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Circular arrangement of *Stipagrostis ciliata* clumps in the Negev, Israel and near Gokaeb, Namibia

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Circles of tufts or tuft remnants of the perennial grass *Stipagrostis ciliata* were found in sandy soils in desert areas of Israel and Namibia. It is suggested that such a circular pattern is due to vegetative propagation of this and other species by means of horizontal rhizomes. The central part of the older specimens dies and detached offspring ramets develop in the periphery of the genet. Other species with similar arrangement of ramets are *Stipagrostis obtusa*, *Asphodelus ramosus* (Liliaceae), and *Cyperus macrorrhizus* (Cyperaceae). The shrubby dicotyledones *Calligonum comosum* and *Artemisia monosperma*, which also produce circles of clumps, are capable of reproducing vegetatively by means of adventive roots and new branches, which are the extension of buried branches in the periphery of the genet.

Keywords: fairy rings; grasses; *Stipagrostis*; desert

Introduction

The formation of clumps arranged in circles in several plant species have drawn the attention of many authors in different parts of the world (Hitchcock, 1935, p. 381; Barbour, 1969; Vasek, 1980; Cox, 1987; Vandenbeld, 1988, p. 191; Danin & Yom-Tov, 1990; Moll, 1991; Lovegrove, 1993) and fall often under the common term 'fairy rings' (Hitchcock, 1935). It has been suggested that certain animals, such as termites, ants, rodents, and mammals, induce local edaphic changes in a circular pattern up to a few metres in diameter. Plants developing in such areas respond to these changes by growing more intensively in the animal affected soil and therefore attain a circular pattern. Theron (1979) suggested that the circular pattern is derived in some cases by allelopathy based on poisonous materials excreted to the soil by *Euphorbia* species.

Another phenomenon causing circular arrangement of clumps or tufts is caused by a certain type of vegetative multiplication. When the old central parts of the original clump dies, younger clumps on its periphery constitute circles of plants detached from each other with a diameter of up to 15m (Barbour, 1969; Vasek, 1980).

Dead plant tufts arranged in circles, mostly more than 2 m in diameter, were shown to the first author by Dr M. Seely, in the Namib Desert near Gokaeb, in an area known locally as the 'Far East', during an excursion of participants of the Dunes '89

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conference. One of Seely's suggestions for explanations of what appeared to be a riddle, referred to Cox's (1987) interpretation of circles of annual plants developed close to Gobabeb, further west of Gokaeb. In the environs of Gokaeb the circles were found in interdune areas and stable shallow sand sheets dominated by a nearly monospecific grassland of the annual form of *Stipagrostis ciliata* (Desf.) De Winter. The first author observed, however, during that excursion, that the dead plant remnants forming the circles were rhizomes of perennial plants and not of annuals.

The following studies of plant morphology and growth habits of a few *Stipagrostis* species in the Negev of Israel support a morpho-ecological explanation for the formation of circles of plants. It seems that this explanation holds true also for *S. ciliata*.

The morpho-ecology of Stipagrosis ciliata

Ecological studies of *Stipagrostis ciliata*, *S. obtusa* (Delile) Nees and *S. plumosa* (L.) Anderson were carried out in the Mishor Yamin-Rotem sand field plain of the northern Negev of Israel about 10 km SE of Dimona (Fig. 1) under 100 mm of mean annual rainfall, which supports a rather rich vegetation (Danin *et al.*, 1964). *S. ciliata* was also studied in sandy areas of the western Negev and also examined by the first author in Namibia, east of Gobabeb.

Entire clumps and tufts of the species studied in Israel were collected in the field, dissected in the laboratory and examined under a dissecting microscope, with an attempt to understand and describe by schematic diagrams their pheno-morphology (Orshan, 1989), i.e. the morphology and life history of each of their organs. Verification was carried out later in the field.

In Israel *Stipagrostis ciliata* is generally a perennial plant but in the extreme desert areas of the southern Negev it may also complete its life cycle within 1 year, turning into a therophyte. In Namibia, in the vicinity of Gokaeb, 210 km SW of Windhoek, it is an annual or a perennial according to the local moisture regime (see also Seely & Ward, 1989). In the northern Negev it grows on stable sand fields. It is found also in other arid habitats, but is practically absent from sites of sand accumulation.

