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ROLE OF DISTURBANCE ON THE SEED BANK AND DEMOGRAPHY OF LEUCUS URTICIFOLIA (LABIATAE) POPULATIONS IN A MARITIME SUBTROPICAL DESERT OF PAKISTAN

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Life history strategies of the *Leucus urticifolia* populations growing in disturbed and undisturbed habitats were studied. Seed banks of both populations were persistent, with greater numbers and more species diversity in undisturbed populations. The undisturbed population showed a 65% allocation to reproduction at maturity as compared with 4% biomass allocation to reproduction in disturbed population. Populations of *L. urticifolia* in an undisturbed subtropical desert community of Karachi, Pakistan, have larger and more persistent seed banks, larger plant size, and higher reproductive allocations as compared with a disturbed community.

Introduction

Long-term seed dormancy in desert annuals helps them to avoid a period of drought (Fenner 1985). Annuals, which constitute 40% or more of the flora, can be the most prevalent form of species, and during long drought, the only form for several years (Kemp 1989), and after rains, seeds in the persistent seed bank become the primary form of recruitment (Aziz and Khan 1994). Persistent seed banks and annual replenishment of seed banks play a crucial role in the long-term survival of annual species in seasonally arid environments (Kemp 1989).

Variation in demography and life history pattern of *Tephrosia strigosa,* a summer annual from the maritime desert of Karachi, was reported by Aziz and Khan (1994). The study showed that *T. strigosa* maintained a persistent seed bank with a substantial loss after the dispersal and that the seed bank flora corresponded closely to the existing vegetation. Recruitment occurred after rainfall, and there was high seedling mortality followed by little change in population size during the vegetative phase. Mortality of *T. strigosa* increased again at the time of flowering, and biomass allocation to reproduction increased with the seedling size (Aziz and Khan 1994).

Disturbance, varying in scale and frequency from grazing to human trampling, affects the position and conditions of seeds within the soil profile and subsequent recruitment and survival. Grazing and competition are the most important environmental forces that affect plant growth and survival (Carman and Briske 1985; Painter et al. 1989). The dynamics of populations in a patchy disturbed environment may be quite complex, and the purpose of this article is to determine the responses for a desert annual.

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Leucus urticifolia R. Br. (Labiatae), a summer annual, is widely distributed in maritime subtropical deserts of Karachi, which are dominated by annual species along with a few shrubby perennials (Chaudhry 1961). Seeds of annual species germinate after the first heavy monsoon rains (June–September). Plants flower and set seed by the end of the wet summer season, die at the beginning of the dry seasons in autumn (October), and pass the unfavorable season from October to June as seed in the soil. Seedlings of *L. urticifolia* start emerging after a substantial uptake of water soon after monsoon showers, and plants complete their life cycle in 50–55 d (M. A. Khan, personal observation). Populations of *L. urticifolia* can grow in full sunlight but are usually present under low-lying shaded areas where they occur in a relatively deep soil profile and grow in association with desert shrubs like *Digera muricata, Abutilon indicum, Prosopis juliflora,* and *Indigofera cordifolia.* Populations can also be found in full sunlight.

The purpose of this study was to investigate the seed bank, demography, and life-history characteristics of populations of the summer annual *L. urticifolia* that have high and low levels of disturbance. Also, the seed banks of associated species were investigated.

Material and methods

The study was conducted at the Karachi University campus (Pakistan) (lat. 24°48′N, long. 65°55′E). This region receives an average of 220 cm of rain per year, with 90% of it falling in the months of June–September. During the months of October–May no rain falls usually, and winter rains, during December and January, are rare. The extent and duration of rainfall are insufficient to support diverse flora. During the summer of 1993 after monsoon rains, two populations of *Leucus urticifolia* were selected for study. The undisturbed population occurred in a relatively shady area and was associated with other desert annuals such as *Aristida mutabilis, Digera muricata, Indigofera cordifolia, Indigofera hochstet-*

teri, and *Cleome brachycarpa*. Some perennials, including *Prosopis juliflora*, *Iphonia grantioides*, *Senna holosericea*, and *Abutilon indicum*, were also present. The disturbed population occurred in a nonshady site and was exposed to trampling by people and grazing by animals and was associated with *D. muricata*, *Rhynchosia minima*, *Sida ovata*, and *A. indicum*.

