Disposition of rainwater under creosotebush

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Abstract:

In desert shrubland ecosystems water and nutrients are concentrated beneath shrub canopies in 'resource islands'. Rain falling on to these islands reaches the ground as either stemflow or throughfall and then either infiltrates into the soil or runs off as overland flow. This study investigates the partitioning of rainwater between stemflow and throughfall in the first instance and between infiltration and runoff in the second.

Two series of 40 rainfall simulation experiments were performed on 16 creosotebush shrubs in the Jornada Basin, New Mexico. The first series of experiments was designed to measure the surface runoff and was performed with each shrub in its growth position. The second series was designed to measure stemflow reaching the shrub base and was conducted with the shrub suspended above the ground. The experimental data show that once equilibrium is achieved, 16% of the rainfall intercepted by the canopy or 6.7% of the rain falling inside the shrub area (i.e. the area inside the shrub's circumscribing ellipse) is funnelled to the shrub base as stemflow. This redistribution of the rainfall by stemflow is a function of the ratio of canopy area (i.e. the area covered by the shrub canopy) to collar area (i.e. a circular area centred on the shrub base), with stemflow rate being positively correlated and throughfall rate being negatively correlated with this ratio.

The surface runoff rate expressed as a proportion of the rate at which rainwater arrives at a point (i.e. stemflow rate plus throughfall rate) is the runoff coefficient. A multiple regression reveals that 75% of the variance in the runoff coefficient can be explained by three independent variables: the rainfall rate, the ratio of the canopy area to the collar area, and the presence or absence of subcanopy vegetation. Although the last variable is a dummy variable, it accounts for 66.4% of the variance in the runoff coefficient. This suggests that the density and extent of the subcanopy vegetation is the single most important control of the partitioning of rainwater between runoff and infiltration beneath creosotebush. Although these findings pertain to creosotebush, similar findings might be expected for other desert shrubs that generate significant stemflow and have subcanopy vegetation. Copyright © 2003 John Wiley & Sons, Ltd.

KEY WORDS drylands; desert shrubs; stemflow; infiltration; throughfall; overland flow; creosotebush; resource islands

INTRODUCTION

The distribution of soil resources in desert shrubland ecosystems is markedly nonuniform (Schlesinger *et al.*, 1990, 1999). Water and nutrients essential for plant growth concentrate beneath shrub canopies in 'resource islands', whereas intershrub areas are relatively dry and devoid of nutrients. Both biotic and abiotic processes (summarized by Schlesinger *et al.* (1996), Schlesinger and Pilmanis (1998) and Dunkerley (2000b)) contribute to the formation of these islands. Abiotic processes often form microtopographic mounds that coincide approximately with the islands. These processes include the deposition of windblown sediments in sheltered locations under shrub canopies, the accumulation of fines beneath shrubs owing to differential rainsplash directing more soil particles toward shrubs than away from them, and the preservation of the surface horizons of former soils under shrubs that recently have invaded grassland habitats. Biotic processes include digging by rodents, which enhances infiltration, the uptake by shrubs of essential nutrients followed by the deposition of

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litter beneath their canopies, the presence of symbiotic nitrogen-fixing bacteria in the shrub-rooting systems, which contribute to the accumulation of nitrogen, and the funnelling of intercepted rainfall down stems to the shrub base. This process is termed stemflow.

Stemflow is favoured by a multistemmed cone-like shrub structure (Navar and Bryan, 1990; Martinez-Meza and Whitford, 1996). Not only does stemflow concentrate rainwater in the soil adjacent to the shrub base but the water is usually rich in nutrients extracted from the leaves and wood of the plant and obtained from dryfall and microbial crusts on the shrub stems (Whitford *et al.*, 1997). Dye tracing indicates that some of the nutrient-rich water penetrates to considerable depths along root channels (Martinez-Meza and Whitford, 1996). This deep storage is available for shrub growth during times of little or no precipitation (Nulsen *et al.*, 1986; Reynolds *et al.*, 1999), thereby affording shrubs a distinct competitive advantage over shallow-rooted plants that are unable to tap this moisture source. Thus, once established, shrubs form self-augmenting entities that are buffered against short periods of environmental stress (Martinez-Meza and Whitford, 1996). As a consequence, shrub-dominated ecosystems are very stable and quite resilient to drought and modest shifts in climate (Schlesinger *et al.*, 1990; Whitford *et al.*, 1995; Reynolds *et al.*, 1999; Dunkerley, 2000b).

