SEASONAL VARIATION IN STRUCTURE, COMPOSITION, PHYTOMASS, AND NET PRIMARY PRODUCTIVITY IN A *LASIURUS SCINDICUS* HENR., AND *CENCHRUS SETIGERUS* VAHL., DOMINATED DRY SANDY DESERT SITE OF KARACHI

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Abstract

Variation in composition, structure, plant biomass and net primary productivity was analyzed in a grass-dominated sandy desert community of *Lasiurus scindicus* Henr., and *Cenchrus setigerus* Vahl., situated within the campus of University of Karachi. Pakistan. Life form indicated a thero-hemi-cryptophytic/geophytic flora. Phytosociological parameters of vegetation were studied at monthly interval from June 1990 to June 1991. The density as well as live biomass-based diversity of the community was generally low and dominance high. The live-biomass-based diversity varied seasonally and was the function of precipitation and soil moisture. On the advent of rain in August with the increase in diversity, the relative abundance pattern tended to approach log-normal distribution which was otherwise geometric. The density-based diversity declined after August rains largely due to very high density of *Tragus roxburghii* (1327 plants.m^{-2}), a small graminoid, which created the condition of very high dominance concentration.

The above ground live plant biomass (LB), was maximum (311g.m^{-2}) in September which was positively related with rainfall and soil moisture content. The effects of rainfall were better represented in the month subsequent to its occurrence and remained noticeable for not more than 50-60 days, when major proportion of LB entered the dead compartment in October. Standing dead (SD) biomass was maximum in November, litter was minimum in August (72.5 g.m^{-2}) and maximum in October (249 g.m^{-2}). Below ground biomass was larger than the above ground biomass. Above ground net primary productivity (ANP) as evaluated by various methods varied from 368 to 587 g.m^{-2}.year^{-1} (x = 448.8 $\pm$ 50.88 g.m^{-2}.year^{-1}; CV = 22.67%). ANP was related positively with biomass-based diversity and negatively with dominance. Below ground Net productivity (BNP) was higher than ANP and amounted to 834.4 g.m^{-2}.year^{-1}. The system transfer functions also indicated that productivity was more below ground-directed. Annual efficiency of energy capture by the primary producers was estimated to be 0.47% on the basis of half of total solar radiation. Annual energy flow diagram through primary producer compartments is constructed.

Introduction

Herbaceous vegetation emerging during monsoon season in arid regions is not only of ecological interest but also possesses considerable potential and utility as pasture. The estimation of productivity and determination of structural characteristics of such vegetation are essential preliminary to the assessment of its ecological efficiency, functional characteristics and economic potential. A great deal of data on the functional aspects of ecosystems has accumulated globally during 1960s and early 1970s, under International Biological Program (IBP) (Lieth & Whittaker, 1975). However, no such data is available from most Asian countries including Pakistan. This led us to undertake investigations on seasonal variation in structure, composition, phytomass and net primary production in a dry sandy site of Karachi dominated by *Lasiurus scindicus* Henr., and *Cenchrus setigerus* Vahl.

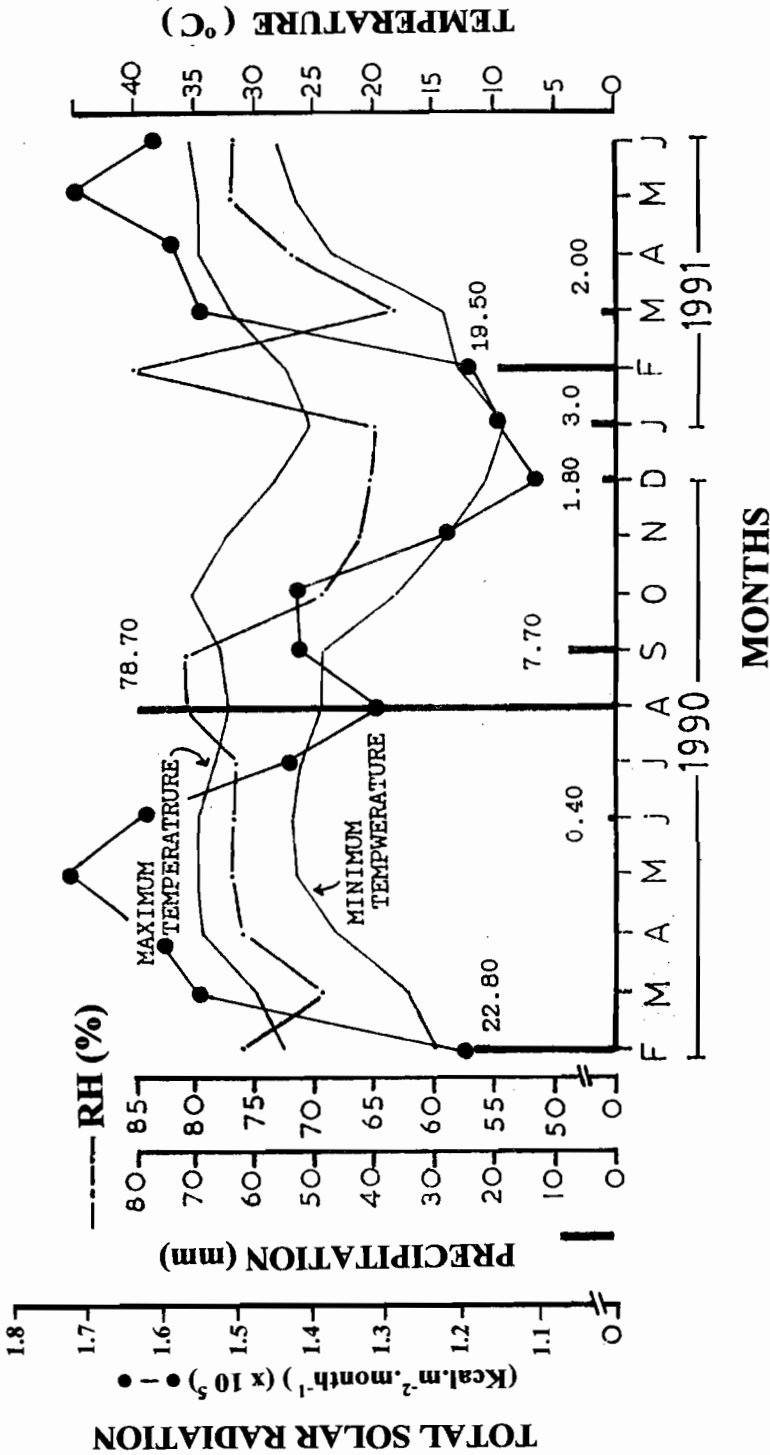*Department of Botany, University of Karachi, Pakistan.

Fig. 1. Climatic pattern of Karachi during study period. Relative humidity (RH, %) at 8:00 AM. Solar radiation data adopted and calculated from Ahmad *et al.*, (1991).
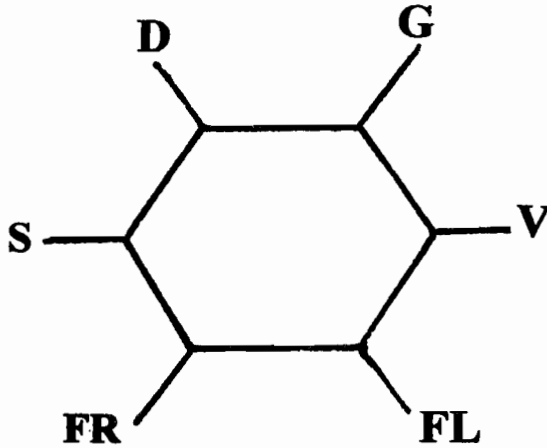
Fig. 2. Phenological stages diagrammatically represented. G, Germination of seeds (seedling 0-2 cm in height in monocots and upto first leaf stage in dicots) or active sprouting of buds in rhizome or root-stock in perennial species; V, Vegetative growth phase; FL, Flowering phase; FR, Fruiting phase; S, Mature seeds; D, Death of plant in annuals and that of aerial parts in perennials, completely or substantially as some perennial grasses remain partially alive above ground during drought.

DESCRIPTION OF THE AREA

The climate of Karachi is of **BWh** type and bioclimate as determined by Holdridge's system falls in the category of **tropical bush formation** (Qadir *et al.,* 1966). The rainfall is irregular and averages below 200 mm; mostly received in summer. Annual potential evapo-transpiration is c.1750 mm (Zubenok, 1977). Minchen (1907) recognized summer (May-October) and winter (November-April), two climatic extremes. The precipitation during the study period has been far below the average. It was 86.8 mm in summer (1990) and 26.3 mm in winter (early 1991) (Fig. 1). The total solar radiation, as calculated and adapted from Ahmad *et al.,* (1991), was maximum in the summer months of May and June and substantially lower in winter months (Fig. 1). The diffuse radiation remained 20 - 30% of the global radiation.

The study site, about 2 ha in size, situated in Karachi University campus was a dry plain of loose sandy (sand: 90%, silt: 9.30%), non-saline (ECe: 0.60 dS.m^{-1}), basic (pH: 8.5) and relatively non-calcarious ($CaCO_3$:13.39%; including alkaline earth carbonates) and with low organic matter (0.15%) and water retaining capacity. Fencing to prevent disturbances as far as possible protected the site.

Materials and Methods

Floristics, life form and phenology

The site was regularly visited for vegetation sampling and plant collection. The species encountered were assigned to various life forms (Raunkiaer, 1934). The phenological data were recorded each month from June 1990 to June 1991. Six phenological stages were noted (Fig. 2).

Field methods:
(i) Abundance: During the last week of each month 30 quadrats of 1 m^2 were laid at random in the field to sample the vegetation for abundance. Most of the grasses were bunch forming and each bunch was regarded as an individual plant. Any portion of sod forming grasses possessing an independent shoot and root was considered as an individual (Singh & Yadava, 1974).

(ii) **Plant** biomass, **standing dead** vegetation and litter: Above ground biomass was evaluated by harvest method dividing the field into three more or less equal areas. On each sampling date five 1m^2 quadrats were randomly laid in each area and divided into 25 x 25 cm subquadrats. From each quadrat two subquadrats were randomly selected and harvested. Thus in all 30 quadrats were sampled on each sampling date. All vegetation was harvested at the ground level (Green, 1959). The litter was gathered after the plot had been cleared. The samples were washed through floatation, dried and weighed. The harvest for each species was kept in separate paper bag, quadratwise. The species were further separated into live and dead parts in laboratory. All samples were dried at 80°C and weighed.

For the estimation of below ground plant material, 25 x 25 x 30 cm monoliths, one from each quadrat were dug out from the field on each sampling date. The soil samples were soaked in water and biomass was screened using 32-mesh-sieve under a jet of water, than was dried at 80°C and weighed.

Vegetation analysis:
(i) **Preliminary** Treatment of data: The importance value index (IVI) for each species was computed by direct summation of relative density and relative frequency following Curtis & McIntosh (1951).

(ii) Quantitative life form and leaf size spectra: Life form and leaf size spectra for each month were prepared on the basis of number of species, their IVI and the live biomass. Leaf area was determined in accordance with Cain & Castro (1959) and each species was assigned to leaf size and life form classes according to Fuller & Bakke (1918) and Raunkiaer (1934). Raunkiaer's system was adopted owing to its simplicity and ease of application. Also, the bulk of the data available for comparison is in Raunkiaerian form. Moreover, the modified system of Ellenberg & Mueller-Dombois (1967) appears particularly suitable for regions of rich flora (Qadir & Shetvy, 1986). The area under study is rather poor in flora.

(iii) Diversity analysis: General diversity was ascertained by information theory function ($\bar{H} = -\Sigma\, p_i.\log p_i$) where p_i is the proportion of density or standing live biomass belonging to the ith species (Margalef, 1957). The equitability was measured by $e = \bar{H}/\bar{H}_{max}$ where $\bar{H}_{max} = \log S$ (Pielou, 1969). The species richness was calculated as $d = S/\sqrt{N}$ (Menhinich, 1964) and $d' = S-1/\log N$ (Margalef, 1957), where S is the number of species in the sample and N is the total density or total standing live biomass of the sample. The diversity was also measured by Mc Intosh's index of diversity (Mc Intosh, 1967).

$$M_c = 1 - \sqrt{\Sigma \, ni^2/N}$$

where n_i is the density or live biomass of ith species.   Dominance was estimated by Simpson's (1949) index (c) and McNaughton (1968) index of community dominance as:

$$c = \Sigma \, pi^2 \text{ and } CDI = Y1 + Y2 /Y * 100$$

where Y1 is IVI or biomass of the leading dominant, Y2 , the IVI or biomass of subordinate species and Y, the total IVI or live biomass of the sample. The dominance-diversity curves (Whittaker, 1965), based on IVI and live biomass were plotted.

Results and Discussion

(i) Floristic composition of the vegetation: Thirty-two species were encountered during sampling period (Table 1) besides a sporadic *Dipcadi erythaceum* whose single individual was once recorded. There were 7 grasses, 8 legumes and 18 other species. There were initio only 9 species in the month of June (1990) which increased to 28 after summer rains. However, gradually the species loss occurred in winter and only 7 live species were recorded in December, and again minimum (5 species) in June, 1991. There were 5 phenerophytes, 7 chamaephytes, 5 geophytes, 1 hemicryptophyte and 14 therophytes. The leaf size spectrum was nanophyllous. Larger number of therophytes appears to be the result of aridity and grazing and browsing in the area in the past. Grass communities are generally dominated by hemicryptophytes (Braun-Blanquet, 1932). Barucha & Dave (1944), however found a grassland association in Bombay area dominated by *Themeda triandra* and *Pseudenthistria hetroclite* to be therophytic. Singh & Yadava (1974) have also reported more therophytes in Varanasi grassland of India.

