

DEMOGRAPHIC STUDIES OF *IPOMOEA SINDICA* STAPF, A DESERT SUMMER ANNUAL

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Abstract

This study focuses on the population ecology of a desert summer annual, *Ipomoea indica* Stapf, the abundant flora after the monsoon rains in Karachi, Sindh. Two sites were selected for the study, designated as site 'A' and 'B'. Site 'A' was dry having low water holding capacity, on the other hand, site 'B' had high water holding capacity. Vegetation was comparatively sparse at site 'A', whereas, relatively high water holding capacity and nutrient status of the soil 'B', presumably enable the population to flourish with higher densities. *I. indica* exhibited Deevey type I survivorship curves at both the sites. Plants inhabiting site 'B' showed better vegetative and reproductive growth than those surviving at site 'A'. Large quantity of seeds were present in the buried seed pool. Their number decreased after the monsoon rains i.e., after the germination of seedlings. Rise in the seed bank was observed after dispersal from the existing vegetation, thus exhibiting persistent type of seed bank. *I. indica* produces heavy seeds in smaller numbers. That's why the dispersal distance travelled by the seeds was less. Most of the seeds fall near the mother plant due to their heavy weight and horizontal growth of plants.

Introduction

Demographic studies are helpful in understanding how physical and biotic environment may affect population's survivorship and fecundity. Environmental factors have strong influence on the demography and productivity in communities dominated by annual plants. An array of factors such as shade (Barkham, 1980), competition (Gross, 1990), plant density (Harper, 1977), seed production (Watkinson & Harper, 1978), and grazing (Bastrenta, 1991) affect the dynamics of natural populations.

Reserves of buried seeds are usually present in all the habitats including forests (Leckie *et al.*, 2000), grasslands (Meerts & Grommesch, 2001), marshes (Leck & Simpson, 1995), as well as man-made ecosystems such as abandoned fields (Leck & Leck, 1998), planted forests (Hill & Stevens, 1981) and cultivated fields (Batanouny *et al.*, 1991), which are of great economic and agricultural importance. They act as a source of a new populations, which prevent the local extinction of species. Seed bank of any area represents not only the present vegetation but also a memory of past vegetation and also determines the future trends of a certain area. Seed bank ensures the germination of seeds at suitable time of the year. In this way they protect the seeds from adverse conditions. Temporal and spatial variations also affect the seed density in the soil (Coffin & Lavenroth, 1989; Shaukat & Siddiqui, 2004).

Seed dispersal or seed rain also plays an important role in natural populations as it affects the demographic pattern and competitive interactions (Miller *et al.*, 1994). Dispersal is the only way for the addition of the seeds to the buried seed reserves. It is also affected by a number of factors such as topography, morphological attributes of seeds / diaspore (Augspurger & Franson, 1987; Okuba & Levin, 1989), wind direction and speed (Telenius & Tortensson, 1989), surrounding vegetation and shape of the seeds (Wajid & Shaukat, 1983), orientation and position of seeds landing on the ground (Peart, 1981), and prominent objects in the vicinity of plants (Westelaken & Maun, 1985). According to Harper (1977), disappearance of annuals from the site depends on its dispersal and

establishment elsewhere. A large number of studies have examined the local dispersal of seeds and shown that most seeds are found near the parent plant. Dispersal curve for wind or animal dispersed seeds usually tends to be leptokurtic (Howe & Westtey, 1986).

Temporal and spatial variations also affect the density of seeds in the soil (Coffin & Lavenroth, 1989). Soil heterogeneity causes spatial heterogeneity of seed populations in the soil (Boudell, 2002). Disturbance varying in scale and frequency from grazing to human trampling also affects the position and composition of seed within the soil profile (Aziz & Khan, 1995, 1996). The present study is designed to study the survivorship patterns, growth rate, biomass allocation and fecundity of *Ipomoea indica* individuals. This paper also elucidates the significance of seed bank and seed rain and its relation with the above ground vegetation.

