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A PRELIMINARY AUTECOLOGICAL
STUDY OF STAAVIA DODII,
FAMILY BRUNIACEAE

Hong

Andrew Gubb
November, 1976

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INTRODUCTION

Staavia dodii is a "rare and endangered" species, belonging to the Family Bruniaceae, which is endemic to South Africa. *Staavia dodii* is restricted and endemic to the Cape of Good Hope Nature Reserve. It occurs in a number of small populations, which are relatively isolated from each other.

Veld fires are comparatively frequent during the summer months in the Cape Peninsula, and a number of *Staavia dodii* populations have been destroyed by fire. Furthermore,ⁱⁿ all senescent populations there are substantially fewer seedlings appearing than senescent bushes dying off.

The possibility of future burning programmes and the ever-present danger of accidental burning of vegetation are two important considerations demanding investigation on *Staavia dodii*, which, like so many other rare and endangered species, has escaped the specific attention of many researchers.

No record could be found of any scientific work on *Staavia dodii*, and the present study was conceived of as a preliminary autecological investigation, focusing on the effects of fire on these isolated populations, and the factors involved in germination.

1 GEOGRAPHICAL DISTRIBUTION

Staavia dodii, an endemic species, is rare and local in the Cape of Good Hope Nature Reserve, which lies in the south-western Cape, at about 34 15'S and 18 31'E. Staavia dodii populations are restricted and occur in the central area of the Cape of Good Hope Nature Reserve extending west to east (map 1).

2 CLIMATIC AND TOPOGRAPHICAL LIMITATIONS

2.1 The general climatic cycle

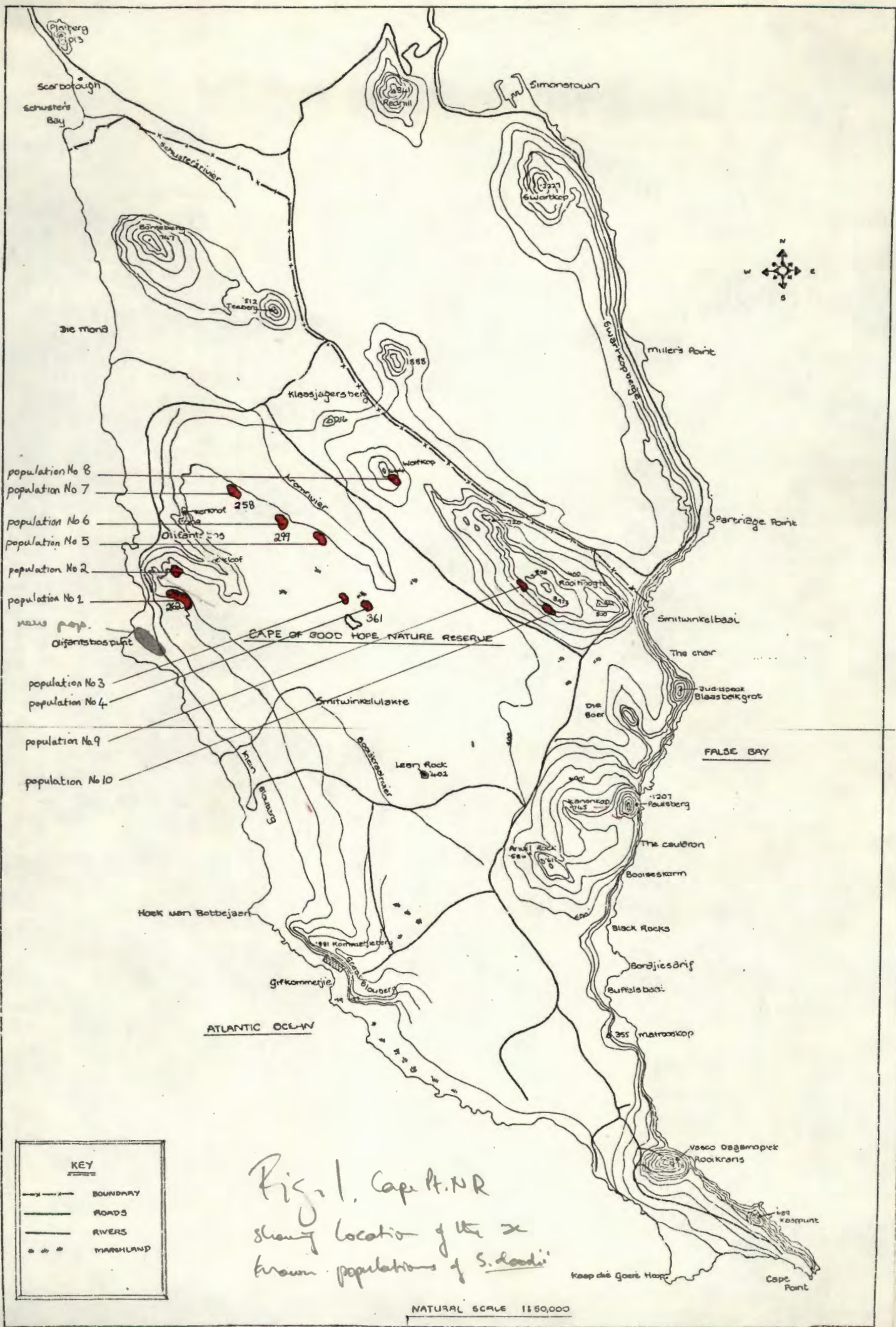
The Cape Peninsula is small and almost surrounded by sea, thus having an equable climate. The climate is of the Mediterranean type, which is characteristically maritime. In summer the stable^{anti-}cyclonic system off the west coast i.e. the South Atlantic High, causes warm dry weather with frequent south-easterly winds (map 2). These winds vary both in intensity and duration, being generally stronger and more lasting in the southern Peninsula.

During winter the area is affected by the eastward moving cyclonic systems of the mid-latitudes. The clockwise movement of the cyclone causes moist north-westerly winds to blow over the Peninsula and cyclonic precipitation occurs (map 3). A cyclonic depression may be followed by another, or fine weather, sometimes lasting over a week, may occur.

The transition between summer and winter is gradual. Furthermore, the so-called summer and winter phenomena are not entirely confined to these seasons - so accentuating the equable nature of the climate.

