

## BIOMASS AND NET PRIMARY PRODUCTION OF PROSOPIS GLANDULOSA (FABACEAE) IN THE SONORAN DESERT OF CALIFORNIA<sup>1</sup>

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### ABSTRACT

*Prosopis glandulosa* var. *torreyana* accounts for nearly 90% of the total plant cover in a mesquite woodland community near Harper's Well along the southern margin of the Salton Sea in the Sonoran Desert of California. Total above-ground biomass in ten individuals studied in detail ranged from 43-760 kg per plant and 1.9-8.5 kg m<sup>-2</sup> canopy area. Stand biomass ranged locally from a high of 23,000 kg ha<sup>-1</sup> near the wash to 3,500 kg ha<sup>-1</sup> in the fringe of this mesquite stand. Net above-ground primary production for 1980 had a mean of 2.2 kg m<sup>-2</sup> canopy for shrub forms and 5.3 kg m<sup>-2</sup> canopy for tree forms. Mean *Prosopis* stand production for 1980 was 3,650 kg ha<sup>-1</sup>, an extremely high value for desert communities. This level of production is particularly high in relation to the low mean annual precipitation of approximately 70 mm. New woody tissues in trunk and branches accounted for 51.5% of the allocation of productivity in *Prosopis*, a remarkably high woody allocation for a desert plant. Only 33.6% of net primary production was allocated to leaves.

SPECIES of *Prosopis* (mesquite) form a dominant woody element in desert and semiarid communities over large areas of the world. In the southwestern United States alone *Prosopis* covers approximately 30 million hectares (Parker and Martin, 1952). Despite the widespread ecological importance of *Prosopis*, few data are available characterizing the stand biomass and productivity of mesquite woodlands. Such data are extremely important for a variety of reasons. First, available published information from plantations of *Prosopis* in South America and Pakistan suggest that net primary production rates for such stands may be remarkably high for desert communities (Salinas and Sanchez, 1971; Ahmed, 1961). Such high levels of net primary production could only be maintained in arid environments by a decoupling of productivity from the usual limiting factors of water stress and nitrogen availability. A second reason for the significance of biomass and productivity studies in *Prosopis* is the increasing importance of energy and food production from arid zone plants. There is a very great potential for *Prosopis* species in this regard, particularly in many third world countries (Felker, 1979).

In this paper we present a detailed analysis of biomass and net primary production in

stands of *Prosopis glandulosa* var. *torreyana*, an ecologically important member of the North American species in the genus. Our primary study site near the southern end of the Salton Sea in the Sonoran Desert of California is a mature mesquite woodland supported by natural ground water. Our approach in this study has been to carry out an intensive investigation of the magnitude and dynamics of the distribution of biomass in both individual plants and an entire mesquite stand. We discuss the seasonality of net above-ground primary production and the relative allocation of production to structural, photosynthetic, and reproductive tissues during the 1980 growing season. This is the first in a series of papers describing the production of *Prosopis* woodlands in relation to seasonal fluxes in water and nitrogen availability.

**MATERIAL AND METHODS**—*Species and site description*—*Prosopis glandulosa* Torr. var. *torreyana* (L. Benson) M.C. John. (often cited as *P. juliflora* var. *torreyana*) has the most widespread range of distribution of any of the North American species. While it is most characteristic of the Sonoran, Mojave and Chihuahuan Deserts, it extends north into the Great Basin and semi-arid grasslands throughout the American southwest. Typical habitats for *P. glandulosa* are washes, stream banks, alkalai sinks, or outwash plains with significant ground water supplies. Individual plants may form trees up to 10 m or more in height or they may form large spreading shrubs with no cen-

