COMPETITIVE INTERACTIONS BETWEEN A PERENNIAL LEGUME SHRUB *INDIGOFERA OBLONGIFOLIA* AND TWO ANNUALS *TEPHROSIA STRIGOSA* AND *CORCHORUS TRILOCCULARIS*

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Abstract

The investigation focuses on competitive interactions between a perennial shrub *Indigofera oblongifolia* and two annuals *Tephrosia strigosa* and *Corchorus triloccularis* as well as the intraspecific competition of the three mentioned species. Both intraspecific and interspecific competitions were inferred using the nearest neighbour distances between pairs of plants. Intraspecific competitive intensity was found to be greater for the annuals than that of the perennial shrub. Interspecific competition between the perennial shrub species and the two annuals was assessed by the reproductive potential of the annuals. The accumulation of phenolics in the roots of annuals was tested in response to competitive stress. The number of flowers (and fruits) in the two annuals were depressed as the distance between annual plant and the shrub (*I. oblongifolia*) declined. By contrast, there was greater accumulation of total soluble phenols in the annuals as the distance of the shrub became closer to the annual. The implications of competitive interactions in structuring the communities are discussed.

Key words: Competition, Annuals, Perennials, Resources, Phenols.

Introduction

One of the most prevalent ecological interactions, which are being extensively investigated in recent years, is competition for limited resources (Vargas-Mendoza & Fowler, 1998; Weis & Hochberg, 2000; Gange *et al*., 2006, Keddy, 2007, 2012). Without gaining a thorough insight of the mechanisms of plant interactions, we can not predict the responses of communities and ecosystems to available nutritional level, species composition patterns and diversity, to elevated atmospheric carbon dioxide levels, response to invasive species and global climate change. Understanding interactions between annuals and perennials is essential to the management and restoration of shrub-dominated habitats. Small–scale spatio-temporal patterns have been recognized to be important in the assembly and organization of communities and separation in time and space can lead to enhanced plant diversity in general and that of annuals in particular (Guo, 1998; Bolker *et al*., 2003; Herben *et al*., 2006). Investigations attempting to disclose spatial distribution patterns of perennial and annual species suggests that biotic interactions, particularly intra- and interspecific competitive interactions are important determinants of community structure, particularly in arid and semiarid vegetation (Cheplick & Wicstrom, 1999; Bolker & Pacala, 1999; Guo *et al*., 2006; Khan & Shaukat, 2000, Facelli & Temby, 2002; Shaukat *et al*., 2003, 2009b). The impact of interspecific competition is usually measured by its effect upon plant growth, neglecting impacts upon other stages of the life cycle such as fecundity which have a direct influence upon individual fitness and the asymptotic population growth rate. The form and reproductive output of plants growing together are affected due to competition as compared to their growth in isolation (Harper, 1977; Ford and Sorrensen, 1992; Sammul *et al*., 2000; Cipollini & Bergelson, 2002).

Many empirical studies have elaborated the importance of local density in survival, growth and reproduction of individuals (Gottleib, 1977; Silander & Pacala, 1986; Miller & Weiner, 1999; Khan & Shaukat, 2000). However, density is a crude measure of competitive or interactive state of a population because individuals react to neighbouring individuals not to the overall density of co-occurring species populations (Goldberg & Landa, 1991; Weiner *et al*., 2001; Bruno *et al*., 2003; Keddy, 2007, 2012). Competing plants can be different regarding size and many physiological and ecological aspects such that considering average individual would compromise the results to a great extent (Berger *et al*., 2008).. Competition between plants has been shown to be exclusively a neighbourhood phenomenon (Mack & Harper, 1977; Turkington & Harper, 1979) and interactions occur only among closely located individuals (Silander & Pacala, 1986; Ford & Sorrensen, 1992; Khan & Shaukat, 1997; Shaukat *et al*., 2003). Thus the distances between neighbours and overall spatial configuration are important determinants (Stoll & Weiner, 2000).

Various techniques and related computational issues have been proposed and addressed to investigate competition under field conditions (Weldon & Slauson, 1986; Golberg, 1994; Crawley & May, 1987; Guo & Brown, 1997; Sammul *et al*., 2000; Miriti *et al*., 2001; Berger *et al*., 2008; Damgaard, 1998, 2004, 2008; Bohn *et al*., 20011). The degree of interspecific and intraspecific competition can be assessed from correlations between nearest-neighbour distances and plant sizes (Welden *et al*., 1988; Cunliffe *et al*., 1990; Yeaton *et al*., 1993; Grundy *et al*., 1994; 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 (Woodell *et al*., 1969; 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 (Fonteyn & Mahal, 1981; Ehleringer, 1984), Furthermore, Ehleringer *et al.* (1991) demonstrated differential utilization of summer rains by annuals, perennial herbs and shrubs, suggesting that the components within the community will respond differentially to the change in precipitation patterns that would have sizable impact on competition and possible alteration in community structure. Since soils in arid regions are often poor in nutrients such as nitrogen and phosphorus the inter- or intraspecific competition can also be attributed to limited supply of soil nutrients (Lentz, 1999; Wiegard & Jutzi, 2001; Hodges, 2003; Tiainen *et al.*, 2006). However, such studies have mostly focused on competition between perennial herbs or shrubs