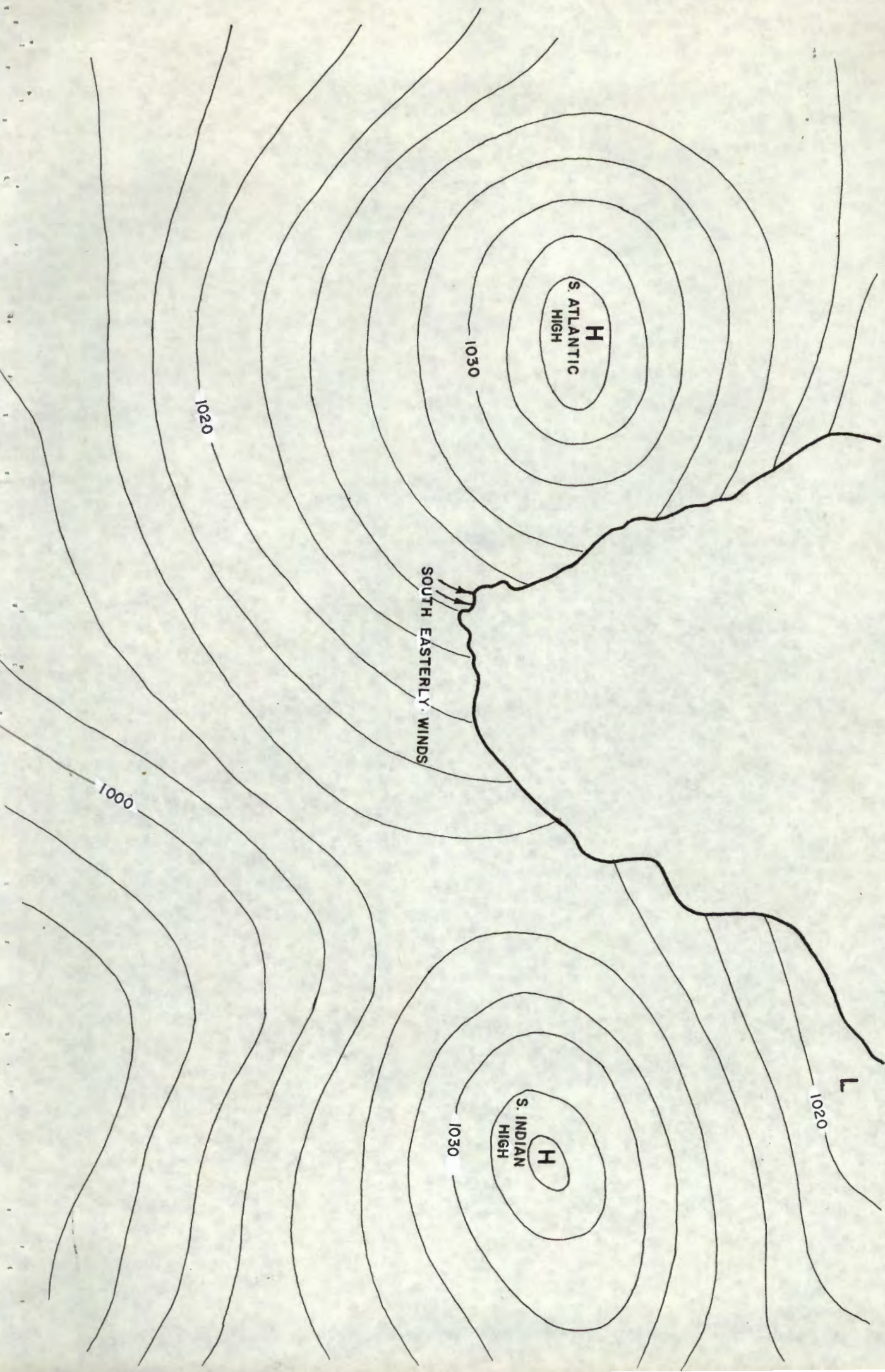
2.2 Climatic influences on the Reserve ¹

1. Climatic data from Taylor, H, (1969)

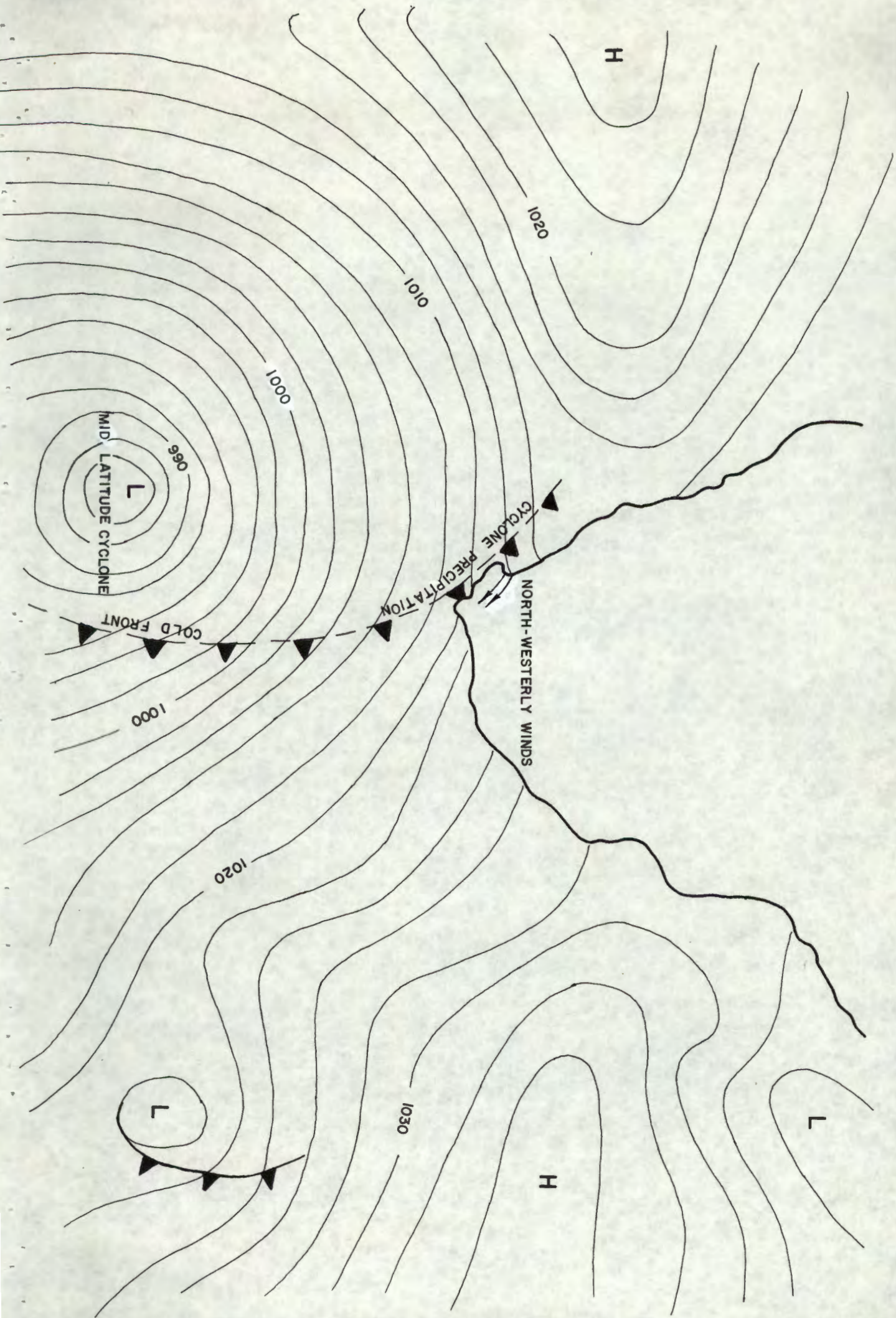


ISOBARIC MAP OF TYPICAL COASTAL PRESSURE SYSTEM AFFECTING THE SOUTH WESTERN CAPE IN SUMMER.

4



ISOBARIC MAP OF TYPICAL COASTAL PRESSURE SYSTEM AFFECTING THE SOUTH WESTERN CAPE IN SUMMER.



2.2.1 Temperature

The exposed weather station at Cape Point is not representative of general conditions in the Reserve, but certain inferences may be made from the data on Simonstown and from the vegetation in the Reserve. The average range in mean daily maxima and minima temperatures at Cape Point is only 4°C, compared with a range of 8.5°C at Simonstown. Cape Point is continually exposed to the cold south-easterly winds, while Simonstown, on the north side of a mountain range, not only receives more insolation, but is also sheltered from some of the summer winds. The xerophytic vegetation of the north slopes in the Reserve suggests that their temperature regimes are more like those of Simonstown.

Seasonal temperature variation is small, being about 5°C at Cape Point and nearly 17°C at Simonstown. It is unlikely that any part of the Reserve experiences frost.

2.2.2 Wind

The dominant climatic factor on the Reserve is wind. Few places are completely sheltered from either the summer or winter winds. The south-easters may blow for a period of a week or more, with intensities of 16km to 40km per hour, gusting to 102km per hour, being frequently recorded at Cape Point. Deformation - caused by strong winds from a constant direction - is characteristic of the coastal vegetation. Because these winds blow mainly in the fire season, they are instrumental in the formation of dunes, so having an important effect on habitat.

The north-westerly winter winds seldom form dunes, but have the effect of scorching the vegetation on the coastal shelf. This is probably a result of wind-borne salt spray. Generally, the Staavia dodii populations are exposed to both summer and winter winds, but are partly protected by rocks.

2.2.3 Precipitation

About 90% of the annual precipitation of the southwestern Cape falls in winter. The average annual rainfall of Cape Point is given as 333mm, which is substantially lower than the surrounding areas. While the extent of the difference may be a result of inaccurate recording, the rainfall of the whole Reserve is generally lower than that of the northern part of the Peninsula.

Fog is more common on the west coast, occurring in all seasons, but particularly during autumn. Fogs on the east coast occur mainly in autumn. Staavia dodii populations are not found in areas of common fog occurrence.