(ii) Temporal Variation **among** dominants: On the basis of IVI, *Cenchrus setigerus* was leading dominant in initial months. After summer rains in August *Tragus roxburghii* germinated in large number and became the leading dominant. As this species began to die in September, *Blepharis sindica* attained the status of leading dominant. In November and December when both *Tragus* and *Blepharis* died, *Dactyloctenium scindicum* attained the dominance. From December onwards till February, *Cyperus atkinsonii* dominated the site and from March onwards to June, *Tephrosia subtriflora* dominated owing to the death of *C. atkinsonii* (Table 2). On live biomass basis, the community was initially dominated by *Aerva javanica*. Later on, *Lasiurus scindicus* became the leading dominant. *C. setigerus* was the second dominant from August to October and then again in February and March. It died in April.

(iii) **Phenology:** Just after few showers of rains in August, the seedlings of annuals and perennials started emerging from the ground. In case of perennials like *A. javanica, S. pakistanica* and grasses like *C. setigerus, L. scindicus, D, scindicum* etc., fresh sprouting started from above ground stem or the underground rhizome. The field became green and the bare areas in the community filled with new plants. Several annual species such as *Digera muricata, Indigofera cordifolia, I. linifolia, Phyllanthus niruri, T. roxburghii* etc., completed their life cycle from August to September (-October). *Launaea nudicaulis* died in September without flowering (Fig.3).

Table 1. Life-form, leaf-size characteristics, mean live biomass (g/sq.m) and occurrence of species encountered during year long sampling of *Lasiurus scindicus* community.

Species	Lf[*]	Ls[***]	Mean live biomass (g/m^2)	Occurrence (No. of months out of 13)
Aerua javanica (Burm.f.) Juss.	PH (nano)	MI	17.53 ± 3.52	9
Blepharis sindica T. And.	TH	MI	8.80 ± 6.42	3
Boerhaavia verticillata Poir	PH	MI	0.67	1
Senna holosericea Fresn.[***]	CH	NN	2.91 ± 2.10	2
Cenchrus pennisetiformis				
Hochst., & Steud ex. Steud.	TH	MI	0.24	1
Cenchrus setigerus Vahl	GE	MI	18.32 ± 9.52	10
Convolvulus scindicus Stocks	CH	NN	0.02	1
Corchorus tridens L.	TH	NN	0.01	1
Cymbopogon jwarancusa (Jones) Schult.	GE	MI	21.47	1
Cyperus atkinsonii C.B.C.	GE	NN	2.50 ± 1.18	10
Cyperus bulbosus Vahl	GE	MI	1.01	1
Dactyloctenium scindicum Boiss.	HE	NN	5.05 ± 1.31	13
Digera muricata (L.) Mart.	TH	MI	0.06	1
Euphorbia dracunculoides Lam.	TH	NN	1.01	1
Fagonia indica Burm.f.	CH	LP	0.86 ± 0.23	2
Indigofera cordifolia[***] Heyne ex Roth	TH	NN	1.54 ± 0.10	2
Indigofera linifolia[***] (Linn.f.) Retz.	TH	NN	2.08 ± 0.96	3
Indigofera oblongifolia[***] Forssk.	PH (nano)	NN	2.01	1
Lasiunus scindicus Henr.	GE	MI	21.67 ± 8.55	13
Leptothrium senegalensis				
(Kunth) W.D. Clayton	TH	NN	2.76 ± 1.82	5
Mollugo cerviana L. Seringe	TH	LP	0.025 ± 0.015	2
Oligochaeta ramosa (Roxb.) Wagenitz.	CH	MI	0.49	1
Polygala abyssinica Fresn.	CH	NN	0.73 ± 0.22	9
Phyllanthus niruri L.	TH	LP	0.01	1
Portulaca sp.	TH	LP	0.20 ± 0.12	7
Prosopis juliflora[***] (Swartz.) DC.	PH	LP	0.07	1
Rhynchosia schimperii[***] Hochst ex Boiss.	CH	NN	11.77 ± 6.06	2
Sida pakistanica S. Abedin	CH	NN	6.70 ± 1.24	12
Tephrosia strigosa[***]				
(Delz.) Sant. & Maheshw.	TH	NN	6.03 ± 3.09	3
Tephrosia subtriflora Baker[***]	CH	NN	3.73 ± 1.5	12
Tragus roxburghii Panigrahi	TH	NN	9.47	1
Tribulus terrestris L.	TH	NN	0.68 ± 0.36	4
Dipcadi erytheceum Webb. & Birth.	GE	MI	-1	

[*]Life form: PH, Phanerophyte; CH, Chamaephyte; HE, Hemi-cryptophyte; GE, Geophyte; TH, Therophyte.
[**]Leaf size: LP, Leptophyll; NN, Nanophyll; MI, Microphyll. [***]Leaf-size based on leaflet.

Table 2. Temporal variation of dominants in a dry sandy desert site of Karachi.

| Month | ------------------------ Dominants ----------------------------- | |
	IVI-based	Live biomass-based
June, 90	*Cenchrus setigerus*	*Aerua javancia*
	Leptothrium senegalensis	*Lasiurus scindicus*
	Dactyloctenium scindicum	*Dactyloctemium scindicum*
July, 90	*Cenchrus setigerus*	*Sida pakistanica*
	Dactyloctenium scindicum	*Aerua javanica*
	Aerua javanica	*Dactyloctemium scindicum*
	Lasiurus scindicus	
August, 90	*Tragus raxburghii*	*Lasiurus scindicus*
	Tephrosia strigosa	*Cenchrus setigerus*
	Indigofera cordifolia	*Aerua javanica*
	C. setigerus	
September, 90	*Blepharis sindica*	*Lasiurus scindicus*
	Indigofera cordifolia	*Cenchrus setigerus*
	Indigofera linifolia	*Aerua javanica*
	Tephrosia strigosa	
October, 90	*Dactyloctenium scindicum*	*Lasiurus scindicus*
	Cenchrus setigerus	*Cenchrus setigerus*
	Cyperus atkinsonii	*Dactyloctemium scindicum*
	Tephrosia strigosa	
November, 90	*Cenchrus setigerus*	*Lasiurus scindicus*
	Tephrosia subtriflora	*Sida pakistanica*
	= *Cyperus atkinsonii*	*Tephrosia subtriflora*
	S. pakistanica	
December, 90	*Cyperus atkinsonii*	*Lasiurus scindicus*
	Lasiurus scindicus	*Cenchrus setigerus*
	Sida pakistanica	*Sida pakistanica*
January, 91	*Cyperus atkinsonii*	*Lasiurus scindicus*
	Tephrosia subtriflora	*Sida pakistanica*
	Cenchrus setigerus	*Dactyloctemium scindicum*
February, 91	*Cyperus atkinsonii*	*Lasiurus scindicus*
	Cenchrus setigerus	*Cenchrus setigerus*
	Tephrosia subtriflora	*Dactyloctemium scindicum*
March, 91	*Tephrosia subtriflora*	*Aerua javanica*
	Cenchrus setigerus	*Cenchrus setigerus*
	Leptothrium senegalensis	
April, 91	*Tephrosia subtriflora*	*Sida pakistanica*
	Cyperus atkinsonii	*Aerua javanica*
	Leptothrium senegalensis	
May, 91	*Tephrosia subtriflora*	*Aerua javanica*
	Cyperus atkinsonii	*Dactyloctemium scindicum*
	Laisurus scindicus	*Sida pakistanica*
June, 91	*Tephrosia subtriflora*	*Aerus javanica*
	Lasiurus scindicus	*Tephrosia subtriflora*
	Dactyloctenium scindicum	
	Aerua javanica	

MONTHS

Fig. 3. Phenological stages of some important species.

Key to the species:

1. *C. setigerus*
2. *D. scindicum*
3. *C. atkinsonii*
4. *B. sindica*
5. *L. scindicus*
6. *T. roxburghii*
7. *T. terrestris*
8. *S. pakistanica*
9. *L. senegalensis*
10. *I. cordifolia*
11. *M. cerviana*
12. *D. muricata*
13. *C. tridens*
14. *T. strigosa*
15. *E. dracunculoides*
16. *P. niruri*
17. *I. linifolia*
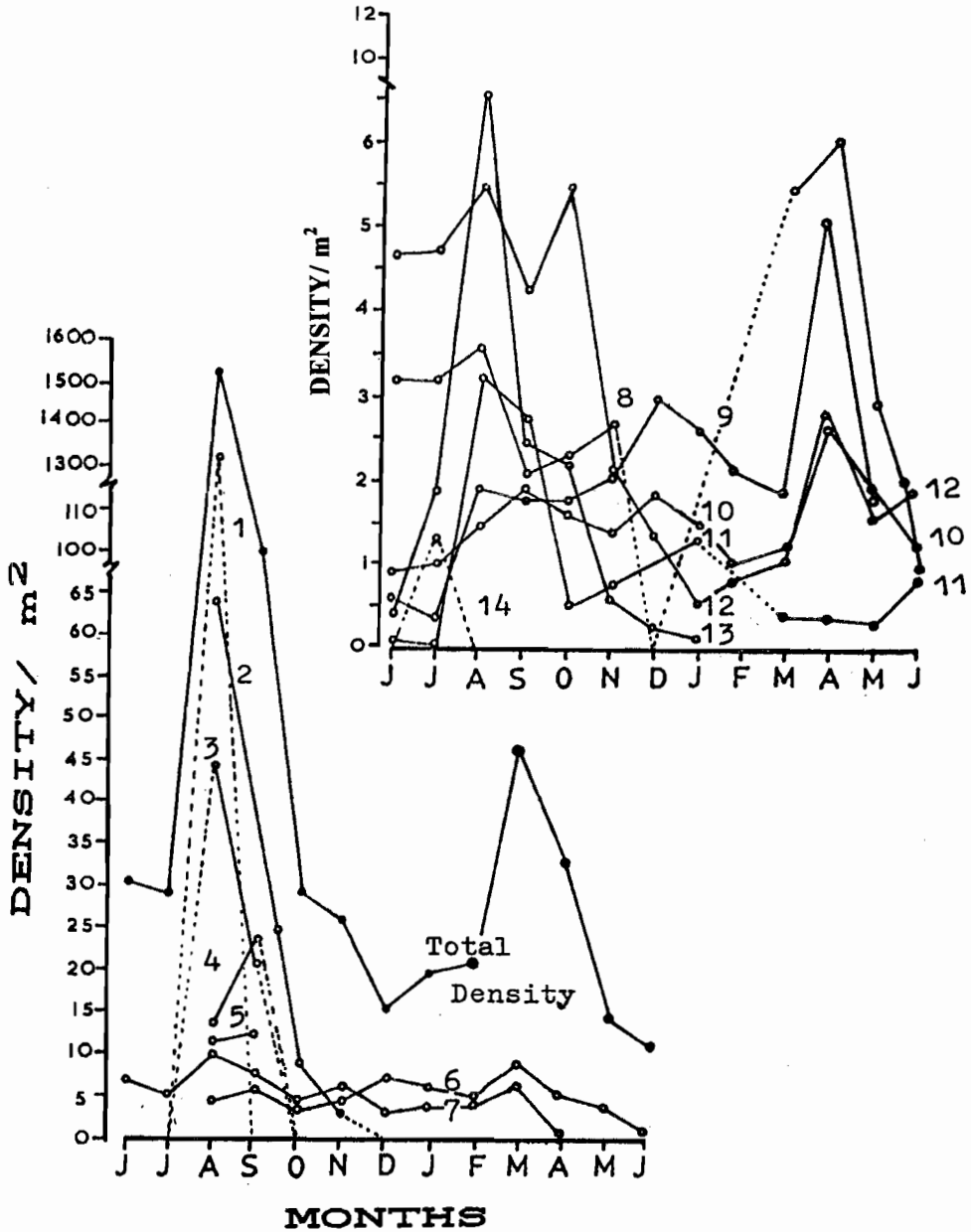18. *L. nudicaulis*

Fig. 4. Variation in density of species occurring in *L. scindicus* dominated site over the period from June, 90 to June 91.

1. *T. roxburghii*, 2. *T. strigosa*, 3. *I. cordifolia*, 4. *B. sindica*, 5. *I. linifolia*, 6. *C. atkinsonii*, 7. *C. setigerus*, 8. *L. senegalensis*, 9. *S. pakistanica*, 10. *L. scindicum*, 11. *Portulaca* sp., 12. *D. scindicum*, 13. *P. abyssinica*, 14. *D. muricata*.

Cyperus atkinsonii flowered in August, underwent seed maturation in September and October and died in October-November. It again grew after rains in February but remained vegetative and died in May. *L. scindicus* flowered during September. *D. scindicum* and *C. setigerus* flowered simultaneously in August, their seeds matured in September-October and both largely died in November. They again appeared after winter rains, flowered but did not produce seeds probably due to early moisture depletion.

The herbaceous vegetation underwent marked seasonal dynamics with the availability of moisture. Such marked seasonality in species distribution, their phenology and performance is common in monsoon grasslands and desert communities (Babu, 1971; Kumar & Joshi, 1972; Singh & Yadava, 1974). Ephemerals and annuals dominate the vegetation, at least numerically, during monsoon season, complete their life cycle within minimum possible time and disappear.