Materials and Methods

Study site: This study was conducted in Karachi, Sindh (Lat. 24° 48 N., Long. 65° 55 E.). This is a dry and semi-arid region, composed mainly of xerophytic vegetation. The precipitation occurs mainly in monsoon (June – September), with an average of 220 cm of rain per year. Due to low rainfall, plant diversity is low. Diverse annual flora that emerges after monsoon showers converts the deserts of Sindh into grassland for a very small period of time. The dry air and moisture deficiency after monsoon season i.e., in the month of late September and October may create drought conditions. Evapotranspiration is also high, particularly in summer.

Two sites were selected for the study. One of the study site is situated within Karachi University campus, called as site 'A' and the other near PCSIR (Pakistan Council of Science and Research Institute), named as site 'B'. Site 'A' is located in a non-shady area. This area is very much exposed to trampling and grazing. Site 'B' is relatively a less disturbed site. It is situated in a shady area. After monsoon rains, water from the adjacent elevated areas moves towards site 'B', thereby creating relatively better moisture regime than that of site 'A'.

The species selected for the study was *Ipomoea indica* (Convolvulaceae). It is a summer annual, commonly found after monsoon rains and also important economically. *I. indica* can also be used as an ornamental plant. It is common in Pakistan, India and other arid parts of the world. Abundant or common in the waste grounds, vacant lots, road-sides and abandoned fields.

Demography: Demography of *Ipomoea indica* was studied by establishing ten 1m² permanent plots within each site. Plots were censused every ten days throughout the growing season. Number of plants surviving in each plot was counted. This data was further used in the construction of conventional life-tables. Survivorship curves were also plotted against time. A chi-squared test was performed to compare the survival rates at the two selected sites.

Growth, biomass allocation and fecundity: At every sampling date (at 10 days interval for 120 days), 10 individuals of each plant species were randomly collected from the outside of each permanent plot from both the sites. Plants were brought to the laboratory, where their size was measured. They were then dried in an oven to a constant dry weights (80°C for 48 hr), and their biomass allocation determined. Fecundity was studied by counting the number of fruits per plant and number of seeds per fruit from the plants collected from the outside of permanent plot.

Seed bank: Twenty soil samples were randomly collected to a depth of 15 cm with a help of 2.5 cm diameter aluminum corer from both the sites. Soil samples were collected at three different phenological states i.e., before rainfall (before germination of seeds), after rainfall (after germination of seedlings) and after seed dispersal. Seeds were sorted out manually with the help of a binocular microscope, identified and counted. A seed album prepared over several years was used for identification purpose. Herbarium specimens were also used.

Dispersal: At each site 10 isolated mature plants of *Ipomoea indica* were chosen prior to seed loss in both the years. Dispersal distance was studied by collecting seeds from 3.8 cm diameter area around each plant from 0-100 cm. Data was taken at alternate days with the initiation of dispersal. Seeds within 3.8 cm diameter area were converted to seeds per decimeter square (seeds / dm²) and a dispersal curve was plotted between number of seeds / dm² and the distance traveled by seeds from the parent plant was calculated.

Soil moisture regime: At both the sites soil moisture regime was determined. Soil samples were collected at monthly intervals from July to October Moisture percentage by weight was determined in the soil and expressed as a percentage of maximum water holding capacity.

$$\text{Water content percent} = \frac{\text{Loss in weight on drying}}{\text{Weight of oven-dried soil}} \times 100$$

Results

Demography: The life tables of *Ipomoea indica* was constructed for site 'A' and 'B' and presented in the Tables 1 & 2. Plants were observed to complete their entire life i.e., from germination to seed maturation in 120 days. Survivorship curves at both the sites followed Deevey type-I (Deevey, 1947), survivorship curve (Fig.

1). Plant density varied significantly ($p < 0.001$) at each site in both the years. Over the entire study period density and mortality were much greater at site 'B'. Most mortality occurred in the later stages of plant life. Comparison of *Ipomoea indica* survivorship curves at both the sites using chi-square and G test showed significant differences at both the sites (Table 3).

