

Interaction of ecology, taxonomy and distribution in some Mesembryanthemaceae

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ABSTRACT

Many taxa of the family Mesembryanthemaceae show close correlations between distribution and environmental factors, e.g. occurrence on limestone or quartzite only, but few cases have been studied in detail. Recent investigations in anatomy, morphology, life cycles, physiology, and in energetic properties indicate that fundamentally different patterns are developed in adaptation to arid conditions, even in reaction to identical edaphic and climatic factors.

On the other hand, little is known about the immediate influence of changes in the natural environment. Studies in populations of the subgenus *Cephalophyllum* of the genus *Cephalophyllum* N.E. Br. show strong correlations between precipitation data and habit, which can superimpose genetic dispositions. In addition, growth forms are well adapted to certain types of plant communities, so that superficially, a diffuse structural pattern results.

Long term studies, in the field and in the greenhouse, of growth forms in relation to time, to precipitation, and to associations, allow first suggestions for adaptive pathways in the evolution of the group, and the results form a basis for taxonomic decisions in this highly confused taxon. Finally, the example offers aspects for the better understanding of interaction between ecology and distribution data.

RÉSUMÉ

INTERACTION DE L'ÉCOLOGIE, DE LA TAXONOMIE ET DE LA RÉPARTITION GÉOGRAPHIQUE CHEZ CERTAINES MÉSEMBRYANTHÉMACÉES

Baucoup de taxons de la famille des Mésembryanthémacées montrent d'étroites corrélations entre la répartition géographique et les facteurs du milieu, par exemple, leur présence seulement sur calcaire ou sur quartzite, mais peu de cas ont été étudiés en détail. De récentes investigations dans les domaines de l'anatomie, de la morphologie, des cycles biologiques, de la physiologie et des propriétés énergétiques indiquent que des modes fondamentalement différents d'adaptation aux conditions arides se sont développés, même en réponse à des facteurs édaphiques et climatiques identiques.

*D'autre part, on connaît peu de choses sur l'influence immédiate des changements dans le milieu naturel. Des études sur des populations du genre *Cephalophyllum* N.E. Br., sous-genre *Cephalophyllum*, montrent de fortes corrélations entre les précipitations et le part qui peuvent déterminer des modifications génétiques. De plus, des formes biologiques sont bien adaptées à certains types de formations végétales, de sorte que superficiellement, il en résulte un mode de structure diffus.*

Des études à long terme, sur champ et en serre, des formes biologiques par rapport à la phénologie, aux précipitations et aux associations, permettent de formuler de premières hypothèses quant aux voies d'adaptation suivies dans l'évolution du groupe; les résultats constituent une base pour le traitement systématique de ce taxon extrêmement confus. Finalement, cet exemple souligne la nécessité de mieux comprendre les rapports qui existent entre l'écologie et la répartition géographique.

INTRODUCTION

Members of the family Mesembryanthemaceae dominate wide areas in the drier parts of southern Africa, yet little information is available on the ecological requirements and exact distribution of species and even genera. This lack of knowledge is mainly due to insufficient taxonomic treatment, but adaptive strategies and population dynamics have also received little attention.

To illustrate the problem of possible interaction, the syndrome of runner formation in the genus *Cephalophyllum* has been studied as an example over five years, and first results allowing suggestions of evolutionary pathways are presented in this paper.

MATERIAL

Populations from the subgenus *Cephalophyllum* of the genus *Cephalophyllum* N.E.Br. have been chosen for the study for several reasons: the members of the subgenus are easy to identify by characters of fruit morphology, leaf shape, and growth form (described as '2. Gruppe' by Hartmann, 1978), they represent a well defined closely related complex; the delimitation of species within the subgenus has been highly uncertain, because no critical evaluation of characters has been undertaken up to now; naming of species dates back to pre-Linnean times (e.g. Dillenius, 1732), but identification is extremely difficult because no types have been prepared, and only few drawings are available; and, finally, the distribution area of the group extends through different climatic regions, so that possible correlations with environmental factors can be examined. Although the taxonomic treatment of the subgenus has not yet been completed and a detailed monograph will be published later,

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the results allow the preliminary delimitation of seven species, based on results of investigations into fruits, flowers, and leaves (for distribution of species see Fig. 1): *C. alstonii* Marloth ex L. Bol.; *C. corniculatum* (L.) Schw.; *C. diversiphyllum* (Haw.) H.E.K. Hartm. comb. nov. (Basionym: *Mesembryanthemum diversiphyllum* Haw., Obs. Mesembr. 228, 1794; Lectotypus = iconotypus: t. 198, fig. 252 in: Dillenius, Hort. elth., 1732); *C. loreum* (L.) Schw.; *C. pillansii* L. Bol.; *C. purpureo-album* (Haw.) Schw.; and *C. tricolorum* (Haw.) Schw.