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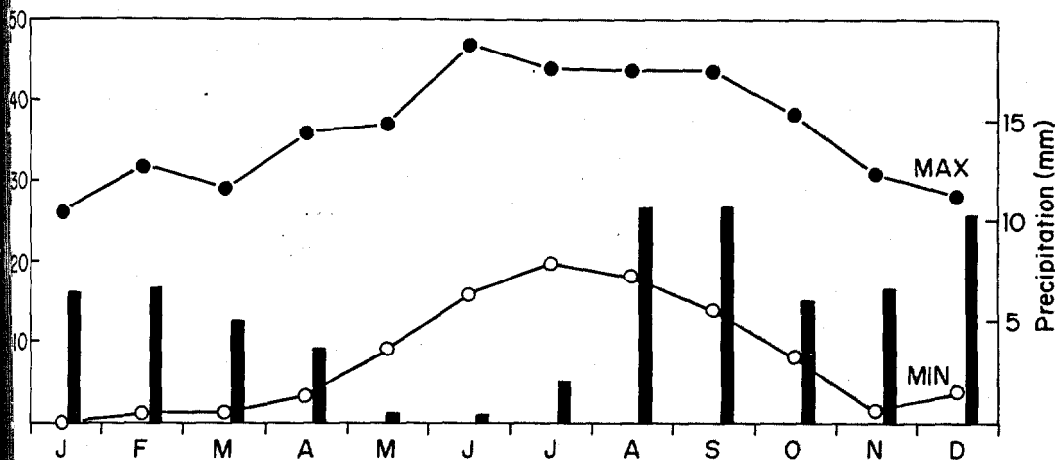


Fig. 1. Mean monthly temperature and precipitation for Brawley, California (20-yr record).

trunk. Both forms are characteristically deciduous with major growth between March and August.

Our primary study site, Harper's Well, is located west of the southern shore of the Salton River, approximately 8 km from the junction of State Highways 78 and 86. The site is on a gently sloping outwash plain from the Fish Creek Mountains, at an elevation of -30 m. The surface soil is a sandy silt with lenses of clay at regular intervals in the profile. The ground temperature appears to be relatively stable at depth, only slightly lower than that recorded more than 50 years ago when the site was the subject of an intensive hydrological study by the U.S. Geological Survey (Meinzer, 1927). Mean annual precipitation is approximately 70 mm, with the majority of rainfall typically occurring from August to March (Table 1). Mean temperatures are highest, 47°C, in July, the driest month of the year.

**Methods**—The above-ground biomass of *Prosopis glandulosa* at Harper's Well was measured by dimension analysis using modifications of techniques described by Whittaker and Marks (1975). The compartments of biomass measured were: primary and secondary trunk, main productive branches, juvenile branches (current year's growth), leaves, inflorescences, and fruits. Primary and secondary trunk were the basal parts of the tree with bark from which productive branches were cut.

Biomass of primary and secondary trunk was determined by measuring the top and bottom diameter and length of each trunk segment to calculate trunk volume. Subsample sections

("cookies") were taken from several trunks for determination of trunk specific weight. Trunk volume multiplied by average trunk specific weight ( $\text{kg dry wt m}^{-3}$ ) gave trunk dry weight. Productive branches were the main branches with thin green bark and many leaves. Juvenile twigs were the new shoots produced at the terminus of the productive branches. Regressions for all these biomass compartments were formulated from a sample of 73 branches representing each of the two growth forms, as depicted in Fig. 2. The shrub forms are shorter individuals (1-3 m) with no main central trunk, while the tree forms are taller (3-6 m) with one main central trunk.

Above-ground productivity was also measured using the techniques of Whittaker and Marks (1975) with some modifications. Sections of various diameter ("cookies") or cores were taken out of trunk and productive branches. Increment cores were extracted with an increment borer. In these "cookies" and cores the average width of 1-yr growth increments over the last 5 yrs was determined. For productive branches this average growth increment regression against diameter was combined with complete diameter and length measurements of the sample branches to result in a regression of average yearly volume of woody increment against branch basal diameter. Average yearly volume increment was multiplied by productive branch specific weight to yield a regression of yearly branch wood production against branch basal diameter. Average yearly wood production was similarly measured for trunks. Clipping production was determined first by formulating a regression between maximum leaf biomass (occurring

