



## Stemflow, throughfall and channelization of stemflow by roots in three Chihuahuan desert shrubs

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(Received 14 June 1994, accepted 22 August 1994)

Three studies were conducted to examine precipitation–vegetation relationships in the multi-stemmed shrubs *Larrea tridentata*, *Prosopis glandulosa* and *Flourensia cernua* in a desert ecosystem. We measured stemflow and throughfall as affected by bulk precipitation, canopy architecture and stem-angles. Using fluorescent dye, we traced root channelization of stemflow water. Stepwise regression analysis showed that the best one-variable model for stemflow in *L. tridentata* was canopy volume, which accounted for 87% of variation. The best one-variable model for stemflow in *P. glandulosa* and *F. cernua* was canopy area, which accounted for 82% of variation in both species. Stemflow data from winter and summer months were statistically compared to determine the influence of leaves on stemflow generation in *P. glandulosa* and *F. cernua*. Stemflow amounts collected during winter months do not differ significantly from those of summer months demonstrating that in these winter deciduous species the absence of leaves during winter months does not affect generation of stemflow. Analysis of variance showed that the percentage of throughfall was different among species suggesting that variations in canopy characteristics could explain, in part, these interspecific throughfall differences. Both stem-angle and stem-length had a significant effect on stemflow generation in *F. cernua* and *L. tridentata*, whereas there was only a significant relationship between stem-angle and stemflow in *P. glandulosa*. Analysis of rhodamine-B dye distribution under shrubs indicated that root channels are preferential pathways for movement of stemflow water into soil, and that this water is potentially the source of soil moisture which allows shrubs to remain physiologically active under drought conditions.

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**Keywords:** stemflow; throughfall; root channelization; *Larrea tridentata*; *Prosopis glandulosa*, *Flourensia cernua*, Chihuahuan Desert

### Introduction

Fertility under desert shrubs nutrient rich 'islands' is well documented (Garcia-Moya & Mckell, 1970; Lajtha & Schlesinger, 1986; Lajtha & Klein, 1988). However, desert

shrubs not only affect the accumulation of nutrients but also the interception, infiltration and storage of water. Although there is information available regarding precipitation-vegetation interactions in forest (Helvey & Patric, 1965; Helvey, 1967; Jackson, 1975), grassland vegetation (Burgy & Pomeroy, 1958; Couturier & Ripley, 1973) and desert vegetation (Glover *et al.*, 1962; Pressland, 1973, 1976; West & Gifford, 1976; Tromble, 1983, 1987; Nulsen *et al.*, 1986; Navar & Bryan, 1990; Navar, 1993; Mauchamp & Janeau, 1993), most of these studies have focused on the importance of rainfall interception by vegetation and subsequent evaporation of that water. With the exceptions of those studies by Glover *et al.* (1962) and Nulsen *et al.* (1986), little research has been carried out on factors affecting stemflow and throughfall, and the redistribution of this water in the soil as it is affected by shrubs.

Since water is limited in semi-arid lands, intercepted water, once partitioned as stemflow and throughfall, could be an important source of soil moisture (Tromble, 1987). Crabtree & Trudgill (1985) concluded that stemflow is only a small part of storm input; however, stemflow drainage rapidly concentrates large volumes of water at the base of trees or shrubs. Stemflow depends not only on precipitation characteristics such as intensity, duration and amount, but also on characteristics of vegetation such as type, morphology and distribution of cover (Branson *et al.*, 1981; Crockford & Johnson, 1983; Crockford & Richardson, 1983, 1987, 1990*b*; Van Elewijck, 1989). Crockford & Richardson (1983, 1987, 1990*b*) reported that the main factors affecting stemflow in a eucalypt forest and *Pinus radiata* D. Don plantation were crown size, tree size, leaf shape, branch angle, bark type and flow path obstructions.

*Larrea tridentata* (DC). Coville (creosotebush), *Prosopis glandulosa* (Swartz) DC. (mesquite), and *Flourensia cernua* DC. (tarbush) are now dominant species in plant communities on what were large areas of grasslands in the Jornada Basin of Southern New Mexico before the turn of the century (Buffington & Herbel, 1965). Creosotebush, mesquite and tarbush share many traits common to water stress tolerant species. However, these three species differ in functional and structural characteristics (e.g. leaf phenology, canopy size and volume, and root system distribution among others) which should result in different patterns of response and persistence as a result of disturbance (Grime, 1977). We studied water redistribution in these three species of shrub in order to evaluate the importance of morphological and phenological differences in desert shrub species as factors affecting stemflow and throughfall.

Several arid zone shrub and small tree species are adapted to intercept relatively high amounts of rainfall, which is redistributed via stemflow to deep layers in the soil profile along root channels (Pressland, 1976). This deep infiltrated water is considered as a possible source of available moisture for plant growth in desert ecosystems even in the absence of accessible water in the upper soil profile (Tromble, 1987). Glover *et al.* (1962), in a study of savanna vegetation in Kenya, described how stemflow water was redistributed and the effect of stemflow water on grass growth beneath the tree canopy in arid and semi-arid ecosystems. Nulsen *et al.* (1986) found that the canopy of mallee vegetation (a shrub-eucalypt association) intercepts water and redistributes it into soil via stemflow at depths as great as 28 m, and that this stored water is possibly used during the dry summer (Specht 1957), cited by Nulsen *et al.* (1986), observed that 'taller and presumably deeper rooted species growing in arid zones channeled water to greater depth than shorter and shallow rooted plants'. We hypothesized that stemflow water in desert shrubs is distributed to deep soil storage by following preferential flow paths along root channels.

If water redistribution and root channelization represents a substantial fraction of the rainfall intercepted by shrub canopies, this could be an important factor in the ability of shrubs to withstand drought conditions.

## Materials and methods

### *Study area*

The primary study area was located on a watershed that varies in elevation from approximately 1200 to 1400 m on the Jornada Long-Term Ecological Research (LTER) site situated on the New Mexico State University College Ranch and USDA Jornada Experimental Range, 37 km north of Las Cruces, New Mexico. The average annual precipitation is 230 mm, with 52% occurring in summer (July – September) from intense and short duration convective storms. The remaining precipitation occurs as scattered low-intensity rainfall, primarily from frontal storms throughout (Nash & Daugherty, 1990). The potential evapo-transpiration is 2290 mm.

