POPULATION STRUCTURE, SPATIAL PATTERN AND REPRODUCTIVE CAPACITY OF TWO SEMI-DESERT UNDERSHRUBS *SENNA HOLOSERICEA* AND *FAGONIA INDICA* IN SOUTHERN SINDH, PAKISTAN

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Abstract

Size class distribution is important in understanding population structure, demography and stability of populations. In this study, the size structures of two semi-desert under-shrub populations, soil characteristics of habitats, spatial pattern of plant populations and reproductive capacity of the populations of two plant species i.e., *Senna holoceracea* and *Fagonia indica* were examined in two different sites. Size class distribution of both species were positively skewed, having greater frequencies in the smaller classes that represents adequate recruitment. This shows adequate recruitment in the populations of both the species. The examination of spatial pattern, using sample plot and plotless methods, disclosed aggregated pattern of both the species populations. Soil characteristics were also found spatially variable, showing higher fertility (organic matter, nitrogen, Ca, Mg and K) underneath the selected plants and lower in the gaps, which is one of the principal cause of aggregation in species populations. Fecundity of the two plants were also found to be different, particularly differences were found in the fecundity of same plant at the two sites which was presumably due to difference in plant size.

Introduction

Comparing the size class distributions of species populations in natural or semi-natural assemblages provide useful information not only on the structure and demography of the populations in different habitats but offer understanding on the stability of populations and communities. The structure of plant populations can be evaluated in terms of age, size and form of the individuals that constitute it (Harper & White, 1974). As the reproductive capacity and survival of plants depends more on size rather than the age (Harper, 1977; Watkinson & White, 1985; Weiner, 1986) it is better to classify the life history of a plant by stages (size) rather than the age (Werner & Caswell, 1977; Kirpatrick, 1984, Caswell, 2001). The structure of a plant population is governed both by abiotic and biotic factors that also have a substantial bearing on the spatial pattern, age grouping and genetic structure of plant populations (Hutchings, 1997). Additionally, these groups of factors also regulate the spatial and temporal changes in the number of individuals in the populations (Watkinson, 1997; Silvertown & Charlesworth, 2001). Size distributions with few individuals in larger size-classes and numerous smaller ones in small-size classes have been reported by several workers (Moore & Bhadresa, 1978; Turner & Rabinowitz, 1983; Weiner, 1985; Knox *et al*., 1989; Arenas & Fernandez, 2000). The size class distributions, often referred to as size hierarchies (Weiner & Solbrig, 1984; Weiner, 1985) reflect various characteristics including the growth rate of individuals that are mainly the result of asymmetric competition (Weiner & Thomas, 1986).Among the biotic factors, competition (Weiner, 1985) and herbivory (Barboza *et al*., 2009) play vital role in size class distribution of individuals. The size distribution reflects the reproductive ability and the recruitment of new individuals (relative to mortality rate) or the prevalence of disturbance regime or events (Harper, 1977). The studies on size structure have been conducted for some tropical plant species in various regions (Moore & Bhadresa, 1978; El-Ghonemy, 1980; Kleier & Rundel, 2004; Mosallam, 2005,

2007; Barboza *et al*., 2009; Al-Sodany *et al*., 2009). However, there is paucity of information on size structure of ecologically or economically important plant species in Pakistan (Saifullah *et el*; 1993; Khan *et al*, 1995, Khan & Shaukat, 1997).

The distribution pattern of plants in space as an outcome of possible regulatory mechanisms involved within the community, has attracted the attention of numerous workers (Greig-Smith, 1983, Dale, 1999). Pattern in a population can be defined (Ludwig & Reynolds, 1986) as a quantitative description of the horizontal distribution of individuals of a species within a community. Spatial pattern of plants reflect multiple ecological processes including competition, predation, allelopathy, herbivory, dispersal, various types of disturbances, plant-microbe interactions and edaphic-topographic characteristics (Janzen, 1970; Whittaker & Levin, 1977; Dale, 1999; Potts, 2003; Woods, 2004). Two contrasting types of spatial pattern are generally exhibited by perennial plants in arid environments. Regular patterns are exhibited by desert shrubs or trees which arise as a result of competition predominantly for moisture and to a lesser degree for nutrients (Phillips & MacMahon, 1981). By contrast plants often show aggregated or contageous distribution pattern that may be the result of a multitude of factors such as limited dispersal, vegetative reproduction, environmental heterogeneity and intraspecific competition (Greig-Smith, 1977; Haase, 1996; Southwood & Handerson, 2000). Aggregated patterns are also caused by harsh physical environments, typically during succession in a homogeneous habitat (Whipple, 1980; Bertness & Callaway,1994; Haase *et al*., 1996). Contagious pattern is generally exhibited at various scales with varied intensity (Greig-Smith, 1983; Dale, 1999).

