

INTRASPECIFIC COMPETITION AND AGGREGATION IN A POPULATION OF *SOLANUM FORSKALII* DUNAL IN A SEMI-ARID HABITAT: IMPACT ON REPRODUCTIVE OUTPUT, GROWTH AND PHENOLIC CONTENTS

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Abstract

This investigation focuses on intraspecific competition in a virtually pure population of *Solanum forskalii* Dunal in a semi-arid area. Intraspecific competition was inferred from correlation between nearest-neighbour distances and plant sizes. In addition, the effect of intraspecific competition on number of leaves, biomass, reproductive output and soluble phenol content was also examined. Plant cover, number of leaves, biomass and reproductive output (number of fruits) were positively correlated with inter-plant distance indicating that intraspecific competition caused reduction in all these parameters as the distance between nearest neighbouring individuals diminished. Soluble phenol content in roots and leaves was found negatively correlated with the nearest neighbouring distance between plant pairs. Accumulation of phenols in response to biotic interaction presumably provides a protective mechanism against the biotic stress of intraspecific competition.

Introduction

Competition for limited resources is one of the most prevalent ecological interactions, and it has been extensively investigated in recent years (Goldberg & Barton, 1992; Vargas-Mendoza & Fowler, 1998; Weis & Hochberg, 2000; Keddy, 2001; Gange *et al.*, 2006). Quantitative studies of plant distribution patterns suggests that biotic interactions, particularly intra- and interspecific competitive interactions are important determinants of the structure of arid and semiarid vegetations (Fowler, 1986; Austin, 1990). The form, reproductive output and chemical composition of plants growing together are affected due to competition as compared to their growth in isolation (Ford & Sorensen, 1992; Hjaelten *et al.*, 1994; Cipollini & Bergelson, 2002; Tiainen *et al.*, 2006; Ormeno *et al.*, 2007). One growing body of information on plant competition comes from investigations that focus on measurement of pairwise interactions among many pairs of species simultaneously (Lehoczky & Reisinger, 2003; Li & Kremer, 2006). These experimentally derived competition matrices may contain useful information on the possible mechanism of plant competition (Keddy & Shipley, 1989). Many empirical studies have demonstrated the importance of local density on survival, growth and reproductive output of individuals (Pacala & Silander, 1987; Khan & Shaukat, 2000; Weis & Hochberg, 2000). However, density is a crude measure of competitive or interactive state of a population because an individual reacts to the effects of neighbours, not to the density of populations (Mack & Harper, 1977). Because of the sessile nature of plants, individuals interfere mainly with close neighbours and therefore the details of the local distribution or 'spatial pattern' of plants within communities are of prime

importance (Antonovics & Levin, 1980; Fowler, 1984; Bergelson, 1993; Khan & Shaukat, 1997; Stoll & Weiner, 2000; Kristensen *et al.*, 2005). Intraspecific aggregation alters the frequency of inter- versus intraspecific encounters so that individuals interfere more with conspecifics (Stoll & Prati, 2001). A great deal of effort has been directed to developing theoretical models which highlight the significance of spatial patterns (Dale, 1999) in ecology but also urges the experimental validation of spatial theory (Tilman & Kareiva, 1997).

Evidence of intraspecific and interspecific competition has been inferred from correlations between nearest-neighbour distances and plant sizes (Phillips & MacMahon, 1981; Cunliffe *et al.*, 1990; Yeaton, *et al.*, 1993; Khan & Shaukat, 1997; Shackleton, 2002; Shaukat *et al.*, 2003). Such results for low rainfall regions have been attributed to impoverished soil moisture status as the limiting resource for the competing neighbouring plants (Shaukat *et al.*, 2003). Experimental removal of closely located individuals, in some earlier studies, resulted in decreased negative xylem water potential of the focal plants, providing evidence that these patterns are the product of root competition for moisture (Ehleringer, 1984). Since soils in arid conditions are often poor in nutrients such as nitrogen and phosphorus, intraspecific competition can also be attributed to limited supply, of soil nutrients, particularly nitrogen (Wiegand & Jutzi, 2001; Tiainen *et al.*, 2006).