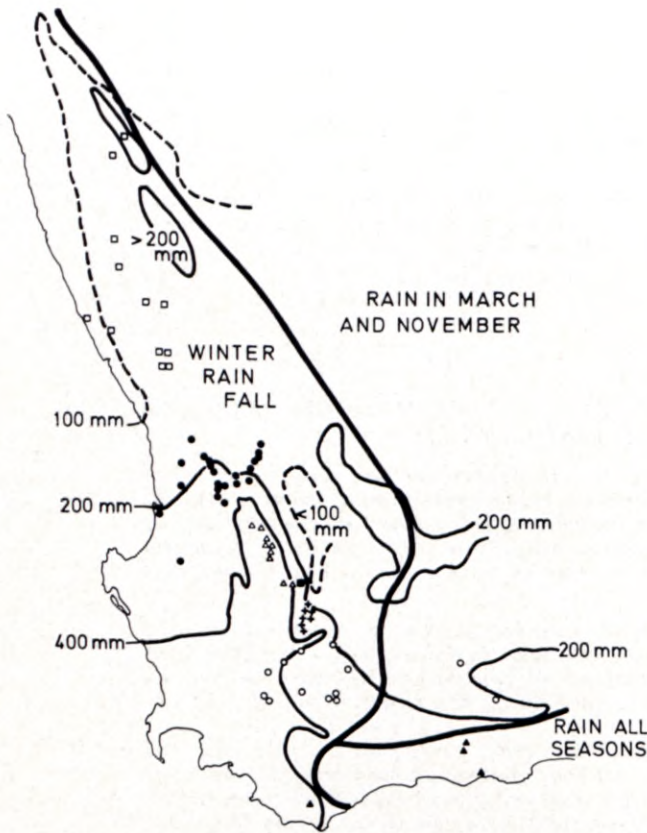


FIG. 1.—Geographical distribution of species of the subgenus *Cephalophyllum* of the genus *Cephalophyllum* N.E. Br. in relation to precipitation. For each species, the amount of rain expected per year is given in brackets; regional differences in rainfall are indicated on the map by thick continuous lines. Rainfall data after Schulze & McGee (1978) and monthly reports from the Weather Bureau, Pretoria. Full square: *C. alstonii* Marl. ex L. Bol. (\pm 200 mm); squares: *C. pillansii* L. Bol. (100–200 mm); crosses: *C. corniculatum* (L.) Schw. (200–400 mm); full circles: *C. tricolorum* (Haw.) Schw. (150–400 mm); circles: *C. purpureo-album* (Haw.) Schw. (<200 \rightarrow 400 mm); full triangles: *C. diversiphyllum* (Haw.) H.E.K. Hartm., comb. nov. (>200 mm); triangles: *C. loreum* (L.) Schw. (> 400 mm).

METHODS

Studies in growth forms in the genus *Cephalophyllum* (Hartmann, 1978) revealed that two fundamental types can be distinguished: flowers can occur in compound, dichotomous, annually-formed inflorescences (Fig. 2), or they can grow singly in leaf axils of long perennial axes (Fig. 3). In the first case, short runners are produced in order to bear the inflorescences. These die off at the end of the season and are replaced by new ones in the following year

(Fig. 2). In the second case, runners persist for several years, they form several new internodes per year, and can reach considerable lengths (to 1 m), but branching is rare (Fig. 3). Intermediate stages exist and it was decided to use the length of runners and their number together with the number of seedlings established per population as parameters to examine development and stability of populations. To describe 'length of runners', the longest runner of each plant in the plot was measured in order to register the maximum potential per plant. From these measurements, the means of populations were calculated. 32 populations of five species of the subgenus *Cephalophyllum* were chosen out of 70 known ones. In small populations ($n < 100$), all plants were recorded, whereas in larger ones representative plots were selected. The study was started in March 1977 — the dry season for most of the distribution area — and recording was repeated annually at about the same time of the year, until 1981. Final examinations are scheduled for February 1982. At least one plant of each population was transferred to greenhouses in Hamburg (Germany), mainly for studies of other characters, in order to achieve a taxonomic classification. Plants are kept at $\pm 10^\circ\text{C}$ at night and $25\text{--}30^\circ\text{C}$ during the day time, receiving additional light of about 5000 Lux for 10

