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**1974 PROGRESS REPORT
[FINAL]**

**DISTRIBUTION AND BALANCE OF BIOMASS AND
NUTRIENTS IN DESERT SHRUB ECOSYSTEMS**

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ABSTRACT

The spatial distribution of nitrogen and carbon was studied in ecosystems of mesquite (*Prosopis velutina*) and paloverde (*Cercidium floridum*) in the Sonoran Desert, 35 km south of Tucson, Arizona. The weight of all ecosystem components was determined and samples collected for total nitrogen and organic analysis. Soil is the dominant nitrogen reservoir for these shrub ecosystems. Over 77% of ecosystem nitrogen was found in the soil; 20% was in shrub biomass; the remainder was in understory vegetation and litter. Carbon was almost equally distributed between soil and biomass. Total ecosystem nitrogen averaged 319 g/m² and carbon averaged 4.5 kg/m². Total nitrogen and carbon in the ecosystem can be predicted with reasonable reliability using linear regression equations with shrub biomass and shrub height as independent variables. Total biomass for both shrub ecosystems was similar and averaged 5.8 kg/m². Linear regression equations relating total ecosystem biomass and shrub height had r² values of 0.7. Paloverde and mesquite shrubs form a center from which properties change in a more or less consistent manner with distance, depending on the ecosystem component. From shrub center to beyond the canopy edge soil nitrogen declined by 50% at the surface and by lesser amounts with depth. Carbon displayed similar trends. Standing understory vegetation and shrub litter for both shrub species decreased as distance from the center of shrubs increased. Vertical gradients for soil carbon and nitrogen were abrupt with little change below the 5- to 15-cm layer.

Seasonal and annual changes in percentage nitrogen and carbon were found for many ecosystem components. Seasonal change in nitrogen of leaves, current growth and branches appeared to be associated with translocation, leaching by precipitation and senescence. Annual nitrogen changes in leaves, flowers, current growth and branches were associated with fluctuations in precipitation which presumably relieved water and nitrogen stresses in the shrubs. Changes in nitrogen of understory vegetation on a seasonal and annual basis appeared to be associated with variations in species composition and nitrogen availability. Cyclic trends detected in the nitrogen and carbon content of mesquite litter and in soil pH relate to phenologic and climatic events.

Limited sampling of honey mesquite (*Prosopis glandulosa*) in the Chihuahuan Desert near Las Cruces, New Mexico, disclosed spatial distribution patterns of biomass and nitrogen very similar to those found in the Sonoran Desert. Carbon distribution was irregular and apparently caused by the young stratified soils found in the study area.

INTRODUCTION

Studies on the spatial distribution of biomass and nutrients provide insight on the relative importance of various ecosystem components and allow first approximations on the flow of nutrients. Over the course of three years, the soil-plant systems of mesquite and paloverde have been sampled at the Santa Rita Experimental Range to identify distributional patterns of nitrogen (N) and carbon (C) and to see if these patterns change seasonally or annually in response to environmental factors. Interim results have been reported earlier (Klemmedson 1974, Klemmedson and Smith 1973).

Studies on spatial distribution of biomass and nutrients in arid areas are limited. Garcia-Moya and McKell (1970) studied a number of species in the Mohave Desert and Moore et al. (1967) investigated *Acacia harpophylla* in Australia. Bjerregaard (1971) and Fireman and Hayward (1952) studied cool desert species. Root and stem tissue generally have low amounts of N; leaves, fruit and flowers vary considerably but all have a higher N concentration than roots and stems. Garcia-Moya and McKell (1970) averaged data from 13 different desert shrubs and found the following mean N percentages: roots 0.8%, stems 0.9% and leaves 1.3% N. In desert zones of Russia, N content of shrub leaves ranged from 1.74 to 4.29% and averaged 2.61%; above-ground perennial parts averaged 1.23% N, and roots had an average value of 1.38% N (Rodin and Bazilevich 1967).

Quantitative information on the spatial distribution of litter is sparse. Holmgren and Brewster (1972) and Tiedemann (1970) found litter weight decreased as distance from desert shrubs increased. Zinke (1962) relates differences in soil properties to variations in the amount and composition of the litter.

Spatial distribution of understory vegetation has received some attention in recent years. Clary and Morrison (1973), Kline and McKell (1974), Muller (1953), Martin (1964), Patten and Smith (1974) and Tiedemann and Klemmedson (1973a, 1973b) have observed greater herbaceous density under the canopy of desert shrubs than in adjacent open areas. Tiedemann and Klemmedson (1973a) relate this increased herbaceous density to more favorable chemical and physical properties under the canopy of shrubs.

Garcia-Moya and McKell (1970), among others, have described shrub-induced patterns in soil N; surface soil N decreased significantly as a function of the lateral distance away from the center of shrubs. Under *Acacia greggii* the soil N content was 0.054% at the base of the shrub, 0.021% at the edge of the crown and 0.020% at a distance of two radii from the stem.

Frankland et al. (1963) found the understory vegetation of oak ecosystems in England was characterized by irregular fluctuations during the year but that biomass increased

during the summer growing season. Weight of litter increased slightly during the fall in response to leaf fall. Ovington et al. (1963) reported weight in both herbaceous and shrub layers of ecosystems sampled in Minnesota increased from April to September then decreased from October to March. Roots and litter did not change in weight during the year.

Miller (1963) and McHargue and Roy (1933) agreed that N is very high in young leaf tissue and decreases with leaf age. Tamm (1951) observed a rapid decrease in leaf N soon after emergence, a steady content from July to October, and then a gradual decrease. The N content just prior to leaf fall represented a five-fold decrease from the value at initial leaf development. Protein hydrolysis and translocation of breakdown products are primary causes for the decrease in leaf N with age (McKee 1962).

During a one-year period, Frankland et al. (1963) noted N in understory vegetation changed little during the year but litter N was at a minimum during the winter and reached a maximum in October. The fall maximum may reflect an increase in litter N during initial breakdown by microorganisms. Bock (1963) has observed this N enrichment and attributes it to N accrual from several environmental sources. In a similar study, Tarrant et al. (1969) showed seasonal variations in percentage N of litterfall. For deciduous species, the N content was highest in the spring and fall and lowest in the winter; coniferous species displayed lowest leaf N in the summer and highest in the spring. Cyclic migration of N within trees appears to be responsible for this observation. Tarrant also noted differences between years; this was attributed to slight shifts in the physical composition of litterfall caused by wind intensity and temperatures.

OBJECTIVES

The objectives of this study were to measure the distribution and balance of biomass carbon and nitrogen in the regime of important desert shrub ecosystems, specifically mesquite (*Prosopis velutina*) and paloverde (*Cercidium floridum*).

Specific objectives are to:

1. Determine the influence of shrub age on distribution of biomass, and on distribution and balance of carbon and nitrogen in individual shrub ecosystems.
2. Measure seasonal changes in biomass, and in distribution and balance of carbon and nitrogen in individual shrub ecosystems.
3. Determine the effect of macroenvironmental factors (precipitation, temperature, radiation), which vary yearly, on increment of biomass and nutrient distribution.

METHODS

Field studies were conducted on a 32-ha site at the Santa Rita Experimental Range, 35 km south of Tucson, Arizona.

Recorded use of the study site began in 1915 when domestic livestock in moderate numbers grazed the area yearlong. From 1957 to the present, grazing has been confined to the May-October period.

The study site is part of an alluvial fan with a slope less than 5% and a northwest aspect. Numerous arroyo channels and small shallow washes dissect the fan. Elevation is 975 m. Sonoita and Anthony Series are the dominant soils in the study area. The Sonoita is found on upland sites while Anthony is generally limited to arroyos and adjacent areas of recent mixed alluvial deposits. Sampling for the study was confined to the Sonoita Series, a loamy mixed, thermic typic haplargid formed on moderately coarse-textured alluvium. The ochric epipedon is sandy loam in texture and up to 13 cm deep; the sandy loam argillic horizon extends to a depth of 71 cm (USDA Soil Conservation Service 1970).

Mesquite is the dominant shrub on both the upland site and along arroyos. On the latter site mesquite is tree-like with a well-defined trunk; it commonly reaches a height of 12 m. On upland sites mesquite averages about 3 m high, has from one to three main stems and is more shrub-like. Cannon (1911) found this leguminous shrub characteristically develops a strong taproot in addition to an extensive lateral system. The lateral spread may be 15 m or more and the taproot commonly extends to a depth of 15 m (Little 1950).

Paloverde, the other dominant in the area, is more abundant along arroyos than on upland sites. This legume has smooth green bark and small leaves that are shed during dry periods. Although it may attain a height of 8 m, individuals on upland sites are generally smaller and shrub-like. The root system is similar to that of mesquite although not as extensive. Numerous other shrubs, cacti and herbaceous species comprise the remainder of the vegetation.

At Tucson (elev. 675 m) the mean July temperature is 30.0 C; the mean January temperature is 10.1 C. Diurnal temperature variation averages 17 C. The dry atmosphere and generally clear skies permit intense surface heating during the day and active radiational cooling at night. Average annual precipitation for the study area is 33.5 cm. Approximately 50% of this falls between July 1 and September 15 as intense convective thunderstorms; another wet period occurs from December through March when more prolonged rainstorms provide over 20% of the yearly total. Relative humidity is low and surface winds are usually light with no important seasonal changes in velocity or direction.

FIELD METHODS

The sampling schedule with number and species of shrubs sampled is shown in Table 1. Paloverde was added as a second species in 1972 at the request of the Biome Director.

