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ON THE VEGETATIONAL DYNAMICS OF CALCARIOUS HILLS AROUND KARACHI

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Abstract

Taken together, the findings reported in this paper suggest the prevalence of a progressive succession which seems to be governed initially by extrinsic factors but subsequently largely by the intrinsic properties of the plants. The major reaction of plants of various stages on the edaphic characteristics involved progressive decrease in soil pH and $CaCO_3$ coupled with the increase in soil depth, organic matter (humus), percentage of silt and clay and the consequent increase in maximum water holding capacity of soil that results in the gradual improvement in moisture regime from pioneer to the climax stage. Community attains progressively greater stability as the vegetation proceeds to the climax but diversity after increasingly initially declines somewhat in the terminal communities pointing to the monopolization of environmental resources by the members of the most stable terminal communities. Improvement in community structure during the sere involves increase in standing crop and to a lesser extent in absolute density, elaboration of stratification, and increase in the proportion of chamaephyte and phanerophytes and of species with relatively bigger leaf size. All the structural changes are related to continuous improvement in moisture and nutrient regimes.

Introduction

A brief account of the syndynamics of calcarious hills around Karachi was given by Choudhri (1961), but this description being based only on a few representative stands, is incomplete. Shaukat & Qadir (1970) conducted an extensive survey of the vegetation of the hills and found a close relationship between the seres and aspect and the nature of the slopes of the hills. However, the edaphic factors governing the distribution of plant communities were not considered. Apparently, no report exists regarding the environmental changes associated with the vegetational progression of the hills in desert condition.

The objectives of the present investigation were a) to provide a quantitative description of the successional pattern including changes in structure and community organization with emphasis on diversity and stability relations, b) to assess the relationships between vegetational dynamics and edaphic variables.

Description of the area

Karachi district lies between the latitude 24°-40', 25°-15' North and between the longitude 65°-51' and 67°-40' East. The hills found in the vicinity of Karachi are calcarious in nature, marine in origin and belong to the upper tertiary period (Pithwala, 1946). The climate of Karachi is of the type 'BWh' of Koppen (1936). The bioclimate of Karachi, determined by Holdridge's (1947) system comes in the category of "Tropical desert bush formation." The details of climatic conditions and geology of the area are described at length elsewhere (Qadir *et.al.*, 1966; Shaukat *et.al.*, 1976).

The wind velocity, temperature and humidity, which are usually high, are the physical forces that cause weathering of rocks and thus play an important role in the dynamics of vegetation of the hills under study.

Materials and Methods

Vegetational sampling: Twenty-four stands situated on the slopes of calcarious hills around Karachi were studied. The stands were selected in such a way as to provide representative samples of various stages of lithosere succession. Criteria for the selection of a stand were adequate size (2 hectare or more) of the sample area and absence of any major disturbance whether physical or biological. The stands were sampled by point-centered quarter method (Cottam & Curtis, 1956).

Vegetational analysis:

Importance value index (I.V.I) of each species was computed in accordance with the practice of Curtis & McIntosh (1951) and averaged for the different stages of the lithosere succession. The dominance was ascertained by the Index proposed by Simpson (1949) as follows: $C = \Sigma pi^2$ where pi = the proportion of I.V.I. Contributed by ith species to the total importance value of a stand. General diversity was determined by the information theory function, $\bar{H} = -\Sigma pi \log_e pi$ (Margalef, 1957), equitability was calculated as $e' = \bar{H}_{max}$ (Pielou, 1969) and species richness was simply the number of species (S). The community maturity was established using the index proposed by Pichi-Sermoli (1948) as follows: Community maturity (CM) = $\frac{\Sigma F'_3}{S}$ where F_3' equals the percentage frequency of a species and S equals the number of species. However, the stability of communities (related to maturity) was also independently evaluated by the application of the 'Community quality index concept' proposed by Vasek *et al*, (1975). This concept is related to stability through life span considerations which is believed to be particularly appropriate for desert communities (cf. Johnson *et al*, 1975). Accordingly, stability is here judged on the basis of the proportion of long-lived perennials.

Species present in the stands were assigned to life-form in accordance with Raunkiaer (1934) and leaf-size of randomly chosen plants of each species were measured and the species classifed according to their leaf-size (Fuller & Bakke, 1918; Raunkiaer, 1934).

The ecological affinities among the perennial species were ascertained by constructing a polar ordination of species following the procedure described by Gittins (1965). The polar ordination technique has been shown to be relatively less vulnerable to the effects of beta-diversity, sample clusters, out-lier samples and is comparatively free from distortions from non-linearity compared to many recently developed mathematically elegant ordination methods (Gauch & Whittaker, 1972; Gauch *et al,* 1977).

Soil analysis:

Soil depth in each stand was noted at 3 (three) different spots in a stand and soil samples were collected. The analysis of soil-texture was carried out by Pipette method (USDA, 1951). Humus content of soil was determined by hydrolysing in 10g of oven dry soil with 10 ml of 30% of H_2O_2; the loss in weight gave the quantity of humus. Soil calcium carbonate ($CaCO_3$) was determined by treating 10g of soil with 20 ml of 10% HCl; the $CaCl_2$ thus formed was filtered and loss in weight represented the approximate $CaCO_3$ content of soil (Qadir *et al,* 1966). Soil pH was measured by Cambridge pH indicator (Pat. No. 63621) after preparing the samples according to Peech *et al* (1947). Maximum water holding capacity (MWHC) of soil was determined acording to the procedure described by Keen (1937).

Taxonomic nomenclature in this paper follows that of Stewart (1972).