Table 1. Life table of *Ipomoea indica* individuals inhabiting site 'A'.

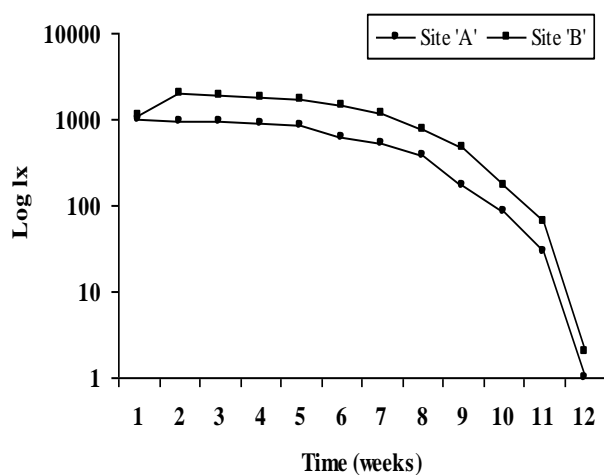
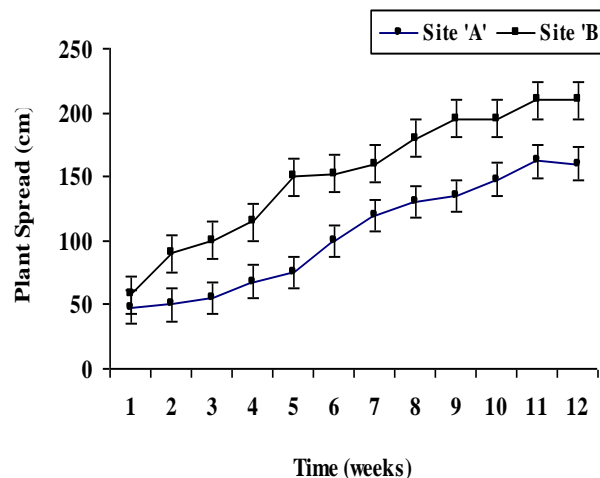
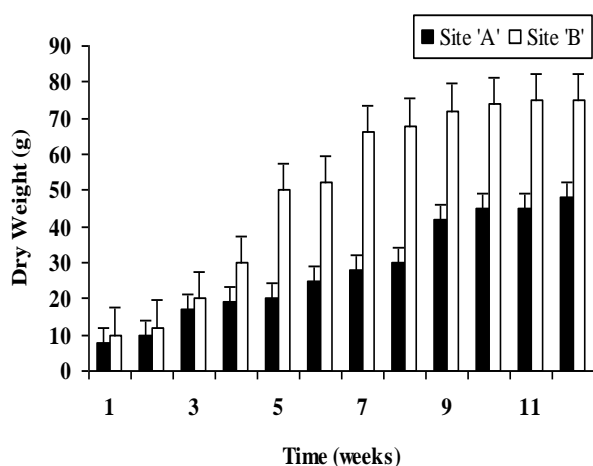
| Age (x) (days) | Numbers surviving (lx) | Numbers dying (dx) | Stationary population (Lx) | Residual life-span (Tx) | Age specific mortality (qx) | Expectancy of further life (ex) |
|-------------------|---------------------------|-----------------------|-------------------------------|----------------------------|--------------------------------|------------------------------------|
| 10 | 1000.00 | 28.91 | 985.54 | 5962.23 | 0.02 | 5.96 |
| 20 | 971.09 | 46.24 | 947.97 | 4976.69 | 0.04 | 5.12 |
| 30 | 924.85 | 17.34 | 916.18 | 4028.72 | 0.18 | 4.35 |
| 40 | 907.51 | 40.46 | 887.28 | 3112.54 | 0.04 | 3.42 |
| 50 | 865.05 | 260.12 | 736.99 | 225.26 | 0.30 | 2.57 |
| 60 | 606.93 | 86.70 | 563.58 | 1488.27 | 0.14 | 2.45 |
| 70 | 520.23 | 144.51 | 447.97 | 924.69 | 0.27 | 1.77 |
| 80 | 375.72 | 202.39 | 274.52 | 476.73 | 0.53 | 1.26 |
| 90 | 173.33 | 860.67 | 129.99 | 202.20 | 0.50 | 1.16 |
| 100 | 86.66 | 57.75 | 57.77 | 72.21 | 0.66 | 0.83 |
| 110 | 28.88 | 28.88 | 14.44 | 14.44 | 1.00 | 1.50 |
| 120 | - | - | - | - | - | - |

