

Reproductive Effort of Some Annual and Perennial Plant Species: Impact of Successional Sequence, Habitat Conditions and Plant Size

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Abstract. The reproductive effort of some annual and perennial plant species was investigated with respect to successional sequence, habitat conditions and plant size. In the psammose succession (dune succession), the reproductive effort (RE) of *Cressa cretica* and *Atriplex griffithii* was significantly greater in the early stage compared to that in late succession. Likewise, in relation to lithosere succession, *Sporobolus arabicus*, *Pluchea lanceolata* and *Vernonia cinerescens* all showed high reproductive effort in early part of succession compared to that of late succession. The annuals (*S. arabicus* and *P. lanceolata*) exhibited greater reproductive effort compared to the perennial species *Vernonia cinerescens*. Examination of the impact of site differences on reproductive effort showed that four grasses including *Setaria intermedia*, *Chloris barbata*, *Cenchrus biflorus*, and *Eragrostis pilosa* were found to have significantly ($P < 0.05$) greater reproductive effort in site 1 (near cultivated field), compared to site 2 (a vacant lot), which had low nutrient level compared to site 1. The reproductive effort of *Sonchus asper* (a composite) did not exhibit significant difference between sites. The investigation of relationships between plant size (volume) and reproductive effort of *Solanum forskalii*, *Senna holosericea* and *Heliotropium ophioglossum* showed positive correlations between plant size and reproductive effort. *Solanum forskalii* and *Senna holosericea*, in particular, exhibited a close association in this respect. It is concluded that: 1) RE is greater in early compared to late succession, 2) RE changes with the habitat and 3) there seems to be a direct relationship between RE and plant size.

Keywords: reproductive efforts, succession, sand dunes, soil analysis, plant-size

Introduction

The survival of an individual (a genet) in a population is determined by a unique combined set of habitat conditions and life-history traits. Temporal pattern of its growth and reproduction is regulated by a variety of features including its growth rate, size, vegetative offspring (if any), the propagules produced per generative episode and the number of such reproductive events that occur during the life-history (Roff, 1992; Stearns, 1992). Each individual is subjected to the force of natural selection, both under the influence of habitat conditions that usually change with time as well as inter- and intra-specific competition. These limiting conditions act as the driving force for the plant to adapt to such life-history traits that would result in fitness (e.g., survival) of the individual and are collectively termed as life-history strategy.

One important aspect of the life-history of plant species in various environments is the resource allocation, i.e.,

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how plants allocate their resources (energy) to different organs and functions (Harper, 1977; Harper and Ogden, 1970) with varied environments (Reekie and Bazzaz, 2005; Lovett-Doust, 1990) in particular to the reproduction (De Jong and Klinkhamer, 2005). The cost of reproduction is generally high which is expressed in the form of reduced growth rate and/or increased death rate (Reekie and Bazzaz, 2005; Bazzaz *et al.*, 1979). The cost of reproduction is also presented as a compromise in the allocation of resources, i.e., current reproduction has an adverse effect on future reproduction and plant growth (Medez and Obesso, 1993; Reekie and Bazzaz, 1992; Fox and Stevens, 1991). Antflinger and Wendel (1997) pointed out the role of inflorescence as a source and sink for carbon assimilation that may lower the cost of reproduction and support frequent inflorescence production thus contribute to increased reproductive effort. Ashman (1994) suggested "dynamic" estimates of the cost of reproduction which is a function of reproductive photosynthesis or respiration, nectar production, or reproductive nutrient resorption to assess

current reproductive investment in order to predict future reproductive effort. The inconsistent evidence for trade-offs between current and future reproduction has prompted much debate regarding the cost of reproduction and the methodology involved for testing it (Bailey, 1992).

Many facets of plant reproduction, such as seed size and number and reproductive potential (Salisbury, 1942) have long been the subject of focus for ecologists. In recent years, a great deal of work has been undertaken on the determination of reproductive effort, the proportion of total energy (biomass) allocated to reproduction in various plant species (Hancock and Pritts, 1987; Watson, 1984; Abrahamson and Caswell, 1982; Soule and Werner, 1981; Bazzaz *et al.*, 1979; Harper and Ogden, 1970) and the allocation of energy to seed production. Among the life-history traits, reproductive effort including floral display and gamete production have paramount effects on plant fitness. The environmental conditions under which reproduction occurs can lead to variation in reproductive effort including floral morphological structures, function and production of seeds (Clifford, 2011). The relative size of plants in a community, as influenced by soil moisture and nutrients, herbivory and competition, appear to be directly correlated with seed size and number (Watkinson and White, 1985; Inouye *et al.*, 1980; Solbrig *et al.*, 1980). A trade-off between seed size and number has been well recognized (Harper, 1977; Werner and Platt, 1976).