Results

a) Stages in the Lithosere:

The successional pattern is interpreted on the basis of the study of contemporaneous spatially separated stands as members of the seres since the process of succession on the calcarious hills is exceptionally slow owing to xeric conditions and hard nature of the lime-stone substratum. Consequently the method of comparison is the only one which was feasible. The vegetational sequence is described below, by arbitrarily dividing the entire lithosere succession in five stages (Fig. 1) for the convenience of description and interpretation.

1. *Early stage:* Initially, on the rocky slopes of the hills, whenever the rock is completely bare, it is occupied by crustose lichens of which the principal ones are *Cladonia* and *Rhizocarpon* (not shown in Fig. 1 as sampling was restricted to shrubs and trees only). These can contribute little or nothing to the processes of weathering but indicate

the suitability of the substratum for further colonization. Lichen establishment is apparently not an essential preliminary to further colonization.

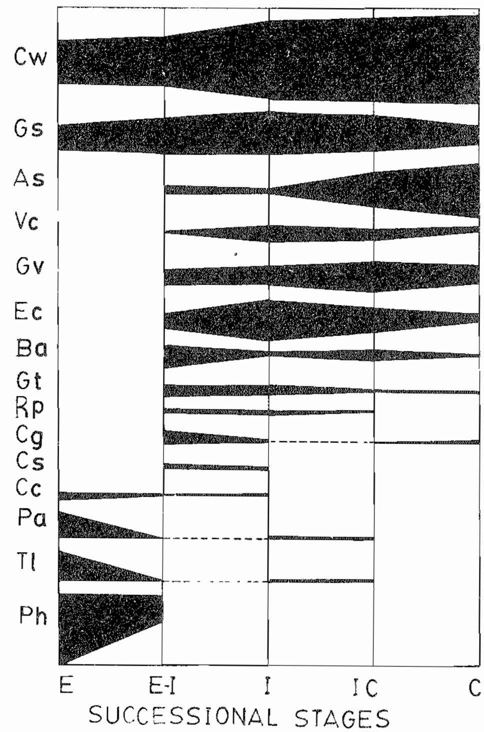


Fig. 1. Relative conspicuousness of shrubs and trees, as indicated by their average importance value index (I.V.I.) in the arbitrarily defined stages of the lithosere succession. Key to symbols: As *Acacia senegal:* Ba, *Barleria acanthoides;* Cc, *Capparis cartilaginea;* Cg, *Cordia gharaf;* Cs, *Commiphora stocksiana;* Cw, *Commiphora wightii;* Ec, *Euphorbia caducifolia:* Gt, *Grewia tenax;* Gv, *Grewia villosa:* Gs, *Grewia sp.* Pa, *Paripolca aphylla;* Ph, *Pulicaria hookeri;* Rp, *Ruellia petula;* Tl, *Taverniera lappacea;* Vc, *Vernonia cinerescens.*

Riccia rafiqii and annual herbs like *Lindenbergia indica, Glossonema varians* and *Kicxia ramosissima* can be seen to be clonizing bare rocks as well as growing in association with crustose lichens. The seeds of the above mentioned herbs possibly germinate on the wind blown sand and humus that accumulates at some microhabitats. *Pulicaria hookeri,* an indigenous shrub, generally occurs as an exochomophyte but sometimes also grows as a lithophyte in association with the above mentioned plants. There pioneer phanerogams are seen to penetrate their roots upto 10 cm. in the rock and play a significant role in the weathering process though physical forces like diurnal temperature fluctuations and high wind velocities and humidity are the more important agencies in this respect. Partly due to abrasion caused by penetrating roots of the pioneer phanerogams and the trapping of wind-blown dust and humus and plant remains and mainly due to the action of physical agents small fragments of rocks and a little quantity of soil is produced which is sufficient to provide favourable conditions for the colonization of the seedlings of shrubs like *Commiphora wightii, Taverniera lappacea, Capparis cartilaginea, Periploca aphylla* and *Grewia* sp. (hybrid of *G. tenax* and *G. villosa*) (Fig. 1). However, long before this initial weathering small crevices in rocks (produced by physical forces) became filled with wind-blown sand and dust. The crevices are colonized by chasmochmophytes like *Viola stocksii, Fagonia arabica, Sporobolus marginatus, Lasiurus hirsutus* and *Pluchea arguta.*

2. *Early intergrading to intermediate:* With the formation of some soil and the enlargement of crevices by the above named chasmochomophytes the flora becomes quite varied. Shrubs like *Euphorbia caducifolia, Cordia gharaf, Commiphora stocksiana, Grewia tenax. Grewia villosa, Vernonia cirerescens* and few seedlings of *Acacia senegal* are able to establish on the shallow soil while *Ruellia petula* and *Barleria acanthoides* invade the enlarged crevices. The importance value of *Pulicaria hookeri* decreases and *Pluchea arguta* and *Taverniera lappacea* loose ground completely to the invading species.

3. *Intermediate:*

The importance value of *Euphorbia caducifolia, Grewia* sp. and *Commiphora wightii* and *Vernonia cinerescens* increase as the depth of soil crust (mingled with gravel) increases.

4. *Intermediate intergrading to climax:*

The importance value of the terminal species like *A. senegal* increases. This plant which in the former stages grows in the form of shrubs. now acquires a tree habit. *Grewia villosa,* a medium sized shrub also attains greater importance but *Grewia sp.* and *V. cinerescens* tend to diminsh. The average importance value of *E. caducifolia,* the giant cactoid-spurge, though declines but actually in some stands it becomes more prominent. However, in most of the stands it seems to loose ground in favour of the more aggressive *C. wightii.* Whenever, *C. wightii* is one of the dominant species, it attains tree-like habit. The strong and deep root systems of *C. wightii* and *A. senegal* contribute a great deal towards soil development.

