PATTERNS OF PLANT ESTABLISHMENT ON A LINEAR DESERT DUNE

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Key words: linear dune, plant establishment, Namib Desert

ABSTRACT

A grass *Stipagrostis sabulicola* (Poaceae) and a succulent *Trianthema hereroensis* (Aizoaceae) constitute the persistent vegetation of the western half of the main Namib Sand Sea. Following unusual, heavy rainfall (> 100 mm) germination of both species occurred over most of the bare dune sand. However, after eleven years of measurement only 11% of the originally established grasses and none of the succulents survived. Sand mobility or moisture rather than seed availability is thought to influence the distribution patterns observed.

INTRODUCTION

The persistent dune vegetation of the western half of the large dune field (34 000 km2) in the southern Namib Desert known as the main Namib Sand Sea consists of two endemic species, a grass *Stipagrostis sabulicola* (Pilger) de Winter (Poaceae) and a succulent *Trianthema hereroensis* Schinz (Aizoaceae). *S. sabulicola* is a large mound-building species with multiple branched and vigorous rhizomes that grows on relatively mobile sand (Yeaton, 1988). Consequently, it is often found in areas of sand deposition where low, soft sand hummocks develop. On linear dunes, it is more often found on the middle to upper plinths (Yeaton, 1988; Seely, in press). *I. hereroensis* is also a mound-building species commonly found in sandy hollows at the base of slipfaces or in depressions on undulating sand sheets. On linear dunes, it occurs more frequently on the lower plinth and dune base (Seely, in press). *S. sabulicola* occurs throughout the main Namib Sand Sea whereas *I. hereroensis* grows from the coast no further than 80 km inland.

Little has been recorded about patterns of germination and establishment of persistent vegetation in mobile desert dune environments experiencing unpredictable rainfall. The occurrence of vegetation in mobile desert sand dunes, and sometimes its zonation, has been noted by a number of authors, for example, Pierre (1958), Leistner (1967), Quézel (1971), Zohary (1973), Felger (1980), Bowers (1982), Walter and Box (1983), Mabbutt (1984), le Houérou (1986), Orshan (1986), Schmida *et al*. (1986) and Yeaton (1988). Danin (1983) described the occurrence of *S. scoparia* in mobile sands of the Negev and its replacement by newly germinated *Artemisia monosperma* as the sands become stabilized.

The non-uniform pattern of establishment of *S. sabulicola* and *I. hereroensis* in mobile sand dunes of the Namib, and of persistent species in desert dunes elsewhere, may result from several factors operating alone or in conjunction:

1. Seeds may be available in some but not all areas of the dune

environment. The sand substrate is highly mobile and seeds could either be removed from an area or buried too deeply for germination. Wind blown seeds accumulate in particular areas of dune habitat such as the base of slipfaces (Robinson and Seely, 1980).

2. Seeds may be available throughout the sand dune environment, but soil moisture conditions for germination may not arise, for example on mobile dune crests and slipfaces (Louw and Seely, 1982: p. 126).

3. Seeds may be available and germination may take place but soil moisture, nutrients or other factors may not support continued growth and establishment.

4. Intra- or interspecific competition for soil moisture or nutrients may affect continued growth and establishment.

5. Predation on plants or seeds may influence plant survival as well as availability of seeds for germination. Oryx feed upon both plant species in the study area (Nott and Savage, 1985a) and seed predation by tenebrionid beetles (S.A. Hanrahan, pers. obs.), birds (Cox, 1983), lizards (Robinson and Cunningham, 1978) and gerbils (Boyer, 1987) has been recorded in these dunes.

In the western, central Namib, mean rainfall is less than 25 mm and unpredictable (Pietruszka and Seely, 1985). In 1976 and again in 1978 over 100 mm of rain fell in this area (Lancaster et al., 1984). These are thought to have been the only rainfall events of this magnitude since 1934 (Walter, 1936). These two events resulted in widespread germination and establishment of the two persistent dune species over large areas of what had been bare dune sand. This occurrence provided an unusual opportunity for observing germination and establishment of S. sabulicola and I. hereroensis. In this paper I describe the pattern of germination, establishment and mortality of vegetation on east and west plinths of a previously bare linear sand dune in the central Namib following two major rainfall events.