Annuals are the important component of the vegetation of arid and semi-arid regions that are known to adapt to variable and unpredictable environments; they play important role in the restoration and conservation of such ecosystems Annuals exploit the resources during the period of favourable environment, complete their life cycle and subsequently remain dormant as seed in soil under unfavourable conditions (Inouye *et al.*, 1980; Whitford & Gutierrez, 1989). The annuals typically exhibit enormous phenotypic plasticity and on a local scale their distribution is largely governed by soil surface characteristics that determine seed accumulation and water retention and also due to the presence of perennials (shrubs) that compete with the annuals growing in the vicinity. Seeds of annuals respond strongly to the presence of established perennial plants in the vicinity which in turn has great impact on persistence (Rees & Long, 1992). Seed production of annuals is suppressed under shrub canopies, in the open areas between shrubs, or both and dispersal distances are generally short (atelochory) and smaller compared to spatial heterogeneity i.e., mosaic developed by shrubs and the interspaces (Venable *et al.*, 2008). Seed dispersal may involve many risks often resulting in substantial loss of propagules, however, those that remain tend to occupy favourable sites (Lavorel *et al.*, 1995). Annual species with greater long-term demographic variation, i.e., year-to-year fluctuation, tend to be those with greater sensitivity of reproductive success to variation among years in summer and/or winter precipitation (Venable & Pake, 1999). It has been argued by some that annuals are weaker competitors than perennials because of former's greater sexual reproductive effort (Gadgil & Solbrig, 1972). Nonetheless, they have the capability to adapt to variable and unpredictable environments. With a few exceptions (Pantastico-Cadas & Venable, 1993; Cheplic & Wickstrom, 1999; Brooks, 2000, 2003; Bender *et al.*, 2002, Facelli & Temby, 2002; DeFalco *et al.*, 2007; Shaukat *et al.*, 2003; HilleRisLambers *et al.*, 2010; Sheley & James, 2014) annuals have been largely ignored in competition studies particularly under field conditions.

Comparatively little is known about the processes structuring communities where annuals contribute a great deal to community composition and structure; one significant process is competition. Here, we investigate intra – and interspecific competition of two annual species in detail and how do they circumvent the problem of competition with the perennials (shrubs) and to what extent they are adversely affected by competitive stress. Facelli & Temby (2002) advocated that the presence of shrubs in arid areas creates spatial heterogeneity that affects the distribution and performance of annual plants present in the landscape. They suggested several possible mechanisms of which root competition plays a significant role. Corbin & D'Antonio (2004) provided evidence on the ability of established native perennial species to limit space available for seeds of annual species to germinate and to restrict the light available to the seedlings thereby reducing the productivity of annuals and some weeds and shifted the balance of competitive interaction in favour of the perennials. Weedon & Facelli (2008) demonstrated that the overall effect of shrubs on the annuals in the arid ecosystem (in South Australia) is negative under the range of water availabilities prevailing during the experiment. With regard to possible allelopathic effects, interactions between annuals and perennials have been investigated under field conditions (Shaukat *et al.*, 1983). Interestingly, many studies have attempted to separate the two mechanisms of interference, *i.e.*, allelopathy from resource competition as a probable cause of observed growth patterns of plants in the field. Inderjit & del Moral (1997) and Williamson (1990) pointed out that separating allelopathy from resource competition was essentially impossible in natural systems (but see Murphy, 2000). Furthermore, any experimental design to distinguish allelopathy from resource competition would necessarily involve conditions that do not duplicate those prevailing in the field. Fowler (1986) stated that the information regarding plant-to-plant interactions (e.g., competition) so as to evaluate the propinquity in this respect among various biogeographic regions, in particular arid regions, is scant. Knowledge of the kind and degree of competitive interactions among species in the field is mandatory for appropriate management of field populations and maintenance of biodiversity. Under field conditions, plants are exposed to a multitude of stresses including biotic stress such as pathogen attack, predation, competition and several abiotic type including drought conditions, paucity of nutrients, acid rain, etc. It has been demonstrated that secondary metabolism may modulate plant responses to varied stresses and thereby confer resistance that eventually increases 'fitness for survival' (Altman & Colwell, 1998). Secondary metabolic pathways in plants play a vital role in providing protection against a variety of stress conditions by producing a range of compounds including phenols, polyphenols, saponins, glycosides, terpenes and glucosinolates that play a crucial protective role against various types of stresses (Seigler, 2001; Cske *et al.*, 2006; Harborne, 2007; Shaukat *et al.*, 2009a, 2009b). Phenolics, in particular, are the major secondary metabolites that are implicated in conferring resistance in plants to a variety of

biotic (Nicholson & Hammerschmidt, 1992; Dixon & Paiva, 1995, Dixon, 2001; Shaukat *et al.*, 2009b) and abiotic stresses (Eliasova *et al.*, 2004; Abreu & Mazzafera, 2005; Geneva & Zozikova, 2007, Edreva *et al.*, 2008; Shaukat *et al.*, 2013). Most phenolic metabolites in plants are linked to phenylpropanoids that are derived from cinnamic acid produced by phenylalanine by the activity of the enzyme phenylammonia-lyase (PAL), the bifurcation point enzyme between primary metabolism (shikimic acid pathway) (see Hermann & Weaver, 1999) and the secondary (phenylpropanoid) metabolism (Dixon & Paiva, 1995). Phenolic compounds in plants are principally synthesized from phenylpropanoid pathway intermediates that include caffeic acid, p-coumaric acid, ferulic acid and sinapic acid. Terpenoid quinones are formed by a combination of the shikimate pathway with the terpenoid pathway (Dewick, 2002). The accumulation of phenolics and /or terpenes owing to competitive stress has been demonstrated by some workers (Hjalten *et al.*, 1994; Siemens *et al.*, 2002; Ormeno *et al.*, 2007; Shaukat *et al.*, 2009b). However, our knowledge is limited regarding how biotc stresses such as competition influence the production of plant secondary metabolites and the possible role of the latter regarding the structuring of communities.