### *Stemflow, throughfall and precipitation relationships*

To determine the fraction of rainfall partitioned as stemflow and throughfall, and also to examine the influence of some canopy parameters (canopy size, canopy volume) on stemflow and throughfall, we selected 13 creosotebush (*Larrea tridentata*), 10 tarbush (*Flourensia cernua*), and 12 mesquite (*Prosopis glandulosa*) plants. A variable number of shrubs was selected in order to achieve a representation of the range of sizes of the species within the study area. Variables that were measured on each shrub included: canopy area, shrub height and canopy volume. Canopy area was calculated by taking the east–west and north–south diameters through the centre of the fullest part of the canopy. Shrub height was measured at the centre of the canopy. Canopy volume for creosotebush was calculated by using the formula for an inverted cone. Canopy volume for mesquite and tarbush were calculated using an upper-half prolate spheroid formula (Ludwig & Reynolds, 1975).

For stemflow collection, all plants in the study were fitted with collection funnels around the main stems or at the root crown. Funnels were sealed to the stem with silicone sealant. The collection funnels were connected by a plastic tube to covered containers where stemflow was stored. Throughfall was recorded with glass containers (canning jars) fitted with plastic funnels. The funnels were placed in the mouth of the jar and covered with a sieve to prevent insects and debris from entering the jar. These jars were placed at mid-point in the shrub canopies. Rainfall was measured by three similar jars with funnels randomly placed in open intershrub spaces within each study area. The average water depth in the intershrub containers was taken as the incoming precipitation. Stemflow, throughfall and precipitation volumes were recorded immediately after each rainfall event from 22 August 1990 to 26 March 1991 (first rainfall period) and from 1 July 1991 to 4 March 1992 (second rainfall period). Once stemflow and throughfall fractions were calculated for each shrub, they were related to total precipitation per storm as recorded in the open area. These fractions were calculated by subtracting them from the total precipitation estimated as intercepted by the canopy of each shrub (gross precipitation), and then each fraction was transformed from volume (ml) to percentage. Depending on the factor to be emphasized, the relationship between interception losses ( $I$ ), gross precipitation ( $P$ ), stemflow ( $SF$ ) and throughfall ( $TF$ ) were determined by the following equations (Branson *et al.*, 1981):

$$I = P - SF - TF \quad (\text{Eqn 1})$$

$$SF = P - TF - I \quad (\text{Eqn 2})$$

$$TF = P - SF - I \quad (\text{Eqn 3})$$

### *Stem-angle and stemflow*

To study the effect of stem-angles on stemflow amounts, three plants of each shrub species (creosotebush, mesquite and tarbush) were randomly selected from the set of plants previously selected in the first experiment. Stem-angles from horizontal were measured with an inclinometer (1 m<sup>2</sup> frame). This frame, constructed with PVC, was sub-divided by placing several inclined strings crossing from one side to one apex at the bottom of the frame at angles of 75, 60, 45, 30 and 15°. The estimation of stem-angles was accomplished by placing the frame vertically on the ground and moving it around the plant to align the stems with string angles on the frame.

Stemflow volumes for each individual stem (different angle) were directly recorded as described for whole shrub measurements. Three rainfall events were used to examine stem-angle effects (20 August, 24 August and 18 September 1992). In addition, other variables measured in this study were length of stems and average stem-diameter. This average was calculated by including both the diameter of main stems, where stemflow collection funnels were placed, and the diameter of secondary branches converging on main stems.

### *Root channelization*

To assess redistribution of stemflow into the soil profile through root channels, rhodamine-B dye powder (Nulsen *et al.*, 1986) was sprinkled on the surface around the base of the trunk (at the root crown) of three selected shrubs of each species. These shrubs were then subjected to simulated rainfall. The approximate depth of water applied to each shrub was 40 mm, which was pumped from a mobile water tank and applied through a sprinkler head attached to a 3 m high PVC pipe placed near each shrub. Two small plastic containers of known volume were placed within the area irrigated, and application of water was stopped when the volume of water inside each container reached 40 mm. Following simulated rainfall, pits were dug adjacent to the treated shrubs in order to map the movement of the dye. Root diameters were recorded for each plant with vernier calipers. Canopy parameters of plants in this part of the study were obtained by the same methodology as in the stemflow measurements. Wetting of soil was mapped by the presence of dye.

### *Statistical analyses*

Regression analysis was used to analyse the relationship between stemflow, as percentage of precipitation ( $Y$ ), and precipitation in mm ( $X$ ) for creosotebush, mesquite and tarbush separately (Lentner, 1975). Stepwise regression analysis using the maximum  $R^2$  improvement procedure was used both to examine the effects of canopy area and canopy volume ( $X$ ) on stemflow ( $Y$ ), and to examine the effects of stem-angle and stem-length ( $X$ ) on stemflow ( $Y$ ), in each species, respectively (Neter *et al.*, 1989; SAS Institute, 1989; Littell *et al.*, 1991). Analysis of variance (ANOVA) was used to evaluate the differences in stemflow and throughfall, as percentage of precipitation, to evaluate the differences in canopy area and canopy volume and to evaluate the differences in stem-angle, stem-diameter and stem-length among species (Lentner, 1975; SAS Institute, 1989). Data on the depth and distribution of rhodamine-B under the soil surface from the root water channelization study were not analysed statistically.