SITE DESCRIPTION AND METHODS

Sand dunes vary across the 120 km width of the central Namib from transverse or crescentic dunes on the coast, linear dunes in the central tract, to star and reticulate dunes on the eastern, inland margin (Lancaster, 1989). Rain, falling mainly in the summer, increases across this distance from a mean value of less than 20 mm on the coast to about 100 mm inland (Lancaster et al., 1984). The study site was situated among the linear dunes, 55 km inland from the coast, where dune heights range to 100 m, dunes are separated by gravel covered interdunes approximately 1.8 km wide and mean annual rainfall is approximately 20 mm (Robinson and Seely, 1980; Seely and Louw, 1980).

A transect 80 m wide and 680 m long was established across a single linear dune (Fig. 1) tending SSE - NNW at 23° 36′ S, 15° 01′ E. The transect was divided into quadrats 40 m by 40 m. On the longer, eastern side of the dune, three sets of four contiguous quadrats (each set 80 m x 80 m), separated by 80 m, were designated as lower, middle and upper regions of the dune plinth. On the shorter, western side of the dune, two sets of four contiguous quadrats were designated as lower and upper plinth. Quadrats were not established in the crest and slipface region of the dune as these very mobile sands (Livingstone, 1987) were devoid of vegetation when the study was initiated.

All living Stipagrostis sabulicola and Trianthema hereroensis in each of the study quadrats were measured and their locations plotted in July 1978, June 1980, November 1983 and October 1989. These plants had germinated mainly in 1976 and, after additional good rain early in 1978, were well established by July 1978. Dead individuals were not included in the sampling. The size of each plant was determined by taking one measurement across its maximum diameter and a second measurement perpendicular to the first and multiplying the two values. Per cent cover within each quadrat was calculated by adding measurements from all plants of a species.

RESULTS

Following the rainfall events of 1976 and 1978, Stipagrostis sabulicola and Trianthema hereroensis germinated and became established on both slopes of the study dune (Fig. 1). With two exceptions noted below, no further germination leading to establishment occurred during the ensuing eleven years of measurement. Greater numbers of S. sabulicola and T. hereroensis germinated on the eastern plinth, whereas more survived on the western plinth. Survivorship of S. sabulicola after each measurement interval was higher on the upper rather than on the lower parts of the dune; survivorship of T. hereroensis after the first two intervals was greater on the lower, western plinth. After eleven years of observations - eleven to thirteen years after germinating rain - only 11% of the originally observed S. sabulicola and none of the T. hereroensis plants had survived.

Per cent cover of both species decreased throughout the observation period with the initial exception of T. hereroensis on the western dune base (Fig. 2). Although cover of S. sabulicola was initially greatest on the middle and upper eastern plinth, after eleven years the upper plinth, east and west, supported the highest cover. Amount and persistence of T. hereroensis cover was highest on the lower western and middle eastern plinth.

Proportion of total cover provided by the two species varied from east to west plinths and between measurements (Fig. 3). Distribution of cover over the dune was more uniform initially, becoming less so with further measurement. After eleven years, two of five areas originally included in the study were devoid of living vegetation. On the east-facing plinth, S. sabulicola always provided more than half of the total cover. On the west-facing plinth, total cover occupied by T. hereroensis ranged between 45% and 65% during the first three measurements. The increase in per cent of total cover by T. hereroensis between the first and second measurements indicated more vigorous initial growth by this species as no germination occurred during this interval.

Mean cover (Fig. 4) of all individual tussocks of S. sabulicola growing at different positions on the dune varied significantly (2-way ANOVA; MS = 85.98, d.f. = 4, F = 8032, $p < 0.01$); mean cover also varied significantly among years (MS = 56.99, d.f. = 3, F = 5.324, p < 0.01). Mean cover of all individual I. hereroensis varied among individuals growing at different positions on the dune (MS = 275.72, d.f. = 4, F = 7.108, p < 0.01) but not among years (MS = 77.32, d.f. = 3, F = 1.993, NS).

DISCUSSION

Distribution of newly germinated individuals of S. sabulicola and I. hereroensis indicated that seed was available at all locations on the east and west plinths. Even though some may have blown away or have been buried too deeply to respond to rainfall, sufficient seed was present to allow germination of plants in all quadrats. Moreover, by June 1978 soil moisture conditions, nutrients and any other factors required for germination and establishment, were present in sufficient quantities to allow the two plant species to grow throughout the plinths.

Crest and slipface regions of the dune were, however, unvegetated. This may have been the result of unavailability of seed, as suggested by the first alternative postulated, or may be the result of high soil mobility or inadequate soil moisture. Our observations do not allow differentiation between these two explanations.