5. *Climax:*

The climax stages are found on the slopes of the hills where substantial soil has been formed and such communities are evidently of two types. The climax communities dominated by *A. senegal* and *C. wightii* are the ones that are more common than the communities where the dominance is shared between *Acacia senegal, E. caducifolia* and *G. villosa.* In the latter type *C. wightii* has relatively much lesser importance value than in the former type.

The wide spread distribution of *C. wightii* throughout the successional stages examined, somewhat confounds its successional position. However, its dominace can be explained on the grounds that it can grow on almost bare rock to fairly high soil dpeths as well as crevices. Furthermore, it is a very drought resistant species (Choudhri, 1961) and has a wide ecological amplitude (Baig, 1966).

b) Ecological affinities among three and shrub species:

Fig. 2 shows the ordination of 15 species in XY, XZ and YZ planes. The distance of species in the three ordination planes and the dissimilarity values of the R-type matrix for random samples of 30 pairs gave significant correlations ($r = 0.569$, $p < 0.001$, $r = 0.520$, $p < 0.01$ and $r = 0.552$, $p < 0.01$ for XY, XZ & YZ planes respectively). indicating that the ordination of species very elegantly portrays the acutal ecological relationships among the species. The ordination used *P. hookeri* and *A. senegal*, the pioneer and the terminal species respectively as the reference points for the construction of primary (X) axis; consequently this axis represents the successional gradient. *T. lappacea* a pioneer undershrub, and *C. gharaf*, a shrub of later stages of the succession furnished the reference set for secondary (Y) axis. Whereas *B. acanthoides*, a plant of crevices and *Grewia* sp., a plant that prevails throughout the successional sequence, provided the end points for the erection of tertiary axis. The distribution of species, in all the three ordination planes, is essentially continuous and discrete clusters and unrecog-

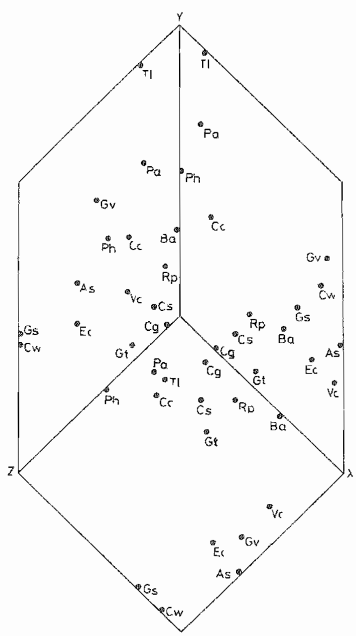


Fig. 2. Species ordination of the 15 shrub and tree species of the calcarious hills. For key to symbols refer to the legend of Fig. 1.

nisable (Fig. 2), providing evidence on the continuous and gradual change in vegetational composition. The pioneer angiosperms, *P. hookeri, T. lappacea, C. cartilaginea* and *Periploca aphylla* are situated on the left side of the XY ordination plane. Species of intermediate stages on weathered rock like *C. gharaf, C. stocksiana* and *G. tenax* and those of enlarged crevices like *Barleria acanthoides* and *Ruellia petula* occupy medium position on the X-axis (central position on XY plane) whereas the dominants of terminal communities viz. *A. senegal, E. caducifolia, V. cinerescens* are located towards the right side of the XY plane. Since *B. acanthoides,* a plant of rock crevices and *Grewia* sp., a plant of soil crust were chosen as the end points for tertiary axis, it portrays the ecological propinquity among the species of rock crevices and that among the species of the flora of the two niches. In the YZ and XZ ordination planes *B. acanthoides* and *R. petula,* the chasmochomophyte occur close together. Early colonizers of rocks like *P. hookeri, T. lappacea* and *C. cartilaginea* are also located either in the vicinity of each other or have somewhat similar positions on the Z-axis. Climax dominants are also situated close together, particularly in the XZ plane.

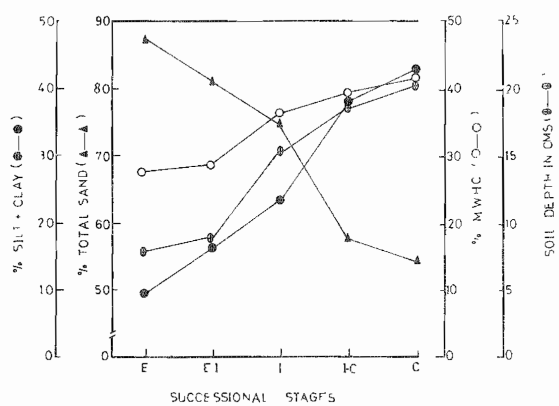


Fig. 3. Changes in soil physical characteristics along the vegetational progression. (MWHC, maximum water holding capacity).

c) *Environmental control of the succession:*

Rational predictions of successional outcome can be made only by considering the environmental factors for a given situation because of the existence of reciprocal interactions of the vegetation and soil. The data on edaphic characteristics of the stands are averaged for the five arbitrarily recongized successional stages (Fig. 3 and 4). Soil properties change dramatically alongwith the advancement of succession. As the succession pro-

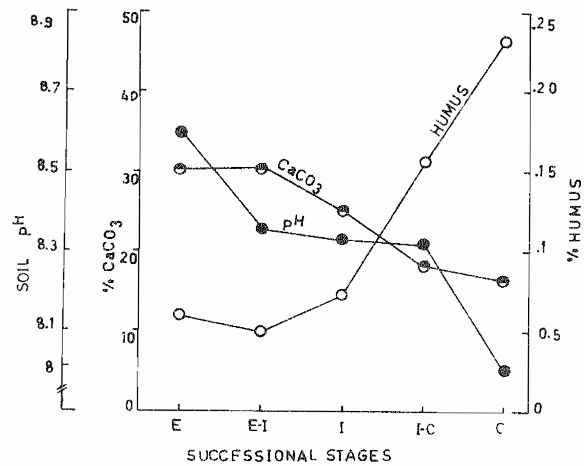


Fig. 4. Changes in soil chemical characteristics along the vegetational progression.