2.3 Topographical limitations

Staavia dodii populations occur on the peaks and upper slopes of hills and ridges characterized by rocky outcrops, but not restricted to any aspect. The ground is dry and the bedrock is very close to the surface. The elevation of the slopes varies from 700m in the west to 200m in the east (table 1).

3 CLASSIFICATION

Staavia dodii belongs to the Order Rosales, Family Bruniaceae, which is endemic to South Africa. Staavia dodii, an erect heath-like shrub, possesses the following characteristics:

a) Leaves: small, spirally imbricate, exstipulate; undivided, lanceolate and three-angled; smooth and longitudinally striated; upper leaves form an involucre around the flower head; apex bears a small projection composed of suberized cells (plate 1); stomata variable; long, slender, unicellular hairs on abaxial and adaxial surfaces - concentrated at apex on immature leaves; hairs have thick walls and narrow lumens; large epidermal cells; thick cuticle, especially on outward-directed abaxial surface.

POPULATION	ELEVATION (ft)
1	210
2	210
3	320
4	360
5	300
6	300
7	250
8	400
9	600
10	600

TABLE 1 : ELEVATION OF STAAVIA DODII POPULATIONS

b) Inflorescence: compressed head or capitulum, surrounded by one or more series of sterile bracts forming an involcre; bears five to ten flowers on broad, flattened axis; development from the centre outwards; racemose; diameter 6 - 12mm, usually 8 - 9 mm; glutinous exudation covers head.

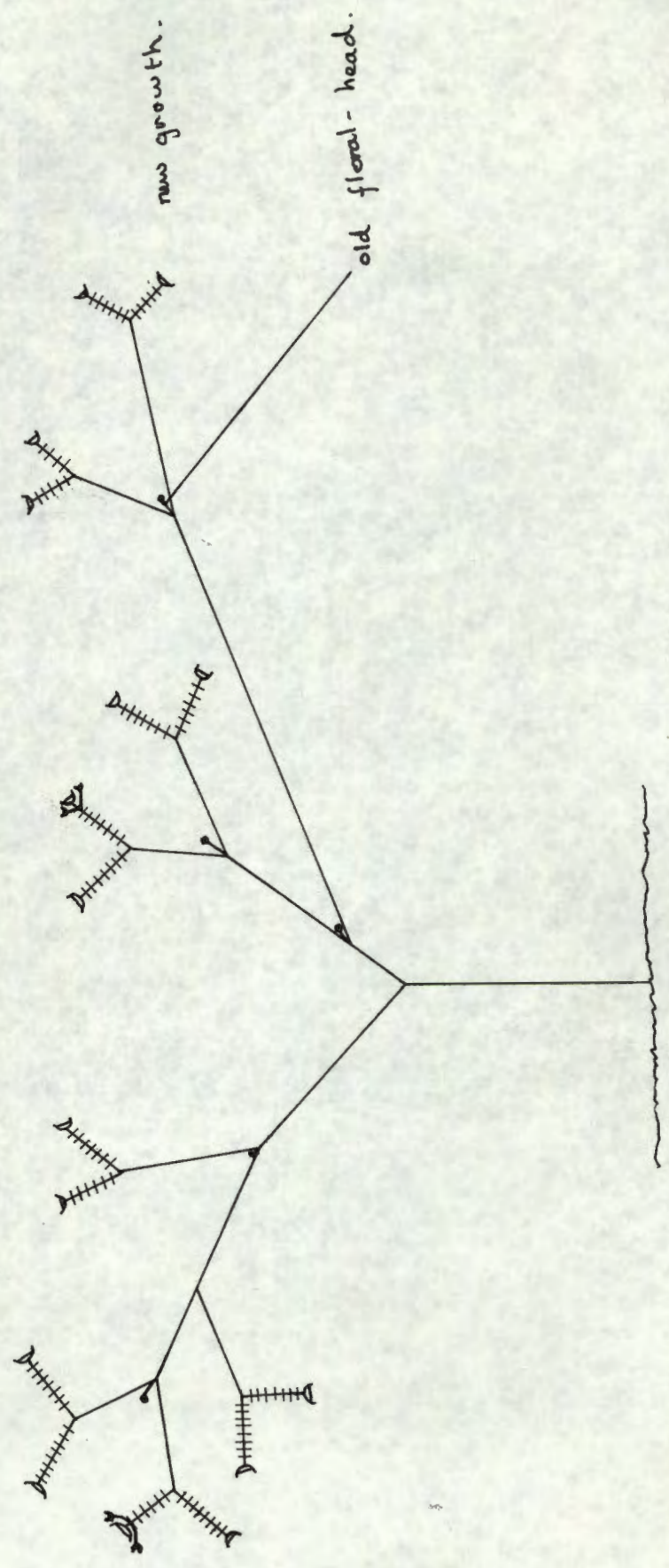
c) Flowers; sessile, bisexual, actinomorphic, less than 5 mm long and 4 - 5 mm wide; surrounded by four to twelve conspicuous involcral bracts which are white - except for black apiculus - wobbly, and usually longer than flowers; thread-shaped bractioles; perianth differentiated into calyx and corolla; obconic calyx tube adnate to ovary and produced slightly above; five sepals unite beyond the ovary; five petals. imbricate in bud, united below, lanceolate, slightly tubed with pouched gland at base of each petal; five stamens. alternate with petals, in one whorl; sagittate-ovate anthers. two thecas opening inwards by longitudinal slits; perigynous ovary, one-celled - sometimes incompletely chambered, generally single carpel contains one ovule, rarely two; pendulous and inverted ovules; single simple style which is short and thick; two stigmas, obliquely terminal and connate; dry, dehiscent fruit - nut with one (two) seeds, extra seed coat - aril; albuminous seeds with endosperm; minute embryo next to hilum.

4 **GENERAL MORPHOLOGY**

4.1 **Growth type**

Staavia dodii may be described as an openly growing ericoid shrub. A characteristic of this type of growth is the "semi-dichotomous" branching of the stem (figure 1, plate 2). The stem generally has no leaves - the leaves occurring at the apices of the branches. The root system is diffuse and extends to a depth of about 1½ metres. Below 15 cm no main tap root is discernable - the roots branching extensively.

Fig 1 'Semi-dichotamous' branching of Stauvia dodii.



4.2 Flowering period

Staavia dodii has a long flowering period lasting from March to September. By the end of April all the flower heads have been produced.

4.3 Seeding period

Seeds ripen on the flower heads from April through to the end of November. It follows that flowers produced early in the season will seed late in April.

4.4 Flowering position

The majority of the flowers are situated towards the outer edge of the head. Fewer flowers occur near the centre (plate 3).