By October 1989 no plants survived on east or west lower plinth and the number of live individuals had decreased markedly elsewhere. Differential mortality among plants growing in different portions of the dunes had occurred. Inter or intraspecific competition for soil moisture must be discounted as a major factor, as plants disappeared from entire regions of the plinth. However, the basis for this differential mortality, soil moisture, nutrients or other factors, was not immediately apparent.

S. sabulicola and I. hereroensis apparently use moisture derived from fog as well as soil moisture for continued growth. S. sabulicola has a system of surface roots that extends more than 10 m from the plant. These roots are able to take up moisture from the upper few millimeters of fog-dampened sand (Louw and Seely, 1980). Other roots do not penetrate more than 1 m below the sand surface. In contrast, I. hereroensis has a very long tap root penetrating several meters below the sand surface (Nott and Savage, 1985b) and fog-water uptake occurs through the leaves (Seely et al., 1977; Nott and Savage, 1985c). Fog-water precipitation increases from dune base to crest (Robinson and Seely, 1980) and availability of larger amounts of fog moisture may have led to greater long term survival of S. sabulicola on the upper plinths.

In 1980 and 1983 no differences in moisture content were measured from different regions of the dune plinths in soil at depths up to 300 mm (< 0.5 % moisture, gravimetrically determined). Thus soil moisture does not appear to provide the only explanation for the observed differential mortality. Moisture gradients on dunes are complex and poorly understood (Yeaton, 1988), however, and moisture at greater depths, or its relative availability from sands of varying grain size, may have contributed to the pattern observed.

Yeaton (1988) found that grass species establishing from rhizomes were found where rates of sand movement were highest and those from seed where sand movement was lowest. These observed patterns of establishment of _S. sabulicola_, and of _I. hereroensis_ although a succulent, partially confirm this pattern. On the transect, the most mobile sand occurred on the upper east and west plinth. However, the least mobile sand occurred on the lower and middle east plinth, the area where the fewest individuals survived. The lower west plinth, although intermediate in sand mobility, supported the highest growth of _I. hereroensis_ while they survived. Although sand mobility may be important for _S. sabulicola_ rhizome development, stable sand is not the only factor representing optimal growing conditions for _I. hereroensis_ growing from seed.

Initial vigour appears to have a possible influence on long term survival of _I. hereroensis_ but not of _S. sabulicola_. By 1980 the largest _I. hereroensis_ individuals with the greatest per cent cover were growing on the lower west plinth. Survival was also highest in this area. In contrast, the largest _S. sabulicola_ individuals with the greatest per cent cover were measured on the upper east plinth in 1980 whereas highest long term survival occurred on the upper west plinth.

Oryx are the major grazing animal in the main Namib Sand Sea. They feed upon both persistent species, and even appear to have a stimulating effect on growth of _I. hereroensis_ (Nott and Savage, 1985a). Oryx are not numerous enough to have a long term negative effect on plant populations. Seeds are an important dietary item to some dune organisms. Lizards and beetles usually feed on seeds accumulated at the base of plants or slipfaces (Robinson and Cunningham, 1978; pers. obs.). In contrast, larks were found to search for seeds at the dune base (Cox, 1983). Despite consumption of seeds by a number of species, extensive germination throughout the dune indicates that seed predation does not determine plant distribution.

Several rainfall events > 15 mm occurred after 1983. These caused germination of _S. sabulicola_ in all quadrats on the east and west plinths. None of the seedlings survived. Extensive germination of _I. hereroensis_ also occurred, and two seedlings became established on the lower west plinth. In view of the infrequent occurrence of rains sufficient to cause extensive germination and establishment (a 42 year interval during this century), exhaustion of the seed bank becomes a consideration. There is no information concerning longevity of seeds of either species nor what proportion of seeds in the soil germinate after a rainfall event. Seed production occurs regularly, however, _S. sabulicola_ setting seed annually in the summer months and _I. hereroensis_ throughout the year. Seed is distributed by wind, although germination patterns after light rainfall events indicate that at least a few of the seeds do not move far from the mother plant.

In the unpredictable, low rainfall conditions of the mobile desert dune sands in the western part of the central Namib, the pattern of establishment of persistent plant species appears to be controlled not by availability or distribution of seed but by differential mortality over time of established plants. Despite the unusual conditions in the Namib, where fog moisture contributes to sustained plant growth, I predict that differential mortality, rather than seed availability, may be the determinant of perennial plant distribution patterns in all mobile sand dunes.

ACKNOWLEDGEMENTS

For assistance with field measurements I thank A. and H. Ebez, L. Praetorius and A. Suttle. Financial support of the Foundation for Research Development and the Transvaal Museum is gratefully acknowledged. The Directorate of Nature Conservation provided facilities and permission to work in the Namib Naukluft Park.

