POPULATION STRUCTURE, INTRASPECIFIC COMPETITION AND PHASIC DEVELOPMENT OF *UROCHONDRA SETULOSA* (TRIN.) C.E. HUBB., A COASTAL HALOPHYTIC GRASS OF PAKISTAN

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Abstract

The population structure, intraspecific competition and phasic development of growth in a population of *Urochondra setulosa* (Trin.) C.E. Hubb., in a dry salt marsh of Hawkes Bay, Karachi, Pakistan, are described. Density and cover values averaged 26000 plants/ha and 1951 sq. m /ha, respectively. Size class distribution was asymmetrical ($X^2 = 37.62$, $p < 0.001$) as 84.8% of the population concentrated in initial classes of plants smaller than 50 cm crown diameter. The crown size data fitted best ($P < 0.001$) to the negative power/ logarithmic equation indicating decreasing rate of mortality with age. Drawn to scale, crown outline diagrams indicated that when a hummock reaches to a critical size of around 60 cm in diameter begins to undergo degeneration and consequent hollowing in crown develops which increases with age. Among various developmental phases, mature hummocks dominated (40%) the frequency distribution, followed by building ones (23%). The frequency of seedlings + seedlings intergrading to pioneer was more or less equal to the frequency of degenerate and eroded phases. The phenomenon of phasic development is cyclic in time though quite incoherent in space. The spatial pattern of the population was contagious as determined through test of fitness of Poisson series and the magnitude of variance/ mean quotient (2.58).

Bivariate Simple Linear Correlation analysis for multiple nearest neighbours measurements indicated significant competitive influence of reference plants extending upto the third neighbour only. Multivariate Canonical Correlation Analysis (CANCOR), however,indicated intense competition only between the reference plant and the second and third nearest neighbours. The first nearest neighbour appeared to exhibit substantially lower competitive interaction with reference plant. The results are discussed in view of population structure, pattern and the biological characteristics.

Introduction

The form and reproductive output of plants growing together are affected due to competition as compared to their growth in isolation (Bleasdale, 1960; Harper, 1961, 1977). Density is a very crude measure of the competitive or interactive state of a population because an individual reacts to the effects of neighbours, not to the density of populations (Mack & Harper, 1977). Competition among plants appears to be purely a neighbourhood phenomenon (Mack & Harper, 1977; Turkington *et. al.*, 1977; Turkington & Harper, 1979) and interactions occur only among sufficiently closely located individuals (Silander & Pacala, 1985; Ford & Sorrensen, 1992). Various models of competition have been proposed (Ford & Sorrensen, 1992). Density has been the basis of some competition models. However, because of plasticity and spatial pat-

terning density is not a good measure for describing and predicting the bahaviour of plant population. As an alternative individual-based models (Houston, 1992) focus on individual plants and their neighbours. The size class analysis and nearest neighbour measurenments were therefore employed to determine the population structure, its dynamics and the competitive effects in an uneven aged, almost pure and visually homogeneous population of a coastal grass, *Urochondra setulosa* (Trin.) C.E. Hubbard. Study Area: The Hawkes Bay region of Karachi (24° 45'-25° N and $66^\circ 45'$ - 67° E) is charaterized by a variety of habitats and well marked vegetational zonation. Some of the dry salt marshes of this area where soil is sandy and somewhat poor in organic matter are predominantly populated by *Urochondra setulosa* forming hummocks about 15 cm high due to accumulation of eolian sand. The moisture supply is scanty mainly due to summer rains averaging around 200 mm or to poor oceanic seepage. The bare flats between hummocks are composed of compact alluvium containing some gravel. The salinity of the saturated extract of upper 20 cm soil profile measures around 53 $dS.m^{-1}$ in the bare flat area and $37 dS.m^{-1}$ in case of the hummock soil. The growth as well as the decay of the plant is slow. Plants such as *Cressa cretica, Aeluropus lagopoides, Cyperus sp.*, may sometimes be seen growing in between the hummocks or colonizing the eroded part of hummocks.

Materials and Methods

To collect data on density and stand cover, 75 quadrats, 1 x 1 m each were laid randomly and sampled in a population of *Urochondra setulosa*. The occurrence of hummocks as discrete plants generally with sufficiently large bare interspaces imposed no difficulty in determining individuals as may occur in many clonal species of grasses. However, clumps that were separated by more than 10 cm with no aboveground tissue connection were adjudged to be individual plants. Crown areas of the plants were calculated by measuring diameter of the crown diagonally at three points as plants exhibited somewhat circular growth form. To estimate the crown cover of deformed individuals, the crown was divided into appropriate geometric figures and the area determined.

To determine the nature of spatial distribution of plants, the observed frequencies of quadrats containing 0, 1, 2, 3.....,n individuals were related to the expected frequencies of the quadrats derived from Poisson series, e^{-m}, me^{-m}, $m^2.e^{-m}/2!$, $m^3.e^{-m}/3!$......, where m is the mean density of individuals. X^2 - goodness of fit was used to evaluate the significance. Variance/mean quotient was also employed to detect the nature of spatial distribution (Ludwig & Reynolds, 1985).