The basic growing unit — ramet — is made up of a stem which is the distal section of a plagiotropic leafy rhizome *sensu* Du Rietz (1931) (Fig. 2, Rk). It has short (1–2 mm long) internodes at its 2–3 cm long leaf-carrying basal part and terminates in an inflorescence the culm of which has three internodes each of 8–30 cm length (Fig. 2, L_{11}–L_{13}). The prophyll (Fig. 2, P) and the first four leaves of the brachyblastic basal part of the ramet bear no buds in their axils (Fig. 2, P, L_1–L_4) while the following five or six leaves (Fig. 2, L_5–L_{10}) have axillary buds subtended by sheaths. The upper part of the first leaf (Fig. 3, Pb, h) has a hyaline part which subtends the rest of the stem while young. It is woolly along the margins of the hyaline part (Fig. 3, Pb, v) and may serve for protection. The lower part of P and L_{1-3} are straw-coloured, either pale-yellow or whitish, whereas the blades of L_4–L_{10} are green. The first leaf with a long blade is L_5. The blades of the leaves L_5–L_{13} are convolute throughout, horseshoe-shaped in transverse section, and densely hairy on the upper surface (cf. De Winter, 1965, p. 317). From amongst some of the buds at the axils of leaves 4–9, new ramets of the order K + 1 develop (Fig. 2(b), R_{k+1}). Their lower brachyblastic part turns into a continuation of the leafy rhizome.

Due to this intensive branching a dense tuft is quickly formed out of every new seedling, a genet which survives the environmental stress. It is made up of many ramets which continue to grow and branch to form a dense rounded tuft with a branched sympodial leafy rhizome reaching a few decimetres in diameter. When the genet grows older its central part dies and deteriorates, leaving a dense tuft of dead stems and roots and thus a circle of satellite independent tufts is formed around the dead centre.