REFERENCES

Bowers, J.E. 1982. The plant ecology of inland dunes in western North America. J. Arid Environ. 5: 199-220.

Boyer, D.C. 1987. Effect of rodents on plant recruitment and production in the dune area of the the Namib Desert. Unpublished MSc thesis, University of Natal, Pietermaritzberg.

Danin, A. 1983. Desert Vegetation of Israel and Sinai. Cana Publishing House, Jerusalem.

Felger, R.S. 1980. Vegetation and flora of the Gran Desierto, Sonora, Mexico. Desert Plants 2: 87-114.

Lancaster, J., N. Lancaster and M.K. Seely. 1984. Climate of the central Namib Desert. Madoqua 14: 5-61.

Lancaster, N. 1989. The Namib Sand Sea. A.A. Balkema, Rotterdam.

Le Houérou, H.N. 1986. The desert and arid zones of northern Africa. In: Ecosystems of the World Vol 12B, Hot Deserts and Arid Shrublands, B. M. Evenari, I. Noy-Meir and D.W. Goodall, eds. Elsevier, Amsterdam. pp. 101-147.

Leistner, O.A. 1967. The Plant Ecology of the Southern Kalahari. Botanical Survey of South Africa Memoir No. 38, Pretoria.

Livingstone, I. 1987. Using the response diagram to recognise zones of aeolian activity: a note on evidence from a Namib dune. J. Arid Environ. 13: 25-38.

Louw, G.N. and M.K. Seely. 1980. Exploitation of fog water by a perennial Namib dune grass _Stipagrostis sabulicola_. S. Afr. J. Sci. 76: 38-39.

Louw, G.N. and M.K. Seely. 1982. Ecology of Desert Organisms. Longman, London.

Mabbutt, J.A. 1984. The desert physiographic setting and its ecological significance. In: Arid Australia. H.G. Cogger and E.E. Cameron, eds. Surrey Beatty and Sons, New South Wales. pp. 87-109.

Nott, K. and M.J. Savage. 1985a. Observations on the utilization of a dune succulent by Namib faunae. S. Afr. J. Sci. 20: 269-271.

Nott, K. and M.J. Savage. 1985b. Root distribution of _Trianthema hereroensis_ in the Namib dunes. Madoqua 14: 181-184.

Nott, K. and M.J. Savage. 1985c. Variation in seasonal and diurnal leaf water potential of a Namib dune succulent. Madoqua 14: 177-179.

Orshan, G. 1986. The deserts of the Middle East. In: Ecosystems of the World Vol 12B, Hot Deserts and Arid Shrublands, B. M Evenari, I. Noy-Meir and D.W. Goodall, eds. Elsevier, Amsterdam. pp. 1-28.

Pierre, F. 1958. Ecologie et Peuplement Entomologique des Sables Vifs du Sahara Nord-Occidental. Publications du centre de recherches Sahariennes série biologie No. 1. pp. 7-332.

Pietruszka, R.D. and M.K. Seely. 1985. Predictability of two moisture sources in the Namib Desert. S. Afr. J. Sci. 81: 682-685.

Quézel, P. 1971. Die Pflanzenwelt. 1. Teil. Flora and Vegetation der Sahara. In: Die Sahara und ihre Randgebiete Vol. 1. H. Schiffers, ed. Weltforum Verlag, München. pp. 429-475.

Robinson, M.D. and A.B. Cunningham. 1978. Comparative diet of two Namib Desert sand lizards (Lacertidae). Madoqua 11: 41-54.

Robinson, M.D. and M.K. Seely. 1980. Physical and biotic environments of the southern Namib dune ecosystem. J. Arid Environ. 3: 183-203.

Seely, M.K., M.P. de Vos and G.N. Louw. 1977. Fog imbibition, satellite fauna and unusual leaf structure in a Namib Desert dune plant, Trianthema hereroensis. S. Afr. J. Sci. 73: 169-172.

Seely, M.K. and G.N. Louw. 1980. First approximation of the effects of rainfall on the ecology and energetics of a Namib Desert dune ecosystem. J. Arid Environ. 3:25-54.

Seely, M.K. Sand dune communities. In: Ecology of Desert Communities. G.A. Polis, ed. University of Arizona Press, Tucson. (in press).

Shmida, A., M. Evenari and I. Noy-Meir. 1986. Hot desert ecosystems: An integrated view. In: Ecosystems of the World Vol 12B, Hot Deserts and Arid Shrublands, B. M. Evenari, I. Noy-Meir and D.W. Goodall, eds. Elsevier, Amsterdam. pp. 379-387.