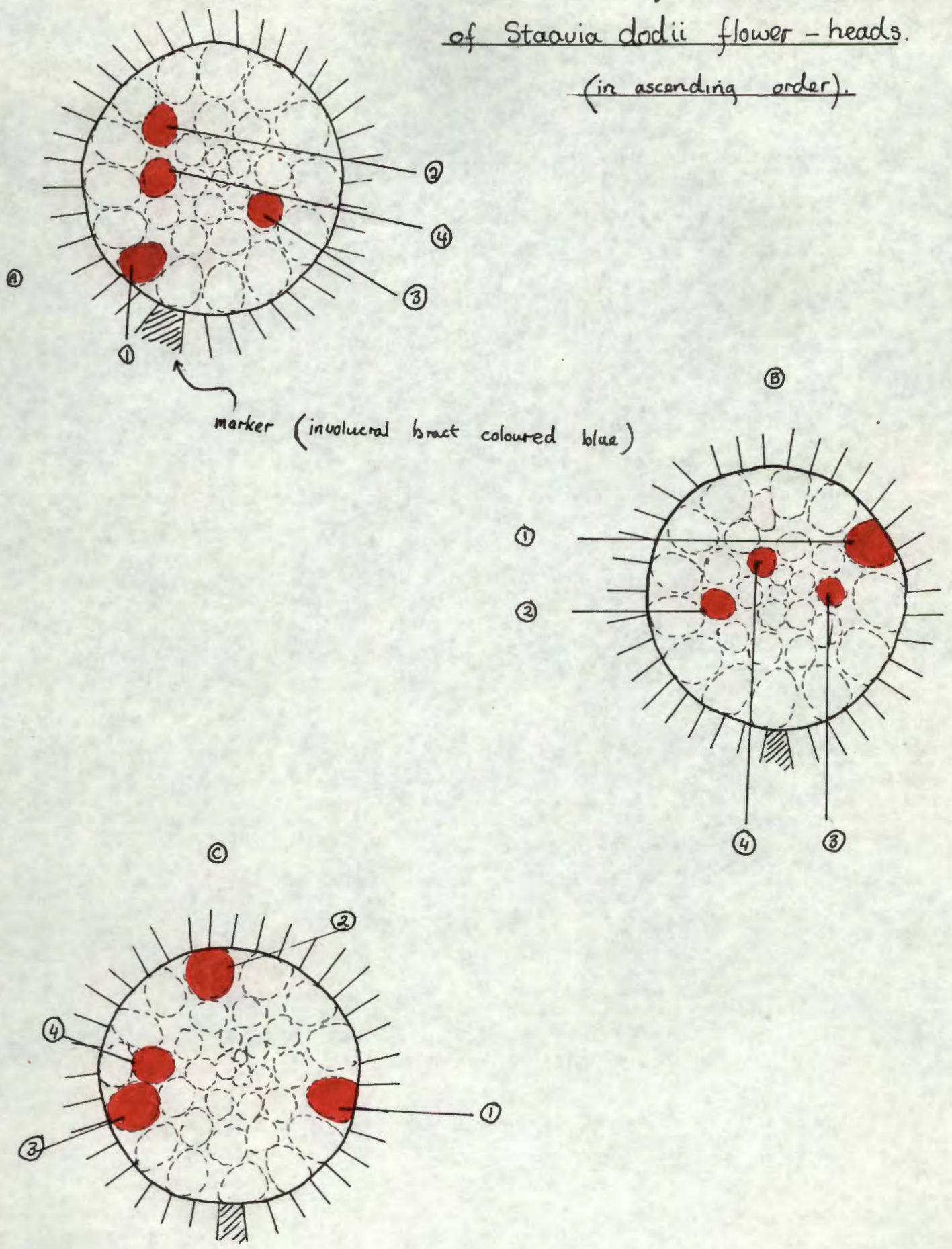
4.5 Rotation flowering

A number of flower heads were marked with tags and the position of the flowers as they appeared, was recorded. This information enabled the following order of flowering to be established (figure 2). The flowers opened from the perimeter inwards in a clockwise direction. The leaves spiral upwards around the stem in a clockwise direction (plate 1), becoming broader and more splayed as they approach the flower head. At the base of the flower head the spiralling leaves are modified further to form an involucre, supporting the flower head. This involucre has two layers, the inner one of which gradually merges with the bracts on the flower head. A similar spiralling (i.e. clockwise) pattern occurs in the flowers which are positioned on a woody receptacle (figure 2).

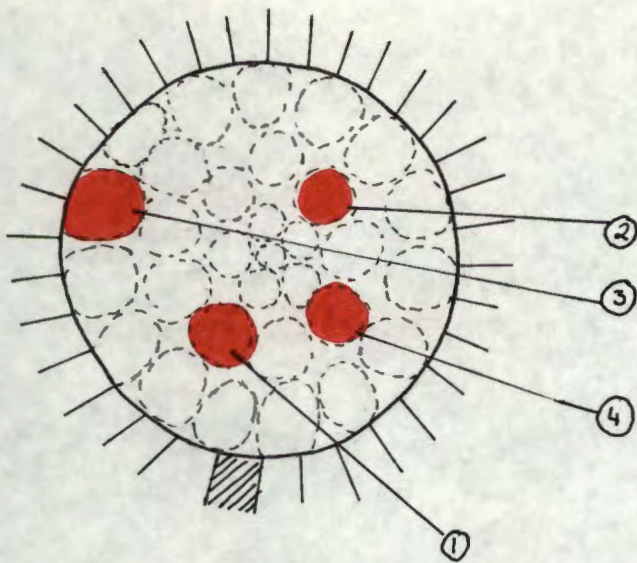
4.6 Seeding

Although there are approximately 30 flowers on a well-developed head, a maximum of ten flowers seed - the other

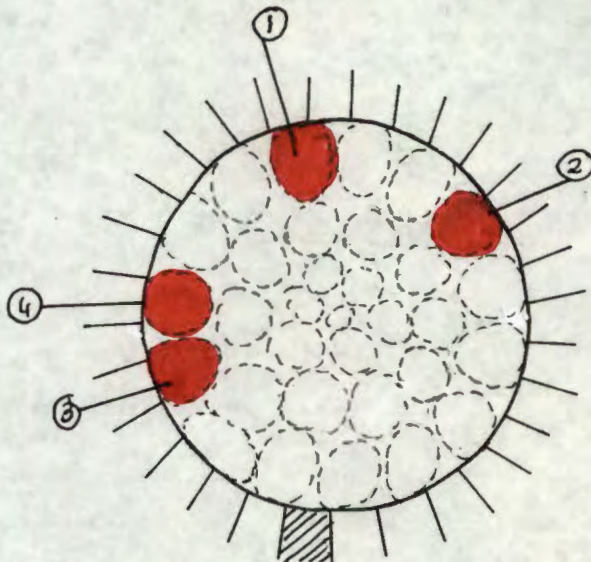
Figure 2 The investigation of Rotation
Flowering in a sample
of *Staavia dodii* flower-heads.
(in ascending order).



d



e



f

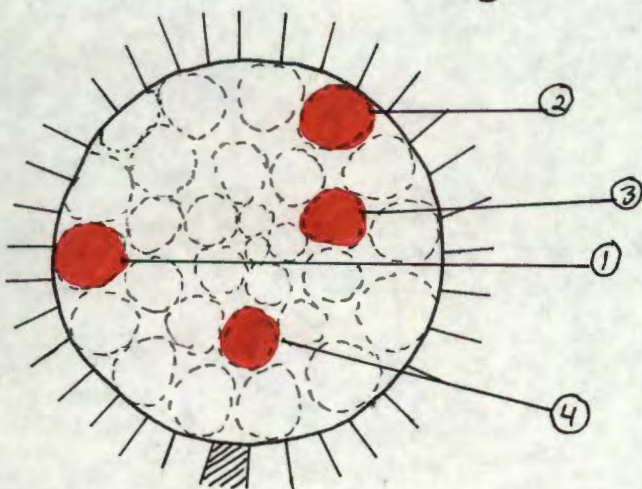
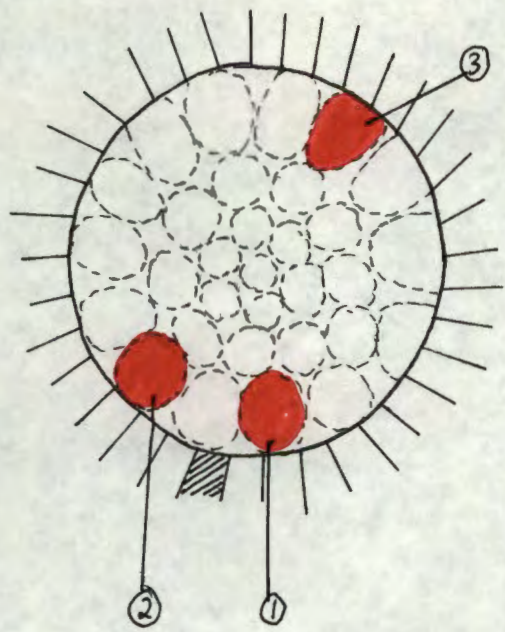
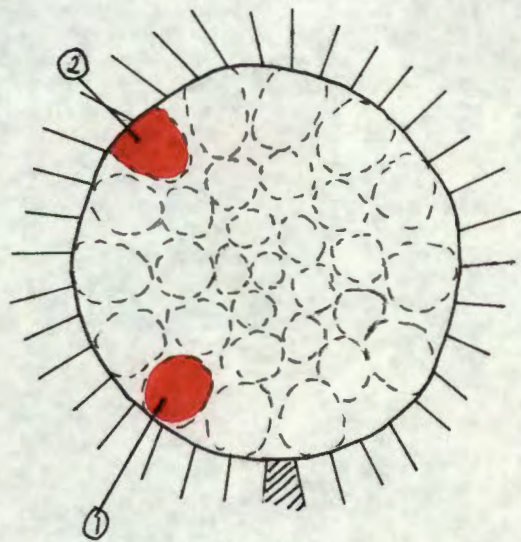