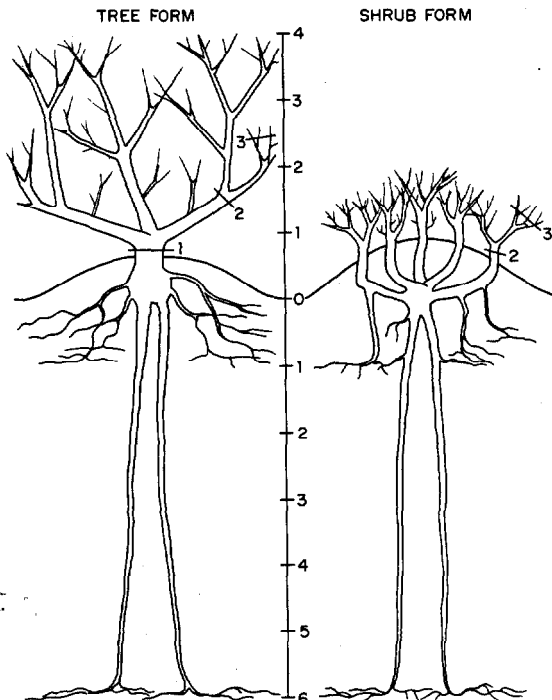


Fig. 2. A diagrammatic representation of two growth forms found in the Harper's Well population of *Prosopis glandulosa*. The numbered transects indicate primary trunk (below 1), secondary trunk (between 1 and 2), productive branches (between 2 and 3) and juvenile twigs (above 3).

in July–August, Sharifi, Nilsen and Rundel, in rev.) and productive branch basal diameter. The current twig production was determined with a regression formulated at the end of the growing season between current twig dry weight and branch basal diameter. Flower and pod production were also determined by formulating regressions between maximum flower or fruit dry weight (May and June respectively, Sharifi et al., in rev.) and branch basal diameter. Clipping production was the sum of leaf, current twig, flower, and fruit production.

Above-ground productivity and biomass were determined for ten individuals (five trees and five shrubs). The trunk sections of each individual were carefully measured to determine trunk volume, lengths, and diameters. Following trunk measurements the basal diameters of all productive branches were measured. The above described regressions were applied to the measurements for each individual to determine biomass and above-ground productivity per individual. One tree was similarly measured, then harvested to ground level to check the accuracy of the applied regression.

Biomass and production per individual were converted to stand biomass and production by first calculating biomass and productivity per canopy volume for the ten measured trees. Biomass per canopy volume was then multiplied by canopy volume per area to estimate stand biomass and productivity. *Prosopis* canopy volume per area was measured in 0.1-ha quadrats. Quadrats were placed every 100 m along two transects across the wash and along the wash. The transects were oriented to best represent the wash woodland vegetation in the area of Harper's Well. Canopy volume was determined by integrating the volume under a hemispheroidal canopy for each tree based on the radius and height of the tree ( $V = \frac{2}{3}\pi r^2 h$ ).

**RESULTS**—The Harper's Well site, dominated by phreatophytic populations of *Prosopis glandulosa*, had a mean ground coverage of 33.9% for this species, a range of 10–77% cover in individual 0.1-ha samples. This species accounts for approximately 90% of the total plant cover in the stand. Scattered shrubs of *Atriplex* and *Larrea tridentata* account for less than 4% of total coverage. Herbaceous grasses and forbs occur at only very low frequencies. Lichen and algal crusts are virtually absent.

Regression curves for the biomass of *P. glandulosa*, calculated from productive branch dimension characteristics, show the strongest association between biomass and basal diameter, while the regressions calculated from juvenile twigs show biomass to be best associated with twig length (Table 1). The two growth forms of *Prosopis* at Harper's Well, however, show different dimensional relationships and therefore require individual biomass and productivity calculations. The regression equations for total branch weight, total twig weight, bare twig weight, and leaf weight all have relatively high statistical accuracy. Regressions between branch diameter and inflorescence or pod dry weight are less accurate (see values of  $r$  and SEE in Table 1).

The predictive ability of our regression equations was evaluated by comparing the total harvested biomass of a representative tree to the estimated biomass from our regressions. Estimated biomass was within 5% of the harvested values for all above-ground compartments measured.

Total above-ground biomass in the ten plants studied showed a large range in total plant biomass, with both mean dry weight and biomass per unit area of canopy of the tree forms greater than that of the shrub forms (Table 2). The above-ground dry weight of individual plants

TABLE 1. Regression equations for *Prosopis glandulosa*. All are based on a power function,  $\log_e y = \log_e a + b \log_e x$