Growth and biomass allocation: Pattern of root and shoot growth for both the sites are presented in Fig. 2. Like other annuals *I. indica* also showed a typical sigmoid curve, characteristic of annuals (plant size plotted against time). Plants inhabiting at site 'B' had significantly ($p < 0.001$) higher growth rates. Total dry weights of all plants increased throughout life (Fig. 3). Dry weights of site 'A' plants were lower than that of site 'B'. Significant differences in the dry

weights of root, stem and leaves were observed in *I. indica* plants, considering time (root, $F = 104.39$, $p < 0.001$; stem, $F = 111.74$, $p < 0.001$; leaf, $F = 686.41$, $p < 0.001$) and site (root, $F = 60.49$, $p < 0.001$; stem, $F = 424.00$, $p < 0.001$; leaf, $F = 288.74$, $p < 0.001$) as factors. Interaction of both the factors (time x site) for root ($F = 10.311$, $p < 0.001$), stem ($F = 10.40$, $p < 0.001$) and leaf ($F = 26.00$, $p < 0.001$) were also significant.

Table 2. Life table of *Ipomoea sindica* individuals inhabiting site 'B'.

| Age (x) (days) | Numbers surviving (lx) | Numbers dying (dx) | Stationary population (Lx) | Residual life-span (Tx) | Age specific mortality (qx) | Expectancy of further life (ex) |
|-------------------|---------------------------|-----------------------|-------------------------------|----------------------------|--------------------------------|------------------------------------|
| 10 | 1000.00 | 16.67 | 991.66 | 6583.23 | 0.01 | 6.58 |
| 20 | 983.33 | 16.67 | 974.99 | 5591.57 | 0.01 | 5.58 |
| 30 | 966.66 | 23.33 | 954.99 | 4616.58 | 0.02 | 4.77 |
| 40 | 943.33 | 76.66 | 904.99 | 3661.59 | 0.08 | 3.88 |
| 50 | 866.66 | 33.33 | 849.99 | 2756.60 | 0.03 | 3.18 |
| 60 | 833.33 | 166.66 | 749.99 | 1906.61 | 0.20 | 2.28 |
| 70 | 666.66 | 266.68 | 533.33 | 1156.62 | 0.40 | 1.73 |
| 80 | 399.98 | 100.01 | 349.97 | 623.27 | 0.25 | 1.55 |
| 90 | 299.97 | 216.64 | 191.65 | 273.33 | 0.72 | 0.91 |
| 100 | 83.33 | 46.67 | 59.99 | 81.65 | 0.56 | 2.97 |
| 110 | 36.66 | 30.00 | 21.66 | 258.33 | 0.81 | 7.04 |
| 120 | - | - | - | - | - | - |

Fig. 1. Survivorship curves for *Ipomoea sindica* individuals inhabiting site 'A' and 'B'.Fig. 2. Plant height (cm) of *Ipomoea sindica* individuals inhabiting site 'A' and 'B'.Fig. 3. The total dry weight (mg/plant) of *Ipomoea sindica* individuals inhabiting site 'A' and 'B'.

Percentage of biomass allocation to the component organs at each site is presented in Fig. 4. At each site plants allocated maximum biomass to reproductive structures in all three species at both the sites. Growth of all vegetative organs (root, stem and leaf) slowed down after the commencement of flowering and fruiting. Reproductive output was maximum at site 'B' in both the years. Flowering at site 'B' was commenced earlier than at site 'A'. At site 'A' *I. sindica* flowered at the age of approximately 60 days. However, at site 'B', flowering began in *I. sindica* when plants were approximately 50 days old.