Plants have evolved various mechanisms to defend themselves from different types of biotic and abiotic stresses. There is evidence that secondary metabolism may modulate plant responses to various forms of stresses and thereby contribute to plant 'fitness for survival' (Altman & Colwell, 1998). By means of secondary metabolic pathways plants produce a wide range of compounds, including phenols, nitrogen-based compounds and terpenes, that play a protective role against a range of stresses (Seigler, 2001; Cseke *et al.*, 2006; Harborne, 2007). In particular, phenolics are the major secondary metabolites that are involved in the protection of plants against a variety of biotic (Nicholson & Hammerschmidt, 1992; Dixon & Paiva, 1995; Harborne, 1999) and abiotic stresses (Eliasova *et al.*, 2004; Abreu & Mazafera, 2005; Ganeva & Zozikova, 2007; Edreva *et al.*, 2008). Accumulation of secondary metabolites such as phenolics and terpenes in response to competitive stress has also been investigated (Hjaelten, *et al.*, 1994; Siemens *et al.*, 2002; Ormeno *et al.*, 2007). However, our knowledge of how biotic factors such as competition influence plant chemistry and its plausible consequences are limited.

The objectives of this study were: 1) to determine the extent of intraspecific competition in an almost pure population of *Solanum forskalii* Dunal growing in a semi-arid area, 2) to examine the spatial pattern in the population and 3) to investigate the effect of intraspecific competition on growth, reproductive output and the soluble phenolic contents of leaves and roots of *S. forskalii*.

Materials and Methods

Study area: The study was conducted at a site located on the Karachi University Campus in Karachi, Pakistan, which has a subtropical maritime desert climate. Average annual rainfall is about 20 cm, most of which is received during the monsoon (summer) season. Since summer temperatures (the end of April through the end of August) are approximately 30 to 35°C, the winter months (November through March) are mild (average of about 20°C). Wind velocity is generally high all year. Vegetation of the study site consisted of an almost pure population of *Solanum forskalii* Dunal., a perennial undershrub. Within the population a few individuals of an annual herb *Peristrophe*

bicalyculata and an annual grass *Aristida adscensionis* were observed. The topography of the area was uniform and level. If the terrain is level it ensures even deposition of rainfall, a very important criterion in spacing and competition studies (Yeaton *et al.*, 1977).

Soil and vegetation analysis: Soil samples were collected from the field at a depth of 30 cm using a soil auger. Five replicate soil samples were collected and analysed. The physical and chemical characteristics of the soil associated with *Solanum forskalii* population were analysed using the methods described in Allen *et al.*, (1986). The vegetation of the area was analysed using 40 1 m² randomly placed quadrates.

Intraspecific competition: The degree of intraspecific competitive interaction was assessed using the nearest neighbour technique (Pielou, 1977) and following the operational definition of Yeaton & Cody (1976). In this method, the distance between randomly chosen individuals and their nearest neighbour is recorded as are the sums of cover area of each nearest neighbour pair. It is reasonable to assume that if these two variables (sum of cover and interplant distance) are positively correlated, then there exists interference between neighbouring individuals (Yeaton & Cody, 1976). Distances and covers of 40 plant pairs were recorded. Besides the usual response variable i.e., cover-area of the pair of plants. We have also recorded the number of leaves/plant, number of fruits/plant (as a measure of reproductive output) and determined the shoot biomass (dried at 70° C for 24 h). Soluble phenol content of leaves and roots of each pair of plants was also determined.

Soluble phenol estimation: Soluble phenol contents were ascertained in leaves and roots of pairs of plants encountered in the plant-to-plant distance sampling. Total soluble phenols were determined in accordance with Gonzalez *et al.*, (2003) with minor modifications. Root or leaf tissues (500 mg) were taken from each plant and separately homogenized in an ice bath with 2 ml 80% Methanol v/v. The homogenate was centrifuged three times at 6000 g for 3 min. One hundred µl of the supernatant was added to 0.5 ml Folin-Ciocalteu reagent and 1 ml of 20% Sodium carbonate. Finally, distilled water was added until a final volume of 10 ml was attained. The mixture was incubated at 40°C for 30 min. and the absorbance of the developed blue colour was read at 750 nm. Catechol was used as standard. The amount of soluble phenols was expressed as µg mg⁻¹ fresh weight.