Many facets of plant reproduction, such as seed size and number and reproductive potential (Salisbury, 1942) have long been the subject of focus for ecologists. In recent years, a great deal of work has been undertaken on the determination of reproductive effort, the proportion of total energy (biomass) allocated to reproduction in

various plant species (Harper & Ogden, 1970; Bazzaz *et al*., 1979; Soule & Werner, 1981; Abrahamson & Caswell, 1982; Watson, 1984; Hancock & Pritts, 1987) and the allocation of energy to seed production. The relative size of plants in a community, as influenced by soil moisture and nutrients, herbivory and competition, appears to be directly correlated with seed size and number (Inouye *et al*., 1980; Solbrig *et al*., 1980; Watkinson & White, 1985). A trade-off between seed size and number has been well recognized (Werner & Platt, 1976; Harper, 1977).

The aims of this investigation were: 1) to examine the size structure of two semi-desert under-shrub populations at two different sites, 2) to determine the soil characteristics at the two sites underneath the under-shrubs and in the open (gaps), 3) to compare the spatial pattern of plant populations using a variety of techniques of pattern detection and analysis and 3) to investigate the reproductive capacity of the two plant species under study in different habitats.

Materials and Methods

Study area: The study area is located in Southern Sindh where two sites were selected for the study because the plant species selected for investigation occurred as dominating species in the vegetation at these sites. Topographically the area comprises predominantly of alluvial plains with varied soil types ranging from loamy soils to loamy sands and also sand dunes near the coast. The two sympatric plant species were selected for the study, viz., *Senna holosericea* (Fresen) Greuter and *Fagonia indica* Burm. That usually occur abundantly on sandy loam to loamy sand soil types in the lower Sindh area. Of the two sites selected, one was located in Karachi University Campus and the other situated near Steel Mill on the National Highway at about 20 kilometre south-east of Karachi city.

Size structure of populations: Each population was sampled by 60 quadrats of 4 X 4m in size. Homogeneity of stands (sites) was assessed visually to comprise of uniformity of vegetation, particularly with respect to the abundance of the two selected species. The height from the ground surface (H) and the average diameter (D) of the plant cover (canopy), based on two perpendicular measurements for each plant of *S. holosericea* and *F. indica* were taken and the volume (V) calculated as a cylinder: $V = \pi r^2 H$ (where r = D/2). Because the ratio of height to diameter varies with the habitat, the estimation of plant volume using the variables H and D seems to be most suitable for expressing the size of shrubs (undershrubs) (Shaltout & Ayyad, 1990, Shaltout *et al*., 2003). The volume estimates were subsequently categorized in seven size classes and absolute frequencies within each size class determined.

Variation in plant size was expressed using Gini's coefficient of size inequality for each of the population. The Gini coefficientis (G´) can be easily computed from unordered plant size data as the 'relative mean difference' i.e., as the mean difference of size between all possible

pairs, divided by mean size (Damagard & Weiner, 2000), as follows:

$$G' = \sum_i \sum_j |X_i - X_j| / 2n^2\mu \qquad i=1,\ldots, n \; ; \; j=1,\ldots,n$$

where X_i and X_j are sizes of a pair of individual, n equals the total number of observations and μ is the mean size. The program GINI was developed by the first author in C^{++} which computes the Gini's coefficient by two different methods...

Reproductive capacity and reproductive effort: For 20 individuals of *S. holosericea* and *F. indica* occurring within the quadrats, number of flowers/fruits were also recorded. Number of seeds within each fruit were counted to determine fecundity. Twenty randomly chosen plants of the two selected species in each of the habitat (sites) were collected along with their roots (by excavating around the roots carefully), the plants were split into root, shoot and reproductive parts to determine the biomass of various parts. After measuring the fresh weight, the plant parts were dried in an oven at 70°C for 24 h and the dry weights determined. Reproductive effort was expressed as follows:

$$\text{Reproductive effort \%} = \frac{\text{Dry weight of reproductive parts}}{\text{Total plant dry weight}} \times 100$$

The relationship between fecundity and plant size was established using correlation coefficient. Likewise correlations were also computed between plant size and reproductive effort.