## Results and discussion

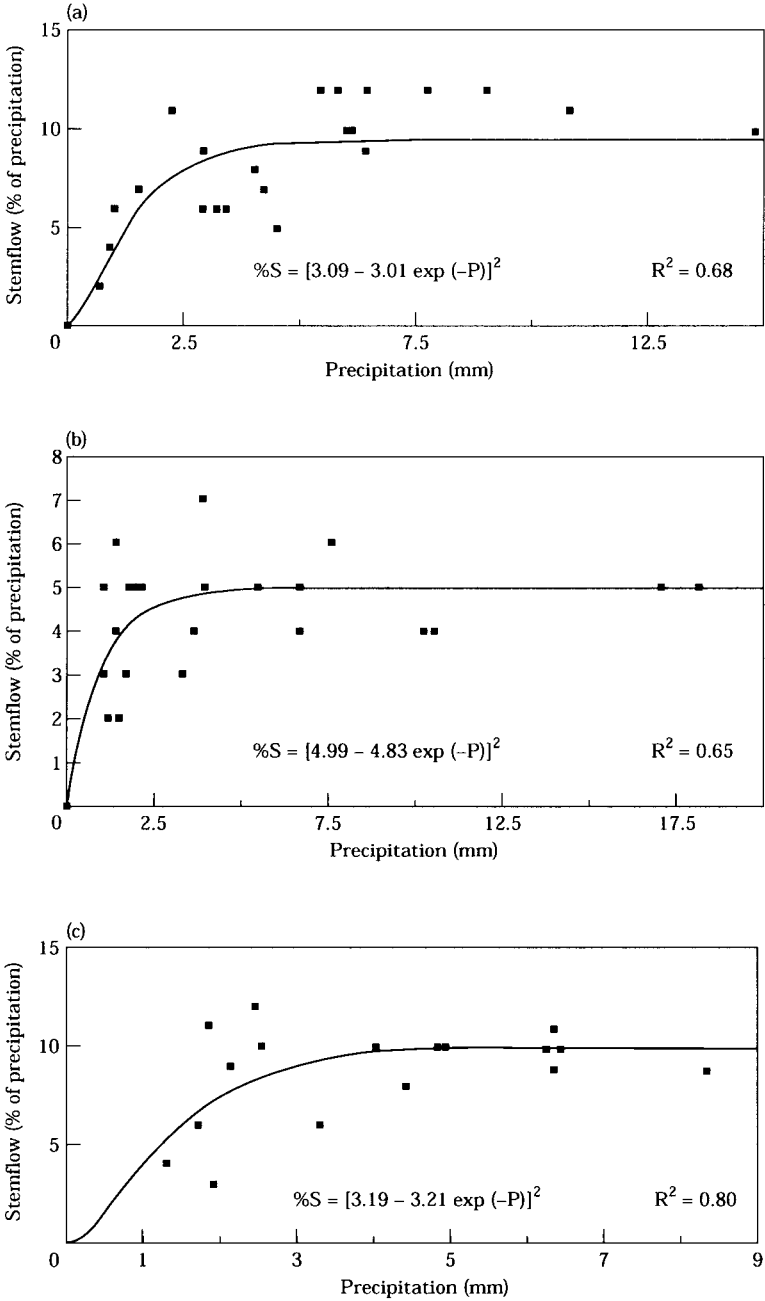
Stemflow amounts in *L. tridentata* averaged 10% of total precipitation with a range of 2–27% in both summer and winter. Similarly, in *F. cernua* stemflow averaged 10.6% in summer and 10.5% in winter with a range of 3–28% and 5–22%, respectively. Average stemflow in *P. glandulosa* was approximately half that measured in other shrubs: 5.4% and 5.3%, range 2–15% and 2–13% for summer and winter rainfall, respectively. Stemflow in *P. glandulosa* was similar to estimates for a dry sclerophyll eucalypt forest (5.6%) and *L. tridentata* and *F. cernua* were similar to stemflow estimates for a *Pinus radiata* plantation in south-eastern Australia (Crockford & Richardson, 1990b). These percentages are considerably lower than stemflow of 42% and 40% estimated for mulga (*Acacia aneura* F. Muell) in arid Australian woodland (Slatyer, 1965; Pressland, 1973), and the average of 32% for malle (*Eucalyptus* scrub formation) in south-western Australia (Nulsen *et al.*, 1986). Stemflow in *P. glandulosa* and the other Chihuahuan desert shrubs were higher than the 1.8% for brigalow (*Acacia harpophylla* F. Muell. ex Benth.) in a subtropical semi-arid forest in central Queensland (Tunstall & Connor, 1981), and also 1.85% for a rainforest in Malaysia (Sinun *et al.*, 1992).

Regression of stemflow as a percentage of precipitation and precipitation depth giving the best fit were similar curvilinear equations (Fig. 1). The best fit for each equation was selected in terms of maximum  $R^2$  values after testing several regression models. These responses are curvilinear since the initiation of stemflow occurs only after the canopies have become saturated, as was reported by Enright (1987).

The slope of percentages of stemflow and the rainfall threshold after which stemflow started to be channelled were different for each species. For creosotebush the curve was asymptotic at stemflow equal to 9.5% (Fig. 1(a)). For mesquite the curve was asymptotic at stemflow equal to 5% (Fig. 1(b)) and for tarbush the curve was asymptotic at stemflow equal to 10.2% (Fig. 1(c)). These results are similar to those reported by Crockford & Richardson (1990b).

The threshold amount of precipitation required before stemflow was initiated ranged between 1.3 mm and 1.8 mm in the three species. For creosotebush and tarbush the curves rise smoothly at rainfalls above 1.3 mm and for mesquite the curve rises after a rainfall threshold of approximately 1.8 mm. These values, although slightly lower, are comparable to the precipitation threshold of 1.5 mm reported by Pressland (1973) for *A. aneura*, with the 1–2 mm of rain reported by Enright (1987) for *Rhopalostylis sapida* H. Wendl. & Drude in south New Zealand and with the 2 mm reported by Navar (1993) for the *Acacia farnesiana*–*Prosopis laevigata* scrub in north-eastern Mexico. These results also suggest that requirements to wet the canopy for each species must be satisfied before stemflow occurs. Therefore, it is clear that rain events of different sizes can generate similar quantities of stemflow and *vice versa*. There was a tendency for the curves of all three species under study to remain relatively flat at precipitation amounts in excess of 6 mm. Accordingly to Pressland (1973), this tendency can be attributed, in part, to stem and leaf drip. Once the foliage and bark is wet, some water droplets fall directly to ground instead of being funnelled to the base of shrubs by stems. A similar situation was suggested by Crockford & Richardson (1990b) in their study of a dry sclerophyll eucalypt forest and a *Pinus radiata* plantation.

Stemflow as percentage of precipitation was significantly different among species (ANOVA  $p < 0.001$ ) which is attributable to morphological differences among the species. Canopy components with different characteristics for each species have to be wetted before stemflow occurs (Pressland, 1973). As suggested for *Diospyros texana scheele* and *A. farnesiana*–*P. laevigata* by Navar & Bryan (1990) and Navar (1993), it is likely that variables such as leaf type and position, bark roughness, branch hydrophobicity, total stem area and number of stems and their inclination could account for these differences.



**Figure 1.** Relationship between stemflow as percentage of precipitation and total precipitation (mm) for (a) creosotebush (*Larrea tridentata*), (b) mesquite (*Prosopis glandulosa*) and (c) tarbush (*Flourensia cernua*).

### *The effect of canopy parameters on stemflow*

Stepwise regression analysis (SAS Institute, 1989) was used to determine the effects of canopy volume and canopy area on stemflow in each species. The best one-variable linear model for stemflow in *L. tridentata* was canopy volume which accounted for 87% of the variation ( $R^2 = 0.87$ ;  $p < 0.001$ )  $S = 17.0 + 20.5 V$  (where  $S$  = stemflow in l and  $V$  is canopy volume in  $m^3$ ). This suggests that plant components of creosotebush such as leaves and stems implicitly included in the canopy volume variable may have significance in the generation of stemflow.