The major objective of this study was to disclose the competitive interactions between a perennial shrub, *Indigofera oblongifolia* Fosskal and two annual herbs including *Tephrosia strigosa* (Dalz.) Santapau & Maheshw. and *Corchorus trilocularis* L. Intraspecic competitive effect for both the annuals and the perennial species (*Indigofera oblongifolia*) were also examined. We also focused on impact of interspecific competition on the reproductive potential of the annual herbs as well as the accumulation of phenolics in the root tissue of the annuals imposed by interspecific competitive stress.

Materials and Methods

Study area: The study was conducted near Pakistan Steel Mills area, nearly 50 km Northeast of Karachi city. The climate of the area has been designated as subtropical maritime desert. In accordance with Holdrige's system, the bioclimate of the area falls into tropical desert bush formation (Shaukat *et al.*, 2014). The average annual rainfall is about 195mm, most of which is received during the monsoon season. A topographically uniform plain area was selected within the study site. A levelled terrain ensures an even deposition of rainfall which is deemed to be an important determinant in spacing and competition studies (Yeaton *et al.*, 1977). The vegetation of the study area was dominated by the perennial shrubs such as *Indigofera oblongifolia* Forssk., *Zizyphus nummularia* (Burm f.) Wight & Arn., *Prosopis cineraria* (L.) Druce, *Prosopis juliflora* (Sw.) DC, *Capparis decidua* (Forssk.) Edgew. , and *Lyceum edgeworthii* Dunal. The abundant annuals included *Aristida adscensionis* L., *Tephrosia strigosa* (Dalz.) Santapau & Maheshw., *Corchorus trilocularis* L. *Tragus biflorus* Panigrahi, *Indigofera cordifolia* Heyne ex Roth., *Cleome viscosa* L. and *C. scaposa* DC.

Vegetation sampling: Phytosociological attributes, namely density and cover of the perennial (shrub) species constituting the principal framework of vegetation in the study area were estimated using point-centred quarter method (see Kent & Koker, 1994). Distances of plants from the centre of the quarter point and plant covers were recorded at fifty sampling points made at regular intervals along a predetermined direction (W to E). The cover of each individual shrub was based on diameter measured as the average of long axis and the maximum width of the canopy perpendicular to the length

Using this field data relative densities (D_3) relative cover (C_3), absolute density (D_2), absolute cover (C_2) and importance value (IV) of the shrub species were calculated. Importance value of species was calculated as (D_3+C_3). Density of the two selected annual species namely *Tephrosia strigosa* and *Corchorus trilocularis* were estimated using fifty 1 m^2 randomly placed quadrats.

Assessment of competition: The degree of intra- and interspecific interactions were assessed using the nearest neighbour technique (Pielou, 1977) and following the operational definition of Yeaton & Cody (1976). The technique involves the measurement of distances between randomly chosen individuals and their nearest neighbours as well as the sums of cover areas of the nearest neighbour pairs. The method works on the principle that if the sums of the covers are positively correlated with the interplant distances then there exists interference between neighbouring individuals (Ehleringer, 1984). It is mandatory that the data on nearest neighbour pairs of individuals should be collected from a topographically uniform area and that the pair of plants should not be separated by a drainage line or a mound such as an 'ant mound'. Furthermore, inter- or intraspecific pair of individuals should not be intersected by the canopy of a third species.

Nearest neighbour distances between randomly chosen individuals of the shrub *Indigofera oblongifolia* and the annuals *Tephrosia strigosa* and *Corchorus trilocularis* were measured. Nearest neighbour distances were measured between the centres of the two canopies and the cover area of each individual measured as outlined above. Measurements of interplant distance and sums of covers were recorded for thirty-five conspecifics of the perennial *I. oblongifolia* and for the two annuals *Tephrosia strigosa* and *Corchorus trilocularis* to assess the degree of intraspecific competition. Interspecific interactions were estimated for the annuals located within a distance of 1.0 m radius from the centre of each randomly chosen *I. oblongifolia* shrub. The individuals of *I. oblongifolia* were chosen randomly to serve as focal plant. For the two annuals *T. strigosa and C. trilocularis*, the number of plants (or seedlings) were recorded at 10 cm intervals up to 1m distance from the centre of *I. oblogifolia.* In addition, the number of flowers (including developing fruits) for the two annuals were also counted per plant as a measure of reproductive potential. The number of flowers (plus fruits) of the annuals and distance from the centre of *I. oblongifolia* were subjected to correlation and regression analysis (Rosner, 2006; Zar, 2009). Additionally, for randomly chosen *T. strigosa* or *C. trilocularis* individuals the nearest neighbour (either conspecific or hetrospecific viz., *I. oblongifolia*) and flowering/fruiting status were recorded.