| y                        | x      | Form  | N  | Range (cm) | a      | b     | r     | SEE <sup>a</sup> |
|--------------------------|--------|-------|----|------------|--------|-------|-------|------------------|
| Branch total dry weight  | Diam   | All   | 73 | 0.81-7.48  | 74.888 | 2.519 | 0.944 | 0.43             |
|                          |        | Tree  | 45 | 0.81-5.62  | 66.134 | 2.676 | 0.982 | 0.26             |
|                          |        | Shrub | 27 | 1.01-7.48  | 69.205 | 2.455 | 0.970 | 0.30             |
| Leaf total dry weight    | Diam   | Shrub | 45 | 0.81-5.62  | 15.265 | 2.301 | 0.967 | 0.31             |
|                          |        | Tree  | 28 | 1.01-7.48  | 13.371 | 2.234 | 0.920 | 0.44             |
| Inflorescence dry weight | Diam   | All   | 22 | 0.81-3.81  | 3.641  | 1.713 | 0.814 | 0.62             |
|                          |        | Tree  | 16 | 0.81-3.81  | 2.994  | 1.671 | 0.798 | 0.74             |
| Seed total dry weight    | Diam   | All   | 21 | 1.38-5.62  | 12.43  | 2.283 | 0.739 | 0.830            |
|                          |        | Tree  | 15 | 1.38-5.62  | 13.65  | 2.380 | 0.777 | 0.830            |
| Juvenile twig dry weight | Length | All   | 48 | 12.5-51.5  | 0.004  | 1.740 | 0.899 | 0.337            |
|                          |        | Shrub | 35 | 10.4-40.4  | 0.011  | 1.534 | 0.914 | 0.24             |
| Juvenile leaf dry weight | Length | Tree  | 50 | 8.0-40.5   | 0.018  | 1.166 | 0.741 | 0.425            |
|                          |        | Shrub | 37 | 8.0-40     | 0.182  | 0.060 | 0.844 | 0.303            |
| Mature twig dry weight   | Length | Tree  | 75 | 8-51.5     | 0.001  | 2.130 | 0.938 | 0.333            |
|                          |        | Shrub | 35 | 8-40       | 0.002  | 1.840 | 0.933 | 0.284            |

<sup>a</sup>SEE = standard error of the estimate.

anged from 43-760 kg, corresponding to 1.9-135 kg m<sup>-2</sup> canopy area. Mean values for all plants sampled were 55.5 kg individual<sup>-1</sup> and 1.92 kg m<sup>-2</sup> canopy respectively. Biomass per unit of canopy volume (1.92 kg m<sup>-3</sup>) was less than biomass per unit canopy area. For this reason stand biomass was calculated from mean tree volume per area of ground within the wash-woodland community. Nevertheless, the mean dry weight per canopy volume is significantly greater for the tree forms

than shrub forms (Table 3). Leaf area index (LAI) was significantly higher in tree than in shrub forms of *Prosopis glandulosa*. This higher LAI resulted from layering due to greater canopy heights in the tree forms.

On a mean plant basis, *Prosopis glandulosa*

TABLE 2. Above-ground biomass for *Prosopis glandulosa* at Harper's Well during August 1980. Two standard errors of the means are shown in parentheses

|                    | Biomass                   |                              |                              | Leaf area index (m <sup>2</sup> m <sup>-2</sup> ) |
|--------------------|---------------------------|------------------------------|------------------------------|---|
|                    | (kg plant <sup>-1</sup> ) | (kg m <sup>-2</sup> /canopy) | (kg m <sup>-3</sup> /canopy) |   |
| <b>TREE FORM</b>   |                           |                              |                              |   |
| 1                  | 100.9                     | 5.53                         | 2.81                         | 2.34  |
| 2                  | 98.5                      | 3.60                         | 1.59                         | 1.74  |
| 3                  | 760.5                     | 8.88                         | 2.72                         | 3.50  |
| 4                  | 189.9                     | 5.68                         | 3.15                         | 2.29  |
| 5                  | 130.5                     | 3.91                         | 1.64                         | 1.44  |
| Mean               | 256.10 (285)              | 5.52 (1.9)                   | 2.38 (0.2)                   | 2.26 (0.8)  |
| <b>SHRUB FORM</b>  |                           |                              |                              |   |
| 1                  | 43.5                      | 3.76                         | 2.35                         | 1.86  |
| 2                  | 74.4                      | 2.11                         | 1.24                         | 1.06  |
| 3                  | 73.1                      | 2.27                         | 1.36                         | 1.03  |
| 4                  | 46.5                      | 2.11                         | 1.24                         | 1.50  |
| 5                  | 43.2                      | 1.92                         | 1.12                         | 0.94  |
| Mean               | 56.11 (16)                | 2.43 (0.7)                   | 1.46 (0.2)                   | 1.28 (0.4)  |
| <b>INDIVIDUALS</b> |                           |                              |                              |   |
| Mean               | 156.10 (144)              | 3.98 (1.5)                   | 1.92 (0.4)                   | 1.77 (0.5)  |

1 = harvested tree.