The best one-variable linear model for stemflow in *P. glandulosa* and *F. cernua* was canopy area, which accounted for 82% of the variation ( $R^2 = 0.82$ ;  $p < 0.001$ ); in *P. glandulosa*  $S = 7.6 + 10.3 A$ ; in *F. cernua*  $S = 4.8 + 3.9 A$  (where  $S$  = stemflow in l and  $A$  = canopy area in  $m^2$ ). These relationships suggest that the effects of twigs and terminal branches included in the total projected canopy area may be more significant than leaves in stemflow generation in these species. *P. glandulosa* has sparse leaf cover and leaves are pinnately compound. *F. cernua* has fewer leaves scattered along the stem in comparison to *L. tridentata* which has dense aggregations of small leaves on terminal branches.

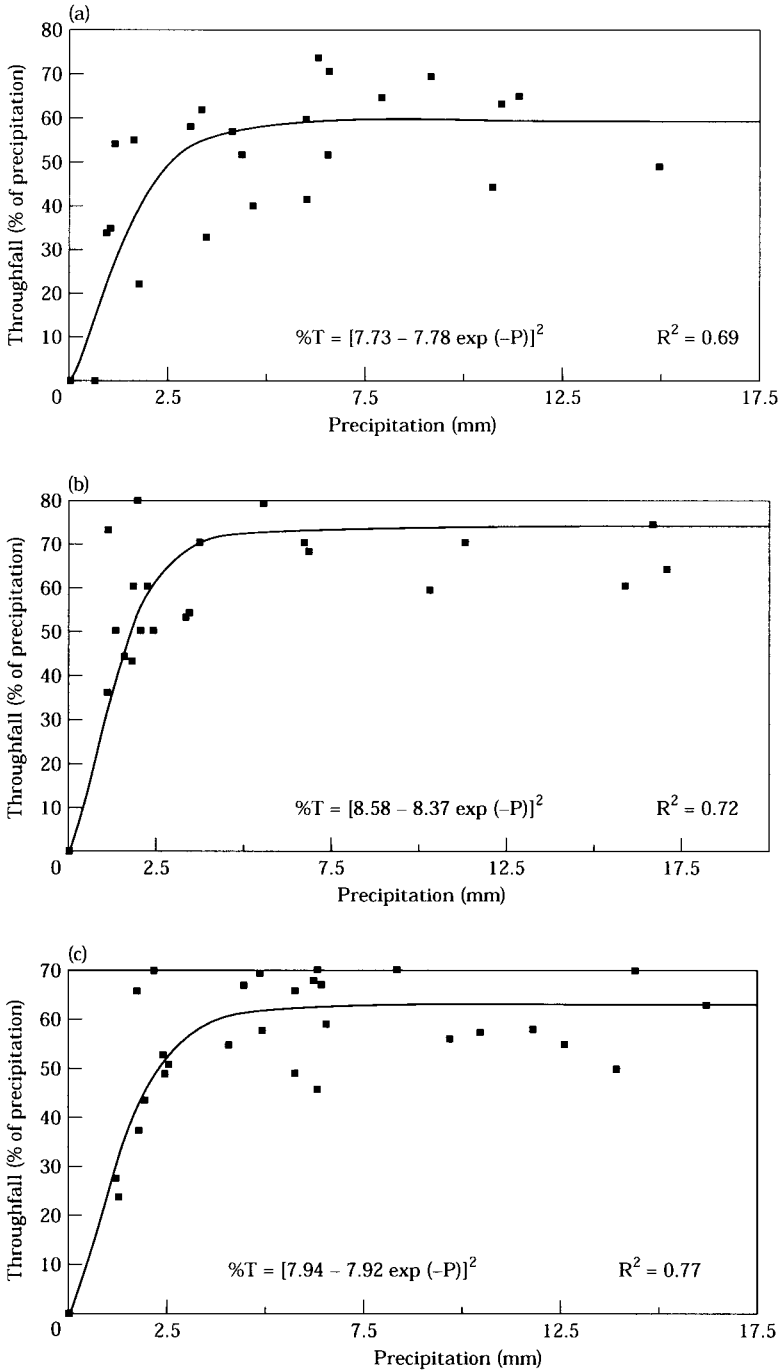
To determine the influence of leaves on stemflow generation in *P. glandulosa* and *F. cernua*, stemflow data from winter months (December–March), when these deciduous shrubs are without leaves, were compared with stemflow data from the summer months (July–November) by ANOVA for each species. There were no differences in stemflow percentages in the three species in winter and summer. The absence of seasonal differences in stemflow in the winter deciduous species, *P. glandulosa* and *F. cernua* is evidence that in these species leaves do not affect the generation of stemflow.

The results show that the volume of precipitation channelized as stemflow varies as a function of canopy area and canopy volume characteristics. There is a positive effect on redistribution of rainwater as shrub size increases. This effect is reflected in a greater water availability under the shrubs, which in turn produces additional plant growth. Thus, large mature shrubs should have greater stability under stressful environmental conditions such as drought.

### *Throughfall*

The average throughfall in creosotebush was 56.0% (range 22–83%) of total precipitation during summer and 55.5% (range 10–80%) in winter. In tarbush throughfall averaged 53.4% (range 9–70%) and 58.2% (range 38–73%) in summer and winter, respectively. In mesquite, average throughfall was 63.5% (range 43–89%) and 62.1% (36–89%). Throughfall in these Chihuahuan desert shrubs was similar to the 55.7% in mulga (*A. aneura*) in an arid Australian woodland (Slatyer, 1965), the average of 60% for a *Eucalyptus* scrub in south-western Australia (Nulsen *et al.*, 1986) and the average of 69% for *Diospyrus texana* in north-eastern Mexico (Navar & Bryan, 1990).

The best fit regression equations were curvilinear for throughfall with different asymptotes for each species (Fig. 2). Throughfall was significantly different among species ( $p < 0.001$ ). There were significant differences in throughfall as percentage of precipitation between *L. tridentata* and *P. glandulosa*, and between *P. glandulosa* and *F. cernua*, but no significant difference between *L. tridentata* and *F. cernua* ( $p < 0.05$ ). The differences in throughfall in *P. glandulosa* appear to be related to the characteristics of the canopy components, but the canopy structure of *L. tridentata* and *F. cernua* appears to be of little importance. The throughfall results for *P. glandulosa* are similar to those reported by Mahendrappa & Kingston (1982). Although different



**Figure 2.** Relationship between throughfall as percentage of precipitation and total precipitation (mm) for (a) creosotebush (*Larrea tridentata*), (b) mesquite (*Prosopis glandulosa*) and (c) tarbush (mm) *Flourensia cernua*.



from *P. glandulosa*, the throughfall pattern in *L. tridentata* and *F. cernua* in our study are similar to those reported by Brandt (1989) and Navar & Bryan (1990). Factors affecting throughfall include leaf size, position, surface texture, the extent of canopy cover, branch arrangement and branch inclination of each species analysed (Crockford & Richardson, 1990a; Bui & Box, 1992). Other variables interact with the canopies (such as rain angle, rain intensity and wind velocity) (Slatyer, 1965; Mahendrapa & Kingston, 1982; Crockford & Richardson 1990c). Since measurements in our study were made at sites that are in close proximity, it is unlikely that storm variables can account for these differences.