Walter, H. 1936. Die ökologischen Verhältnisse in der Namib-Nebelwüste (Südwestafrika) unter Auswertung der Aufzeichnungen des Dr. G. Boss (Swakopmund). Jahrb. Wiss. Bot. 84: 58-222.

Walter, H. and E.O. Box. 1983. The Karakum desert: an example of a well-studied eu-biome. In: Ecosystems of the World, 5, Temperate Deserts and Semi-deserts. N.E. West, ed. Elsevier, Amsterdam. pp. 105-159.

Yeaton, R.I. 1988. Structure and function of the Namib dune grasslands: characteristics of the environmental gradients and species distributions. J. Ecol. 76: 744-758.

Zohary, M. 1973. Geobotanical Foundations of the Middle East. 2 Vols. Gustav Fischer Verlag, Stuttgart.

Figure Captions

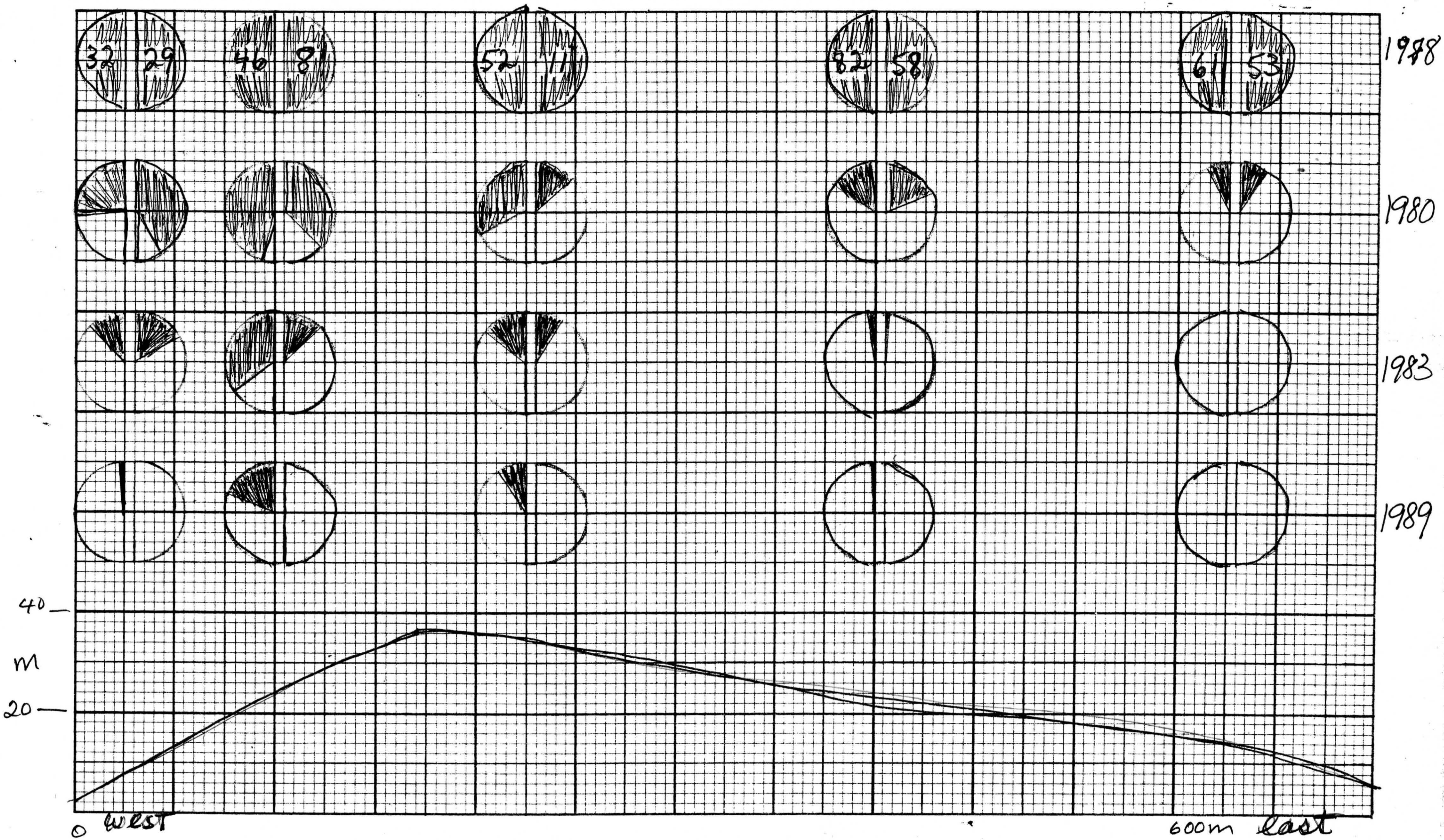
1. Profile of a linear dune in the central Namib. Per cent survival of Stipagrostis sabulicola (left half of circles) and of Trianthema hereroensis (right half of circles) in July 1978 (top), June 1980, November 1983 and October 1989 (bottom). The original number of plants present in 1978 is indicated in each half circle.