Soil analysis: Soil samples were collected from each site from a depth of 0-30 cm using a soil auger. Soil samples were collected underneath *Senna holosericea* and *Fagonia indica* and from the gaps between the shrubs. Four cores were collected from soils underneath the selected plant species each and from the gaps between the shrubs at each site. Soil pH was measured by making a paste of 10g soil in 50 ml deionized distilled water (1:5 ratio) using a Jenway pH-meter. Organic matter content was determined by loss on ignition method (Dean, 1974). Exchangeable Ca, Na and K were determined using a flame photometer (Allen *et al*., 1986). Maximum water holding capacity of soil was ascertained by the method described by Keen (1931). Total Kjaldhal nitrogen was determined using the method of Bremner & Shaw (1958). Available PO_4 was determined colorimetrically using ammonium molybdate reagent (Allen *et al*., 1986).

Detection of spatial pattern: Perry *et al*., (2002) suggested employing several different techniques to quantify spatial pattern. Accordingly, the spatial patterns of *Senna holosericea* and *Fagonia indica* were detected using four different methods– two distance based (plotless) methods and two quadrat-based methods.

1. The index α proposed by Pielou (1960) which employs the mean of squared distances between randomly selected sampling origins and their nearest individuals ώ was used, as follows:

$$\alpha = \acute{\omega} \, \pi \, \rho$$

where ρ equals the independently determined population density. The population density was estimated using

quadrat method as described above. The expected value of this index under the assumption of CSR (complete spatial randomness) is (n-1)/n, where n equals the number of points. Forty point-to plant distances were measured. The value of α that is significantly greater than expected indicates aggregation of individuals while a value significantly less than the expected indicates a regular distribution pattern. Greig-Smith (1983) gave 95% confidence limits for the index.

2. An alternative approach is suggested by Hopkins (1954) which employs both point-to-plant and plant-to-plant distances. Hopkins uses as a 'coefficient of aggregation' the ratio of the sum of squared distances between a random point and their nearest neighbouring individuals (ω), to the square of distances between the individuals and their nearest neighbouring individuals (r), i.e., provided the same number of measurements are made (n=40 in this study) between random points and the nearest individuals and the distances between individuals and their nearest neighbouring individuals:

$$A = \Sigma\, \omega^2 / \Sigma\, r^2$$

The coefficient is unity for complete spatial randomness (CSR), >1 for aggregated distributions, and <1 for regular distributions. The departure of A from unity is tested for significance in the following manner. The parameter x = A/ (1+A) has value of 0.5 for CSR with a variance of 1/(4(2n+1)). Thus (x - 0.5) may be regarded as a normal deviate (Z) with zero mean and standard error equal to 1/(2√(2n+1)). Hopkins also provided a chart (of incomplete beta distribution) showing values of x at different probability levels at various sample sizes (Greig-Smith, 1983). 3) Morisita's index (Morisita, 1971) which is unaffected by random thinning was used as one of the quadrat-based method, as follows:

$$I\delta = Q\, \Sigma\, Xi\, (Xi - 1)/ N\, (N-1)$$

where N= Σ Xi , Q equals the number of quadrats and Xi are the number of individuals in each quadrat. The significance of Iδ was checked using an F-distribution:

$$F = (\, I\delta\, (N-1)+Q-N)/(Q-1))$$

which is tested against υ1 = Q and υ2 = ∞ . 4) Based on the quadrat data, the popular variance/mean ratio was also computed. The variance/mean ratio of 1 corresponds to CSR, a ratio >1 indicates aggregation, while a ratio <1 implies regular distribution. The significance of the ratio is determined using a t-test where the expected value is 1 (for CSR) and the standard error (SE) of the ratio is:

$$SE = (2/(n-1))\, \tfrac{1}{2}$$

with n equal to the number of quadrats (Greig-Smith, 1983). Simulation studies have shown that the methods used here for detection of spatial pattern are adequately powerful against both aggregate and regular alternatives (Shaukat, 2001). In addition to the above mentioned tests of significance developed for different pattern detection methods, 500 Monte Carlo simulations were performed using uniform random distributions in a sampling window A with the given plant density incorporating the edge effect (Connors & Bowers, 1987; Shaukat, 2001; Shaukat & Siddiqui, 2004; Illian *et al.*, 2008).