(iv) **Density variation of species:** The density of the community increased exponentially with the advent of summer rains (Fig. 4). It was 1530 plants m^{-2} after rains compared to 31 plants m^{-2} in June. *T. roxburghii* (small ruderal graminoid) alone contributed 86.68% of the total density i.e., 1327 plants m^{-2}. *T. strigosa* had density of 64 plants m^{-2}. The density declined drastically during September and attained minimum value in December. The second peak of density increase occurred in March after February rains. The overall density in May, 1991 was substantially lower than that of May, 1990 (initial value). It could be due to more severe drought this year.

The post-rainfall thinning in the community may be due to two reasons. Firstly, it may be due to stronger selective pressure in earlier phases of life cycle. Greater degree of mortality of seedlings in sexually reproducing plants has been shown to be related with the genetic load of unfit genotype (Sarukhan, 1976). Secondly, the post-rainfall moisture depletion may also be crucial, as seedlings are more vulnerable to moisture loss. This is also evident from highly significant positive correlations of density with rainfall (P) and soil moisture content (SM) through different months of observation:

$$\text{Density}/m^2 = 1.5872 + 19.3192P \text{ (mm)} \pm 32.662$$
$$r^2 = 0.9944 \ t = 44.02$$
$$\text{adj. } r^2 = 0.9938; \ p < 0.0001; \ F = 1939.48$$

$$\text{Density}/m^2 = 196.584 + 334.72 \text{ SM} \pm 87.81$$
$$r^2 = 0.9592 \ t = 16.09$$
$$\text{adj. } r^2 = 0.9555; \ p < 0.001; \ F = 258.85$$

(v) Biomass dynamics:

Above ground live biomass (LB): The above ground live biomass varied considerably through different months and among and within various species (Fig. 5; Table 3). LB increased exponentially from 20.6 $g.m^{-2}$ in June, 1990 to 310.8 $g.m^{-2}$ in September, declining thereafter gradually uptill January (24.2 $g.m^{-2}$), as it gradually entered the dead and litter compartments. After February rains, LB again slightly increased to 43 $g.m^{-2}$. It was 34 $g.m^{-2}$ in May, 1991.
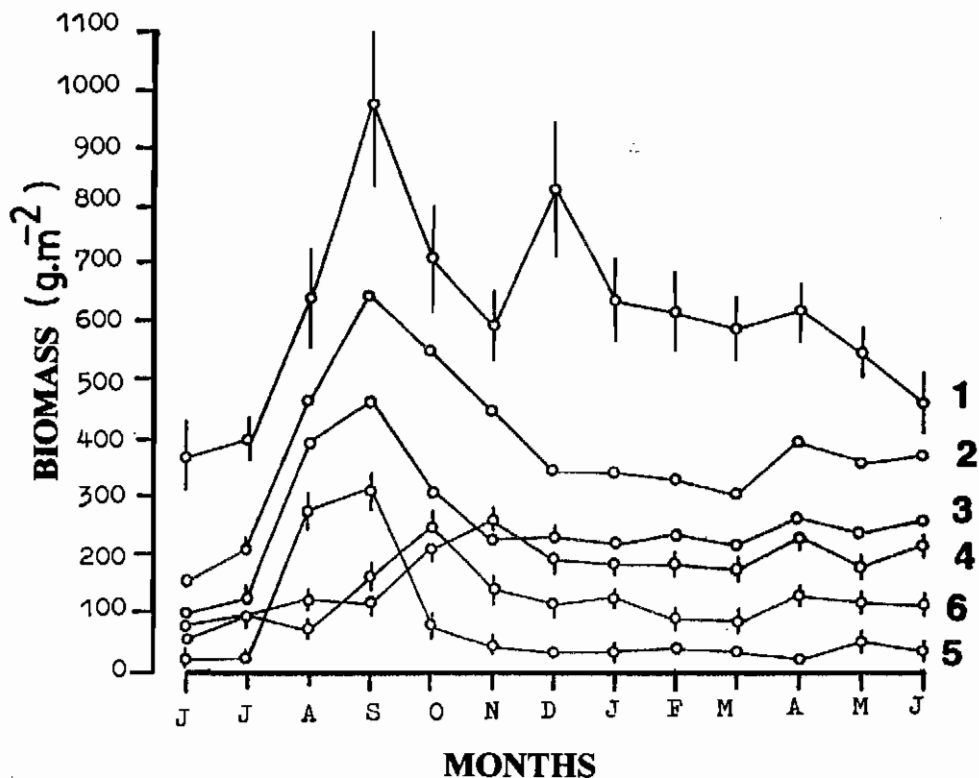
Fig. 5. Variation in biomass components. Below ground biomass expressed in g per 0.3 m³ monolith. 1. Below ground biomass, 2. Above ground standing crop, 3. Total above ground biomass, 4. Above ground dead biomass, 5. Above ground live biomass, 6. Litter.

Temporal variation in live biomass apportionment among grasses, legumes and other species: LB proportion of species other than legumes and grasses was high initially (54.9-69.6%) but on advent of rains grasses came up and dominated the site up till February with LB proportion varying from 55.8 to 74.0%. Legume component increased during monsoon season up till November (9.8-16.3%) but declined later on due to exclusion of annual legumes from 5 species in August to only 1 in November (Table 4). The proportion of species other than grasses and legumes increased from March onwards reaching to 85.6% in June largely due to the death of grasses (*C. setigerus* and *D. scindicum*) and legumes. LB during this part of year was mainly composed of *A. javanica* and *S. pakistanica*.

Seasonal variation in life-form and leaf-size spectra: Substantial variation occurred in life form and leaf-size spectra, when constructed on the basis of number of species, their IVI or live above ground biomass. LB-based spectra, being more applicable, reliable and reflective to real species performance, were chosen here for the description of the seasonal behaviour of the community. Geophytic class was dominant for a period from August to February. Later on this class declined and proportion of Phaner-

Table 3. Values of liver standing biomass (g.m⁻²) of various species occurring in different months in *L. scindicus* dominated dry site

Species	June,90	July	August	September	October	November	December	January,91	February	March	April	May	June
A. javanica	10.04	4.48	26.53	26.64	4.27	-	-	-	-	22.24	7.60	26.48	29.11
B. sindica	-	-	2.91	21.65	1.83	-	-	-	-	-	-	-	-
B. verticillata	-	-	0.67	-	-	-	-	-	-	-	-	-	-
C. holosericea	-	-	-	-	5.01	-	-	-	0.81	-	-	-	-
C. penniseriformis	-	-	-	0.24	-	-	-	-	-	-	-	-	-
C. setigerus	0.72	0.28	63.42	84.89	11.67	1.58	7.38	1.01	8.87	3.41	-	-	-
C. scindicus	-	-	0.02	-	-	-	-	-	-	-	-	-	-
C. tridens	-	-	0.01	-	-	-	-	-	-	-	-	-	-
C. jwarancosa	-	-	21.47	-	-	-	-	-	-	-	-	-	-
C. atkinsonii	0.65	-	12.78	3.64	0.32	0.43	1.63	1.01	2.11	1.05	-	1.30	-
C. bulbosus	-	-	1.01	-	-	-	-	-	-	-	-	-	-
D. scindicum	1.77	1.16	10.47	9.68	13.00	5.43	1.99	2.12	4.00	1.69	1.00	12.82	0.55
D. muricata	-	-	0.06	-	-	-	-	-	-	-	-	-	-
E. dracunculoides	-	-	1.01	-	-	-	-	-	-	-	-	-	-
F. indica	-	-	-	-	-	-	-	0.63	1.10	-	-	-	-
I. cordifolia	-	-	1.44	1.64	-	-	-	-	-	-	-	-	-
I. linifolia	-	-	2.45	3.58	0.27	-	-	-	-	-	-	-	-
I. oblongifolia	-	-	-	-	-	-	-	-	2.01	-	-	-	-
L. scindicum	6.55	4.83	67.93	105.40	22.97	22.50	13.17	14.12	16.98	2.14	1.05	3.12	0.91
L. senegalensis	-	-	10.01	1.35	-	1.05	-	-	-	1.00	0.40	-	-
M. cerviana	-	-	0.01	0.04	-	-	-	-	-	-	-	-	-
O. ramosa	-	-	-	-	-	-	-	-	0.49	-	-	-	-
P. abyssinica	0.13	0.14	1.67	1.40	4.09	0.72	0.49	0.39	-	1.58	-	-	-
P. niruri	-	-	0.0	-	-	-	-	-	-	-	-	-	-
Portulaca sp.	0.01	-	0.10	0.19	0.02	0.93	-	-	-	0.02	-	0.13	-
P. juliflora	-	-	0.07	-	-	-	-	-	-	-	-	-	-
R. schinperii	-	-	-	17.084	5.71	-	-	-	-	-	-	-	-
S. pakistanica	0.50	8.72	11.93	15.68	9.26	8.51	4.62	3.92	4.01	2.62	9.15	5.05	-
T. strigosa	-	-	6.82	10.94	0.32	-	-	-	-	-	-	-	-
T. subtriflora	0.26	-	15.50	5.10	2.65	4.22	1.12	1.01	2.68	1.62	2.76	4.45	3.44
T. roxburghii	-	-	9.47	-	-	-	-	-	-	-	-	-	-
T. terrestris	-	-	1.59	0.90	-	0.02	-	-	0.21	-	-	-	-
	20.63	19.97	269.36	310.75	81.39	45.39	30.45	24.21	43.27	37.37	21.96	53.35	34.01

The values rounded to two decimal places.

Table 4. Apportionment of live standing biomass into grasses, legumes and other species.

Month	Components		
	Grasses	Legumes	Others
June, 90	9.04[*]	0.253	11.326
	43.64[**]	1.225	54.929
	3[***]	1	5
July	5.99	-	13.700
	30.43	-	69.570
	2	-	3
August	182.75	26.274	59.321
	68.10	9.790	22.106
	6	5	15
September	201.592	39.050	70.134
	66.764	12.933	23.227
	5	5	8
October	47.637	13.952	23.775
	55.804	16.344	27.852
	3	5	6
November	30.559	4.217	10.617
	67.321	9.290	23.389
	4	1	5
December	22.540	1.120	6.790
	74.023	3.678	22.299
	3	1	3
January, 91	17.247	1.010	5.950
	71.254	4.173	24.573
	3	1	4
February	29.548	5.503	7.920
	68.763	12.806	18.431
	3	3	5
March	8.232	1.616	27.520
	22.030	4.325	73.646
	4	1	5
April	2.448	2.760	16.752
	11.148	12.569	76.284
	3	1	2
May	15.944	4.453	32.952
	29.886	8.347	61.767
	2	1	4
June	1.455	3.440	29.011
	4.290	10.146	85.565
	2	1	1

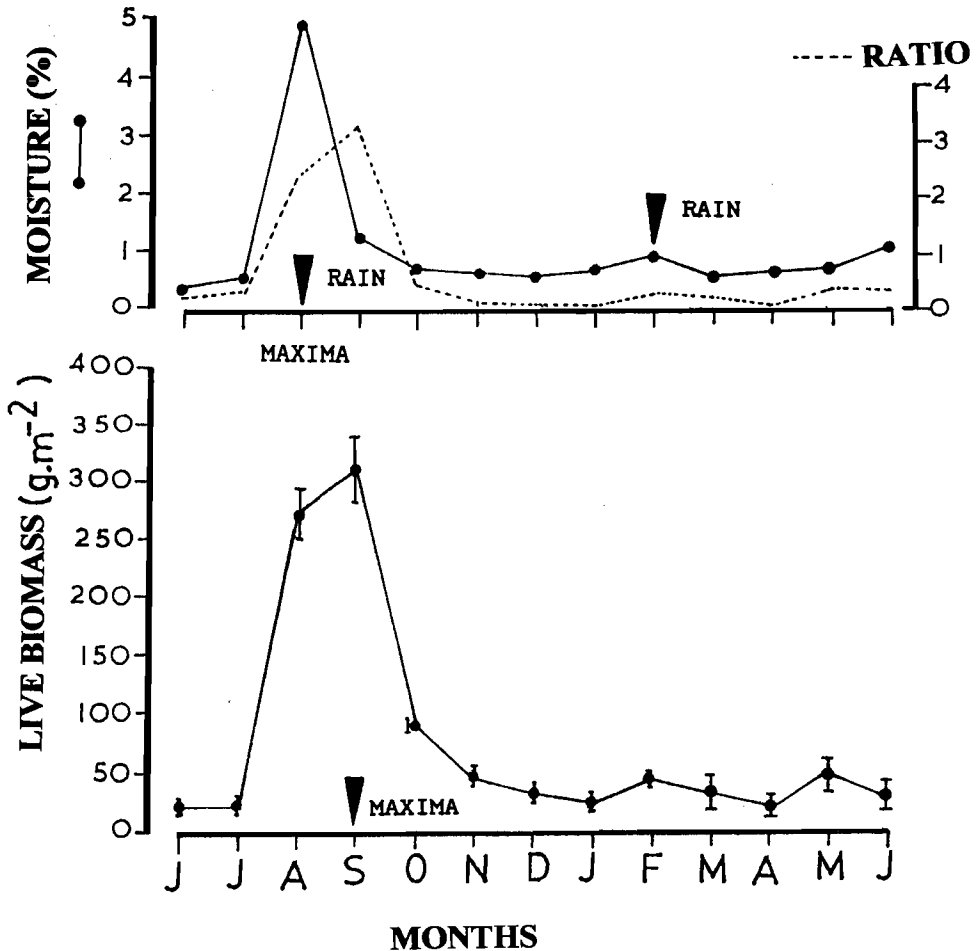[*] Live biomass (g.m^{-2}), [**], Percentage proportion, [***], The number of liver species.

