D	0.876	8.0
Soil-plant system	Ln C = 6.973 + 1.187 H	0.883	6.4	C = -11959 + 5694 A	0.906	6.9

[1]CV_b = Coefficient of variation for regression
[2]DM = dry matter; H = shrub height (m); D = average crown diameter; A = crown area (m^2)

Table 6. "Best equations," based on R^2 values, for estimating dry matter, nitrogen and carbon for selected components of mesquite and palo verde soil-plant systems.

Component	Velvet mesquite			Palo verde		
	Equation	R^2	CV_b[1]	Equation	R^2	CV_b
			Dry matter (Kg/shrub)			
Small branches	Ln B = -3.084 + 0.218 H + 1.347 D -0.120 A[2]	0.934	25.8	Ln B = -3.735 + 0.632 H - 0.231 A + 1.835 D	0.952	15.8
Large branches	Ln B = -5.420 + 0.585 H + 2.420 D - 0.235 A	0.951	19.6	Ln B = -3.710 + 2.274 D - 0.253 A + 0.462 H	0.981	8.6
Deadwood	Ln B = -5.962 + 0.348 H + 2.710 D - 0.280 A	0.934	29.2	Ln B = -5.156 + 0.427 H + 2.254 D - 0.260 A	0.909	39.6
Shrub shoot	Ln B = -3.196 + 0.493 H + 1.937 D - 0.185 A	0.969	10.5	Ln B = -2.331 + 1.979 D - 0.219 A + 0.416 H	0.984	5.9
Shrub shoot and root	Ln B = -2.824 + 0.479 H + 1.898 D - 0.184 A	0.971	9.3	Ln B = -2.284 + 1.991 D - 0.217 A + 0.394 H	0.981	6.4
Standing crop and litter	Ln B = -2.153 + 0.500 H + 1.650 D - 0.155 A	0.975	7.9	Ln B + -1.784 + 1.791 D - 0.193 A + 0.431 H	0.978	6.3
			Nitrogen (g/shrub)			
Small branches	Ln N = -0.471 + 0.357 H + 1.224 D - 0.110 A	0.916	11.0	Ln N = -1.634 + 0.683 H - 0.258 A + 2.048 D	0.934	9.5
Large branches	Ln N = -4.857 + 0.745 H + 3.015 D - 0.315 A	0.912	18.0	Ln N = -1.619 + 2.364 D - 0.256 A + 0.454 H	0.980	5.4
Deadwood	Ln N = -4.772 + 0.506 H - 0.318 A + 2.981 D	0.908	19.5	Ln N = -3.639 + 0.617 H + 2.359 D - 0.285 A	0.901	18.0
Shrub shoot	Ln N = -0.437 + 0.681 H + 1.676 D - 0.168 A	0.968	6.2	Ln N = 0.140 + 1.972 D - 0.215 A + 0.426 H	0.982	3.9
Shrub shoot and root	Ln N = -0.105 + 0.649 H + 1.684 D - 0.171 A	0.968	5.8	Ln N = 0.189 + 1.980 D - 0.213 A + 0.406 H	0.980	4.1
Standing crop and litter	Ln N = 0.405 + 0.637 H + 1.521 D - 0.149 A	0.971	5.3	Ln N = 0.544 + 1.864 D - 0.199 A + 0.420 H	0.985	3.3
Soil	Ln N = 3.852 + 1.371 D - 0.109 A	0.978	2.6	Ln N = 3.668 + 1.301 D - 0.135 A + 0.275 H	0.971	2.7
Soil-plant system	Ln N = 3.794 + 1.361 D - 0.113 A + 0.132 H	0.982	2.4	Ln N = 3.670 + 1.369 D - 0.140 A + 0.292 H	0.980	2.3
			Carbon (g/shrub)			
Small branches	Ln C = 2.907 + 0.218 H + 1.374 D - 0.123 A	0.933	5.3	Ln C = 2.241 + 0.661 H - 0.233 A + 1.834 D	0.949	4.6
Large branches	Ln C = -2.281 + 0.574 H + 3.565 D - 0.366 A	0.852	15.7	Ln C = 2.315 + 0.491 H + 2.257 D - 0.253 A	0.980	3.0
Deadwood	Ln C = -1.039 + 0.327 H + 3.159 D - 0.330 A	0.914	10.1	Ln C = 0.356 + 0.540 H + 2.350 D - 0.281 A	0.896	8.9
Shrub shoot	Ln C = 2.845 + 0.477 H + 1.958 D - 0.186 A	0.968	4.1	Ln C = 3.741 + 1.951 D - 0.216 A + 0.431 H	0.984	2.3
Shrub shoot and root	Ln C = 3.228 = 0.463 H + 1.920 D - 0.185 A	0.970	3.7	Ln C = 3.788 + 1.967 D - 0.214 A + 0.406 H	0.980	2.5
Standing crop and litter	Ln C = 3.981 + 0.486 H + 1.671 D - 0.157 A	0.974	3.3	Ln C = 4.264 + 1.789 D - 0.193 A + 0.430 H	0.979	2.5
Soil	Ln C = 5.939 + 1.377 D - 0.108 A	0.973	2.3	Ln C = 5.818 + 1.216 D - 0.123 A + 0.134 H	0.963	2.5
Soil-plant systems	Ln C = 5.875 + 0.256 H + 1.431 D - 0.124 A	0.984	2.0	Ln C = 5.927 + 1.462 D - 0.149 A + 0.331 H	0.980	1.9

[1]Coefficient of variation for regression.
[2]H = shrub height (m), D = average crown diameter (m), A = crown area (m^2).

was not dominantly best for estimating N in palo verde shrub systems (Table 5).