Computer programs for all the statistical analyses were developed by the first author (S.S.S.) in C++ or FORTRAN 77 and are available as a package on request (also see Shaukat & Siddiqui, 2004).

Results

Size class structure: The results of size class distribution of the two species *Senna holosericea* and *Fagonia indica* are illustrated graphically in Fig. 1a,b and Fig. 2a,b respectively. Frequency distribution of *Senna holosericea* at both the sites showed close to normal distribution with some positive skewness though it was non-significant (Table 1).Similarly, kurtosis for both species was non-significant. Moderate values of Gini's index G were found for both populations at the two study sites. The first two classes (small-size classes) of *S. holosericea*, contributed 54.6 and 45 percent plants of *Senna holosericea* measured at site 1 and site 2 respectively. The last three size-classes (larger classes) of *S. holosericea* generally had low frequencies at both the sites examined. The size-class distribution of *Fagonia indica* showed unimodal distributions with low frequencies in last four size classes. The first two classes representing young plants or seedlings contributed 56.2 and 35.7 percent of the total frequency at sites 1 and 2 respectively.

Table 1. Gini, skewness, kurtosis, mean and standard error of individual sizes of *Senna holosericea* and *Fagonia indica* at two sampling sites.

Parameter	*Senna holoceracea*		*Fagonia indica*	
	Site 1	Site 2	Site 1	Site 2
Gini Index	0.535	0.502	0.551	0.441
Skewness	1.460	1.217	1.521	1.172
Kurtosis	1.500	0.520	1.143	0.524
Mean	91.280	126.720	101.780	106.130
SE	7.936	9.630	9.938	7.207

Soil properties: The soil properties at the two sites are given in Table 2. Soil nutrients (organic matter, total N, available PO_4 and exchangeable K^+, Ca^{++} and Mg^{++}) underneath *Senna holosericea* and *Fagonia indica* were significantly greater (P at the most 0.05) compared to the gaps between the undershrubs. However, water holding capacity and pH of soil under the shrubs and in the open spaces did not differ significantly. Comparison of soils underneath the two species showed that exchangeable Ca^{++} had greater concentration in the soil under *Senna occidentalis* than that of *Fagonia indica*.(P<0.05). The soil nutrient levels were also found to differ between sites. Soil nutrients including exchangeable Ca, Mg and available phosphate were significantly (p<0.05) higher at site 2 compared to site 1.
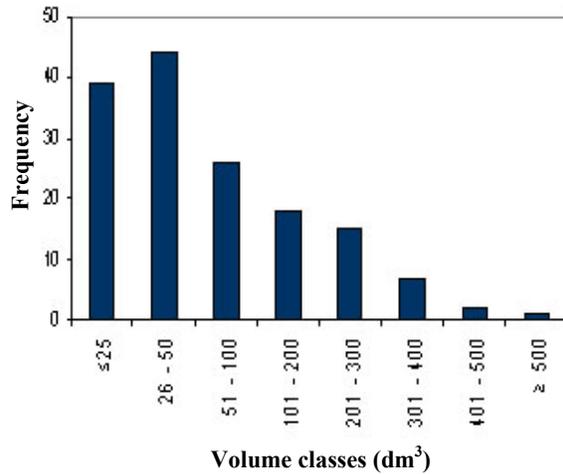
Fig. 1a Frequency curve of volume classes of *Senna holosericea* at site 1.
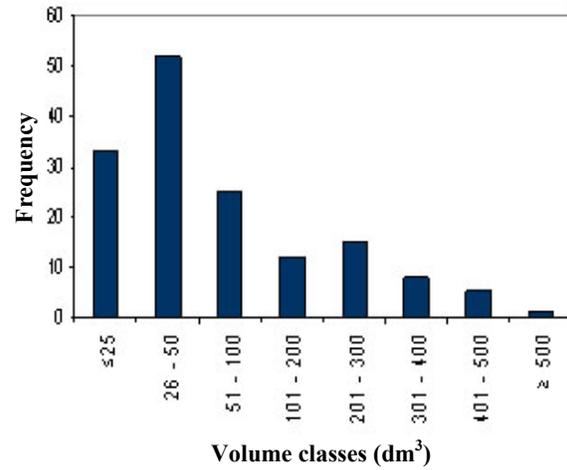