After a shrub was randomly selected from a pool of 50 plants, its height, diameter and basal area were measured (DSCODE A3UKB01). Plots (.093 m²) were located on a north-south line running through the center of the shrub at

the following points: 1) at 1/3, 2/3 and 3/3 the north and south canopy radii (CR); and 2) at 4/3 the north and south canopy radii, but at least 1 m beyond the edge of the crown. At each of the above points, live and dead standing understory vegetation was harvested within the plot (A3UKB04). Litter was also collected from each plot (A3UKB05). Material collected from north and south plots at the same canopy position was combined into one sample, thus making the sample .186 m² in area.

Shrubs were harvested to ground level and separated into leaves, flowers, fruit, current growth (woody growth less than one year old), branches less than 1 cm in diameter, branches greater than 1 cm in diameter and deadwood. Branches and deadwood were weighed to the nearest 0.5 kg; other components were weighed to the nearest gram. Random samples were taken of all shrub components (A3UKB02).

Soil columns were collected from each of the vegetation plot locations and at the center of the shrub. Surface dimensions of the columns were 8 x 10 cm; the columns were separated into four depths: 0-5, 5-15, 15-30 and 30-60 cm. All soil (A3UKB09), rocks and shrub roots (A3UKB03) in the column were removed; samples taken at the same depth and crown position were combined into one sample.

The shrub with its above- and below-ground components, the understory vegetation, litter and soil to a depth of 60 cm was defined as a shrub ecosystem.

LABORATORY METHODS

The understory vegetation was separated into live and dead herbs, shrubs and succulents. Litter was separated into that from the overstory shrub (shrub litter) and that from the understory vegetation (understory litter). All organic samples were oven-dried at 70 C, weighed and ground in a Wiley mill to pass a 40-mesh sieve.

Soil samples were passed through a 2-m sieve; soil passing the sieve was corrected for fine earth adhering to the coarse fraction. During the sieving process roots were removed from the soil and handled in the same manner as other organic samples (A3UKB03). Samples of fine earth for laboratory analysis were ground in a Spex Mixer/Mill to pass a 100-mesh sieve.

Analyses for total nitrogen by the Kjeldahl method (Bremner 1965) and for organic carbon by the dry combustion method (Allison et al. 1965) using a LECO high-frequency induction furnace, were run on above-ground biomass (A3UKB06), understory species (A3UKB07), litter (A3UKB08) and soil (A3UKB09).

For purposes of comparing properties of the shrub ecosystems with that of the adjacent nonshrub system, data from the 0/3-3/3 positions were used to represent the shrub system, while those from the 4/3 position were used to represent the adjacent ecosystem. The area involved for these estimates was determined by calculating the area of

Table 1. Sampling dates, number of shrubs and species sampled during the study period (A3UKB01-09)

Date	No. Shrubs of Each Species Sampled	Species
May 1971	5	Mesquite
Sept.-Oct. 1971	5	"
Feb. 1972	5	" and Palo Verde
April-May 1972	5	"
Sept.-Oct. 1972	5	"
Jan. 1973	3	"
May 1973	3	"
Sept. 1973	3	"

Table 2. Distribution of shrub biomass in ecosystems of average size mesquite and paloverde shrubs (A3UKB02-03)

Component	Mesquite Ecosystem		Palo Verde Ecosystem	
	kg/m ²	%	kg/m ²	%
Leaves	.142	2.8	.016	0.3
Flowers	.002	----	.007	0.1
Fruit	.003	0.1	.004	0.1
Current Growth	.014	0.3	.123	2.4
Branches < 1 cm	.374	7.5	1.065	21.2
Branches > 1 cm	2.725	54.4	2.914	58.0
Deadwood	1.072	21.4	.539	10.7
Roots	.680	13.6	.360	7.2
Total	5.012		5.028	

concentric rings represented by each of the plot locations. Each sample was multiplied by the area of the ring in which it occurred. The area of the adjacent ecosystem was set equal to the total area of the shrub ecosystem.

RESULTS AND DISCUSSION

DISTRIBUTION OF BIOMASS

Shrub Biomass

Mesquite averaged 3.3 m in height and 21.2 m² in canopy projection; paloverde averaged 3.5 m in height and 15.1 m² in canopy projection. The two shrub species were almost identical in total biomass (Table 2) and averaged slightly over 6 kg oven dry. Over half of this biomass was in large branches and bole material. For mesquite, deadwood made up the next largest portion of biomass and apparently accumulates on the shrub over time. Insects seem to play a significant role in branch mortality. Paloverde is relatively free of insect pests and deadwood was only half of that found on mesquite. Small branches and current growth account for much more biomass in paloverde than in mesquite. In light of low leaf biomass on paloverde, it appears the small green branches carry on a substantial portion of the photosynthesis (Peattie 1953). Root biomass was similar for both species. However, root data should be interpreted with caution because of the small plot size and depth of sampling.

Table 3. Spatial distribution of understory biomass (A3UKB04)

Understory Component	Canopy Position			
	1/3 CR	2/3 CR	3/3 CR	4/3 CR
	g/m ²			
	Mesquite			
All Species	221.2 ^{a*}	141.0 ^{ab}	127.0 ^{ab}	70.0 ^b
Herbaceous Species	138.9 ^a	83.4 ^{ab}	44.1 ^b	43.1 ^b
	Palo Verde			
All Species	234.9 ^{ab}	359.4 ^a	144.8 ^b	127.0 ^b
Herbaceous Species	154.0 ^a	133.9 ^a	59.8 ^b	28.2 ^b

*Within any given row, figures that lack one or more common letters are significantly different at the 95% level.

Table 4. Seasonal changes in understory biomass (A3UKB04)

Understory Component	Season		
	Spring	Fall	Winter
	g/m ²		
	Mesquite		
All Species	147.5 ^{a*}	118.9 ^a	161.5 ^a
Herbaceous Species	44.1 ^a	73.2 ^{ab}	138.9 ^b
	Palo Verde		
All Species	307.7 ^a	187.6 ^a	154.3 ^a
Herbaceous Species	56.7 ^a	105.1 ^a	120.1 ^a

*Within any given row, figures that lack one of more common letters are significantly different at the 95% level.

As size or age of shrub changes, the distribution of biomass among shrub components changes. To evaluate this, percentage distribution of shrub components was regressed against height, biomass and canopy projection of shrubs as independent variables. When site and environmental conditions are invariate, these parameters are assumed to correlate well with shrub age. Age determination was not attempted for all shrubs since it is extremely difficult for mesquite and often subject to considerable error. However, observations indicated that the oldest mesquite shrub was approximately 60 years old and the youngest shrub about 5 years old.

As mesquite shrubs increase in height, the percentage of leaves, current growth and small branches decreases while the percentage of large branches increases. A nonsignificant correlation for deadwood indicates no change in deadwood with size. Regression equations and their r^2 values for various shrub components are as follows:

		r^2
Leaves	$Y = 13.1 - 2.4x$	0.32
Current growth	$Y = 2.4 - 0.5x$	0.21
Small branches	$Y = 53.7 - 11.4x$	0.54
Large branches	$Y = 11.9 - 12.9x$	0.70

High variation, leading to low correlation coefficients, was particularly noted in small size shrubs. Regression statistics for paloverde were quite similar to those for mesquite.

Changes in biomass of shrub components occur with seasons but in most cases changes were small and nonsignificant. Flowers were present sporadically throughout the summer. Mesquite had leaves at all seasons but only a small fraction persisted until winter. Paloverde was leafless during the winter and sometimes leafless in spring and fall. According to Shreve and Wiggins (1964), paloverde leaves develop after wet periods and persist for only 6 to 10 weeks. While immature fruit were found occasionally during spring, the bulk of the fruit was collected in fall and by winter all fruit had been shed. Biomass of current growth was lowest in spring and increased throughout the summer and fall; most of this woody growth occurred during summer.

Except for mesquite fruit, annual changes in biomass of shrub components were not statistically significant. Mesquite fruit production in 1972 was significantly greater than in either 1971 or 1973. Precipitation from May to September (period of fruit production) was greater in 1972 than in either 1971 or 1973.

Understory Biomass

Biomass of all species and the herbaceous component of understory for both shrubs decreased as distance from the center of the shrub increased (Table 3). For mesquite, the 4/3 CR position had only 32% of the biomass for all species as that found at the 1/3 CR position. A similar trend held for paloverde. Other authors (Muller 1953, Tiedemann and Klemmedson 1973b) have noted increased vegetative density under the canopy of desert shrubs compared to open areas. Tiedemann and Klemmedson (1973b) associated increased herbaceous growth under shrubs with better soil conditions.

Although understory biomass of both shrubs shows no change from season to season, the herbaceous component for mesquite shrubs is significantly higher in winter than in spring (Table 4). Weight of understory herbs (live and dead) in winter is over three times that in spring and the fall value lies between the two extremes. Based on work by Martin (1964), perennial herbs attain most of their growth during the summer rainy season. A second growing period may occur in winter if sufficient precipitation is received. The high herbaceous biomass observed in winter probably reflects production for both summer and winter growing periods. Although most perennial herbaceous species are dormant during the normally dry spring, shrubs, succulents and annual herbs initiate growth in the spring, thus maintaining a rather constant understory throughout the year. While the herbaceous component of understory biomass of paloverde ecosystems shows the same seasonal pattern as mentioned for mesquite, the trend is not significant.

No significant differences were found in the annual distribution of understory biomass or in any of its components. Large fluctuations in annual precipitation compensated for dry periods. Three years is too short a time to show annual changes of this kind.