Fig. 6. Relationship between soil moisture content (at 15-20 cm depth) and the standing liver biomass of dry *Lasiurus* site. The dotted line represents live: dead biomass ratio.

ophytes increased to dominate the spectrum for March and June. Therophytic class was only represented after rains. Its LB-based proportion was low but moderate to high on the basis of number of species or IVI (Table 5). Microphyllous and nanophyllous classes dominated the spectra. Mesophyllous class was only present in August with insignificant magnitude. Leptophyllous elements were, however, relatively conspicuous if adjudged on the basis of number of species.

It follows from the results that the site underwent a significant physiognomic change during summer monsoon period only if viewed on the basis of number of species or their IVI. Such a change was, however, quite insignificant on the basis of LB proportion allocated to the therophytes. It may, presumably be due to low rainfall during the observation period.

Table 5. Life-form and leaf-size spectra of *L. scindicus* site. Data in percentage.

Month	Life-form*					Leaf-size**			
	PH	CH	HE	CR/GE	TH	LP	NN	MI	MS
June. 90 a)	22.22	22.22	11.11	22.22	22.22	11.11	55.55	33.33	-
b)	9.03	7.46	21.24	40.57	25.80	1.81	50.41	47.79	-
c)	48.93	4.32	8.62	38.59	0.004	0.04	15.63	84.36	-
July	16.66	33.33	16.66	33.33	-	-	50.00	50.00	-
	13.48	22.97	21.64	46.87	-	-	39.65	60.35	-
	24.24	44.37	5.82	25.61	-	-	50.16	49.36	-
August	10.71	21.42	3.57	14.29	46.43	10.71	57.14	32.14	3.57
	1.84	6.16	1.25	9.85	76.99	3.77	82.38	13.85	0.61
	10.16	10.85	3.90	54.09	12.99	0.06	31.71	68.19	0.03
September	5.00	15.00	5.00	15.00	60.00	5.00	70.00	25.00	-
	1.63	3.89	1.77	19.54	63.71	3.87	65.49	30.65	-
	8.57	12.87	3.11	62.36	13.02	0.06	22.99	76.95	-
October	7.14	35.71	7.14	21.43	28.57	7.14	71.43	21.43	-
	3.75	27.67	15.19	30.30	23.57	3.93	75.36	20.72	-
	4.99	31.31	15.22	45.63	0.28	0.03	51.12	47.69	-
November	-	30.00	10.00	30.00	30.00	10.00	70.00	20.00	-
	-	30.77	8.09	45.29	17.43	4.01	67.71	28.28	-
	-	29.63	11.96	54.06	4.39	0.02	44.61	53.95	-
December	14.28	28.57	14.28	28.57	14.28	14.29	57.14	28.57	-
	8.95	16.73	9.29	53.23	11.80	11.80	62.09	26.11	-
	-	20.46	6.53	73.00	-	-	27.72	72.27	-
January, 91	-	42.86	14.28	42.86	-	14.29	57.14	28.57	-
	-	38.14	5.01	61.88	-	0.31	68.88	30.81	-
	-	24.58	8.76	66.69	-	2.59	34.90	62.50	-
February	9.09	45.45	9.09	27.27	-	9.90	54.55	36.36	-
	0.48	37.88	5.61	55.76	-	0.48	67.65	31.87	-
	4.68	21.15	9.30	54.37	0.48	2.55	55.13	42.31	-
March	8.03	25.00	8.03	25.00	33.94	8.34	58.33	3.33	-
	5.73	33.79	4.63	36.60	20.29	2.09	61.58	36.33	-
	59.52	15.59	4.52	17.64	2.74	0.06	25.58	74.35	-
April	12.50	25.00	12.50	25.00	25.00	12.50	62.50	25.00	-
	3.06	34.57	7.91	33.04	21.43	4.21	79.20	16.58	-
	34.61	54.24	4.55	4.77	1.82	-	60.62	39.38	-
May	14.29	28.57	14.29	28.57	14.29	14.29	57.14	28.57	-
	6.18	34.68	11.75	42.32	5.33	5.07	71.89	23.04	-
	49.64	17.81	24.04	8.43	0.09	0.24	44.27	55.48	-
June	20.00	20.00	20.00	20.00	20.00	20.00	40.00	20.00	-
	16.82	29.82	19.74	24.62	7.84	9.01	49.55	41.44	-
	85.52	10.15	1.61	2.68	-	-	11.75	88.24	-

*. PH, Phanerophyte; CH, Chamaephyte; HE, Hemi-cryprtophyte; CR/GE, Cryptophyte/Geophyte; TH, Therophyte. **. LP, Leptophyll; NN, Nanophyll; MI, Microphyll; MS, Mesophyll. a) Based on the number of species; b) Based on the IVI of the species; c) Based on the standing live biomass of species.

Relationships between above ground live biomass and soil moisture content and climatic variables: The magnitude of LB was associated positively with soil moisture content and precipitation. However, a time lag phenomenon was apparent i.e., the biomass maxima occurred in the month subsequent to that of the occurrence of precipitation (Fig. 6). Walter (1979) has demonstrated a direct relationship between moisture avail-ability and above ground biomass. Hullet & Tomaneck (1969) also showed a direct relationship of seasonal estimated total forage production with May + June precipita-tion in a clay upland range site in Western Kansas. Sala *et al.*, (1988) have reported similar results. Live: Dead biomass ratio behaved in similar manner as the live bio-mass.

The relationship of LB ($g.m^{-2}$) with climatic variables e.g., atmospheric tempera-ture ($^{\circ}C$) (mean monthly, T), relative humidity at 8:00 AM (RH), precipitation, mm (P), solar radiation, $MJ.m^{-2}.day^{-1}$ (SR) and soil moisture content, (SM), as determined by linear and multiple correlation and regression, is presented below:

LB of this site exhibited non-significant correlation with T (r = 0.2060), RH (r = 0.4179) and SR (r = 0.0989). It related positively with P and SM (variation accounted for c. 34 and 41 %, respectively), as follows:

LB = 52.066 + 2.8078 P $\pm$ 78.185
r^2 = 0.3991, t = 21.703; adj. r^2 = 0.3445 p< 0.021; F = 7.305

LB = 21.03 + 53.739 SM $\pm$ 74.138
r^2 = 0.4597, t = 3.059, adj. r^2 = 0.4106 p< 0.011; F = 9.358

Regression analysis with lag (-1) transformed climatic variables indicated no signif-icant correlation with T (-1) (r=0.335) and RH (-1) (r=0.4232). P (-1), SR(-1) and SM (-1), however, related significantly with LB as follows:

LB = 55.0185 + 3.1977 P (-1) $\pm$ 72.389
r^2 = 0.5171, t = 3.273, adj. r^2 = 0.4688 p< 0.008; F = 10.706

LB = 277.547 - 10.358 SR (-1) $\pm$ 85.905
r^2 = 0.3199, t = -2.169, adj. r^2 = 0.2519 p< 0.055; F= 4.703
LB = 24.459 + 55.9004 SM (-1) $\pm$ 85.905
r^2 = 0.5123, t= 3.24, adj. r^2 = 0.4636 p< 0.009; F = 10.5023

The linear combinations of variables namely T (-1), P (-1) and SR (-1) explained 95.94% variability in LB as shown by the following equation.

LB = 74.595 + 8.0605 T (-1) + 2.959 P (-1)- 12.3488 SR (-1) $\pm$ 19.991
                    t=10.085   t=10.859   t=10.358
                    p<0.0001   p< 0.0001   p< 0.0001
r^2 = 0.9705; adj. r^2 = 0.9594 ; F = 87.838

None of the lag (-2) transformed independent variables except T (-2) related with LB significantly. Even T (-2) itself accounted for only 23.98% variability in LB as follows:

$$LB = 223.423 + 12.375 \text{ T } (-2) \pm 89.094$$
$$t = 2.038$$
$$r^2 = 0.3158; p < 0.072; adj. r^2 = 0.2398, F = 4.16$$

The linear combination of lag (-2) transformed climatic variables, however, accounted for 92.53% variability in LB as follows:

$$LB = 103. 111 + 7.994 \text{ T } (-2) + 6.382 \text{ RH } (-2) + 28.506 \text{ P } (-2) -$$
$$t = 3.368 \qquad t = 4.38 \qquad t = 6.644$$
$$9.827 \text{ SR } (-2) - 525.386 \text{ SM } (-2) \pm 27.924$$
$$t = -5.643 t = -6.831$$
$$r^2 = 0.9627; adj. r^2 = 0.9253 \ p < 0.0001, F = 25.783$$

None of the lag (-3) transformed variables or their linear combinations yielded significant correlation with LB. It appears that effects of rains within its given pattern and magnitude, persisted for not more than 50-60 days. Indeed, major proportion of live biomass that emerged after August rains entered the dead compartment during October.

Seasonal variation in species diversity and dominance: Species diversity, an important attribute of structure, function and organization was calculated on the basis of density as well as the live biomass of the constituent species because the best measure of importance of a species in a community may be its productivity which both expresses its biological activity and indicates the share of the environmental resource it utilizes (Vasender, 1984). The vegetation of the site was simple in its organization as the species diversity remained low (S, d, e, H̄) and dominance high (c and CDI). Diversity based on density declined substantially after rains in August. On the basis of biomass, however, H̄ and Mc had nearly maximum value for this month (Table 6). H̄ averaged to 0.6445 ± 0.065 and varied about 26% around the year. The decline of diversity in August if viewed on the basis of density is understandably due to very high density of *Tragus roxburghii* (1327 plants.m^{-2}) which created the conditions of high dominance concentration in this month. The temporal variation in diversity, as observed here, is also reported by Singh & Misra (1969) in grasslands of Varanasi, India and Imura (1981) in stored-product insect fauna in barley mills of Japan. Species diversity tends to be low in physically controlled ecosystems and high in biologically controlled ones (Tramer, 1969; Odum, 1971). If it is true, the community under study is controlled biologically only for a short period of time. Indeed, there is no such entity as wholly biologically controlled or wholly physically controlled community in nature (Smith, 1980). The community is rather influenced by the interaction of the two. These results are similar to those reported by Khan *et al.*, (1989) for coastal grass - dominated communities.

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Table 6. Temporal variation in diversity, equitability, species richness
and dominance in *L. scindicus* site.

Month	S	H	Mc	e	d	d'	c	CDI
June, 90 a)	9	0.6690	0.4797	0.7011	0.6862	3.5778	0.2707	55.9900
b)	9	0.5776	0.4097	0.6054	1.9824	6.0883	0.384	80.4695
July	6	0.7224	0.5467	0.9284	0.7023	2.6838	0.2055	56.3695
	6	0.5686	0.4419	0.7306	1.3426	3.8462	0.3115	67.8482
August	28	0.2997	0.1314	0.2071	0.2066	6.3321	0.7545	52.3610
	26	0.9794	0.6142	0.6922	1.5872	10.2923	0.1488	48.9474
September	20	0.9763	0.6292	0.7504	0.6044	6.2521	0.1375	30.1801
	18	0.7296	0.5412	0.5812	1.0210	6.8191	0.2066	63.0205
October	14	1.0002	0.6567	0.8727	0.8397	5.3192	0.1180	28.9900
	14	0.7322	0.6222	0.6389	1.5155	6.7323	0.1427	42.1385
November	10	0.8671	0.6043	0.8671	0.7433	3.9858	0.1566	37.0600
	10	0.6662	0.4465	0.6661	1.4843	5.4348	0.30636	68.3289
December	7	0.6853	0.4818	0.8100	0.5133	2.2036	0.2685	53.2250
	7	0.6593	0.4730	0.7802	1.2686	4.0431	0.2778	67.4877
January, 91	7	0.6914	0.5177	0.8182	0.4962	2.6098	0.2326	50.9000
	8	0.5998	0.3833	0.6641	1.6263	5.0578	0.3804	74.5340
February	11	0.9321	0.6220	0.8963	0.8564	4.5106	0.1499	45.1470
	11	0.7975	0.5306	0.7658	1.6781	6.1237	0.2203	59.4590
March	12	0.7411	0.5726	0.6867	0.5529	4.1152	0.1827	41.5650
	10	0.6470	0.3852	0.6470	1.6359	5.7252	0.3779	68.6360
April	8	0.7724	0.5660	0.8553	0.4040	2.6996	0.1883	42.8550
	6	0.5869	0.4397	0.7543	1.2804	3.7258	0.3139	76.2840
May	7	0.8451	0.5238	0.8392	0.4586	2.5348	0.2268	50.6200
	7	0.6045	0.4307	0.7153	0.9584	3.4742	0.3241	73.6730
June	5	0.6278	0.4855	0.8955	0.5330	4.1144	0.2477	54.4660
	4	0.2297	0.1378	0.3816	0.6869	1.9608	0.7434	95.7112

a, Based on density; b, Based on live standing biomass $(g.m^{-2})$.