The relationships between environmental factors and resource allocation pattern expressed in different populations of a species have not been fully explored. In the late 1960's ecologists began to develop theories pertaining to evolutionary basis of resource allocation patterns of which the pioneering work was that of (Reekie and Bazzaz, 2005; Harper and Ogden, 1970). Life-history theory predicts that a short juvenile period and high reproductive effort should be favoured in adverse or stochastic environment, where the life span is unpredictable and mortality is age and size independent (Torang *et al.*, 2010; Silvertown *et al.*, 2001; Kozlowski, 1992; Stearns and Koella, 1986). By contrast, delayed reproduction and lesser reproductive effort should be an optimal strategy in more stable environment, where mortality declines with age or size (Torang *et al.*, 2010). Harper *et al.* (1970) suggested that the intensity of competition is a function of habitat maturity and as a result, early successional species are exposed to low

competitive stress and are primarily annuals with high reproductive effort, while species appearing in later part of a particular sere face greater competitive stress, are usually perennials and have lower reproductive effort (Newell and Tramer, 1978; Gadgil and Solbrig, 1972). High proportions of energy allocated to vegetative parts were thought to confer fitness in a long-term severe struggle for existence in resource-limited stable environments (McNaughton, 1975; Gaines *et al.*, 1974; Abrahamson and Gadgil, 1973). Abrahamson (1975) studied the reproduction of *Rubus hispidus* L., in relation to habitats of a secondary succession and found that the total reproductive effort (sexual and vegetative reproduction) declined with increased maturity of the site. Some studies comparing reproductive effort of a single species under different environmental conditions have shown contradictory results (Holler and Abrahamson, 1977; Van Andel and Vera, 1977; Werner and Rioux, 1977). In accordance with Hancock and Pritts (1987) two hypotheses have been tested with regard to the association of reproductive effort and successional maturity: 1) reproductive effort declines as succession progresses and 2) perennials have a lower reproductive effort than annuals. They found significant negative trend between reproductive effort and successional progression. Abrahamson (1979) showed that the species from early succession had higher reproductive effort than did herbs from late succession. Roos and Quinn (1977) found that early successional field population of *Andropogon scoparius* had a higher reproductive effort and a shorter developmental time (as indicated by dates of first anthesis) than populations of older successional field. Swamy and Ramakrishnan (1988) found that in late succession reproductive effort of *Mikania micrantha* was lesser compared to that of early succession. Comparing the annuals against the perennial with respect to their reproductive effort, Hancock and Pritts (1987) found that annuals had consistently greater reproductive effort than the perennials. Ploschuk *et al.* (2005) stated that seed yield and allocation to reproduction are actually lower in several perennial weeds compared with closely related annual crops. Similarly, Djordjevic-Miloradovic (1997) examining the changes in reproductive effort of *Tussilago farfara* populations demonstrated similar results. Silvertown and Dodds (1996) concluded that annuals have greater reproductive allocation compared to perennials. Nonetheless, certain studies have shown greater allocation to reproduction in perennial crops (DeHaan *et al.*, 2003; Pimm, 1997).

McNamara and Quinn (1977) compared the populations of the annual *Amphicarpum pushii* Kunth and found the reproductive effort to differ with sites which was explained on the basis of differences in micro-environments. They further stated that the apparent trend of differential allocation of reproductive biomass in relation to site conditions, could be adaptive for this fugitive species and could result either from phenotypic plasticity or may be due to local genetic differentiation. Tallowin (1977) working with *Festuca contracta* T. Kirk showed that the sexual reproductive effort declined significantly with increasing habitat severity, principally exposure to high winds. Reduced floret and seed production resulting from severe habitat conditions have also been reported in *Phleum alpinum* (Callaghan and Lewis, 1971). Li *et al.* (2005) investigated the reproductive effort of *Artemisia halodendron* in two contrasting habitats and reported that plants inhabiting the less eroded semi-fixed habitats (dunes) produced more flowering shoots, greater dry weight of flowering shoots, dry weight of seeds and reproductive effort than those inhabiting the more eroded mobile dunes. He *et al.* (2009) examined the reproductive effort of an annual plant *Corispermum elongatum* Bunge in two types of sandy habitats and found significant effect on the pattern of reproductive allocation. The resource allocated to reproduction was size-dependent and also affected by habitat types. Torang *et al.* (2010) tested among-population differentiation in reproductive effort of *Primula farinosa* L., using sites that differed widely in soil depth and water retaining capacity and found that reproductive effort varied among populations and negatively correlated with soil depth. Soule and Werner (1981) stated that the relationship between environmental conditions and the resource allocation patterns have not yet been fully worked out. This raises the need of further studies along this line.