Table 5. Spatial distribution of shrub and understory litter (A3UKB05)

Component	Canopy Position			
	1/3 CR	2/3 CR	3/3 CR	4/3 CR
	g/m ²			
	Mesquite			
Mesquite litter	581.3 ^{a*}	451.0 ^a	121.1 ^b	29.1 ^b
Understory litter	160.4 ^a	161.5 ^a	116.3 ^a	155.5 ^a
	Palo Verde			
Palo Verde litter	394.6 ^a	179.9 ^b	86.8 ^{bc}	23.2 ^c
Understory litter	436.6 ^a	253.4 ^a	158.7 ^a	277.3 ^a

*Within any given row, figures that lack one of more common letters are significantly different at the 95% level.

Litter Phytomass

Shrub litter displayed a strong horizontal gradient for both species; the 4/3 CR position contains approximately 1/20 of the litter found at the 1/3 CR position (Table 5). Regression analysis shows a good relation between shrub height and weight of shrub litter at 1/3 and 2/3 CR positions with r^2 values of 0.6 for both species. The correlation drops off for 3/3 and 4/3 CR positions and is nonsignificant for paloverde. Accumulations of shrub litter at the canopy edge and beyond are dependent on wind, erosion and other agents.

Understory litter did not vary spatially under the shrubs (Table 5). This is difficult to explain since understory biomass did vary significantly. Perhaps the combined effect of differential amounts of herbage and differential rates of decomposition caused the nonsignificant trend observed.

Although the fall of leaves and fruit is definitely seasonal, the residual litter and addition of deadwood throughout the year are sufficient to mask these effects. An annual trend in litter weight was unexpected since the sources of litter showed no annual trend.

Distribution of Total Biomass in Shrub Ecosystems

In order to compare the distribution of biomass in shrub ecosystems with that in adjacent ecosystems, comparable areas were considered and data reduced to a square meter basis. Plot data for all components of the ecosystem except above-ground shrub biomass were adjusted by the proportion of the canopy area represented by the plot location; thus the 1/3 CR position, typically high in shrub mulch, makes only a relatively minor contribution (areawise) to shrub ecosystem litter. The 4/3 CR position is now termed the adjacent ecosystem.

The bulk of biomass in shrub ecosystems is in above-ground shrub biomass (Table 6). Shrub roots make up the next largest portion; understory biomass and litter combine to make up about 12% of total ecosystem biomass for both mesquite and paloverde shrubs. This distribution pattern is similar to that for a subtropical semiarid forest in Australia (Moore et al. 1967). Our estimates of root biomass,

Table 6. Distribution of total biomass in shrub ecosystems and in their adjacent ecosystems (A3UKB02-05)

Component	Mesquite Ecosystem		Adjacent Ecosystem	
	kg/m ²	%	kg/m ²	%
Aboveground Mesquite Biomass	4.33	76.0	----	----
Mesquite Roots (0-60 cm)	0.68 ^{a*}	11.9	0.10 ^b	27.8
Understory Biomass	0.16 ^a	2.8	0.07 ^b	19.4
Mesquite litter	0.38 ^a	6.7	0.03 ^b	8.3
Understory litter	0.15 ^a	2.6	0.16 ^a	44.4
Total Ecosystem Biomass	5.70 ^a	----	0.36 ^b	----

	Palo Verde Ecosystem		Adjacent Ecosystem	
	kg/m ²	%	kg/m ²	%
Aboveground Palo Verde Biomass	4.67	80.2	----	----
Palo Verde Roots (0-60 cm)	0.36 ^a	6.2	0.12 ^a	21.8
Understory Biomass	0.26 ^a	5.3	0.13 ^a	23.6
Palo Verde litter	0.21 ^a	3.6	0.02 ^b	3.6
Understory litter	0.27 ^a	4.6	0.28	50.9
Total Ecosystem Biomass	5.82 ^a	----	0.55 ^b	----

*Within any given row, biomass figures that lack one of more common letters are significantly different at the 95% level.

even for the 60-cm depth, appear low compared to the trend reported for other desert shrubs by Holmgren and Brewster (1972), Bjerregaard (1971) and Garcia-Moya and McKell (1970). Differences in species, environment, sampling methods and other factors make comparisons of root biomass difficult and tenuous at best.

When the mesquite ecosystem and its adjacent ecosystem are compared, significant differences occur in root biomass, understory biomass, shrub litter and total ecosystem biomass (Table 6). In view of the above discussion, these differences are to be expected. Based on our limited sample, root biomass in the adjacent ecosystem was only 1/7 that of the mesquite ecosystem. Paloverde ecosystems and their associated adjacent ecosystems show patterns of biomass distribution so similar to that of mesquite that they are not discussed separately.

Significant differences in total biomass between paloverde and mesquite shrub ecosystems were limited to shrub litter; weight of mesquite shrub litter was significantly higher than that of paloverde (Table 6). This follows from greater weight of leaves and deadwood in mesquite shrubs (Table 2). No differences in biomass were observed for adjacent ecosystems of the two shrub species. Regression analysis showed that total biomass of the shrub ecosystems could be predicted from shrub height with r^2 values of 0.73 and 0.70 for mesquite and paloverde, respectively. Values of r^2 for estimating biomass of individual compartments ranged from 0.28 to 0.43.

Table 7. Average nutrient concentration of shrub components sampled in the spring, fall and winter (A3UKB06)

Component	%N		%C		C:N	
	Mesquite	Palo Verde	Mesquite	Palo Verde	Mesquite	Palo Verde
	Leaves	2.95 ^{a*}	3.89 ^b	46.6 ^a	42.5 ^a	16.4 ^a
Flowers	3.81 ^a	3.59 ^a	43.8 ^a	44.3 ^a	11.9 ^a	12.7 ^a
Fruit	2.32 ^a	2.84 ^a	43.9 ^a	45.2 ^a	17.1 ^a	17.1 ^a
Current Growth	2.01 ^a	2.61 ^b	45.1 ^a	43.4 ^a	23.4 ^a	17.7 ^b
Branches < 1 cm	1.51 ^a	1.58 ^a	43.2 ^a	42.2 ^a	29.2 ^a	28.2 ^a
Branches > 1 cm	1.13 ^a	1.12 ^a	42.7 ^a	43.0 ^a	39.4 ^a	40.1 ^a
Deadwood	1.01 ^a	0.93 ^a	40.9 ^a	40.5 ^a	43.1 ^a	46.6 ^a
Roots	1.55 ^a	1.17 ^a	45.7 ^a	44.1 ^a	29.5 ^a	40.3 ^b

*For any given nutrient and within any given row, figures that lack one or more common letters are significantly different at the 95% level.

NUTRIENT CONCENTRATION IN BIOMASS AND SOIL

Shrub Biomass

Plant tissues consisting mostly of young growing cells (i.e., leaves, flowers, fruit and current growth) have the highest percentage N (Table 7). The synthesis of amino acids and proteins, which contain from 12 to 19% N (Salisbury and Ross 1969), is normally highest in young growing cells (Webster 1959). Of the living plant components, large branches are lowest in N.

Paloverde leaves contain considerably more N than mesquite leaves. During spring both shrubs have similar concentrations of leaf N, but for the remainder of the year, paloverde leaves are high and mesquite leaves relatively low in N. Since paloverde leaves are shed soon after the end of wet periods (Shreve and Wiggins 1964), N values for paloverde leaves probably reflect reduced losses through translocation during senescence and leaching by precipitation. Mesquite leaves remain attached until late winter and probably lose substantial amounts of N through senescence and leaching. Current growth is the only other shrub component showing a significant difference in N percentage between species. Presumably, the higher N content of current growth branches of paloverde is related to the capacity of paloverde stems to carry on photosynthesis (Peattie 1953). In most cases the concentration of N in mesquite and paloverde is at least two times greater than that reported for other desert trees and shrubs (Moore et al. 1967, Egunjobi 1969, Garcia-Moya and McKell 1970, Bjerregaard 1971).

Carbon concentration was less variable in shrub components than N. Young growing tissues of mesquite and paloverde had the highest C concentration; deadwood was lowest in C (Table 7). The average C percentage for all shrub components for paloverde and mesquite (42.8%) is slightly lower than a nominal value of 45% used by Olson (1970).

Table 8. Seasonal change in nutrients of mesquite shrubs (A3UKB06)

Component	Season		
	Spring	Fall	Winter
		N%	
Leaves	3.51 ^{a*}	2.82 ^b	2.25 ^c
Current Growth	2.27 ^a	1.77 ^b	2.00 ^{ab}
Branches less than 1 cm	1.36 ^a	1.52 ^b	1.74 ^c
Branches more than 1 cm	1.03 ^a	1.16 ^{ab}	1.26 ^b
Roots	1.56 ^a	1.55 ^a	1.52 ^a
		C%	
Leaves	46.7 ^a	47.3 ^a	45.3 ^b
Current Growth	44.7 ^a	45.9 ^b	44.9 ^{ab}
Branches less than 1 cm	43.3 ^a	43.3 ^a	42.9 ^a
Branches more than 1 cm	42.8 ^a	43.3 ^a	41.7 ^b
Roots	45.9 ^a	46.0 ^a	45.3 ^a
		C:N Ratio	
Leaves	13.7 ^a	16.8 ^b	20.3 ^c
Current Growth	20.4 ^a	26.6 ^b	22.9 ^{ab}
Branches less than 1 cm	32.4 ^a	28.8 ^b	24.8 ^c
Branches more than 1 cm	43.2 ^a	38.8 ^{ab}	34.1 ^b
Roots	31.1 ^a	31.0 ^a	31.9 ^a

*Within any given row, figures that lack one of more common letters are significantly different at the 95% level.