Forty soil cores per population were randomly collected using a soil corer (2.5-cm diameter, 4.9-cm^2 area, with a depth of 15 cm) before germination (July 1993), after germination (August 1993), and after dispersal of seeds (November 1993) from parent plants. Twenty soil samples of each collection were watered, and the seeds were allowed to germinate under natural outdoor conditions and were monitored regularly for 6 wk. The approximate maximum temperature was 35°C and minimum was ca. 25°C. As seedlings emerged they were identified and later removed, and the soil was turned over every week to facilitate further germination. Seeds from the other 20 samples were manually extracted with the help of a binocular microscope and identified.

Twenty permanent quadrats (20 × 20 cm) per population were established subjectively to sample the population densities soon after the appearance of *L. urticifolia* seedlings following substantial rainfall during the 1992 growing season. Permanent quadrats were placed at regular intervals (1½ m). After 5-d intervals, 10 seedlings were randomly collected from the area close to each quadrat and washed, and the roots, shoots, leaves, flowers, and fruits were dried at 80°C to a constant weight. At the end of the growing season, prior to seed dispersal, all of the plants surviving in quadrats were harvested and washed, and then roots, shoots, leaves, flowers, and fruits were separated. Number of leaves, flowers, and fruits was recorded. All parts of the plant were then oven-dried at 80°C to a constant weight.

Statistical analysis of the data was carried out using the computer program of Statistical Package for Social Sciences (SPSS). Data were analyzed using means and LSD ($P < 0.05$) procedures.

Results

Seed bank

Seeds of nine species were found in the soil samples collected from the undisturbed population, and the seeds of seven of those species germinated (table 1). Seeds of *Prosopis juliflora* and *Abutilon indicum*, which did not germinate, were sorted out from the samples. Seeds of only five species were observed in samples collected in the disturbed population, and the seeds of four of those species germinated (table 2). Seed bank size for both sites was significantly ($P < 0.0001$) re-

Table 1

Mean number of seeds sorted out (a) and germinated (b) in soil samples (seeds m^{-2}) collected at three phenological states from the undisturbed population (± SE)

Species	Life form	Before germination		After germination		After dispersal	
		a	b	a	b	a	b
Leucus urticifolia	Annual	23,469.2 ± 816.3	19,387.6 ± 1020.4	9591.7 ± 408.2	12,244.8 ± 687.4	15,714.2 ± 816.3	21,863.6 ± 1456.4
Prosopis juliflora	Perennial	10,816.2 ± 1020.4	0	4285.7 ± 865.2	0	0	0
Indigofera cordifolia	Annual	6530.6 ± 1010.2	5306.1 ± 1020.4	0	2040.8 ± 20.5	12,857.0 ± 2040.8	11,836.5 ± 1020.4
Indigofera hochstetteri	Annual	11,020.3 ± 854.2	4285.7 ± 845.2	6530.6 ± 768.4	4081.6 ± 204.1	11,836.6 ± 1224.5	10,204.0 ± 204.1
Aristida mutabilis	Annual	16,734.6 ± 204.1	13,673.4 ± 612.24	4081.6 ± 2040.8	6326.5 ± 408.2	13,673.4 ± 1224.5	12,448.9 ± 204.1
Iphonia grantioides	Perennial	3877.5 ± 845.2	3877.5 ± 816.3	2040.8 ± 627.2	3673.4 ± 408.2	6530.6 ± 204.1	4081.6 ± 204.1
Digera muricata	Annual	18,367.2 ± 204.1	5306.1 ± 816.32	9591.8 ± 408.2	2653.0 ± 612.2	22,652.9 ± 875.3	7551.0 ± 451.2
Cleome brachicarpa	Annual	0	0	2040.8 ± 784.2	0	6326.5 ± 204.1	0
Tephrosia strigosa	Annual	4081.6 ± 612.2	0	0	0	0	0

Table 2

MEAN NUMBER OF SEEDS SORTED OUT (a) AND GERMINATED (b) IN SOIL SAMPLES (seeds m^{-2}) COLLECTED AT THREE PHENOLOGICAL STATES FROM THE DISTURBED POPULATION (± SE)