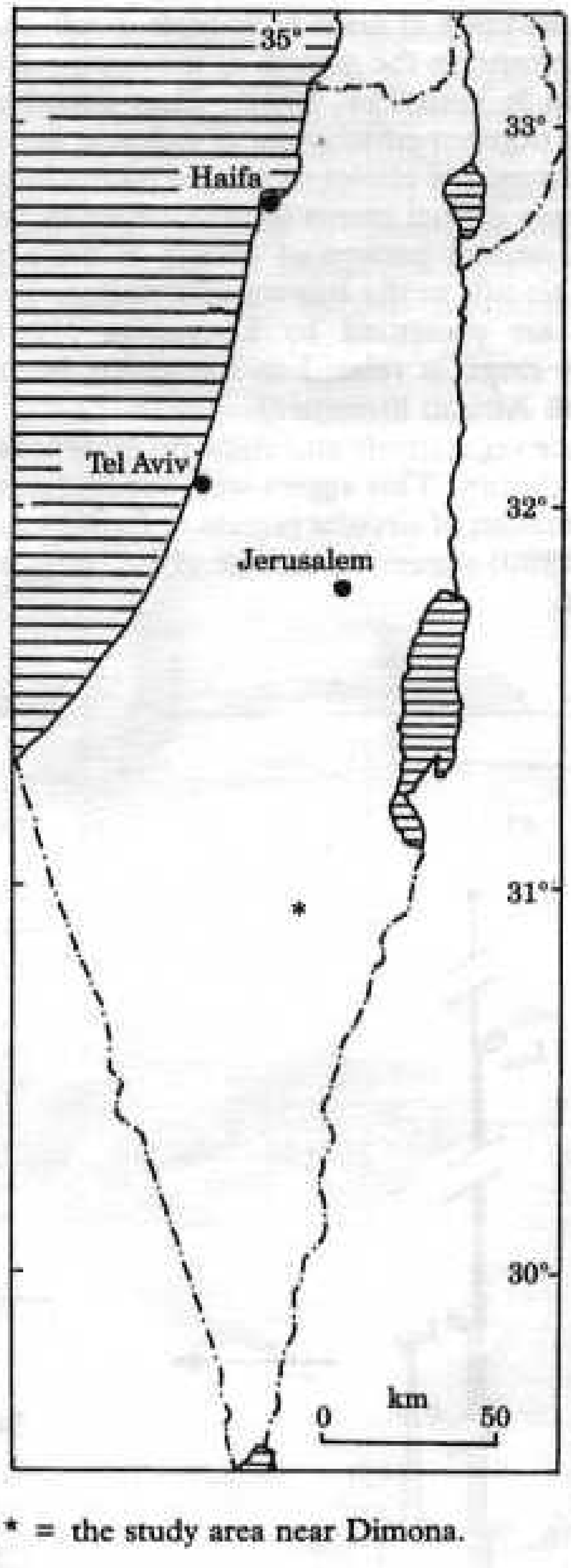

Figure 1. Location map; * = the study area near Dimona.

Similar circles of plants were observed in Israel of *Stipagrostis obtusa, Asphodelus ramosus* L., *Cyperus macrorrhizus* Nees, *Calligonum comosum* L'Hér, and *Artemisia monosperma* Delile. The circles in all these species occur in stable sand sheets. All these species are capable of reproducing vegetatively. Cauline adventitious roots are formed on each ramet which enable the ramets to become independent entities arranged in a circle.

Discussion

Circular arrangement of plants may be derived from different causes. One group of plant species may be regarded as responding to animal activity which locally changes the edaphic conditions. Addition of manure by male gazelles to Mediterranean soils in their 'marking stations' promotes the growth of the composite *Silybum marianum* (L.) Gaertn. in circles (Danin & Yom-Tov, 1991). They found a similar response of the same plant species to the nutrient enrichment of soil near nests of harvesting ants. Cox (1987) attributes the existence of circles of annual plants in Namibia, near Gobabeb, to rodent activity. Whereas annual plants were involved in all the previous examples, Moll (1991) relates the circular pattern of growth in the perennial grass *Stipagrostis giessii* Kers in northern Namib to the impact of termites. Two aerial photographs of circles in desert areas are presented by Lovegrove (1993, p. 41). The latter's explanation of the 'fairy rings' is related to harvesting termites' activity (known as 'heuweltjies' in the South African literature).

Other species reproduce vegetatively and show no evident faunal relationship for the circular pattern of their clumps. This agrees with the findings at Barbour (1969) and Vasek (1980) for the formation of circular ramets of *Larrea tridentata* (DC.) Cov. in the Mojave Desert. Vasek (1980) suggested the age of 11,700 years for the oldest circular clumps in his study area.