The C:N ratios for both species were low (11 to 46), especially for young, actively growing tissues. These low ratios have implications in microbial decomposition of plant material. When leaves, flowers and fruit are shed from shrubs and utilized by soil microorganisms, rapid decomposition and release of plant-available N can be expected. Decomposition of deadwood will be much slower because of the high C:N ratio.

Leaf N in both mesquite and paloverde changed significantly with seasons (Tables 8 and 9). Loss of N from leaves began sometime after the spring flush of growth and continued into winter dormancy. McKee (1962) states that protein is hydrolyzed in older leaves and the products translocated to other plant parts, thus reducing leaf N. Losses of leaf N may have occurred through leaching by precipitation (Tukey et al. 1957). The seasonal decrease of N in current growth may be partially caused by growth and maturity. In the spring, new branch tips are short, immature and growing rapidly; a high N content is expected. In the fall, growing tips are presumably still high in N but woody material had developed and matured behind the growing tips. Older wood contains less N; thus overall N content of current growth decreases from spring to fall. Small and large mesquite branches have lower N in spring than in fall and winter. Evidently, N is translocated in spring from storage sources into regions of active growth. In the fall and winter, products of photosynthesis are being stored in these woody tissues, thus increasing their N concentration. This pattern was not evident in paloverde.

Table 9. Seasonal change in nutrients of paloverde shrubs (A3UKB06)

Component	Season		
	Spring	Fall	Winter
	N%		
Leaves	4.18 ^{a*}	3.48 ^b	----
Current Growth	3.20 ^a	2.15 ^b	2.48 ^b
Branches less than 1 cm	1.63 ^a	1.48 ^a	1.63 ^a
Branches more than 1 cm	1.15 ^a	1.19 ^a	1.02 ^a
Roots	1.28 ^a	1.18 ^a	1.04 ^a
	C%		
Leaves	43.2 ^a	41.6 ^b	----
Current Growth	43.5 ^a	43.3 ^a	43.4 ^a
Branches less than 1 cm	42.1 ^a	42.6 ^a	42.2 ^a
Branches more than 1 cm	42.9 ^a	43.7 ^a	42.7 ^a
Roots	44.2 ^a	44.1 ^a	44.0 ^a
	C:N Ratio		
Leaves	10.4 ^a	12.0 ^b	----
Current Growth	14.1 ^a	21.2 ^b	18.0 ^b
Branches less than 1 cm	26.7 ^a	30.6 ^a	27.4 ^a
Branches more than 1 cm	39.1 ^a	37.9 ^a	43.5 ^a
Roots	35.1 ^a	42.0 ^a	43.9 ^a

*Within any given row, figures that lack one or more common letters are significantly different at the 95% level.

Table 11. Percentage nitrogen for shrub components sampled in the spring (A3UKB06)

Component	Spring 1971-72	Spring 1973
	N%	
	Mesquite	
Leaves	3.19 ^{a*}	4.58 ^b
Flowers	3.41 ^a	4.88 ^b
Current Growth	1.89 ^a	2.79 ^b
Branches less than 1 cm	1.39 ^a	1.25 ^a
Branches more than 1 cm	1.11 ^a	0.79 ^b
Roots	1.49 ^a	1.88 ^a
	Palo Verde	
Leaves	3.94 ^a	4.51 ^a
Flowers	3.35 ^a	3.91 ^b
Current Growth	3.08 ^a	3.40 ^a
Branches less than 1 cm	1.62 ^a	1.63 ^a
Branches more than 1 cm	1.25 ^a	0.99 ^a
Roots	1.29 ^a	1.28 ^a

*Within any given row, figures that lack one of more common letters are significantly different at the 95% level.

Mesquite leaves were lower in C percentage in winter; paloverde were lower in C in the fall. Exact reasons for these small changes in C are not known.

C:N ratios changed generally for many shrub components. In most cases change in N seems responsible for the change in the ratio.

Mesquite leaves, flowers and current growth were higher in N in 1973 than in 1972; N in large branches was quite low in 1973 (Table 10). The latter result is surprising in view of no differences due to years in small branches. Some of these same responses also occurred in paloverde. It appears the spring N content caused most of those differences. Table 11 gives spring N percentages on an annual basis; differences between years are quite striking for mesquite and may relate to precipitation. Precipitation was unusually heavy for the February through April 1973 period (96.5 mm) compared to the 1971-72 averaged value (12.7 mm) for this same period. Moreover, this spring period in 1973 was slightly cooler than in either 1971 or 1972. Mineralization and movement of nitrate in the soil could be important factors in this response. Additional N uptake by the plant did not increase biomass; it only resulted in higher concentrations of N in leaves, flowers, current growth and roots. Large branch N was significantly lower in 1973, perhaps indicating that greater amounts of N were translocated during the wet spring. Finally, it may be speculated that additional N in shrub components in 1973 represents luxury consumption. While paloverde showed the same pattern as mesquite, only one component showed a significant difference. Smaller sample size may be responsible for the lack of significance. It is apparent in Table 10 that annual changes in C are small compared with those of N and perhaps not biologically significant.

Table 10. Annual change in shrub nutrients* (A3UKB06)

Components	Nitrogen, %		Carbon, %		
	1971	1972	1971	1972	1973
	Mesquite				
Leaves	3.06 ^{ab**}	2.96 ^a	3.69 ^b	47.1 ^a	46.7 ^a
Flowers	3.67 ^a	3.16 ^a	4.88 ^b	45.3 ^a	43.6 ^b
Fruit	2.33 ^a	2.45 ^a	1.75 ^a	44.9 ^a	43.6 ^a
Current Growth	2.11 ^{ab}	1.76 ^a	2.28 ^b	46.0 ^a	44.9 ^b
Branches less than 1 cm	1.38 ^a	1.51 ^a	1.43 ^a	43.2 ^a	43.6 ^a
Branches more than 1 cm	1.21 ^a	1.11 ^a	0.87 ^b	42.6 ^a	44.1 ^a
Roots	1.47 ^a	1.48 ^a	1.82 ^a	44.3 ^a	46.4 ^b
	Palo Verde				
Leaves	----	3.69 ^a	4.51 ^b	----	42.1 ^a
Flowers	----	3.35 ^a	3.91 ^b	----	45.8 ^a
Fruit	----	3.07 ^a	2.55 ^a	----	44.5 ^a
Current Growth	----	2.61 ^a	2.78 ^a	----	43.4 ^a
Branches less than 1 cm	----	1.50 ^a	1.65 ^a	----	42.3 ^a
Branches more than 1 cm	----	1.27 ^a	1.01 ^b	----	43.1 ^a
Roots	----	1.19 ^a	1.31 ^a	----	44.1 ^a

* Means of spring and fall values.

**Within any given row and for a particular nutrient, figures that lack one or more common letters are significantly different at the 95% level.

Table 12. Nutrient content of understory vegetation (A3UKB07)

Component	N, %	C, %	C:N
<u>Mesquite</u>			
Herbs, Live	1.43	40.3	28.2
" Dead	1.07	39.7	37.1
Shrubs, Live	1.23	42.2	34.3
" Dead	0.83	44.8	53.9
Succulents, Live	0.73	38.6	52.9
" Dead	1.05	34.5	32.8
<u>Palo Verde</u>			
Herbs, Live	1.45	40.9	28.1
" Dead	1.03	40.7	39.7
Shrubs, Live	1.22	44.7	36.6
" Dead	0.75	44.3	59.3
Succulents, Live	1.10	36.9	33.6
" Dead	0.87	34.1	39.0

Understory Phytomass

Nitrogen concentration for understory components was similar for mesquite and paloverde (Table 12). The living herb component of understory vegetation had the highest N concentration. Live succulents were especially low in N; dead succulents contained more N than live succulents. Factors responsible for this are not known.

Of the understory components, shrubs were high in C percentage and succulents were low; the percentage of C did not change appreciably from living to dead, thus suggesting little decomposition. The C:N ratios were generally higher for dead understory components, thus reflecting a differential loss of nitrogen and carbon in standing dead vegetation.

No significant spatial pattern was detected in the concentration of N and C in understory vegetation.

In the understory of mesquite shrubs, all components are lower in N in spring than in fall or winter (Table 13). Paloverde shows this same trend but differences are not significant. Uptake of N by understory vegetation can be expected to be higher during late summer and winter when the soil is occasionally moist than in spring when precipitation is ordinarily deficient. A difference in species composition of understory vegetation may be another factor contributing to low spring N percentages of understory vegetation.

Higher N in understory vegetation of both shrubs in 1973 than in 1971 or 1972 (Table 14) is apparently a response to greater winter-early spring moisture in 1973. Annuals were more abundant in 1973 than in either of the preceding years; they often contain a relatively high N percentage. Annual differences in C percentage, although significant, are fairly small and of unknown biological significance.

Table 13. Seasonal change in percentage nitrogen of understory vegetation (A3UKB07)

Component	Season		
	Spring	Fall	Winter
<u>Mesquite</u>			
Total Understory	1.08a*	1.21 ^b	1.20 ^b
Live Herbs	1.28 ^a	1.54 ^b	1.44 ^{ab}
Dead Herbs	0.99 ^a	1.16 ^b	1.04 ^{ab}
<u>Palo Verde</u>			
Total Understory	1.07 ^a	1.21 ^a	1.14 ^a
Live Herbs	1.35 ^a	1.54 ^a	1.47 ^a
Dead Herbs	0.96 ^a	1.10 ^a	1.02 ^a

*Within any given row, figures that lack one or more common letters are significantly different at the 95% level.