The relationship between interplant spacing and crown size variation was determined by multiple nearest neighbour measurements following Smith (1979) and Bell (1981). Twenty five reference plants were chosen at random. The random points were established by random co - ordinates and the nearest plant to the random point was considered as a reference plant. The distance from the reference plant to each of the four nearest neighbours (d_i, i = 1, 2, 3, 4) were measured from the centre of the plants. The cover of the plant was calculated by mean of crown diameters along three different radii. The terminal solitary and cylindric spike of *Urochondra setulosa*, being

compact and stout, is retained by the plant for considerable period of time and the plant collects dust due to its recretophytic and pubescent habit. This makes the current year's spikes easily identifiable from the remnant spikes of last year's growth. The current and last year remnant fecundities (Cf and Lf, respectively) of the plants were thus determined by counting the current year and remnant spikes present on the plants. The sum of Cf and Lf represented total fecundity (Tf). A matrix (A) of combined crown cover values of the reference plant and the i th nearest neighbour ($\triangle$ i, i = 1, 2, 3, 4) was generated. Similarly matrices (C, L, T and CD) were generated for combined crown diameter (cdi, i = 1, 2, 3,4), combined current fecundity (Cfi, i= 1, 2, 3 ,4), combined last year remnant fecundity (Lfi, i = 1,2,3,4), combined total fecundity (Tfi, i = 1, 2, 3, 4) and combined crown diameters (Cdi, i = 1,2,3,4) values, respectively. Complementary distance matrix (D) was represented by four distances, d1, d2, d3, d4, between reference plant and the ith nearest neighbour. Linear correlation and regression analyses between distance (di) and corresponding combined cover ($\triangle_j$), current , remnant and total fecundities (Cf, Lf and Tf) were performed to determine the relationship between plant size and the proximity of the eighbours. Furthermore, the sum of cover areas, current fecundity, remnant fecundity and total fecundity ($\triangle_5$, Cf_5, Lf_5 and Tf_5, respectively) of reference plant and the four nearest neighbours in a sampling point were correlated with the area of the circle (Ad_4) whose radius is equal to the distance of the fourth nearest neighbour, d_4 (Bell, 1981). To investigate the relationship of variation in plant size with the cover areas of the smallest (Asmp), the largest plant (Algp) and the total cover percentage of five plants (in relation to the area of the circle whose radius is equal to the distance, d_4), the coefficient of variation in cover (CV_c = s / $\bar{X}$ * 100, s = st. deviation; $\bar{X}$ = mean) was calculated for the five plants cover values in each sampling circle. CV_c was correlated with Asmp, Algp and $\triangle_5$/Ad_4. Similar analysis was performed with reproductive parameters of the plants (Cf_5, Lf_5 and Tf_5).

In the population under study, in some cases the distance of the third neighbour (d3) plus the radius of its crown (r3) was larger than the distance of the fourth neighbour (d4) plus the radius of its crown (r4). Therefore, following Khan *et. al.*, (1993), the parameter of total cover proportion ($\triangle$5/Ad') was also calculated in relation to the area (Ad') of the circle with radius equal to max (d4 + r4 , d3 + r3). Correlations between $\triangle$ 5/Ad' and CVc, Ad' and CV_c and Ad' and $\triangle_5$ were computed. Similar analysis was performed for data on current, remnant and total number of spikes.

To perform multivariate canonical correlation analysis (CANCOR), data of matrix (CD) of combined crown diameter values of reference and the ith nearest neightbour (cdi, i-1.2.3,4) and complementary distance matrix (D) were transformed as square root + 0.5. The transformed matrices were employed to compute canonical correlations using the package of Orloci & Kenkel (1985). The advantage of determining canonical correlation is that the information inherent in the intraset and interset covariance structure is not lost.

Age-related population structure was investigated by determining size-class frequencies by apportionment of the sampled individuals into size-classes of 10 cm crown diameter. Dispersion and location parameters were calculated to check the normal distribution.
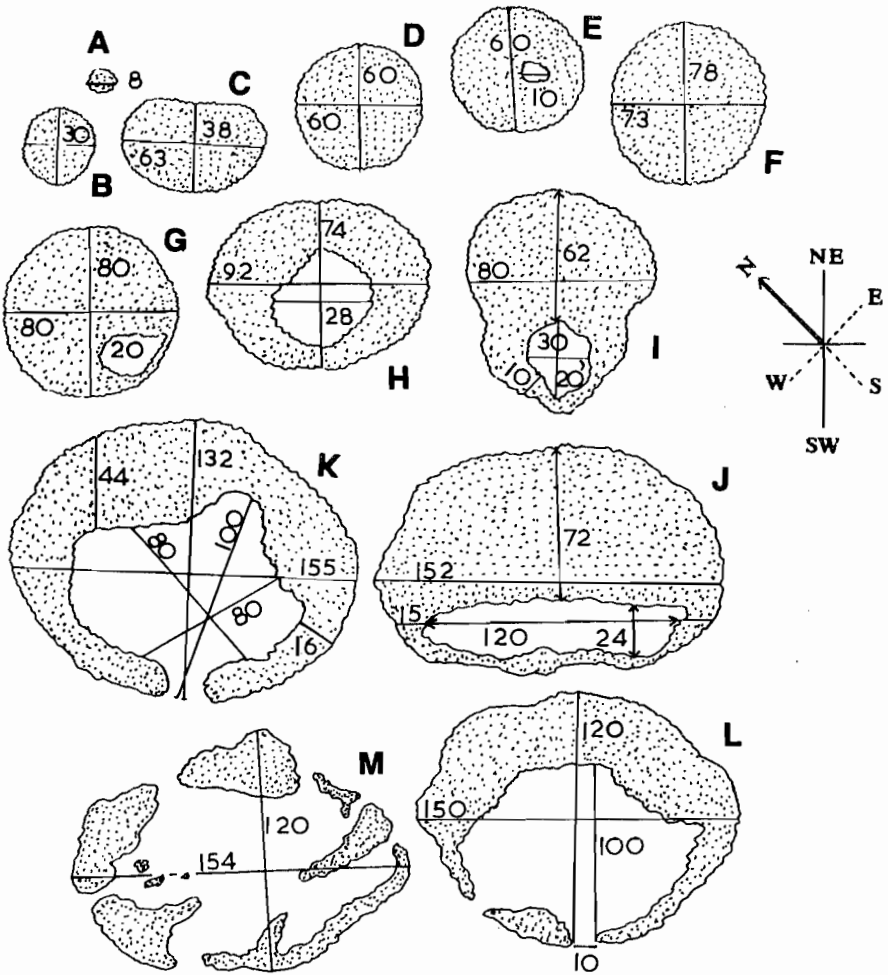
Fig.1. Crown outline diagrams drawn to scale to show phasic development of *Urochondra setulosa* colonized hummocks in a dry salt marsh of Hawkes Bay, Kaachi.