TABLE 3. Summary of mean structural characteristics for shrub and tree forms of *Prosopis glandulosa* at Harper's Well

|   | Shrub form |    | Tree form |
|---|------------|----|-----------|
| Canopy height (m)                                 | 2.0        | ** | 3.3       |
| Canopy volume (m <sup>3</sup> )                   | 42.2       | *  | 121.6     |
| Canopy area (m <sup>2</sup> )                     | 24.8       |    | 41.3      |
| <b>Biomass allocation (%)</b>                     |            |    |           |
| Trunk   | 30.1       |    | 41.8      |
| Branch  | 51.9       |    | 52.0      |
| Twigs   | 1.3        |    | 0.7       |
| Leaves  | 10.1       | *  | 7.6       |
| Reproduction                                      | 10.9       | *  | 4.3       |
| Leaf area index (m <sup>2</sup> m <sup>-2</sup> ) | 1.3        | *  | 2.3       |
| Biomass/tree (kg plant <sup>-1</sup> )            | 56.1       |    | 256.0     |
| Biomass/canopy area (kg m <sup>-2</sup> )         | 2.4        |    | 5.5       |
| Biomass/canopy volume (kg m <sup>-3</sup> )       | 1.5        | *  | 2.4       |
| <b>Allocation of NPP (%)</b>                      |            |    |           |
| Wood  | 53.8       |    | 47.8      |
| Twigs   | 4.3        |    | 2.9       |
| Leaves  | 31.6       |    | 33.5      |
| Reproduction                                      | 34.3       | *  | 16.4      |
| Production/tree (kg plant <sup>-1</sup> )         | 17.8       |    | 60.5      |
| Production/canopy area (kg m <sup>-2</sup> )      | 0.8        |    | 1.3       |
| Production/canopy volume (kg m <sup>-3</sup> )    | 0.5        |    | 0.5       |
| Biomass accumulation ratio                        | 3.1        | *  | 4.1       |

\*\* = significant difference at P = 0.05.

TABLE 4. Net annual above-ground production of *Prosopis glandolosa* at Harper's Well. Two standard errors of the means are shown in parentheses

|                 | Woody increment<br>(kg plant <sup>-1</sup><br>yr <sup>-1</sup> ) | Clipping production<br>(kg plant <sup>-1</sup><br>yr <sup>-1</sup> ) | Leaf production<br>(kg plant <sup>-1</sup><br>yr <sup>-1</sup> ) | Total production<br>(kg plant <sup>-1</sup><br>yr <sup>-1</sup> ) | Production/<br>canopy area<br>(kg m <sup>-2</sup> yr <sup>-1</sup> ) | Biomass<br>accumulation<br>ratio BAR |
|-----------------|--|--|--|---|--|--------------------------------------|
| TREE FORM       |  |  |  |   |  |                                      |
| 1               | 13.0   | 9.0  | 8.7  | 22.0  | 1.21   | 4.59                                 |
| 2               | 14.1   | 15.1   | 7.6  | 29.2  | 1.07   | 3.37                                 |
| 3               | 94.6   | 82.4   | 57.3   | 177.0   | 2.07   | 4.30                                 |
| 4               | 23.0   | 17.7   | 17.1   | 40.7  | 0.97   | 4.42                                 |
| 5               | 17.4   | 16.3   | 9.3  | 33.7  | 1.01   | 3.87                                 |
| Mean            | 32.4 (35.0)  | 28.1 (30.5)  | 20.0 (21.2)  | 60.5 (65.2)   | 1.26 (0.23)  | 4.11 (0.75)                          |
| SHRUB FORM      |  |  |  |   |  |                                      |
| 1               | 6.7  | 7.4  | 4.2  | 14.1  | 1.22   | 3.09                                 |
| 2               | 11.2   | 12.9   | 7.3  | 24.1  | 0.68   | 3.09                                 |
| 3               | 9.3  | 11.8   | 6.6  | 21.1  | 0.66   | 3.37                                 |
| 4               | 8.4  | 8.6  | 5.9  | 17.0  | 0.77   | 2.74                                 |
| 5               | 6.6  | 6.2  | 4.1  | 12.8  | 0.57   | 3.38                                 |
| Mean            | 8.4 (1.9)  | 9.4 (2.9)  | 5.6 (1.4)  | 17.8 (4.8)  | 0.78 (0.08)  | 3.14 (0.23)                          |
| ALL INDIVIDUALS |  |  |  |   |  |                                      |
| Mean            | 20.4 (17.7)  | 18.8 (15.1)  | 12.8 (16.0)  | 39.1 (32.7)   | 1.02 (0.14)  | 3.62 (0.42)                          |