Interestingly, for the part of year when diversity was low, the associated diversity-dominance curves were linear exhibiting geometric distribution and for the part of year when diversity was high the curves exhibited a tendency to approach log-normal distribution (Fig. 7). The geometric distribution implies that the most successful species preempts a fraction 'k' of the available resources, next a fraction `k' of the remainder and so on (May, 1975). This phenomenon may be atrributed to species poor and environmentally stressful conditions (Whittaker, 1975). In such communities the phenomenon of dominance is strongly developed. Anderson *et al.*, (1979) also observed geometric distribution of biomass among species of sub-alpine herbaceous meadow of North Pole Basin, Colorado, which they atrributed to largely the soil moisture conditions. The sigmoid type of curve on the other hand, is characteristic of communities with more
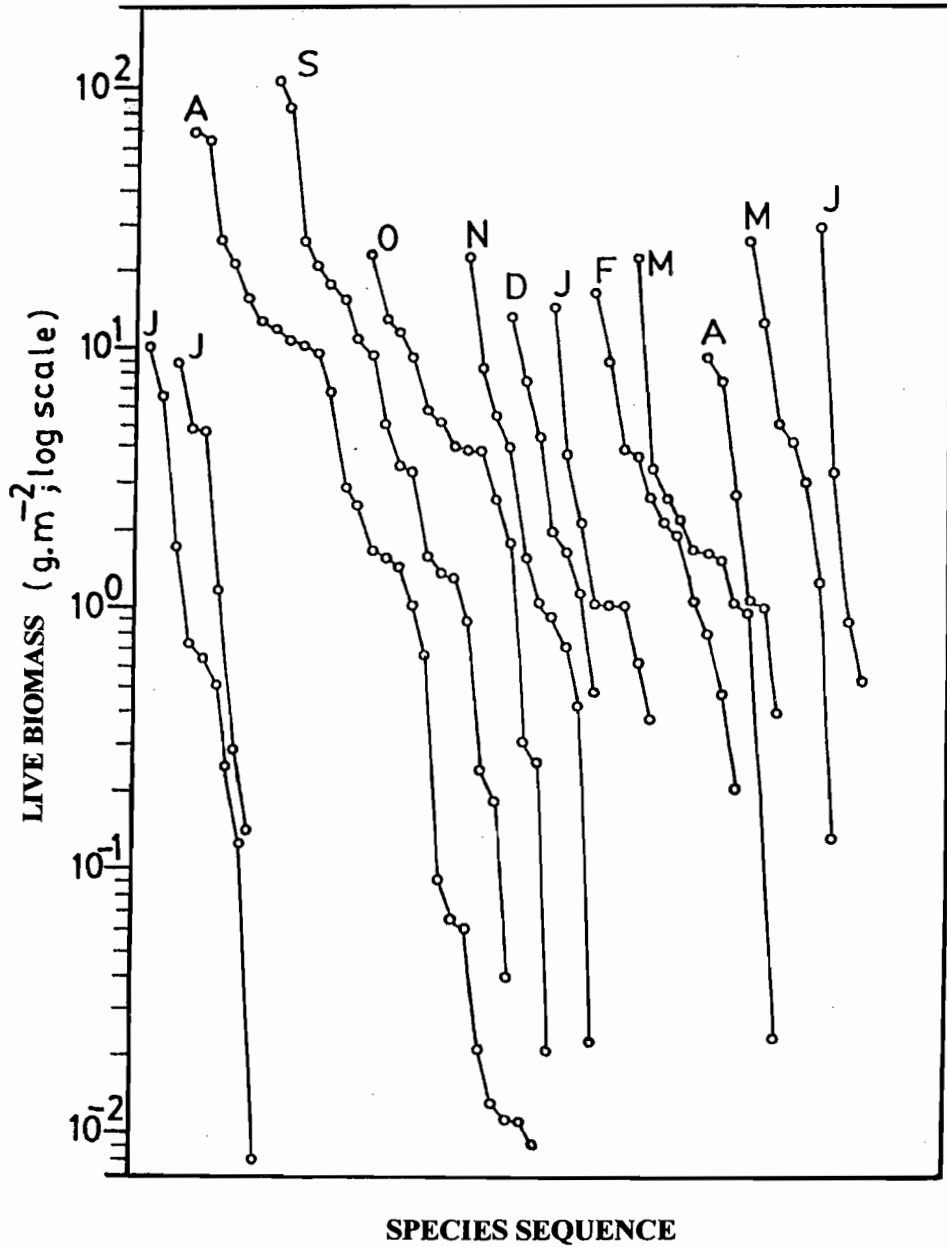
Fig. 7. Dominance-diversity curves for *L. scindicus* community drawn on semi-log plot on the basis of live biomass of the constituent species occuring during June, 90 and June, 91.

competitive species. None of the species usurps a especially large portion of niche space and there is large 'middle class' species utilizing similar portions of niche space. This feature of vegetation associates with high diversity situation (Yodzis, 1978).

Climatic relations of diversity and dominance: The simplest measure of diversity, S (number of species) as well as $\bar{H}$ exhibited significant positive correlation with amount of rainfall whereas dominance, CDI showed inverse relationship. $\bar{H}$ also related positively with soil moisture content (SM,%). The following predictive equations clearly signify that diversity was stimulated by moisture availability in this dry sandy site.

$$S = 8.5005 + 0.2253 \; P \; (mm) \pm 3.5386$$
$$t = 4.792$$
$$r^2 = 0.6761; \; p < 0.001 \qquad (1)$$
$$adj. \; r^2 = 0.6466 \; F = 22.96$$

$$S = 6.4297 + 3.9257 \; SM \; (\%) \pm 3.70$$
$$t = 4.472$$
$$r^2 = 0.6460; \; p < 0.001 \qquad (2)$$
$$adj. \; r^2 = 0.6135 \; F = 20.05$$

$$\bar{H} = 0.5986 + 0.00527 \; P \; (mm) \pm 0.1290$$
$$t = 3.076$$
$$r^2 = 0.465 \; p < 0.011$$
$$adj. \; r^2 = 0.4136, \; F = 9.464 \qquad (3)$$

$$CDI = 70.8096 - 0.30034 \; P \; (mm) \pm 12.379$$
$$t = 1.826$$
$$r^2 = 0.2326; \; p < 0.095 \qquad (4)$$
$$adj. \; r^2 = 0.1628, \; F = 3.215$$

Rain - induced diversity stimulation in natural grass communities of sodic soils of Karanal, India, has also been reported by Sinha *et al.*, (1988).

Growth patterns of some important species: A study of growth patterns of species exhibited in the field is important as it provides understanding of production trends of a community (Singh, 1968). The change of growth in present studies was expressed in terms of log ratio following Singh (1968):

Log ratio = 10 x D.wt. $(g.m^{-2})$ at given later date/ D.wt. $(g.m^{-2})$ on the initial date.

Lasiurus scindicus showed one peak of growth prominently. The second peak (for winter) was inconspicuous. *C. setigerus* showed somewhat fluctuating growth pattern and disappeared in the month of April. The growth spurt of summer was, however, prominent. *D. scindicum* exhibited two peaks: one from August to October and other in May. *C. atkinsonii* showed one peak in summer from August to October. Its growth remained fluctuating thereafter. Major increase in biomass of *S. pakistanica* was evi-
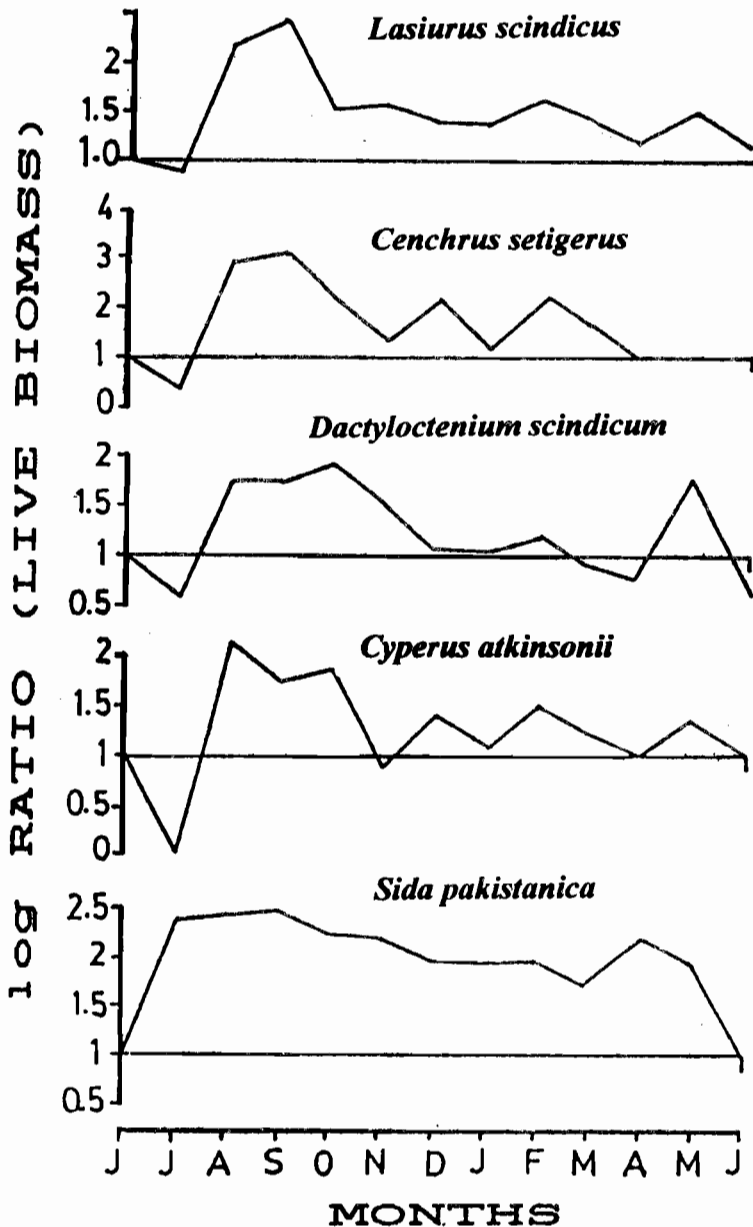
Fig. 8. Changes in live standing biomass of species occurring in dry *L. scindicus* site.

dent in July to September, then it gradually declined uptill March. Second spurt oc-
curred in April. A pattern of reduced growth in winter is presumably related to adverse
moisture regime in winter (Fig. 8). It is evident from Fig. 9 that annual legumes like *I.
linifolia, I. cordifolia* and *T. strigosa* exhibted practically no standing dead biomass
associated with alive plants during their entire life span. They were either wholly alive
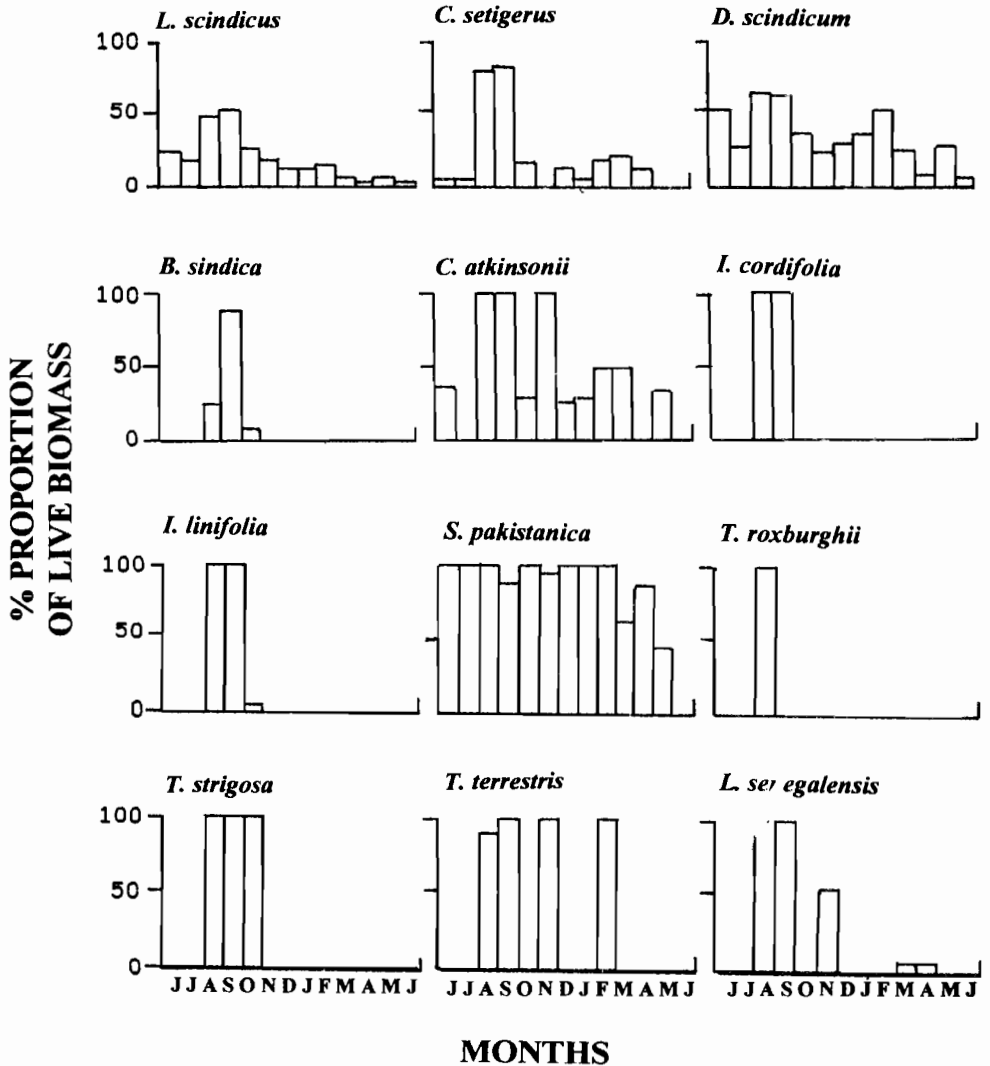
Fig. 9. Per cent proportion of live biomass for some constituent species of *L. scindicus* dominated site.

or wholly dead. Their death, like their emergence, was remarkably synchronous. These species died in October. *S. pakistanica* exhibted somewhat similar trend and died in June. The standing dead biomass proportion in perennial grasses such as *C. setigerus, L. scindicus* and *D. scindicum* was substantial around the year except that it decreased significantly in summer rainy season. It appears that the magnitude of standing dead biomass associated with a plant is a phenomenon, which is species specific and varies with growing season. The pattern of live: dead biomass proportion as observed in grasses appears to be due to their morpho-ecological peculiarities. They retain, at least a part of leaf, even if dead, with stem due to sheathing leaf-base to protect intercalary meristems. The leaves of dicotyledons are, generally, abscized immediately after the leaves are dead.