The combined cover was calculated for each nearest neighbour (conspecific) pair. These values were regressed against their corresponding interplant distance to assess the strength of the relationships between the independent and the dependent variables. The analysis of variance for regression was performed for all three species to check the significance (Zar, 2009).Additionally, product-moment correlation coefficient and coefficient of determination were computed for combined cover versus interplant distance for the shrub and the two annuals (Zar, 2009). The effect of distance on flowering status was determined by arbitrarily grouping *T. strogosa* and *C. triclocularis* individuals found at various distances from *I. oblongifolia* five classes as follows: 0-20, 20-40, 40-60, 60-80 and 80-100 cm. A chi-square contingency test was employed to assess the association between flowering/fruiting designation and the distance category of the annuals and the shrub using mean as the expected value (Zar, 2009). Computer programs for all the statistical analyses were developed by the first author (S.S.S.) in C++ and FORTRAN 77 and are available from the senior author on request.

Estimation of soluble phenol content: Total soluble phenol content was ascertained in roots of pairs of plants chosen in the plant-to-plant distance sampling. Soluble phenol content was estimated following the procedure described by Gonzalez *et al.* (2003) with slight modifications. Plant tissues (500mg) from each plant were homoginized in an ice bath with 2ml methanol v/v. Subsequently, the homogenate was centrifuged thrice at 6000g for 3 min. One hundred μl of the supernatant was added to 0.5ml Folin-Ciocalteau reagent and 1ml of 20 percent sodium carbonate. Lastly distilled water was added to achieve a final volume of 10ml. The mixture was then incubated at 40° C for 30 min. The absorbance of the blue colour obtained was read at 750 nm on a Shimadzu (model UV-1800) spectrophotometer. Gallic acid was employed as standard. The Soluble phenol content was expressed as μg mg^{-1} fresh weight.

Results

Analysis of vegetation composition showed a total of 18 perennials (shrubs) of which *I. oblongifolia* was the first dominant species with an importance value (IV) of 45.8 while *Zizyphus nummularia* was second dominant (IV=26.8) (Table 1). *Prosopis juliflora* an exotic and invasive species from South America was recorded as third dominant. The rest of the perennials had IV less than 20. Eight species had importance value (IV) less than 8.

A significant positive correlation (r=.787 , p<0.01) was found between nearest neighbour distance (D) and the sum of cover (C) for pairs of the shrub *Indigofera oblongifolia* (Fig. 1).With the increase in interplant distance sum of cover also increased. The linear regression equation for this relationship is as follows:

$$D = 0.841 + 0.587C \pm 0.491 \quad R^2 = 0.619 \qquad F=61.92 \ (p<0.001)$$

Likewise, significant positive correlations were found for nearest neighbour distance (conspecific) and the sum of cover for the annuals *Tephrosia strigosa* (r=0.879, p<0.001) (Fig. 2) and *Corchorus trilocularis* (r=0.896, p<0.001) (Fig. 3). The regression equation for *T. strigosa* between distance (D) and cover (C) is as follows:

$$D = 0.076 + 0.710C \pm 0.272 \quad R^2 = 0.678 \qquad F = 129.29 \ (p<0.001)$$

The corresponding regression equation for *Corchorus trilocularis* is given below:

$$D = 0.924 + 0.347 \pm 0.034 \quad R^2 = 0.803 \qquad F=154.91 \ (p<0.001)$$

Table 1. Phytosociological attributes of shrubs (perennials) of semi-desert shrub community in the vicinity of Pakistan Steel Mills.

| Species	D_3	C_3	D_2	C_2	IV
Zizyphus nummularia	11.5	15.3	188.4	241.11	26.8
Indigofera oblongifolia	21.0	24.8	343.9	253.03	45.8
Prosopis cineraria	9.0	10.6	147.4	277.12	19.6
Prosopis juliflora	11.5	13.2	188.4	697.08	24.7
Capparis decidua	6.5	8.5	106.5	223.65	15.0
Lycium edgeworthii	8.0	3.4	131.0	113.97	11.4
Salvadora oleoides	5.5	2.0	90.0	262.81	7.5
Pteropyrum olivierii	4.5	2.3	73.71	70.02	8.7
Vernonia cinerescens	6.0	2.7	98.28	86.48	12.8
Euphorbia caducifolia	5.0	7.8	81.9	352.17	12.8
Iphiona grantioides	2.5	0.3	40.95	31.46	2.8
Prosopis glandulosa	2.5	0.5	40.95	39.37	3.0
Cadaba fruticosa	1.5	0.8	24.57	29.48	2.3
Solanum surattense	1.5	0.4	24.57	10.56	1.9
Calotropis procera	1.5	0.8	24.57	35.13	2.3
Heliotopium ohioglossum	1	0.3	0.16.38	18.21	1.3
Ochradenus baccatus	0.5	0.1	0.19	0.134	0.6
Leptadenia pyrotechnica	0.5	0.2	0.19	0.151	0.7
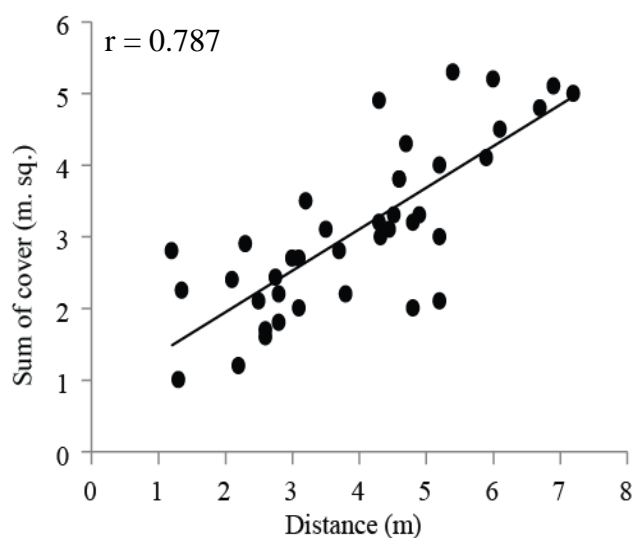
Fig. 1. Relationship for *Indigofera oblongifoliai* near Pakistan Steel Mills of sum of covers for 40 pairs of plants and their distance.
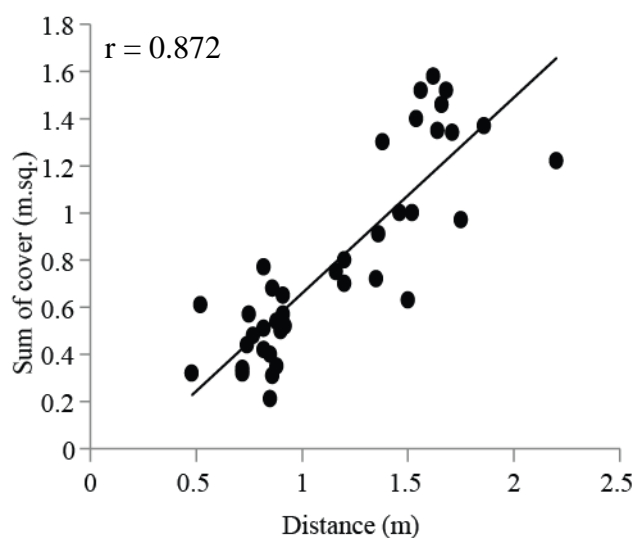