The un-shaded part in the numbers indicate the hummock/hollow size in cms. A. Seedling plus seedling inter-grading to poineer stage, B. building, C-G, Mature; H-J, Degenerate, K-M, Eroding stage. Winds are predominantly from west or south-west. see text for further explanation.

Various phasic stages of the plant were ascertained on the basis of plant size, its radial expansion and morphology, ground characteristics and the deformities in the crown of the plant i.e., the hollowing of the central part of the hummock and distortion in circular growth form of the plant. The outline diagrams of some hummocks were, therefore, drawn on suitable scale and their distribution among six convenient phases viz., seedlings, pioneer, building, mature, degenerate and eroded was determined.

Results and Discussion

Urochondra setulosa, a caespitose perennial with erect or geniculately ascending rigid culms and short rhizome, exhibitd phasic development in dry saline flats of Hawkes Bay, Karachi (Fig. 1 & 2). Many species have been reported to exhibit phasic development but mostly from temperate areas (Kershaw,1960, 1962, 1973, 1975; Barclay-Estrup, 1971). The recorded examples from tropical areas are only a few. Pemadasa (1981) reported such cyclic dymnamics in tropical vegetation of coastal salt marsh of Sri Lanka, composed mainly of *Arthrocnemum indicum.* Drawn to scale crown outline diagrams of some *Urochondra* hummocks of various sizes are presented in Figure 1. The near-circular form of hummocks in initial to mature stages of development are strongly deformed with age and continuous intrinsic and extrinsic environmental changes. Only when hummock reaches a critical size of around 60 cm diameter it begins to undergo degeneration and consequent hollowing in crown which increases in size with time. The accumulation of eolian sand on leeward side of hummock under predominant southwesterly and westerly winds (for most part of the year; March - October) and consequent leeward growth of underground rhizome causes deformation in crown and gradual enlargement of the hollow more towards the seaward (southwestern) margins of the hummocks. This is probably the reason that hollow is consistently seen to be located in the southwestern part of the mature and degenerate types of hummocks and as a result of which the southwestern extremities of the hummocks are eroded earlier. The bare areas thus created may sometimes be colonized by *Cressa cretica, Limonium stocksii, Aeluropus lagopoides or Cyperus* sp. Such a phenomenon of phasic development over a population, cyclic in time though quite incoherent in space as indicated by varying frequency of various developmental phases (Fig. 3).
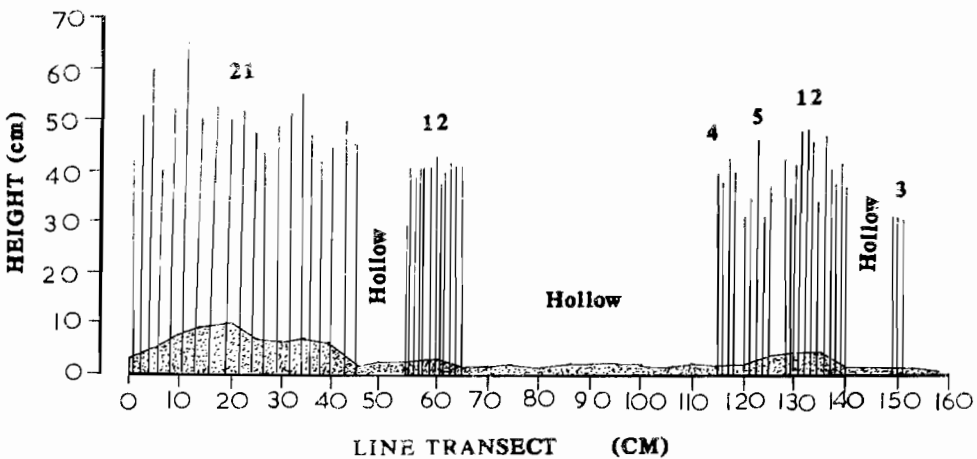

Fig.2. Line transect across a *Urochondra setulosa* hummock in NE-SW direction showing number of tillers touching the line transect (figures above the bars) their height including spike if present and thickness of the soil accumulated above the ground surface (shaded part).
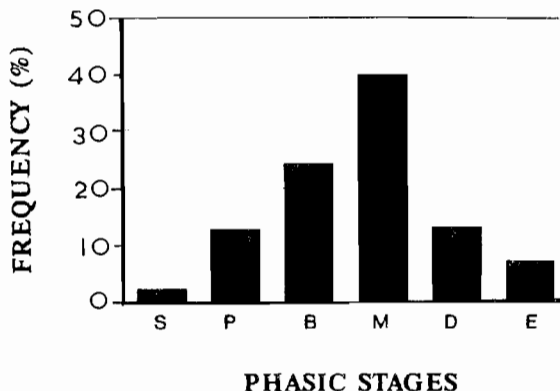
Fig.3. Distribution of individuals of *Urochondra setulosa* into various phasic stages.
S. Seedlings, P. Pioner, B. Building, M. Mature. D. Degenerate. E. Eroding.

The population is largely composed of mature hummocks (40%) followed by building ones (23%). The frequency of seedlings + seedlings intergrading to poineer was more or less equal to the frequency of degenerate and eroded phases. This indicates that the developmental changes are being replicated many times over the entire population as a series of phases occurring at a number of points at any given instant in time. Likely the cyclic changes are unidirectional representing the fluctuations about the mean value (Kershaw, 1973). The population may thus be viewed as fairly stable under the given set of environmental conditions.