Table 3. Curve comparison of *Ipomoea sindica* individuals at site 'A' and 'B', using chi-squared test.

| Time period | χ^2 | Significance | G |
|-------------|----------|--------------|--------------|
| 01 | 0.26 | n.s. | 0.25 |
| 02 | 0.03 | n.s. | 0.03 |
| 03 | 2.14 | n.s. | 2.27 |
| 04 | 4.28 | 0.05 | 5.07 |
| 05 | 10.39 | 0.01 | 10.60 |
| 06 | 4.07 | 0.05 | 4.13 |
| 07 | 5.42 | 0.05 | 5.44 |
| 08 | 8.59 | 0.01 | 8.71 |
| 09 | 3.48 | 0.05 | 3.55 |
| 10 | 6.66 | 0.01 | 6.47 |
| Total | 45.92 | 0.001 | 46.55 |

Similarly, in the year 2001 percent reproductive biomass of all three species was significant for time ($F = 29.94$, $p < 0.001$), site ($F = 19.37$, $p < 0.001$) and species ($F = 3.39$, $p < 0.05$) factors. First order interactions i.e. time x site ($F = 0.98$, $p < 0.001$), time x species (0.89 , $p < 0.01$) and site x species ($F = 0.06$, $p < 0.05$) were also significant.

Interaction of all three factors i.e., time x site x species ($F = 1.98$, $p < 0.001$) was also found significant. Biomass allocated to components organs is presented in fig. 4. Plants allocated higher amounts of biomass to reproductive organs. Percent dry weight allocated to vegetative organs decreased with the onset of flowering. *I. sindica* flowered at the age of about 50 days at site 'A' and about 45 days at site 'B'.

Table 4. Seeds / m² extracted from the soil samples collected at three different phonological states from site 'A' and 'B' (Mean Standard Error).

| Plant species | Before rainfall | | After rainfall | | After dispersal | |
|-----------------------|--------------------|--------------------|--------------------|--------------------|--------------------|---------------------|
| | Site 'A' | Site 'B' | Site 'A' | Site 'B' | Site 'A' | Site 'B' |
| <i>I. sindica</i> | 22925.38 ± 0.03 | 34388.07 ± 1.17 | 5290.47 ± 0.75 | 8817.45 ± 0.23 | 24688.87 ± 0.12 | 52904.73 ± 0.55 |
| <i>C. viscosa</i> | 43205.53 ± 0.22 | 23444.38 ± 1.17 | 14107.92 ± 0.56 | 24688.87 ± 0.56 | 70539.64 ± 0.22 | 102282.98 ± 0.35 |
| <i>D. muricata</i> | 26452.36 ± 0.75 | 51141.24 ± 0.22 | 6172.21 ± 0.35 | 37915.06 ± 0.55 | 37915.06 ± 0.15 | 61722.19 ± 0.28 |
| <i>T. subtriflora</i> | 1763.49 ± 1.05 | 4408.72 ± 0.15 | - | - | - | 1763.49 ± 0.45 |
| <i>C. aucheri</i> | 881.74 ± 0.08 | 1763.49 ± 0.15 | 1763.49 ± 0.33 | 881.74 ± 0.55 | 881.74 ± 0.33 | 526.98 ± 0.88 |
| <i>T. terrestris</i> | 881.74 ± 0.17 | - | - | 1763.49 ± 0.23 | 1763.49 ± 0.11 | - |
| <i>G. gynandra</i> | 1763.49 ± 0.05 | - | - | - | 3526.89 ± 0.38 | - |
| <i>C. brachycarpa</i> | - | 2645.23 ± 0.35 | - | 881.74 ± 0.23 | - | 4408.72 ± 0.58 |
| <i>R. minima</i> | - | 3536.98 ± 0.38 | - | - | - | 1763.49 ± 0.33 |
| <i>L. urticifolia</i> | - | 2645.23 ± 0.55 | - | - | - | 3526.98 ± 0.56 |
| <i>P. juliflora</i> | - | 881.71 ± 1.00 | - | 881.74 ± 0.23 | - | 881.74 ± 0.18 |
| <i>A. mutabilis</i> | - | 326.98 ± 1.28 | - | 881.74 ± 0.33 | - | 4408.72 ± 0.35 |
| <i>Z. nummularia</i> | - | 881.74 ± 0.34 | - | 881.74 ± 0.34 | - | 881.74 ± 0.34 |