allocated the largest amount of standing biomass to branch wood (51.9%). Trunk wood accounts for 33.1%, while current twigs, leaves, and reproductive tissues had 1.0, 8.7, and 6.3% respectively of the biomass. The allocation of dry weight to biomass compartments varied between plants. Tree 4, for example, had long trunk sections so that its percentage of biomass in such tissues (50.7%) was high. Overall there was a much lower relative allocation of biomass to trunk tissues of 33.1%. There was no significant difference between tree and shrub forms in the allocation of biomass to trunk and productive branches (Table 3). Shrub forms however allocate significantly more relative biomass to leaves (10.1%) than the tree forms (7.1%). Yet the LAI of tree forms was higher than shrub forms due to the greater leaf biomass of tree forms and the taller canopy of tree forms resulting in canopy layering. Reproductive effort (relative allocation of biomass to reproductive organs) was variable between individuals with shrub forms having a significantly greater reproductive effort. Total biomass and productivity per individual is predominantly higher in tree forms than shrub forms although these differences are not significant.

Annual above-ground productivity for 1980 is shown in Table 4 for all individuals studied. Most production in these plants occurs through woody increment (sum of trunk plus productive branch wood increment). Shrub forms had a lower above-ground productivity rate than the tree forms for all compartments although

productivity per canopy volume is similar between tree and shrub forms. Clipping production (sum of leaf and juvenile twig increment) was approximately 50% of total production for both growth forms. The biomass accumulation ratio (BAR), calculated as total above-ground biomass over net annual above-ground production, is significantly lower in shrubby forms than in trees (Table 3), suggesting slower growth rates.

Above-ground biomass and net primary production for mesquite at Harper's Well is represented on a stand basis in Table 5. Stand above-ground biomass ranged from 3,500 kg ha<sup>-1</sup> in the fringe of the stand to 21,700 kg ha<sup>-1</sup> along the main wash area. A similar range in above-ground productivity from the stand fringe (900 kg ha<sup>-1</sup> yr<sup>-1</sup>) to the main wash area (5,700 kg ha<sup>-1</sup> yr<sup>-1</sup>) was observed. The average above-ground biomass of 14,000 kg ha<sup>-1</sup> and average above-ground production of 3,600 kg ha<sup>-1</sup> yr<sup>-1</sup> are extremely high in relation to the low rainfall regime in which they grow.

DISCUSSION—Although there is an increasing body of literature describing biomass and productivity for natural plant communities, relatively few data are available for North American desert communities (Szarek, 1979; Ehleringer and Mooney, in press). However, some comparisons with these limited data are possible. Overall, the net above-ground productivity (NPP) of *Prosopis* stands at Harper's Well are far higher than the range of above-ground NPP for other desert communities

TABLE 5. Comparative biomass and productivity of desert woodlands and shrub communities