Species	Life form	Before germination		After germination		After dispersal	
		a	b	a	b	a	b
Leucus urticifolia	Annual	12,244.8 ± 204.1	15,510.1 ± 1632.6	6326.5 ± 408.16	4285.7 ± 204.1	10,612.2 ± 2449.0	11,836.6 ± 204.1
Digera muricata	Annual	10,204.0 ± 408.2	12,448.9 ± 612.2	5714.2 ± 408.2	2040.8 ± 105.2	14,693.8 ± 2449.0	13,673.4 ± 816.3
Abutilon indicum	Perennial	2040.8 ± 1224.5	0	0	2040.8 ± 110.5	0	0
Rhynchosia minima ...	Annual	6122.4 ± 204.1	6326.5 ± 408.2	0	0	0	10,612.2 ± 408.2
Sida ovata	Annual	3673.4 ± 204.1	6530.6 ± 2244.9	2040.8 ± 816.3	4081.6 ± 2244.9	2653.0 ± 945.0	5510.2 ± 3775.5

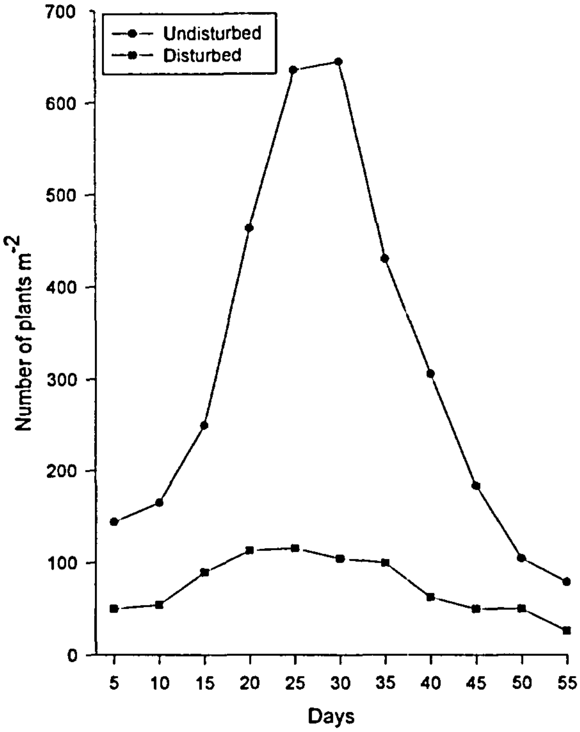

Fig. 1 Survivorship curve of undisturbed and disturbed population of *Leucus urticifolia.*

duced after recruitment and was replenished after the seed dispersal.

DEMOGRAPHY

Survivorship curves of both populations showed significantly ($P < 0.0001$) different patterns (fig. 1). *Leucus urticifolia* completed its life-cycle, from germination to seed production, in 55 d. Density of plants progressively increased and peaked around 25–30 d. In the undisturbed population, the peak density was 645 ± 2 plants m^{-2}, while 118 ± 51 plants m^{-2} occurred in disturbed population. After 30 d the density of plants in both populations substantially declined.

GROWTH AND REPRODUCTION

Pattern of root and shoot growth in both populations of *L. urticifolia* showed a progressive increase with age (fig. 2). Seedling growth in undisturbed populations was greater than in the disturbed population. Leaf production in *L. urticifolia* starts when plants were ca. 8-d-old (fig. 3). Leaf production was slow at the initial stages of the life-cycle, but leaf number increased considerably with age. Leaf number was higher in the undisturbed than in the disturbed population. In the undisturbed population, onset of flowering and fruiting occurred earlier than in the disturbed population (fig. 3). Numbers of flowers and fruits produced by plants in the undisturbed population were significantly higher than in the disturbed