The population of *U. setulosa* in coastal dry marsh of Hawkes Bay, Karachi, although exhibited very high density (26000 plants/ha^{-1}) is quite open as the value of cover averaged to 1951 m^2.ha^{-1} only. No plant larger than a meter in crown diameter was encountered in sampling. The population as determined by size class frequency (Fig. 4) based on crown diameter values was not distributed normally (X^2 = 37.624, p < 0.001). The larger part (84.8%) of the population concentrtated in initial classes composed of plants smaller than 50 cm crown diameter. However, seedlings in real sense (measuring less than 5 cm in crown) were extremely low in number (2.5%). In arid regions seedling recruitment is spasmodic coinciding with the rainfall (Bell, 1981). Since the population was studied after around 50 days of 70 mm summer rainfall, the initial class appeared to be composed of the new recruits in this population whose number is considerably lower than that expected through extrapolation of best fit negative power/logarithmic equation as given below:

$Log_e Y$ = 5.50993- 0.95131 $Log_e X$ r = 0.7412 N= 10, t = 4.83   t = 3.12
p < 0.001 p < 0.014   F = 9.75
$Log_e Y$ = 3.80255 - 0.03509 X   r =- 0.9037 N= 10, t = 11.2 t =5.97
p < 0.001 p < 0.001   F = 35.6239

From the data it appears that individuals of *U. setulosa* should have decreasing rate of mortality with age (Hett & Loucks, 1971). The lower number of seedlings than expected suggested some sort of mutually disadvantageous interactions among plants
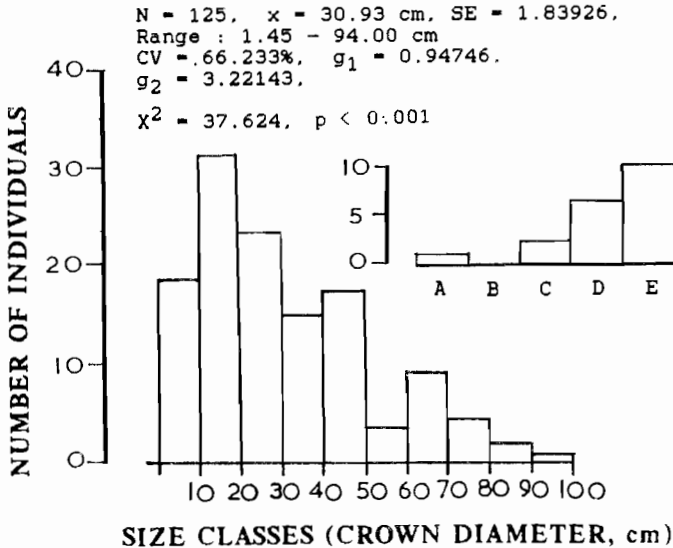
N = 125,   x = 30.93 cm, SE = 1.83926,
Range : 1.45 - 94.00 cm
CV =.66.233%, g_1 = 0.94746,
g_2 = 3.22143,

x^2 = 37.624, p < 0.001

SIZE CLASSES (CROWN DIAMETER, cm)

Fig.4. Size class distribution of individuals of *Urochondra setulosa* in a coastal dry salt marsh near Goth Abdul Rehman. Paradise point, Karachi. The inlet depicts further distribution of individuals belonging to the initial class. Classes in inlet are: A, upto 2 cm, B, 2 to 4: C, 4 to 6: D. 6 to 8 and E.* to 10 cm. The hypothesis that population is normal of mean 30.9228 and St. deviation 20.56351 can be rejected at the 95% confidence level.

causing elimination of smaller individuals from the population. Besides competitive exclusion, some other factors could also be important such as the direct or indirect effects of climate, seed crop size, potential of seedling establishment or load of unfit genotypes etc., (Bell, 1981; Sarukhan, 1976). King & Woodell (1973) suggested that in arid conditions such competitive exclusion of smaller individuals would result into spatially regular pattern. The spatial pattern of population, in our case, as determined through the test of fitness of Poisson series (Table 1) and the magnitude of variance/ mean quotient (2.58), was found to be contagious which may probably be best attributed to larger number of relatively denser patches of growth due to young recruits in the population after summer rains. Anderson (1971a) summarized some population trends in a few dry land environments. He noted that young individuals in a population tended to form spatial contagions that disappeared with age due to elimination of individuals from high density patches. Thus originally patterned population mosaic eventually became randomly scattered. Moreover, in population where mortality rate should decrease with age and competition becoming intense among mature plants that saturate the potential root zone, elimination of smaller individuals should be intensified. Yeaton (1978) found competitive elimination of smaller individuals in uneven-aged *Pinus strobus* population which exhibited random spatial pattern. It was suggested that regular patterns are rare as most population exist over time sufficient to reproduce offsprings occupying space among parents and simultaneously older plants are removed from the area due to senescence, biotic factors and the random events. Even in arid regions

Table 1. Test for goodness of fit of Poissonian series
$$(\epsilon^{-m}, m.e^{-m}, m^2.e^{-m}/2!, \ m^3.e^{-m}/3!....).$$

Number per Quadrat	Number of Observed	Quadrats Expected	Difference	$X^2 = (O-E)^2/E$
0	18	5.5705	12.4295	27.73393
1	13	14.4834	-1.4834	0.15192
2	16	18.8283	-2.8283	0.42486
3	5	16.3179	-11.3179	7.84995
4	8	10.6066	-2.6066	0.64059
5	5	5.5155	-0.5155	0.04817
>5	10	3.6778	-6.3322	10.86771
Total	75	75		$X^2 = 47.71713*$

$N = 75$; $\overline{x} = m = 2.60$; $e = 2.7182818$, $e^{-m} = 0.0742735$; variance $= 6.702703$; variance: mean ratio, $v/m = 2.57796$ (t = 9.5984; p <0.001). St. error of v/m ratio = 0.163989.

*, df= 5; p < 0.001.

where competition for water is keen, contagious or random patterns are more common than regular (Anderson, 1971b; Greig-Smith & Chadwick, 1965; Khan *et al.*, 1993). Khan & Shaukat (1996) have reported the distribution of *Avicennia marina* to be random in the mangrove habitat of Rehri, Karachi. It may be emphasized here that the development of a pattern in plant populations may be the result of the variation in population dynamics affecting the pattern over time (Bell, 1981). Moreover, the interactions and adjustments among species in three dimensional space are reported to give some interesting spatial patterns in natural mixed forests (Ishizuka, 1984).