| Dominant taxon                 | Community                   | Stand age | Mean precipitation (mm yr <sup>-1</sup> ) | Above-ground biomass (kg ha <sup>-1</sup> ) | Net primary production (kg ha <sup>-1</sup> yr <sup>-1</sup> ) | Biomass accumulation ratio | Reference                   |
|--------------------------------|-----------------------------|-----------|---|---|--|----------------------------|-----------------------------|
| <i>Prosopis glandulosa</i>     | wash/woodland, California   | 25        | 70  | 13,973                                      | 3,695  | 3.85                       | present study               |
| <i>P. velutina</i>             | bajada, Mexico              |           | 300                                       | 5,012                                       |  |                            | Klemmedson and Barth, 1975  |
| <i>P. glandulosa</i>           | bajada, Mexico              |           | 300                                       | 2,890                                       |  |                            | Klemmedson and Barth, 1975  |
| <i>Larrea tridentata</i>       | desert scrub, California    | 70        | 440                                       | 3,300                                       | 910  | 3.65                       | Chew and Chew, 1975         |
| <i>L. tridentata</i>           | desert scrub, Arizona       | 12        | 200                                       | 3,892                                       | 917  | 4.24                       | Whittaker and Neiring, 1975 |
| <i>Cercidium microphyllum</i>  | wash woodland, Arizona      | 25        | 278                                       | 3,429                                       | 512  | 6.69                       | Whittaker and Neiring, 1975 |
| <i>C. microphyllum</i>         | bajada, Arizona             |           | 250                                       | 5,028                                       |  |                            | Klemmedson and Barth, 1975  |
| <i>Artemisia tridentata</i>    | Great Basin sage, Nevada    | 17        | 250                                       | 3,679                                       | 1,128  | 3.23                       | Balgh et al., 1974          |
| <i>Ambrosia dumosa</i>         | Great Basin sage, Nevada    |           | 190                                       | 3,004                                       | 580  | 5.18                       | Turner and McBrayer, 1974   |
| <i>Triplex vesicaria</i>       | chenopod scrub, Australia   | 50        | 180                                       | 900   | 300  | 3.0                        | Noble, 1977                 |
| <i>Sarcobatus vermiculatus</i> | desert scrub, Negev, Israel |           |   | 763   |  |                            | Evenari et al., 1975        |
| <i>Artemisia herba-alba</i>    | desert scrub, Algeria       |           |   | 1,367                                       |  |                            | Rodin et al., 1972          |
| <i>Sarcobatus vermiculatus</i> | semidesert, Iran            |           |   | 2,600                                       |  |                            | Moore and Bhadresa, 1978    |

Table 5). Considering the low mean annual precipitation of approximately 70 mm at Harper's Well, above-ground net primary production is higher than one would expect from classical relationships between precipitation and productivity (Whittaker, 1978). This enhanced productivity and biomass of *Prosopis* is clearly related to the phreatophytic nature of the water relations in our study stands at Harper's Well, which allows uncoupling of production from limitation by water resources. Investigations currently in progress have demonstrated that ground water supplies the majority of water utilized by mesquite at Harper's Well. A pattern of phreatophytic utilization of water has been described for *P. tamarugo* in northern Chile (Mooney et al., 1980), and has been generally inferred for other species of *Prosopis* in rainfall areas.

On the basis of an individual plant or on a canopy coverage basis, the above-ground NPP of *Prosopis* far exceeds that of other desert shrubs and trees which have been studied. The above-ground productivity per plant at Harper's Well was 39.6 kg yr<sup>-1</sup> (Table 4) in

comparison to values such as 0.53 kg yr<sup>-1</sup> for *Cercidium microphyllum* in Arizona (Whittaker and Neiring, 1975) and 0.90 kg yr<sup>-1</sup> for individual *Larrea tridentata* (Chew and Chew, 1975). On a canopy area basis *Prosopis* produced 1.02 kg m<sup>-2</sup> yr<sup>-1</sup>, 10 times the level of 0.09 kg m<sup>-2</sup> yr<sup>-1</sup> for *Larrea* reported by Whittaker and Neiring (1975).

Our stand values of above-ground NPP for *Prosopis* are still lower than those reported for plantations of other species of the genus. High-density plantations of seven *Prosopis* taxa in Pakistan have been found to yield up to 8,000 kg ha<sup>-1</sup> yr<sup>-1</sup> (equal to 0.8 kg m<sup>-2</sup> yr<sup>-1</sup>) of wood in an area of 250 mm yr<sup>-1</sup> precipitation (calculated from Ahmed, 1961, using a wood specific gravity of 0.7). Tree densities in these stands were as high as 11,000 trees per hectare. Studies of *P. tamarugo* in the Pampa del Tamarugal of the northern Atacama Desert in Chile have reported NPP of pods and leaves alone of up to 12,700 kg ha<sup>-1</sup> yr<sup>-1</sup> or 1.27 kg m<sup>-2</sup> yr<sup>-1</sup> (Salinas and Sanchez, 1971). This high level of leaf and pod production (1.27 kg m<sup>-2</sup> yr<sup>-1</sup>) seems remarkable since leaves and re-

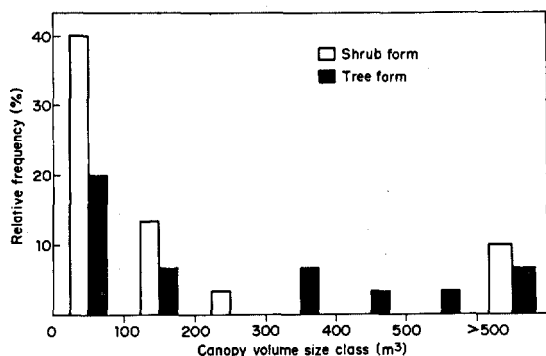


Fig. 3. Frequency histogram of *Prosopis glandulosa* size classes at Harper's Well, California.

productive tissues accounted for only about 58% of the NPP ( $0.59 \text{ kg m}^{-2} \text{ yr}^{-1}$ ) at Harper's Well (see Table 3).