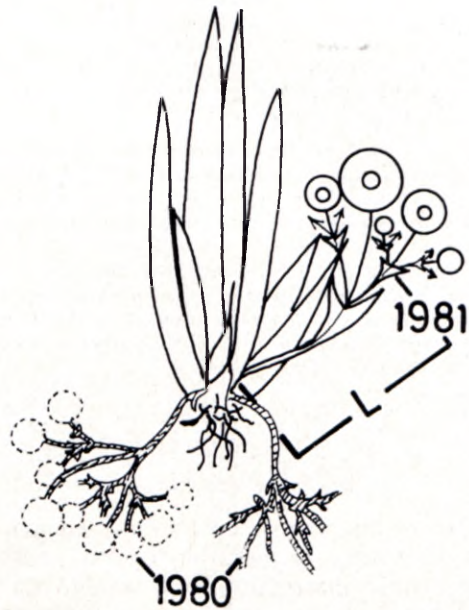


FIG. 2.—Plant with annual runners. 1980 = last year's inflorescences, 1981 = flowering inflorescence, L = length of runner.

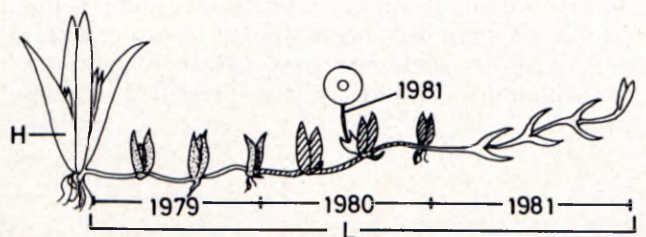


FIG. 3.—Plant with persistent runner; years of growth hatched differently. L = length of runner, H = head of plant.

hours per day. They are watered twice per week in winter, and once per month in summer, with gradual changes in spring and autumn.

ECOLOGY AND DISTRIBUTION OF SPECIES

It is known from other genera in the family Mesembryanthemaceae [e.g. *Odontophorus* N.E.Br. (Hartmann, 1976)] that infrageneric taxa can be correlated with distribution to rainfall patterns. Species of the subgenus *Cephalophyllum* show tendencies towards correlations of this type (Fig. 1), which include amount and seasonal distribution of rain as parameters.

Of particular interest is the distribution of *C. purpureo-album*: it occurs from areas where more than 400 mm annual precipitation is expected to regions with less than 200 mm of rain per year; in addition, rainfall can be registered in different seasons. In this species, leaf length has been found to be correlated with the amount of annual precipitation. The western populations develop longer and thicker leaves than the eastern ones, and an infraspecific cline is formed. The gradient of the ecocline is determined by the differences in amount of rainfall per year, irrespective of seasons.

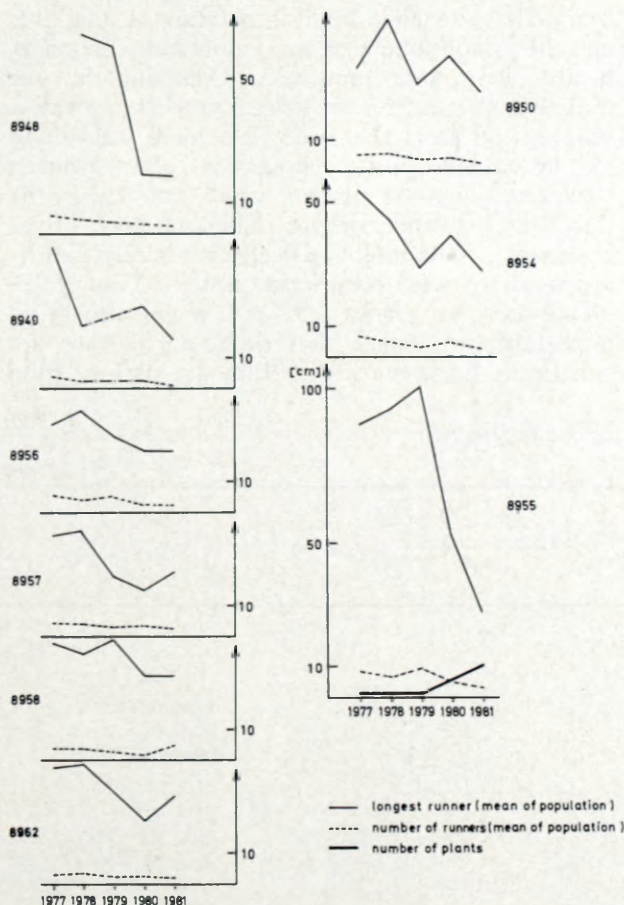


FIG. 4.—Annual changes in length and number of runners in *Cephalophyllum tricolorum* (Haw.) Schw. The ordinates represent both length in cm and number of runners; on the abscissa, the years are indicated. The figures at left are collecting numbers, one per population; populations are arranged in parallel north-south series from top to bottom, reflecting the geographic distribution. Each point on the curves represents the mean value per one year.

