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Rainfall patterns in the Gran Desierto, Sonora, Mexico

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The Gran Desierto is the driest region of the Sonoran desert. A detailed statistical study of its rainfall patterns, based on fitting gamma probability distributions, showed that seasonality does not vary within the area, but that both the expected amount of rainfall and the frequency of rainy periods are lower towards the west. Biogeographic variation in this region seems to be strongly associated with rainfall patterns through the varying efficiency of water use by the species involved. The predominance of microphyllous shrubs over cacti and drought-deciduous perennials in the more arid west is attributed to their greater efficiency of water use.

Introduction

Some continuous physical variables present no bounds within their normal ranges, while other variables present definite lower (or upper) bounds. Temperature, for example, when measured in degrees Celsius, can take values above or below zero. Although in theory absolute zero (−273°C) represents an unsurpassable lower boundary, in practice the statistical behaviour of temperature within the range of climatological data is that of unbounded variables.

Rainfall data, on the other hand, are typically zero-bounded values, i.e. rainfall can never present values below zero. In areas where rainfall is very abundant, periods with little or no rainfall will be rare and the data series will approach a typical bell-shaped distribution. However, in more arid climates, periods with no rainfall can be frequent and the resulting data distribution will be highly skewed. Statistically, this is a point of great importance. While the frequency distributions of continuous non-bounded variables are expected to approach a Gaussian (normal) function, the distributions of zero-bounded variables tend to be markedly skewed when the average approaches zero. This is shown in Fig. 1, where both the normal distribution (an unbounded probability density function) and the gamma distribution (a zero-bounded p.d.f.) are shown for three different means. While in unbounded, symmetric distributions the mean always coincides with the most frequent value or mode, in zero-bounded distributions there is an increasingly greater ratio between the mean and the mode as the mean of the distribution takes lower values. For a given variance, zero-bounded variables tend to show a symmetric bell-shaped dispersion function for high means, and a highly skewed J-shaped distribution for low means. The latter is the case with rainfall data from arid environments.

As the average of zero-bounded data gets lower, (a) the skewness of the distribution increases and (b) the relative variability of the data (i.e. the variance in relation to the

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mean) becomes very high. Both the high variability and the skewness of the distribution make the arithmetic mean an unsuitable statistic for characterising the rainfall regime of arid climates. This fact has long been noted by many authors. Shreve (1964), for example, wrote that 'in regions of low rainfall the figures showing the monthly or annual totals, or even the averages for 10 or 15 years, have relatively little significance'. For this reason, a series of authors (e.g. Thom, 1958; Hastings & Turner, 1965; Panofsky & Brier, 1968; García, Vidal *et al.*, 1973, Carrillo & Casas, 1974; Mosiño & García, 1978, 1979, 1981; Crutcher & McKay, 1978; García & Vidal, 1981; Coe & Stern, 1982; Stern & Coe, 1982) have used the gamma distribution for the analysis of rainfall data. Following these ideas, and some new proposals of our own, in this paper we characterise the rainfall regime of the Gran Desierto and analyse its relation to large-scale phytogeographical variations in plant distribution.

The study area

The Gran Desierto, which is among the driest and most extreme deserts in North America, is an area of approximately 15,000 km^2 in the north-western part of Sonora, Mexico. Its approximate limits are the U.S. border to the north, the delta of the Colorado River to the west, the Gulf of California to the south and the 112° 40′ meridian to the east. It has recently been the object of increasing scientific interest for its striking natural features. These include its volcanic geology (Gutmann, 1976; Lynch, 1982), its vegetation (Felger, 1980), its archaeology (Hayden, 1967, 1969, 1976, 1982), and in general the great diversity of its geography and resources (Ives, 1964; May, 1973).

In addition to its extreme aridity, it presents two aspects which set it apart from the rest of the Sonoran desert in Mexico: (a) it has more than 5000 km^2 of active sand dunes and (b) it includes the volcanic shield of El Pinacate, which has an extension of more than 2000 km^2. The inland dunes originated from sediments blow eastwards from the delta of the Colorado River (Merriam, 1969; McKee & Breed, 1976). It is thought that it took more than 10,000 years for these dunes to develop (Felger, 1980). The system is formed mainly by crescentic, barchan and stellar dunes of considerable height (more than 100 m in some parts). Originated mostly from sediments of volcanic origin, this dune system is probably the largest in the American continent. Sand of marine origin, composed chiefly of shell fragments, forms a narrow band of longitudinal dunes near the coast (Ives, 1959).

The volcanic shield, also of recent geologic origin, was formed during the Quaternary in a series of eruptions that ranged from the Pleistocene to the late Holocene. Because of its striking volcanic landscape, the geology of the Pinacate has been well studied (e.g. Arvidson & Mutch, 1974; Bull, 1974; Gutmann, 1976; Lynch, 1982). The older ranges in the region, all of pre-Tertiary origin, lie in a NW–SE direction, parallel to the main local faults (Cortés, Fernandez *et al.*, 1976). These ranges are formed by intrusive and metamorphic rocks of different ages (Merriam, 1972). Paleozoic gneiss and Cretaceous granite are the most abundant. Tertiary rocks in the area are all of extrusive origin, mostly basalt and tuffs erupted before the Pinacate was formed.

Vegetationally, the western part of the Gran Desierto is a typical floristic representative of the Lower Colorado Valley subdivision of the Sonoran desert. This subdivision is dominated by a microphyllous desert with *Larrea tridentata* and *Ambrosia dumosa* as characteristic species. The eastern part of the Gran Desierto, near the town of Sonoyta, forms part of the Arizona Uplands subdivision, which is dominated by crassicaulescent vegetation, with *Cercidium microphyllum*, and *Opuntia* spp. (chollas and prickly-pears) as characteristic species (Shreve, 1964). Towards the coast, seawater intrusions and saline spray determine the occurrence of a coastal desert with dominance of *Atriplex* spp., *Frankena palmeri* and various other halophytes. A detailed description of the vegetation in the central part of the Gran Desierto can be found in Felger (1980).