Structural differences between shrub and tree forms of *Prosopis glandulosa* at Harper's Well are summarized in Table 3 and Fig. 2. Mean height and volume of canopy are both greater in trees than shrubs. Biomass per unit of canopy volume and BAR are also significantly greater. While LAI is significantly higher in trees, shrubs allocate a significantly greater proportion of their biomass to leaves, as well as to reproductive structures, than do trees.

Field surveys of the relative occurrence by size class of shrub and tree forms of *Prosopis* at Harper's Well indicate a preponderance of smaller individuals (Fig. 3). Shrub forms dominate the smaller size classes while trees are relatively more frequent in the larger classes. Huge shrub-form individuals with greater than  $500 \text{ m}^3$  canopy volumes occur around low dunes adjacent to our stands. These canopies form rings around the margins of the dune, with central areas composed almost entirely of dead woody tissues.

Our regression analyses of above-ground biomass and production from basal diameter provide an accurate basis to determine above-ground NPP. A validation test of our estimates was conducted by totally harvesting a tree estimated to be 181.6 kg in weight. Our harvested biomass was 189.9 kg, only 4.4% above the estimated biomass. Since considerable amounts of stem wood is commonly buried in large *Prosopis* mounds, these figures do underestimate total production of non-root tissues. To date we have only a preliminary estimate of what below-ground stem and root biomass may be, based on our complete harvesting of a representative tree-form individual. The total live above-ground biomass of this individual was

189.9 kg (see Table 2). Careful excavation, however, found 49.2 kg of additional trunk biomass below-ground, almost 30% of the above-ground total. Since 33% of the mean above-ground production occurred in the trunk, a doubling of actual trunk biomass (to include below-ground trunk tissues) would increase our estimates of above-ground NPP by approximately 15%, or  $4,420 \text{ kg ha}^{-1} \text{ yr}^{-1}$ . An addition of an estimated below-ground production could increase NPP to over  $8,000 \text{ kg ha}^{-1} \text{ yr}^{-1}$ .

The allocation of biomass to new tissues during the 1980 growing season for *P. glandulosa* is quite consistent in both tree and shrub forms. New woody tissues of pre-existing branches and trunks together accounted for 51.5% of new NPP, with values ranging from 41–59% in the ten individuals studied. This is a surprisingly large allocation to woody tissue for a desert plant. The next largest category of allocation was to new leaf tissues which comprised 32.6% of new production (Table 3). Such allocation relationships are similar to those of other more mesic forest types (Whittaker 1966).

While structural differences between tree and shrub forms of *P. glandulosa* are highly significant in many respects, it is difficult to determine whether this dichotomy is genetic or habitat-related. Shrub forms are characteristic of the outer edges of the mesquite stands at Harper's Well, while tree forms predominate near the wash adjacent to the well itself. Stands to the south where the water table is at a depth of 12 m are dominated by low shrubby *Prosopis* averaging only 1 m in height (Meinzer, 1927). Thus, ground water relationships may be a very important factor influencing an individual's development into a tree or a shrub form. The significance of genetic variability cannot be ignored, however. The genus *Prosopis* is well-known for intraspecific morphological variation (Peacock and McMillan, 1965; Graham, 1960). Such variability is apparent even in common garden plantations (Felker, pers. commun.).

The data collected during this investigation suggest that wash woodlands dominated by *Prosopis glandulosa* are characterized by high above-ground biomass and high above-ground productivity in comparison to other desert communities with similar environmental conditions. Mesquite above-ground productivity at Harper's Well is particularly high in relation to the low rainfall which characterizes the upper Sonoran Desert of California. Therefore, mesquite productivity seems to be decoupled from limitation by surface water resources.

These productivity data indicate a high potential for production of wood, leaves, and pods in managed stands of mesquite in marginal agricultural areas with low surface water resources. Investigations are continuing to evaluate seasonal productivity, phenology, and the magnitude of herbivory for *Prosopis glandulosa* at Harper's Well.

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