Detection of spatial pattern: Perry *et al.*, (2002) suggested employing several different techniques to quantify spatial pattern. Accordingly, the spatial pattern of *S. forskalii* was detected using four different methods— two distance based (plotless) methods and two quadrat-based methods. :) The index α proposed by Pielou (1960) which employs the mean of squared distances between randomly selected sampling origins and their nearest individuals ω was used, as follows:

$$\alpha = \omega \pi \rho$$

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. Pielou (1962) also 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 (1959) 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 $1/(2\sqrt{(2n+1)})$. Hopkins (1951) 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:

$$I_{\delta} = Q \Sigma X_i (X_i - 1) / N (N-1)$$

where $N = \Sigma X_i$, Q equals the number of quadrats and X_i are the number of individuals in each quadrat. The significance of I_{δ} was checked using an F-distribution:

$$F = (I_{\delta} (N-1) + Q - N) / (Q - 1)$$

which is tested against $v_1 = Q$ and $v_2 = \infty$. 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

$$SE = (2/(n-1))^{1/2}$$

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 (Shaukat, 2001; Shaukat & Siddiqui, 2004).

Table 1. Physical and chemical properties of soil associated with the population of *Solanum forskalii*.

Characteristics	Units	Values	Characteristics	Units	Values
Sand	g kg ⁻¹	726	Organic matter	g kg ⁻¹	2.3
Silt	g kg ⁻¹	161	CaCO ₃	g kg ⁻¹	136
Clay	g kg ⁻¹	113	Available PO ₄	ppm	9
Moisture content (July)	%	13.7	Total N	%	0.16
Moisture content (October)	%	8.6	Exchangeable K	ppm	42
Max. water holding capacity	%	28.9	pH	-	7.8

Results

Vegetation and soil analysis: The results of vegetation analysis disclosed that *Solanum forskalii* was the predominant species with a relative density of 95.4% while relative density of *Peristrophe bicalyculata*, *Chloris barbata* and *Cleome brachycarpa* was 2.1, 1.6 and 0.9 % respectively. The absolute density of *Solanum forskalii* was 16.82 per m².

The physical and chemical characteristics of the soil of study site are outlined in Table 1. On the basis of the analysis of the texture, the soil is sandy loam. The soil has alkaline pH, high in CaCO₃, while the moisture content was low particularly in October when the sampling was performed. In general, the nutrient contents of the soil, available phosphate, and total nitrogen content and exchangeable potassium have low concentrations. The organic matter content of the soils was also poor.

Intraspecific competition: A significant positive correlation ($r=0.642$, $p<0.001$) was found between nearest neighbour distance (D) and average covers (C) for pairs of *S. forskalii* individuals (Fig. 1a). With the increase in interplant distance the average cover also increased (Fig. 1a). The following linear regression equation expresses this relationship:

$$C = 19.556 + 8.847 D \pm 54.46$$

The ANOVA for the simple regression revealed a significant linear regression ($F=68.24$, $p<0.001$). The coefficient of determination $R^2 = 0.4122$, indicates that 41.22% of variance in the combined cover) of nearest neighbour plant pairs is accounted for by the variation in the distance between nearest neighbour pairs of *S. forskalii*. Similarly, the relationships between the nearest neighbour distances (D) with the number of leaves (L) and the shoot biomass (B) were also significant ($r = 0.661$, $p<0.001$; $r = 0.687$, $p<0.001$ respectively) (Fig. 1b,c). The linear regression equations pertaining to these relationships are as given below:

$$L = 11.38 + 1.533 D \pm 14.559$$

$$B = 0.770 + 0.131 D \pm 1.064$$

The F-ratios for these regression analyses were $F=38.69$, $p<0.01$ and $F=34.48$, $p<0.01$ respectively, while the corresponding coefficients of determination (R^2) were 0.436 and 0.471, respectively. The correlation between nearest neighbour distances distance (D) and the average number of fruits (representing reproductive output) in pairs of plants (F_R) was significant ($r = 0.515$, $p<0.01$) (Fig. 2a). The regression equation expressing the relationship between distances and average number of fruits is