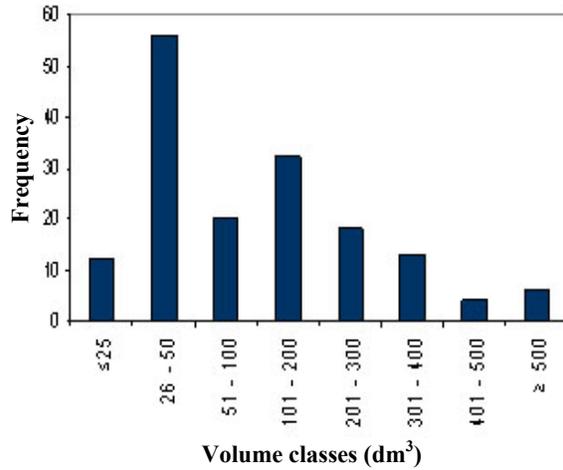Fig. 2a. Frequency curve of volume classes of *Fagonia indica* at site 1.

Fig. 1b. Frequency curve of volume classes of *Senna holosericea* at site 2.
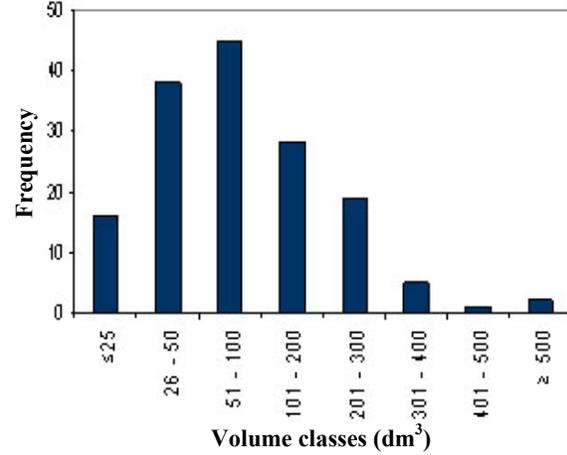

Fig. 2b. Frequency curve of volume classes of *Fagonia indica* at site 2.

Table 2. Soil Properties of the two sites. Each value is mean of four replicates. Means are followed by SE.

Soil property	Site 1			Site 2		
	Senna	*Fagonia*	**Open**	*Senna*	*Fagonia*	**Open**
Max water holding capacity	29.8 ± 0.6	29.5 ± 0.7	27.2 ± 0.8	30.4 ± 0.5	31.8 ± 0.7	27.8 ± 0.7
pH	7.8 ± 0.1	7.7± 0.2	8.1 ± 0.2	8.0 ± 0.2	7.8 ± 0.2	8.0 ± 0.3
Organic matter %	0.53 ± 0.05	0.47 ± 0.04	0.33 ± 0.04	0.62 ± 0.04	0.50 ± 0.04	0.36 ± 0.04
Total N %	0.25 ± .0.05	0.22 ± 0.03	0.12 ± 0.03	0.27 ± 0.05	0.25 ± 0.04	0.16 ± 0.02
Exchangeable K^+	22 ± 2	20 ± 3	14 ± 2	26 ± 2	24 ± 2	13 ± 2
Exchangeable Ca^{++}	49 ± 3	37 ± 4	26 ± 3	62 ± 3	44 ± 5	33 ± 5
Exchangeable Mg^{++}	25 ± 4	23 ± 3	13 ± 2	30 ± 4	26 ± 4	15 ± 3
Available PO_4	16 ± 3	14 ± 3	5 ± 1	23 ± 2	24 ± 3	7 ± 3

Spatial pattern: The results of distance based indices of pattern detection are presented in Table 3. Hopkins index A values for *Sennan holosericea* were 1.648 and 1.584 for sites 1 and 2 respectively that indicate significant aggregation (p<0.01). The index A values of 1.426 and 1.825 of *Fagonia indica* for sites 1 and 2 were also found significant (p<0.05 and p<0.001 respectively) showing aggregated distribution. Likewise, the values of Pielou's index also disclosed significant clustered distribution pattern for *S. holosericea* (p<0.05 and p<0.01) for sites 1 and 2 respectively. The variance/mean ratios for *Senna holosericea* pertaining to sites 1 and 2 were 1.726 and 1.666 which differed significantly (p<0.05) from 1 (the value for complete spatial randomness) showing aggregated distribution pattern (Table 3). Similarly, the variance/mean ratios of 1.840 and 1.834 for *Fagoia indica* also significantly (p<0.01) exceeded unity disclosing aggregated pattern. The Morisita's index of pattern detection for the two species was also found significant as indicated by the significant F-ratios (Table 4).