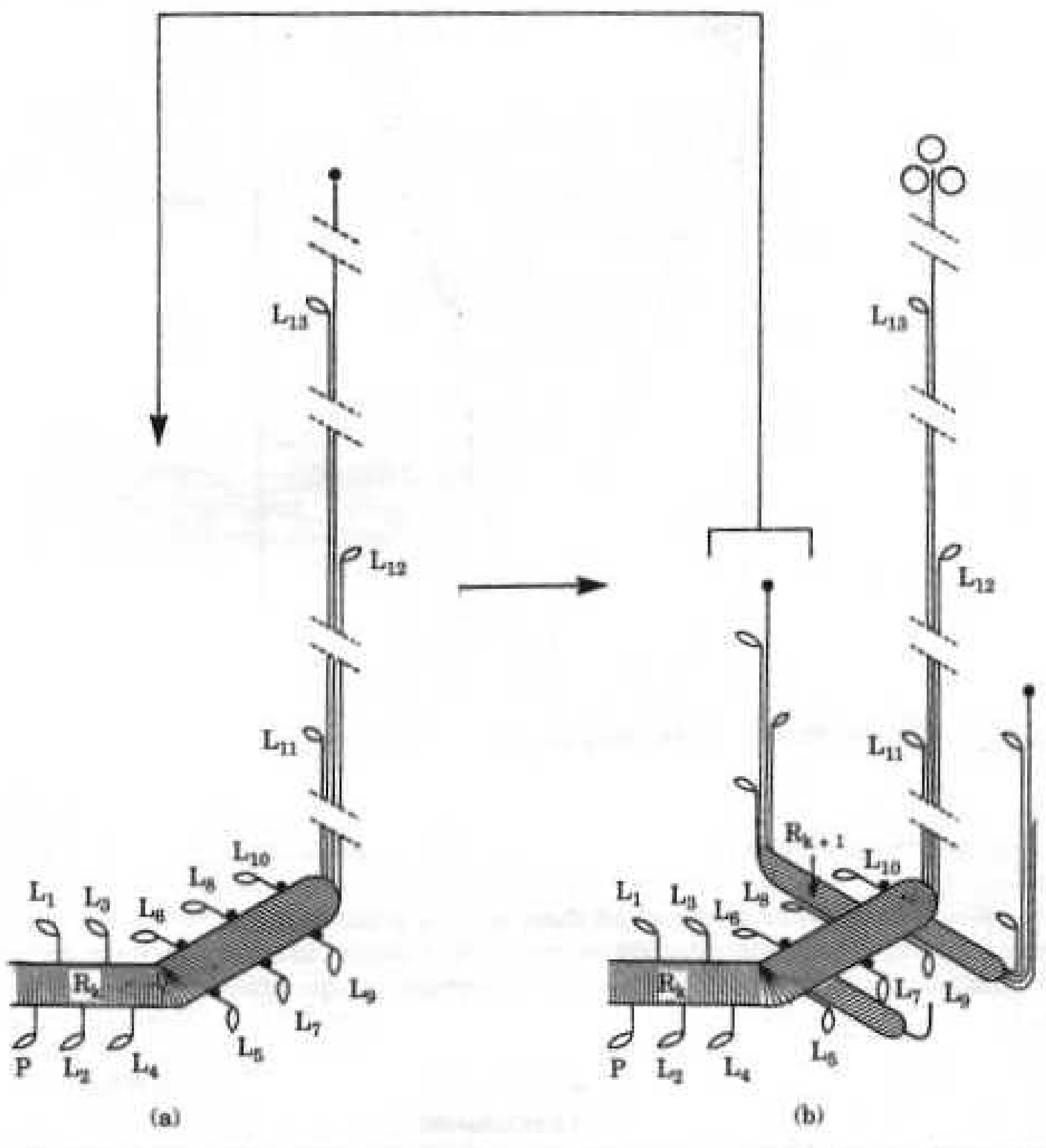

Figure 2. Schematic presentation of structure and development of *Stipagrostis ciliata*: (a) A single young ramet of the order R_k;P, L_{1-L13} location of the leaves in their age sequence. (b) A ramet of the order R_k with branches of the order R_{k+1} at the axils of L_5, L_8, and L_9.

Our findings in growth habits and circle formation of *Stipagrostis ciliata* and other species in the desert areas of Israel suggest that the formation of circles there is due to their morpho-ecology affecting their growth characteristics.

Specimens of *S. giessii* were also examined at the Kew Herbarium. It is suggested that further investigations on the circles of this species should be carried out, since *S. giessii* has the same growth form as that of *S. ciliata* and therefore its circular clumps might be derived in the same way as described above for the latter species.

The formation of plant circles as a result of growth processes described above could