With ln N as the Y variable, multiple regression improved the precision of estimating N in most components of mesquite and palo verde systems (Tables 5 and 6). R^2 values were increased from 0.05 to 0.15 units; CV_b values also were improved (Table 6). For mesquite, the first independent variable entered was height, except when estimating N in soil or in the entire soil-plant system. For those cases, average crown diameter was the first independent variable entered. For palo verde, average crown diameter was the most important independent variable.

Organic Carbon

Results of regression analysis for C were similar to that for dry matter and N. In all components of mesquite and palo verde (except palo verde leaves and twigs) carbon could be estimated with any combination of X and Y variables attempted with significant simple regression coefficients (at $p<0.01$, except for roots). Precision of equations was highest for the perennial shrub components and those involving summation of component values, less satisfactory for shrub leaves and current twigs, understory and litter, and lowest for roots. For dry matter and N, ln C = f (height) was the most satisfactory simple regression equation for mesquite for 9 of 13 components, and r^2 and CV_b values were comparable to those for dry matter and N equations (Table 5).

No one simple regression form was most satisfactory for palo verde. Ln C = f (average crown diameter) gave the best fit for roots, understory and litter components; C = f (crown area) gave the best fit for shrub branches, shoot total, shrub total and standing crop plus litter; ln C = f (height) gave the best fit for deadwood (Table 5). Multiple regression improved the precision for predicting C in both velvet mesquite and palo verde systems over that provided by simple regression equations (Table 5 and 6).

Rate of Nitrogen and Carbon Accumulation

Many authors (Fireman and Hayward 1952, Zinke 1962, Garcia-Moya and McKell 1970, Tiedemann and Klemmedson 1973, Barth 1980) have observed that perennial plants, particularly shrubs, tend to accumulate soil nutrients beneath their canopies. This phenomenon results from the nutrient cycling process and when effective may be attributed to several processes. These include (a) absorption of nutrients by roots from beyond the crown area of the plant or from lower soil layers and substratum and eventual deposition of litter under the crown, (b) fixation of nutrients by the plant or an associated symbiotic organism, (c) net import of nutrients by fauna that use the plants for nesting, resting, roosting, or feeding, and (d) movement by wind or water. Although many researchers have noted this phenomenon, none, to our knowledge, have sought to quantify the accumulation pattern as a function of shrub size or age.

In a soil-plant system where inputs exceed outputs (i.e. net accumulation occurs), we expect the regression coefficients to be positive and significantly different from zero; in such cases the regression coefficient indicates the rate of accrual of the nutrient. The graphs and related statistics in Figure 1 portray substantial differences between velvet mesquite and palo verde regarding accumulation of N and C. Most striking is the difference in the soil component. Soil under palo verde did not accumulate N or C with increase in shrub size, whereas that under velvet mesquite accrued N at the rate of 11.2 g/m² per meter of height ($p<0.05$) and C at the rate of 0.11 kg/m² per meter of height ($p<0.05$). For the soil-plant system, C was accumulated at a highly significant ($p<0.01$) rate in both mesquite and palo verde. Rate of N accumulation in the palo verde system was only about half that of mesquite with less confidence in the estimate (Fig. 1). Average crown diameter and crown area were not as satisfactory as height as measures of N and C accumulation.