Size-dependent variation in reproductive effort is now a fairly well known phenomenon. Size is a better predictor of reproductive status than age (Waugh and Aarssen, 2012; Hanzawa and Kalisz, 1993). It has been noticed that plants have to attain a minimum size below which they do not reproduce regardless of age (Lacey, 1986). Size-dependent variation in reproductive effort in plants has been theoretically predicted a long time ago (Gadgil and Bossert, 1970). Samson and Werk (1986) gave a simple model for the examination of the pattern of reproductive allocation. Their results suggested that much of the variation in reproductive effort can be

explained on the basis of intrinsic size effects rather than extrinsic factors. However, in many studies of reproductive effort, size dependent effects have been completely ignored. Ohlson (1988) investigated the size-dependent reproductive effort in the populations of *Saxifraga hirculus*. In *S. hirculus* the probability of flowering increased with plant size, which has also been reported for some other species as well (Pritts and Hancock, 1983; Van der Meijden and Van der Waals-Kooi, 1979). Welham and Setter (1998) studied the size-dependent reproductive effort of *Taraxacum officinale* Weber populations and found that reproductive effort increased linearly with increasing vegetative biomass but the slope for the population from alfalfa field (disturbed site) was significantly greater than that derived from undisturbed sites with high grass density. Mendez and Obeso (1993) reported a linear relationship between reproductive allocation and plant size in *Arum italicum*. Mendez and Karlsson (2004) found reproductive biomass to be size-dependent in all the studied populations of *Pinguicula vulgaris* L. Likewise, Kawano and Mikaye (1983) working with five species of *Setaria* found greater fecundity and reproductive biomass above a threshold size to be size-dependent. Hartnett (1990) reported that the sexual reproductive effort in four clonal composites was a monotonically increasing function of ramet size. Pino *et al.* (2002) demonstrated a linear relationship between reproductive biomass and vegetative biomass in *Rumex obtusifolius* indicating a size dependent reproductive pattern.

The principal objectives of the present study were: 1) to investigate the impact of successional sequence on the reproductive effort of some annual and perennial plants, 2) to examine the effect of site differences on the reproductive effort of some plants and 3) to relate reproductive effort with plant size.

Materials and Methods

Study sites. All study sites were located in Karachi city, southern Sindh, Pakistan or its vicinity. The physiographic situations ranged from plains to sand dunes to calcareous hills around Karachi. The study sites were located within the greater Karachi. In all, 8 sites were sampled site 1=Sandspit, site 2=Clifton, site 3=Paradise point, site 4=Gdap, site 5=Cultivated field in Karachi university campus, site 6=Vacant lot near Dept., of Statistics, university of Karachi, site 7=Karachi university campus near Dept., of Physiology, university of Karachi, site 8=near Pipri. The soils were in general coarse

textured and poor in nutrients and organic matter. The soil from each site was collected with a soil auger (except at Paradise Point, where soil was very shallow) to a depth of 25 cm. Soils were analysed physically and chemically. Soil texture was determined using a set of sieves of various sizes. Soil pH was determined in a soil paste (1:5, soil: distilled water) using a Jenway pH meter (Model 3505). The characteristics of the soils pertaining to individual experiments are given in appropriate sections.

Effect of successional sequence. Reproductive effort of five species was investigated in two different series. One successional sequence was that of sand dune system prevailing at Sandspit and Clifton area in Karachi, southern Sindh, Pakistan. The unstabilized, mobile dunes at Sandspit (having sparse vegetation cover) can easily be distinguished from stabilized (fixed) dunes that have plenty of vegetation cover, particularly that of *Ipomoea pescaprae* L. R. Br., a dominating species in the late psamosere succession. *I. pescaprae* horizontally spreads on the dunes profusely (stems trailing, rooting at the nodes), binds the sand and prevents it from moving in bulk. Such dunes are situated in Clifton area though most of them have now been destroyed due to rapidly growing construction work. The plant species chosen for the study were *Atriplex griffithii* Moq and *Cressa cretica* L., both being perennial halophytic under-shrubs occur sympatrically. The dune vegetation at Sandspit is dominated by *Suaeda fruticosa* Forssk, *Salsola imbricata* Forssk., *Salvadora persica* Linn., *Atriplex griffithii*, *Cressa cretica*, *Zygophyllum simplex* Linn., and *Ipomoea pescaprae* as well as grasses such as *Halopyrum mucronatum* (Linn.) Stapf, *Aeluropus lagopoides* (Linn.) Trin., *Urochondra setulosa* (Trin) C.E. Hubbard and a sedge *Cyperus conglomeratus* subsp., *curvulus* (Boeck) Kukkonen. The vegetation at Clifton area (undisturbed permanent dunes) is dominated by *Ipomoea pescaprae*, *Suaeda fruticosa*, *Salsola imbricata*, *Heliotropium bacciferum* subsp. *lignosum* (Vatke) Kazmi, *Cressa cretica* (all shrubs or undershrubs) and grasses including *Dichanthium annulatum* (Forssk) Stapf., *Lasiurus hirsutus* (Forssk) Boiss and *Aeluropus lagopoides*.