ceeds the soil depth increases more or less gradually. However, a sharp increase in soil depth occur at the intermediate stage. Alongwith the course of lithosere succession soil texture becomes finer, i.e. the percentage of sand particles decreases whilst silt + clay increases, with the consequence that the maximum water holding capacity (MWHC) is increased (Fig. 3), resulting presumbaly in increasingly more favourable moisture regimes. With the death and decay of plants, particularly the annuals that each year contribute a good deal of organic matter to the soil, the humus content of soil continuously increases along with successional march. Since all the shrubs and the tree found on the calcarious hills are deciduous, the annual contribution of leaves from these plants also plays a preeminent role in the increment of the humus content.

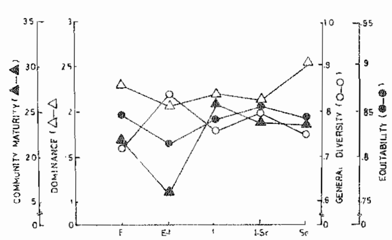
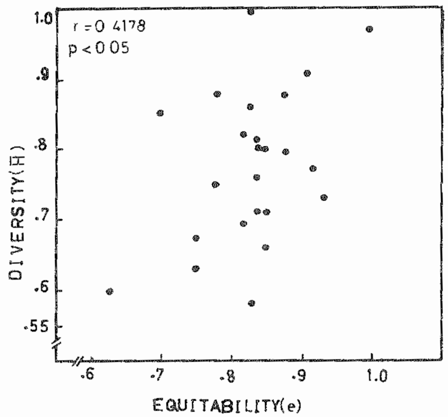


Fig. 5. Changes in community maturity, dominance, general diversity and equitability of shrub and tree species during the lithosere succession.

The soil $CaCO_3$ content and pH decreases as the vegetation proceeds from early to climax stage. A significant correlation ($r = 0.647$, $p < 0.01$) exists between pH and soil $CaCO_3$ content.



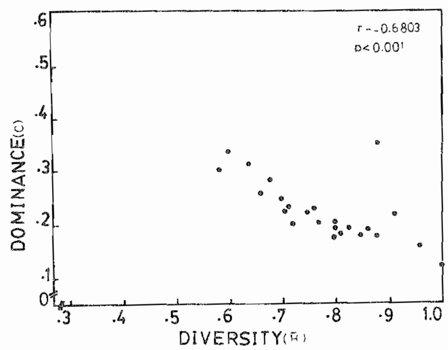


Fig. 6. Relationship between general diversity and equitability.
Fig. 7. Relationship between dominance and general diversity.

d) *Dominance, diversity and stability relations:*

Fig. 5 shows the changes in general diversity (H), equitability (e), dominance (c) and community maturity (CM), based on trees and shrubs, during the vegetational progression. Initially the general diversity is low and increases sharply in the 'early intergrad-

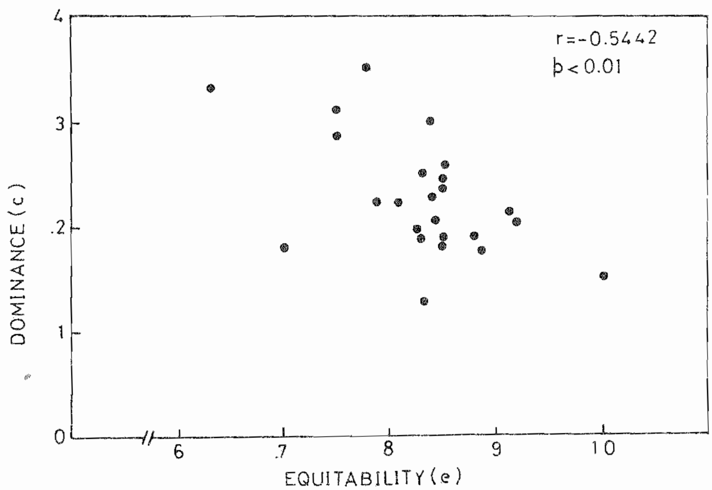


Fig. 8. Relationship between dominance and equitability.

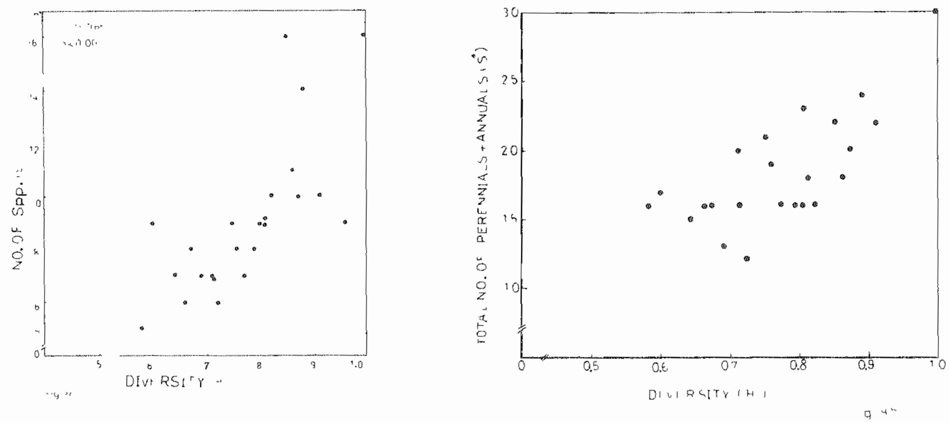


Fig. 9 (a) Relationship between richeness (s) of shrub and tree species and their general diversity.
Fig. 9 (b) Relationship between total number of species (s*) and general diversity of shrubs and trees. See text for explanation.