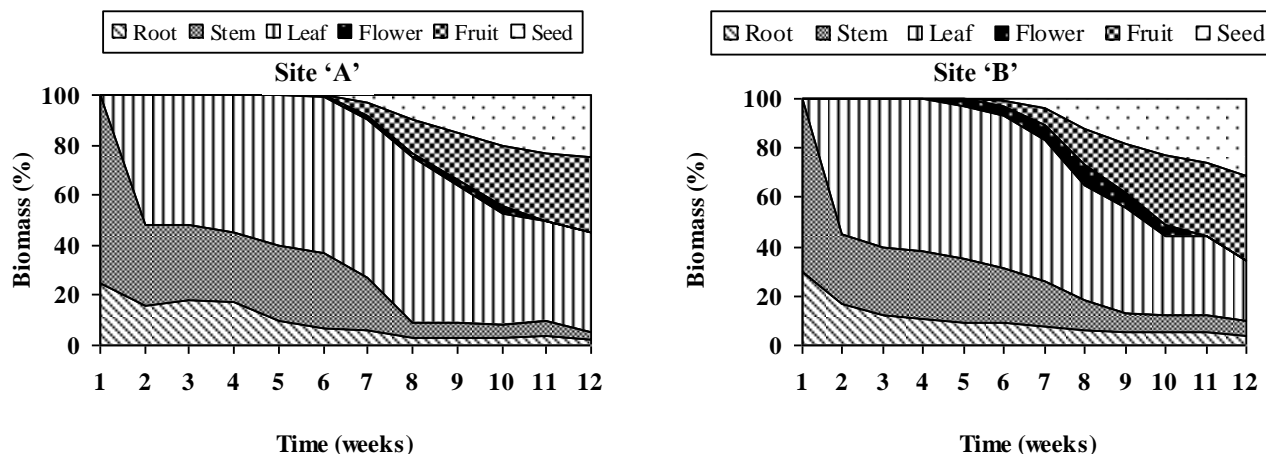


Fig. 4. Biomass allocation (%) of *Ipomoea sindica*, to component organs at site 'A' and 'B'.

Seed bank: Seeds of 7 species were sorted out from the soil samples at site 'A' while 5 species occurred in the above ground vegetation whereas, seeds of 11 species were sorted out from site 'B' samples and only 8 were present on the ground (Table 4).

Seeds of the following species were sorted out from the soil samples collected from site 'A': *Ipomoea sindica*, *Cleome viscosa*, *Digera muricata*, *Tephrosia subtriflora*, *Chrysopogon aucheri*, *Tribulus terrestris* and *Gynandropsis gynandra*. With the exception of *C. aucheri* and *T. terrestris*, all the above-mentioned species were present in the above ground vegetation.

Samples collected from site 'B' contained seeds of the following species: *Ipomoea sindica*, *Cleome viscosa*, *Digera muricata*, *Aristida mutabilis*, *Cleome*

brachycarpa, *Rhyncosia minima*, *Zizyphus nummularia*, *Leucas urticifolia*, *Tephrosia subtriflora*, *Chrysopogon aucheri* and *Prosopis juliflora*. Interestingly, *A. mutabilis*, *T. subtriflora* and *P. juliflora* were not present in the existing vegetation.