The other successional sequence was a lithosere associated with calcareous hills near Paradise Point and Gadap area. The species investigated were two annuals namely *Sporobolus arabicus* Boiss and *Pluchea arguta* Boiss and a perennial species *Vernonia cinerescens* Schultz-Bip. The vegetation at Paradise Point which

represented early succession consisted of under-shrubs such as *Iphiona grantioides* (Boiss) Anderb, *Ruellia patula* Jacq., *Ruellia longifolia* (Stocks) T. Anders, *Barleria acanthoides* Vahl and *Pulicaria hookeri* Jafri and grasses such as *Chrysopogon aucheri* (Boiss) Stapf, *Cymbopogon jwarancusa* (Jones) Schultes and, *Sporobolus arabicus*, etc. Whereas, the vegetation at Gadap area representing late succession was dominated by *Commiphora wightii* (Am) Bhandari, *Grewia tenax* (Forsk) Fiori, *Euphorbia caducifolia* Haines, *Vernonia cinerescens* SchBip, *Grewia villosa* Willd. and *Acacia senegal* (L) Willd. In this mature type of vegetation both *Sporobolus arabicus* and *Pluchea arguta* are infrequent. *S. arabicus* often occurs in abundance after the monsoon rains. At least five plants of each of the selected species were randomly collected from the study sites. Plants included the roots and the underground parts (if any) and placed in between blotting papers, kept in plant presses and brought to the laboratory. The plants were split into vegetative and reproductive parts (flowers, fruits, seeds and peduncle if present) oven dried at 75 °C for 24 h and weighed. The reproductive effort (RE) was determined as $RE = (\text{reproductive weight} / \text{total dry weight}) \times 100$.

Data on reproductive effort were subjected to analysis of variance (ANOVA) followed by Fisher's least significant difference (LSD) test, performed at a rejection probability level = 0.05.

Effect of habitat conditions. Five sympatrically occurring species were chosen for this study of which four were grasses, namely *Setaria intermedia* Roem. & Schult., *Chloris barbata* Swartz, *Cenchrus biflorus* Roxb., *Eragrostis pilosa* (L) P. Beauv and one annual Composite *Sonchus asper* (L) Hill. All of these species occurred in a cultivated field in Karachi university campus where vegetables are grown, served as one habitat (site 1). Except for *Sonchus asper*, that grows in winter, the grasses were sampled during summer. The other sampling site for these species was located in a vacant lot (site 2) near Statistics Department, university of Karachi where all the six species were found and sampled. The plants were chosen randomly except *Sonchus asper* which was infrequent and had to be sampled deterministically. The entire plants including underground parts were collected. The rest of the procedure was the same as outlined above. The soil samples from both sites were also collected and analysed physically and chemically in accordance with the procedures mentioned earlier.

Effect of plant size. Three perennial species were chosen *Solanum forskalii* Dunal, *Senna holosericea* (Fresen) Greuter and *Heliotropium ophioglossum* Stocks ex Boiss., *Solanum forskalii* population was located at Karachi university campus (near department of Physiology) and it was almost a pure population so that intraspecific competition was greater than interspecific competition (Shaukat *et al.*, 2009). The population of *Senna holosericea* and *Heliotropium ophioglossum* were located near Pepri (about 35 km from Karachi city on National Highway) and the two species occurred sympatrically. Circumference was measured of thirty plants of each species, and the volume of each plant was calculated as a cylindrical shaped structure (Shaukat *et al.*, 2012; Shaltout *et al.*, 2003). The entire plants, together with roots were collected and brought to laboratory in polythene bags. The reproductive effort was determined as described above. Product moment correlation coefficients were calculated and linear regressions was performed between plant size (volume) and the reproductive effort. All programs including DISPERS (for computation of mean and SE), ANOVA to compute analysis of variance and the post-hoc test “least significant difference” LSD, and CORREG to perform correlation and linear regression were written by the first author (SSS) in C++ and are available on request. Similar programs written in BASIC are also available by Ahmed and Shaukat (2012).