Figure 2 (contd)

g



h



i

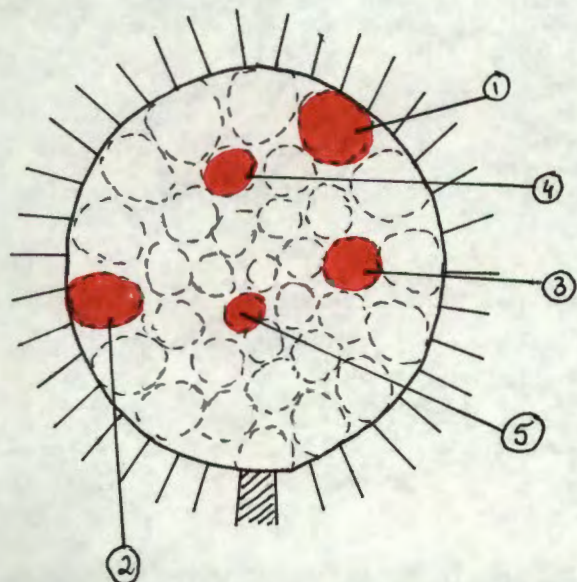
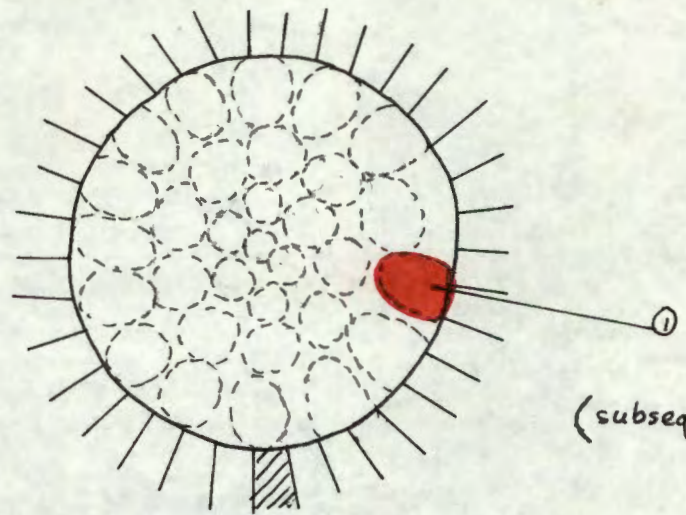


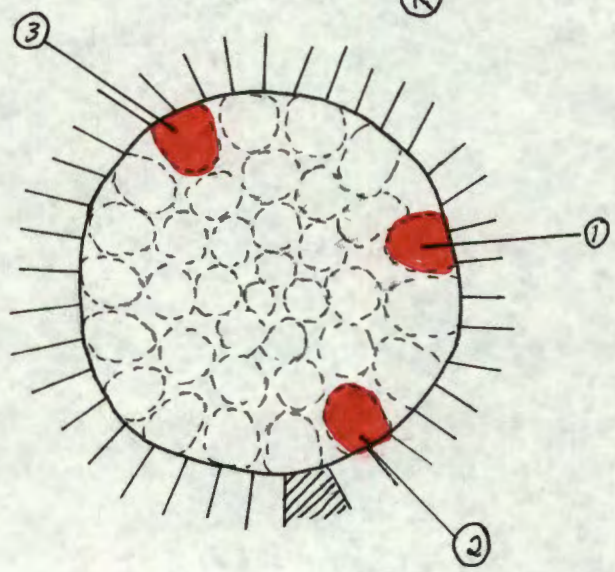
Figure 2 contd

(j)



(subsequently died).

(k)



flowers possibly not being pollinated. Just as the number of flowers produced depends on the population age, so does the number of flowers seeding.

4.7 Coppicing

No true coppicing was observed, although Population 8 showed an example of "partial coppicing" when a mature shrub had been destroyed - apart from a few viable terminal branches. The rate of growth of the new shoots was more rapid than the surrounding seedlings (plates 4 and 5). This is as a result of the roots of the destroyed plant remaining functional. The terminal branches of this plant remained functional until such a time as the coppiced shoots had become well-established and sufficiently photosynthetically active to maintain the root system.

4.8 The position of the flower heads on the shrub

The flowers occur on the terminal branches of the shrub facing outward (plate 6). Thus, when dispersed, the majority of seeds fall outside the shrub foliage cover. A well-established mature bush may have as many as 200 to 300 flower heads, which leads to high number of seeds being produced per bush per season.

4.9 Shoot production

Shoot production took place from the beginning of June, or shoots may appear as buds prior to this period. Two (occasionally three) shoots are produced just below the the flowers. In the event of shoots appearing early, small flower heads may develop at their apices. The development of shoots is slow until flowering has been terminated. Consequently, terminal branches of a mature shrub with a cluster of 3 to 4 flowers may be observed - two or three flower heads being extremely small with 1 to 2 flowers per head, and the fourth flower head, belonging to the original branch, being large in diameter.

4.10 Seed development

Flowers open for a period of about 4 days, during which time the flowers are pollinated. The flower closes subsequently, and remains closed for an approximate period of 6 weeks, whereupon the carpel of the ovary, having died, forms a light brown husk. The base of the ovary tears away from the receptacle, and the surrounding mass of bracts exert pressure on the edges of the now loose ovary - so forcing the dry fruit upwards above the level of the flower head. A concurrent splitting open and folding back of the carpels occurs (plate 7). Once the dry dehisced fruit is resting partly above the flower head, the dry carpels, using the bracts as a lever, fold right back, having the appearance of a pair of jaws (plate 8). The light brown seed, resting in the dry dehisced carpel, is free (plate 7). The folding back of the carpels continues with the tip of the stigma digging into the mass of bracts, suspending the base of the fruit above the bracts.

This system of seed exposure may be compared to the exposure of the fertile gleba of the Gasteromycetes fungus, *Geastrum* - a genus of the Order Lycoperdales. The exposed seed is removed from the dry dehisced fruit coat by means of branch shaking in windy conditions, it is displaced by raindrops (empty carpel, plate 8).

4.11 The effect of wind

Long branches tend to droop or break off at the base - especially in senescent populations. This appeared to be the result of the buffeting effect of the wind. The breaking of branches was more apparent in areas where large Leucodendron species, Leucospermum species and protea bushes had died off, leaving gaps in the vegetation - so resulting in funnelled wind gusts blowing onto Staavia dodii shrubs.

Many scattered dead shrubs are found in senescent populations. It is difficult to determine whether this is due to wind buffeting or not. The dead shrubs displayed characteristic twisting of the stems at ground level (plate 9) - a feature apparent in exposed shrubs as well (although no broken branches occur). Shrubs protected from wind by Protea bushes or large boulders have healthy stems with no twisting (Plate 10).

In recently matured populations (eg. Population 3), no broken branches or dead shrubs occur. In these populations, vegetation height is uniform - so affording Staavia dodii maximum protection on all sides (Plate 11).

5

VARIATION OF FLOWER-HEAD SIZE WITH AGE

Staavia dodii flower-head size depends broadly on three factors:

- a) the age of the plant
- b) the age of the population
- c) the position of the plant in relation to environmental factors.

Population age depends on when the population was last destroyed by fire. About 400 flower heads per population were measured from a large sample of shrubs in each population. The sample was kept as large as possible, with a minimum of flower heads per/shrub being measured - so attempting to reduce the possibility of sampling errors and of variation occurring due to environmental factors (table 2).