LONG TERM CHANGES IN RUNNER LENGTH AND NUMBER OF RUNNERS

Results of measurements and countings of runners over five years show distinct correlations to modes of runner formation, which will be discussed for each species.

In *C. tricolorum*, where persistent runners are developed, remarkable lengths have been measured (Fig. 4), but due to wide variation in values, no distinct limits can be given. Since the fluctuation in values does not concur simultaneously in all populations (compare e.g. 8954 and 8955, or 8957 and 8958 in Fig. 4), changes seem mainly to depend on local factors, and widespread influences can be excluded; dynamics of distinct populations will be discussed separately (section 6).

In *C. purpureo-album* (Fig. 5A) and *C. alstonii* (Fig. 5C), which develop annual runners as axes of inflorescences, the length seldom exceeds 10 cm, and consequently, variation is low. Similar values are found in *C. corniculatum* (Fig. 5D), a species with annual runners under favourable conditions, but these runners can become persistent and elongate in unfavourable situations.

In *C. loreum*, runner length shows a continuous increase from the northern to the central populations (Figs 1 & 5B), which is paralleled by an increased life span of runners in this series, thus presenting a geographic cline. The two south-eastern populations possess values closer to the centre of the cline. They cannot be linked up with the sequence.

The number of runners per plant can reach 10 in all species, but mean values per population rarely exceed 5. In general, it can be seen that an increase in the number of runners coincides with an increase in length of longest runners when mean values of populations are considered. In order to test the constancy of runner length and numbers, the mean values of populations per year are compared (Fig. 6). Although distinct centres can be identified in the diagram, it is also obvious that overlapping occurs. In general, it can be expected that annual runners (inflorescences) do not exceed 12 cm in length (open circles and squares in Fig. 6), whereas persistent runners reach 15 cm at least (dots in Fig. 6). The intermediate positions of *C. loreum* (L.) Schw. (triangles in Fig. 6) are discussed in section 7.

DYNAMICS OF POPULATIONS

Together with the recording of runners, the number of established seedlings was counted, and the general situation was observed. From these results, first insights into the dynamics of populations in arid habitats can be gained.

Most spectacular changes occur in the species *C. tricolorum* (Fig. 4), and, in addition, the development of a new population could be followed in this species (Table 1). The vigorous single plant was regarded as a fresh colonizer in 1977, because no dead remains of conspecific individuals were detected nearby, and the nearest living population of