Numerous studies have measured stemflow on desert shrubs (e.g. Pressland, 1973; Navar and Bryan, 1990; Mauchamp and Janeau, 1993; Martinez-Meza and Whitford, 1996; Whitford et al., 1997). Although data are relatively abundant on the proportion of rainfall that becomes stemflow, comparisons among these data are problematic because different studies have used different methods. Even so, there is little doubt that the process of stemflow is effective in concentrating water at the shrub base, but it is less clear what becomes of this water after it reaches this location. The traditional view is that most, if not all, stemflow infiltrates in the immediate vicinity of the shrub base (e.g. Pressland, 1973, 1976; Mauchamp and Janeau, 1993; Dunkerley and Booth, 1999). However, Navar and Bryan (1990) recognized that the infiltrability of the soil adjacent to the shrub base may be less than the rate at which stemflow arrives at the collar, and they suggested that the stemflow simply spreads over the soil surface until it all eventually infiltrates. This spreading, however, may not be uniform, as some stems carry more water than others and so deliver water unevenly to the shrub base. Indeed, where the ground surface is bare, we have observed microchannels radiating from the shrub base. Such channels imply that all stemflow does not infiltrate and that sufficient water flows across the ground surface beneath the shrub to form these channels. This flow represents a loss of water and nutrients from the resource island (Schlesinger et al., 1999). Significantly, we have not observed such channels under shrubs with dense subcanopy vegetation. Thus, it may be inferred that runoff rates are sensitive to the presence or absence of subcanopy vegetation.

In addition to stemflow, rainwater reaches the ground beneath desert shrubs as throughfall. Throughfall may be divided into free throughfall, which is the above-canopy rainfall that reaches the ground through gaps in the canopy, and released throughfall, which refers to intercepted water that falls from leaves and branches (Dunkerley, 2000a). Inasmuch as the canopy of a desert shrub typically covers less than half the shrub area (i.e. the area bounded by the circumscribing ellipse) (Mauchamp and Janeau, 1993; Wainwright *et al.*, 1999), it is clear that most of the rain falling within a shrub area reaches the ground as free throughfall. Free throughfall on to susceptible soils (i.e. sandy loams and loamy sands) (Poesen, 1992) unprotected by subcanopy vegetation may cause crusting and so promote surface runoff. At the same time, subcanopy vegetation may enhance infiltration by increasing soil organic matter and macroporosity through root decomposition and faunal activity. Although it seems obvious that subcanopy vegetation should promote infiltration, the effect of subcanopy vegetation on infiltration beneath desert shrubs has not been studied previously. One of the goals of this study, therefore, is to investigate this phenomenon.

In order to understand better the function and dynamics of resource islands and the growth and survival of the shrubs rooted in them, additional data are needed on the partitioning of rainwater into stemflow and throughfall in the first instance and into infiltration and runoff in the second. Thus the objectives of the study are twofold: (i) to design and carry out rainfall simulation experiments that will illuminate the partitioning processes, and (ii) to elucidate the factors that control these processes. The study is confined to creosotebush

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(Larrea tridentata), the most abundant perennial in the North American warm deserts (Shreve, 1942; Mabry et al., 1977; Smith et al., 1997).

FIELD AREA AND METHODS

The study was undertaken within the Jornada Long-term Ecological Research (LTER) Site (32°31'N, 106°47'W), 40 km north of Las Cruces, New Mexico, on the bajada surface fringing Summerford Mountain. The area is typical of the northern Chihuahuan Desert and has a mean annual rainfall of 24.5 cm distributed unevenly over two seasons. The summer (June to September) rains are monsoonal in character, with the moisture originating in the Gulf of Mexico. Approximately 60% of the annual rainfall occurs during this season as intense, short-duration, convective storms. Winter and spring rains (October to May) are usually frontal in character, with the moisture coming from the Pacific Ocean. Rainfall events are of low intensity and tend to be prolonged, sometimes lasting for several days.

Persistence is an important rainfall property, as it indicates the likelihood of a wet (dry) day being followed by another wet (dry) day and, hence, the likelihood that soil moisture levels will be high (low) at the start of a rainfall event. An analysis of daily rainfall data by Wainwright (in press) indicates that the probabilities of a wet (dry) day being followed by another wet (dry) day are 0.02 and 0.06 (0.29 and 0.83) during the summer and winter, respectively. These statistics indicate that rainfall events are generally well spaced in both summer and winter, so that soil moisture levels are usually low at the start of a rainfall event. Low soil moisture levels have implications for the time to equilibrium runoff that are discussed below.

Owing to its dominance in the North American warm deserts, creosotebush has been well studied, and information on its morphology, biology, chemistry and distribution may be found in a variety of publications (e.g. Mabry *et al.*, 1977; Reynolds, 1986; Smith *et al.*, 1997, pp. 93–106; Reynolds *et al.*, 1999). Creosotebush has a structure that is well suited to funnelling intercepted rain to the shrub base. Numerous slender stems radiate upward from a central root (or stem) cluster at ground level (see photographs in Wainwright *et al.*, 1999), and each branch terminates in greenish twigs that bear small, evergreen, vertically orientated leaves (Smith *et al.*, 1997). The above-ground architecture of the shrub ranges from conical with large exterior stem angles to hemispherical with small exterior stem angles (Whitford *et al.*, 1996). Although the shrubs selected for this study have a wide range of mean exterior stem angles (i.e. $25 \cdot 2^{\circ}$ to $63 \cdot 0^{\circ}$), there is no significant correlation (r = 0.32, t = -1.25, p = 0.23) between this measure of shrub shape and stemflow flux (cm³ h⁻¹). Consequently, shrub shape is omitted from the remaining analyses.