Standing dead biomass (SD), litter & total above ground biomass: The standing dead biomass varied greatly with different months and reached to the maximum in November when live biomass entered the dead compartment due to drought. SD biomass decreased during monsoon season (Table 7 & Fig. 5). The litter component was maximum in October (249 $g.m^{-2}$) and minimum in August (72.5 $g.m^{-2}$). Obviously, it underwent decay and decomposition after rains. The above ground standing biomass (live + dead) was maximum in September and minimum in June; averaging around 249.8 $\pm$ 25.9 g/m^2, which was comparable to average standing above ground biomass within enclosures of high sub-alpine snow zone herbaceous meadow (207.5 $\pm$ 5.3 g/m^2) (Anderson *et al.*, 1979) and to that of many grass communities of Pakistan coast (Khan *et al.*, 1989). The total standing crop (live + dead + litter) was maximum in September (647 $g.m^{-2}$) (Fig. 5).

Below ground biomass: The below ground biomass fluctuated with time and its magnitude was larger than that of above ground biomass (Fig. 5). Most of the perennial grasses in arid regions are bunch forming in habit which are known to have higher root/shoot ratio (Odum, 1971). Scischab *et al.*, (1985) have reported below ground biomass in *Eleocharis rostellata* varying from 1.6 to 12.9 times of the above ground biomass depending upon the habitat.

Above ground net primary productivity (ANP): When measured by direct harvest method, ANP is usually represented by the peak standing crop i.e., the total amount of herbage at the end of growing season, or by the sum total of the maximum weights attained by the individual species (Sims & Singh, 1971). The peak standing crop and ANP could only be identical in case the vegetation is composed of species which stop growing at single instant of time and where mortality occurs only during the post growth period (Weigart & Evans, 1964). Even if it is the case, Malone (1968) reported that "summation of individual species" peak growth results in 12% greater estimate of production compared to that by peak standing crop method. Moreover, in case the vegetation is composed of species that attain maximum weight at different times, the summation of peak method may estimate nearly 2 times that of peak standing crop. If mortality and disappeared standing dead are included this disparity may further increase to 2.5 to 5 times greater estimate of ANP than peak standing crop (Weigart & Evans, 1964). Kelly *et al.*, (1974) have proposed another approach "the positive increase sum method" to estimate ANP. In the present study ANP was estimated by the following methods:

(a) Difference Method: The positive increase in the standing crop (live + dead + litter) on successive sampling dates.

(b) Summation of peak values of individual species: The values of peak biomass of individual species are summed, and from this the total value for initial observation is subtracted. The difference would represent ANP. The biomass of initial observation is considered to be carry-over from the preceding season. Table 8 presents the estimation of ANP of this site by this method.

Table 7. Values of standing dead biomass (g.m^{-2}) of various species occurring in different months in *L. scindicus* dominated dry site[*].

Species	June,90	July	August	September	October	November	December	January,91	February	March	April	May	June
A. javanica	0.70	0.74	-	2.37	-	22.91	2.17	4.18	3.02	32.46	-	10.60	10.00
B. sinica	20.33	11.06	9.80	2.72	24.15	1.54	6.79	4.21	5.01	4.09	7.50	1.34	6.23
C. holosericea	-	-	-	-	1.14	-	-	-	-	-	-	-	-
C. pennisetiformis	-	1.70	-	0.50	-	-	-	-	-	-	-	-	-
C. setigerus	22.35	31.62	15.61	14.72	67.68	77.49	51.38	49.92	43.28	28.54	67.86	51.06	46.18
C. prostratus	2.09	-	-	-	-	-	-	-	-	-	-	-	-
C. tetragonoloba	-	0.09	-	-	-	-	-	-	-	-	-	-	-
C. jwarancosa	-	-	5.40	-	-	-	-	-	-	-	-	-	-
C. atkinsonii	1.58	3.40	0.27	-	11.63	-	4.87	2.68	2.13	2.30	4.65	3.33	1.96
D. scindicum	1.66	3.12	3.17	3.20	22.83	19.66	5.05	4.00	3.69	6.72	14.98	28.70	11.01
H. ophioglossum	-	-	-	-	0.27	-	0.32	-	-	-	-	-	-
I. cordifolia	6.54	4.70	-	-	4.03	0.13	0.97	0.23	0.18	0.41	-	2.41	0.06
I. linifolia	-	-	-	-	2.82	-	-	-	-	-	-	-	-
L. scindicum	24.02	28.86	88.87	85.44	75.42	126.23	109.23	110.26	118.86	94.20	113.25	61.17	123.77
L. senegalensis	1.17	2.74	-	-	7.83	0.74	8.50	6.27	6.13	4.73	14.86	9.05	9.88
M. cerviana	-	-	-	0.56	-	-	-	-	-	-	-	-	-
P. abyssinica	-	-	-	-	-	-	-	-	0.13	-	-	-	-
Portulaca sp.	0.001	-	0.30	-	-	-	-	-	0.22	-	-	-	-
R. schimperii	-	-	-	-	-	-	-	-	-	-	-	-	-
S. pakistanica	-	-	-	2.38	-	0.29	-	0.49	-	1.88	1.98	7.77	6.50
T. strigosa	-	-	-	-	-	0.13	0.63	-	-	-	-	-	-
T. subriflora	0.024	0.82	0.20	0.08	-	3.90	3.45	3.21	3.12	3.39	1.64	1.98	3.05
T. roxburghii	-	-	-	6.93	2.01	0.08	1.39	1.06	-	-	-	-	-
T. terrestris	-	-	0.13	-	-	-	-	-	-	-	-	-	-

[*]The values rounded to two decimal places.

Table 8. Estimation of net aboveground primary productivity through summation of peak biomass of individual species.

Species	Biomass (g.m^{-2}) (June)	Peak Biomass (g.m^{-2})
A. javanica	10.04	26.64
B. sinica	-	21.65
C. holosericea	-	5.01
C. setigerus	0.72	84.89
C. jwarancosa	-	21.47
C. atkinsonii	0.65	12.78
D. scindicum	1.77	13.00
F. indica	-	1.10
I. cordifolia	-	1.64
I. linifolia	-	3.53
I. oblongifolia	-	2.01
L. scindicum	6.55	105.40
L. senegalensis	-	10.01
P. abyssinica	0.13	4.09
R. schimperii	-	17.85
S. pakistanica	0.50	15.68
T. strigosa	-	10.94
T. subtriflora	0.25	15.50
T. roxburghii	-	9.47
T. terrestris	-	1.59
Other[*]	0.01	4.55
Total:	20.63	388.79
ANP: 368.16 g.m^{-2}		

[*], Includes species contributing less than 1.00 g.m^{-2} biomass each.

(c) **Positive increase sum method:** The positive increase in biomass of the individual species are summed on successive sampling dates through the year.

(d) **Sum of positive changes in biomass plus mortality:** The positive changes in the above ground biomass on sampling dates are summed. The positive increase in standing dead for only those sampling dates during which positive difference also occurred in above ground biomass are summed. This last sum is regarded to be the production not reflected in the biomass increment. The total of the two sums is considered as ANP.

The ANP estimates obtained with these methods are given below:
a) 586.72 g.m^{-2}
b) 368.16 g.m^{-2}
c) 464.25 g.m^{-2}
d) 375.96 g.m^{-2}

$\bar{X}$ = 448.77 $\pm$ 50.88 g.m-^{2}; CV = 22.67%

Table 9. Linear correlation and regression between proportional change in diversity or dominance indices and the proportional change in live biomass during successive round the year sampling of a desert plant community.

Parameters	r	a	b	F	p
∴ LB/∴S (Y/X)	0.9829	0.4265	3.4925	285.45	0.0001
⌐LB/∴H	0.7683	1.2331	8.7041	14.404	0.004
⌐LB/∴Mc	0.4719	1.1828	5.6812	2.8640	0.120
⌐LB/ ⌐e	0.0555ns	-	-	-	-
⌐LB/ ⌐d	0.2257ns	-	-	-	-
⌐LB/ ⌐d'	0.9324	1.0218	5.9453	66.519	0.0001
⌐LB/ ⌐c	-0.4268	1.6594	-2.7039	2.2273	0.1000
⌐LB/⌐CDI	-0.4015	1.2687	-5.3183	1.9210	0.2480

The mean rate of production thus ranged from 1.00 to 1.61 g.m^{-2}.day^{-1} ($\bar{X} = 1.23 \pm 0.14$). It is obvious that ANP values as calculated by the above methods, varied around 23%. Singh & Yadava (1974) when working with tropical grassland of Kurukshetra, India presented ANP estimates that varied by c. 30% with these methods. Jukola-Sulonen (1983) also reported substantial variation in ANP when estimated by different methods. Estimate obtained with method - d has been used here for further discussion as it lends itself well for the seasonal apportionment of ANP.

Our estimate of ANP (448 g.m^{-2} year^{-1}) for this sandy site is comparable to estimates reported for other arid lands. The productivity for deserts and semi-deserts is reported to vary between 10 to 250 g.m^{-2} year^{-1} (Whittaker & Likens, 1975). ANP for nine grass community types of American desert (Sims & Singh, 1971) varied from 107 g.m^{-2} for ungrazed shortgrass prairie at Pentex, Texas to 512 g.m^{-2} for the grazed tallgrass at Osage, Oklahoma. Clark & Jacoby (1994) have reported the production of *Sporobolus virginicus* salt marsh in Australia amounting as large as 852 g.m^{-2} year^{-1}. Our estimate is, however, similar to ANP of burned prairie (462 ± 49 g.m^{-2}) of Texas, USA, composed of several grasses and sedges but lower than that of unburned site of this prairie (Harcombe *et al.*, 1993).

Diversity relations of productivity: With the assumption that increase in live biomass (LB) is reflected in the primary productivity in the monthly harvest data, proportional change in diversity and LB for successive observations were calculated as current value minus previous value over the previous value. Correlation and regression analyses between proportional changes in diversity and LB were undertaken to investigate the relationship between them. A hypothesis that diversity for a bare area (no species) should be zero, likely the productivity should be zero, make this approach apparently workable in determining the relationship between diversity and productivity. Johnson *et al.*, (1975) have adopted this approach when investigating diversity-productivity relations in Mojave desert road side vegetation. It is evident from Table 9 that proportional

change in biomass (◢LB) correlated significantly positively with ◢ S, ◢H, ◢Mc and ◢d' but negatively with ◟c. No correlation was observed with ◢CDI.

The results reported on diversity-productivity relations are controversial. Auclair *et al.*, (1976) reported inverse relationship whereas Singh & Misra (1969) reported positive correlation between them. Diversity is principally a mechanism which generates community stability while dominance is a mechanism which generates community production (Margalef, 1965; Mc Naughton, 1967). Our results, however, do not appear in agreement to this contention. Diversity whether expressed in simplest form of number of species (S) or as H or Mc appear to generate productivity in this arid, dry sandy and non-saline site which supports Singh & Misra (1969) who suggested that diversity appears to generate productivity and dominance makes a system stable. Johnson *et al.*, (1975) have also indicated such a relationship between diversity and productivity. In arid regions, just the same factor- more available water probably stimulates both diversity and productivity and probably the best measure of diversity is the number of species. Positive association of LB with the amount of precipitation and the soil moisture content as observed by us is also indicative of the same contention. However, all types of arid ecosystems including dry and moist salinity-affected areas which are characterized with low diversity-high dominance situation leading to more and more monopolization by lesser and lesser number of species should critically be evaluated before making generalizations with respect to diversity-productivity relationships in desert environment.

Below ground net primary productivity (BNP): There are numerous difficulties and inaccuracies in measurement of BNP as have been indicated by many workers (Dahlman & Kucera, 1965; Singh, 1967; Lieth, 1968; Singh & Yadava, 1974). The results are affected by many factors: time of greater root development, losses due to organic root secretions, sloughing off of root hairs, root caps and cortical layers, translocation of organic materials to the soil and fungal components and consumption of roots by soil animals, etc. Therefore, the estimates of BNP should be viewed with constraints and limitations imposed by the available methods. In the present studies BNP was estimated by a summation of the significant positive peaks in the below ground biomass on the successive sampling dates. BNP for the site in question amounted to 834.4 $g.m^{-2}$ year^{-1}. Obviously, it is higher than ANP. Studies of many workers have indicated that plants in arid and stressful conditions allocate greater biomass proportion to the below ground parts (Pearson, 1965; Struik & Bray, 1970). Pearson (1965) reported that in grazed and ungrazed communities of Idaho desert, 80% and 65% of the plant biomass, were underground. He was of the contention that grazing could have stimulated the root growth. Sims & Singh (1971) have also observed higher BNP than ANP in desert communities of Texas and Oklahoma.