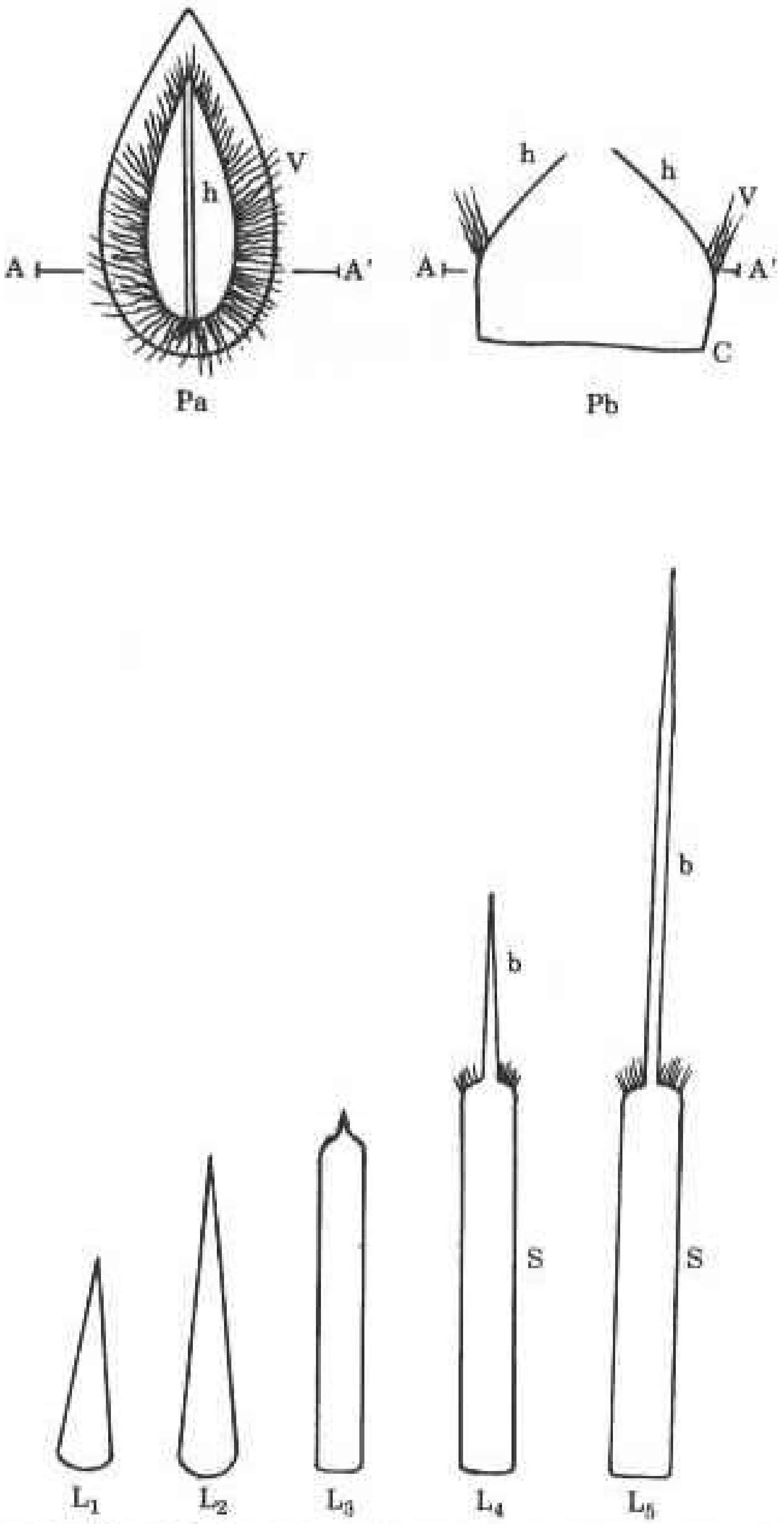

Figure 3. Leaves of *C. ciliata*: Pa, back view of the lowermost leaf (prophyll); Pb, a transverse section of Pa along the line A–A'; C, straw coloured section; h, hyaline section; v, hairs; L_{1}-L_{5}, 1st to 5th leaves; b, blade; S, sheath.