Fig. 2. Relationship for *Tephrosia strigosa* near Pakistan Steel Mills of sum of covers for 40 pairs of plants and their distance.
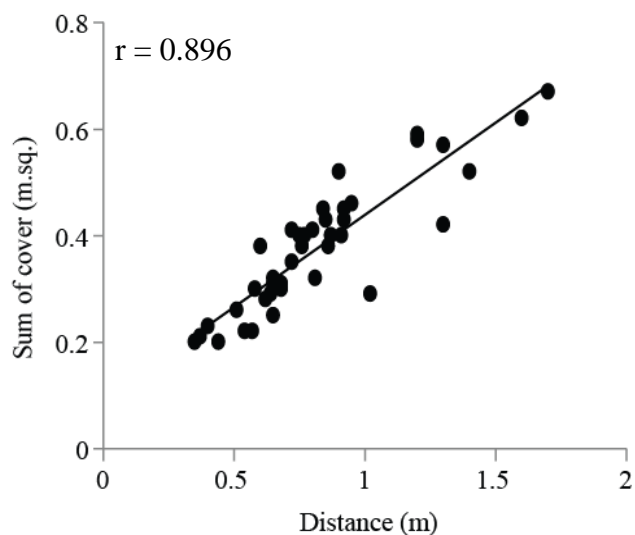

Fig. 3. Relationship for *Corchorus triloccularis* near Pakistan Steel Mills of sum of covers for 40 pairs of plants and their distance.

The flowering status of annuals was evaluated against the shrub *I. oblogifolia* and conspecifics. Overwhelming majority of the two annuals (*T. strigosa* and *C. triloccularis*) that had conspecific as the nearest neighbour showed flowering (94.1% and 88.6.8% for *T. strigosa* and *C. triloccularis* respectively) while 6.9 and 11.4% of the two annual species failed to flower (Table 2). However, when growing together with *I. oblongifolia* (shrub) *T. strogosa* and *C. tricloccularis* showed 80.9 and 77.3% flowering while 19.9 and 22.7% respectively failed to bloom. Test of association between flowering/ nearest-neighbour showed significant association between flowering and the kind of nearest neighbour plant, i.e., conspecific or the shrub ($\chi2=10.45$, $p<0.01$; G=11.44) for *T. strgosa* and ($\chi2=3.90$, $p<0.05$; G=4.06) for *C. triloccularis*. Further analysis of the flowering status of annuals and the arbitrary distance categories (of 20cm distance intervals) from the perennial shrub (*I. oblongifolia*) (Fig. 4a,b) showed significant positive association (chi-square) between the flowering of the two annuals and distance from the perennial shrub, $\chi2 = 26.71$, $p<0.001$, for *T. strigosa* and $\chi2=14.59$, $p<0.01$ for *C. triloccularis*. Fig. 5a,b shows the relationship between soluble phenol content of the annual *Tephrosia strigosa* and *Corchorus triloccularis* at various distance categories from the perennial shrub *Indigofera oblongifolia*. The total soluble phenol content of *T. strogosa* increased with increasing distance categories from the perennial shrub (F=29.85, $p<0.001$) (Fig. 5a). Likewise, soluble phenol content of *Corchorus triloccularis* was also elevated (Fig. 5b) as the plants were located at a greater distance from the shrub *I. oblongifolia* (F=46.45, $p<0.001$).