### *Stem-angle and stemflow*

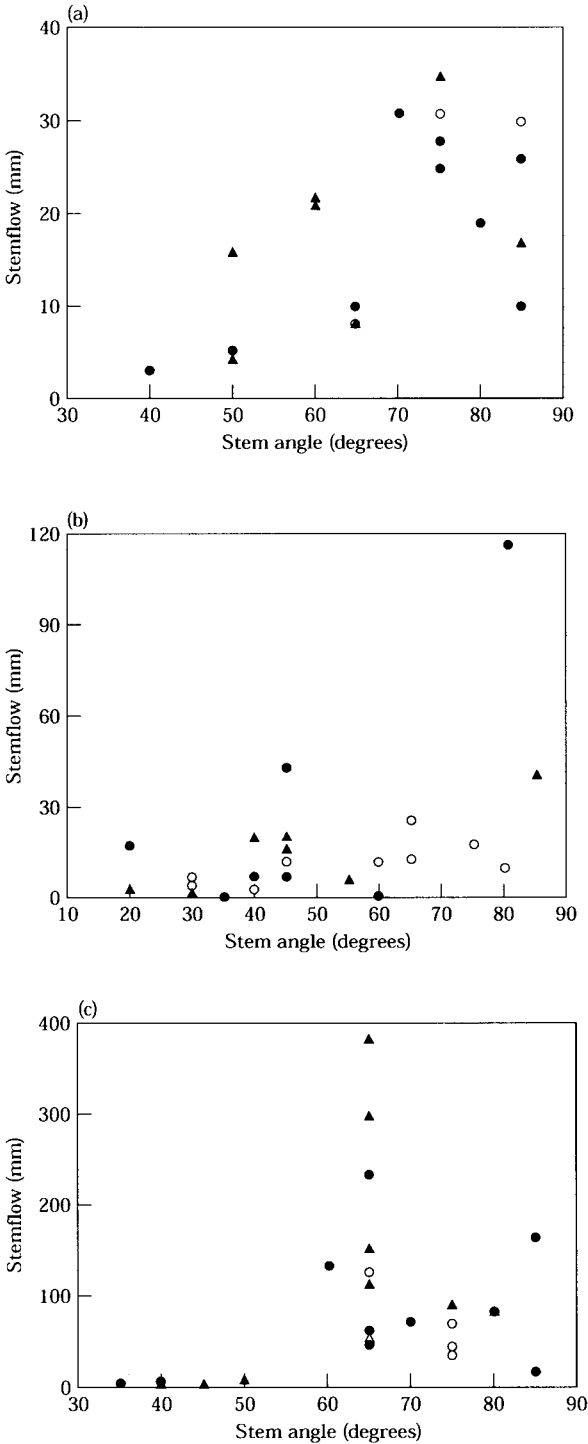
Stepwise regression models (SAS Institute, 1989) of measured variables and stemflow for each species showed that the best one-variable linear model in mesquite (*P. glandulosa*) was stem-angle accounting for 21% of the variability of collected stemflow ( $R^2 = 0.21$ ;  $p < 0.0001$ ); regression equation  $S = -3.1 + 0.3 A$  (where  $S$  = stemflow in mm and  $A$  = stem-angle in degrees). Stemflow yields were higher in shrubs with upward oriented branches than stemflow amounts with horizontally oriented branches. In this species maximum stemflow amounts were reached at stem slope angles of about 70–75° (Fig. 3(a)). Navar & Bryan (1990) observed that shrubs with more vertically projected stems collected higher amounts of stemflow.

In tarbush (*F. cernua*) stepwise regression detected significant effects of stem-angle and stem-length which accounted for 50% of the variability of collected stemflow ( $R^2 = 0.5$ ;  $p < 0.001$ ); regression equation  $S = -51.0 + 0.5 A + 0.7 L$  (where  $S$  = stemflow in mm,  $A$  = stem-angle in degrees and  $L$  = stem-length in cm). In tarbush, although there was some stemflow on branches at angles less than 40°, stemflow amounts were higher on branches with angles equal to or greater than 45° (Fig. 3(b)) and with lengths above 70 cm. These results suggest that differences in stemflow for this species may be attributed both to the effect of more vertically inclined stems and a larger surface area due to longer stems. These variables have been reported to be significant in other species (Crockford & Richardson, 1987; Navar & Bryan, 1990).

In creosotebush stem-angle and stem-length accounted for 41% of the variability of collected stemflow ( $R^2 = 0.4$ ;  $p < 0.001$ ); regression equation  $S = -108.0 + 0.5 A + 1.0 L$  (where  $A$  = stem-angle in degrees and  $L$  = stem-length in cm). Stemflow volumes were higher on stems with angles equal to or greater than 65°, and there was little stemflow at stem-angles equal to or less than 50° (Fig. 3(c)). In those stems with angles equal to or greater than 65°, stem-length was as important as stem-angle funnelling stemflow to the root crown. However, in stems with angles less than 50°, stem-length appears to be unimportant in stemflow generation. In creosotebush, steeply inclined stems combined with longer stems have a greater potential for contributing to stemflow generation than shorter more horizontal stems. Thus, *L. tridentata* is similar to many other shrubs and trees (Helvey & Patric, 1965; De Ploey, 1982; Crockford & Richardson, 1987; Herwitz, 1987; Navar & Bryan, 1990; Navar, 1993).