The Lower Colorado Valley subdivision is the hottest and driest part of the Sonoran desert. It is characterised by its extreme floristic and structural simplicity, with dominance of microphyllous shrubs, a low abundance of cacti, and in general a low richness of perennial species which is compensated in part by a relatively large flora of herbaceous ephemerals. The Arizona Uplands subdivision is, by comparison, wetter and cooler, and occupies areas of higher elevations. It is floristically and structurally more complex, showing a greater variety of life-forms with an abundant and diversified flora of cacti. Trees in the Lower Colorado Valley desert are rare. Most of them are phreatophytes (*Prosopis* spp.), restricted to areas with a shallow water-table. In the Arizona uplands, both microphyllous (e.g. *Olneya tesota*) and aphyllous (e.g. *Cercidium microphyllum*) trees are frequent on rocky hillsides and along washes and *arroyos*. *Cercidium microphyllum* is a characteristic species here, common in most habitats. Ives (1964) described this area as an 'arborescent desert'.

Methods

The gamma distribution

The gamma distribution is a two-parameter probability density function given by the equation

$$f(x) = \frac{1}{\beta\, \Gamma(\gamma)}\, x^{(\gamma-1)}\, e^{-x/\beta}; \qquad \beta > 0,\ \gamma > 0, \tag{1}$$

where x is a random variable (amount of rainfall in our case), and F(x) is the probability density, such that $\int_0^{\infty} f(x) = 1$, and $f(x) = 0$ for all $x < 0$. That is, the distribution has a zero lower bound but shows no upper bounds in the field of positive real numbers. β is the scale parameter, and γ is the shape parameter. $\Gamma(\gamma)$ is the ordinary gamma function of γ, such that

$$\Gamma(\gamma) = \int_0^{\infty} x^{(\gamma-1)}\, e^{-x}\, dx. \tag{2}$$

The gamma distribution is positively skewed (Fig. 1), the skewness being inversely related to the shape parameter γ. For $\gamma > 1$, the distribution is bell-shaped; for $\gamma < 1$ the distribution is J-shaped and the intercept at the origin becomes infinite. For $\gamma = 1$, the distribution becomes exponential with intercept $1/\beta$.

The first moment about the origin (μ_1') is

$$\mu_1' = \beta\gamma, \tag{3}$$

and the second, third and fourth moments about the mean are, respectively (Thom, 1958)

$$\mu_2 = \sigma_2 = \beta^2 \gamma \tag{4}$$

$$\mu_3 = 2\beta^3 \gamma \tag{5}$$

$$\mu_4 = 3\beta^4 \gamma(\gamma + 2). \tag{6}$$

For the particular case of the gamma distribution, skewness, which is measured as $g_1 = \mu_3/(\mu_2)^{3/2}$, simplifies to $g_1 = 2/\sqrt{\gamma}$. As γ increases, the skewness approaches zero and the distribution approaches normality. The mode of the distribution can be calculated as $Mo = \beta(\gamma - 1)$ for $\gamma > 1$. When $0 < \gamma \leqslant 1$, the mode is zero. Approximate estimates of γ and β can be obtained from equations (4) and (5), by using the sample estimators of μ and σ.

$$\hat{\gamma} = (\bar{x}/s)^2, \tag{7}$$

$$\hat{\beta} = s^2/\bar{x}. \tag{8}$$

Mosiño & García (1981) used these formulae for the estimation of γ and β from climatological data with good results. The maximum likelihood estimators of γ and β used in this study are somewhat more complex to calculate, although they can be shown to be more consistent and efficient in statistical terms (Thom, 1958). $\hat{\gamma}$ is calculated as

$$\hat{\gamma} = \frac{1 + \sqrt{1 + 4A/3}}{4A} \tag{9}$$

where $A = \log \bar{x} - [(\Sigma \log x)/n]$. When an x-value is zero it is taken arbitrarily as $1/(n + 1)$, where n is the number of observations, to avoid the indeterminancy of log 0 (García, Vidal *et al.* 1973). $\hat{\beta}$ is calculated as

$$\hat{\beta} = \bar{x}/\hat{\gamma}. \tag{10}$$

By an even more complex but elegant statistical analysis, Coe & Stern (1982) used generalised linear models (GLM) to estimate these parameters by a regression-type procedure. In their approach, the estimated values $\hat{\gamma}$ and $\hat{\beta}$ for any month are not only related to the data series for that month, but are also functionally related to the data series of all other months by a generalised linear function.

Integrated between two points (x_1, x_2), the gamma distribution gives the probability that a certain sample value will fall between these bounds. Hence, the interest is not on the gamma distribution itself, but rather on its integral. Previously, the integration of the function has been done as an expansion of series or of continued fractions (Thom 1958; García, Vidal *et al.*, 1973). Pearson (1951) tabulated values of the integral of the gamma distribution from zero to large values of x, for different values of γ and β. For this study, we used a less precise but simpler procedure which is, in addition, extremely easy to programme. The whole gamma distribution, for the estimated $\hat{\gamma}$ and $\hat{\beta}$ parameters, was divided into small intervals along the independent variable. The area of each interval was integrated numerically and added to the total. The numerical integration method used was a third-order Newton–Cotes quadrature formula (Ralston & Rabinowitz, 1978). The precision of the procedure was improved by making the size of each interval—or segment—inversely related to the absolute value of the slope of the function. Based on the fact that $f(x) = 1$, we could estimate the integration error for some trial runs. This was always less than 0·001.