Table 14. Effect of year on percentage N and C of understory vegetation* (A3UKB07)

Nutrient	Year		
	1971	1972	1973
<u>Mesquite</u>			
N	1.07a**	1.17ab	1.23b
C	42.4 ^a	38.9 ^b	41.1 ^a
<u>Palo Verde</u>			
N	----	1.02 ^a	1.36 ^b
C	----	42.1 ^a	41.0 ^b

* Means of spring and fall values.

**Within any given row, figures that lack one or more common letters are significantly different at the 95% level.

Litter Phytomass

No statistical differences were found for either shrub in percentage N of shrub litter with distance from the shrub center (Table 15). Carbon percentage showed only a few significant differences and the C:N ratio is almost constant from position to position. Mesquite litter is consistently higher in percentage N than paloverde litter; component composition of the litter is responsible for this difference. Mesquite litter receives large annual increments of N-rich leaves while paloverde litterfall is largely woody and low in N (Table 2).

Understory litter of mesquite and paloverde shrubs is significantly lower at the 4/3 CR position than at any of the other positions (Table 15). Under the protection of the shrub canopy the light, N-rich components of understory litter are not dispersed by wind and water to the same extent they are beyond the protection of the canopy. At the 4/3 CR position, litter contains more of the bulkier, N-poor components of understory litter. Spatial differences in species composition of understory vegetation and their fertility status may contribute to this pattern (Tiedemann and Klemmedson 1973a, 1973b).

Table 15. Spatial change in nutrients and C:N ratio in shrub and understory litter (A3UKB08)

Component	Canopy Position			
	3/3 CR	2/3 CR	3/3 CR	4/3 CR
<u>Mesquite</u>				
Mesquite litter N, %	1.61 ^{a*}	1.57 ^a	1.62 ^a	1.64 ^a
" " C, %	39.2 ^{ab}	38.8 ^a	39.8 ^{ab}	40.5 ^b
" " C/N	25.4 ^a	26.2 ^a	25.8 ^a	26.6 ^a
Understory litter N, %	1.41 ^a	1.36 ^a	1.24 ^a	0.99 ^b
" " C, %	38.0 ^a	38.2 ^a	36.6 ^a	36.7 ^a
" " C/N	28.9 ^a	30.3 ^a	31.5 ^a	41.8 ^b
<u>Palo Verde</u>				
Palo Verde litter N, %	1.26 ^a	1.39 ^a	1.39 ^a	1.38 ^a
" " C, %	37.5 ^a	37.8 ^a	38.5 ^a	39.7 ^a
" " C/N	32.0 ^a	29.1 ^a	31.2 ^a	31.4 ^a
Understory litter N, %	1.37 ^a	1.34 ^a	1.20 ^a	0.93 ^b
" " C, %	37.5 ^a	37.7 ^a	37.4 ^a	37.4 ^a
" " C/N	31.5 ^a	32.3 ^a	34.1 ^a	44.0 ^b

*Within any given row, figures that lack one or more common letters are significantly different at the 95% level.

Percentage C in understory litter does not change with position, but the C:N ratio is significantly higher for both species at the 4/3 CR position (Table 15). C:N ratios under the shrub canopy average 31.4 while that for the 4/3 position averages 42.9; thus indicating a more favorable environment under the canopy for decomposition and nutrient release.

The N concentration of mesquite litter portrays a cyclic trend; the maximum concentration is reached in winter after fall of N-rich leaves while the minimum is reached in fall (Table 16). Tarrant et al. (1969) found seasonal changes in N content of red alder litter and attributed the differences to phenological events of the overstory vegetation. The N percentage of paloverde did not change seasonally. Carbon percentage of litter of both shrubs was significantly lower in fall than in spring and winter. This is reasonable because of ideal conditions for microbial decomposition in late summer. Moreover, C percentage is likely to be high immediately after periods of most intense litterfall.

Some annual changes in nutrient content of shrub litter were detected (Table 17). Nitrogen percentage of paloverde litter was significantly higher in 1973 than in 1972; the explanation for this difference is not clear. The C:N ratio significantly decreased over the study period and reached its lowest point for both shrubs in 1973.

Percentage N of understory litter was significantly higher for both shrubs during 1973. This reflects the wet spring of 1973 and an abundance of herbaceous species, especially annuals, high in N. The C:N ratio reflects the increased N content of understory litter; the 1973 C:N ratio is more favorable to microbial decomposition and nutrient release than that of preceding years. These data suggest that rates of

Table 16. Seasonal change in nutrients and C:N ratio in shrub and understory litter (A3UKB08)

Component	Season		
	Spring	Fall	Winter
<u>Mesquite</u>			
Mesquite litter N, %	1.64 ^{ab*}	1.50 ^a	1.73 ^b
" " C, %	40.0 ^a	38.6 ^b	40.6 ^a
" " C/N	25.2 ^a	27.5 ^a	24.4 ^a
Understory litter N, %	1.17 ^a	1.30 ^a	1.29 ^a
" " C, %	38.4 ^a	36.6 ^b	36.9 ^{ab}
" " C/N	36.6 ^a	31.6 ^a	29.9 ^a
<u>Palo Verde</u>			
Palo Verde litter N, %	1.44 ^a	1.31 ^a	1.31 ^a
" " C, %	38.8 ^a	37.2 ^b	38.9 ^a
" " C/N	29.8 ^a	29.5 ^a	33.4 ^a
Understory litter N, %	1.24 ^a	1.25 ^a	1.13 ^a
" " C, %	37.7 ^{ab}	36.2 ^a	38.6 ^b
" " C/N	33.8 ^a	33.3 ^a	39.3 ^a

*Within any given row, figures that lack one or more common letters are significantly different at the 95% level.

decomposition and nutrient release to the soil may fluctuate considerably as environmental factors combine to make conditions more or less favorable for decomposition.

Soil

The horizontal distribution of soil N observed here for mesquite and paloverde follows a consistent pattern similar to that observed by others (Zinke 1962, Fireman and Hayward 1952, Garcia-Moya and McKell 1970). At all depths, N is highest at the 0/3 CR position where the influence of the shrub is greatest and continually decreases as distance increases (Tables 18 and 19). For both shrub species, soil N declines by 50% from the 0/3 to the 4/3 CR position in the surface horizon but by only 15% in the 30-60-cm horizon. Soil C follows the same consistent pattern with distance as reported for N above. The patterns of soil N and C percentage relate directly to the distribution of biomass and nutrient concentration described earlier for the shrubs (including roots), the understory species and the litter that these plants produce. These plants function to concentrate nutrients and maintain them in the cycling pool by virtue of processes described in references cited above and thereby decrease the amount of N lost through leaching and soil movement.

Tables 18 and 19 show the height concentration of N at the center of the shrub. In coniferous systems, Zinke (1962) noted soil N was low near the tree bole and increased to a maximum 1 to 1.5 m from the bole. Low N near the bole resulted from the accumulation of bark low in N. Mesquite and paloverde shrubs do not have a central stem but are branched at the ground or within a few feet of the ground. Without the tall, straight stem typical of conifers, bark litter is not concentrated around the bole in these desert shrubs. The pattern of bark shedding is not known for these desert shrubs.

Table 17. Annual change in nutrients and C:N ratio in shrub and understory litter* (A3UKB09)

Component	Year		
	1971	1972	1973
<u>Mesquite</u>			
Mesquite litter N, %	1.49 ^{a**}	1.58 ^a	1.68 ^a
" " C, %	40.2 ^a	38.9 ^a	38.4 ^a
" " C/N	29.2 ^a	25.5 ^b	23.8 ^b
Understory litter N, %	1.14 ^a	1.14 ^a	1.56 ^b
" " N, %	36.3 ^a	39.3 ^b	36.7 ^a
" " C, %	36.8 ^a	37.2 ^a	24.5 ^b
<u>Palo Verde</u>			
Palo Verde litter N, %	----	1.31 ^a	1.49 ^b
" " C, %	----	38.4 ^a	37.5 ^a
" " C/N	----	32.1 ^a	25.9 ^b
Understory litter N, %	----	1.10 ^a	1.50 ^b
" " C, %	----	37.6 ^a	35.8 ^a
" " C/N	----	34.2 ^a	23.2 ^b

* Means of spring and fall values.

**Within any given row, figures that lack one or more common letters are significantly different at the 95% level.

Table 18. Spatial distribution of some soil properties for mesquite shrubs (A3UKB09)

Depth in cm	Position				
	0/3 CR	1/3 CR	2/3 CR	3/3 CR	4/3 CR
<u>N%</u>					
0-5	.072 ^{a*}	.060 ^b	.052 ^b	.040 ^c	.035 ^c
5-15	.050 ^a	.038 ^b	.033 ^{bc}	.030 ^c	.028 ^c
15-30	.038 ^a	.032 ^b	.029 ^{bc}	.028 ^c	.026 ^c
30-60	.028 ^a	.026 ^{ac}	.025 ^c	.024 ^{bc}	.022 ^b
<u>C%</u>					
0-5	.769 ^a	.569 ^b	.487 ^b	.370 ^c	.304 ^c
5-15	.489 ^a	.321 ^b	.278 ^{bc}	.241 ^c	.227 ^c
15-30	.339 ^a	.283 ^b	.238 ^c	.227 ^c	.213 ^c
30-60	.234 ^a	.215 ^{ac}	.191 ^{bc}	.187 ^b	.177 ^b
<u>C:N Ratio</u>					
0-5	10.61 ^a	9.52 ^b	9.25 ^{bc}	9.25 ^b	8.63 ^c
5-15	9.55 ^a	8.40 ^b	8.34 ^b	8.08 ^b	8.18 ^b
15-30	8.77 ^a	8.77 ^a	8.28 ^a	8.01 ^a	8.10 ^a
30-60	8.27 ^a	8.12 ^a	7.70 ^a	7.91 ^a	8.85 ^a
<u>pH</u>					
0-5	6.5 ^a	6.8 ^b	6.8 ^b	6.8 ^b	6.9 ^b
5-15	6.7 ^a	7.1 ^b	7.1 ^b	7.0 ^b	7.0 ^b
15-30	6.8 ^a	7.2 ^b	7.2 ^b	7.2 ^b	7.1 ^b
30-60	7.1 ^a	7.3 ^a	7.2 ^a	7.3 ^a	7.3 ^a

* Within any given row, figures that lack one or more common letters are significantly different at the 95% level.