The seed population of all the species showed significant differences ($p < 0.001$) among the three collections and also between years. Number of seeds of all species declined significantly ($p < 0.001$) after the first collection (before rainfall). Number of seeds in the third collection (after dispersal) was also significantly higher ($p < 0.001$) than the second collection (after seed germination). That is higher number of seeds were sorted out from the samples collected after dispersal of seeds from the parent plant. Lowest number of seeds was sorted

out from the samples collected after rainfall i.e., after germination of seeds. *I. sindica* seeds showed significant differences with time ($F = 3697.75$, $p < 0.001$) and site ($F = 2214.03$, $p < 0.001$). Interaction of both the factors also showed significant differences ($F = 604.19$, $p < 0.001$).

Seed dispersal: Dispersal seems to be more directional. Almost all seeds dispersed towards east due to westerly blowing winds. *I. sindica* dispersed seeds at the end of the growing season when leaves senesced. The general pattern of seed dispersal at both the sites are presented in the Fig 5. The pattern of dispersal varied with each site. Seeds of *I. sindica* were found to be dispersed around parent plant and usually traveled small distances. Seeds collected from site 'B' was significantly greater ($p < 0.001$) than site 'A' plant (*I. sindica*, $F = 12764.72$, $p < 0.001$). Interaction of both the factors for *I. sindica* ($F = 320.97$, $p < 0.001$) was also found to be significant.

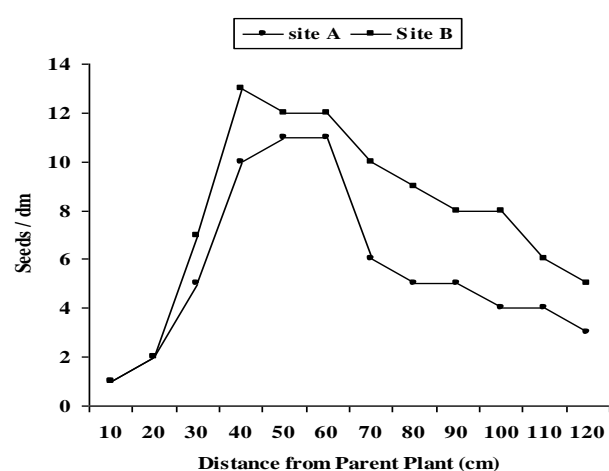


Fig. 5. Dispersal distance (cm) traveled by the seeds of *Ipomoea sindica* at site 'A' and 'B'

Soil Moisture content: Soil moisture content at site 'A' and 'B' was highest in the month of August followed by July and September. Lowest soil moisture content was recorded in the month of October. Moisture content showed significant among months ($F = 8.49$, $p < 0.001$) and site ($F = 34.72$, $p < 0.001$) in 2000. Whereas, interaction of month \times site exhibited low significance ($F = 0.25$, $p < 0.05$).

Discussion

The detailed demographic analysis of *Ipomoea sindica* elucidates the natality and mortality of individuals relative to a change in actual population size. Plants exhibited greater density at site 'B'. It might be due to better soil moisture regime at site 'B'. Elevated moisture levels would lead to greater germination of the annuals as their germination is controlled by light, temperature and soil moisture (Baskin & Baskin, 1989). Survivorship of *I. sindica* showed an increase in the early phase of life cycle and loss of individuals in the later part of life.

This indicates that later stages of life cycle are more susceptible to the vagaries of the environment such as depletion of moisture. Greater mortality in the later stages of life cycle is the result of low soil moisture levels and high evaporation rate from soil surface in the month of September and October that lead to desiccation of plants and the eventual mortality of plants due to drought (Fox, 1990).

The resource allocation pattern of plants is fundamental aspects of their life-history strategies (Nault & Ganon, 1988). At both the sites root dry weights were lowered than other component organs. Overall dry weight of roots was greater at site 'B'. Site 'A' is relatively less favourable than site 'B', mainly because of low moisture levels in deeper horizons of soil. Harper (1977) made the generalization that plants grown in moisture depleted zones tend to adjust their root to shoot ratio in favour of shoots.