Results and Discussion

Effect of successional sequence. The soil characteristics of early and late dune succession are given in Table 1. The soils of both the successional sequence are extremely sandy with low water retaining capacity. The soils of late succession at Clifton area have greater organic matter and slightly greater levels of nutrients. Salinity is greater at Sandspit presumably because of nearness of sea and the salt spray. The reproductive effort of the five species in relation to successional sequence is shown in Table 2. The two species chosen for the psamosere (sand dune) succession showed greater reproductive effort for early succession compared to late succession. *Cressa cretica* responded to successional sequence more than did *Atriplex griffithii* showing greater disparity between early and late successional stages. It is possible that the reproductive effort of *A. griffithii* is slightly underestimated because of the loss of seeds as a consequence of wind dispersal. Wind speed at the coast is in general high and the seeds of *A. griffithii* are anemochoric.

Table 1. Soil characteristics of unstabilized shifting and fixed sand dunes at Sandspit and Clifton respectively, Mean \pm Standard Error (SE)

Soil characteristics	Unstabilized dunes	Fixed dunes
Coarse sand %	57.24 \pm 2.15	45.36 \pm 1.85
Fine sand %	40.53 \pm 1.52	49.54 \pm 1.77
Silt and clay %	2.23 \pm 0.31	5.10 \pm 0.84
Water holding capacity	5.20	8.04
pH	8.2	7.9
Organic matter %	0.280	0.438
Total Kjeldahl nitrogen	0.58	0.088
Exchangeable Ca	44	62
Exchangeable Mg	5.0	9.0
Electrical conductivity	20	18
EC (μ s/cm)		

Table 2. Mean and range and SE (standard error) of reproductive effort of species in early and late psamosere and lithosere succession, Rows means not sharing the same letter are significantly different(P=0.05)

Sere/Species	Early succession		Late succession	
	Range	Mean \pm SE	Range	Mean \pm SE
Psamosere				
<i>Atriplex griffithii</i>	8-19	12.8 \pm 1.4 ^a	6-11	8.2 \pm 0.8 ^b
<i>Cressa cretica</i>	10-24	17.4 \pm 1.6 ^a	8-17	11.5 \pm 1.7 ^b
Lithosere				
<i>Sporopolous arabicus</i>	18-26	21.2 \pm 1.27 ^a	12-21	17.5 \pm 1.24 ^b
<i>Pluchea arguta</i>	16-27	23.5 \pm 1.47 ^a	9-19	15.3 \pm 0.85 ^b
<i>Vernonia cinerescens</i>	13-21	16.7 \pm 0.87 ^a	10-15	12.4 \pm 0.92 ^b

The soil properties of the hill slopes of early and late succession are given in Table 3. The soil texture in the late succession is slightly finer with greater percentage of silt plus clay and consequently has greater maximum water holding capacity. Organic matter % and the concentrations of exchangeable Ca, Mg and K were also at a higher level in late succession compared to early succession. The reproductive effort of all three test species was higher in the early succession compared to late lithosere succession. The annuals namely *Sporobolus arabicus*, an annual grass and *Pluchea arguta*, an annual forb showed high reproductive effort 21.2 and 23.5, respectively. The perennial species *Vernonia cinerescens* also showed high reproductive effort in the early lithosere succession. Compared to the reproductive effort of psamosere progression the reproductive effort was higher for species in the lithosere succession. Hancock and Pritts (1987) concluded that

Table 3. Soil characteristics of calcareous hills at early (Paradise Point) and late succession (Gadap)

Soil characteristics	Early succession	Late succession
Coarse sand %	51.8 ± 1.27	38.2
Fine sand %	28.7 ± 1.47	33.5
Silt and clay %	19.5 ± 0.82	28.3
Water holding capacity	20.6	28.3
pH	7.8	7.6
Organic matter %	0.341	0.568
Total Kjeldahl nitrogen	0.210	0.431
Exchangeable Ca	52 ± 2	61 ± 3
Exchangeable Mg	28 ± 2	32 ± 2
Exchangeable K	18 ± 1	26 ± 3