BNP and ANP as well as their production rates were higher in summer than in winter (Table 10). Major growth spurt in our region is, indeed, after summer rains. The length of growing season, of course, depends upon the distribution and the magnitude of rain, and it generally extends from August to October. Total net production (TNP) and the production rates were also higher in summer. The turn over rates of the below ground biomass was calculated by the method proposed by Dahlman & Kucera

Table 10. Seasonal apportionment of above- and belowground
production and production rates.

Season[*]	Net production $(g.m^{-2})$	Rate of production $(g.m^{-2}.day^{-1})$	Rainfall (mm)
Aboveground production			
Summer	344.6	1.873	86.8
Winter	31.4	0.173	26.3
Annual	376.0	1.030	113.1
Belowground production			
Summer	586.0	3.184	86.8
Winter	248.4	1.372	26.3
Annual	834.4	2.286	113.1
Total net production			
Summer	930.6	5.057	86.8
Winter	279.8	1.546	26.3
Annual	1210.3	3.316	113.1

[*]. After Minchen (1907).

Table 11. Maximum belowground biomass and turnover rates.

Season[*]	Max. belowground biomass $(g.m^{-2})$	BNP $(g.m^{-2})$	Turnover
Summer	980.0	586.0	0.598
Winter	835.2	248.4	0.297
Annual	980.0	834.4	0.51

[*]. After Minchen (1907).

(1965); Turn over = BNP/ Max., below ground biomass. The turn over of below ground biomass was larger after summer rains (major precipitation peak) than in winter (Table 11). Presumably, after summer rains the old and dead roots of perennials decompose due to high temperature and thus rapid microbial activity. Simultaneously, the ephemerals and annuals grow in this season and perennials translocate down assimilates to form new underground components. During winter, low temperature coupled with low precipitation keeps the turn over restricted. It is clear, however, that great proportion of biomass (85%) is replaced in a year. Turn over as high as 97% has been reported for *Panicum* community by Singh & Yadava (1974). The replacements ranging from 19% to 68% for nine arid sites have been reported by Sims & Singh (1971).

Total net primary productivity (TNP): The total net primary productivity of the site was 1210 g.m^{-2} year^{-1}. Murphy (1975) has presented data on TNP of tropical ecosystems including grasslands. TNP for perennial grasses from India ranged from 650 to 3510
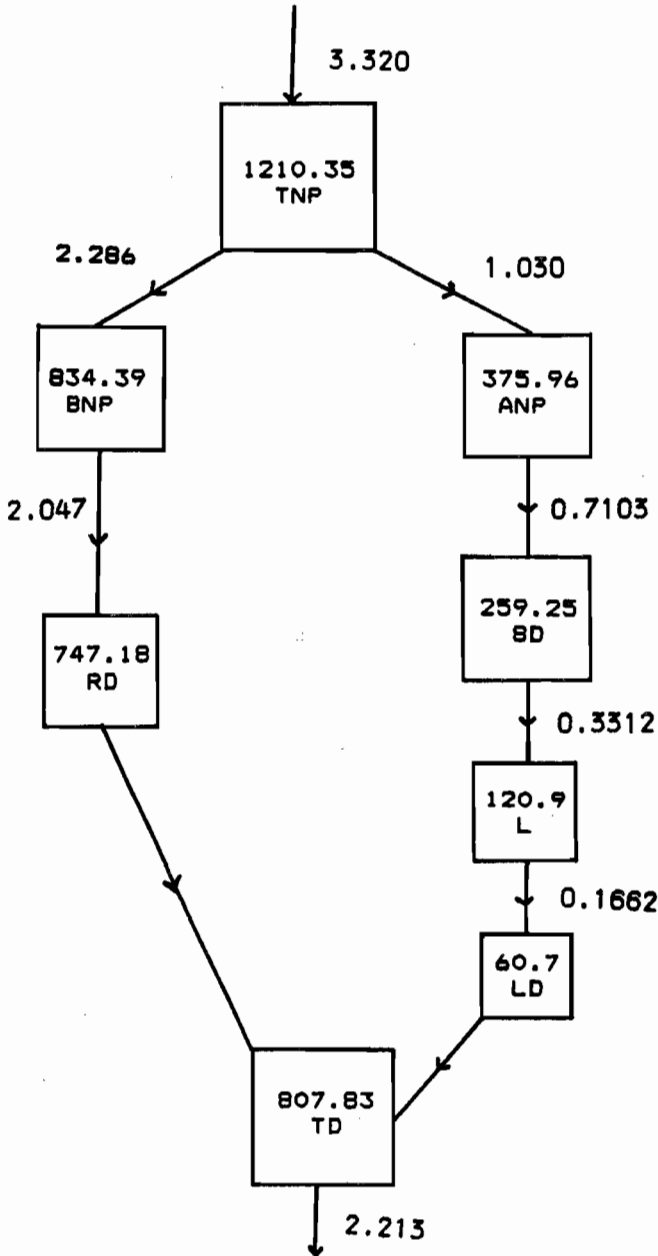
Fig. 10. Net primary production, accumulation and disappearance rates during the whole year period in *L. scindicus* dominated community compartment: $g.m^{-2}$. The accumulation and disappearance rates: $g.m^{-2}.day^{-1}$. Compartment symbols: TNP, total net productivity; ANP Above ground net productivity; BNP, Below ground net productivity; SD Standing dead; L, Litter; LD, Litter disappearance; RD, Root disappearance; TD, Total disappearance.

g.m^{-1} year^{-1} for sites that received 700-1000 mm rainfall. TNP for *Panicum miliare* dominated community was reported to be 3538 g.m^{-2} year^{-1} (Singh & Yadava, 1974). Low values of TNP in our case may be attributed to the arid conditions. Besides, the community productivity is a function of a number of factors like periodicity of rainfall, its magnitude and distribution over time, evapo-transpirational rate, solar radiation, soil permeability and fertility, number and nature of species entering the community composition and their characteristics, grazing pressure in the area etc., (Sims & Singh, 1971; Murphy, 1975; Steen, 1980; Sala *et al.*, 1988).

Net accumulation **and** disappearance rates: A block diagram constructed to depict accumulation and disappearance rates is presented in Fig. 10. The value on the arrow represents the rate of accumulation and disappearance on a per-day basis. SD, L, LD and TD were calculated following Singh & Yadava (1974). The transfer from live to standing dead compartment was calculated by summation method of the positive changes in standing crop of dead material on successive sampling dates where as transfer of standing dead to litter compartment was calculated by the negative changes in the standing crop of the dead material summed on successive sampling dates. The litter disappearance was estimated as LD = (initial amount of litter + litter production) - (amount of litter in the end).

The disappearance of below ground biomass was represented by summation of negative changes in the below ground biomass on successive sampling dates. TD is the sum total of RD + LD. From this block diagram some sort of annual sheet for dry matter may be prepared (Table 12). It may be observed that an amount of 103.3 g.m^{-2} remain unaccounted for in the balance sheet which may be taken care if following assumptions are made:

(a) That only source of transfer from ANP is through SD and SD may be calculated as: SD = (initial amount of biomass + ANP) - (Biomass at the end). This will transfer the 'unaccounted for' biomass to SD compartment.

(b) The value in the L compartment may now be calculated in a different manner in order to balance for SD:

L = |Initial Standing Dead + SD] - [Standing Dead at the End].

The litter disappearance will then be:

LD = |Initial Litter + L] - [Litter at the end]

Computation with these assumptions would ultimately transfer the 'unaccounted for' biomass to TD through SD, L and LD. There are evidences that some direct transfer of live biomass to the litter compartment may take place (Golley, 1965). The wastage of green vegetation may take place due to grasshopper activity (Mitchell, 1973), ants, other insects and small mammals (Currie & Goodwin, 1966). Nest-forming birds may have directly removed some biomass as some local birds were seen removing *Tragus roxburghii*, a small-sized tender graminoid. It was also seen in the nests of some birds in the vicinity. In addition to these factors some of the 'unaccounted for' biomass could be due to respiration by plants in dry periods when they can not photosynthesize. Some material must have also been translocated downward to help plants survive the unfavourable season (Struik, 1965; Singh & Yadava, 1974). Some loss of litter must have taken place during gales, which is a common feature in arid and semi-arid areas.

Table 12. An annual balance sheet of dry matter.

Compartments	Biomass $(g.m^{-2})$
ANP	
Initial biomass	20.6
ANP	375.9
Total input into the system	396.5
Transfer to SD	259.2
Biomass at the end	34.0
Total output	293.2
Unaccounted for	103.3
BNP	
Initial biomass	376.8
BNP	834.4
Total input into the system	1211.2
Disappearance of the biomass	747.2
Biomass at the end	464.0
Output	1211.2
Unaccounted for	0
SD	
Initial biomass	80.5
SD production	259.2
Input into the system	339.7
Transfer to litter	120.8
SD at the end	219.2
Output	340.1
Unaccounted for	0.4
Litter	
Initial	56.4
Litter production	120.9
Input into the system	177.3
Litter disappearance	60.7
Litter at the end	116.6
Output	177.3
Unaccounted	0

The greater estimates for SD, L and LD calculated in accordance with the above-given assumptions amounted to 362.6, 223.8 and 163.6 $g.m^{-2}$, respectively, for this site.

System transfer functions (Tfr): Tfr is the quantity by which the system block multiplies the input block to generate output (Golley, 1965). It reflects the orientation of the functioning of an ecosystem in space and time (Sims & Singh, 1971). The Tfr were calculated on the whole year basis using the values of various compartments in the block diagram and also the values of greater estimates.

Table 13. System transfer functions (Tfr).

Compartments	Tfr (annual)	Tfr (annual)*
TNP to ANP	0.311	
ANP to BNP	0.689	
ANP to SD	0.689	0.964
SD to L	0.466	0.617
ANP to L	0.322	0.595
L to LD	0.502	0.731
BNP to RD	0.894	
TNP to TD	0.667	0.803

*Based on greater estimates of SD, L, LD and TD. TNP, Total net primary production; ANP, Aboveground net primary production; BNP, Belowground net primary production; SD, Standing dead; L, Litter disappearance; RD, Belowground biomass disappearance.

Tfr data (Table 13) indicated greater below ground-directed productivity (68.9%) in this site exhibiting typical desert conditions. Some 69% (96.44% if greater estimates are considered) of ANP entered the SD compartment and 47% (62% on the basis of greater estimate) of SD was directed to litter production. Some 50% on normal estimate basis and 73% on greater estimate basis, of litter, is decomposed. The total loss of TNP through TD was 67% (80% on greater estimate basis).

Efficiency of energy capture (EEC): To investigate EEC, calorific values of live and dead standing biomass of important species and that of composite samples of litter and below ground biomass were determined by adiabatic bomb calorimeter by forming compact pellets oven-dried powdered material and re-drying the pellets at 80°C. The pellets were burnt in bomb under 30 atm. O_2 pressure using platinum wire. Ash contents were determined by combustion in muffle furnace. The mean calorific values of *D. scindicum* and *C. setigerus* on dry wt. and ash-free basis as well were more or less equal and *L. scindicum* had somewhat higher value. The calorific values were generally higher in August and September (October) (Table 14 and Fig. 11) after summer rains and February and March after winter rains. Peak values were generally associated with peak vegetative and reproductive growth. The calorific values for the months of May and June and rainless July were generally low. These results are similar to those reported by Singh & Yadava (1973) for some graminoids of India. The calorific values on dry wt. basis for litter varied considerably from 2398 cal.g^{-1} in April to 3866 cal.g^{-1} in the initial month and 3803 cal.g^{-1} in September (Fig. 12) after rainy season growth. The lower value in August appears to be the result of the weathering effect. The fluctuation in the calorific values of standing dead material is presumably due to the varied values of the source material belonging to different species and the weathering effect. In the below ground biomass (Fig. 12) the calorific values dry wt. basis ranged from 2828 cal.g^{-1} in April to 4257 cal.g^{-1} in post-rain month of October.

Table 14. Calorific values (g.m⁻¹) of live and standing dead biomass of some perennial and annual/ephemeral species emerging after rains in *L. scindicus* community.

Species	Jun,90	Jul	Aug	Sept	Oct	Nov	Dec	Jan,91	Feb	Mar	Apr	May
A. javanica		*	3817									
B. sinica			* 2864									
				** 2382								
C. setigerus	* 2592	2633	2534	2573	3151	3180	3212	2836	3151	2630	3280	2642
	** 2707	2799	2720	2952	3592	3472	3501	3008	3466	2962	3628	2957
	*** 3007			2845	2539	3011	3786		4743	4393	3470	2185
C. atkinsonii		*	3652									
C. bulbosus		*	3449									
D. scindicum	* 2737	2698	1582	3060	2903	2914	2981	2513	2992	3165	3271	3278
	** 3026	3006	1721	3279	3201	3159	3321	2728	3320	3443	3564	3480
		***	3502		3336		3274		3221		2756	3526
I. cordifolia		*	3168									
I. linifolia							*		2870			
I. oblongifolia							*		3924			
							**		3729			
L. scindicum	* 3473	2960	3464	3952	3686	3956	3585	3562	3804	3011	2932	3492
	** 3680	3330	3785	4169	4010	4097	3773	3861	4023	3338	3071	3669
		***	3653		2790			3721	3497			3227
L. senegalensis		*	2899									
O. ramosa							*		2852			
R. schimperii			* 3850									
				*** 3082								
S. pakistanica			* 3394			3180					2943	
			** 3073		2710						2845	
T. strigosa			* 3503									
			** 3001									
T. subtriflora			* 3392									
			** 2999									
T. roxburghii			* 3770									
			** 3498									

The values rounded to two decimal places.
*D. wt. basis of live biomass, **On ash-free basis of live biomass. ***D. wt. basis of standing dead biomass.