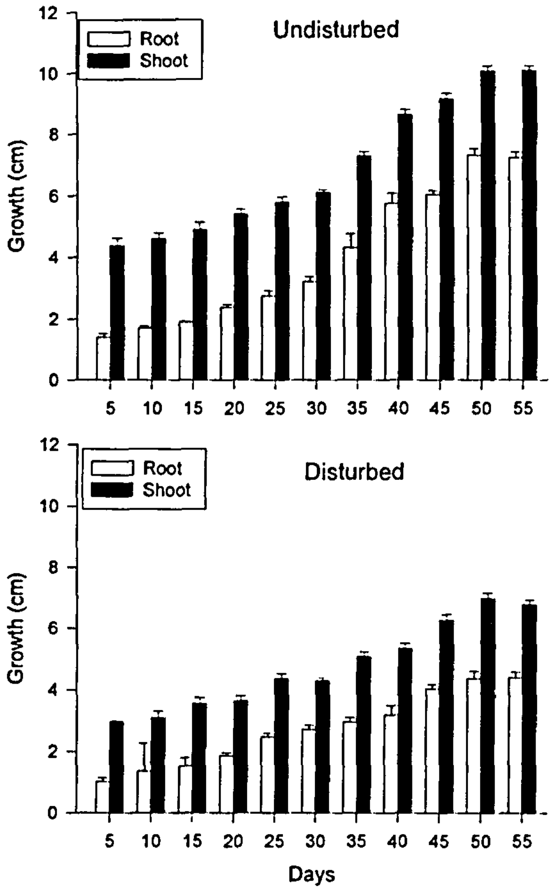

Fig. 2 Root and shoot growth (cm) of *Leucus urticifolia* in the undisturbed population and the disturbed population.

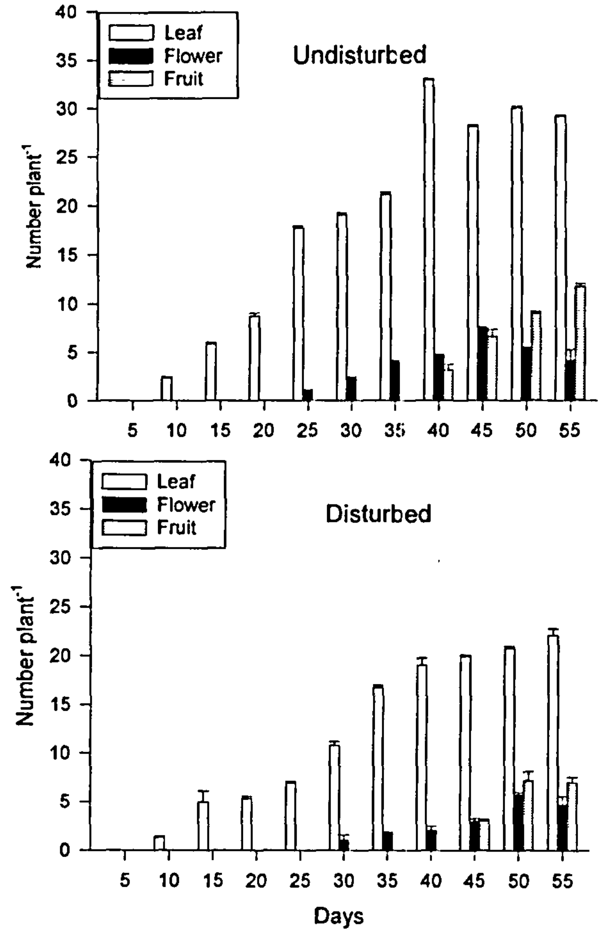

Fig. 3 Leaf, fruit, and flower numbers of *Leucus urticifolia* in the undisturbed population and the disturbed population.

population. A two-way ANOVA of root and shoot growth and number of leaves, flowers, and fruits indicated significant main effects and their interaction effect for population and time in days (table 3).

Biomass allocation

Dry weights of roots, stems, and leaves were slightly higher in undisturbed populations (data not shown), and flower and fruit weight was significantly ($P < 0.0001$) higher. Relative biomass allocation to roots and stems decreased with age in both populations, but decreases in allocation to stems in disturbed population were more substantial (fig. 4). Biomass allocation to leaves showed a mixed pattern in the undisturbed population but showed a progressive increase in the disturbed population. Plants in the undisturbed population (fig. 4) allocated a maximum of 65% of their biomass to reproduction, whereas those in the disturbed population (fig. 4) allocated only 4% of their biomass to reproduction.