$$F_R = -0.797 + 0.179 D \pm 1.918$$

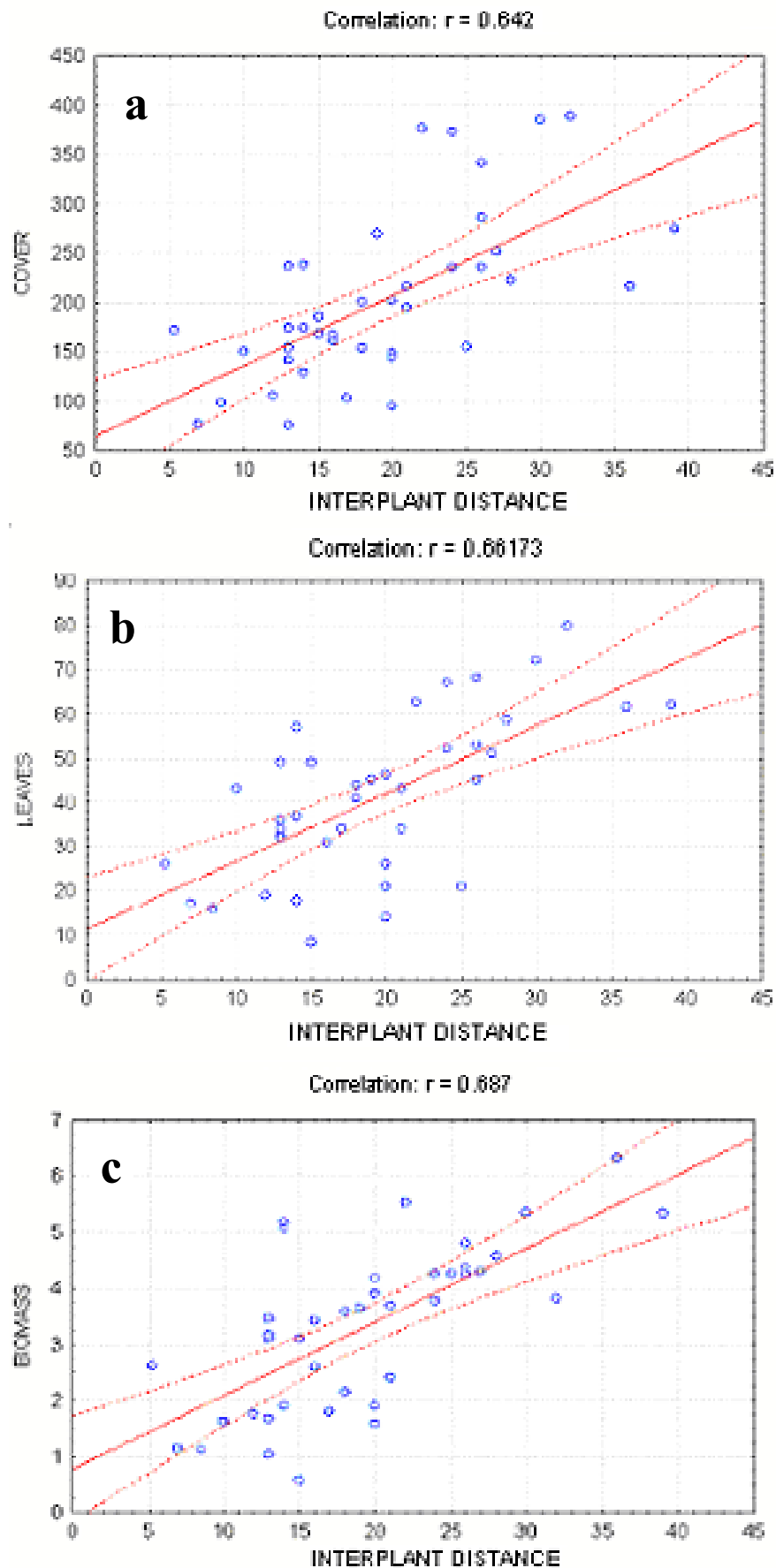


Fig. 1. a, Relationship between mean cover (cm^2) and inter-plant distance; b, relationship between mean number of leaves and inter-plant distance; c, relationship between biomass(g) and inter-plant distance.