ing to intermediate' stage but subsequently declines and then remains more or less steady at a slightly higher level than that of the early stage. The equitability component of diversity declines in the 'early to intermediate' stage but thereafter increases and runs somewhat parallel to general diversity. On the other hand, dominance at first declines then remains practically at the same level upto 'intermediate intergrading to climax' stage but increases sharply in the climax communities. The community maturity index declines initially but then increases sharply in the intermediate stage and then diminishes very slightly. These community attributes are generally dependent on one another. General diversity is significantly positively correlated with equitability ($r = 0.417$, $p < 0.05$; Fig. 6). In contrast dominance, as expected, is strongly inversely related to general diversity ($r = -0.680$, $p < 0.001$; Fig. 7) and to the equitability ($r = -0.544$, $p < 0.01$; Fig. 8). The number of trees and shrubs species represented species richness (S) and had a highly significant positive correlation with general diversity ($r = 0.716$, $p < 0.001$; Fig. 9a) and the total number of species (herbs + trees = S*) exhibit the same relationship ($r = 0.724$, $p < 0.001$, Fig. 9b). On the other hand, community maturity index bears a signifcant inverse relationship with general diversity ($r = -0.601$, $p < 0.01$; Fig. 10) and the number of species (S) also bears the same relation with community maturity ($r = -0.582$, $p < 0.01$; Fig. 11). An attempt was made to relate general diversity to edaphic variables but no discernable trends were seen except in case of the proportion of sand particles in soil which showed a curvilinear relationship with $\bar{H}$ (Fig. 12).

Changes in community stability (related to maturity) based on life span considerations are depicted in Fig. 13, which shows the relative density of short, long and very long-lived species in the different stages of the succession. The proportion of the average relative density of short-lived species declines dramatically during the course of the progression whilst that of very long-lived species shows a continuous increase. The propor-

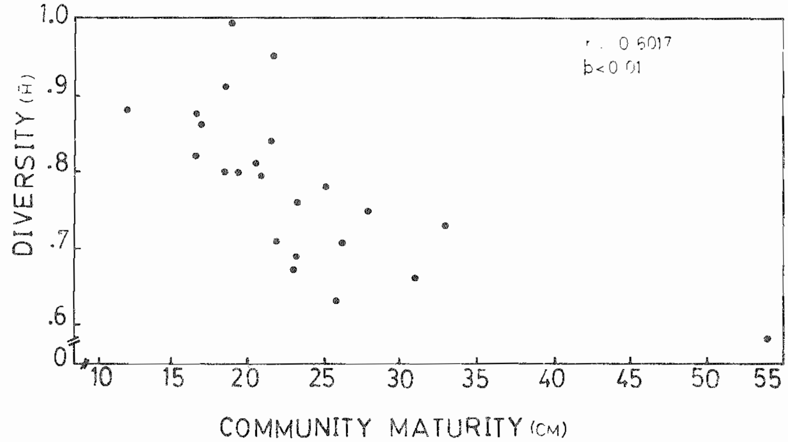


Fig. 10. Relationship between community maturity and general diversity.

tion of long-lived species after increasing intially drops somewhat but on the whole the density of long-lived + very long-lived species increases sharply with the advancement of succession, indicating the increasing community stability alongwith the course of succession.

e) Changes in vegetational structure:

The term 'structure' is used here in the sense as under stood by Dansereau (1957:147), i.e. 'structure' in the present text refers to the growth form, stratification and coverage; the leaf size spectra are also included in this section for convenience and

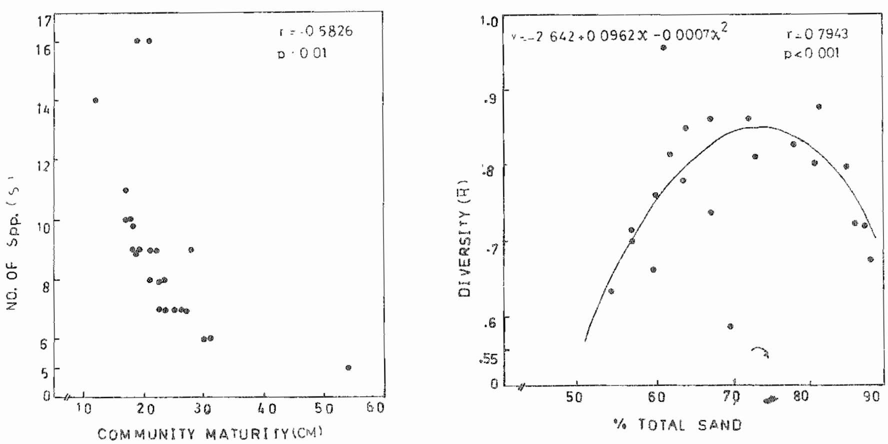


Fig. 11. Relationship between community maturity and species richness.
Fig. 12. Relationship between total sand percentage and general diversity.