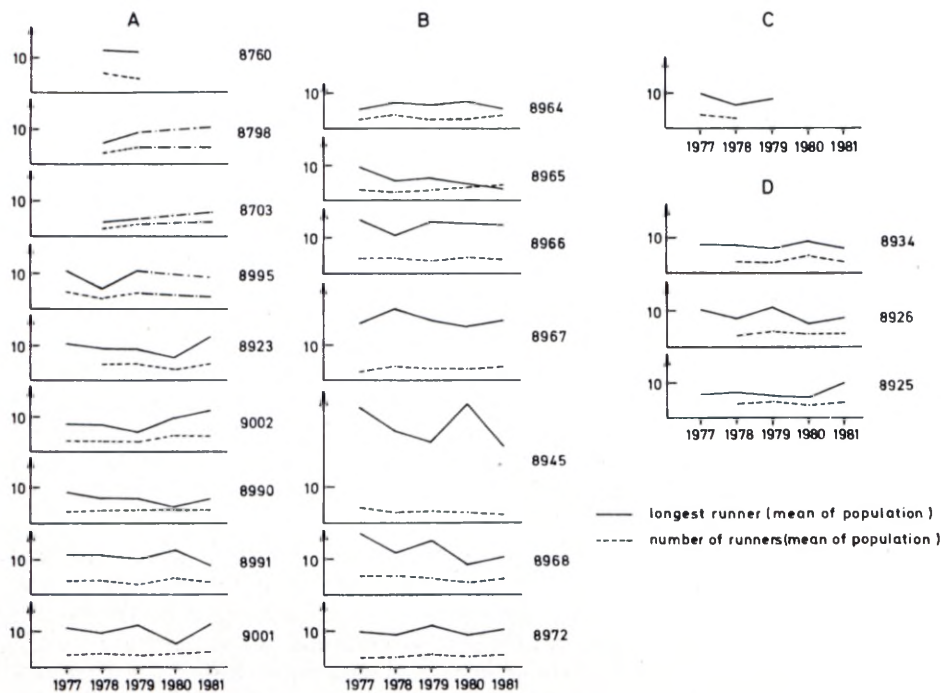


FIG. 5.—Annual changes in runner length and number. The figures at left are collection numbers, ordinates indicate numbers of runners and length (in cm) and points represent mean values per one year. A, *C. purpureo-album* (Haw.) Schw., the populations are arranged from east to west in the sequence from top to bottom, and can therefore be correlated to increasing amounts of rainfall per year (compare Fig. 1). B, *C. loreum* (L.) Schw., populations are arranged in north-south sequence from top to bottom, the top five ones representing a cline in increasing length of runners; C, *C. alstonii* Marl. ex L. Bol.; D, *C. corniculatum* (L.) Schw., populations are arranged in a north-south sequence from top to bottom.

the species was located 4 km away. No seedlings have been observed, although fruits have been formed. Instead, the plant developed side branches (Table 1, 1979), and the primary runners died away (Table 1, 1980), thus allowing secondary centres to develop into new plants (1980, 1981). In this case, the reduction in runner length (Fig. 4) is clearly correlated to an increase in number of plants (Table 1).

Similar models of dynamics can be seen in other populations of *C. tricolorum*, but causal factors can rarely be determined. An exception is presented by population *Hartmann* 8948, in which moles were reported in 1979, their activity resulting in a decrease of runner length in 1980 (Fig. 4, 8948). In

general, it can be expected that populations of *C. tricolorum* in their young phases are composed of few large plants. An increase in number mainly seems to be reached by disintegration of long axes and the establishment of new plants from secondary heads (short side branches). Consequently, the initially high value for the longest runners of plants is reduced, while at the same time more individuals can be counted. Older populations often form an entangled mass of runners which can hardly be traced back to their origins. Although none of the observed populations has declined entirely, hardly any seedlings have been found either (35 out of 929 plants seen, i.e. about 3,5%). It might also be of importance to realize that these populations are genetically homogeneous, if they are derived from

TABLE 1.—Dynamics of a new population (*Hartmann* 8955)

Year	Number of plants	Number of runners	Length of longest runner (cm)	Notes
1977	1	8	88	—
1978	1	6	93	—
1979	1	9	100	long runners with side branches
1980	5	5 5 3 3 6	30 84 30 16 102 $\bar{x} = 52,4$	original runners dying out, new ones forming from secondary centres
1981	10	? 2 1 7 3 1 2 2 1 4	62 27 20 38 15 15 17 22 20 33 $\bar{x} = 26,9$	

Note: values of numbers of runners and length of longest runner for 1980 and 1981 are arranged in such a way that corresponding positions refer to the same plant.