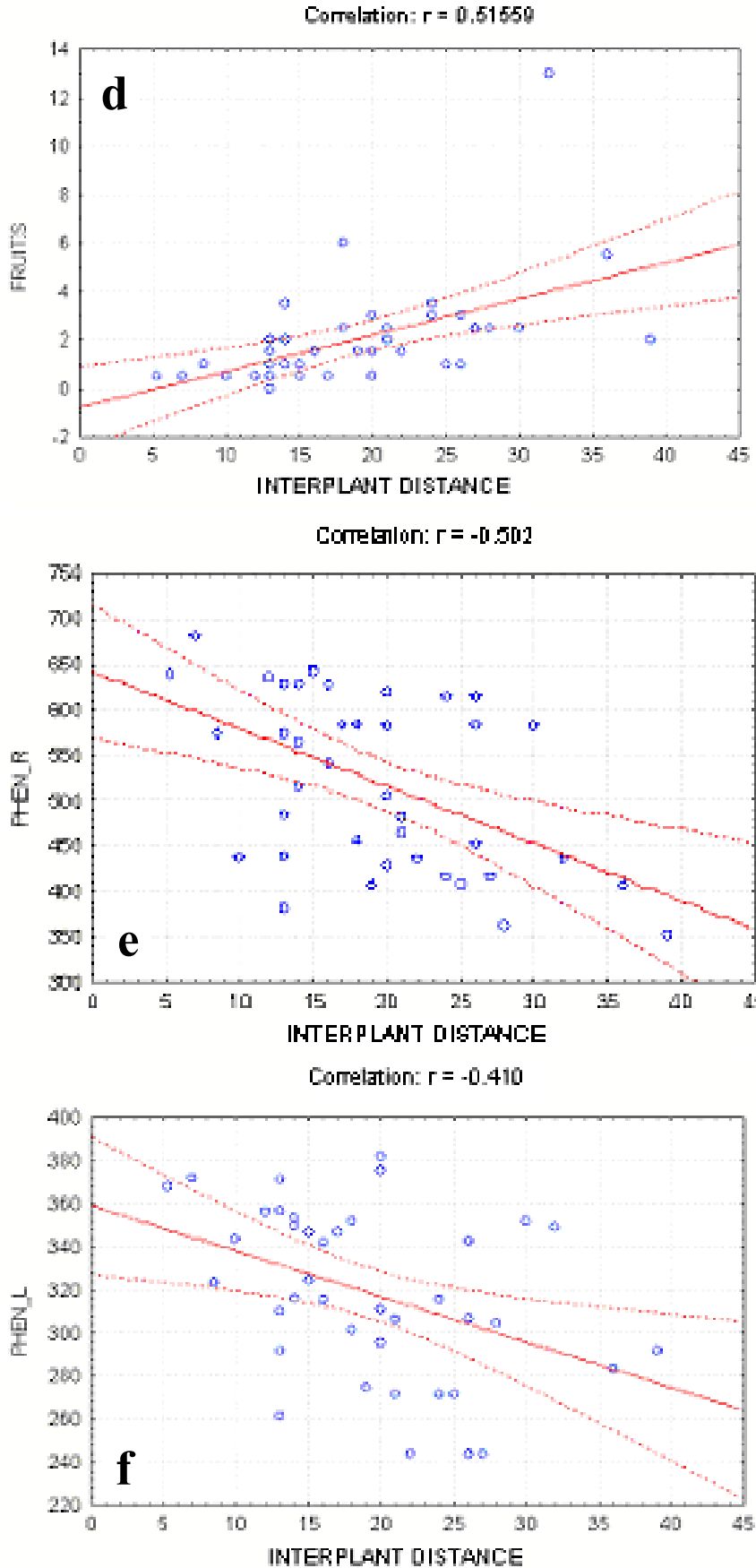


Fig. 2. d, Relationship between number of fruits and inter-plant distance; e, relationship between root phenol (Phen_R) (and inter-plant distance, f, relationship between leaf phenol (Phen_L) and inter-plant distance.