Discussion

Leucus urticifolia populations exhibited much variation in seed bank, demography, and reproduction characteristics at disturbed and undisturbed sites, but both populations have a persistent seed bank. Comparisons of the populations indicated a pattern of greater seed bank, recruitment, mortality, and reproduction in the less disturbed population than in disturbed population. It is also possible that some other unknown site factors varied between sites. *Leucus urticifolia*

Table 3

Results of two-way analysis of variance of characteristics of individual plants × population × days

Dependent variable	Days (d)	Population (P)	d × P
	Independent variable		
Number of leaves	3298.7***	3249.9***	157.8***
Number of flowers	951.9***	516.1***	120.3***
Number of fruits	2519.4***	787.6***	153.2***
Root length	3654.8***	9251.4***	530.7***
Shoot length	652.7***	2587.8***	176.1***

*** $P < 0.001$.

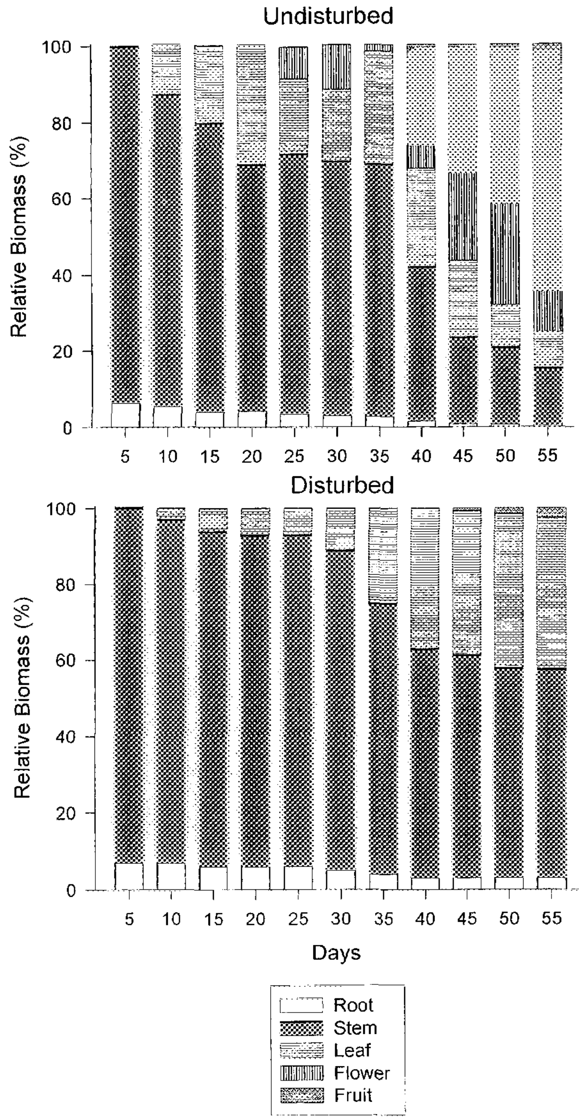

Fig. 4 Biomass allocation pattern (%) of *Leucus urticifolia* in the undisturbed population and the disturbed population.

grows well under shaded conditions and the disturbed population was located in this kind of area.

Seed bank and current vegetation of both populations are closely related and the seed bank flora can be used to predict vegetation of that habitat (M. A. Khan, unpublished data). The seed bank of both populations showed a persistent nature. The size of the seed bank in undisturbed populations (*L. urticifolia* = 23,469 seed m^{-2}; total = 71,426 seed m^{-2}) was twice that of the disturbed population (*L. urticifolia* = 12,244 seed m^{-2}; total = 34,283 seed m^{-2}). Persistent seed banks of annuals were also reported for *Salicornia europaea* (Jefferies et al. 1983), *Atriplex triangularis* (Khan and Ungar 1986), and *Tephrosia strigosa* (Aziz and Khan 1994). As expected, the seed reserve decreased significantly ($P < 0.0001$) after the rainfall but did not completely disappear and increased significantly after the dispersal of new seeds. There appears to be a small decline in total seed bank from the time of dispersal to the time of germination, which may be due to predation or death of seeds.

High intensity of disturbance results in a decrease in diversity of species and of the seed bank flora. In a Pakistani desert, most of the perennials maintain a transient seed bank (Khan 1990, 1993; Zaman and Khan 1992), since seed germination is not the predominant mode of recruitment. Most of the ramet recruitment takes place through the vegetative growth of rhizomes and stolons (Aziz 1994). Production of large genetic variation in the form of seeds could be the ultimate strategy for long-term survival. Few seedlings were reported during the last 8 yr of study at this site (M. A. Khan, personal observation). Desert annuals, in contrast, maintain a persistent seed bank (Aziz and Khan 1994) because their fitness depends upon their recruitment through seed germination. Some of the dispersed seeds were also lost during the dormant period, but they maintained a more or less persistent seed bank. The results presented here agree with those for *Tephrosia strigosa,* an annual from the same area (Aziz and Khan 1994).