Table 3. Values of pattern detection indices for *Senna holosericea* and *Fagonia indica* at two sites, based on distance methods (Peilou's α and Hopkins A) and the respective probabilities based on the test statistic.

Index/probability	Senna holosericea		Fagonia indica	
	Site 1	Site 2	Site 1	Site 2
Hopkins A	1.648	1.584	1.426	1.825
X	0.622	0.613	0.6100	0.646
Probability	<0.01	<0.01	<0.05	<0.001
Peilou's α	1.390	1.680	1.936	1.308
Probability	<0.05	<0.01	<0.001	<0.05

Table 4. Values of mean, variance, variance/mean ratio, Morisita's index and the respective probabilities for *Senna holosericea* and *Fagonia indica* at two sites.

Index/probability	Senna holosericea		Fagonia indica	
	Site 1	Site 2	Site 1	Site 2
Mean density./ha	1166.62	1103.50	852.76	974.92
Mean No/quadrat	1.7266	1.7666	1.3674	1.834
Variance	3.2229	2.9436	2.516	2.874
Variance/mean	1.726	1.666	1.840	1.834
t-value	2.7668	2.5369	3.200	3.175
Probability	<0.05	<0.05	<0.01	<0.01
Morisita's index	1.383	1.372	1.609	1.442
F-ratio	1.673	1.667	1.840	1.823
Probability	<0.05	<0.05	<0.01	<0.01

Table 5. Reproductive effort of the two species.

Sites	Senna holosericea		Fagonia indica	
	Site 1	Site2	Site 1	Site 2
Number of fruits	94±67.8	130±86.6	477±351.2	549±430.6
Number of seeds	663±411.7	961±669.5	2380±1923.0	2753±2232.6
Reproductive effort	22.65±3.63	29.33±4.28	12.35±2.02	18.78±3.59

Reproductive capacity and reproductive effort: The number of fruits and reproductive capacity (fecundity) of both the species *Senna holosericea* as well as *Fagonia indica* were significantly (p<0.05) greater at site 2 compared to site 1 (Table 5). The fecundity of *F. indica* was remarkably greater than that of *S. holosericea*. The reproductive effort of *Fagonia indica* was found significantly (p<0.001) greater than that of *Senna holosericea.* For both the species, RE was significantly greater (p<0.05) at site 2 compared to that of site 1. An examination of

the relationship between plant size and reproductive capacity (fecundity) showed that large plants were associated with greater fecundity. Correlation coefficients were calculated between plant size and the number of seeds produced (Table 6). The correlation coefficients were found to be highly significant for *Senna holosericea* for both the sites (p<0.01). Similarly, correlation coefficients between number of seeds counted per plant and the size of plants of *Fagonia indica* were also significantly correlated (p<0.05).

The correlation coefficients between plant size and reproductive effort for both *Senna holosericea* (p<0.05 and p<0.01 for sites 1 and 2 respectively) and *Fagonia indica* (p<0.05 for both sites 1 and 2) were found to be significant (Table 7).

Table 6. Correlation coefficients between number of seeds per plant and the size of plants. of *Senna holosericea* and *Fagonia indica* at two study sites.

Sites	Senna holosericea		Fagonia indica	
	Site 1	Site 2	Site 1	Site 2
Correlation Coefficient	0.563	0.618	0.478	0.529
Probability	<0.01	<0.01	<0.05	<0.05

Table 7. Correlation coefficients between reproductive effort and plant size of *Senna holosericea* and *Fagonia indica* at two study sites.