2. Mean per cent cover (± S.E.) of Stipagrostis sabulicola (•) and Trianthema hereroensis (o) in quadrats (n = 4) at four times of measurement on the lower and upper west plinth and on the upper, middle and lower east plinth.

3. Percentage of total cover in quadrats (n = 4 per area) on east (above) and west (below) plinths of a linear dune (u = upper, m = middle, l = lower) at four measurement periods.

4. Mean per cent cover (± S.E.) of individual Stipagrostis sabulicola plants on the west lower (1, n = 32, 17, 8, 1) and upper (2, n = 46, 42, 32, 18) plinth and the east upper (3, n = 52, 34, 15, 10), middle (4, n = 82, 26, 4, 1) and lower (5, n = 61, 9, 0, 0) plinth at four measurement periods; mean per cent cover (± S.E.) of individual Trianthema hereroensis plants on the west lower (1, n = 29, 24, 10, 0) and upper (2, n= 8, 6, 2, 0) plinth and the east upper (3, n = 11, 3, 2, 0), middle (4, n = 58, 22, 1, 0) and lower (5, n = 53, 10, 0, 0) plinth at four measurement periods.

(1)



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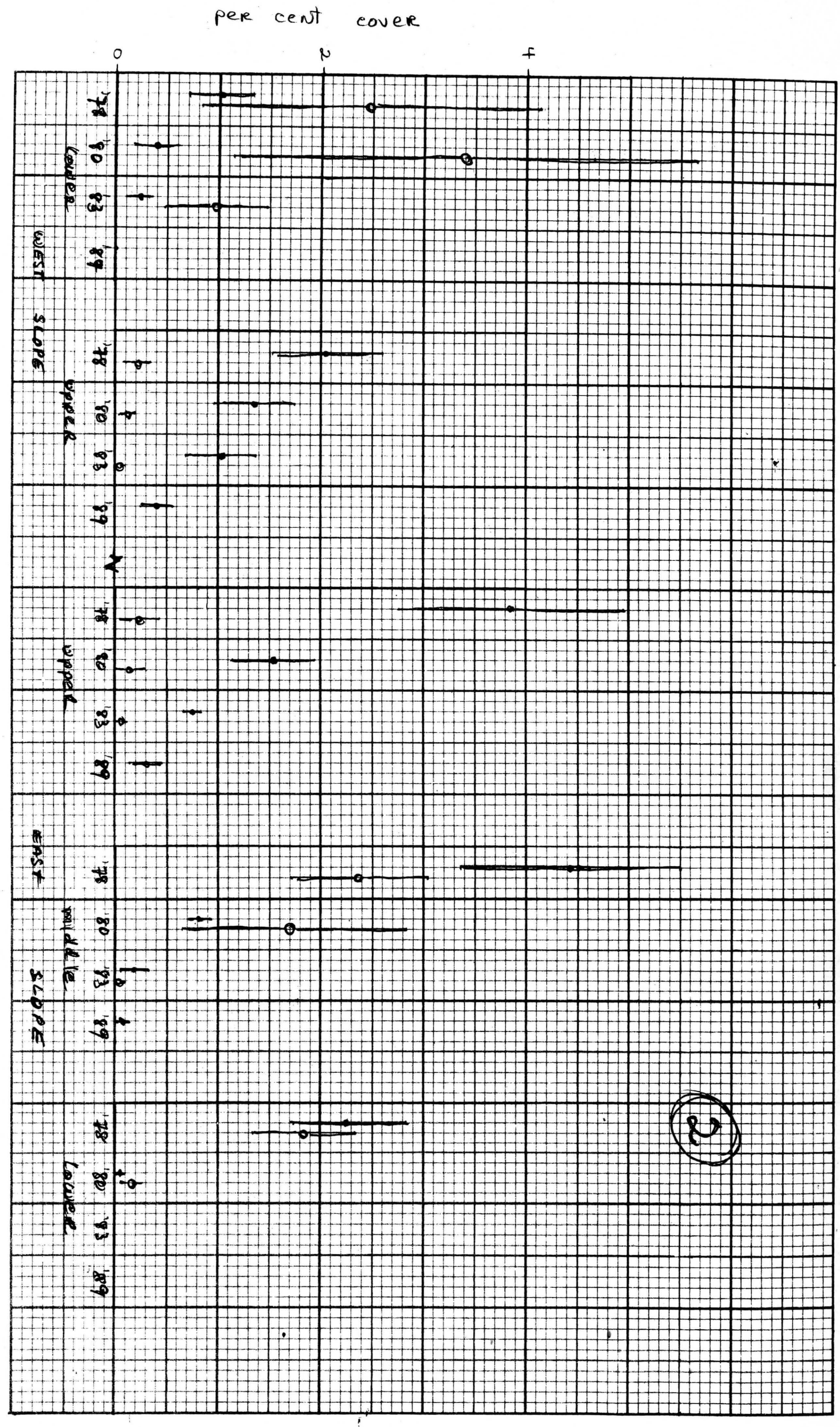