reproductive effort in general declines with the onward progression of succession. Harper *et al.* (1970) suggested that intensity of competition is correlated with habitat maturity and as a consequence, early successional species, which are primarily annuals, have large reproductive effort, while species dominating the later part of sere, which are usually perennials, have smaller reproductive effort. The changes in reproductive effort in the present study during psamosere contrasts with the findings of He *et al.* (2009) who found greater reproductive effort of *Corispermum elongatum* growing on fixed or stabilized dunes compared to that on mobile or embryonic dunes. On the other hand, present study accords with the findings of Gleeson and Tilam (1990) who found that the reproductive biomass declined during successional progression. Likewise, Swamy and Ramakrishnan (1988) found that the reproductive effort of *Mikania micrantha* was greater in 3 year old field compared to that of 12 years fallow field. In later succession, plants showed adaptation for survival and competition and also increased allocation to rosette and root because they serve as perennating organs. Roos and Quinn (1977) reported that in early successional field population of *Andropogon scoparius* had higher reproductive effort and a shorter developmental time than population of older site. Djordjevic-Miloradovic (1997) working on the reproductive effort of *Tussilago farfara* growing on coal ash and found greater reproductive effort of *T. farfara* in early succession (1-2 years) compared to 8-9 years old population. In the mature stage of succession, plants exhibited adaptations to vegetative way of reproduction.

The annual species *Sporobolus arabicus* and *Pluchea arguta* exhibited greater reproductive effort compared

to the perennial species *Vernonia conerescens*. Annuals generally colonize in early succession in heterogeneous, unpredictable and xeric environments and exposed to low competitive stress, therefore, they devote more energy to reproduction. Ploschuk *et al.* (2005) demonstrated greater allocation to reproduction in annual compared to perennial *Lesquerella* crop. Usually perennials which face greater competitive stress, as they predominate the mid and later succession, have lower reproductive effort (Newell and Tramer, 1978; Gadgill and Solbrig, 1972).

Influence of habitat. The soil analysis of the two study sites (cultivated field, site 1 and vacant lot, site 2) are presented in Table 4. The soil was sandy loam at site 1 while it was loamy sand at site 2. The proportion of silt + clay was considerably higher at site 1. Likewise, the soil of site 1 also had greater percentage of organic matter and the nutrients. In particular, nitrogen percentage was significantly ($P < 0.05$) higher in the arable field soil. All the grass species including *Setaria intermedia*, *Chloris barbata*, *Eragrostis pilosa* and *Cenchrus biflorus* were found to have significantly ($P < 0.05$) greater reproductive effort in site 1 compared to site 2 (Table 5). However, a dicot weed *Sonchus asper* did not show a significant difference in the reproductive effort between the two sites. It is apparent that in most of the species tested the reproductive effort declined significantly with the habitat severity. The cultivated field undoubtedly having better moisture regime due to irrigation and better nutrient regime owing to fertilizer application as well as good aeration afforded to the roots resulted in enhanced reproductive effort to increase the population size. Although, it must be borne in mind that in this

Table 4. Soil characteristics of two sites at Karachi University campus (cultivated field (Site 1) and vacant lot (Site 2))

Soil characteristics	Site 1 (near field)	Site 2 (vacant lot)
Coarse sand %	41.4	44.8
Fine sand %	31.5	32.4
Silt and clay %	27.1	22.8
Water holding capacity	32.2	25.2
pH	7.7	7.7
Organic matter %	0.853	0.437
Total Kjeldahl nitrogen	0.430	0.240
Exchangeable Ca	78±3	50±2
Exchangeable Mg	32±2	27±2
Exchangeable K	25±1	19±2

Table 5. Range and mean reproductive effort of 5 replicate plants of each species. Means followed by a different letter in a row are significantly different at $P=0.05$

Species	Site 1		Site 2	
	Range	Mean	Range	Mean
<i>Setaria intermedia</i>	9-15	13.77±0.79 ^a	8-12	9.7±0.72 ^b
<i>Chloris barbata</i>	12-19	15.2±1.2 ^a	11-15	12.0±0.69 ^b
<i>Cenchrus biflorus</i>	25-33	31.7±1.3 ^a	22-30	26.4±1.1 ^b
<i>Eragrostis pilosa</i>	18-27	24.5±1.4 ^a	16-23	18.8±1.3 ^b
<i>Sonchus asper</i>	15-21	18.6±0.92 ^a	11-19	16.9±1.2 ^a