Sites	Senna holosericea		Fagonia indica	
	Site 1	Site 2	Site 1	Site 2
Correlation Coefficient	0. 470	0.636	0.508	0.470
Probability	<0.05	<0.01	<0.05	<0.05

Discussion

The populations of both the under-shrubs showed variation in size-structure as evidenced by moderate values of Gin's index (G´).The size differences in the plant populations are presumably the direct result of differences in growth rates of individuals in the populations. Secondly, asymmetric competition might be an additional factor promoting the size inequality of the populations (Weiner, 1990). As larger plants, with greater competitive ability, suppress the growth of smaller plants (Weiner & Thomas, 1986; Weiner, 1990), the one-sided competition would presumably accentuate the differences in growth rates between mature and juvenile individuals.

The study indicated that the size-class frequency distribution of *Senna holosericea* was to some degree positively skewed with high percentages in the first two size classes indicating a high rate of recruitment of new individuals in the populations. Similarly, the populations of *Fagonia indica* at both the sites also had considerably large percentage of individuals in small size classes though the percentage frequency of small individuals was slightly lesser at site 2 compared to that of site 1. However, the populations of both the investigated species

exhibited ample recruitment of young (juvenile) individuals. In any stable population an excess of juveniles over the mature individuals is expected (Crisp & Lange, 1976; Moore & Bhadresa, 1978; Goldberg & Turner, 1986; Mosallam, 2005). The positively skewed size-class distribution may represent rapidly growing populations with high reproductive capacity. Nonetheless, such a distribution may also indicate high age-specific mortality rates in the lower size-classes (Hara, 1988, Weiner *et al*., 2001; Shaltout *et al*., 2003)

All the four methods of pattern detection indicated aggregated distribution pattern for both *Senna holosericea* and *Fagonia indica* populations at two different study sites. The two distance-based methods, i.e., Pielou's α and Hopkins' A have been shown to be sufficiently powerful against both aggregate and regular alternatives (Shaukat, 2001). In addition to the classical tests, empirical distributions using Monte Carlo simulation were also generated for each test (Shaukat & Siddiqui, 2005) which confirmed the prevalence of aggregated distribution of the populations. The quadrat-based method of variance/mean ratio depends to a certain extent on the size of the quadrat (Greig-Smith, 1983). However, the quadrat size used was neither two small nor excessively large and probably represented the scale of aggregation inherent in the populations. Aggregated spatial pattern in desert shrubs has often been reported (Skarpe, 1991; Haase, 1995; Hegazy & Kabiel, 2007). Studies on structure and dynamics of plant populations have demonstrated that that the spatial distribution can be influenced by several biotic factors, including seed dispersal pattern, probability of seedling survival, as well as abiotic factors such as soil moisture and nutrient regimes (Janzen, 1971; Hubbell, 1980; Borcard *et al*., 1992; Messaoud & Houle, 2006; Humphreys *et al*., 2008). Prentice & Werger (1985) and Dayong (1990) suggested that aggregation is initiated by the clustered seedling establishment due to environmental control and/or limited seed dispersal. Caylor *et al*. (2003) advocated that the distribution of suitable regeneration sites and subsequent patterns of seedling establishment may play a crucial role in determining the spatial patterning of desert shrubs. In fact, a large number of fruits and seeds were observed underneath or at the periphery of the respective under-shrubs (S.S. Shaukat, personal observations). Moreover, often a number of conspecific seedlings of the species were recorded in the close vicinity of the large individuals of the species. Thus, with the establishment of offspring around the parent plant, clumping would eventually develop.

The study demonstrated that certain soil characteristics were spatially variable and some soil chemical characteristics differed markedly in soils beneath and between the shrubs (i.e., in the gaps) in the desert ecosystem under study. Such "islands of fertility" in arid and semi-arid areas have often been reported (Burke, 1989; Hook *et al.*, 1991; Schlesisinger *et al*., 1996). Similarly, Gutierrez *et al*., (1993) found remarkably high concentrations of nitrogen, phosphorus and organic matter underneath than outside the shrubs. Likewise, Li *et al*., (2007) found fertile island formed by the shrubs or patches of *Tamarix* spp. enriched with soil nutrients and higher level of available nitrogen at greater depth compared to