Population 1; This population is situated on the west coast between spot heights 259 and 262. A section of the population was destroyed by fire about 5 years ago. This section has an average flower-head diameter of 8.88 mm for young plants (which have flowered for 1 - 2 seasons); 9.04 mm for young mature plants and 9.98 mm for "young" plants. (These plants have 1 - 5 flower heads, 5 - 15 flower heads and more than 15 flower heads respectively.) The average size of flower head in this

Populations

Diameter. (m.m.)

<u>Pop.</u>		
1.		6.86.
2.		7.23.
3.		9.11.
4.		6.55.
5.		6.43.
6.		6.72.
7.		7.28.
8.		6.62.
9.		—
10.		—

Table 2 : Variation of flower-head size with age

community is 9 mm. In the western area of this population, there is a section which has older senescent plants (15 - 20 years). These plants have an average flower-head diameter of 6.86 mm.

Population 2: This population, which is senescent, lies north-west of Population 1, overlooking the area called "Die Kloof." The flower heads have an average diameter of 7.23 mm.

Population 3: Lying west of spot height 361, this population occurs in the firebreak which is burnt every 9 years. The plants are mature and have vigorous, healthy growth with the diameter of the flower heads being 9.11 mm on average.

Population 4: The average flower-head diameter of this extremely senescent population (20 - 25 years), occurring on spot height 361, is 6.55 mm.

Population 5: Occurring ^{south-east} of spot height 299, the average flower-head diameter of this population is 6.73 mm. Senescent growth is apparent.

Population 6: This population occurs at spot height 298, and the average flower-head size is 6.172 mm. Senescent growth is apparent.

Population 7: Occurring at spot height 258, senescent growth is apparent in this population. The average flower-head diameter is 6.72 mm.

Population 8: This population lies on the peak of Wolfkop, spot height 464. Prior to 1975 there were about 35 - 40 shrubs. In 1975 a bush fire destroyed all except two shrubs which had a flower-head diameter of 6.62 mm. Clearly this sample is not sufficient to be representative of the whole population, and the size of the flower head might well be due to environmental factors.

Populations 9 and 10: Two further populations occur, on the southern slopes of spot heights 808 and 902. However, these populations were totally destroyed by fire in 1975 and no data on flower-head size are available.

6 POLLINATION

6.1 Pollinating agents

No specific study of the pollinating agents was made and such observation was restricted to a general level. Upon daytime investigation of the flower heads, the following animals were noted as possible pollinating agents:

Vertebrates: Birds - sugar birds

Invertebrates: Beetles

Wasps

Bees

Ants

6.1.1 Birds as pollinators (ornithophily)

On several occasions the sunbird (Nectarinidae) was seen visiting Staavia dodii bushes. Sugar is the primary attractant for these birds, which hop from flower to flower. To facilitate pollination, visits must be regular. Since the sunbird visits were irregular, and appeared to be almost accidental while flying en route from one colourful bush to another (eg. Erica species and Aspalathus capensis^{plate 10}), it may be concluded that these birds, while playing a small part in pollination, are of very little importance to Staavia dodii populations.

6.1.2 Beetles as pollinators (cantharophily)

→ Hemiptera! A ♀
Various Coleoptera, both of the chewing and sucking type, visited Staavia dodii flowers heads, with stink-bugs being the most common variety observed. The majority of

chewing beetles were observed eating the ray-florets - perched on the flat disc of the flower head, facing outward with their bellies rubbing over the flower. Thus they were in a favourable position for pollinating the flowers. Although the mouth parts (perpendicular to the body axis) are in an orthognathic position facilitating the licking of nectar from the open, flat flowers, this was not observed.

By way of contrast, the sucking beetles (which were more common) did lick the nectar from the individual flowers on the flower head. It was concluded that these sucking beetles are of relative importance to the pollination of Staavia dodii - being attracted to the flower by nectar odours rather than colour.

6.1.3 Hymenoptera as pollinators

a) Ants (formicidae): Ants were frequently observed walking in the flowers, but generally only in one's and two's. The high carbohydrate level (nectar) serves as an attractant; however, due to the small number of ants seen on the flowers, ants were not classed as general pollinators.

b) Wasps (vespidae); A variety of species, generally small in size, were noted. The wasps lapped up the nectar, and it was concluded that they visited the flowers only for nectar, which is a source of carbohydrate to maintain their energy metabolism. Since the visits were infrequent, wasps were classified as unreliable and unsteady pollinators.

c) Bees (melittophily):

i) Honey-bees: This bee visited the Staavia dodii flowers irregularly and was not considered to be of much importance as a pollinator.

ii) Bumble-bees: The bumble-bee (the common Bombus species found throughout the Cape) was classed as one of the main pollinating agents, being the most regular visitor to the Staavia dodii flowers. The bumble-bee niche is fully established in the vicinity ,

in old, rotting Protea logs, and the bee is the most versatile and active pollinator in the Staavia dodii populations.

Other colourful plant species especially the bushy species such as Aspalathus capensis (plate 12) in the Staavia dodii population attract the Bumble-bee. While en route from one Aspalathus capensis bush to the next, the bumble-bee will settle on a Staavia dodii bush and visit a number of flowers. The Staavia dodii flower, as a result of its toughness and general open formation, is not damaged by the bumble-bee.

Thus a pair of bumble-bees (inhabiting a dead Protea bush within a Staavia dodii population) being extremely territorial, may monopolize the community. This favours the pollination of Staavia dodii, as the bees will spend the whole day "working" on the population. Both the structure and behaviour of the bumble-bee show distinctive adaptation which facilitate their feeding off the Staavia dodii communities. However, it must be borne in mind that the possibility exists that, although the bumble-bee is an important pollinator of Staavia dodii, this pollination may be indirect; that is to say, the bumble-bees are attracted originally by the colourful plant species in the community, with the scent of the nectar in the Staavia dodii flower heads becoming more important at close quarters. Thus, while Staavia dodii is a source of nectar for the bumble-bee, the other colourful species could possibly provide pollen. This may well be a complex evolutionary specialization on the part of Staavia dodii; such a suggestion however, is speculative, and more intensive investigation would be required to validate it.

7 SEED DISPERSAL

7.1 Agents

No seed dispersal agents for Staavia dodii were observed. The role of wind and rain in facilitating dispersal has been discussed previously.

7.2 Dispersal position

Litter from the bases of nature bushes was collected and the seeds spitted out. The distance of the litter (moving radially outwards from the plant) was recorded, and it was found that the majority of seeds fell under and around the Staavia dodii shrub. This supports the suggestion that the seeds are dispersed by wind buffeting, and no agents are responsible for the dispersal of seeds - possibly because the testa is tough and thick enough so as to pass through the intestine of vertebrates, such as birds, baboons etc, virtually undamaged. The fact that seeds found further afield were resting against Restia tussocks and surface rocks suggests that these seeds were carried by water.

8 SEEDLING DISTRIBUTION

8.1 Unburnt areas

Very few seedlings are found in those populations which have not been burnt in the last 10 years. Population 4 had a single seedling 32 centimetres in height - probably 2 to 3 years old. Some populations contained no seedlings, while Populations 6 and 7 had 6 and 4 seedlings respectively, only two of which were under 3 years old (Population 6). Even Population 3 which is at most 9 years old, contained very few seedlings (Plates 41, 42 and 43).

8.2 Burnt areas

This includes sections of Population 1,8,9 and 10 burnt about 5 years ago, and Populations 8,9 and 10 burnt less than a year ago. All four populations show extensive seed germination and seedling growth. Population 8 has approximately 2 000 seedlings originating from 35-40 pre-fire senescent shrubs. Seedlings occupy areas in the original population as well as areas near the burnt vegetation, that is the area occupied by pre-fire shrub. The seedlings found further afield are obviously a result of seeds being carried by wind and water. The question arises whether the seedlings occupying new areas will reach maturity or not. However this is a point requiring further investigation at a later point in time.

No seedlings occur in close proximity to the two remaining mature shrubs in Population 8. It is possible that the Staavia dodii shrub releases toxins into the soil which prevent germination of seeds in the immediate vicinity, so reducing the competition for survival factors (i.e. light, nutrients, water etc). The contrast between the observed pattern of seed dispersal and seedling growth is important. It will be recalled that in Populations 2,3,4,5,6,7 the seeds were found mainly around and under the Staavia dodii bushes, whereas in the burnt areas (where extensive seed germination occurs), the seedlings generally grow in a ring about 2,5 metres away from the mature shrub (figures 3 and 4).