Table 19. Spatial distribution of some soil properties for paloverde shrubs (A3UKB09)

Depth in cm	Position				
	0/3 CR	1/3 CR	2/3 CR	3/3 CR	4/3 CR
<u>N%</u>					
0-5	.069 ^{a*}	.065 ^a	.055 ^b	.045 ^c	.036 ^c
5-15	.038 ^a	.037 ^a	.033 ^a	.028 ^b	.027 ^b
15-30	.032 ^a	.030 ^{ab}	.029 ^{abc}	.027 ^{bc}	.026 ^c
30-60	.027 ^a	.025 ^a	.026 ^a	.024 ^a	.023 ^a
<u>C%</u>					
0-5	.689 ^a	.581 ^b	.494 ^{bc}	.419 ^c	.306 ^d
5-15	.307 ^a	.266 ^{abc}	.286 ^{ab}	.243 ^{bc}	.219 ^c
15-30	.252 ^a	.231 ^a	.243 ^a	.225 ^a	.213 ^a
30-60	.232 ^a	.200 ^a	.194 ^a	.195 ^a	.181 ^a
<u>C:N Ratio</u>					
0-5	9.84 ^a	9.04 ^{bc}	8.82 ^{bc}	9.20 ^{ab}	8.50 ^c
5-15	8.12 ^a	7.91 ^a	8.46 ^a	8.39 ^a	8.00 ^a
15-30	7.77 ^a	7.75 ^a	8.27 ^a	8.15 ^a	8.10 ^a
30-60	7.43 ^a	7.39 ^a	7.38 ^a	7.32 ^a	7.34 ^a
<u>pH</u>					
0-5	7.21 ^a	7.20 ^a	7.10 ^a	6.91 ^a	7.00 ^a
5-15	7.29 ^a	7.26 ^a	7.23 ^a	7.12 ^a	7.11 ^a
15-30	7.37 ^a	7.37 ^a	7.30 ^a	7.25 ^a	7.22 ^a
30-60	7.43 ^a	7.39 ^a	7.38 ^a	7.32 ^a	7.34 ^a

*Within any given row, figures that lack one or more common letters are significantly different at the 95% level.

For mesquite shrubs, soil pH was consistently low at the 0/3 CR position and increased significantly at other positions. The concentration of biomass near the shrub center and the acidifying effect of organic matter accumulated near the shrub center as it decomposes produce this pH pattern. Tiedemann and Klemmedson (1973b) observed a pH of 5.3 in the leachate from a sample of dried mesquite leaves. No soil pH pattern was observed under paloverde; this is reasonable in view of the low leaf biomass of paloverde. For both species, soil N is reduced by approximately 50% and soil C by 60% from the 0- to 5-cm layer to the 30- to 60-cm horizon. Abruptness of the vertical gradient in the upper soil layers is a reflection of vegetation type and the arid environment. Charley and Cowling (1968) noted that biologically induced vertical gradients become sharper with increasing aridity because biological activity in most arid climates is confined to the first few centimeters of soil.

Soil pH increases with depth in these ecosystems. This is a function of soil genesis and the distribution of organic matter. Soil carbonates are dissolved by precipitation and removed from upper soil horizons. Dissolved carbonate is precipitated at lower soil depths, thus accumulating and raising the pH. The addition of acidic organic matter and its decomposition have an acidifying effect on the soil. This effect is greatest at the soil surface, particularly under shrubs where litter accumulates and decreases with depth.

Table 20. Depth function for soil nutrient (all canopy positions averaged) (A3UKB09)

Depth in cm.	N, %	C, %	C:N	pH
Mesquite				
0-5	.052 ^{a*}	.500 ^a	9.45 ^a	6.77 ^a
5-15	.036 ^b	.311 ^b	8.51 ^b	6.97 ^b
15-30	.031 ^c	.260 ^c	8.38 ^b	7.11 ^b
30-60	.025 ^d	.201 ^d	7.97 ^c	7.28 ^c
Palo Verde				
0-5	.054 ^a	.490 ^a	9.08 ^a	7.08 ^a
5-15	.033 ^b	.264 ^b	8.18 ^b	7.20 ^b
15-30	.029 ^c	.233 ^{bc}	8.01 ^b	7.30 ^{bc}
30-60	.025 ^d	.200 ^c	8.01 ^b	7.37 ^c

*Within any given column, figures that lack one or more common letters are significantly different at the 95% level.

The C:N ratio also decreases with depth; this gradient is well established in the literature for most soils. Although data in Table 20 are averaged for all canopy positions, individual canopy positions all showed a decrease in C and N and an increase in pH with depth. Magnitude of change was greatest at the center position.

Soil N and C did not change with seasons. These nutrients are at, or close to, steady-state conditions and as such are not expected to be influenced by short-term seasonal changes unless the change is great. The depth function for soil pH shows a strong seasonal pattern (Table 21). At all depths, pH is higher during winter than during fall or spring. During the spring when plants are actively metabolizing, soil pH usually declines. In the fall, plant activity is diminished but microbial decomposition may still be high and acids produced by this process may account for low fall pH values. During winter, soils are drier, colder and biotic activities are reduced; hence, pH values tend to rise.

Soil pH was higher in 1973 than in either 1971 or 1972 for both paloverde and mesquite (Table 22). Especially high pH values in the fall of 1973 may be related to the lack of precipitation in the summer of 1973. Dry conditions may have lowered microbial decomposition, leaching of acidic products of decomposition, and nutrient absorption by plants, thus permitting accumulation of soluble salts with a resultant pH increase.

AMOUNT OF NUTRIENTS IN THE ECOSYSTEM

In both mesquite and paloverde ecosystems, over 77% of ecosystem N was found in the soil, 18% was in shrub biomass and less than 4% was in understory vegetation and litter (Table 23). Importance of the soil as a large reservoir of N is obvious.

In the adjacent ecosystem for both species, shrub roots and understory litter are the largest contributors to the scant biomass N pool. The lack of substantial amounts of biomass in the adjacent ecosystem results in the soil containing essentially all the N.

Table 21. Seasonal changes in soil pH (A3UKB09)

Depth in cm.	Spring	Season	
		Fall	Winter
Mesquite			
0-5	6.7 ^{a*}	6.6 ^a	7.1 ^b
5-15	6.9 ^a	6.9 ^a	7.3 ^b
15-30	7.0 ^a	7.0 ^a	7.4 ^b
30-60	7.2 ^a	7.2 ^a	7.4 ^b
Palo Verde			
0-5	7.1 ^{ab}	6.9 ^a	7.2 ^b
5-15	7.2 ^{ab}	7.1 ^a	7.3 ^b
15-30	7.3 ^{ab}	7.1 ^a	7.5 ^b
30-60	7.3 ^a	7.3 ^a	7.5 ^b

*Within any given row, figures that lack one or more common letters are significantly different at the 95% level.

Table 22. Annual changes in soil pH*

Depth in cm.	Year		
	1971	1972	1973
Mesquite			
0-5	6.7 ^{a**}	6.4 ^a	7.0 ^b
5-15	6.9 ^a	6.7 ^a	7.1 ^b
15-30	7.0 ^a	6.8 ^a	7.3 ^b
30-60	7.3 ^a	7.0 ^b	7.5 ^c
Palo Verde			
0-5	----	6.8 ^a	7.4 ^b
5-15	----	7.0 ^a	7.4 ^b
15-30	----	7.0 ^a	7.5 ^b
30-60	----	7.1 ^a	7.6 ^b

* Means of spring and fall values.

**Within any given row, figures that lack one or more common letters are significantly different at the 95% level.

When shrub ecosystems and their respective adjacent ecosystems are compared, significant differences exist for all components except understory litter and, in the case of paloverde, shrub roots. Lack of significance in N in understory litter reflects the absence of spatial patterns in biomass and percentage N for understory species noted in previous sections.

The above-ground shrub biomass and soil contain similar amounts of C (Table 24). Shrubs, understory biomass and litter combine to account for less than 12% of total C. In contrast to N, C accumulates in vegetative matter and is relatively more immobile in soil.

Carbon distribution in adjacent ecosystems was similar for both shrub species. Carbon was concentrated in the soil because there is no appreciable above- and below-ground accumulation of woody biomass. The contrast between shrub ecosystems and adjacent ecosystems for C is similar to that for N. For most components, the adjacent ecosystem contained only a small fraction of the C found in the shrub ecosystem. For the total ecosystem, shrub ecosystems contained more than 2.5 times the C found in adjacent ecosystems.