Thus, the probability for any month of having rain equal to, or above, a certain threshold k is calculated as $P(k) = \int_k^\infty f(x)$. Usually, the monthly average is taken as a meaningful threshold value. Likewise, the median of the distribution can be calculated as the threshold value whose probability is 0·5. A similar, though non-parametric, approach has been taken by Button and Ben-Asher (1983), for the probabilistic analysis of the occurrence of individual storms in the Negev desert. The recurrence interval of a given storm is defined as $RI = (N + 1)/R$, where N is the number of recorded storms and R is the rank of the particular storm under consideration (one, for the storm with the highest precipitation; N for the storm with the lowest). Thus, the probability for a new rainfall event to exceed in precipitation the storm of rank R is $P = 1/RI$.

The measurement of seasonality

The rainfall patterns in deserts tend to be so variable that it is often difficult to judge the existence of seasonal trends. The comparison of monthly averages through an analysis of variance is of little use with data from arid zones because (a) the average, as we have seen is a poor indicator of the most probable value, (b) the dispersion of the data is usually very high and (c) the data is strongly non-normal and hence violates the normality assumption that is inherent of Fisher's variance–ratio distribution (F) test (Kendall & Stuart, 1977).

Statistically, seasonal variations exist when some months of the year concentrate abundant rains with a significantly higher frequency than other months. If for, say, 30 years of rain data we could classify each month as either 'rainy' or 'dry', then we could count the frequency with which each month appears as 'rainy' in the 30-year series. If some months show significantly higher frequencies than other months, then it could be said that statistically, there is a significant seasonal trend. If, on the other hand, the months do not differ significantly in their frequencies, we cannot reject the null hypothesis that the rain distribution is non-seasonal.

The problem reduces then to classifying each month as either 'rainy' or 'dry'. However, dryness is a relative concept in ecological terms. In a desert with, say, 100 mm of annual rainfall, a month with 50 mm is a 'rainy' period. In a rainforest with, say, 3000 mm of annual rainfall, a month with 50 mm is definitely a 'dry' month. Therefore, the classification of any period as 'dry' or as 'rainy' has to be done by comparing it with the statistical distribution of the whole series. An appropriate way to do this is by reducing the whole series of rainfall data for n periods (e.g. months), to an equivalent series with p periods of equal rainfall and $(n-p)$ periods of no rainfall at all, subject to the restriction that the new series shows the same probability distribution. That is, the new series has to show the same $\hat{\gamma}$ and $\hat{\beta}$ values as the original series (and hence the same mean, mode and variance, and also the same rainfall probability for any particular time period). Our original series of data is statistically equivalent to a new series with p rainy periods and $(n-p)$ dry periods. Then we can count the first p more rainy periods of our original data series and assign them as rainy periods, while the rest of the series will be classified as dry. This is really forcing our data, which vary continuously, into a binary 'caricature' that is fitted by the same probability distribution.

Let us take as an example the monthly rainfall for Puerto Peñasco during the year 1971 (see Table 1). The parameters of the gamma distribution for that series can be calculated from equations (7) and (8). Using the (biased) estimators of γ and β, the calculations for $\hat{\gamma}$ become

$$\hat{\gamma} = \frac{(n-1)}{n^2} \frac{(\Sigma x)^2}{\Sigma x^2 - (\Sigma x)^2/n}, \tag{11}$$

$$= \frac{(n-1)}{n} \frac{1}{\frac{n \Sigma x^2}{(\Sigma x)^2} - 1}. \tag{12}$$

Similarly, the calculations for $\hat{\beta}$ become

$$\hat{\beta} = \frac{1}{(n-1)} \left(\frac{n \Sigma x^2}{\Sigma x} - \Sigma x\right). \tag{13}$$

Now let us assume that the total rainfall (Σx) is divided into p months of equal rainfall (r) each. Equation (12) now becomes

$$\hat{\gamma} = \frac{(n-1)}{n} \frac{1}{\frac{n p r^2}{p^2 r^2} - 1}. \tag{14}$$

Table 1. *Monthly rainfall at Puerto Peñasco during 1971:* p = *3·1 months,* r = *20·1 mm,* E = *0·258. The months are classified into two categories (dry or rainy) according to their rainfall (see text for details).*

Month	Rainfall	Reduced series	Classification
Jan	—	—	Dry
Feb	—	—	Dry
Mar	—	—	Dry
Apr	4·5	1·8	Dry
May	—	—	Dry
Jun	—	—	Dry
Jul	—	—	Dry
Aug	19·0	20·1	Rainy
Sep	28·1	20·1	Rainy
Oct	8·5	20·1	Rainy
Nov	—	—	Dry
Dec	2·0	—	Dry

which simplifies to

$$\hat{\gamma} = \frac{(n-1)}{n} \frac{1}{n\frac{1}{p} - 1} \tag{15}$$

Similarly, equation (13) can now be written as

$$\hat{\beta} = \frac{1}{(n-1)} \left(\frac{n\,p\,r^2}{p\,r} - p\,r \right), \tag{16}$$

which simplifies to

$$\hat{\beta} = \frac{1}{(n-1)} (n\,r - p\,r). \tag{17}$$

From equations (12) and (15) it is clear that

$$p = \frac{(\Sigma\, x)^2}{\Sigma\, x^2}, \tag{18}$$

and from equations (13) and (17) it can be deduced that

$$r = \frac{\Sigma\, x^2}{\Sigma\, x}. \tag{19}$$

For our example in Table 1, the value of p is 3·1 months, and the value of r is 20·1 mm. Hence, the first p months (i.e. 3 months, rounded to the nearest integer) are considered relatively rainy, and the rest of the months are relatively dry. Note, from equation (15), that the value of p depends on the value of $\hat{\gamma}$, and hence on the shape of the probability distribution of rainfall, but not on the actual quantities. Hence, p is an adequate and valid measure of rainfall concentration on a given data series. It measures the evenness of the distribution, or the proportion of relatively wet periods, with independence of the actual quantities.