Furthermore these seedlings grow against small shrubs such as Erica species and Restionaceae species, and more commonly between cracks or against boulders and flat rocks. This is possibly a result of seedlings being washed against a hard substrate. Many seedlings occur in clusters of 10-20 seedlings (Plates 36, 37).

A transect (30m x 4m) of Population 8 seedling distribution was taken, showing the effect of rain run-off on seed dispersal (figure 5). This area was selected for the following reasons:

- a) the area chosen contained a section where no Staavia dodii had occurred previously
- b) the area colonized was an enlargement of an area previously occupied by a Staavia dodii population

Seed dispersal from a Senescent
Stavia dodii shrub.

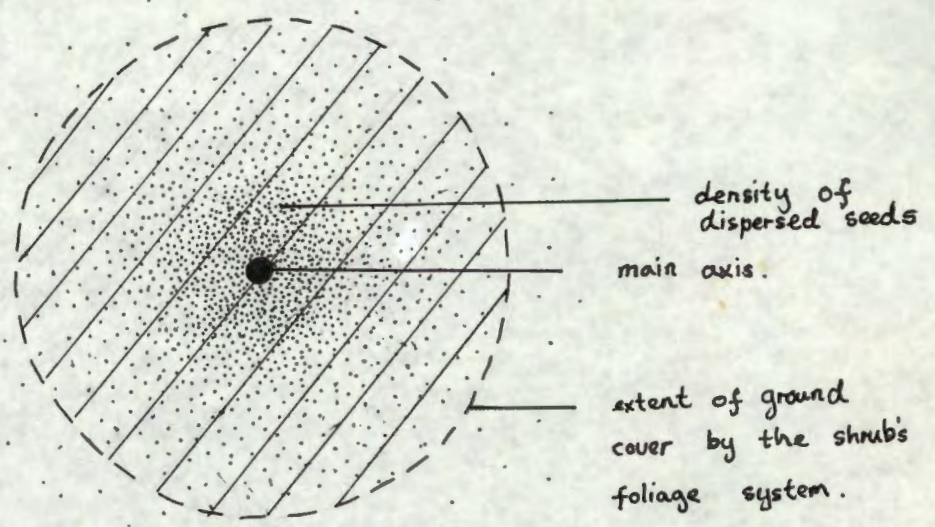


FIGURE 3

Seedling distribution (seed dispersal)
in the vicinity of a fire - destroyed
Staavia dodii shrub.

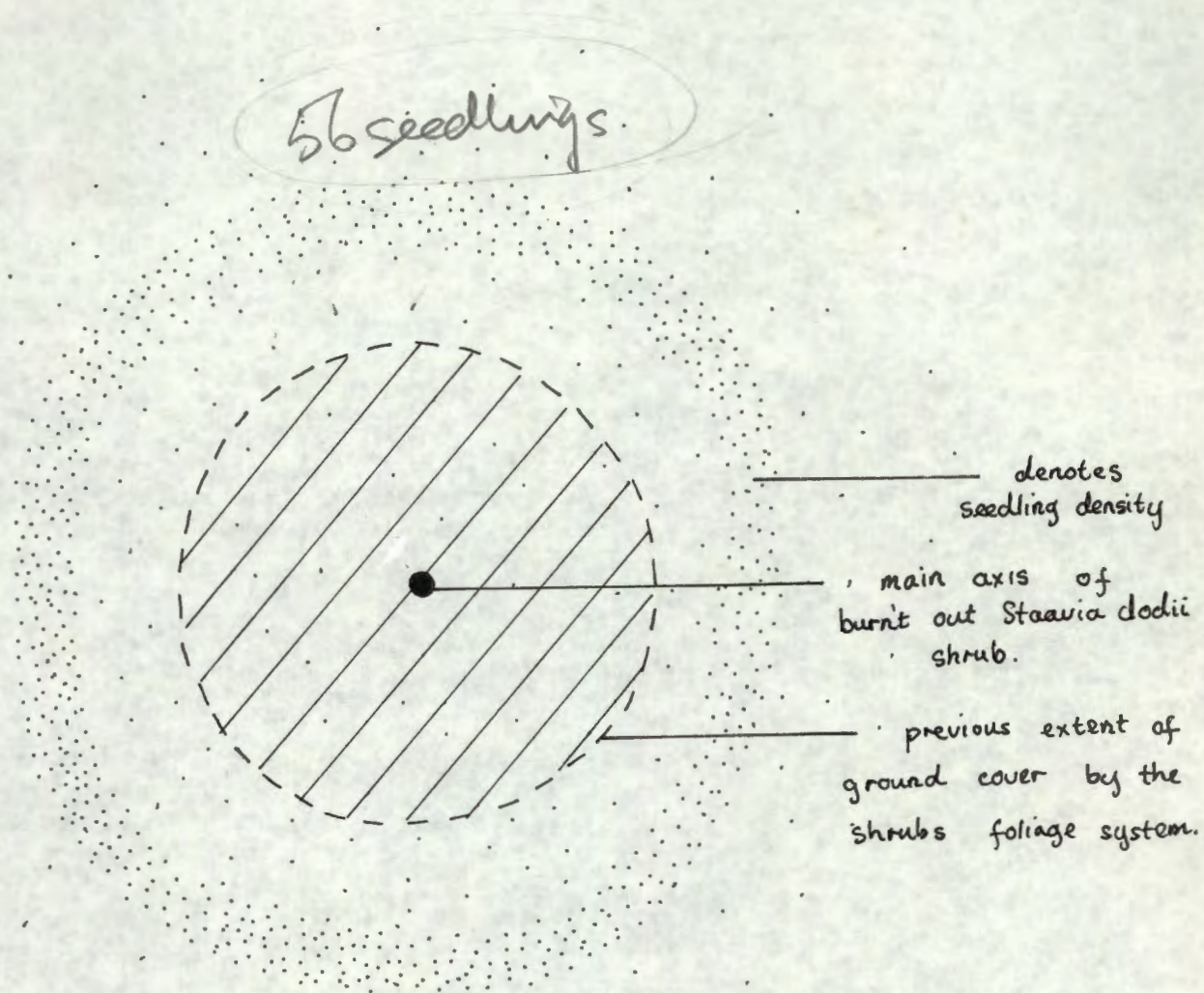


FIGURE 4

FIGURE 5 a. A Profile of the Seedling distribution
in the Wolfkop Transect.

(transect is 4 metres in width).