inter-shrub spaces. It was suggested by Winton & Burke (1995) that the importance of the presence of plants on localized soil lineaments can be so great as to diminish the species specific response to the extent that the differentiation, after alteration of soil properties, no longer exist. In the present study, at site 1 soils underneath *S. holosericea* and *F. indica* differed significantly with regard soil organic matter and exchangeable calcium while at site 2 soils differed with respect to exchangeable potassium and available phosphorus. Likewise Hirobe *et al*., (2001) found ample differences in soil properties such as total N, total C, C/N ratio, exchangeable K, Na, Ca, and Mg of soils collected underneath the shrubs of *Artemisia ordosia* and *Sabina vulgaris* in Mu Us desert, China. Greater amounts of nutrients beneath the shrubs and in close vicinity, facilitates the germination, seedling establishment and survival of seedlings, generally the conspecifics (Callaway, 1995; Callaway *et al*., 2002). Plants occurring in the fertile microhabitats produced as a result of aggregation of shrubs, with greater nutrient accumulation in soil, are shown to produce more flowers and fruits and greater seed mass as a consequence of facilitation (Turado & Pugnaire, 2003). Thus, facilitation by inducing variations in the reproductive output may play a major role in the demography and dynamics of plant populations.

Large differences in the reproductive capacity (fecundity) of the two under-shrubs *S. holosericea* and *F. indica* were found. Salisbury (1942) noted such differences in reproductive capacity of various species and suggested that they may be the consequence of different selective pressures and can be attributed to the ability of a species to persist in time and space (Harper *et al*., 1970; Harper & White, 1974). Marked variation in the between site fecundity was recorded for both the species. Fecundity of *Senna holosericea* was found to be remarkably greater at site 2 than at site1. The average plant size (volume) of *Senna holosericea* was significantly greater at site 2 compared to site 1. Although the size of *Fagonia indica* plants was also somewhat greater at site 2 than at site 1 but the difference was not statistically significant. It has been shown that fecundity depends more on plant size rather than age (Herrera, 1991; Hanzawa & Kalisz, 1993). The variation in plant size is therefore a good estimate of relative fitness within species which is demonstrated in several species and strong correlations between plant size and number of seeds produced are recorded (Inouye *et al*., 1980; Solbrig *et al*., 1980; Watkinson & White, 1985; Aarssen & White, 1992).

The reproductive potential of both the species under study and in particular, that of *Senna holosericea* is much greater then their actual seed production. Reproductive losses that resulted in ovary, fruit and seed abortion and non-availability of pollen constitute the major pre-dispersal losses (Boieiro *et al*., 2009). In addition, seed predators inflicted considerable losses in both the species, particularly in *Senna holosericea* where about 10 percent of the seeds are eaten by the larvae of Curculionids (S.S. Shaukat, personal observations). Phytophagous insects associated with the flowers cause large losses in reproductive potentials in some legumes (Breedlove & Ehlich, 1972; Heithaus *et al*., 1982). Seed predation is known to be an important factor regulating seed production

in many plant species including other species in the genus *Senna* (*Cassia proparte*) (Whitehead & Kingslover, 1975; Baskin & Baskin, 1977; Lee & Bazzaz, 1982).

The results indicated great deal of variability in reproductive effort (estimated as the ratio between reproductive and total biomass) varied both within sites and between sites in response to austere moisture supply which is a critical dynamical component of life history strategies of the desert shrubs in heterogeneous, unpredictable and xeric environments. Site to site variations in reproductive effort (RE) have been shown and significant negative trends between RE and successional maturity have been demonstrated (Hancock & Pritts, 1987). Life history traits such as growth rate, reproductive capacity and phenotypic plasticity are all subject to selection pressure (Bradshaw, 1965; Stearns, 1977; Stearn & Hoekstra, 2005). Like fecundity, the reproductive effort was also found to be dependent on individual size, with larger plants having greater reproductive effort than the smaller plants. Size dependent variation in reproductive effort in plants was theoretically predicted by Gadgil & Bossert, (1970). Similar to *S. holosericea* and *Fagonia indica*, in a number of perennial species an increasing relationship between reproductive effort and plant size has been empirically demonstrated (Samson & Werk, 1985; Hartnett, 1990; Schimid & Weiner, 1993). Likewise, numerous studies have quantified interpopulational variation in mean reproductive effort (cf. Evenson, 1985; Reekie & Bazzaz, 2005).

Estimates of reproductive success based on the absolute fecundity of individual plants (e.g., Herrera, 1990), and demographic aspects (Travis & Henrich, 1986) should be considered instead of, or in addition to , routinely used measures of reproductive success describing the relative success of reproductive structures such as flowers and fruits.

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