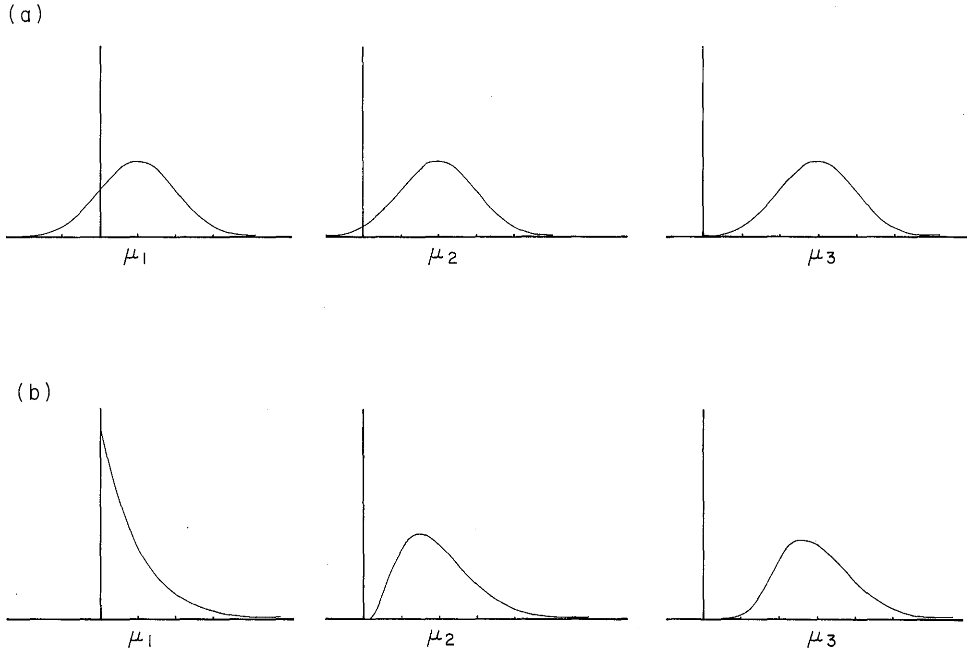

Figure 1. (a) Probability density function for a continuous unbounded statistical variable (normal distribution) with means μ_1, μ_2 and μ_3. (b) Probability density function for a continuous, zero-bounded statistical variable (gamma distribution) with means $\mu_1 = 1$, $\mu_2 = 2$, and $\mu_3 = 3$. For all functions the variance (σ^2 is equal to unity and $\int_0^\infty f(x)\,dx = 1$.

It is interesting to note that the equation for p (eqn. 18) is identical to what is known in probability theory as the 'diversity number of order 2' (Rényi, 1976; Hill, 1973; Ezcurra, 1980). Its statistical properties as a measure of heterogeneity, or of the number of 'apparent states' of a data series, are well known. The value of p ranges between one for data series with all the rainfall concentrated in one month, and n for data series showing complete evenness or homogeneity. The relation $E = p/n$ is a relative measure of evenness (also known as equitability or regularity) in the data. For rainfall data, E is an inverse measurement of rainfall concentration, with values $E = 1/n$ for complete concentration in one period and $E = 1$ for complete regularity. For the example in Table 1, E is 0·258, indicating that relatively rainy months occurred in only 25·8% of the period under study.

Results

Rainfall probabilities

The gamma probability density function was used to analyse the rainfall distribution of the monthly data series from three stations in the Gran Desierto: San Luis Río Colorado (1949–1975), Puerto Peñasco (1948–1975) and Sonoyta (1949–1975). The statistical analysis was made for every individual month through the whole series, and for the annual totals. The results of the analyses for the annual series from each station are shown in Figs 2, 3 and 4. In all cases, the goodness of fit as evaluated by a G-test (Sokal & Rohlf, 1969) was acceptable, i.e. there were no significant differences between the observed series and the gamma p.d.f. taken as the null hypothesis.

The most skewed rainfall distribution is observed in San Luis Río Colorado ($g_1 = 2{\cdot}035$),

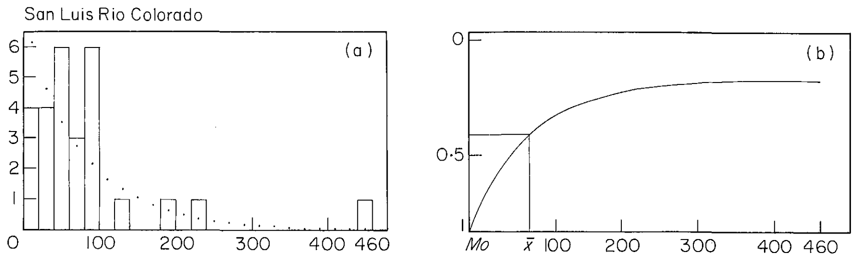

Figure 2. Annual rainfall in San Luis Río Colorado. (a) Observed frequency distribution with the theoretical gamma values indicated by points. (b) Accumulated gamma right-tail probabilities, indicating the probability of the mean (x) and of the mode (*Mo*).

while the highest degree of symmetry in the data series is observed in Sonoyta ($g_1 = 1{\cdot}003$). It is interesting to note that while San Luis Río Colorado and Puerto Peñasco show no significant differences in their annual averages, the shape of their probability distributions is quite different. In San Luis the mode is zero, indicating that years with no rainfall are the most frequently expected case. In Puerto Peñasco, the mode is 48·68 mm, indicating a less skewed distribution and hence a higher constancy of rainfall.

The analysis of the monthly data showed that, with the exception of July for Sonoyta, all the modes are equal to zero. This indicates a J-shaped probability distribution for every month in which no rainfall is the most frequently expected case. It is interesting to note that, although the July monthly average in Sonoyta is lower than that of August, the skewness in July was lower, indicating a more uniform rainfall pattern for this month. Figure 5 shows the median and the mean rainfall values for each month, and the probability of getting rainfall equal to, or higher than, the mean. It is important to note that in most cases these probabilities are below 0·3, indicating that rainfall equal to, or above, the monthly average will occur in less than 30% of the years, while no rainfall is the most frequently expected case for all months in San Luis Río Colorado and Puerto Peñasco, and for all months except July in Sonoyta.