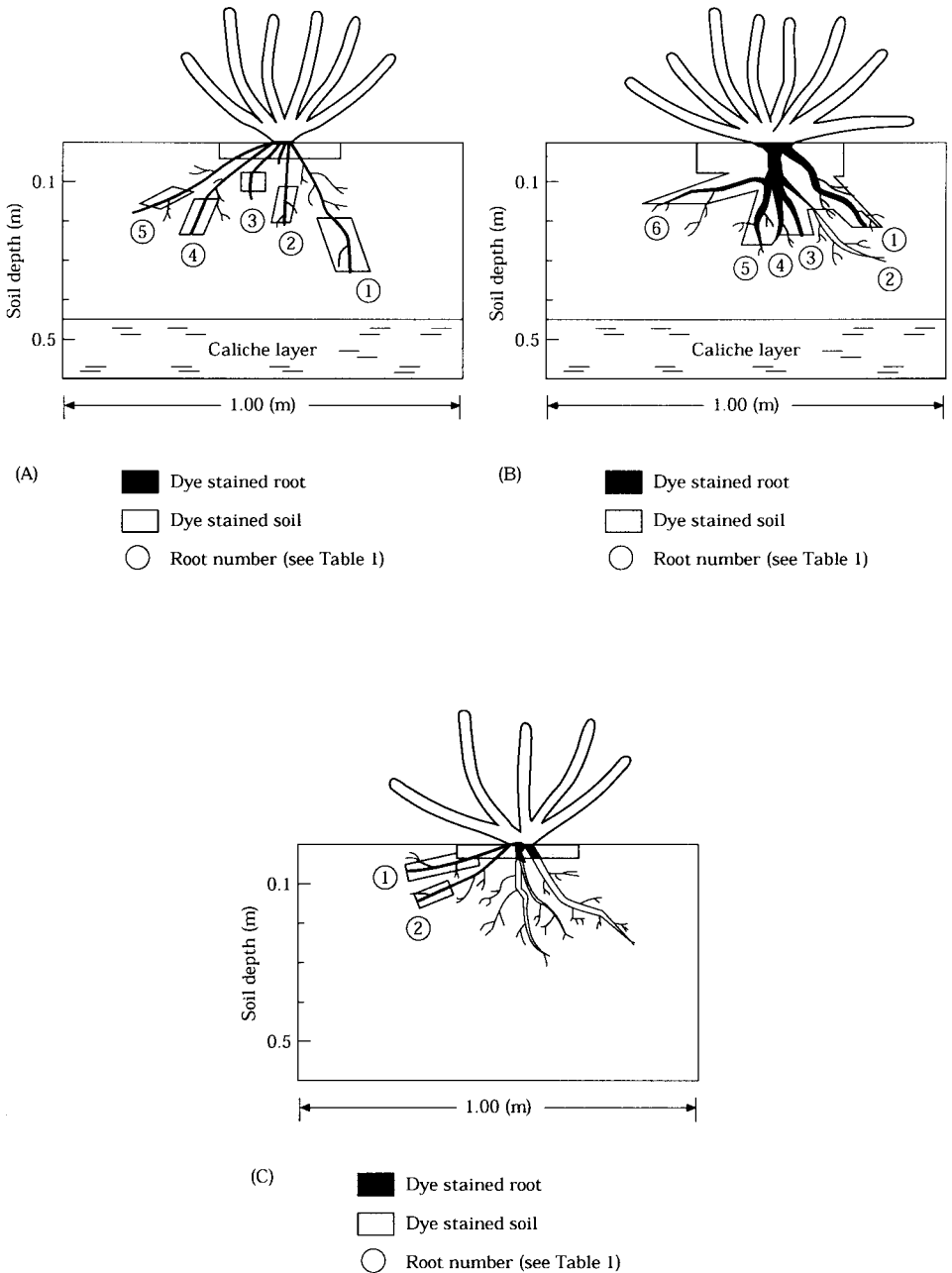
### *Root water channelization*

In *L. tridentata*, dye movement was localized along main roots (Fig. 4, plants A–C). The depth of dye ranged from 5 to 35 cm. The minimum depth of dye was observed on the largest shrub (largest canopy area and canopy volume) and the maximum depth was observed on the creosotebush with the smallest canopy measurements (Table 1).



**Figure 3.** Relationship between stem-angle and stemflow volume for (a) mesquite (*Prosopis glandulosa*), (b) tarbush (*Flourensia cernua*) and (c) creosotebush (*Larrea tridentata*). (○ = plant 1; ● = plant 2; ▲ = plant 3).

The presence of dye-stained soil was observed in the first 10 cm under the soil surface along the wetting front and at sites of soil profile where dye reached its maximum depth through root channels (Fig. 5, plants A-C).



**Figure 4.** Rhodamine-B dye in root and soil under three *L. tridentata* plants: A, B and C.

In *F. cernua*, dye depth ranged from 14 cm on the largest shrub to 20 cm on the smallest shrub (Table 1). The dye was uniformly distributed along the main root of the shrubs and was present in the soil immediately surrounding those roots (Fig. 5, plants A-C). This lateral movement of dye in the soil at this site may be due to the influence of soil texture on rhodamine-B dye solution. According to Trudgill (1987), soil water dye tracing with rhodamine-B is known to suffer from adsorption problems in soil with high clay content. Rhodamine-B dye is cationic and therefore strongly adsorbed on clay exchange sites (Nulsen *et al.*, 1986). Since there is a higher clay content in the soils of the *F. cernua* site, this could explain the presence of the dye in the soil immediately surrounding the main root.

In *P. glandulosa* dye movement was detected on the main root of shrubs, although some secondary roots were observed to be stained (Fig. 6, plants A-C). Dye depth values ranged from 16 to 37 cm. The maximum depth of dye was detected under the shrub with the largest canopy values, and the minimum depth of dye was observed under the shrub with the smallest canopy (Table 1). There was no dye in the soil