The F-ratio was significant ($F = 13.75$, $p < 0.01$) while the corresponding coefficient of determination (R^2) was 0.265 which implies that 26.5% variation in fruit weight depended on the interplant distance.

Besides the growth and reproductive output parameters, the chemical response due to competitive stress was also investigated. A significant correlation coefficient was obtained between the interplant distance between nearest neighbours (D) and their average phenolic contents of roots (P_R) ($r = -0.502$, $p < 0.001$) (Fig. 2b,c). Likewise, the correlation coefficient between interplant distance and the phenolic content of leaves (P_L) the nearest neighbours was also significant ($r = -0.410$, $p < 0.001$). The linear regression equations for these relationships are:

$$P_R = 642.24 - 6.31 D \pm 83.798$$

$$P_L = 359.06 - 2.111 D \pm 36.101$$

The corresponding F-ratios resulting from ANOVA for phenol content of roots and leaves as regressed against interplant distance were found significant, $F = 12.836$, $p < 0.05$; and $F = 7.704$, $p < 0.05$, respectively while R^2 for these relationships were 0.252 and 0.168 respectively.

Spatial pattern: Pielou's index α was found to be 2.394 which is significantly ($p < 0.01$) greater than the expected value (0.975) indicating an aggregated distribution. Hopkins' test yielded a value of $A = 1.534$ and that of $x = 0.6053$. Testing the x value against the theoretical distribution (chart given by Hopkins) significant ($p < 0.01$) aggregation in the population was indicated. Morisita's index gave a value of $I_\delta = 1.1730$, which when tested against theoretical F-distribution ($F = 3.980$; $v_1 = 39$, $v_2 = \infty$) was found significant ($p < 0.001$) indicating an aggregated distribution. Lastly, the variance/mean ratio of 3.986 was highly significant ($p < 0.001$) pointing to an aggregated distribution at the quadrat size used. It is noteworthy that Monte Carlo simulation tests for all the four pattern detection indices revealed significant (P at the most 0.01) aggregation of the population, thereby confirming the results of the classical tests.

Discussion

The determination of the functional significance of negative species interactions in the assembly and maintenance of plant communities of arid regions has been the objective of numerous ecological investigations. One of the methods frequently employed in such studies is the nearest neighbour analysis, most workers employ Pielou's (1962) method wherein distance between randomly-chosen individuals and their nearest neighbour is recorded, as are sums of covers of each nearest neighbour pair. It is postulated that if these two variables are positively correlated then there is interference between neighbouring individuals (Yeaton & Cody, 1976; Philips & MacMahon, 1981). The nearest neighbour analysis performed for *Solanum forskalii* disclosed the existence of a negative interaction between conspecific closest neighbouring individuals. A high value of product-moment correlation coefficient ($r = 0.642$) provides evidence of a fairly intense intraspecific competition (Yeaton *et al.*, 1985). It is assumed that a higher degree of correlation indicates stronger competitive interaction which limits more effectively the size attained by the smaller individual as a function of its distance from its nearest

neighbour (Cunliffe *et al.*, 1990). Since larger plants may use more of a limiting resource than smaller ones, other individuals do not survive quite so close to a larger plant.

The average number of leaves in the nearest neighbouring individuals and their average shoot biomass also were found to be positively linearly correlated with the interplant distance, providing evidence on the prevalence of intraspecific competition in *Solanum forskalii*. The association of lesser number of leaves/plant associated with the closely located individuals suggests that soil moisture is one of the limiting factor and the smaller leaf-area due to lesser number of leaves would minimize the rate of water loss by transpiration. Decreased overall photosynthesis by the plant owing to fewer leaves results in suppression of biomass production by such individuals. Likewise, we also obtained a positive correlation between the average number of fruits/plant (reproductive output) and nearest neighbouring distance of *S. forskalii* Cunliffe *et al.*, (1990), Bergelson (1993) and Shaukat *et al.*, (2003) found decreased reproductive output of plants in response to intra- and interspecific competition.