Mean calorific values representative to different producer compartments were calculated as a function of calorific values of live and dead components of important species entering the community composition and the litter and below ground biomass collected during the observation period. Such values for above ground live, standing dead, litter and below ground biomass were 3321, 3286, 3161 and 3251 cal.g⁻¹, respectively.
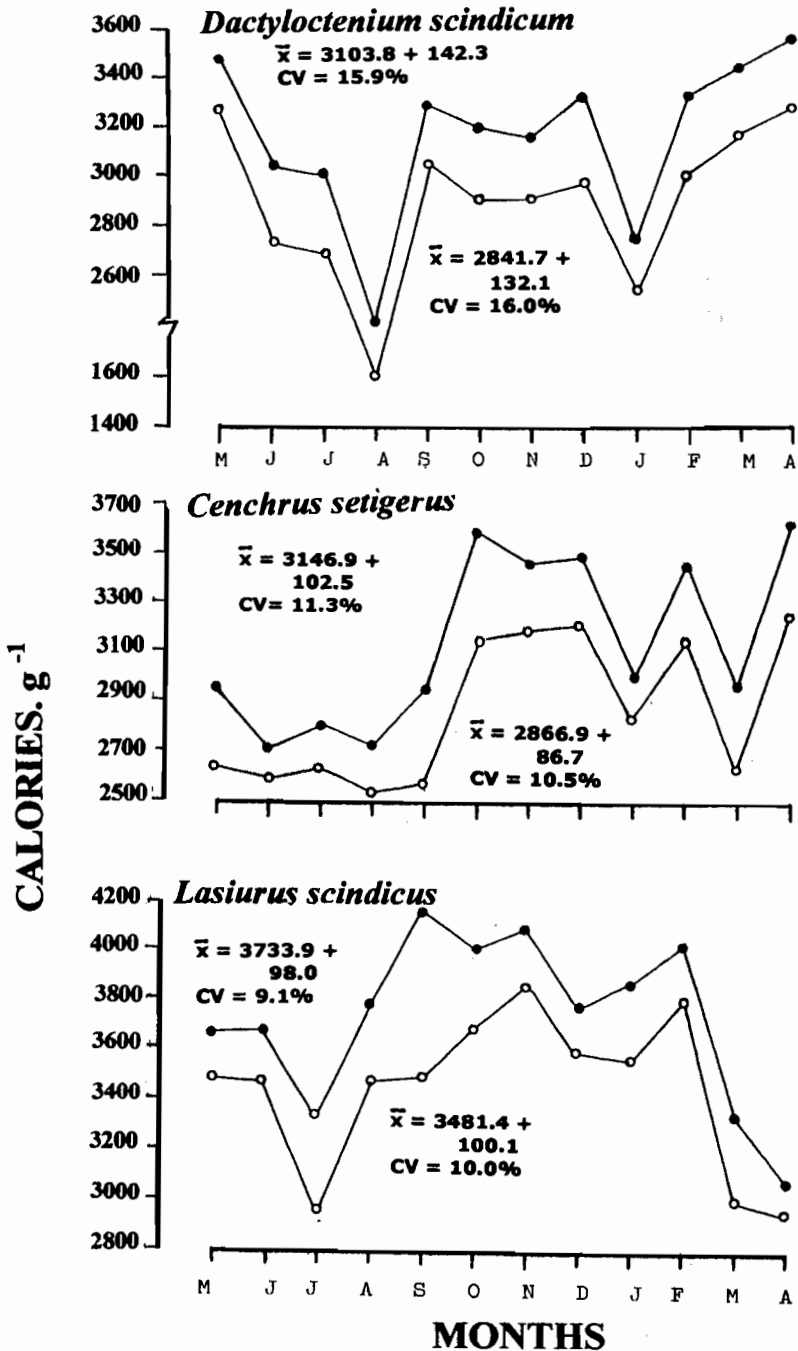
Fig. 11. Variation in calorific value of live above ground biomass of *D. scindicum*, *C. setigerus* and *L. scindicus* throughout the year, (solid circle: Ash-free biomass, open circle: on dry wt. basis.
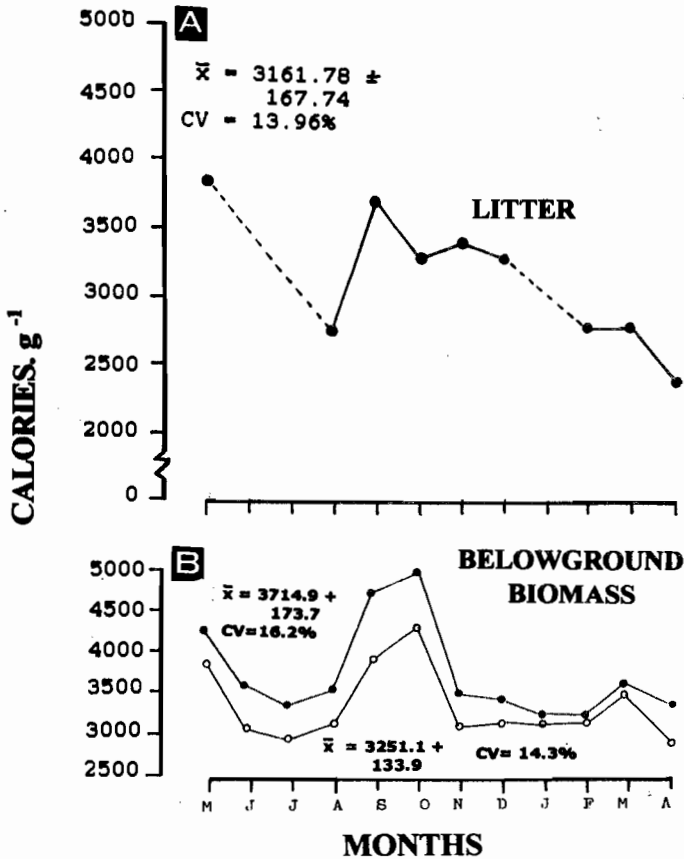
Fig. 12. Variation in calorific value of litter (A) and below ground biomass (B) of dry *L. scindicum* sit. (open circle: on dry wt. Basis and closed circle: on ash-free basis).

Efficiency is the ratio of output (calories in vegetation) to input (radiant energy) (Botkin & Malone, 1968). When it is based on total radiation, it is referred to as "relative efficiency" and when it is based on photosynthetically efficient radiation (0.4 - 0.7 (m), it is called "absolute efficiency". For calculation of energy capture efficiency, Botkin & Malone (1968) have opined that the actual amount of light intercepted by the canopy should be considered. Since, data on interception and albedo is not available, 50% of total incident solar radiation is termed here as usable incident solar radiation following the practice of Singh & Yadava (1974). This amount is roughly equivalent to the solar radiation available to plants for photosynthesis (Daubenmire, 1959; Singh & Misra, 1968; Yokum, 1961; Sims & Singh, 1971, 1978).

In the present studies, efficiency is determined on the basis of calorific values of ash-containing matter of species-samples as suggested by Murphy (1975). Based on the usable solar radiation, EEC in ANP, BNP and TNP of this dry site amounted to 0.15, 0.32 and 0.47%, respectively. In grasslands situated in different parts of the world the value of EEC of 0.1 to 5.1% have been reported (Golley, 1960, 1965, 1968; Botkin &
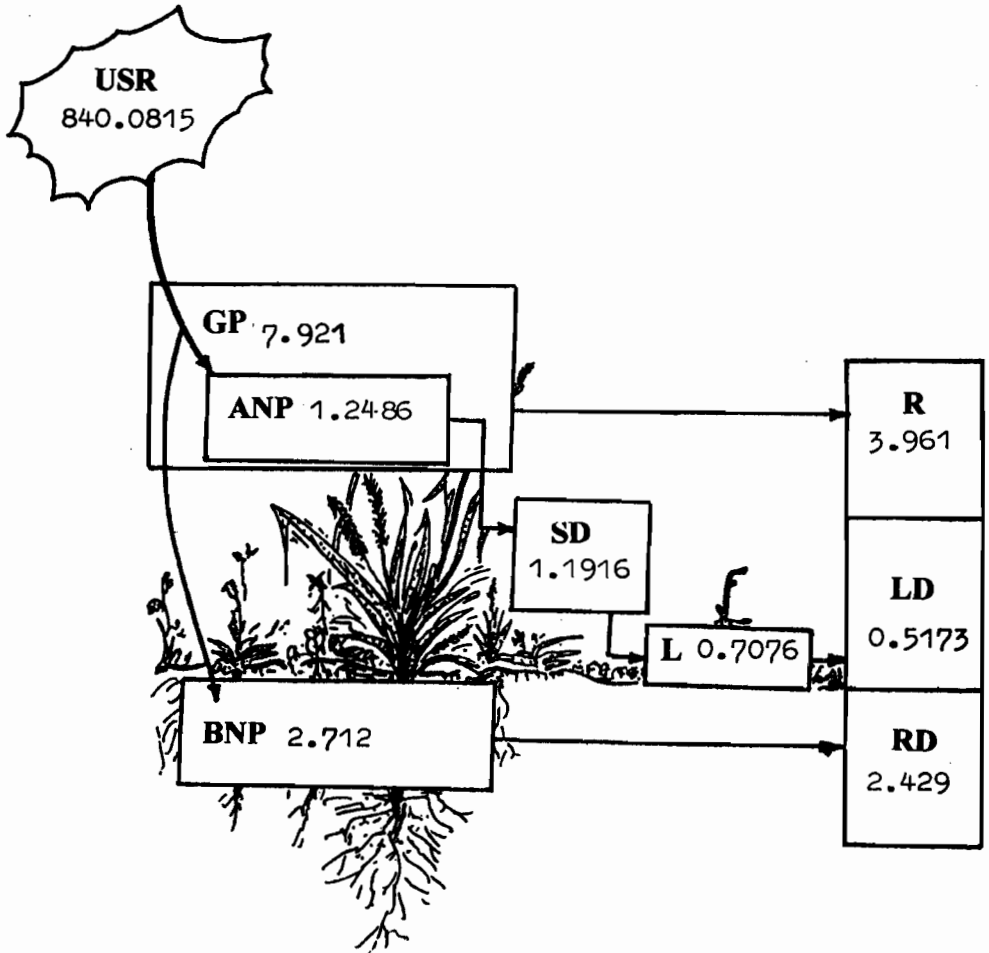
Fig. 13. Annual energy flow through producer compartments in a dry site. All values in Kcal.m^{-2} (x 1000).

Malone, 1968; Sims & Singh, 1971, 1978; French, 1979; Coupland, 1979). The perennial grasses of Japan were reported to have ANP-EEC 0.51% based on photosynthetically available radiation for growing season and 0.35% on annual basis. For desert community of Arizona ANP-EEC was much low around 0.06% only and for alpine tundra (xeric) community around 0.2% (Jordon, 1971). Misra & Misra (1989) have reported efficiency value of 0.81% for perennial *Aristida setacea* dominatecd community receiving rainfall as high as 1200mm and situated in Brahampur on the coastal belt of Bay of Bengal. Data on EEC for grass dominated communities of Pakistan is not available for comparison. However, Chughtai *et al.*, (1978) have presented EEC estimate for a cultivated legume (*Phaseolus acontifolius*) from Peshawar to be 0.26 and 0.56% on the basis of total solar incident and photosynthetically available radiation, respectively. Comparison with estimate is difficult because their data is based on a time-period of one growing season (one month). However, grasses, particularly C_4, are far more effi-

cient CO_2 utilizers than legumes (C_3 plants) and better adapted to high insolation and temperature (Mott & Popenoe, 1977).

Annual energy flow (AEF): An estimate of AEF through the primary producer compartments is depicted in Fig. 13. The new symbols used in the diagram are usable solar radiation = USR, gross primary production = GP and respiration = R. The values of GP and R are hypothetical being based on the assumption that generally 50% of the gross primary productivity is realized as net primary production and 50% is dissipated via respiration (Odum, 1971). For SD, L, and LD compartments, their greater estimates are used to construct AEF diagram.

Some 68.5% of the energy fixed in TNP moved towards below ground production and 32,5% stayed above ground. The energy that dissipated through root and litter disappearance constituted 74.4%. Nearly 25% of the total energy fixed in TNP remained surplus in this site. The greater energy allocation in BNP appears related with the effects of grazing to which this site has been exposed over past years (Pearson, 1965; Smith, 1980). The net surplus of 25% of total energy fixed in this community indicates its tendency to move towards a scrub forest type (cf. Golley, 1972). In arid regions this process is obviously very slow. Under conditions of disturbance such sites are being rapidly colonized by *Prosopis juliflora*, an aggressive exotic species. At several places it has indeed changed the physiognomy of the landscape (Khan & Ahmad, 1992).

As environmental conditions in arid areas vary considerably over years with intermittent droughts and irregular precipitation, long-term studies could only provide more reliable and practically useful production estimates for this fragile and young ecological system. Moreover, the energetics of our grass-dominated systems should be investigated in a network of localities representing different agro-ecological zones of Pakistan to develop better eco-developmental strategy for our rangelands.

Acknowledgement

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