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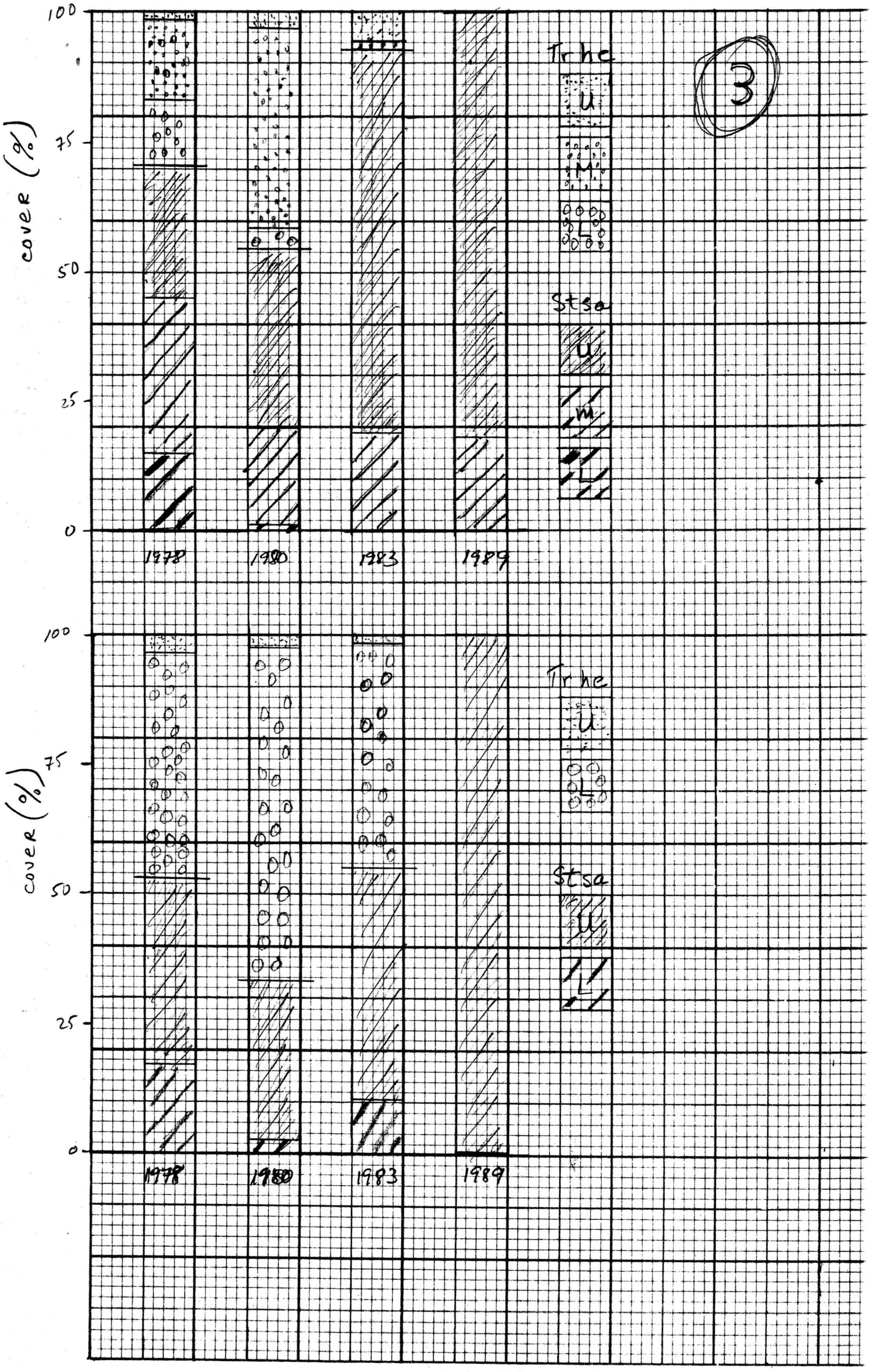