U. setulosa, a sexually reproducing grass, retains terminal stout spikes for considerable time so that both current as well as last year's remnant spikes may often be seen together on the same plant that are easily distinguished. The number of spikes/plant although is a crude reproductive parameter, was recorded in the present study. In this respect the population comprised of 4 types of plants - i) plants with no spikes, ii) plants with current spikes only, iii) plants with last year's spikes only and iv) plants with both current as well as last year's remnant spikes. Around 58% of the plants belonged to the last category and around 23% to the first category generally represented by smaller individuals of average crown diameter of $11.7 + 0.82$ cm (range : 4.5 - 20 cm, CV= 38.5%) (Fig. 5). The number of spikes/plant for the current year's growth ranged from 0-74 and the last year's remnant spikes/plant ranged from 0 - 42, averaging $6.93 + 0.98$ and $7.54 + 0.84$, respectively. The distribution of spikes amongst the plant was in all the cases positively skewed with larger proportion of plants with no spike or only a few spikes (Fig.6). This corresponded well with the trend of plant size distribution as evident from the following relationship:
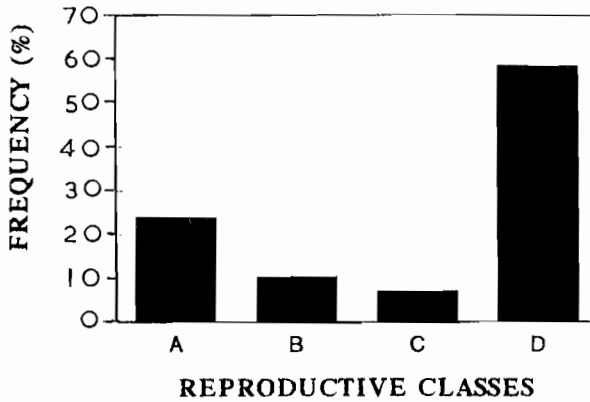
REPRODUCTIVE CLASSES

Fig.5. Distribution of individuals of *Urochondra setulosa* into various reproductive classes.

A.   Plants with no spikes.   C.   Plants with last year remnant spikes only.

B.   Plants with current year spikes only.   D.   Plants with both current and last year remnant spikes.

Number of current spikes/plant =

$$-4.065 + 35.558 \text{ Crown Diam (m)} + 8.22$$
$$t = 3.06, t = 9.91$$
$$p < 0.002, p < 0.001$$
$$r = 0.6664, F = 98.24, df = 123$$

Last Year's Remnant spikes/plant

$$-2.996 + 34.093 \text{ Crown Diam (m)} + 6.25$$
$$t = 2.96, t = 12.50$$
$$p < 0.003, p < 0.0001$$
$$r = 0.7481, F = 156.30, df = 123$$

Total Number of Spikes/plant =

$$-7.289 + 70.197 \text{ Crown Diam (m)} + 11.01$$
$$t = 4.09, t = 14.60$$
$$p < 0.0001, p < 0.0001$$
$$r = 0.7964, F = 213.23, df = 123$$

Most of the reference plants were generally spike bearing and the first nearest neighbours to them were generally non-spike bearing in most of the cases (Fig. 7). The proportion of spike bearing plants as well as the number of spikes/plant gradually increased in second, third and fourth nearest neighbours (Table 2, Fig. 7). To this effect two hypotheses may be propounded- a) that the competition between the reference and the first nearest neighbours is keen enough to reduce growth as well as the reproductive output of the first neighbour, b) that the plants of first nearest neighbour category are largely smaller in size and have not as yet reached the reproductive age. To examine these hypotheses techniques of simple linear correlation and multivariate canonical correlation analysis were employed. Linear regression and correlation analy-
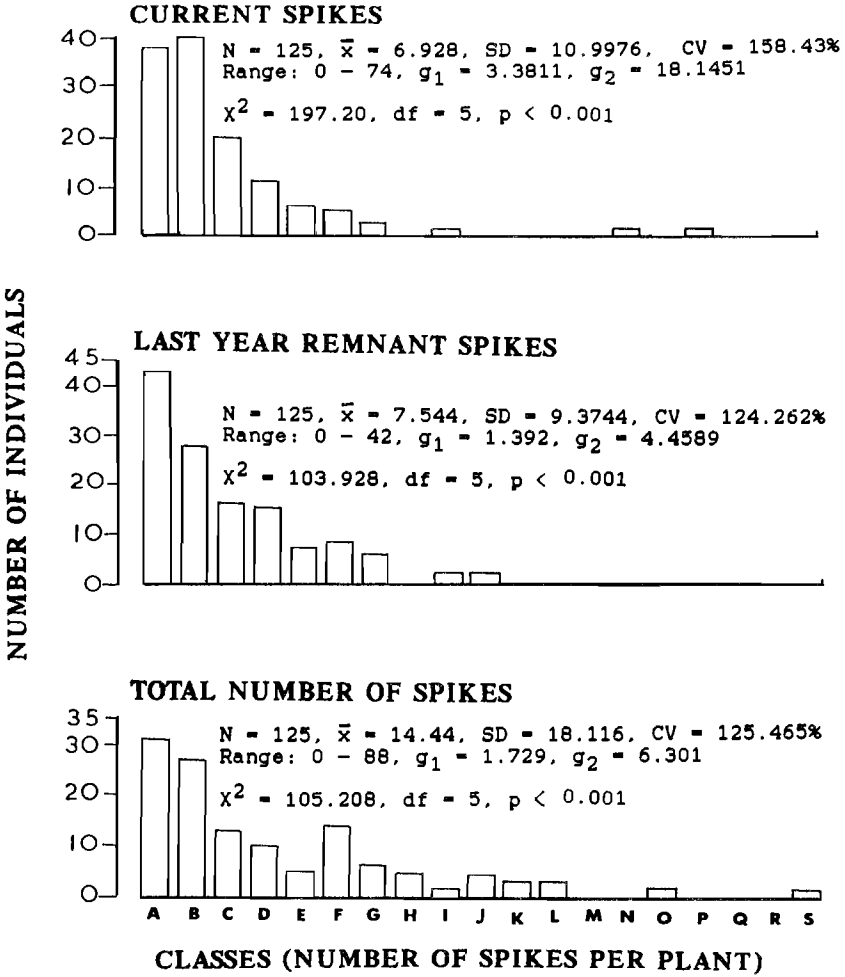
CURRENT SPIKES