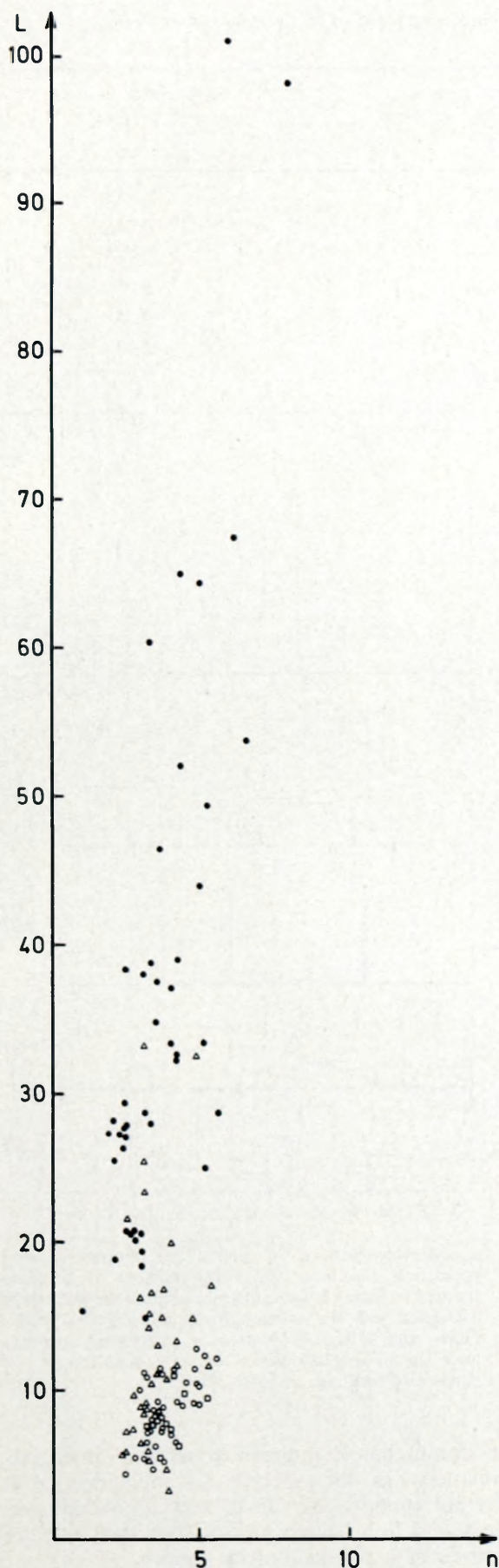


FIG. 6.—Comparison of runner length (L in cm) and runner number (n) of different species. Full square: *C. alstonii* Marl. ex L. Bol.; triangles: *C. loreum* (L.) Schw.; circles: *C. purpureo-album* (Haw.) Schw.; full circles: *C. tricolorum* (Haw.) Schw. Each symbol represents the mean value of one population in one year.

one single plant, like *Hartmann* 8955. Furthermore, it should be noted that flowering is not abundant in the species, and even further reduced in greenhouse cultures.

In the species *C. purpureo-album* (Fig. 5A), *C. alstonii* (Fig. 5C) and *C. corniculatum* (Fig. 5D), little variation in length of longest runners has been found. The limited growth can be interpreted as an economic adaptation, because the runners are only used during a single season. Thus, the loss of material is kept low.

In *C. purpureo-album*, a particularly high rate of germination and establishment of seedlings has been observed: young plants without runners can amount to 60% of a population. Mean values for seedlings over five years exceed 10% in general. Since hardly any vegetative reproduction occurs, a high rate of germination is required to keep the species in existence. The life span that plants of *C. purpureo-album* can reach under natural conditions, in comparison with plants of *C. tricolorum*, has not yet been investigated. Plants of both species have been kept in culture for seven years now without showing signs of decline.

Three populations of *C. corniculatum* have been recorded, between which the proportion of seedlings varies widely (*Hartmann* 8925: 4%, $n = 143$; *Hartmann* 8926: 26%, $n = 339$; *Hartmann* 8934: 5%, $n = 184$), and shows no correlation at all to lengths of runners (compare Fig. 5D).

Of *C. alstonii*, only one small population is known, in which the number of plants varied from 15 to 11 during the investigation. It was impossible to identify seedlings, because the population was in poor condition and adult plants without runners existed. The possibility cannot be excluded that fruits and plants are removed by collectors, since the species is considered particularly interesting by amateur growers in Europe.

Like *C. corniculatum*, *C. loreum* varies considerably in proportions of seedlings but, in the last-named species, the percentage of seedlings of a population is correlated to the prevailing length of longest runners in that population (Table 2 and Fig. 5B): the more seedlings that are established, the more shorter runners can be expected in the adult plants.

The example of *C. loreum* stresses the fact that dynamics of populations can follow either strategy: if little material is invested into vegetative parts (short runners), many seedlings are established under normal natural conditions (10–60% in one population); if much material is used for production of vegetative parts (long runners), less is invested into sexual reproduction and only few seedlings are developed (3–5%).

POPULATION DYNAMICS IN RELATION TO CLIMATIC CHANGES

The composition of population has been shown to vary from year to year, a process which can be expected to depend on climatic factors. For a first

TABLE 2.—Correlation between length of runners and proportion of seedlings in *Cephalophyllum loreum*

Collection number (Hartmann) arranged in N-S- sequence	Length of runners (highest annual means in cm)	Seedlings in % over five years
8964	8,74	26,15
8965	9,18	10,74
8966	14,90	3,19
8967	20,00	8,07
8945	33,68	4,55
8968*	17,00	12,60
8972*	11,00	9,70

* Geographically separated populations.

test, amount and frequencies of rainfall have been analysed and correlated with one another.