Seasonality

The monthly totals for the whole data series from each of the three Gran Desierto stations were subject to the analysis of seasonality explained earlier. The p values obtained showed 27·4 rainy months for San Luis Río Colorado (27-year series), 47·8 for Puerto Peñasco (28-years series) and 85·3 for Sonoyta (27-year series). The r values obtained (i.e. the rainfall value for a typical rainy month) were 78·8 mm for San Luis Río Colorado,

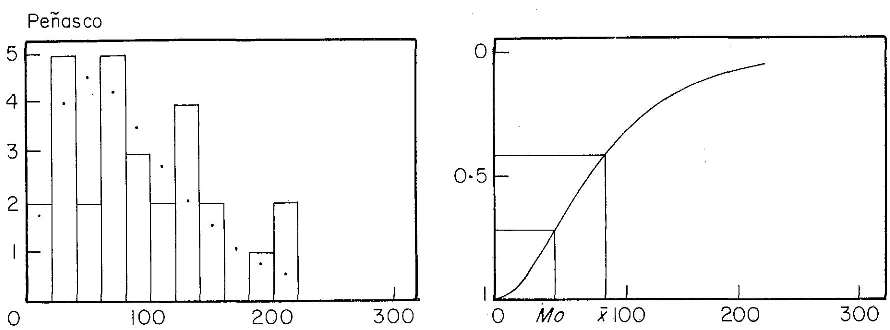

Figure 3. Annual rainfall in Puerto Peñasco. Symbols as in Fig. 2.

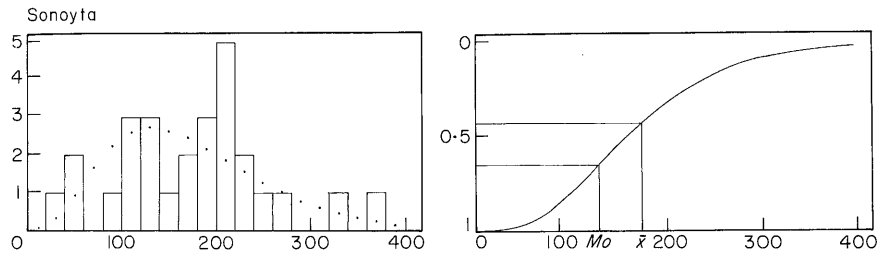

Figure 4. Annual rainfall in Sonoyta. Symbols as in Fig. 2.

53·1 mm for Puerto Peñasco and 55·7 mm for Sonoyta. The lowest equitability was observed in San Luis Río Colorado (E = 0·08), followed by Puerto Peñasco (E = 0·14). Sonoyta shows a higher equitability (E = 0·26), which indicates a higher frequency of relatively wet months and hence a more uniform rainfall pattern (Fig. 8).

It is interesting to note that while the expected annual rainfall—as expressed by the mean or the mode—decreases from east to west, both the concentration of rain ($1 - E$) and

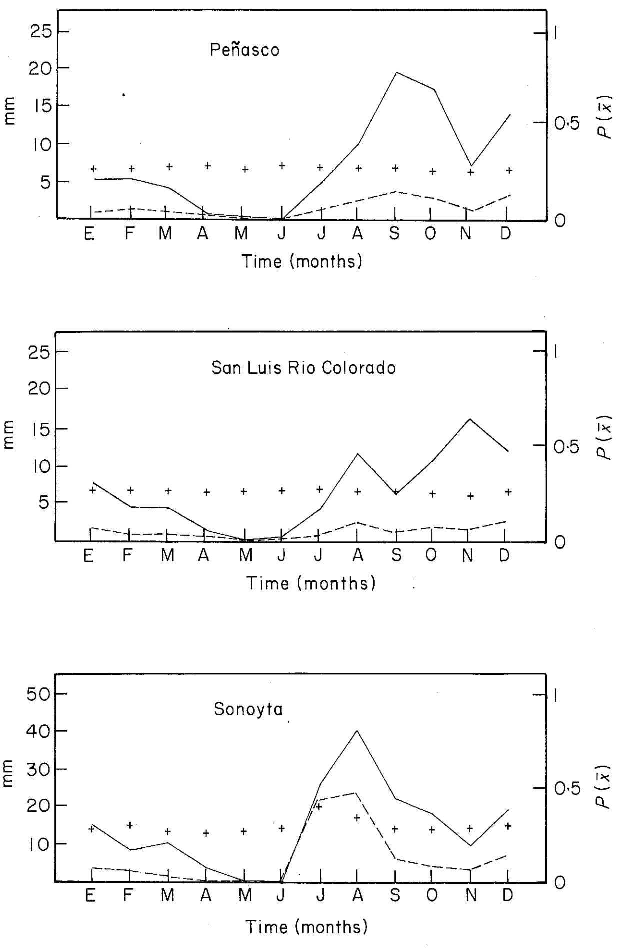

Figure 5. Monthly rainfall in San Luis Río Colorado, Puerto Peñasco and Sonoyta. —— Monthly means; --- monthly medians; -·-·, probability of rainfall equal to, or above, the mean.