habitat competition is likely to be more severe because of the crop. It is observed that these grasses or weeds generally do not grow in close neighbourhood of the crop plant. Moreover, the grasses tested here usually grew near the periphery of the field thereby avoiding direct competition from the crop plant but take advantage of better growth conditions of the cultivated field. On the other hand the same grasses when growing sympathetically in the semi-natural community (Site 2) are subjected to interspecific competition. Also they are subjected to feeding activity of phytophagous insects and exposed to high wind velocity (3-4 miles/h). Besides, competitive stress could be an important factor responsible for decreased reproductive effort under the condition of co-occurrence of a number of species including the grasses and other perennial herbs and shrubs. Tallwin (1977) examined the sexual reproductive performance of *Festuca contracta* (T. Kirt) demonstrated that seed production declined with increasing habitat severity. Reduced floret and seed production because of severe habitat conditions has also been found in another grass *Phleum alpinum* (Callaghan and Lewis, 1971). Li *et al.* (2005) studied the reproductive effort of *Artemisia halodendron* in two contrasting habitats. Plants growing on the less eroded semi-fixed habitats (dunes) produced greater number of flowering shoots, higher dry weight of flowering shoots, seed dry weight increased reproductive effort than those inhabiting the more eroded mobile dunes, thereby demonstrating the negative effect of habitat severity. The results of the current study suggest that the between population variation in reproductive effort in relation to site conditions observed in the field largely reflects phenotypic plasticity in response to local environmental conditions. Phenotypic plasticity with respect to reproductive effort has also been reported for *Polygonum cascadenense* by Hickman (1975). On the

other hand, local genetic differentiation can be ruled out as this process is favoured by selection when spatial differences in environmental conditions are consistent over time and seed dispersal between habitats is limited. In the present study the two habitats were not too far from each other (about 300 m) and gene exchange was highly likely to occur between populations (in fact the two populations can be regarded as part of a metapopulation) and both the habitats may be categorized as temporary and disturbed, thereby restricting the chances of long-term selection pressure.

Effect of plant size. The soil characteristics of the two sites namely Site 1 (Karachi university campus near department of Physiology) and site 2 (Peprri 35 km from Karachi city) are given in Table 6.

Table 6. Soil characteristics of two sites where plants size and RE studies were performed

Soil characteristics	Karachi university	Peprri
Coarse sand %	72.6	70.1
Fine sand %	16.1	16.3
Silt and clay %	11.3	13.6
Water holding capacity	29.2	30.8
pH	7.8	8.0
Organic matter %	0.35	0.32
Exchangeable Ca	22±2	50±2
Exchangeable Mg	49±2	62±3
Exchangeable K	25±1	30±2
Available PO ₄	16	24
Total Kjeldahl nitrogen	0.38	0.42

The relationships between plant size (volume) and reproductive effort for the three species, namely *Solanum forskalii*, *Senna holosericea* and *Heliotropium ophioglossum* are shown in Fig. 1-3, respectively. Product moment correlation coefficients were calculated between plant size (volume) and reproductive effort (RE). All three species showed significant positive correlation between plant size and reproductive effort: *Solanum forskalii* $r=0.721$ ($P<0.001$), *Senna holosericea* $r=0.749$ ($P<0.001$), *Heliotropium ophioglossum* $r=0.0.443$ ($P<0.05$). The range of variation in RE varied among the species. Reproductive effort ranged between 9.2 to 20.1% for *Solanum forskalii*, 8.2 to 17.3% for *Senna holosericea* and 5.7 to 16.4% for *Heliotropium ophioglossum*. The regression equations between plant size (PS) and

reproductive effort (RE) are give below for the three species:

Solanum faskalii

$$PS=10.502+0.0134 RE \quad R^2=52.0\% \quad R^2 \text{ adj}=50.3\%$$

Senna holosericea

$$PS=8.331+0.0161 RE \quad R^2=56.2\% \quad R^2 \text{ adj}=54.6\%$$

Heliotropium ophioglossum

$$PS=10.201+0.0103 RE \quad R^2=19.6\% \quad R^2 \text{ adj}=16.7\%$$

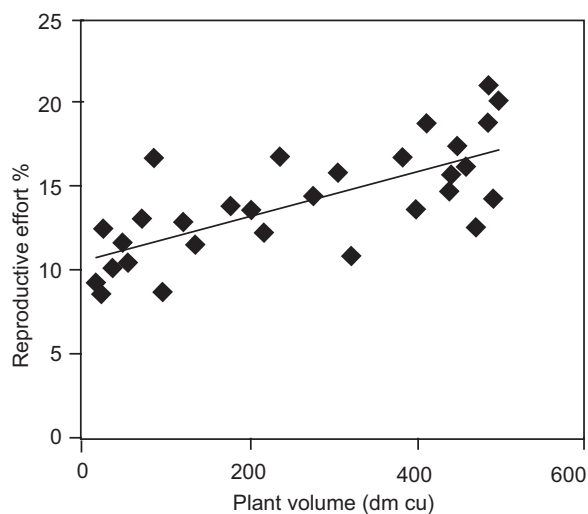


Fig. 1. Relationship between size of *Solanum faskalii* individuals and % reproductive effort. Linear regression line is fitted to the data, $R^2=52.0\%$.