Nutrient supply in the soil environment is extremely heterogeneous, varying both spatially and temporally at scales relevant to plant roots (Hodge, 2003) and plays a significant role in intraspecific competition and in determining plant size hierarchies (Facelli & Facelli, 2002). The measurements of total nitrogen and the available phosphorus content in the field gave relatively low values for these nutrients in soil indicating the paucity of these resources, thereby influencing the response of roots pertaining to acquisition of these resources by the plants. The resource acquisition ability of the closely located individuals may be adversely affected due to the stresses to which the roots are exposed. The reduction in cover, number of leaves, shoot biomass and the reproductive output can all be attributed to resource competition for moisture and nutrients in closely located individuals.

A high degree of negative correlation was found between the average phenol content (of roots and leaves) of the nearest neighbouring individuals and their interplant distance for *Solanum forskalii*. Secondary metabolites such as phenolics and terpenes are known to play a major role in the adaptation of plants to the changing environment and in overcoming stress constraints (Seigler, 2001). Natural selection favours the production of secondary metabolites with multiple functions because they provide protection to plants from unpredictable biotic and abiotic factors. Plant phenolics have long been regarded as defenses against pathogens and herbivores (Dixon & Paiva, 1995) and provide protective mechanism against a variety of abiotic stresses (Eliasova *et al.*, 2004; Abreu & Mazafera, 2005; Ganeva & Zozikova, 2007; Edreva *et al.*, 2008). Competitive stress is also known to result in the accumulation of phenolics and terpenes (Hijaltem, *et al.*, 1994; Siemens *et al.*, 2002; Ormeno *et al.*, 2007). Our results provide additional support regarding accumulation of secondary metabolites (phenolics) in root and leaves in response to intraspecific competitive stress. Secondary metabolic pathway is physiologically important as it provides the means of channeling and storing carbon compounds, accumulated from photosynthesis, during periods when nitrogen is limiting or whenever leaf growth is curtailed. However, to establish the protective role of any secondary metabolite, it is necessary to monitor the concentration over the life cycle of the plant and to survey the population, to determine specific localization within tissue and perform bioassays against associated microorganisms, insects and other predators (Harborne, 1999). Secondary metabolites may vary irregularly in their distribution within the plant or within populations yet they may still provide protection. The protective role of phenolics may be due to structural stabilization of cell-wall through condensation-polymerization of

phenols and quinones. Secondly, they can provide photoprotective mechanism, *i.e.*, by altering the absorbance of visible and UV-radiation. Thirdly, they act as powerful antioxidant and antiradical agents (Harborne, 1999; Edreva *et al.*, 2008).

All four methods of pattern detection indicated aggregated dispersion pattern for the *Solanum forskalii* population. The two distance-based methods used here 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 which confirmed the prevalence of aggregated distribution of the population. 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 too small nor excessively large and probably represented the scale of aggregation inherent in the population. A number of workers have demonstrated that aggregated pattern leads to greater intensity of intraspecific competition (Stoll & Weiner, 2000; Kristensen *et al.*, 2005) as the occurrence of individuals in close vicinity in the biological space would increase the probability of interference among the conspecifics, particularly when the individuals are uniformly distributed within the clumps (Ross & Harper, 1972).

In conclusion, evidence is presented on the prevalence of a significant component of intraspecific competition in the population size-structure by demonstrating a highly significant correlation between interplant distance on one hand and the average cover, number of leaves and biomass on the other. In addition, the reproductive output (number of fruits/ plant) was also positively correlated with the distance between pairs of nearest neighbour plants pointing to the dependence of reproductive output on competition. Low moisture and nutrient regimes seem to be the principal causes involved in the resource competition. The prevalence of aggregated pattern in the population promotes the intensity of intraspecific competition by increasing the probability of intraspecific contacts. Accumulation of soluble phenols in the roots and leaves of the competing plants apparently provides a protective mechanism against the biotic stress due to competition and also possibly against other biotic and abiotic stresses. Together with theoretical models on spatial patterns and dynamics, controlled experiments and field observations on competition such as the present study provide significant insight into understanding of the patterns and processes involved in the structuring of plant communities.

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