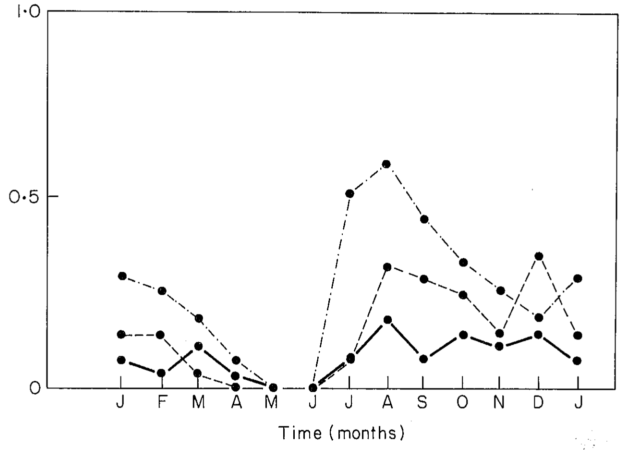

Figure 6. Seasonality in the Gran Desierto. The lines show the relative frequency of rainy spells for every month in each station. Frequencies were calculated as a percentage of the total number of recorded years. ———, San Luis Río Colorado; –––, Puerto Peñasco; –·–·, Sonoyta.

the amount of rain of a typical rainy month (r) increase towards the west. Sonoyta, which vegetationally belongs to the Arizona Uplands subdivision of the Sonoran desert, shows a greater number of wet months (i.e. a greater regularity in the rainfall pattern), but the amount of rain in a typical wet month (r) is higher towards the west. That is, towards the Lower Colorado Valley subdivision of the Sonoran desert, the total amount of rainfall decreases and there are fewer rainstorms (indicated by a lower E value), but the intensity of each rainstorm seems to be higher.

With the p values for the three series—calculated on a 324 month basis for San Luis and Sonoyta (1949–75) and on a 336 month basis for Puerto Peñasco (1948–75)—the first p more rainy months were identified for each station. If a month were consistently dry, it would never be classified as rainy in any of the recorded years. On the other hand, if a month were consistently rainy, it would be classified as such in a good number of the recorded years. Hence, by dividing the frequency with which each month is classified as

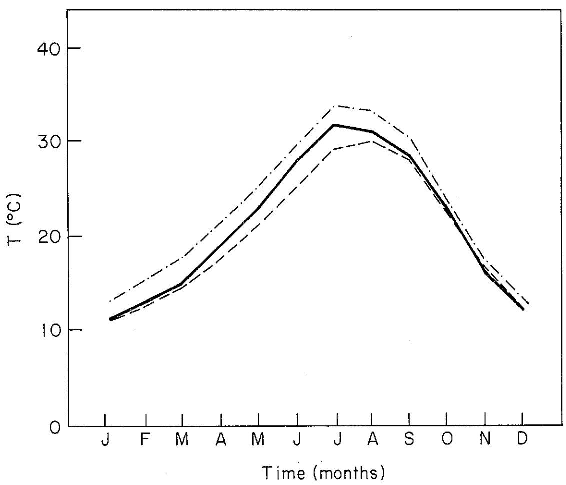

Figure 7. Mean monthly temperatures for the three stations in the Gran Desierto.

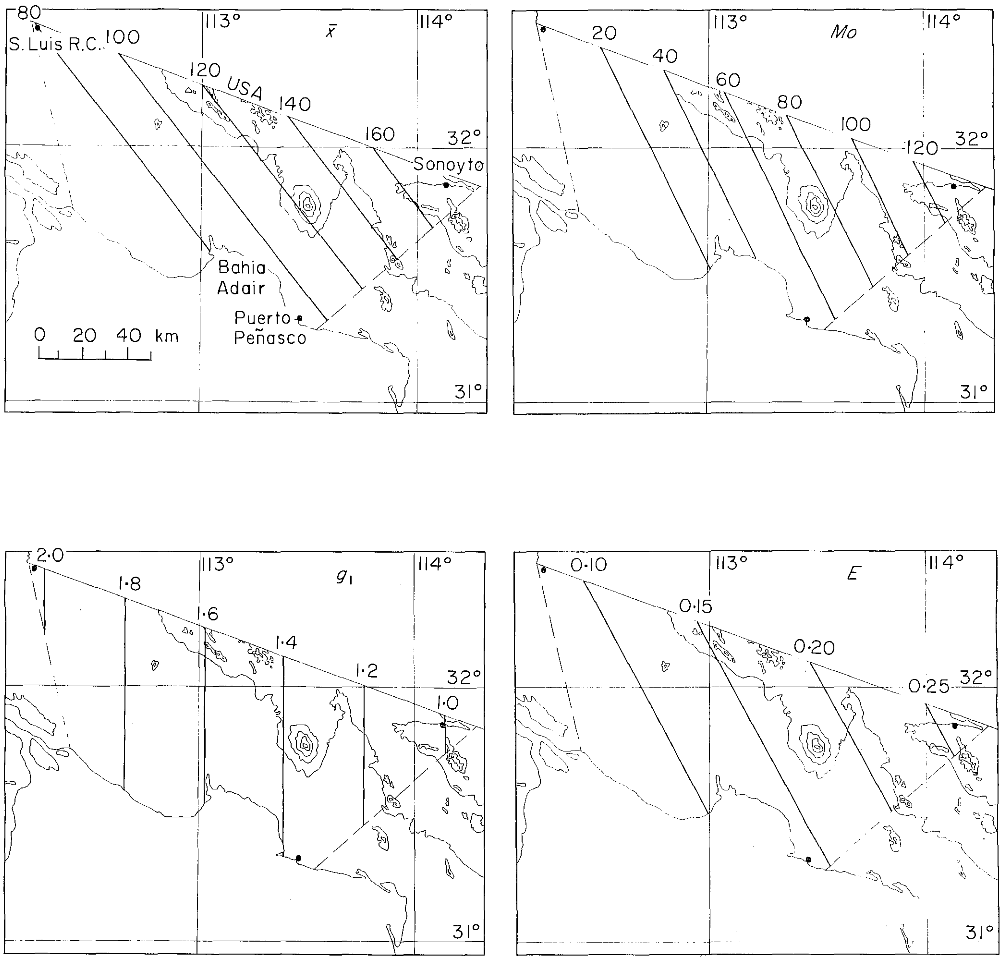

Figure 8. Geographic variation in the rainfall pattern within the Gran Desierto. The maps show the variation in the mean (x), mode (Mo) and skewness (g_1) of the annual rainfall, and in the evenness (E) of the monthly rainfall.

rainy by the total number of years, the relative frequency of rainy spells for every month was calculated. These values are estimators of the probability, for every particular month, of having a relatively high rainfall. The results of this analysis are shown in Fig. 6. (In mathematical terms, the procedure can be described as follows: Let x_{ij} be the rainfall registered during month i of year j, from a series of s years with a total of n months, where, obviously, $n = 12\,s$. If the x_{ij} values are ranked in decreasing order, any period (x_{ij}) will be counted as rainy if its rank is lower than p, and will be counted as dry if its rank is higher. If f_i is the frequency of rainy spells for month i in the whole series of s years, then $q_i = f_i/s$ is the relative frequency of rainy periods and is an estimator of the probability of having high rainfall in a given month i.)