Three samples of creosotebush shrubs, herein designated samples A, B and C, were selected for this study. Sample A comprised seven shrubs, sample B six shrubs and sample C three shrubs. Two criteria were used in the selection of these shrubs. The first was that the shrubs in samples A and C should have bare ground surfaces beneath their canopy, whereas those in sample B should have vegetated ground surfaces. For simplicity, the former are hereafter referred to as 'bare shrubs' and the latter as 'vegetated shrubs'. The dominant vegetation beneath the latter shrubs is muhley grass (*Muhlenbergia porteri*). The second criterion was that each sample should include a variety of shrub sizes, as previous studies have shown that stemflow volumes are related to this property (Martinez-Meza and Whitford, 1996; Whitford *et al.*, 1997). In the present analysis, shrub size is represented by canopy area A_{CA} (cm²). Canopy area was estimated by taking a vertical photograph of each shrub, projecting the photograph on to a scaled grid, counting the grid intersection points overlain by the canopy, and multiplying by the area of the grid square. In addition, the height H (cm), length L (cm) and width W (cm) of each shrub were measured, and the area of the circumscribing ellipse $A_{SH} = \pi[(LW)/2]^2$ (cm²), herein termed the shrub area, was calculated. The data for H, L, W and A_{SH} are recorded along with A_{CA} in Table I.

Two series of experiments were performed on each shrub and are summarized in Table II. The first series was designed to measure the surface runoff from the shrub area, whereas the second was designed to measure the stemflow reaching the shrub base. In both series a rainfall simulator (Luk *et al.*, 1986) was set up over

Sample ^a	Length ^b (cm)	Width ^c (cm)	Height (cm)	Canopy area (cm ²)	Shrub area ^d (cm ²)	Exterior stem angle ^e (tan)
A	160	150	130	8134	18 852	0.61
А	285	215	172	28 206	48 1 3 2	0.56
А	161	160	129	6182	20234	1.43
А	201	168	140	5744	26 5 25	0.78
А	200	190	150	5203	29 849	1.31
А	150	125	190	7191	14728	1.96
А	250	230	160	15777	45 166	0.58
В	187	140	110	9541	20564	0.68
В	229	210	176	12747	37775	1.16
В	210	203	157	14610	33 486	0.76
В	280	240	185	19 049	52786	1.15
В	256	250	216	17414	50272	0.97
В	227	210	119	14 434	37 445	0.86
С	125	96	110	6046	9426	1.18
С	158	153	115	13 254	18989	0.68
С	310	230	194	26913	56 006	0.47

Table I. Shrub properties

^a Samples A, B and C have bare, vegetated and bare ground surfaces, respectively.

^b Maximum diameter of the canopy.

^c Measured perpendicular to the maximum diameter.

^d Area of the circumscribing ellipse.

^e Measured using the method of Whitford et al. (1996) and Wainwright et al. (1999).

the shrub, and artificial rain was applied (Wainwright *et al.*, 1999) until the runoff rate in the first series and the stemflow rate in the second series stabilized, indicating that equilibrium (steady state) conditions had been achieved (Figure 1). Equilibrium conditions are studied here because multiple experiments were performed on most shrubs (e.g. at different rainfall rates). As a result, soil moisture and canopy storage at the start of each experiment were different, making the study of non-equilibrium conditions problematic. That this study is confined to equilibrium conditions is not meant to imply that the redistribution of rainwater during non-equilibrium conditions is inconsequential, rather the study of these conditions is simply impractical given the research design of this study.

In the first series of experiments an adjustable collar made of sheet aluminum was pushed into the ground around the shrub base, and the soil adjacent to the collar was tamped down to minimize any increase in

Sample	Number of	Ground surface	Series 1: grow	th position	Series 2: suspended
	shrubs		Collar position	Target rainfall rate (cm h ⁻¹)	Target rainfall rate (cm h ⁻¹)
A	7	Bare	5-7 cm from base	14.4	14.4
В	6	Vegetated	Edge of sub-canopy vegetation	3.6, 7.2, 14.4	3.6, 7.2, 14.4
C	3	Bare	 (1) 5-7 cm from base (2) Edge of shrub canopy (3) Midway between (1) and (2) 	 (1) 3.6, 7.2 and 14.4 (2) 14.4 (3) 14.4 	3.6, 7.2, 14.4