Stem dry weights also followed the same pattern, but their weights were considerably higher than roots. Leaf biomass allocated to site 'B' plants was much greater than site 'A' plants. Higher leaf biomass of site 'B' plants increased the photosynthetic functions, thus enhancing the vegetative and reproductive growth of site 'B' plants. Leaf biomass increased early in the life, but decreased later. This decrease is associated with an increase in the reproductive structures.

Flowering in plants inhabiting site 'B', commenced earlier than plants surviving at site 'A'. Reproductive effort of site 'B' plants was considerably higher than site 'A' plants. Fox (1990), suggested that annual plants in hot deserts show considerable variation in flowering time, due to unusual degree of phenotypic plasticity, which is adaptive (Lacey, 1986). Like vegetative growth, the reproductive growth of site 'B' plants were much better than site 'A' plants, due to the depletion of resources at site 'A'. Vegetative and reproductive performance of site 'B' plants were much better than those inhabiting site 'A'. Overall, plants from the two sites allocate greater resources to various reproductive functions.

Plant populations in any area consist of two parts, an above ground phase i.e., vegetation and a buried viable seed reserve in the soil. Comparison between above and below ground species composition discloses the interaction between vegetation and seed reserves in the past (Aziz & Khan, 1996; Qaderi *et al.*, 2002; Shaukat & Siddiqui, 2004). Seeds of annual plant species in our study area remain dormant in the soil and recruitment depends on monsoon rain which triggers germination. The seeds germinate at any time during summer when enough moisture is available. Annual species in our study area form persistent seed bank presumably because of enforced dormancy. *C. viscosa* is the most abundant species in the seed bank samples followed by *D. muricata* and *I. sindica*. Whereas, *I. sindica* is the most dominant annual in the overlying vegetation of both site 'A' and 'B'. It is due to the fact that each capsule of *I. sindica* produced maximum of five seeds, whereas number of seeds per fruit in *C. viscosa* sometimes reach up to 30-40.

Seed densities varied significantly in the three sampling periods. Seed bank depletion of annuals was significant following to monsoon showers due to seedling emergence. By mid October there was a significant rise in the seed bank due to seed production and dispersal of new seeds, following type-IV seed bank in accordance with Thompson & Grime (1979). Seeds of the constituent species of the vegetation were well represented in the seed bank. But not all of seed bank species were represented in the above ground vegetation. *T. terrestris* was absent from the study site 'A', while *A. mutabilis*, *T. subtriflora* and *P. juliflora* were absent from site 'B', suggesting that these species came through dispersal from adjacent areas. Alternatively, they could be the common species of the past. Invasion of other species might led to intense competition and with the passage of time they became represented only by their seed banks. Similarly, Kitajima

& Tilman (1996) reported that species composition of *Agropyron* species in the soil seed bank do not follow the changes in the above ground vegetation, great discrepancies were observed between the above ground vegetation and seed banks. On the other hand, Meerts & Grommesch (2001), found a strong correlation between soil seed bank and above ground vegetation in a heavy-metal polluted grasslands at Prayon (Belgium). Presence of other species in the seed bank samples indicates the historical species composition of our study sites, which appear to be more diverse.

Seed dispersal affects plant populations in two ways. Firstly seeds may augment or deplete local populations, thus affecting population size and secondly dispersing seeds in any area may act as founders of new populations. Seeds of *I. sindica* were dispersed near the parent plants due to their large sizes. Most of the *I. sindica* seeds which are relatively larger in size fall near the parent plant. An alternative explanation of short distance dispersal of *I. sindica* seeds is that this plant is a creeper. Although the plant spreads but does not spread vertically. Pacala (1986) suggests that short dispersal distances may facilitate coexistence by increasing the degree of interspecific spatial segregation. Limited dispersal creates "biotic" spatial heterogeneity (Pacala, 1989). Crawley & May (1987) have shown that the only way by which an annual is able to persist in any community is by its potential to colonize empty sites as a result of seed dispersal. The role of secondary dispersal by wind, ants or any other agencies could be important in this respect.

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