One population of *C. purpureo-album* (Hartmann 9001) grows near Worcester in the Cape, from where precipitation data on a monthly basis are available. Comparison of data indicates, that the amount of rain in one year is correlated to the number of established seedlings in March/April of the following year (Fig. 7). It is suggested that the rate of reproduction by seeds in this population is directly influenced by the available moisture. Closer investigation (Fig. 8) into the seasonal distribution of rainfall reveals even more limited correlation factors: rains occurring out of season, like the summer rains in January and February 1979, do not result in an increased number of seedlings as counted in March 1979. Obviously, only winter rain allows the germination and subsequent growth of seedlings, whereas at the same time the amount of this rain determines the number of seedlings per population. On the other hand, no influence of rainfall on length or number of runners has been detected, although the fact of annual runner production suggests possible interrelations (Fig. 7).

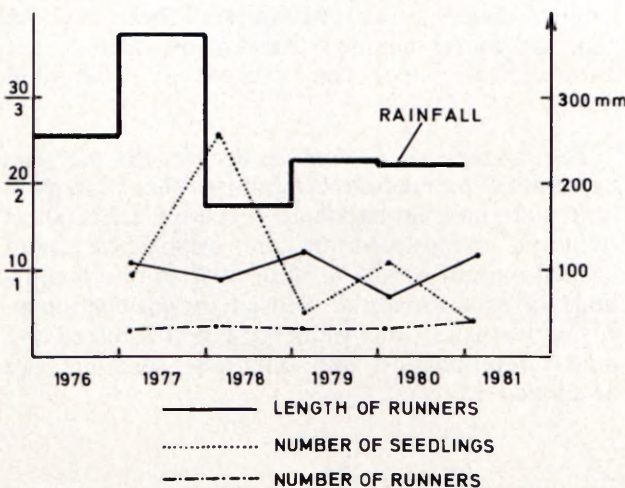


FIG. 7.—Dynamics of one population in relation to precipitation (Hartmann 9001). Amount of annual precipitation (in mm) = thick continuous line. Number of seedlings = dotted line; number of runners = broken dotted line; length of runners (in cm) = thin continuous line.

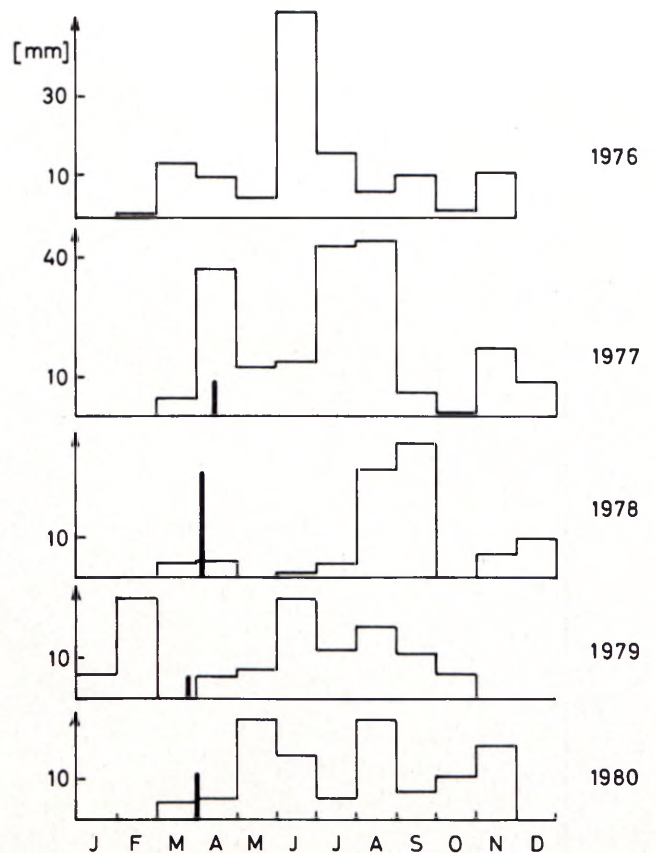


FIG. 8.—Monthly pattern of rainfall at Worcester, near population Hartmann 9001. The number of seedlings counted in March is indicated by a vertical line and can be correlated with the amount of rainfall: abundant winter rains result in high proportions of established seedlings. Note the missing correlation between summer rain and number of seedlings in early 1979.

It should be of interest to analyse analogous correlations in the species *C. tricolorum* with persistent runners, but up to now no locality has been found from where precipitation data and the existence of a population are known.