Table 23. Distribution of nitrogen in shrub ecosystems and in their adjacent ecosystems (A3UKB06-09)

Components	Mesquite Ecosystem		Adjacent Ecosystem	
	(g/m ²)	%	(g/m ²)	%
Aboveground Mesquite Biomass	53.2	16.5	----	----
Mesquite Roots (0-60 cm)	9.4 ^{a*}	2.9	1.6 ^b	0.7
Understory Biomass	1.7 ^a	0.6	0.6 ^b	0.3
Mesquite Litter	5.8 ^a	1.8	0.4 ^b	0.2
Understory Litter	1.9 ^a	0.6	1.3 ^a	0.6
Soil (0-60 cm)	249.5 ^a	77.6	213.2 ^b	98.2
Total Ecosystem	321.8 ^a	----	217.1 ^b	----
	Palo Verde Ecosystem		Adjacent Ecosystem	
	(g/m ²)	%	(g/m ²)	%
Aboveground Palo Verde Biomass	59.8	18.9	----	----
Palo Verde Roots (0-60 cm)	3.9 ^a	1.2	1.3 ^a	0.6
Understory Biomass	2.5 ^a	0.8	1.0 ^b	0.5
Palo Verde Litter	2.6 ^a	0.8	0.2 ^b	0.1
Understory Litter	2.9 ^a	0.9	2.2 ^a	1.0
Soil (0-60 cm)	244.8 ^a	77.3	216.1 ^b	97.8
Total Ecosystem	316.6 ^a	----	221.0 ^b	----

*Within any given row, figures that lack one or more common letters are significantly different at the 95% level.

The two shrub ecosystems differed in the amounts and distribution of N and C only in root and shrub litter. Amount of root N was significantly higher for mesquite than for paloverde systems. This difference reflects a more extensive root system and high N percentage in mesquite roots (Tables 2 and 7). Nitrogen and C in shrub litter were higher for mesquite ecosystems. Shedding of large quantities of leaves and deadwood by mesquite shrubs produces this difference. Mesquite and paloverde ecosystems accumulate and distribute N and C in essentially the same manner. Comparison of adjacent ecosystems for the two species showed no statistically significant difference.

Predicting amounts of nutrients in shrub ecosystems from ecosystem properties gives mixed results (Table 25). For mesquite, shrub height was a better indicator of ecosystem N and C than shrub biomass; for paloverde, both independent variables were of approximately equal value in predicting ecosystem nutrients. In all cases, ecosystem C was more precisely predicted than N. Over 50% of ecosystem C is found in above-ground biomass, and shrub biomass and height are closely related to above-ground biomass. Most of the ecosystem N is in the soil and soil properties cannot be accurately predicted using shrub parameters. Nutrients in adjacent ecosystems could not be predicted using parameters of shrub ecosystems.

Equations such as those in Table 26 provide a fast method to assess the approximate N and C status of desert shrub ecosystems and provide an important means for monitoring the status of nutrient cycles over large areas. In an area

Table 24. Distribution of carbon in shrub ecosystems and in their adjacent ecosystems (A3UKB06-09)

Components	Mesquite Ecosystem		Adjacent Ecosystem	
	(g/m ²)	%	(g/m ²)	%
Aboveground Mesquite Biomass	1845.0	40.8	----	----
Mesquite Roots (0-60 cm)	313.1 ^{a*}	6.9	43.9 ^b	2.3
Understory Biomass	66.9 ^a	1.5	29.8 ^b	1.6
Mesquite Litter	145.5 ^a	3.2	11.5 ^b	0.6
Understory Litter	55.7 ^a	1.2	60.6 ^a	3.2
Soil (0-60 cm)	2096.9 ^a	46.4	1740.3 ^b	92.3
Total Ecosystem	4523.1 ^a	----	1855.5 ^b	----
	Palo Verde Ecosystem		Adjacent Ecosystem	
	(g/m ²)	%	(g/m ²)	%
Aboveground Palo Verde Biomass	1985.3	44.4	----	----
Palo Verde Roots (0-60 cm)	158.9 ^a	3.6	50.3 ^a	2.6
Understory Biomass	106.0 ^a	2.4	55.2 ^a	2.8
Palo Verde Litter	76.8 ^a	1.7	9.5 ^b	0.5
Understory Litter	101.1 ^a	2.3	102.0 ^a	5.2
Soil (0-60 cm)	2043.9 ^a	45.7	1747.0 ^b	88.9
Total Ecosystem	4472.0 ^a	----	1964.0 ^b	----

*Within any given row, figures that lack one or more common letters are significantly different at the 95% level.

Table 25. Linear regression equations relating shrub biomass and height to weight of nitrogen or carbon in the shrub ecosystem (A3UKB01-09)

Dependent	Variables		r ²	Equation
	Independent			
<u>Mesquite</u>				
Ecosystem N, g/m ²	Shrub Biomass (kg)		.53	y = 270.0 + 0.45X
" C, "	" "		.61	y = 3246.4 + 11.18X
" N, "	Shrub Height (m)		.58	y = 195.8 + 37.72X
" C, "	" "		.72	y = 1297.3 + 965.44X
<u>Palo Verde</u>				
Ecosystem N, g/m ²	Shrub Biomass (kg)		.23	y = 286.5 + 0.36X
" C, "	" "		.59	y = 3461.6 + 12.19X
" N, "	Shrub Height (m)		.27	y = 236.5 + 25.36X
" C, "	" "		.57	y = 1864.2 + 800.32X

adjacent to the study area, Fish and Smith (1973) calculated percent cover of shrubs by imagery and found cover for mesquite was 8.2%; that for paloverde was 0.8%. Using these figures, N and C per hectare were determined where the adjacent ecosystem represented the area not occupied by these two shrubs (this probably gives a low estimate since the area between shrubs was not extensively sampled). On this basis, 2281 kg/ha of N and 21,563 kg/ha of C were found in the study area. Approximately 95% of the N was found in the soil; 82% of the carbon is in the soil. The literature contains numerous examples of N and C on an aerial basis; these estimates range both higher and lower than the figures presented above.

Table 26. Distribution of biomass in honey mesquite ecosystems and in their adjacent ecosystems (A3UKB06-09)

Component	Mesquite Ecosystem		Adjacent Ecosystem	
	(kg/m ²)	%	(kg/m ²)	%
Aboveground Mesquite Biomass	1.64	56.8	----	----
Mesquite Roots (0-60 cm)	0.59	20.3	0.02	21.1
Understory Biomass	0.11	3.8	0.03	27.5
Mesquite Litter	0.20	7.0	----	0.9
Understory Litter	0.35	12.1	0.06	50.5
Total Ecosystem	2.89	----	0.11	----

SHRUB-INDUCED NUTRIENT PATTERNS IN THE CHIHUAHUAN DESERT

In the foregoing study, investigation of shrub-induced nutrient patterns was limited to a small area of the Sonoran Desert. At the request of the Desert Biome Director, a very limited number of shrub systems were sampled in the Chihuahuan Desert to learn how the change in environment might affect nutrient distribution in mesquite. At the Jornada Experimental Range 10 km east of Las Cruces, New Mexico, an area was chosen for sampling which appeared to typify environments of honey mesquite (*Prosopis glandulosa*, formerly *P. juliflora* var. *glandulosa*) in the northern Chihuahuan Desert. Light grazing has been practiced in the area for many years but human disturbance has not been significant.

At this site, honey mesquite grew to less than 4 m in height and was of the multi-stem variety. Many shrubs were growing on slight mounds, an apparent result of accumulating aeolian material that partially covers the plant base.

Associated vegetation includes soaptree yucca (*Yucca elata*), snakeweed (*Gutierrezia* spp.) and sandbur (*Cenchrus* spp.). Grasses are scarce but individuals of bristlegrass (*Setaria* spp.) and dropseed (*Sporobolus* spp.) can be found.

Soils appeared structureless with very limited vertical differentiation; texture throughout the profile was loamy sand. These soils would probably be classified as a torrifuvent. In many places the soil was being actively transported by wind.

Climate of the Chihuahuan Desert is somewhat cooler and drier than the Sonoran Desert. Mean temperatures are 4.0 C for January and 26.0 C for July. Precipitation averages 22.5 cm annually; 50% of the total is received from June to August. Spring is typically dry with high evaporation and wind.

Three shrubs, representing the available size range, were selected at random and harvested during late August 1972. These shrubs averaged 1.4 m in height and 3.8 m² in canopy projection. Field and laboratory methods were identical to the above-described studies. Statistical analyses were not attempted.

Table 27. Distribution of biomass and nutrients in honey mesquite ecosystems of average size (A3UKB02)

Component	Biomass		Nutrients	
	kg/m ²	%	N	C
Leaves	.178	8.0	3.01	46.7
Fruit	.021	0.9	3.08	43.4
Current Growth	.104	4.7	1.56	45.4
Branches < 1 cm	.486	21.8	1.40	45.3
Branches > 1 cm	.421	18.9	1.29	43.9
Deadwood	.430	19.3	1.35	43.8
Roots	.590	26.5	1.64	45.2
Total Biomass	2.230			

Table 28. Spatial distribution of litter and understory biomass and nutrients (A3UKB04-05)

Components	Position			
	1/3 CR	2/3 CR	3/3 CR	4/3 CR
	Biomass (g/m ²)			
Understory Biomass	81.4	122.7	115.7	29.6
Shrub Litter	302.0	260.8	31.7	1.4
Understory Litter	720.0	335.0	66.0	54.7
	N, %			
Shrub Litter	1.74	1.94	1.36	1.55
Understory Litter	1.24	0.86	0.84	1.04
	C, %			
Shrub Litter	39.41	39.01	41.93	43.22
Understory Litter	37.15	40.16	37.90	39.29

Distribution of Biomass

Shrub biomass was not concentrated in any one component but was dispersed over branches, deadwood and roots (Table 27). Almost 20% of the biomass was in deadwood; a similar percentage was noted in velvet mesquite. Leaves, fruit and current growth accounted for slightly over 13% of total biomass, or about four times the amount of velvet mesquite. Leaves accounted for much more of the biomass for velvet than for honey mesquite. It should be recalled that the data for velvet mesquite (Table 2) reflect the mean for three sampling dates, including the leafless winter period. Less than 20% of the shrub biomass was in large branches, compared with nearly 60% in velvet mesquite in the Sonoran Desert (Table 2). The other marked difference between velvet and honey mesquite was in root biomass; over 25% of the biomass of honey mesquite was in roots compared with 10% for velvet mesquite and paloverde.