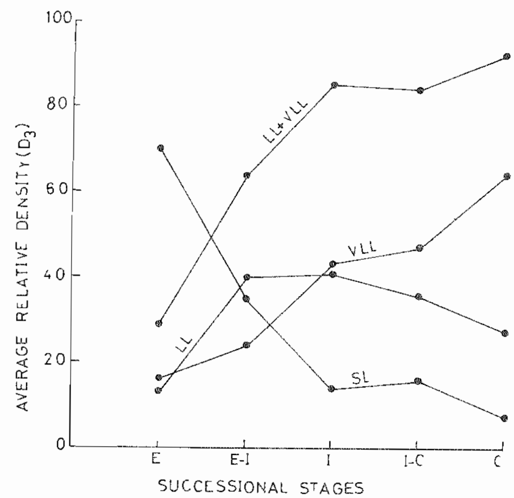


Fig. 13. Changes in community stability during the succession as indicated by the average relative density (D_3) of short-lived(SL), long-lived (LL) very long-lived (VLL) and long-lived+very long-lived shrubs and trees.

because they indicate community function that is corollary to community structure. The sequence of life form invasions and their progression along with the lithosere succession are depicted in Fig. 14. In the early stage of succession the greatest proportion is that of hemicryptophytes whereas phanerophytes and chamaephytes have relatively much lesser

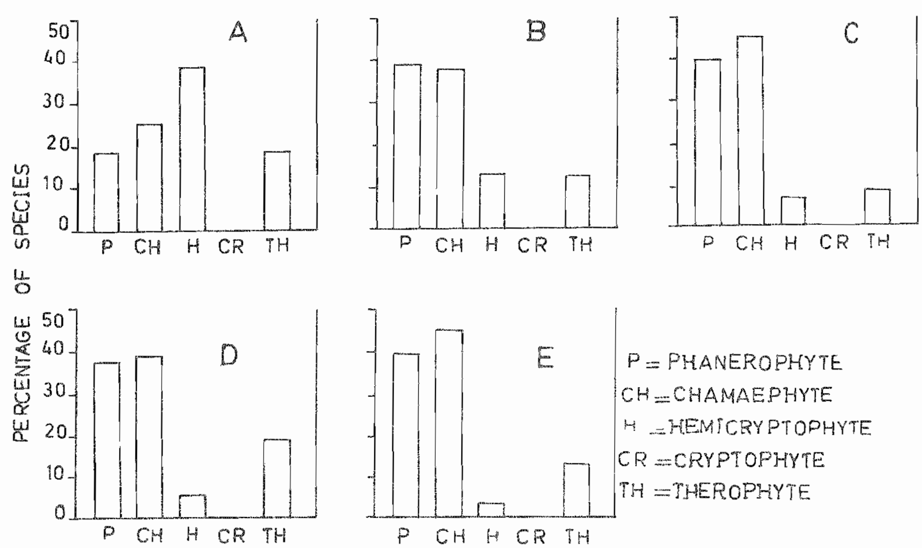


Fig. 14. Life-form spectra in the various stages of the lithosere sucession. A, early; B, early intergrading to intermediate; C, intermediate; D, intermediate intergrading climax and E, climax.

proportion. Cryptophytes were totally absent throughout the progression. In the 'early intergrading to intermediate' stage suddenly the proportion of phanerophytes and chamaephytes increases considerably but that of hemicryptophytes declines. More or less this trend is maintained subsequently but in a more gradual manner. Within the domain of successional sequence, the therophytes are quite substantial in the early stage, they decline somewhat upto intermediate stage but thereafter slightly increased. In climax stage the greatest contribution to the community structure is that of chamaephytes followed by phanerophytes.

In the early stage of succession the stratification is poorly developed and the only discernable continuous layer of vegetation is the herb stratum whereas the shrubs are sparse and are mostly straggling and hardly form a recognizable layer. With the advancement of the vegetation the density of shrubs increases and also many tall shrubs like *E. caducifolia, C. stocksiana, C. gharaf* invade the community whereas small shrubs like *P. hookeri, P. aphylla* and *T. lappacea* decrease in importance with the result that the shrub stratum becomes pronounced and the average height is increased (Fig. 15). The average height of the various strata was calculated by two methods (Fig. 15). Firstly by dividing the average height of each species by the total number of species comprising a given stratum and secondly (for shrubs and trees only) by calculating the weighted average of the height of each stratum taking the cognizance of the relative cover of the component species). In the early stage only herb and shrub strata are recognizable and the tree stratum becomes apparent in the 'intermediate intergrading to climax' stage when *C. wightii* and *A. senegal* acquire a tree habit with pronounced trunks. The height of shrub stratum increases continuously during the vegetational progression as shown by the

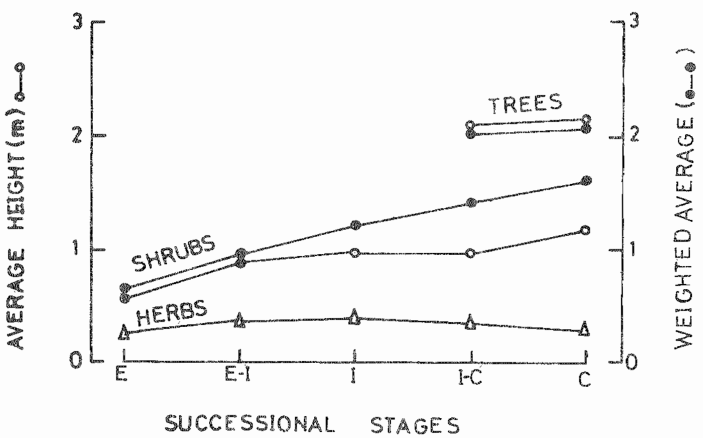


Fig. 15. Changes in average height of herb, shrub and tree species and the weighted average (pro-portional cover x average height of species belonging to the given stratum) of shrubs and trees along the lithosere succession. Note that trees appear only in intermediate intergrading to climax stage.

weighted average height of shrubs. The height of tree stratum is also slightly higher in the climax stage compared to the 'intermediate intergrading to climax' stage (Fig. 15) owing to the increased height as well as increased relative cover of trees. In the intermediate intergrading to climax stage the relative cover of shrubs ranges from 19.8 to 61.00% ($\bar{X}$ = 34.00%) and that of trees 39.80 to 82.61% ($\bar{X}$ = 66.00%) whereas in the climax shrubs from 7.85% to 10.57% ($\bar{X}$ = 8.04%) and trees form 89.43% to 92.15% ($\bar{X}$ = 84.96%) of the total tree and shrub components. The average height of *C. wightii* and *A. senegal* are plotted in Fig. 16 that shows a continuous increase in the height of these two species with the vegetational advancement except that the average height of *A. senegal* slightly drops in the intermediate stage.