Discussion

The present study has demonstrated that both intra- and interspecific competition are important in the field and play a significant role in the structuring of plant community and in altering the reproductive output of neighbouring plants that could have important bearing on the population dynamics of individual species as well as interactive dynamics of multispecies. Competition studies under natural conditions frequently employ nearest neighbour analysis to assess the intensity of intra- and interspecific competition using nearest neighbour analysis we employed the method developed by Pielou (1977) wherein the distance between randomly chosen individuals and its nearest neighbour is recorded, as are the sums of sizes of each of the nearest neighbouring pair. It is postulated that if these two measures are correlated then there exists competition between the neighbouring individuals (Yeaton & Cody, 1976; Phillips & MacMahon, 1981). High degree of correlation between interplant distance and sum of covers of conspecific pairs provided convincing evidence on the prevalence of intaspecific competition in the shrub *Indigofera oblongifolia* as well as in the two annuals *Tephrosia strigosa* and *Corchorus triloccularis*. The intensity of competition as determined by the product-moment correlation coefficient, r (Yeaton *et al.*, 1985) was greater for the two annuals (smaller plants) compared to that of the perennial shrub (larger plant). It is assumed that a greater degree of correlation coefficient indicates stronger competitive interaction. This accords well with the findings

of Cunliffe *et al*. (1990) who obtained greater correlation for the annual (*Gorteria diffusa*) compared to that of the perennial shrub (*Lepoldita constricta*). The hypothesis of greater importance of intraspecific competition compared with interspecific competition is, in theoretical works, often used as a criterion for coexistence (often known as Lotka-Volterra coexistence criterion (see e.g. Tilman, 1982; Freed & Cann, 2014; Shchekinova *et al*., 2014) and evidence has often been provided in several field investigations (Brendse, 1983; Johansson & Keddy, 1991). However, despite the accumulation ample amount of evidence regarding competition between annuals and the perennials (shrubs) particularly under arid conditions, some studies maintain the prevalence of facilitation phenomenon in which native perennial (shrub) species support a greater abundance of exotic annuals than interspaces, indicating overall facilitation of exotic annuals by the native perennials (Holzapfel & Mahal, 1999; Tielborger & Kadman, 2000a, Holzapfel *et al*., 2006; Abella *et al*., 2011; Abella & Smith, 2013). Both

Competition and facilitation can prevail intra- and interspecifically. Tielborger & Kadman (2000b) advocated that temporal environmental variation sway the balance between facilitation and interference (competition) in desert plants. Likewise, Weedon & Facelli (2008) demonstrated that perennial plants facilitate understorey annual species in arid lands through the modification of spatial patterns of resources and conditions. Such a response can result from a balance between simultaneously positive and negative interactions, whether direct or indirect. This balance is readily shifted depending on temporal variability in available water. On the other hand, DeFalco *et al*. (2007) highlighted the potential for the decline of perennial species in an undisturbed habitat in the Mojave desert through direct interaction with an exotic annual grass *Bromus madritensis*. As *Bromus* continues to integrate into the native flora and dominate the landscape, the composition of species within these communities, especially the shorter-lived perennial grasses, are subject to change even in the absence of wildfire.

Table 2. The flowering status of *Tephrosia strigosa* and *Corchorus triloccularis* when their nearest neighbour was either conspecific or the shrub *Indigofera oblongifolia*.

Species	Nearest neighbour	Flowering	Non-flowering
T. strigosa	Conspecific	113	07
	Shrub	136	32
C. triloccularis	Conspecific	70	09
	Shrub	82	24

Competition for limited resources is usually regarded as the most significant force for interference. Keeping in view the conditions of the study area, light is apparently not a limiting factor, particularly in an open community such as the one under investigation. Water is the most likely a limiting factor (Harrington, 1991; Casper & Jackson, 1997; Craine & Dybzinski, 2013) but competition for nutrients (Gutierrez *et al*., 1988; Drenovsky & Richards, 2004, 2005; Dybzinski & Tilman, 2007) cannot be ruled out. Under arid conditions shrubs are expected to have either deep or extensive root system (usually >1.5 m) (Gibbens & Lenz, 2001). Excavation of root systems of a few individuals of *I. oblongifolia* in the field disclosed that their root systems spread laterally to the extent that they overlapped and mingled between the closely located individuals. This also lends support to the standpoint regarding the role of root competition in plant spacing under arid conditions (Phillips & MacMahon, 1981). The root system of the annual herbs was mostly <0.5 m (usually 20-35cm) deep (personal observations). Studies on desert plants have demonstrated that soil moisture depletion resulting from the uptake by roots occurs more rapidly from the immediate vicinity of the plant axis, and gradually spreads outwards (Campbell & Harris, 1977; Richards & Caldwell, 1987; Lobet *et al*., 2014). Furthermore, the upper soil layer dries out more quickly after rain-showers than the deeper horizons which retain enough moisture for much longer duration (Huxman *et al*., 2004; Shaukat & Siddiqui, 2007). Since the root system of annuals in general, including *Tephrosia strigosa* and *Corchorus triloccularis* are invariably shallow (<0.4m) and located close to the surface, these plants presumably face greater shortage of moisture in the

later phases of their growth, due to evaporation of moisture from the soil surface, compared to shrubs that possess deeper and more extensive root system. Thus, interspecific root competition is most intense in the upper soil horizon (0-0.5m) (Gibbens & Lenz, 2001). This could also be the major reason for greater intensity of intraspecific competition faced by the individuals of the annuals *T. strigosa* and *C. triloccularis*.