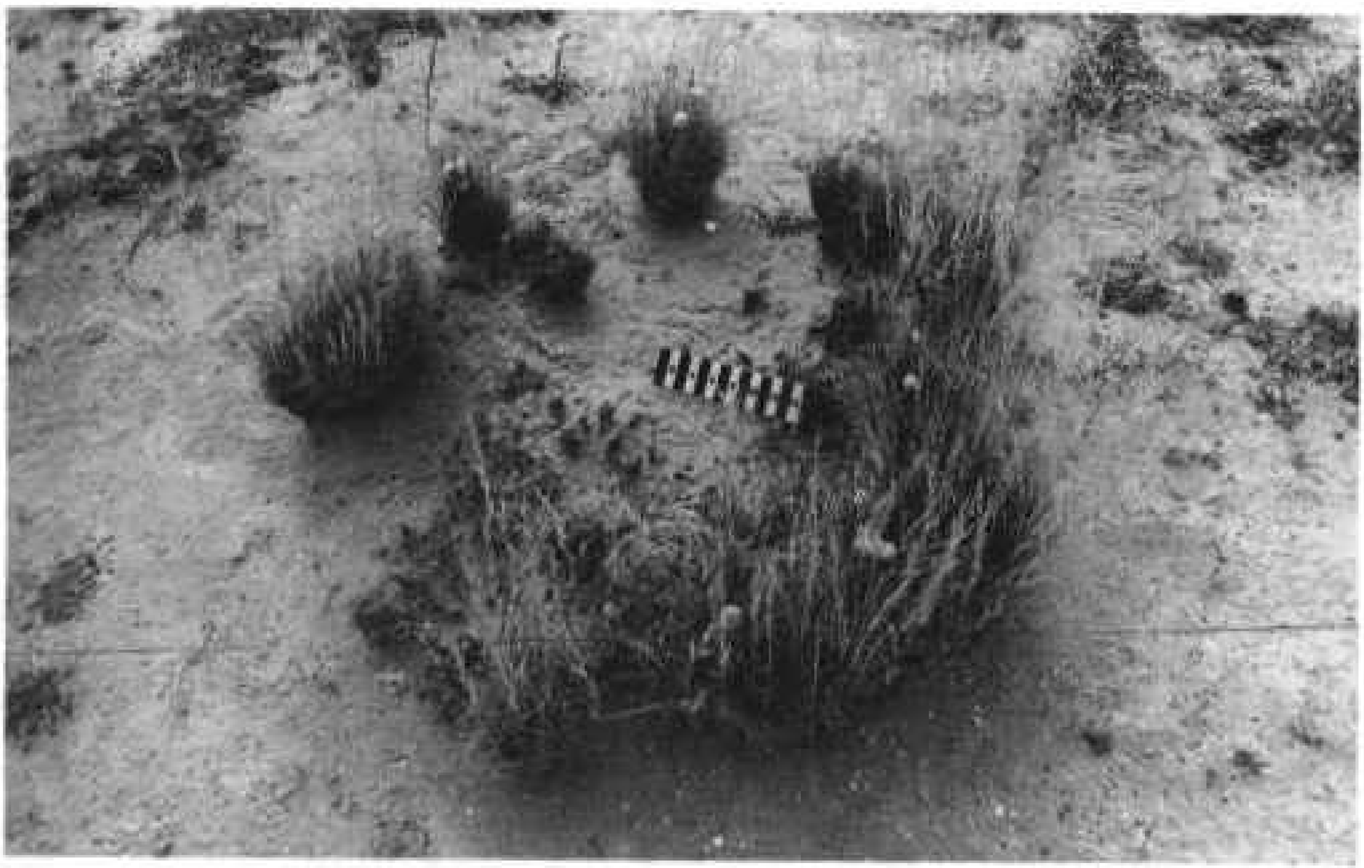

Figure 4. A circle of *Stipagrostis ciliata* in the western Negev, all the independent tufts in the circle are ramets of the parent plant which lived years ago in the centre. Bar = 15 cm.

perhaps account for the circles of dead *S. ciliata* found near Gokaeb, east of Gobabeb, Namibia. Lovegrove's (1993) photograph 39 of Sussusviei area resembles much the circles of remnants of the perennial tufts of *Stipagrostis ciliata* observed by the first author in the Gokaeb area of Namibia. The circles in his photograph 40 are circles of annual plants whereas those of photograph 39 are of perennials.

A few questions may be raised with regards to the circular arrangement of the tufts near Gokaeb. What are the conditions that enable the development of *Stipagrostis ciliata* as the perennial form in the interdune gravelly soil in that area of Namibia and what is the growth rate of clumps of the latter in Namibia? By solving these questions one may know how long the conditions which enabled the development of such large circles have prevailed for and what the absolute age of the rhizomatous remnants of *S. ciliata* in the circles in Namibia is. The use of radiocarbon dating techniques may help to solve these questions.

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