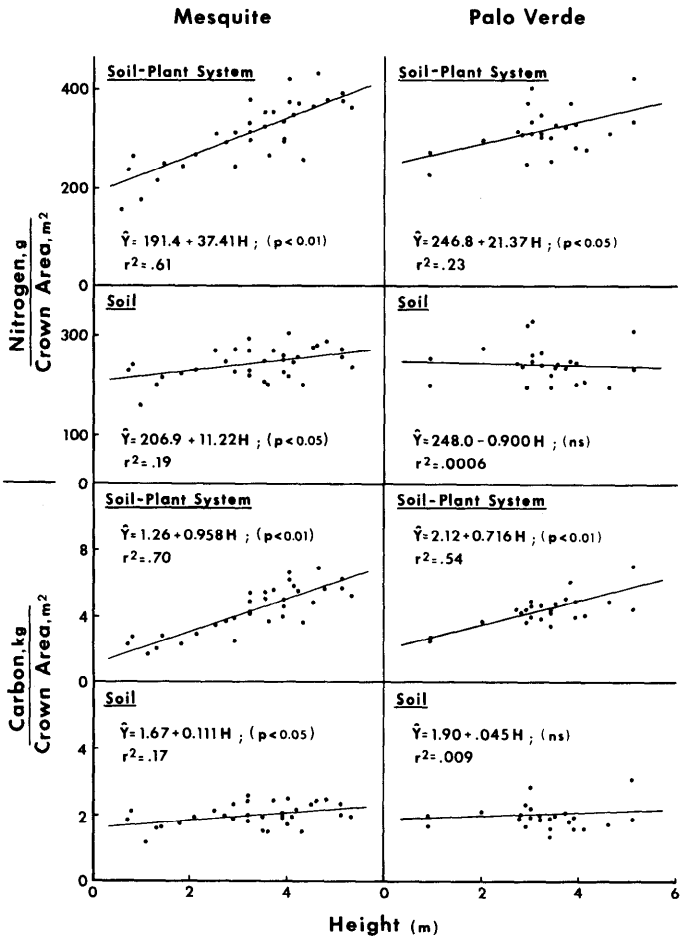

Fig. 1. *Accumulation patterns for nitrogen and carbon in the soil and the soil-plant system of velvet mesquite and palo verde shrubs as a function of height of shrub. Significance of regression coefficients is shown in parentheses following the equations.*

Discussion

Aside from academic questions on how shrubs accumulate and distribute dry matter and nutrients as they grow from seedlings and reach maturity, there are practical reasons for understanding the relationships discussed here. Mesquite has been a favored firewood for years and this use is expanding. But new uses of mesquite (Felker 1979) and other shrubs as a protein source for livestock (Bracker 1972, Thayer and Young 1973), for pulpwood (Laundrie 1958), charcoal (Durso et al. 1973), and as a potential energy substitute for fossil fuels (Wiley and Manwiller 1976) are increasing with rapidly changing economic and energy conditions in the United States. With trends toward more intensive use of shrubs and more sophisticated land management, regression relations similar to those shown here are being used to estimate dry matter on an areal basis (Whisenant and Burzlaff 1978, Meewig et al. 1979) and to predict such things as the flammability of fuels (Brown 1976, Rothermal 1972) and the export of nutrients in logging and pulpwood operations (Klemmedson 1976).

Using the regression equations discussed above, dry matter or amount of nutrient in components of the shrub system of interest can be estimated through combined use of aerial photographs and ground sampling. On a site adjacent to our study area Fish and Smith (1973) demonstrated that percentage cover of various shrubby and succulent species (including velvet mesquite and palo verde) could be inventoried with aerial photographs with good results and considerable cost savings over ground samplings. Though not included in their paper, Fish and Smith (1973) also measured shrub density by species from aerial photographs. These data used in combination with ground sampling for shrubs heights and crown dimensions would facilitate use of the regression equations discussed here to estimate dry matter or nutrient parameters of interest over extensive areas. With some sacrifice in precision, but a savings in cost, good estimates of dry matter and nutrients could be obtained solely from suitable aerial photographs. This would entail use of regression equations using only average crown diameter or crown area as independent variables. Presumably, these equations could be expanded to other nutrients or categories of dry matter required for specific needs. We have not determined the extent to which relationships determined here vary with changes in the habitat.

We have no experimental evidence to explain the contrasting patterns of N and C accumulation in velvet mesquite and palo verde in Figure 1. These functions indicate mesquite is somewhat more effective in accumulating C and considerably more effective in accumulating N than palo verde. The root absorption-litter deposition mechanism appears the most plausible explanation of these differential patterns of accumulation. Velvet mesquite is notorious for its extensive lateral and vertical root systems (Cannon 1911, Parker and Martin 1952, Phillips 1963). In the absence of information on the palo verde root system we assume it is less extensive than that of mesquite. We can hypothesize that a more extensive root system in velvet mesquite, enabling greater absorption of ammonium, nitrate, bicarbonate, and carbonate ions from outside the soil-plant system sampled could account for the differential in N and C accumulation observed.

Fixation of CO_2 via photosynthesis was undoubtedly the dominant mechanism for accumulation of C to these systems, but we have no reason or experimental evidence to expect that the photosynthetic process results in more C fixed per unit of height or crown area of mesquite than in palo verde. Fixation of N_2 was probably not a factor in accrual of N to these systems. Nodules were not found on roots of the 58 shrubs examined and researchers have not detected effective symbiotic N_2 fixation in woody legumes or nonlegumes in the Arizona desert. Although animal activities and aeolian effect may cause a net influx of nutrients to these systems, there is no evidence to substantiate this or show that the effects are differential between mesquite and palo verde.

The manner in which the two species distributed accumulated N and C within their soil-plant systems (Fig. 1) raises some interesting questions. Why were N and C accumulated in the soil component of the mesquite soil-plant system, but not in that of the palo verde system? The weight of dry matter. N and C in litter of palo verde was considerably less than that in mesquite; it also differed by component composition (Tables 1, 2, and 4). Is the production of litter in the palo verde system at a level where inputs just balance outputs, thus maintaining a steady-state of C and N in the soil component? Or is some other factor(s) responsible for maintenance of steady-state conditions in soil under the palo verde? These questions must remain unanswered here and await the results of further studies for possible answer.

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