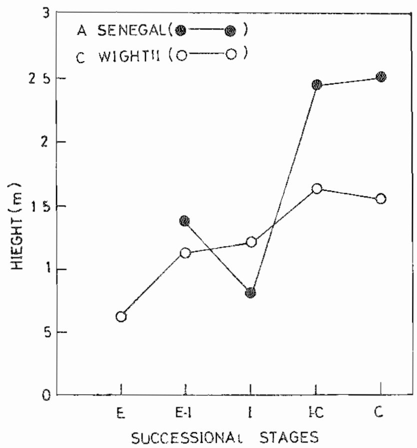


Fig. 16. Changes in average height of *Acacia senegal* and *Commiphora wightii* during the lithosere.

The absolute cover (standing crop) increases rather rapidly as the vegetation progresses from early to sub-climax stage (Fig. 17). However, the increase in absolute density is only slight, indicating that the increment in the standing crop is mostly due to increase in crown (average cover) of the individual shrubs and trees. An attempt was made to relate standing crop to edaphic variables and significant correlations were obtained with the percentage humus ($r = 0.614$, $p < 0.01$), % maximum water holding capacity (MWHC) ($r = 0.768$, $p < 0.001$) and % $CaCO_3$ ($r = -0.677$, $p < 0.001$). A multiple regression equation was developed with the above edaphic variables as the independent variables and the standing crop as the dependent variable; this equation is as follows:

Standing crop = 75.578 + 0.725% Humus + 1.659% MWHC + 0.411% $CaCO_3$ ± 0.624.

Multiple correlation coefficient (R): 0.7755, $p < 0.001$

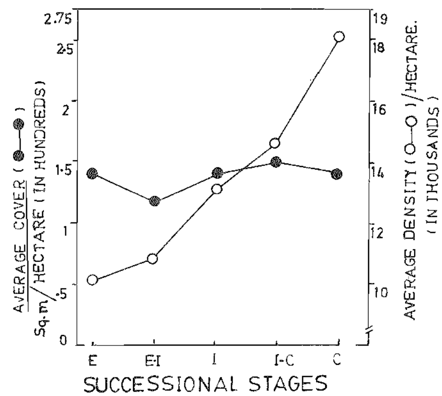


Fig. 17. Changes in average absolute cover (sq.m/ha) and average density per hectare during the succession.

Changes in leaf size spectra during the vegetational progression are depicted in Fig. 18. The most outstanding feature of the leaf size spectra is the high proportion of leptophylls and complete absence of mesophylls in the early stage. Mesophylls appear in the intermediate intergrading to climax stage and subsequently increase in proportion. The proportion of leptophylls also increase upto the intermediate intergrading to climax stage but in the climax their proportion slightly declines. In general, it is quite evident that the proportion of plants with bigger leaves increases as the vegetation proceeds from early to the climax stage.

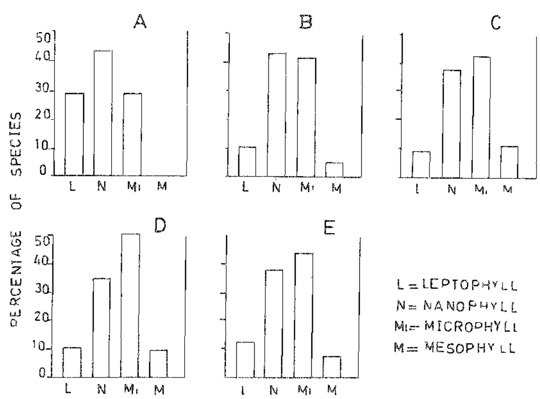


Fig. 18. Rounkiaer's leaf size spectra of the flora of calcarious hills during various stages of succession. A, early; B, early intergrading to intermediate; C, intermediate; D, intermediate intergrading to climax; E, Climax.

Discussion and Conclusions

The process of lithosere succession in arid regions like Karachi is rather different from those in the humid parts of the country. In this region, high humidity of atmosphere, greater diurnal temperature fluctuations and high wind velocities are the more important forces that cause the weathering of rock in the initial stages rather than the activity of cryptogamic flora which is poorly represented in the vegetation undoubtedly due to scanty rainfall. Thus, initially the allogenic forces predominate. Subsequently, however, the succession process is chiefly governed autogenically. The roots of initial colonizers of rock crevices and to a much lesser extent those of the occupants of bare rock help to force open the fissures. The mechanical force exerted by the penetrating roots as well as the accompanying liberation of CO_2 contribute toward rock disintegration. As the succession progresses the soil depth gradually increases and soil texture becomes increasingly finer in response to the activity of the roots of the component plants of various stages. With the increase in proportion of finer particles the maximum water holding capacity of soil also increases resulting in steadily improving moisture regime. The $CaCO_3$ content and pH of soil decline as the vegetation proceeds from early to climax stage. Since the succession involves rock weathering and soil formation, the calcarious material is broken down into increasingly smaller particles. Furthermore, the limestone undergoes chemical weathering and continuously gets converted into soluble calcium bicarbonate that leaches out of the soil resulting in decrease of pH. Obviously, this is the reason for the significant positive correlation found between soil $CaCO_3$ and pH (Salisbury, 1921). Since the decrease in $CaCO_3$ content favours the uptake and availability of certain nutrients, likely the nutrient regime is expected to be continuously improving. Alongwith the advancement of succession the humus content of soil increases steadily, partly because of death and decay of the biota of successive stages and partly because of the annual accumulation of leaf litter from deciduous trees and shrubs. The accumulating humus not only binds the soil particles but also increasingly facilitates the availability of nutrients.