Rate of mortality in *L. urticifolia* increased with the onset of flowering. Individuals from the undisturbed population exhibited greater mortality, presumably due to a greater allocation of resources to reproduction and density-dependent factors. Two other causes of mortality appeared to be competition and drought. In the case of the disturbed population, where recruitment was very low due to disturbance, drought, and high sunlight, the mortality could be due to the density-independent factors. Wu and Jain (1979) observed that density-dependent mortality occurred in species of *Bromus,* while density-independent mortality was reported for *Vulpia fasciculata* (Watkinson and Harper 1978) and *Cakile edentula* (Keddy 1989).

Plant size was positively correlated with the reproductive performance of plants. Plants of the undisturbed population were taller and healthier and produced more flowers and fruits. Similar results were reported for *Fragaria vesca* (Chabot 1978), *Erigeron canadensis* (Reghr and Bazzaz 1979), *Carduus nutans* (Lee and Hamrick 1983), and *Erucastrum gallicum* (Klemow and Raynal 1983).

The resource allocation patterns of plants are a fundamental aspect of their life-history strategies (Nault and Gagnon 1988). Reproductive strategies of plants can be studied in terms of biomass-allocation patterns (Harper 1967). The availability of resources often being limited, their allocation to various plant structures or functions may be done according to several possible compromises that maximize local fitness of a plant (Harper 1977). The life-history strategy of plant species is in part the result of a selection for an optimal allocation of limited resources to vital functions such as growth, reproduction, or the maintenance of vegetative structures (Abrahamson 1979). Thus, plant species exhibit resource allocation patterns that are the result of both their genotype and their environment (Cartica and Quinn 1982; Hume and Cavers 1983).

Biomass allocation to reproduction varied greatly in the two populations. The population in an undisturbed habitat allocated 65% of its resources to reproduction at the final stages of its life-cycle as compared with 4% in the population growing in the disturbed habitat. In habitats that were early successional or highly disturbed, plants tended to allocate a greater proportion of their total biomass to reproductive structures when compared with plants of late successional or less disturbed areas (Abrahamson and Gadgil 1973; Gaines et al. 1974; Abrahamson 1975, 1979). In some cases these differences in reproductive allocation of biomass between habitats were environmentally cued, plastic response of plants (Hickman 1975; Abrahamson and Hershey 1977). Reproductive effort in some populations decreased with an increase in disturbance, such as trampling and grazing in *Rumex crispus* (Maun and Cavers 1971) and *Anthyllis vulnerania* (Bastrenta 1991). Differences in biomass allocation to reproduction could be attributed to light and drought. *Leucus urticifolia* plants thrive in shady and moist conditions, and the undisturbed population was growing under such conditions. However, the disturbed population was growing in open and dry conditions in addition to being exposed to more disturbance, and the significant reduction in biomass allocation could be attributed both to microenvironmental factors and to disturbance regimes.

The results of this investigation indicate that the seed bank of undisturbed subtropical deserts of Karachi, Pakistan, have larger persistent and transitory seed banks than do disturbed areas. Plants in undisturbed areas are large and have greater reproductive allocation than are those of disturbed areas.

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Literature cited

Abrahamson WG 1975 Reproductive strategies in dewberries. Ecology 56:721–726.

——— 1979 Patterns of resource allocation in wildflower populations of fields and woods. Am J Bot 66:71–79.

Abrahamson WG, MD Gadgil 1973 Growth form and reproductive effort in goldenrods (*Solidago*, Compositae). Am Nat 107:651–661.

Abrahamson WG, B Hershey 1977 Reproductive allocation and growth of *Impatiens capensis* (Balsaminaceae) in two habitats. Bull Torrey Bot Club 104:160–164.

Aziz S 1994 Population ecology of a desert perennial halophyte *Cressa cretica* Linn. MPhil diss. University of Karachi, Pakistan.