A two-way ANOVA was performed on the relative frequency values for all months in the three stations. Significant variations were found both between stations ($P < 0{\cdot}05$) and between months ($P < 0{\cdot}01$). A Student-Newman-Keuls multiple comparison test indicated that Sonoyta has significantly higher occurrences of rainy months than the other two stations ($P < 0{\cdot}05$). Although Puerto Peñasco shows, in general, higher frequencies than San Luis Río Colorado (also indicated by a higher E value), the differences between these two curves present only a very weak significance ($P < 0{\cdot}15$).

When the three curves were compared by means of a contingency table analysis, it was found that their relative shapes do not differ significantly, i.e. the observed frequencies for each station do not differ significantly from the pooled total monthly frequencies taken as the null hypothesis. This indicates that the relative seasonal variation in the three stations is similar, with corresponding periods of low and of high frequencies of rainfall.

As no significant differences were found between the seasonal pattern of the three stations, the pooled frequencies were used to characterise the seasonal trends for the whole area. A *G*-test (Sokal & Rohlf, 1969) showed that pooled rain frequencies depart significantly from equidistribution with a minimum in early summer (May and June) and a maximum in August. Partial *G*-values, as used by Ezcurra & Montaña (1984), showed that the frequency of rainy spells in April, May and June is significantly below expected random variation, while the frequency in August is significantly above chance departure from equidistribution ($P < 0{\cdot}01$ in all four cases). It must be concluded, therefore, that April, May and June are consistently dry months, while August tends to be a relatively rainy period in the Gran Desierto.

Discussion

Winter rains in the Sonoran desert are brought by the infrequent incursions of migratory cyclones (i.e. Pacific frontal storms) when the Westerlies make their annual shift southwards (Hastings & Turner, 1972; Mosiño, 1964, 1966). As the sun advances north in late winter, the low pressure systems move northwards and are replaced by high pressure cells. Thus, the Sonoran desert comes under the influence of the dry eastern edge of the Pacific high. No frontal storms can reach the area and drought intensifies, giving rise to a dry and increasingly hot period, the 'arid fore-summer' (Hastings & Turner, 1972). In the Gran Desierto this dry period occurs mostly in May and June (Fig. 6), when the frequency of rainy months is zero.

At the end of June, the Pacific anticyclone moves towards the north-west, and the Sonoran desert comes under the influence of the Bermuda high's western edge, which is associated with moister and more stable masses of air. Some of these masses can extend over the Continental Divide and loose their moisture over the unstable atmosphere of the desert. Thus, July marks the beginning of the summer thunderstorms in the Gran Desierto, which reach a peak in August when the frequency of rainy spells is significantly higher than average (Fig. 6). Although there is a significant summer peak in rain frequency, winter rains are probably very important for plant growth. Winter frontal storms are less intense, sometimes producing a gentle drizzle that can last for hours or even days. Monsoon-type storms in summer are more intense, and discharge their water in a very short time. Thus, for a similar amount of rain, winter storms will incorporate more moisture into the soil, while summer storms will generate more runoff. At the same time, winter temperatures are significantly lower ($P < 0{\cdot}0001$) than summer temperatures (Fig. 7), which in the Gran Desierto can reach daily peaks of up to 56°C (May 1973). For this reason, it is predictable that both direct evaporation and evapotranspiration will be much higher in summer.

The seasonal trend is similar for the three stations, as no significant differences were found between their relative frequencies. If each station is analysed separately, though, seasonal variation is more significant for Sonoyta, which has a higher frequency of rainy months (and higher *E* values), while the trend is statistically weaker in San Luis, where rainy months are rarer. It is important to note that although some months show significantly higher frequencies of rainy spells than others (e.g. August against May), all months had rainy periods in only a small proportion of the registered years (Fig. 6). With the exception of the August series in Sonoyta, which showed rainy periods in 52% of the years, all the rest of the monthly series in the three stations showed rainy spells in less than 50% of years. This underlines the extremely arid character of the Gran Desierto and its great variability in rainfall pattern; even in the relatively rainy months, the most likely outcome is little or no rain.

Annual precipitation values also vary considerably between stations. Figure 8 shows the behaviour of the mean, mode, evenness (calculated over the monthly series) and skewness. The isonomes were calculated by fitting a plane to the three data points, although they are probably curved considerably by the rain shadow of the Pinacate volcanic shield. While San Luis and Peñasco are practically at sea level, Sonoyta is 400 m above sea level, at the base of the Arizona uplands. Elevation and slope in Sonoyta create a rain shadow and induce a higher precipitation than in the first two stations. It can be seen that while rain quantities, as indicated by the averages, closely follow the altitudinal gradient, the other parameters have a higher east–west component in their variation. That is, annual rainfall distribution is more skewed, less regular and presents a lower mode at San Luis than at Puerto Peñasco, although both stations have a similar rainfall average and are at the same altitude. It is possible to conclude that, towards the Lower Colorado Valley, in the west of the Gran Desierto, the relative variation and the unpredictability of the rainfall pattern are higher.