The present study also provides evidence on the prevalence of a fair degree of interspecific competition between the shrub *Indigofera oblongifolia* and the annuals (*T. strigosa* and *C. triloccularis*). An important effect of this negative interaction in which *I. oblongifoia* played a dominating negative role mostly because of its size (and the deep and profuse root system) was that it repressed the establishment of the annuals in its close vicinity which could be because of its size and its greater resource requirement. The importance of size in interspecific competition has often been emphasized (Kull & Zobel, 1991; Sammul *et al*., 2000; Allen *et al*., 2007). However, reduction in root growth of the perennial due to soil heterogeneity in its own patches may occur and possibly provided opportunity for inferior competitors, i.e., annuals to increase their root biomass in these patches. These patterns were also presumably reflected in the size hierarchies above-ground in our data. Root distributions can be determined by spatial heterogeneity of soil biota and abiotic regimes, affecting plant below-ground competitive interactions reflecting corresponding changes in the above ground parts. Thus, spatial heterogeneity of soil may contribute to plant species coexistence despite diffuse competition under arid conditions.
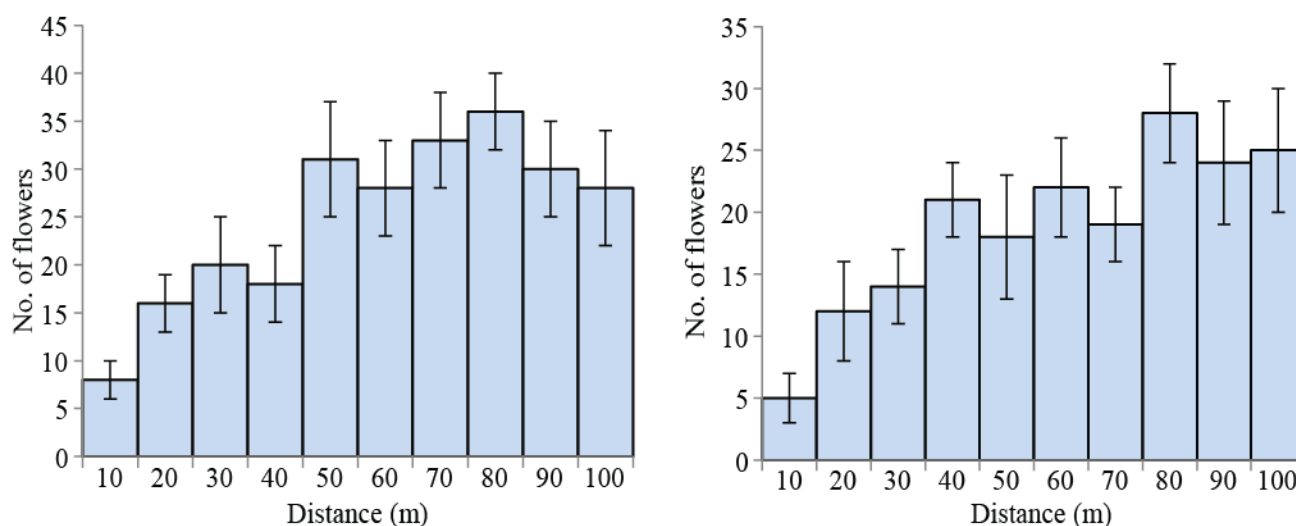
Fig. 4. Mean number of flowers (+ fruits if any) produced per plant of a) *Tephrosia strigosa* and b) *Corchorus triloccularis* at various distance from the shrub *Indigofera oblongifolia*. Bars associated with mean are ± standard errors.
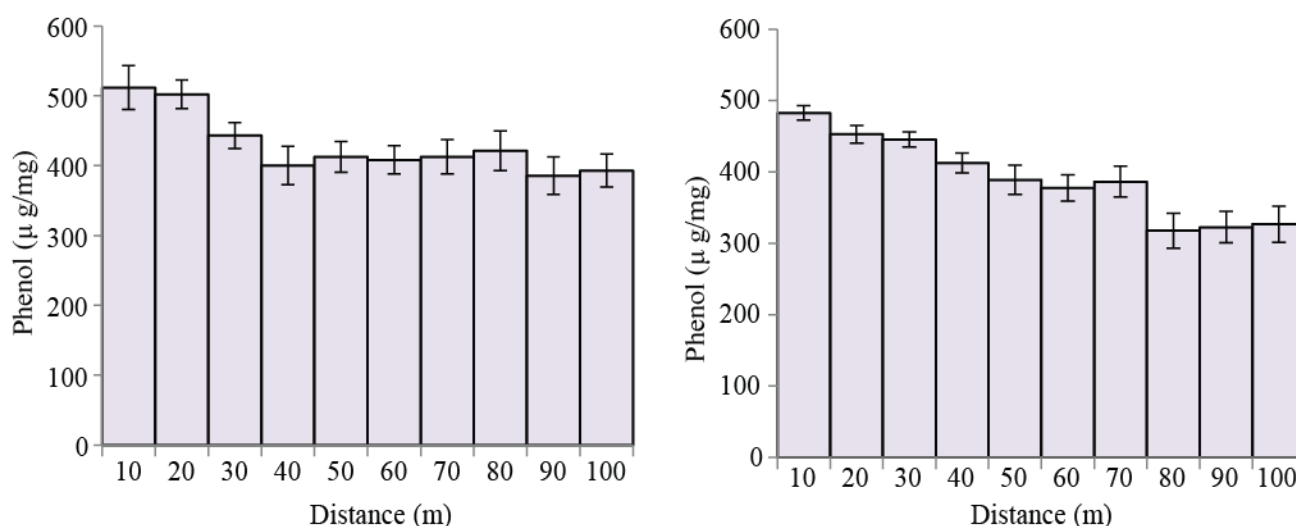

Fig. 5. Mean phenol content μg/mg produced in root of two annuals at various distances from the shrub (*Indigofera oblongifolia*). a) *Tephrosia strigosa*, b) *Corchorus triloccularis*. Bars associated with means are ± standard deviations (SE are too small to be shown clearly).