The variability in the composition of seral stages found in the field strongly suggests that the sere is not a strictly organized sequence of changes, but rather a general trend of change in vegetation of loosely ordered complexity (Whittaker, 1957: 203). Such a trend would agree with *Gleason's* individualistic concept of the plant community (McIntosh, 1975), each stage in the sere being product of the accessibility of plant propagules and environmental shifting. The absence of discrete point clusters and the continuous dispersion of species in the various planes of the species ordination also provide evidence on the individualistic behavior of the species as well as the existence of the vegetational continuum. The terminal communities of climax communities were either dominted by *A. senegal* and *E. caducifolia* or by *A senegal* and *C. wightii.* This variation in the dominance of terminal communities support the climax pattern hypothesis proposed by Whittaker (1953), which allows for a continuity of climax types varying gradually in response to variation in environmental conditions of the terminal communities and not neatly separable into discrete climax types. The climax pattern hypothesis of Whittaker is merely an extension of the continuum concept of vegetation. The climax communities were recognized on the basis of relative stability of plant communities, independently of physiographic stability as suggested by Whittaker (1953). The most important increases of community stability are the species composition and structure of the community (Whittaker, 1953; Doubenmire, 1968). If the species composition of a community remains relatively constant over a period of several decades (ecological time scale), one may speak of a stable community. Thus the communities where long and very long-lived species had very high proportion (> 90%) were recognized as climax communities.

The general diversity was low in the earrly stage of succession but it increased suddenly and subsequently declined and then remained more or less steady at a slightly higher level than that found initially. The subject of diversity trends in succession has become a somewhat confused and a controversial issue. Margalef (1963a, 1969) and Monk (1967) demonstrated that progression leads in the direction of high species diversity. In another article, Margalef (1963b) hypothesized that following initial increase in diversity along succession, diversity tends to become stabilized or to decrease slightly as a result of competitive exclusion and other community changes. The present results corroborate the latter view. Whittaker (1965) also comments that so far as the data can be interpreted in relation to community development or succession they suggest that diversities may both increase during succession and decrease during parts of succession. The community maturity index (CM) of Pichi-Sermoli; which works on the principle "that the greater the frequency percent of each species of lesser the number of sporadic species, the more mature is the community", shows a trend which is more or less the mirror image of that of general diversity ($\bar{H}$). The abrupt fall in CM in the early intergrading to intermediate stage is coupled with the sudden increase in diversity and this is obviously due to increase in the number of sporadic species. In the intermediate stage, however, the CM rises sharply associated with the fall in the diversity level because of the competitive elimination of the pioneer species. Thereafter, CM shows small but reciprocal changes, along with the changes in diversity levels. The scatter diagram of diversity ($\bar{H}$) and CM plotted for individual stands disclosed the same negative relationship.

Dominance is somewhat high in early stage as these communities are constituted by few pioneer species. With the invasion of new species the dominance declines, as the community advances, but the dominance once again attains a high level in the climax communites. Dominance exhibited a strong inverse relationship with general diversity as well as with its equitability component. Such an inverse relationship between dominance and diversity has also been demonstrated by a number of workers, e.g. McNaughton (1968), Glenn-Lewin (1975) and Shaukat *et al* (1978). The high dominance in the climax community coupled with low diversity clearly demonstrates the capability of terminal species to monopolize the environmental resources.

The measures of diversity viz., general diversity, equitability and species richness were found to be significantly correlated among themselves which accords with the findings of Auclair & Goff (1971) and Hurlbert (1971). Both the components of general diversity viz., species richness and equitability appeared to be equally important in governing the general diversity as both richness and equitability were more or less equally well correlated with the general diversity.

Community stability that was judged on the basis of the combined proportion of long and very long-lived species in the vegetation was found to increase along with the progression and the climax communities attainted the greatest stability. However, general diversity somewhat declined in the terminal communities and did not show a positive relationship with stability. Thus we are led to question the often quoted postualte of modern ecology that stability increases with diversity (Elton, 1958; see also Wilson & Bossert, 1971). However, the demonstration by May (1973) that diversity and stability do not go together in mathematical models as well as in the 'natural world' seems noteworthy in this regard. The low diversity high stability situations have also been reported by Daubenmire (1966) for north western forests of America and by Johnson *et al* (1975) for Majave desert.

The community structure changes dramatically during the lithosere progression. Plant community in the early stage is simple unstratified with low coverage, being composed of high proportion of hemicryptophytes with the major proportion of species belonging to small leaf size classes. As the vegetation progresses the plant community differentiates into herbs and shrub and in the later stages the tree stratum becomes most conspicuous. In the early stage plant cover is scanty but the coverage increases rather sharply as the vegetation progresses towards the climax a result of the increasing proportion of chamaephytes and phanerophytes. Leaf size spectra also changes remarkably during the succession. The proportions of leptophylls and nanophyls decline whilst that of microphylls and mesophylls show an increasing trend from early to climax stage indicating the gradual improvement in moisture regime.

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