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Figure 1. Runoff and stemflow hydrographs for shrub 5, sample A. Rainfall rate is $13.5 \text{ cm } h^{-1}$. Collar area is 552 cm^2

infiltration resulting from insertion of the collar. The purpose of the collar was to demarcate an area around the shrub and to direct the infiltration excess from that area through plastic tubes into sample bottles, which were replaced every 30 s. The water in these bottles was then weighed, giving a record of runoff from the collar area A_{CO} (i.e. the area inside the collar). For the bare shrubs in sample A the collar was inserted 5 to 7 cm from the shrub base, and a single rainfall simulation experiment was conducted on each shrub at a target rate of 14.4 cm h⁻¹. The collar was located at a near-constant distance from the shrub base because the edge of the resource island could not be readily identified.

In contrast, for the vegetated shrubs in sample B the collar was inserted into the ground around the edge of the subcanopy vegetation, which was considered to be the boundary of the resource island. Three rainfall simulation experiments were performed on each shrub at target rates of 3.6, 7.2 and 14.4 cm h⁻¹ (accomplished by using 1, 2 and 4 nozzles on the simulator). The recurrence intervals for these rainfall rates with durations of 5 min are <1 year, <2 year and about 25 years, respectively (Abrahams *et al.*, in press). Rainfall rates are given for durations of 5 min because the average time to equilibrium runoff at a rainfall rate of 14.4 cm h⁻¹ on a dry soil is 5.7 min for the 16 shrubs in this study. For the shrubs in sample C rainfall simulation experiments were performed with the collar at three different locations: at the edge of the canopy, close to the shrub base, and midway between these two positions. Simulations at a target rate of 14.4 cm h⁻¹ were conducted with the collar in all three collar locations. Additional simulations were undertaken at target rates of 3.6 and 7.2 cm h⁻¹ with the collar at its innermost position.

For the second series of experiments each shrub was sawn off at ground level and secured in a clamp above a 20-L bucket into which all stemflow drained. The bucket was covered to exclude throughfall. During each experiment the water level in the bucket was measured at 30-s intervals and subsequently converted to a volume using a calibration curve. Each experiment was run until the rate of filling of the bucket stabilized, signifying that equilibrium stemflow had been achieved. Rainfall simulations were performed on each shrub at the same target rates as were applied when the shrub was in its growth position. Inevitably, rainfall rates measured during each pair of experiments differed slightly. The two rainfall rates were therefore averaged and the mean rate was used in all calculations. Eighty experiments were undertaken, 40 on the suspended shrubs and 40 on the shrubs in their growth position. The data obtained from these experiments are summarized in Table III. In this table and elsewhere in this paper the term 'flux' refers to a volume per unit time (cm³ h⁻¹), whereas the term 'rate' signifies a flux per unit area or a length per unit time (cm h⁻¹).

Neglecting evaporation, the hydrological budget of a shrub area at equilibrium is given by