Negative effect of desert shrubs on annuals at different levels of water availability has also been demonstrated by Weedon & Facelli (2008). The number of individuals of both the annuals establishing < 20 cm from the shrub were significantly lesser compared to those found >20 cm away from the shrub. Our findings do not seem to agree with the statement of Grime (2001) that competition will be less important in habitats with water scarcity because plant growth would be limited by water shortage rather than competition. The interspecific competitive effect also resulted in a decreased reproductive potential as evidenced by the observation that a large number of individuals of the two annuals *Tephrosia strigosa* and *Corchorus triloccularis* failed to produce flowers when located in a close vicinity of the shrub *I. oblogifolia*. Furthermore, the reproductive output as measured by the number of flowers and fruits produced per individual, was considerably lower for the annuals (*T. strigosa* and *C. triloccularis*) that were growing in the close vicinity of the perennial shrub *I. oblongifolia*. This can readily be attributed to interspeccfic competition for moisture and also perhaps for nutrients (see below).

Another effect of inter- as well as intraspecific competition was the accumulation of soluble phenols when plant species at hand were located in close vicinity. In other words as the distance was reduced between pairs of plants, average soluble phenol content of roots was elevated. Accumulation of phenols is regarded as a defence mechanism in plants to cope with different types of stresses (Dixon & Paiva, 1995; Dixon, 2001; Garcia-Calderon *et al*., 2015). There is evidence that secondary metabolism may modulate plant responses to various forms of stresses and thereby contributes to plant fitness for survival (Altman & Colwell, 1998). By means of secondary metabolic pathways plants produce a wide range of compounds of various chemical classes, including phenols, nitrogen based compounds, and terpenes, that play a protective role against a range of stresses (Larcher, 2003; 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; Lattanzio *et al*., 2006; Shaukat & Khan, 2009) and abiotic stresses (Dustin &

Cooper-Driver, 1992; Furlan *et al.*, 1999; Eliasova, 2004; Abreu & Mazafera, 2005; Michalak, 2006; Ganeva & Zozikova, 2007; Edreva *et al.*, 2008; Shaukat & Khan, 2009; Shaukat *et al.*, 2013; Krol *et al.*, 2014; Duman & Sivaci, 2015). Accumulation of secondary metabolites such as phenolics and terpenes in response to competitive stress has also been demonstrated (Hjaelten *et al.*, 1994; Agostini *et al.*, 1998; Siemens *et al.*, 2002; Ormeno *et al.*, 2007; Shaukat *et al.*, 2009; Losada *et al.*, 2009). Though as to what extent the phenolics accumulated in these annual plants help in withstanding competitive pressure and the structuring of plant communities is not known yet. Presumably, the mortality rate of the annuals in close vicinity of the shrub will be greater as evidenced by greater stressed faced by such plants. This would obviously create an association pattern as well as a dispersion pattern of the annuals under study. The shrub *Indigofera oblongifolia* and one of the annual *Tephrosia strigosa* belong to Fabaceae (Leguminoseae) and possess root nodules (that contain N-fixing bacteria) whereby they are able to fix nitrogen, presumably enough for their own need. Therefore, with respect to the interaction between *I. oblongifolia* and *T. strigosa*, competition for nitrogen, if any, can be assumed to be minimal despite the fact that soil nitrogen content is poor. However, interspecific competition between the shrub *I. oblongifolia* and the annuals *T. strigosa* and *C. triloccularis*, also presumably involves resource competition for nutrients such as phosphorus and potassium that have low concentrations in the soil. For the individuals that established further away from the shrub, competitive pressure by the conspecific neighbours of the annual species presumably increased later in the season (mid-September- October).

Davis *et al.* (2000) have shown that the resources fluctuate within plant communities and therefore provide opportunities for some species to gain competitive advantage during certain seasons. From the studies utilizing nearest neighbour analysis (Cunliffe *et al.*, 1990; Shaukat *et al.*, 2003) and on the distribution pattern of desert shrubs (or small trees) (Fonteyn & Mahal, 1981; Shaukat *et al.*, 2012; Wang *et al.*, 2013), it becomes evident that biotic interactions are potentially of major functional significance in structuring of communities. Furthermore, diffuse competition (*sensu* Freed & Cann, 2014) between the shrub *I. oblongifolia* with other plant species whether annual herbs or perennial shrubs could also be a major force of interactive dynamics of populations and structuring of the community operating in the plant assemblage under investigation. Also local conditions within the community, particularly in arid regions, greatly influence the community structure, e.g., patches of soil associated with depressions may have elevated organic matter content as well as better soil moisture regime (Harris & Facelli, 2003). Attempts are made to test whether relative competitive ability can predict the composition of communities, and to what extent this might vary with prevailing environmental conditions in the communities. Results of some studies demonstrate that in general the predictive models based upon plant traits can be reasonably employed to achieve these goals (Grime, 2001; Freckleton & Watkinson, 2001; Fraser & Keddy, 2005). Of course, the predictivity would

vary with the environmental conditions. However, the underlying mechanisms of the resulting patterns remain obscure. The search for general quantitative relationships in nature is fundamental to the advancement of theoretical and applied ecology (Keddy, 2005; Shipley, 2010). Plant traits, such as relative competitive ability (e.g., by means of production and accumulation of phenols), may provide an important clue for improved predictive capability.

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