N = 125, $\bar{x}$ = 6.928, SD = 10.9976, CV = 158.43%
Range: 0 - 74, g_1 = 3.3811, g_2 = 18.1451

x^2 = 197.20, df = 5, p < 0.001

LAST YEAR REMNANT SPIKES

N = 125, $\bar{x}$ = 7.544, SD = 9.3744, CV = 124.262%
Range: 0 - 42, g_1 = 1.392, g_2 = 4.4589

x^2 = 103.928, df = 5, p < 0.001

TOTAL NUMBER OF SPIKES

N = 125, $\bar{x}$ = 14.44, SD = 18.116, CV = 125.465%
Range: 0 - 88, g_1 = 1.729, g_2 = 6.301

x^2 = 105.208, df = 5, p < 0.001

A B C D E F G H I J K L M N O P Q R S

CLASSES (NUMBER OF SPIKES PER PLANT)

NUMBER OF INDIVIDUALS

Fig.6. Distribution of *Urochondra setulosa* individuals amongst the fecundity classes: A. Plants with no spikes; B,1-5 spikes per plant; C.5-10, D.10-15.S.85-90 spikes per plant. The hypothesis that the populations are normal can be rejected at the 95% confidence level.

Table 2. Fecundity per plant in terms of number of inflorescences (spikes) in *Urochondra setulosa*.

| Fecundity | Reference Plant | I | ------Nearest Neighbour----- | | | |
			II	III	IV	$\bar{x}$
Current	*7.68	0.84	3.36	7.56	15.3	26.93
	±1.17	±0.30	±0.96	±1.53	±3.87	±0.98
	**75.99	180.81	142.96	102.68	126.43	158.43
Last Year	11.48	1.92	3.52	7.48	13.32	7.54
(Remnant)	+2.36	+0.99	+0.95	+1.38	+2.31	+0.84
	97.39	259.50	135.28	92.15	86.68	124.26
Total	18.80	2.76	6.88	15.44	28.64	14.44
	±3.05	±1.25	±1.75	±2.63	±5.51	±1.62
	81.16	226.82	127.29	85.11	97.60	125.47

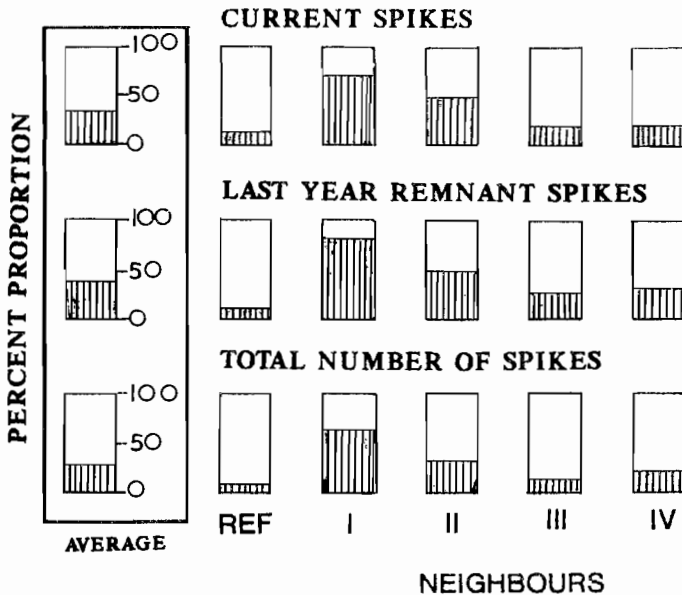*, mean + SE; **, CV = Coefficient of variation (%); N = 25, in each case.

Fig.7. Percentage proportion of reproductive (unshaded) and non-reproductive plants (shaded) amongst the randomly selected reference plants and their first four nearest neighbours in an old population of *Urochondra setulosa*. The inlet represents the over all averages.

Table 3. Linear correlation and regression analyses.

Parameters	r	a	b	F
d_1 (x)/Δ_1 (y)	0.6789***	0.1685	0.8215	19.66
d_2 (x)/Δ_2 (y)	0.5133**	0.2369	0.5168	8.23
d_3 (x)/Δ_3 (y)	0.4880*	0.2634	0.6017	7.19
d_4 (x)/Δ_4 (y)	0.2234ns	-	-	-
d_1 (x)/ Cf_1 (y)	0.4439*	2.2843	14.2093	5.65
d_2 (x)/ Cf_2 (y)	0.4946*	-0.1783	17.0638	7.45
d_3 (x)/ Cf_3 (y)	0.4490*	-1.0918	20.4386	5.81
d_4 (x)/ Cf_4 (y)	0.3341ns	-	-	-
d_1 (x)/ Lf_1 (y)	0.1706ns	-	-	-
d_2 (x)/ Lf_2 (y)	0.2694ns	-	-	-
d_3 (x)/ Lf_3 (y)	0.2759ns	-	-	-
d_4 (x)/ Lf_4 (y)	0.0230ns	-	-	-
d_1 (x)/ Tf_1 (y)	0.2980ns	-	-	-
d_2 (x)/ Tf_2 (y)	0.4025*	4.3706	32.7000	4.44
d_3 (x)/ Tf_3 (y)	0.4280*	2.7071	39.7539	5.16
d_4 (x)/ Tf_4 (y)	0.2282ns	-	-	-
Ad_4 (x)/Δ_5 (y)	0.6965***	0.0426	0.1580	21.66
Δ_5/Ad_4/ CVc (y)	-0.0299ns	-	-	-
Asmp (x)/ CVc (y)	-0.5098**	109.774	-781.104	8.07
Algp (x)/ CVc (y)	0.4817*	78.525	70.773	6.95
Ad' (x)/Δ_5 (y)	0.7903**	0.0237	0.1069	38.26
Δ_5/Ad'(x)/CVc (y)	0.1624ns	-	-	-
Ad_4 (x)/Cf_5 (y)	0.6289***	2.5063	10.006	15.04
Cf_5/Ad_4 (x)/ CVcf (y)	0.4998*	79.9397	3.3883	7.66
Cfsmp (x)/ CVcf (y)	-0.0510ns	-	-	-
Cflgp (x)/ CVcf (y)	0.3627!	99.9764	0.8510	3.49
Cf_5/Ad'(x)/ CVcf (y)	0.4796*	76.4886	5.6081	6.80
Ad' (x)/Cf_5 (y)	0.7169***	1.1121	6.8176	24.32