Rainfall patterns and biogeographic subdivisions

One of the most striking differences between the Arizona Uplands subdivision of the Sonoran desert, in the east of the Gran Desierto, and the Lower Colorado Valley subdivision towards the west, is the relatively low abundance of trees and cacti in the latter, coupled with a relatively high abundance of microphyllous shrubs and ephemerals (Shreve, 1964). The few trees that can be seen to the west of the Gran Desierto are mainly tornillos (*Prosopis pubescens*) and mesquites (*Prosopis glandulosa*), associated with a fresh-water table near the surface.

From the rainfall analysis presented in this paper, it is clear that the Lower Colorado Valley subdivision has significantly less and more variable rainfall than the Arizona Uplands subdivision, although seasonal variation seems to be similar in both. Because temperatures are higher in the Lower Colorado Valley (Fig. 7), the water balance in this area will show the most extreme deficits. It seems, therefore, that ephemerals and microphyllous shrubs (particularly *Larrea tridentata* and *Ambrosia dumosa*) can tolerate better than cacti the extreme drought and the high unpredictability of rainfall that predominate towards the west.

Based on Walter & Stadelmann's (1974) detailed classification of osmotic spectra in desert plants, Jones, Turner *et al.* (1981) classified drought resistance in plants into three main types: (a) drought escape, (b) drought tolerance at high tissue water potential and (c) drought tolerance at low tissue water potential. In the Gran Desierto, the first group includes summer and winter ephemerals and, to a lesser extent, root and bulb perennials. The second group includes cacti, other succulents, and drought-deciduous perennials, while the third group is formed mostly by xeromorphic shrubs with small leaves, thick cuticles and depressed stomata.

In very extreme arid conditions with highly unpredictable rain, plants that escape drought will survive long dry periods as buried seeds, tubers, bulbs or other buried plant parts. Extreme summer temperatures and highly unpredictable summer storms (which, as discussed above, tend to penetrate less into the soil profile than winter storms) explain the fact reported by Shreve (1964) that, in the Lower Colorado Valley, winter ephemerals are more frequently observed than summer ephemerals. Kemp (1983) has shown that winter and summer ephemerals have similar drought tolerance, but differ mainly in their temperature tolerance and carbon fixation metabolism; winter ephemerals have a C_3 metabolism and usually present a rosette leaf arrangement before flowering, while summer ephemerals usually present a more erect growth and a C_4 metabolism.

Under field conditions, xeromorphic perennials with low tissue water potential (e.g. *Larrea tridentata*) can be more efficient in the use of water than cacti and other succulents with CAM metabolism. Szarek (1979) measured the WUE (Water Use Efficiency, defined as the weight of CO_2 fixed per unit weight of water transpired) of different desert plants for one year, and reported mean WUE values of 0·0109 for true xerophytes with C_3 metabolism, 0·0115 for *Atriplex canescens* (a C_4 xerophyte), and 0·0053 for *Opuntia basilaris* (a prickly-pear cactus; all the species reported by Szarek are present in the Gran Desierto). Year-long WUE for *O. basilaris* was lower than that of the other groups, and also much lower than the relatively high WUE attributed to CAM plants under laboratory conditions. The high WUE values of microphyllous xerophytes possibly explain the fact that these plants tend to occur in drier soils than other desert perennials. For example, Yang and Lowe (1956), describing soil and plant variation along a topographical gradient in the Arizona uplands, reported that the typical *Larrea–Ambrosia* associated of lower *bajadas* occurs in soils with less available moisture than the *Cercidium–Cereus* association which is found in upper *bajadas* and rocky hillsides. The former is dominated by microphyllous shrubs, while the latter is floristically and physiognomically richer, particularly in cacti and drought-deciduous trees. Ephemerals which, as discussed above, can also survive well under extremely arid conditions, present, on average, lower WUE values than most desert perennials (Wallace & Szarek, 1981). The strategy of these plants is to maximise photosynthesis when water is available, at the expense of water use efficiency, and to remain in a dormant form under unfavourable conditions.

Following Walter & Stadelmann's (1974) analysis of water relations in desert plants, the typical microsclerophyllous xerophytes of the Lower Colorado Valley subdivision can be described as plants with a low and constant water potential, capable of restricting transpiration during drought periods. The tissue water potential and the leaf surface hardly decrease during the dry season. When the habitat is exceptionally dry, they enter into a kind of resting period, reducing their gas exchange and hence their photosynthetic rate. This strategy seems to yield a highly efficient use of water and the capacity to survive in extremely dry and unpredictable conditions, out-competing the strategies of stenohydrous xerophytes, which lose their leaves during dry periods, and of cacti which accumulate water through an extensive and superficial root system.

Conclusions

The characterisation of climate is becoming a frequent problem encountered by plant ecologists analysing large scale variation in plant distribution (e.g. Austin & Yapp, 1978). In deserts, the main problem when analysing climatic data is how to estimate expected statisical values from highly skewed rainfall distributions. Clearly, the mean becomes an unsuitable measurement of expected precipitation for these environments. The parameters of the gamma distribution seem to yield appropriate environmental descriptors that can be correlated with plant distribution. The probability distribution approach to the study of rainfall patterns also allows the measurement of regularity (or evenness) of the rainfall series, and the study of seasonal trends.

The main climatic difference between the Lower Colorado Valley subdivision of the Sonoran desert and the Arizona Uplands subdivision is in the frequency and regularity of rainfall rather than in the proportion of summer and winter rains. No significant differences were detected in the seasonal pattern of rainfall between these two areas, but highly significant differences were observed in the frequency of rainy periods and in the regularity of the rainfall pattern, the Lower Colorado Valley being less regular and having lower frequencies of rainy spells.

Microphyllous shrubs dominate in the Lower Colorado Valley, where rainfall is highly unpredictable (i.e. frequencies of rainy periods are low and the precipitation pattern is very irregular). Drought-deciduous trees and shrubs, as well as cacti and other succulents, increase their relative abundance in the less arid environment of the Arizona uplands. The dominance of microphyllous xeromorphic perennials in the drier parts of the Gran Desierto is probably due to their greater efficiency in water use.

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