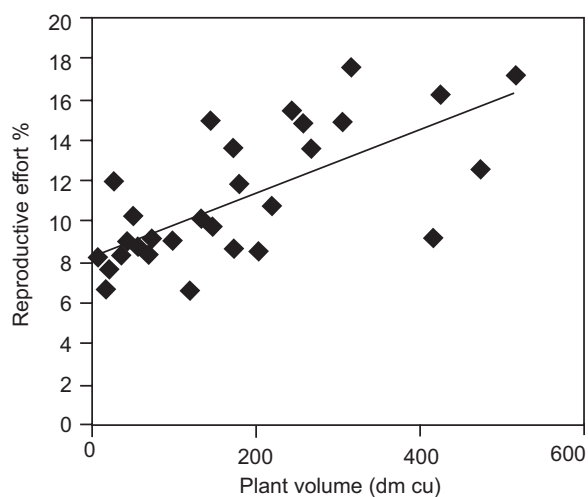


Fig. 2. Relationship between size of *Senna holosericea* individuals and % reproductive effort. Linear regression line is fitted to the data, $R^2=56.2\%$.

High values of coefficient of determination (R^2) indicate that most of the variation in reproductive effort is the result of variation in the plant size (volume). Apart from linear regression, other forms of regression were also tried. Linear relationships provided better fits to the observed data than logarithmic, power or exponential models for each of the species.

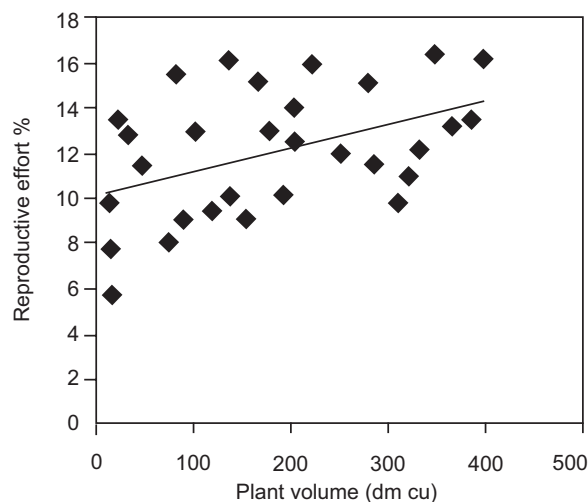


Fig. 3. Relationship between size of *Heliotropium ophioglossum* individuals and % reproductive effort. Linear regression line is fitted to the data, $R^2=19.6\%$.

Size dependent variation in reproductive effort has been demonstrated in a number of empirical investigations (Ohlson, 1988; Kawano and Masuda, 1980; Gaines *et al.*, 1974; Abrahamson and Gadgil, 1973). Usually the reproductive effort increases with increasing plant size (Mendez and Karsson, 2004; Aarssen and Jordan, 2001; Welham and Setter, 1998; Schmid and Weiner, 1993; Hartnett, 1990). Good direct evidence of the pattern of size-dependent reproductive effort and linear relationships between reproductive biomass and vegetative biomass in some perennial species has been provided by Weaver and Cavers (1980) and Waite and Hutchings (1982). On the other hand, Shipley and Dion (1992) found no evidence for size-dependent reproductive effort in a number of herbaceous species. Ohlson (1988) showed that in site with low pH, low nutrients and water supply no relationship existed between seed production and ramet size. However, under favourable site conditions fecundity was directly correlated with the ramet size. Nonetheless, the relationships between RE and size have not been studied under semi-desert

or desert conditioned for the under-shrubs. Furthermore, it is noteworthy that the relationship between plant size (volume) and reproductive effort is highly significant for all three species investigated in our study as shown by high magnitudes of correlation coefficient. These results corroborate the findings of Aarssen and Jordan (2001). All three plant species tested in this study were under-shrubs and not much is known regarding the relationship between size and reproductive effort in these life-forms. The results of isometric relationship parallels the results of an earlier within species study which disclosed that reproductive output per unit plant size is constant across plants of different sizes when size variation is predominately controlled by environmental variation and plants are harvested at final stage of development (Clausen and Aarssen, 1994). A large plant obviously has greater resources to support high fecundity (and/or large seed size) and therefore, high reproductive effort. The limitation of the current study is that it is a snapshot of the situation with regard to the magnitude of reproductive effort as it based on a single year of field observations. In those studies where workers have considered between year variations it has been found that that RE varies from year-to-year (Ohlson, 1988; Soule and Werner, 1981). More importantly, the relationship between RE and plant size can change from year-to-year (Ohlson, 1988). Thus, it is recommended that, in order to study the relationship between RE and plant size, the study should be conducted for at least three years at different sites ranging from nutrient and moisture austerities to high nutrient and moisture regimes or along environmental gradients.

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