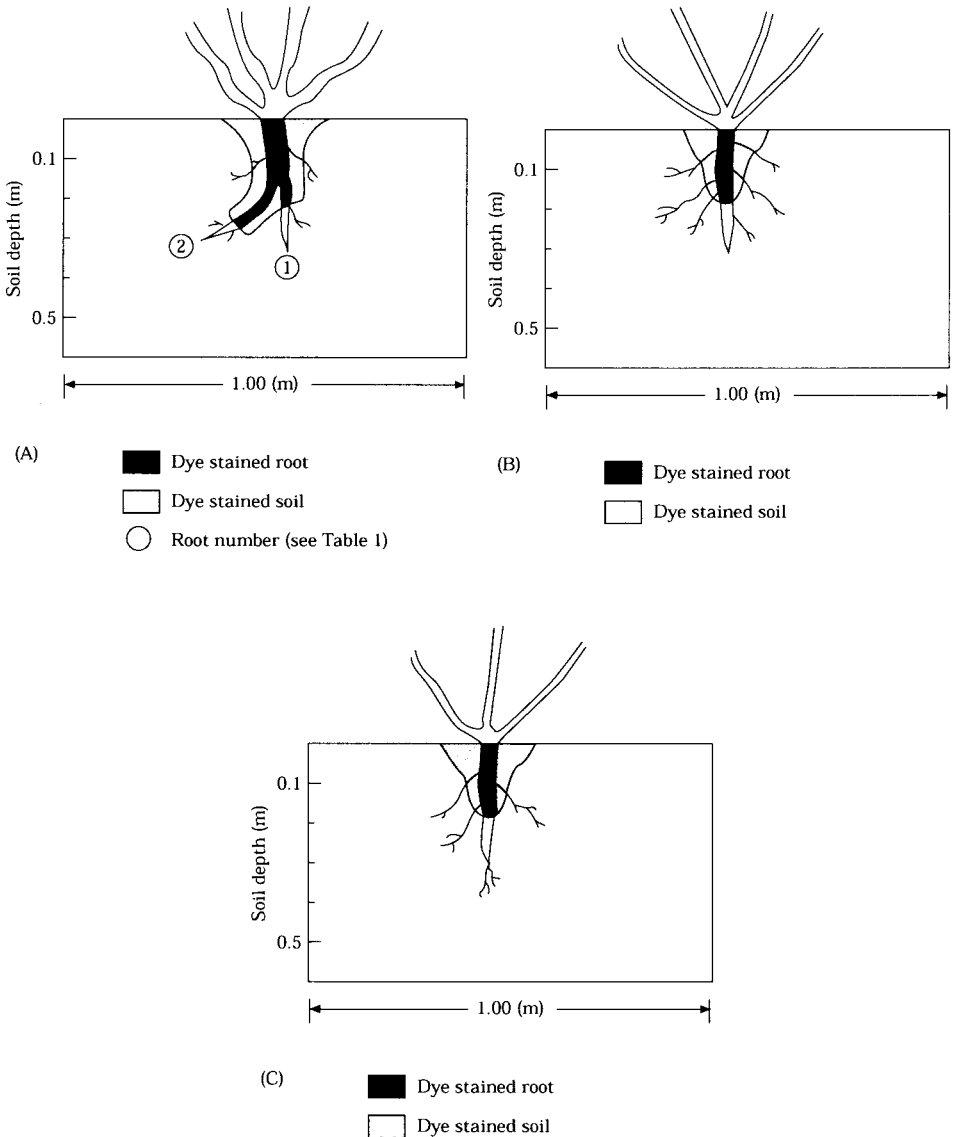
**Table 1.** Dimensions of canopy, root diameters and depth of dye along roots of creosotebush (*Larrea tridentata*), mesquite (*Prosopis glandulosa*) and tarbush (*Flourensia cernua*)

| Species              | Plant            | Canopy                 |                          | Root* | Avg. root diameter (mm) | Depth of dye (cm) |    |
|----------------------|------------------|------------------------|--------------------------|-------|-------------------------|-------------------|----|
|                      |                  | Area (m <sup>2</sup> ) | Volume (m <sup>3</sup> ) |       |                         |                   |    |
| <i>L. tridentata</i> | A                | 1.474                  | 0.344                    | 1     | 7.3                     | 35                |    |
|                      |                  |                        |                          | 2     | 6.2                     | 20                |    |
|                      |                  |                        |                          | 3     | 7.1                     | 15                |    |
|                      |                  |                        |                          | 4     | 5.7                     | 25                |    |
|                      |                  |                        |                          | 5     | 5.7                     | 17                |    |
|                      | B                | 2.688                  | 1.183                    | 1     | 3.4                     | 23                |    |
|                      |                  |                        |                          | 2     | 7.4                     | 18                |    |
|                      |                  |                        |                          | 3     | 18.6                    | 25                |    |
|                      |                  |                        |                          | 4     | 13.9                    | 25                |    |
|                      |                  |                        |                          | 5     | 12.4                    | 26                |    |
|                      |                  |                        |                          | 6     | 15.5                    | 16                |    |
|                      | C                | 3.464                  | 2.599                    | 1     | 2.9                     | 5                 |    |
|                      |                  |                        |                          | 2     | 10.0                    | 10                |    |
|                      |                  |                        |                          | 3     | 35.0                    | 20                |    |
|                      |                  |                        |                          | 4     | 80.0                    | 35                |    |
| <i>P. glandulosa</i> | A                | 2.910                  | 13.808                   | 1     | 60.0                    | 16                |    |
|                      |                  |                        |                          | 2     | 23.1                    | 25                |    |
|                      | B                | 4.246                  | 14.079                   | 1     | 22.2                    | 36                |    |
|                      |                  |                        |                          | 2     | 23.1                    | 25                |    |
|                      |                  |                        |                          | 3     | 35.0                    | 20                |    |
|                      | C                | 5.940                  | 27.876                   | 4     | 80.0                    | 35                |    |
|                      |                  |                        |                          | 1     | 18.1                    | 18                |    |
|                      |                  |                        |                          | 2     | 14.1                    | 20                |    |
|                      |                  |                        |                          | 3     | 6.5                     | 36                |    |
|                      |                  |                        |                          | 4     | 16.3                    | 37                |    |
|                      |                  |                        |                          | 5     | 9.1                     | 37                |    |
|                      |                  |                        |                          | 6     | 60.0                    | 22                |    |
|                      | <i>F. cernua</i> | A                      | 0.363                    | 0.447 | 1                       | 21.5              | 18 |
|                      |                  |                        |                          |       | 2                       | 12.8              | 20 |
|                      |                  | B                      | 0.568                    | 0.539 | 1                       | 24.5              | 17 |
| 2                    |                  |                        |                          |       | 12.8                    | 20                |    |
| C                    |                  | 0.636                  | 0.846                    | 1     | 41.4                    | 14                |    |
|                      |                  |                        |                          | 2     | 12.8                    | 20                |    |

\*Root numbers refer to those in Figs 4-6.

surrounding the main roots of shrubs except in the first 10 cm under soil surface at the edge of the wetting front (Fig. 7, plants A–C).