$$Q_{\rm F} + F_{\rm F} = S_{\rm F} + T_{\rm F} = P_{\rm F} \tag{1}$$

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						Table III	. Results of	rainfall sin	nulation exp	eriments					
Sample	Shrub number	Surface ^a	Rainfall rate $(\operatorname{cm} h^{-1})$ $P = P_{\mathrm{F}}/A_{\mathrm{S}}$	Canopy area (cm^2) A_{CA}	Time to equilibrium stemflow (min)	$\begin{array}{c} \text{Stemflow} \\ \text{flux} \\ (\text{cm}^3 \ h^{-1}) \\ S_{\text{F}} \end{array}$	$\begin{array}{l} {\rm Stemflow} \\ {\rm rate} \\ ({\rm cm}{\rm h}^{-1}) \\ S' = S_{\rm F}/A_{\rm CA} \end{array}$	Stemflow rate $(\operatorname{cm} h^{-1})$ $S = S_{\mathrm{F}}/A_{\mathrm{CO}}$	Throughfall rate $(\operatorname{cm} h^{-1})$ $T = T_{\mathrm{F}}/A_{\mathrm{CO}}$	$\begin{array}{c} \text{Collar} \\ \text{area} \\ (\text{cm}^2) \\ A_{\text{CO}} \end{array}$	Time to equilibrium runoff (min)	$\begin{array}{c} {\rm Runoff}\\ {\rm flux}\\ ({\rm cm}^3~{\rm h}^{-1})\\ {\cal Q}_{\rm F} \end{array})$	$\begin{array}{c} \text{Runoff} \\ \text{rate} \\ (\text{cm } h^{-1}) \\ \mathcal{Q} = \mathcal{Q}_{\mathrm{F}}/A_{\mathrm{CO}} \end{array}$	Runoff coefficient $Q/(S+F)$	Infiltration rate $(\text{cm } h^{-1})$ $F = F_{\text{F}}/A_{\text{CO}}$
A	- 0 m 4 m 0 t		14-6 11-8 15-4 14-5 13-5 13-5	8134 28206 6182 5744 5203 7191	2.75 2.75 2.75 2.25 2.25 2.25	23 076 100 836 32 220 23 724 27 972 30 240	2.84 3.57 5.21 5.38 5.38 5.38	62.37 50.34 45.25 37.18 50.67 54.00	11.89 9.64 12.53 11.78 10.95 11.98	370 2003 712 638 552 552	3.5 5.5 6.67 5.25 5.25	18540 36072 29844 23580 23148 23148 27252	50.11 18.01 41.92 41.93 48.66	0-61 0-30 0-83 0-85 0-85	24.15 41.98 15.87 12.01 19.69 17.32
В	00	9 >>>>>;	12.1 16.3 16.5 9.3 9.3	9541 9541 9541 9541 12747 12747	0.0 4.83 2	7/436 19026 8154 2718 43337 19026	$\begin{array}{c} 4.91\\ 1.99\\ 0.28\\ 3.40\\ 1.49\\ 1.49\\ \end{array}$	134-20 6-73 2-89 0.96 3-90	9.80 13.41 3.33 13.89 7.84	2826 2826 2826 2826 11 109 11 109	3-08 15 11	54288 14148 0 9864 828	9.42 09 5.01 0.00 0.03 0.07	0.87 0.00 0.05 0.05	49.92 15.13 10.59 4.29 16.90
	0 m m m 4 4 4	>>>>>>>>>	2.8 9.2 15.1 2.1 .7	12 747 14 610 14 610 14 610 19 049 19 049	4 5 5	6342 44 394 23 783 8879 8879 57 078 20 612 7978	0.50 3.04 3.00 1.08 0.42	0.57 5.60 3.00 1.12 2.88 1.11	2.36 12.82 3.37 5.89 5.89 3.03	11 109 7929 7929 7159 7159	ν 4	0 16560 0.36 0 2808 28.8	0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.0	0.00 0.00 0.00 0.00 0.00 0.00 0.00 0.0	2.93 16.33 4.49 8.77 8.77
	. ה ה ה ה ה ה		13.1 7.1 3.5 7.6 4.7	17414 17414 17414 14434 14434 14434	0 0	66591 31710 13952 30301 17441 4757	3.82 1.82 0.80 1.21 0.33	8.83 8.83 4.21 1.1.85 8.06 8.06 2.20	10.83 5.85 5.85 6.22 3.87 3.87	7539 7539 2164 2164	2.33	41436 0 32112 6984 0 0	5.50 0.00 3.23 0.00 0.00	0.26 0.00 0.50 0.24 0.00	14-16 10-05 4-70 11-05 6-07
υ	0000	四 四 四 四 四 四 四 五 </td <td>17.6 17.8 8.8 3.6 17.8 17.4 9.6</td> <td>6046 6046 6046 6046 6046 13254 13254 13254 13254</td> <td>1.3 1.45</td> <td>12 684 12 684 7610 3171 56 021 56 021 56 021 19 026</td> <td>2:10 2:10 1:26 1:26 1:28 1:42 1:42</td> <td>1.79 5.06 82.36 49.42 49.42 49.42 4.16 10.89 35.50 35.50</td> <td>15.71 14.96 15.87 7.11 7.11 2.95 16.16 14.95 7.84</td> <td>7085 2506 154 154 154 13471 5143 531 531</td> <td>6 7</td> <td>78 840 38 880 11 160 6588 2808 151 560 58 320 58 320 45 360 19 764</td> <td>11.13 15.51 72.54 42.78 18.23 85.42 85.42 85.42</td> <td>0.77 0.94 0.81 0.88 0.88 0.72 0.58 0.58 0.58 0.93</td> <td>6.38 4.51 13.75 5.31 9.07 3.425 6.42</td>	17.6 17.8 8.8 3.6 17.8 17.4 9.6	6046 6046 6046 6046 6046 13254 13254 13254 13254	1.3 1.45	12 684 12 684 7610 3171 56 021 56 021 56 021 19 026	2:10 2:10 1:26 1:26 1:28 1:42 1:42	1.79 5.06 82.36 49.42 49.42 49.42 4.16 10.89 35.50 35.50	15.71 14.96 15.87 7.11 7.11 2.95 16.16 14.95 7.84	7085 2506 154 154 154 13471 5143 531 531	6 7	78 840 38 880 11 160 6588 2808 151 560 58 320 58 320 45 360 19 764	11.13 15.51 72.54 42.78 18.23 85.42 85.42 85.42	0.77 0.94 0.81 0.88 0.88 0.72 0.58 0.58 0.58 0.93	6.38 4.51 13.75 5.31 9.07 3.425 6.42
	0 0 0 0 0 0 0	88888	4.3 16.5 16.9 9.2 4.5	13 254 26 913 26 913 26 913 26 913 26 913	1.45	9513 44 394 44 394 44 394 22 197 8879	0.72 1.65 1.65 1.65 0.82 0.33	17.92 1.26 4.85 36.96 18.48 7.39	3.47 14.50 13.95 13.16 7.43 3.62	531 35113 9156 1201 1201 1201	4.07	7128 325080 79560 58189 25344 3060	13.42 9.26 8.69 48.45 21.10 2.55	1.04 0.52 0.39 0.97 0.73	7-96 6-51 10-11 1-67 4-81 8-46
^a B, baı	е: v, ve£	getated.													