In the absence of rainfall data, associations of plants could serve as indicators for climatic factors, but information in this field is extremely limited. Preliminary notes on associations in which the populations of *C. loreum* occur, indicate close

correlations between runner formation and flora: plants with shortest runners (Fig. 5B) grow in the most northerly locality together with ericaceous and restionaceous elements, probably a typical fynbos association. Following the series of populations further to the south, more succulent elements occur and the number of fynbos associates is reduced and, at the same time, the length of runners increases considerably (Table 2 and Fig. 5B). The change is probably determined by differences in precipitation, the most northern population representing the highest localities inhabitable by the genus, and receiving relatively high amounts of rain. Towards the south, the localities are situated at lower altitudes and receive less rain (Taylor, 1978), since they are sheltered from west rains by the Cedar Mountains and the Koue Bokkeveld Mountains. Therefore, in the centre of the series, *Elytropappus rhinocerotis* (Renosterbos) is dominant whereas towards the south succulent shrubs increase in proportion.

Further detailed investigations into the associations and the tentative correlations to length of runners and seedling establishment are scheduled.

DISCUSSION AND CONCLUSIONS

The results permit a preliminary understanding of mechanisms that govern the distribution of taxa via ecological factors. It is clearly shown that species of one genus can exhibit marked differences in population dynamics. In this case, two dispersal strategies can be emphasized alternatively, the alternatives being reduced to survival mechanisms under extreme unfavourable conditions in each respective group. Changes in populations can be influenced by amount and time of rainfall through the establishment of seedlings, yet no general adaptive trend can be recognized within the group. The distribution map (Fig. 1) clearly shows that growth forms with short annual runners occur in the regions with low precipitation (*C. pillansii*, 100–200 mm of rain per year) as well as in areas where higher rainfalls are expected (*C. purpureo-album*, up to 400 mm annual precipitation). Therefore it seems unlikely that either of the extreme growth forms can be considered to represent an original stage. Rather, it can be assumed that a putative ancestor possessed ambivalent potentials, which were realized depending upon prevailing conditions. It is suggested that the constant extremes have evolved from an ancient stock with variable growth forms and that fixing of genetic pattern has taken place. Consequently, species with a single growth and reproduction type are seen as final stages in evolutionary lines, and *C. pillansii*, *C. tricolorum*, *C. purpureo-album* and *C. alstonii* as highest evolved species. In contrast, the instability in growth form and reproduction types indicate that in *C. loreum* and *C. corniculatum*, primitive features of the group have been preserved. If these interpretations are correct, the evolution of

the group probably started in associations bordering fynbos and receiving less than 250 mm of annual precipitation. Depending on the extension of suitable areas in different geological times, the total region inhabited by the subgenus might have been much greater, and the restricted distribution found today may represent the result of retreats.

It must remain open at this stage of investigation whether the assumed processes reflect similar evolutionary lines for the entire family. Certainly, the conclusions agree with results from anatomical studies of leaf surfaces (Ihlenfeldt & Hartmann, in press), which place the genus *Cephalophyllum* between xeromorphic and non-xeromorphic surface types, evolution being supposed to have developed from non-xeromorphic types.

Finally, it seems important to realize that different types of population dynamics can be correlated to different taxa, thus presenting a set of characters of considerable potential for taxonomic conclusions.

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REFERENCES

- DILLENIUS, J. J., 1732. Hortus elthamensis, seu plantarum rariorum . . . London.
- HARTMANN, H., 1976. Monographie der Gattung *Odontophorus* N.E.Br. (Mesembryanthemaceae Fenzl). *Bot. Jb.* 97: 161–225.
- HARTMANN, H., 1978. Zur Kenntnis der Gattung *Cephalophyllum* N.E.Br. *Bot. Jb.* 99: 264–302.
- HARTMANN, H., in press. Untersuchungen zum Merkmalsbestand und zur Taxonomie der Subtribus Leipoldtiinae Schw. der Familie Mesembryanthemaceae Fenzl.
- IHLENFELDT, H.-D., & HARTMANN, H., in press. Leaf surfaces in Mesembryanthemaceae. *Bot. J. Linn. Soc.*
- SCHULZE, R. E. & MCGEE, O. S., 1978. Climatic indices and classification in relation to the biogeography of southern Africa. In M. J. A. Werger, *Biogeography and ecology of southern Africa*. The Hague: Junk.
- TAYLOR, H. C., 1978. Capensis. In M. J. A. Werger, *Biogeography and ecology of southern Africa*. The Hague: Junk.