Honey mesquite apparently alters the environment under its canopy in a manner favorable to the establishment of other vegetation. Biomass of understory plants is considerably heavier under the shrub canopy than beyond the canopy edge (Table 28). This agrees with observations at the Santa Rita site.

Litter of both shrub and understory species decreased dramatically as distance from the shrub increased. Shrub litter at the 4/3 CR position contained only 1/300 of the shrub litter found at the 1/3 CR position. Wind is undoubtedly an important factor in establishing this pattern. Litter which falls in less protected portions of the shrub understory (3/3 and 4/3 CR positions) evidently was removed by wind and accumulated at the 1/3 and 2/3 CR positions. The low-growing, multi-stemmed nature of honey mesquite favors accumulation of windblown organic debris.

The bulk of the biomass in honey mesquite ecosystems was found in above-ground portions of the shrub. When roots are added, honey mesquite accounts for 75% of the total biomass in the ecosystem it dominates. Litter accounted for nearly one-fifth of total biomass in the honey mesquite system. In the Sonoran Desert, more biomass is distributed in shrub components and considerably less in understory litter. Distribution of biomass in adjacent ecosystems differs little from Sonoran to Chihuahuan Deserts; in both areas, understory litter accounts for approximately 50% of the biomass. Mean biomass of the total ecosystem for both shrub and adjacent ecosystems in the Chihuahuan Desert is less than half of that found in the Sonoran Desert.

Concentration of Nutrients in Biomass and Soil

The shrub biomass was characterized by an expected high N concentration in young growing components and lower N in deadwood and branches (Table 27). Percentage C was fairly constant; no noteworthy trends were evident. In general, honey mesquite contained slightly less N than similar components in velvet mesquite and paloverde. Phenological studies indicate that differences among species in N concentration are more likely the effect of species and environmental differences than the effect of differences in sampling date.

Understory vegetation averaged 2.0% N and 38.5% C; spatial differences in concentration of these nutrients were not apparent. N concentration in understory vegetation is higher in the Chihuahuan Desert and C concentration slightly lower compared with the Sonoran Desert. Part of the difference may be due to the higher proportion of herbaceous species, typically high in N, in the honey mesquite understory than that observed under velvet mesquite. Shrubs were rarely a part of understory biomass here and succulents were absent.

Shrub litter contained 1.85% N and 40.9% C, whereas understory litter averages 0.99% N and 38.3% C. No distinct spatial pattern for N and C was evident in these litters (Tables 2 and 7). Concentrations of N and C in honey mesquite litter were very similar to those found in litter of velvet mesquite and slightly higher than those found in litter of paloverde. Understory litter for honey mesquite was considerably lower in N concentration than that for Sonoran Desert shrubs. This is surprising in view of the high concentration of understory vegetation. The extraneous organic debris that honey mesquite appears to accumulate may have a low N concentration. The C:N ratio for understory litter is 39.0, a higher value than that found in the

Table 29. Spatial distribution of soil properties for honey mesquite ecosystems (A3UKB09)

Depth in cm.	Canopy Position				
	0/3 CR	1/3 CR	2/3 CR	3/3 CR	4/3 CR
	<u>N, %</u>				
0-5	.083	.090	.061	.045	.033
5-15	.042	.040	.031	.028	.029
15-30	.038	.034	.032	.032	.030
30-60	.029	.028	.029	.026	.027
	<u>C, %</u>				
0-5	.99	1.06	.85	.66	.59
5-15	.61	.61	.41	.40	.48
15-30	.55	.49	.41	.44	.45
30-60	.64	.59	.59	.68	.67
	<u>C:N Ratio</u>				
0-5	11.93	11.78	13.93	14.67	17.88
5-15	14.53	15.25	13.23	14.29	16.55
15-30	14.47	14.41	12.81	13.75	15.00
30-60	22.07	21.07	20.34	26.15	24.81
	<u>pH</u>				
0-5	8.1	8.0	8.2	8.3	8.3
5-15	8.2	8.1	8.3	8.4	8.4
15-30	8.1	8.1	8.3	8.4	8.2
30-60	8.1	8.1	8.2	8.3	8.2

Sonoran Desert and one that indicates a slower rate of decomposition.

The distribution of soil nutrients under honey mesquite is portrayed in Table 29. For the surface layer, soil N decreased by over 60% from 1/3 to 4/3 CR positions. This soil N pattern was evident in lower soil layers but the magnitude of change between positions lessens with depth. This shrub-induced soil N pattern is very similar to that found for paloverde and velvet mesquite near Tucson. However, percentage N in the surface horizon under shrub canopies is higher in the Chihuahuan Desert. This may reflect greater incorporation of organic residue in the surface soil, an apparent result of wind action. Subsurface N percentage averages approximately 10% higher in honey mesquite ecosystems than in velvet mesquite and paloverde ecosystems. Carbon in the surface horizon declines with distance from the shrub center; for lower soil layers the pattern is irregular. This did not occur in Sonoran Desert soils. Unlike velvet mesquite, honey mesquite did not have a noticeable effect on soil pH. The apparent periodic addition of aeolian soil material to the shrub ecosystem and the smaller shrub size (and possibly younger shrubs) may be important factors in the lack of a horizontal pH gradient.

There is an abrupt vertical gradient in soil N from the surface to the 5- to 15-cm layer, but below the surface there is no significant change to 60 cm (Table 30). This pattern is very similar to that found in the Sonoran Desert; the

Table 30. Distribution of soil nutrients with depth (means for five positions) (A3UKB09)

Depth in cm.	N, %	C, %	C/N	pH
0-5	.062 ^{a*}	.831 ^a	13.40 ^a	8.2 ^a
5-15	.034 ^b	.502 ^a	14.76 ^a	8.3 ^a
15-30	.033 ^b	.469 ^a	14.21 ^a	8.2 ^a
30-60	.028 ^b	.632 ^a	22.57 ^a	8.2 ^a

*Within any given column, figures lacking one or more common letters are significantly different at the 95% level.

magnitude of values is only slightly higher for the Chihuahuan Desert. Percentage soil C shows no significant change with depth, a pattern unlike that found for paloverde and velvet mesquite. High variation and a small sample size may explain the lack of vertical pattern. However, other factors may be involved. The soil seems to be a fluvent and thus associated with recent geomorphic surfaces. In the study area it appeared as if new soil may have been high in C due to soil-litter mixing by wind. It takes approximately 100 to 200 years for subsurface organic matter to decompose; this stratified carbonaceous material would mask soil C patterns induced by shrubs (D. M. Hendricks, University of Arizona, pers. comm.). pH showed no pattern with depth; this is another indication of a recent soil where weathering has not yet leached carbonates to lower depths.

Amount of Nutrients in the Ecosystem

Shrub biomass accounts for just under 11% of the total N found in honey mesquite ecosystems; litter and understory vegetation account for less than 3% while soil makes up the bulk (86%) of ecosystem N. This distribution pattern is quite similar to that noted for Sonoran Desert shrubs. However, because of greater accumulation of shrub biomass in the Sonoran Desert ecosystems, they have relatively more N above ground in the shrub biomass and less in the soil. Total ecosystem N is essentially the same for all three ecosystems. In the ecosystem adjacent to that of honey mesquite, soil contains most of the N. A similar pattern was noted for adjacent ecosystems of paloverde and velvet mesquite although slightly more N was distributed in biomass in those ecosystems. Total N in the adjacent ecosystem is higher in the Chihuahuan Desert and appears to result from slightly higher N concentrations in lower soil horizons.

Distribution of the amount of C in honey mesquite ecosystems is similar to that for N except that the above-ground shrub biomass accounts for slightly more (11.5%) of the total C (Table 31). In the Sonoran Desert, shrub biomass accounted for almost half of the C in the shrub ecosystem. Lack of smaller accumulation of biomass in the Chihuahuan Desert system plus high contents of soil C cause this shift in distribution of ecosystem C. Total C for the shrub ecosystem is higher for honey mesquite than for Sonoran Desert species despite smaller shrub size. High concentration of soil C is evidently the controlling factor.

Table 31. Amount and distribution of nitrogen and carbon in honey mesquite and adjacent ecosystems (A3UKB06-09)

Components	Mesquite Ecosystem (q/m ²)		Adjacent Ecosystem (q/m ²)	
	q/m ²	%	q/m ²	%
Nitrogen				
Aboveground Mesquite Biomass	25.48	7.8	----	----
Mesquite Roots (0-60 cm)	10.05	3.1	0.40	0.2
Understory Biomass	1.97	0.6	0.71	0.3
Mesquite Litter	3.70	1.1	0.02	----
Understory Litter	3.42	1.0	0.55	0.2
Soil (0-60 cm)	281.35	86.3	252.94	99.3
Total Ecosystem	325.97	----	254.62	----
Carbon				
Aboveground Mesquite Biomass	731.7	11.5	----	----
Mesquite Roots (0-60 cm)	264.3	4.1	10.4	0.2
Understory Biomass	40.7	0.6	10.8	0.2
Mesquite Litter	72.2	1.1	0.6	----
Understory Litter	136.6	2.1	20.7	0.4
Soil (0-60 cm)	5132.9	80.5	5160.7	99.2
Total Ecosystem	6378.4	----	5203.2	----

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