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where Q_F is the runoff flux, F_F is the infiltration flux, S_F is the stemflow flux and T_F is the throughfall flux, and P_F is the rainfall flux. Although this equation is valid for a shrub area, it does not apply to smaller areas within the shrub area in general and to smaller (collar) areas centred on the shrub base in particular. This is because stemflow redistributes rainwater within the shrub area, concentrating it in the vicinity of the shrub base. As a result, the quantity of rainwater received at any point may be quite different from the rainfall at that point. The difference may be quite large and so must be taken into account in any study of desert shrubs and their associated resource islands. To obtain a better understanding of this phenomenon it is necessary to investigate the disposition of rainwater by stemflow and throughfall.

STEMFLOW AND THROUGHFALL

Equilibrium stemflow conditions are achieved rapidly after the start of rain (Figure 1). For the 16 shrubs in this study, time to equilibrium averaged just 2.4 min under a target rainfall rate of 14.4 cm h^{-1} (Table III). Once equilibrium has been attained, changes to canopy storage and evaporation rates from plant and soil surfaces are so small (<1% of the lowest simulated rainfall rate (Wainwright, in press, table 2)) that for practical purposes they can be assumed to be zero.

It follows from this assumption that all rain falling within a shrub area reaches the ground by either stemflow or throughfall. If P_F and S_F are measured, as they are in this study, T_F for the shrub area may be calculated by subtracting S_F from P_F . However, as explained above, for smaller (collar) areas within the shrub area, such a calculation gives erroneous results because stemflow redistributes the rainwater. A different approach is therefore required that takes into account this redistribution.

Stemflow

Stemflow fluxes were measured during the 40 experiments on the suspended shrubs. Logically S_F is linearly related to the product of the canopy area A_{CA} and rainfall rate *P*. This is confirmed by a non-linear multiple regression which yields the equation

$$S_{\rm F} = a A_{\rm CA} P = 0.16 A_{\rm CA} P \tag{2}$$

with a coefficient of determination $R^2 = 0.69$. To convert S_F to stemflow rate S', both sides of Equation (2) are divided by A_{CA} . Thus

$$S' = S_{\rm F}/A_{\rm CA} = aP = 0.16 P$$
 (3)

(Figure 2), which signifies that, regardless of the size of the shrub, once equilibrium is achieved an average of 16% of the rainfall intercepted by the canopy is funnelled to the shrub base as stemflow. The remaining 84% reaches the ground as released throughfall. In the present sample of 16 shrubs, the canopy covers an average of 42% of the shrub area, leaving 58% uncovered and exposed to free throughfall (Table I). It follows that on average $\{100 \times [0.58 + (0.42 \times 0.84)]\} = 93.3\%$ of above-canopy rainfall reaches the ground beneath a shrub as throughfall, whereas a meager 6.7% reaches it by stemflow. This result suggests that perhaps more attention should be paid to throughfall and its role in the hydrology of desert shrubs than traditionally has been the case.

As the foregoing analysis is concerned with the disposition of rainfall intercepted by the canopy, stemflow rate S' is computed by dividing S_F by A_{CA} . The following analysis, however, focuses on the change in the ratio of the stemflow rate to the rainfall rate as collar area changes. Consequently, stemflow rate S is calculated by dividing S_F by A_{CO} . Because the centre of the collar area is occupied by the shrub base, A_{CO} can never be smaller than the basal area of the shrub. Substituting $S' = S(A_{CO}/A_{CA})$ into Equation (3) and rearranging leads to

$$S/P = 0.16A_{\rm CA}/A_{\rm CO} \tag{4}$$

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Figure 3. Graph of S/P against A_{CA}/A_{CO}

Equation (4) indicates that S/P is linearly related to A_{CA}/A_{CO} . This is confirmed by Figure 3, which shows that the equation is a good fit to the experimental data reported in Table III.