Table 3. (Cont'd)

Parameters	r	a	b	F
Ad_4 (x)/Lf_5 (y)	0.7474***	0.6286	11.5504	29.10
Lf_5/Ad_4 (x)/ CVlf (y)	0.1306ns	-	-	-
Lfsmp (x)/ CVlf (y)	-0.4051*	126.1243	-12.9739	4.52
Lflgp (x)/ CVlf (y)	-0.1995ns	-	-	-
Lf_5/Ad' (x)/ CVlf (y)	0.0834 ns	-	-	-
Ad' (x)/Lf_5 (y)	0.7400***	2.9190	6.9564	27.86
Ad_4 (x)/ Tf_5 (y)	0.8017***	3.4336	21.3767	41.35
Tf_5/Ad_4 (x)/ CVtf (y)	0.4281·	70.7809	1.6290	5.16
Tfsmp (x)/ CVtf (y)	-0.1198ns	-	-	-
Tflgp (x)/ CVtf (y)	0.1359ns	-	-	-
Tf_5/Ad'(x)/ CVtf (y)	0.4112*	77.2050	2.0679	4.68
Ad' (x)/ Tf_5 (y)	0.8496***	5.5540	13.5158	59.68

di,i=1,2,3,4; Distances of the four nearest neighbours from the reference plant, in m. Δ i, i=1,2,3,4; Combined cover values of the reference plant and the ith nearest neighbour, in sq.m.Δ_5; Sum of cover values of the reference plant and all the four nearest neighbours. Cf_i, i=1,2,3,4; Combined current spikes of the reference plant and the ith nearest neighbour. Lf_i, i=1,2,3,4; Combined number of last year spikes of the reference plant and the ith nearest neighbour. Tf_i, i=1,2,3,4; Combined total number of spikes of the reference plant and the ith nearest neighbour. Ad_4; Area of the circle whose radius is equal to the distance, d_4. Δ_5/Ad_4; Ratio of summed plant area in the circle to the area of the circle whose radius is equal to distance , d_4. CVc, Coefficient of variation (%) in cover values of the reference plant and its neighbours. Asmp, Cover area (sq.m) of the smallest plant in the circle. Algp, Cover area (sq.m) of the largest plant in the circle. Ad'; Area of the circle whose radius is equal to the distance, d_3 +r_3 or d_4 + r_4, which one is larger, where r_3 and r_4 are the crown radii of third and fourth nearest neighbour, respectively. CVcf, CVlf and CVtf; Coefficients of variation (%) in current, last year and total number of spikes of reference and the nearest neighbours, respectively. Cf_5, Lf_5 andTf_5 are the sum of current, last year and total number of spikes of reference plant and the nearest neighbours in the circle, respectively. Cfsmp, Lfsmp and Tfsmp are the current, last year and total number of spikes of the smallest plant in the circle, respectively. Cflgp, Lflgp and Tflgp are the current, last year and total number of spikes of the largest plant in the circle, respectively.

***, p < 0.001;   **, p < 0.01;   *, p < 0.10;   ns, non-significant.

sis between combined cover (Δ_i) and interplant distance (di) indicated positive correlations for only first three nearest neighbours (Table   3). The combined values of current spikes/plant also gave similar relationship with di. The combined values of last year remnant spikes/plant and di exhibited no significant relationship though combined values of total number of spikes/plant and di yielded significant correlation with second and third neighbours only. The results of this technique indicate that smaller the distance between the plants, larger is the potential of intraspecific competition (Smith, 1979). This is also indicated by significant positive correlation between sum of cover values of reference plant and all the four neighbours (Δ_5) and the area of the circle (Ad_4) whose radius equalled to the distance of the fourth neighbour (d_4). Smith (1979) also reported similar relationship in almost pure population of *Croton menthodarus*. Although no correlation between the coefficient of variation in cover values (CV_c) and cover percentage (Δ_5/Ad_4) was seen, the area of the smallest plant of the group (Åsmp) related inversely with CV_c (p < 0.01). CV_c, however, related positively with the area of the largest plant (Algp) (p < 0.05). The negative relationship between Asmp and CV_c and positive relationship between Algp and CV_c in the present case may probably be attributed to the fact that since larger part of the populaion (84.8%) concentrated in initial size classes composed of plants smaller than 50 cm crown diameter (40% of the total plants were lesser than 20 cm in crown diameter), inclusion of smaller individual in the group lowers the variation whereas inclusion of larger plant (possibly >50 cm in diameter) increases the variation. Also, under non-random spatial distribution, such a relationship is more likely.

The significant positive correlation of parameters based on number of spikes/plant such as Cf_5, Lf_5 and Tf_5 with the area of the circle of radius d_4 further indicated competition amongst the reference and its neighbours to a degree that is enough to significantly reduce the reproductive output of the plants. It may, however, be noted that the measure Δ_5/Ad_4 has the tendency of overestimating the total cover proportion because considerable part of the crown of fourth nearest neighbour and sometimes that of the third nearest neighbour as well is excluded from the circle whose radius is equal to the distance of the fourth neighbour, d_4. The total cover proportion, therefore, when expressed in relation to the area of the circle with radius equal to max ($d_4 + r_4$, $d_3 + r_3$), the area of the circle (Ad') yielded highly significant correlation with Δ_5 (r=0.7903, p < 0.001, r^2 = 0.6246) with an overall improvement of 13.95% in accounting for the variation as compared to that in case of Δ_5 vs Ad_4 (r=o.6965, p < 0.001, r^2 = 0.4851). Such an improvement to some extent was also observed in case of correlations yielded for Tf_5 against Ad' and Cf_5 against Ad'. which is similor to our previous reports (Khan *et al.*, 1993).