Aziz S, MA Khan 1994 Life-history strategies of a desert summer annual *Tephrosia strigosa* willd. Bangladesh J Bot 23:139–46.

Bastrenta B 1991 Effect of sheep grazing on the demography of *Anthyllis vulneriana* in Southren France. J Ecol 79:275–284.

Carman JG, DD Briske 1985 Morphologic and enzymic variation between long term grazed and non-grazed populations of the bunch grass *Schizachyrium scoparium* var. *frequens*. Oecologia 66:332–337.

Cartica RJ, JA Quinn 1982 Resource allocation and fecundity of populations of *Solidago sempervirens* along a coastal dune gradient. Bull Torrey Bot Club 109:299–305.

Chabot BF 1978 Environmental influences on photosynthesis and growth in *Fragaria vesca*. New Phytol 80:87–98.

Chaudhry II 1961 The vegetation of Karachi. Vegetatio 74: 229–246.

Fenner MF 1985 Seed ecology. Chapman & Hall, New York.

Gaines MS, KS Vo, JL Hamrick, J Caldwell 1974 Reproductive strategies and growth pattern in sunflowers (*Helianthus*). Am Nat 108:889–894.

Harper JL 1967 Darwinian approach to plant ecology. J Ecol 55:247–270.

——— 1977 Population biology of plants. Academic Press, New York.

Hickman JC 1975 Environmental unpredictability and plastic energy allocation strategies in the annual *Polygonum cascadense* (Polygonaceae). J Ecol 27:689–701.

Hume L, PB Cavers 1983 Resource allocation and reproductive and life-history strategies in widespread populations of *Rumex crispus*. Can J Bot 61:1276–1282.

Jefferies RL, A Jensen, D Bazely 1983 The biology of the annual *Salicornia europaea* agg. at the limits of its range in Hudson Bay. Can J Bot 61:762–777.

Keddy PA 1989 Experimental demography of a sand-dune annual *Cakile edentula* growing along an environmental gradient in Nova Scotia. J Ecol 69:615–630.

Kemp PR 1989 Seed banks and vegetation processes in deserts. Pages 257–281 *in* MA Leck, VT Parker, RL Simpson, ed. Ecology of soil seed banks. Academic Press, San Diego.

Khan MA 1990 The relationship of seed bank to vegetation in a saline desert community. Pages 87–92 *in* DN Sen, S Mohammad, eds. Marvels of seeds. Proceedings of International Symposium on Environmental Influences on Seed and Germination Mechanism—Recent Advances in Research and Technology. Department of Botany, University of Jodhpur, India.

——— 1993 Relationship of seed bank to plant distribution in saline arid communities. Pak J Bot 25:73–82.
Khan MA, IA Ungar 1986 Life-history and population dynamics of *Atriplex triangularis.* Vegetatio 66:17–25.
Klemow KM, DJ Raynal 1983 Population biology of an annual plant in a temporally variable habitat. J Ecol 71: 691–703.
Lee JM, JL Hamrick 1983 Demography of two natural populations of musk thistle (*Carduus nutans*). J Ecol 71:927–936.
Maun MA, PB Cavers 1971 Seed production and dormancy in *Rumex crispus.* I. The effect of removal of cauline leaves at anthesis. Can J Bot 49:1123–1130.
Nault A, D Gagnon 1988 Seasonal biomass allocation patterns in wild leek (*Allium tricoccum* Ait.), a spring geophyte. Bull Torrey Bot Club 115:45–54.
Painter EL, JK Detting, DA Steingraeber 1989 Grazing history, defoliation and frequency-dependent competition: effect on two North American grasses. Am J Bot 76:1368–1379.
Reghr DDL, FA Bazzaz 1979 The population dynamics of *Erigeron canadensis,* a successional winter annual. J Ecol 67:923–933.
Watkinson AR, JL Harper 1978 The demography of a sand dune annual: *Vulpia fasciculata.* I. The natural regulation of populations. J Ecol 66:15–33.
Wu KK, SK Jain 1979 Population regulation in *Bromus rubans* and *B. mollis:* life-cycle components and competition. Oecologia 39:337–357.
Zaman AU, MA Khan 1992 The role of buried viable seeds in saline desert plant community. Bangladesh J Bot 21:1–10.