Throughfall

Above-canopy rainfall also reaches the ground as throughfall. Under equilibrium conditions the relationship between throughfall rate T and rainfall rate P has the form (Pressland, 1976)

$$T = T_{\rm F}/A_{\rm CO} = bP = bP_{\rm F}/A_{\rm CO} \tag{5}$$

The coefficient b in this equation may be calculated from

$$b = \{(1 - C_{\rm CO}) + [C_{\rm CO}(1 - a)]\}$$
(6)

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where a = 0.16 regardless of shrub size. The first term on the right-hand side of the equation pertains to free throughfall and the second to released throughfall. The proportion of the collar area covered by the canopy C_{CO} may be estimated from

$$C_{\rm CO} = 1 - (1 - C_{\rm SH}) \left(\frac{A_{\rm CO}}{A_{\rm SH}}\right) \tag{7}$$

where C_{SH} is the proportion of shrub area A_{SH} covered by canopy. Given that the average value of C_{SH} is 0.42 in the present sample of 16 shrubs (see above), Equation (7) indicates that as $A_{\text{CO}}/A_{\text{SH}}$ increases from 0 to 1, C_{CO} decreases from 1 to 0.42—that is, Equation (7) assumes that the canopy cover over the shrub base is 1 and that it diminishes with distance from the shrub base. Furthermore, Equation (6) signifies that as C_{CO} declines from 1 to 0.42, *b* increases from 0.84 to 0.93. Knowing *b*, *T* can be calculated for any collar area using Equation (5).

Redistribution of rainwater

A measure of the redistribution of rainwater by stemflow is provided by the dimensionless ratio (S + T)/P, which may be partitioned into S/P and T/P. As S/P is given by Equation (4), it remains only to develop an expression for T/P. When $A_{CA}/A_{CO} = 1$, (S + T)/P = 1, S/P = 0.16 (Equation (4)), and by subtraction T/P = 0.84. The expression for T/P will therefore equal 0.84 when $A_{CA}/A_{CO} = 1$ and will asymptotically approach 0 as A_{CA}/A_{CO} becomes large. These requirements are met by an equation of the form

$$T/P = 0.84/(A_{\rm CA}/A_{\rm CO})^x$$
 (8)

where x is unknown and must be determined by regression. A non-linear regression was therefore carried out for the 40 experiments on the suspended shrubs and yielded x = 0.16 with $R^2 = 0.65$. The complete equation for (S + T)/P is

$$\frac{(S+T)}{P} = \frac{S}{P} + \frac{T}{P} = 0.16 \left(\frac{A_{\rm CA}}{A_{\rm CO}}\right) + \left(\frac{0.84}{(A_{\rm CA}/A_{\rm CO})^{0.16}}\right)$$
(9)

Equations (4) and (9) are displayed in Figure 4. The value for S/P is given by Equation (4), and T/P is obtained by subtracting Equation (4) from (9). Equation (9) is useful in that it demonstrates that the division of rainwater between stemflow and throughfall is a function of A_{CA}/A_{CO} , with S/P being positively correlated and T/P negatively correlated with A_{CA}/A_{CO} . The next step is to investigate the fate of rainwater once it reaches the ground.

RUNOFF AND INFILTRATION

Starting with a dry soil (soil moisture content <2%) and with a target rainfall rate of 14.4 cm h⁻¹, the average time to equilibrium runoff is 5.1 and 6.9 min for the bare and vegetated shrubs, respectively (Table III). Equilibrium runoff is therefore much less common than equilibrium stemflow. In fact, it is probably quite rare during summer thunderstorms but more frequent during winter frontal storms, which are characterized by prolonged, low-intensity rainfalls. Still, as Figure 1 illustrates, the approach to equilibrium stemflow and equilibrium runoff is initially very rapid. Consequently, although equilibrium is rarely achieved, conditions approaching equilibrium are common, and these conditions can be represented reasonably well by equilibrium equations.

At equilibrium, rainwater inputs (S + T) into a collar area equal outputs (Q + F), where Q is the runoff rate and F is the infiltration rate. Further, (S + T) and (Q + F) both equal P where $A_{CA}/A_{CO} \le 1$ and exceed P where $A_{CA}/A_{CO} > 1$. As a result, the relationship between (Q + F)/P and A_{CA}/A_{CO} is the same as that between (S + T)/P and A_{CA}/A_{CO} (Equation 8). It follows that inasmuch as (S + T) is independent of ground surface properties, so is (Q + F). In contrast, the component variables Q and F are very sensitive to these properties.



Figure 4. Graph of (S + T)/P against A_{CA}/A_{CO} showing the data from 40 pairs of experiments and the best-fit relationship (Equation 9). Equation (4), which relates S/P to A_{CA}/A_{CO} , is included on the graph for comparison

This can be seen in the following analysis of the runoff coefficient and its controls. The runoff coefficient is conventionally defined as Q/P. However, this definition is inappropriate in the case of subcanopy shrub hydrology because P does not represent the rate at which water is arriving at any point on the surface. A better indicator of this rate is (S + T), and so a better definition of the runoff coefficient is Q/(S + T). Thus, Q/(S + T) indicates the proportion of rainwater input that is lost from any collar area by surface runoff. Where a collar is positioned so that the area it encloses corresponds to the resource island, Q/(S + T) indicates the proportion of the resource island.