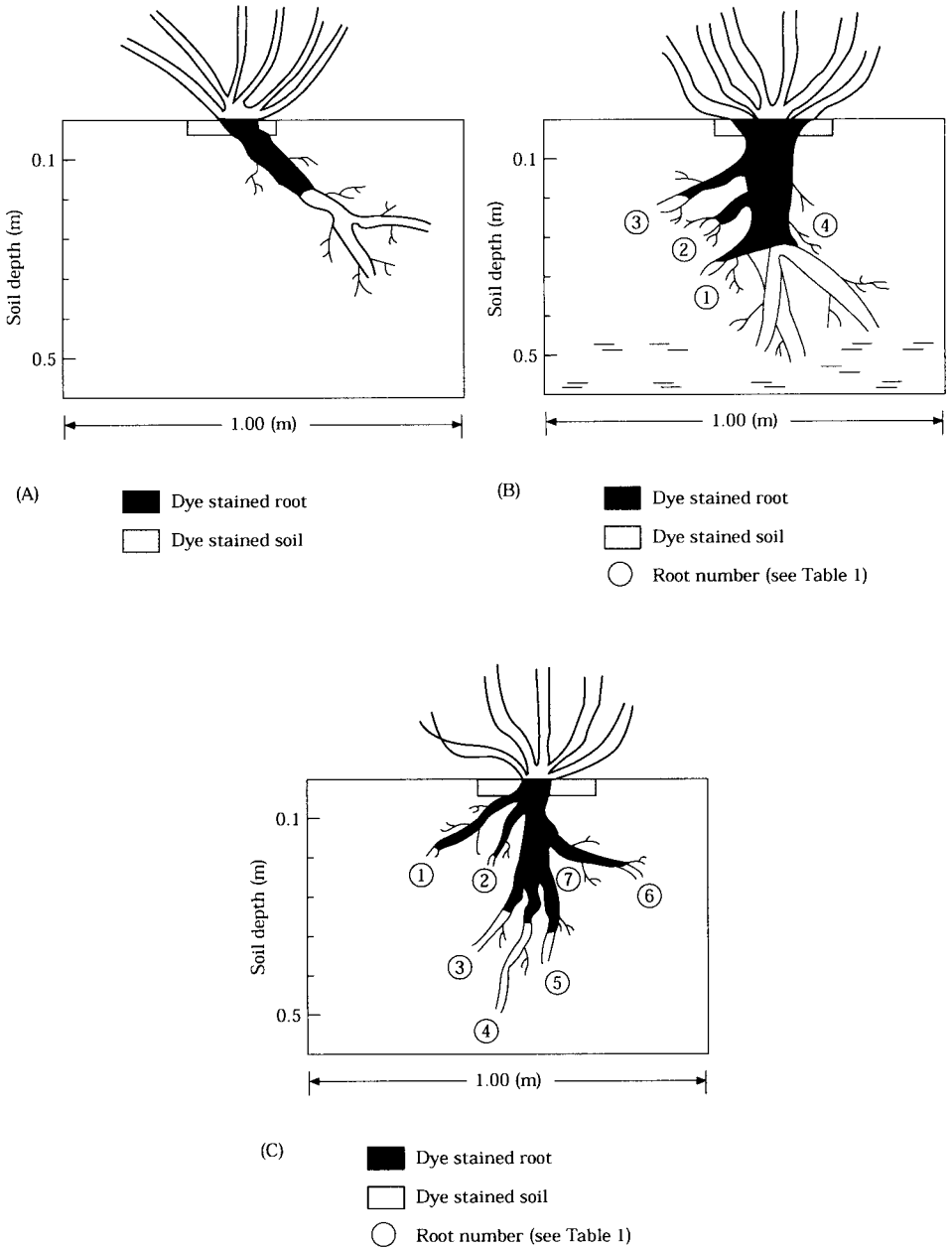
Allison & Hughes (1983) and Nulsen *et al.* (1986) suggested that under mallee (*Eucalyptus* scrub), soil water tracer showed that water from stemflow was transported to depth via root channels where water is presumably stored for use during the dry summer months. The deeper penetration of dye along the roots of mesquite appears to be a function of the height and structure of these shrubs as suggested by Nulsen *et al.*



**Figure 5.** Rhodamine-B dye in root and soil under three *F. cernua* plants: A, B and C.

(1986). Pressland (1976) reported that root distribution of mulga (*Acacia aneura*) is such that stemflow water can readily infiltrate the soil.

The dye tracer study shows that stemflow from intercepted rainfall enters the soil



**Figure 6.** Rhodamine-B dye in root and soil under three *P. glandulosa* plants: A, B and C.

preferentially along root channels to deep storage, and that the depth of stemflow infiltrated via root channels varies as a function of shrub canopy and root distribution characteristics.

Our studies show that shrubs and small trees can redirect a portion of intercepted rainfall via stemflow to deep storage along root channels. This redirected water is thus available to the shrub roots at depths and locations where it is not available to potentially competing plants growing under the canopy of the shrub. Stemflow-root channelized water is thus available for growth and survival of the shrubs when climatic conditions are unfavourable for growth of other plants. This scenario was hypothesized by Nulsen *et al.* (1986) for mallee scrub. Small shrubs in which all stem-angles are greater than 45° should be particularly efficient in redistribution of water by stemflow-root channelization. Water stored around the deeper roots of these shrubs uncouples growth of the shrubs from short-term precipitation. In the Chihuahuan Desert where the predictable season of rainfall is mid- to late summer, water stored via this mode is particularly important for C<sub>3</sub> shrubs such as those examined in this study. The primary period of growth for these shrubs is April through June, the driest period of the year in the Chihuahuan Desert. In this kind of climatic regime, redistributed rainfall may account for the success of C<sub>3</sub> shrubs.

Our data also showed that as the size of shrubs increased, the proportion of intercepted moisture resulting in stemflow increased. Once shrubs exceed some critical size (1 m<sup>2</sup> canopy area in *L. tridentata* and *F. cernua* and 10 m<sup>2</sup> in *P. glandulosa*) the shrubs form 'self-augmenting' entities which are uncoupled from the vagaries of short term climatic variation. Plants that are uncoupled from short-term variations in climate should be more resistant to climatic fluctuations and other environmental stresses. Our studies also suggest that variation in the morphology of *L. tridentata* is in part determined by water availability and the nature of the soil as a rooting medium. The importance of deep water storage in the physiology of desert plants has been suggested by the work of Caldwell & Richards (1989). We suggest that the deep water stored by desert shrubs may be used to access nutrients in shallow soil via the hydraulic lift mechanism (Caldwell & Richards, 1989). Water redistribution by desert shrubs must therefore be considered an essential property of these plants that contributes to the stability of shrub communities in harsh environments.

This research was funded in part by NSF Ecosystems Program Grant No. BSR 90-06621. W.G. Whitford was supported by the U.S. Environmental Protection Agency, Environmental Monitoring Systems Laboratory-Las Vegas. The research described herein has not been subjected to the Agency's peer and administrative review. Therefore the conclusions and opinions drawn are solely those of the authors and should not be construed to reflect the views of the Agency.

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