Whatever synthetic variables chosen for the detection of competition using simple linear correlations, the technique suffers from an inherent drawback of loss of information on intraset and interset covariance structure of the matrices involved. Alternatively, canonical correlation analysis offers a multivariate approach which more effectively discloses the intensity of intraspecific competition (Khan & Shaukat, 1990; 1996; Khan *et. al.*, 1993).   The   first and second canonical correlation (R_1 and R_2) were found to be 0.7741 and 0.6358   (Table 4). These canonical correlation explained 48.74% and 32.88% (cummulatively around 82%) variability in the combined crown

Table 4. Results of canonical correlation analysis. The data of distance and crown diameter matrices transformed as square root + 0.5.

Canonical Variate I * 48.738 % *(cummulative : 48.738%)	$R^2 = 0.5992$	$R = 0.7741$
Canonical Variate II * 32.878 % *(cummulative : 81.616%)	$R^2 = 0.4042$	$R = 0.6358$
Canonical Variate III * 18.04 % *(cummulative : 99.658%)	$R^2 = 0.2218$	$R = 0.4709$
Canonical Variate IV * 0.9822 *(cummulative : 100.00%)	$R^2 = 0.0121$	$R = 0.1099$

Wilks lambda (\ ) = 0.2570; p = 4 , q = 4.
$X^2 = 33.053$, df = 16, p < 0.05.
*, the magnitude of variation accounted for.

diameter values by the nearest neighbour distances. The degree of relationship between the two sets is expressed by Wilks lambda ($\lambda=0.2570$, $X^2 = 33.053$, p < 0.05). Other canonical correlations (R_3 and R_4) were found to be non-significant. The high order of first and second canonical correlations indicated strong competitive effects among the individuals of *U. setulosa*. Both the intraset and interset correlations of distance and combined crown diameters against second canonical variate U_2 and V_2 are low suggesting negligible competitive effects of the reference plant extending to the fourth nearest neighbour (Table 5). In essence, CANCOR analysis indicates

Table 5. Intraset and intersat correlations with the first two canonical variates.

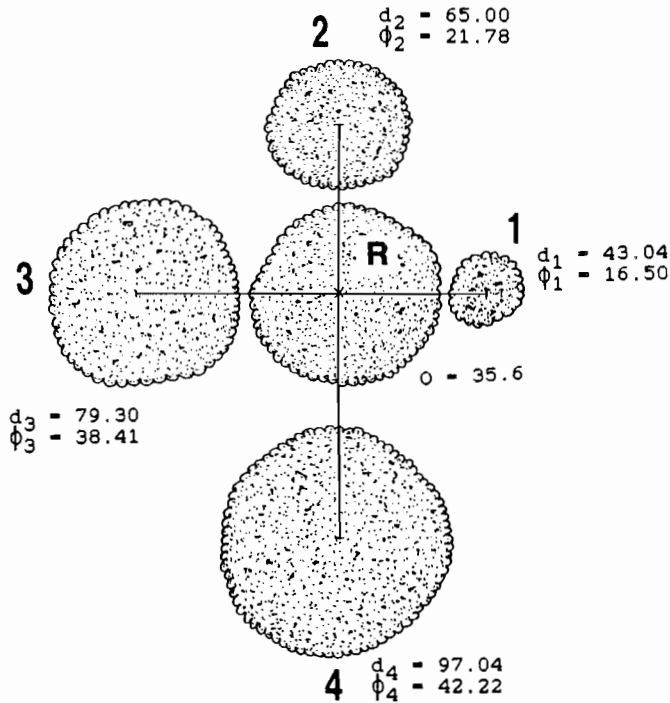| Variable	Intraset		Interset	
	U_1	U_2	V_1	V_2
d_1	0.4925	0.8367	0.3811	0.5319
d_2	0.7665	0.2497	0.5930	0.1589
d_3	0.8147	0.2072	0.6304	0.1318
d_4	0.9912	0.0730	0.7669	0.0644
	V_1	V_2	U_1	U_2
C_1	0.3763	0.8806	0.2911	0.5599
C_2	0.8222	0.3189	0.6361	0.2028
C_3	0.5243	0.3416	0.4056	0.2172
C_4	0.9756	0.1928	0.7549	0.1226

Fig.8. The relationship of mean crown diameters and distances of the first four nearest neighbours with respect to the reference plant in *Urochondra setulosa* population. d, Diameter (cm), Crown diameter (cm). N = 25.

that competition is most intense between the reference plant and the second and third nearest neighbour and the first nearest neighbour seems to exhibit substantially lower competitive interaction. Figure 8 diagramatically represents the situation of crown covers and the distances of the first nearest neighbours with respect to the reference plant. Since *U. setulosa* exhibit phasic development, the competition is expected to be the most severe in the mature and mature to degenerating phases of the cycle as the shoot and the lateral roots of neighbours come gradually closer. The first nearest neighbour although in close proximity of the reference plant seems to exert no substantial competitive effects on reference plant due to their low crown diameter (16.5 cm) and frequent absence of spikes suggesting that their morphology is more of an age-repeated phenomenon rather than the outcome of competitive interaction. The contradiction between bivariate and multivariate approach regarding the competitive effect of first nearest neighbour is due to the fact that the later technique takes into account the interaction among the first four nearest neighbours in addition to the interaction with the reference plant, whereas the bivariate technique ignores the intraction amongst the four neighbours. Thus the results of CANCOR are more reliable than those of the bivariate analysis.

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