To understand the controls of Q/(S + T), a stepwise multiple regression analysis was performed with Q/(S + T) as the dependent variable and P, A_{CA}/A_{CO} and D as the independent variables, where D is a dummy variable that takes the value of 1 for bare shrubs and 0 for vegetated ones. Inasmuch as this study is concerned with infiltration and runoff at equilibrium, the eight experiments in which there was no runoff were omitted from the regression analysis. The first variable to enter the regression equation was D, which accounted for 66.4% of the variance in Q/(S + T). The second variable to enter was A_{CA}/A_{CO} , which increased the explained variance to 70.0%, and the last variable to enter was P, which raised the explained variance to 75.0%. The intercept, however, was not significantly different from 0 at the 0.05 level. Consequently, the intercept was set equal to 0 and the regression repeated. The final regression equation is

$$\frac{Q}{(S+T)} = 0.011P + 0.0072 \left(\frac{A_{\rm CA}}{A_{\rm CO}}\right) + 0.38D \tag{10}$$

with $R^2 = 0.74$. The relative contributions of P, A_{CA}/A_{CO} , and D to the explained variance in Q/(S + T) are indicated by the standardized partial regression (beta) coefficients, which are 0.25, 0.36 and 0.61, respectively.

Thus, D emerges as the independent variable with the strongest influence on Q/(S + T). Given the limited ability of a dummy (or binary) variable, such as D, to represent an interval-scale variable, such as the density and extent of subcanopy vegetation, it may be inferred that the actual correlation between subcanopy vegetation and Q/(S + T) is even stronger than that indicated by the above regression analysis. Indeed, it seems fair to conclude that subcanopy vegetation is the single most important factor controlling the disposition of rainwater between infiltration and runoff beneath creosotebush. Subcanopy vegetation controls infiltration and runoff by intercepting rainfall, thereby preventing raindrop impact from sealing the soil surface, and by increasing soil organic matter and macroporosity through root decomposition and faunal activity. Although these findings

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pertain to creosotebush with a ground cover of muhley grass, similar findings might be expected for other desert shrubs that generate significant stemflow and have a subcanopy vegetation.

CONCLUSION

When equilibrium runoff conditions prevail, virtually all rain falling on to a desert shrub and its associated resource island reaches the ground as stemflow or throughfall. In the past, considerable emphasis has been placed on the role of stemflow in concentrating intercepted rainwater at the shrub base. However, the present study of creosotebush suggests that once equilibrium is achieved, regardless of the size of the shrub, only about 16% of intercepted rain water reaches the ground as stemflow. Allowing for the fact that the canopy covers 42% of the shrub area, it can be seen that only 6.7% of the above-canopy rainfall reaches the ground as stemflow, whereas 93.3% reaches it as throughfall. These findings suggest that more attention should be paid to throughfall as a source of water for resource islands than has hitherto been the case.

The proportions of the above-canopy rainfall rate *P* that reach the ground as stemflow and throughfall are denoted by S/P and T/P, respectively. Equations (4) and (9) show that when the ratio of the canopy area A_{CA} to the collar area A_{CO} equals 1, then S/P = 0.16, T/P = 0.84 and (S + T)/P = 1. The degree to which stemflow alters the spatial distribution of rainfall by diverting a portion of it to the shrub base is quantified by the dimensionless ratio (S + T)/P, which is controlled by A_{CA}/A_{CO} . As A_{CA}/A_{CO} increases, (S + T)/P increases, and the proportion of the rain water reaching the ground by stemflow increases.

Once rainwater reaches the ground, it may infiltrate or runoff as overland flow. A measure of the relative importance of infiltration and runoff is provided by the runoff coefficient Q/(S + T). A multiple regression reveals that P, A_{CA}/A_{CO} and D (i.e. a dummy variable equal to 1 where the subcanopy ground surface is bare and 0 where it is vegetated) account for 75% of the variation in Q/(S + T). The most important of these predictive variables is D, which alone explains 66.4% of the variance in Q/(S + T). Taking into consideration the amount of variance explained by D and the limitations inherent in using a dummy variable to represent an interval-scale variable, it is concluded that the density and extent of subcanopy vegetation is probably the single most important factor controlling the disposition of rainwater between runoff and infiltration. Although these findings pertain to creosotebush with a ground cover of multey grass, similar findings might be expected for other desert shrubs that generate significant stemflow and have subcanopy vegetation.

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