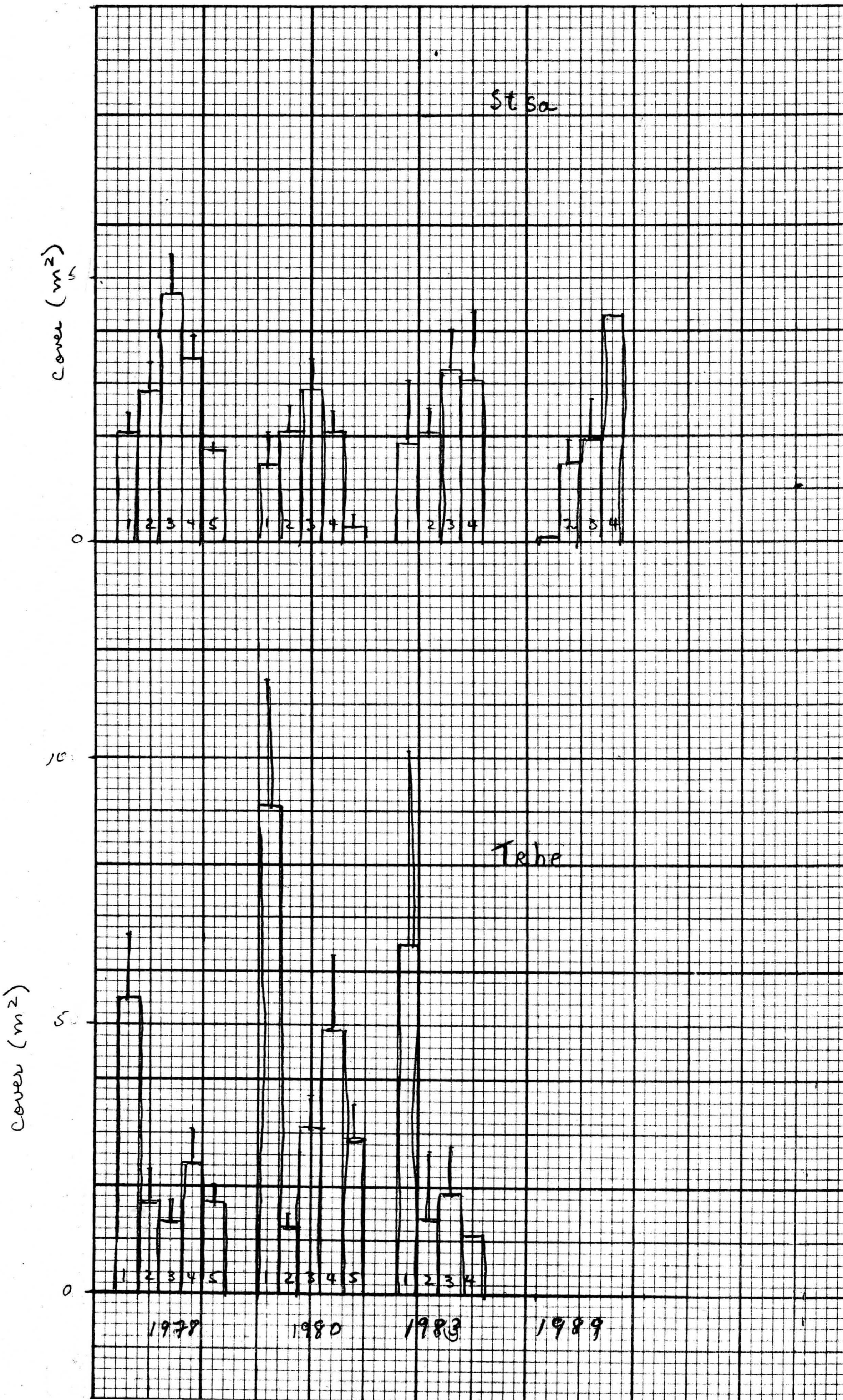
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