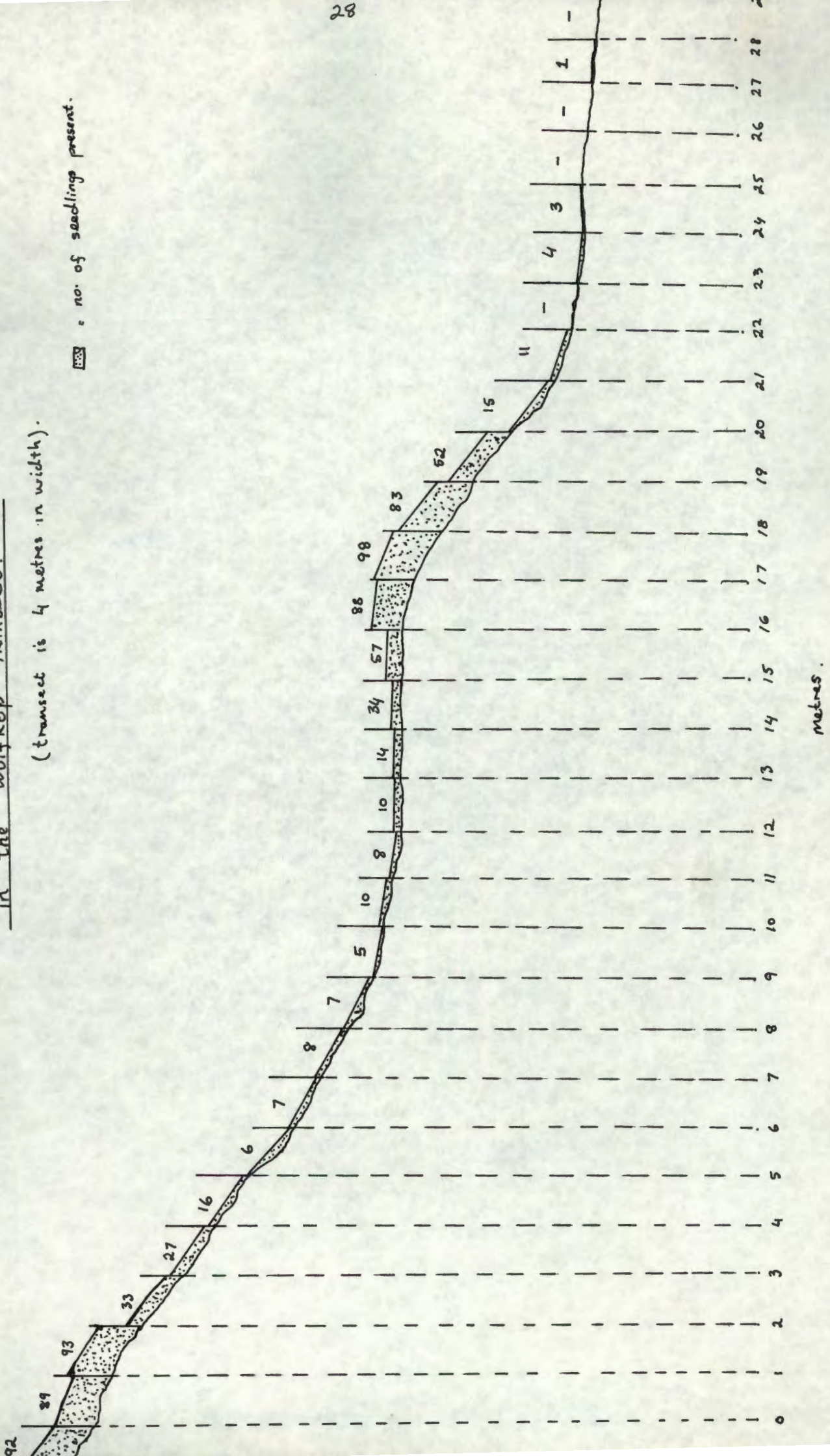



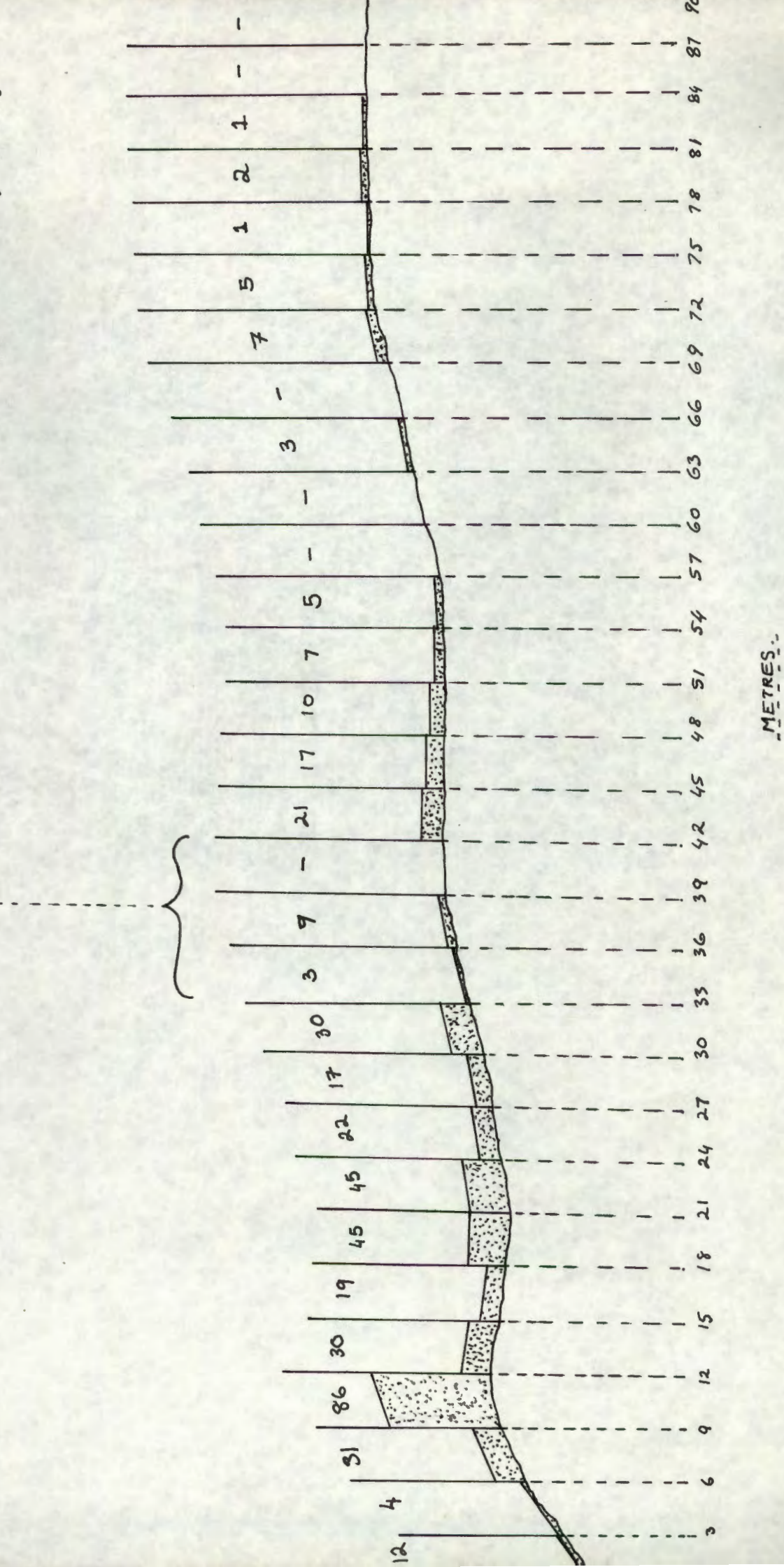
Figure 5 b.

Profile of the Seedling distribution
in the Population No. I transect.

(transect 10 metres in width).

Large flat boulder.

 = number of seedlings.



METRES.

Change in seedling numbers with distance.

METRES	SEEDLINGS
0-1	92
1-2	89
2-3	93
3-4	33
4-5	27
5-6	12
6-7	6
7-8	7
8-9	8
9-10	7
10-11	5
11-12	10
12-13	8
13-14	10
14-15	14
15-16	34
16-17	57
17-18	88
18-19	98
19-20	83
20-21	52
21-22	15
22-23	11
23-24	—
24-25	4
25-26	3
26-27	—
27-28	—
28-29	1
29-30	—

TABLE 3

- number of seedlings per metre fall-off moving from the centre of the population, outwards.

- c) the area favoured seed dispersal by rain run-off, having a slope of about 25%
- d) the area is especially suitable for future monitoring of the population, to establish the percentage survival of the seedlings. There is a possibility that a built-in mechanism could be in operation, favouring ideal Staavia dodii shrub density in areas openly available to Staavia dodii. This would result in an ideal density existing within the bounds of the Staavia dodii niche, and seedlings in outlying areas would die off.

This transect (figure 5, table 3) showed the seedling population as being higher on the lower levels of the slopes, beyond the boundary of previous Staavia dodii populations

9

SEEDLING AGE GROUPS

In Populations 1,8,9,10 groups of common seedling heights occurred. In order to overcome the difficulty of establishing the age of Staavia dodii bushes, method of age determination was devised using data from the seedling transects.

The average height of seedlings in Populations 8,9 and 10 (destroyed by fire 1 year ago) was 6.64cm, with a minimum of 2.1cm and a maximum of 11.9cm. Approximately 10% of seedlings were less than 3cm and 10% above 8 cm. These seedlings could be a maximum of 1 year old.

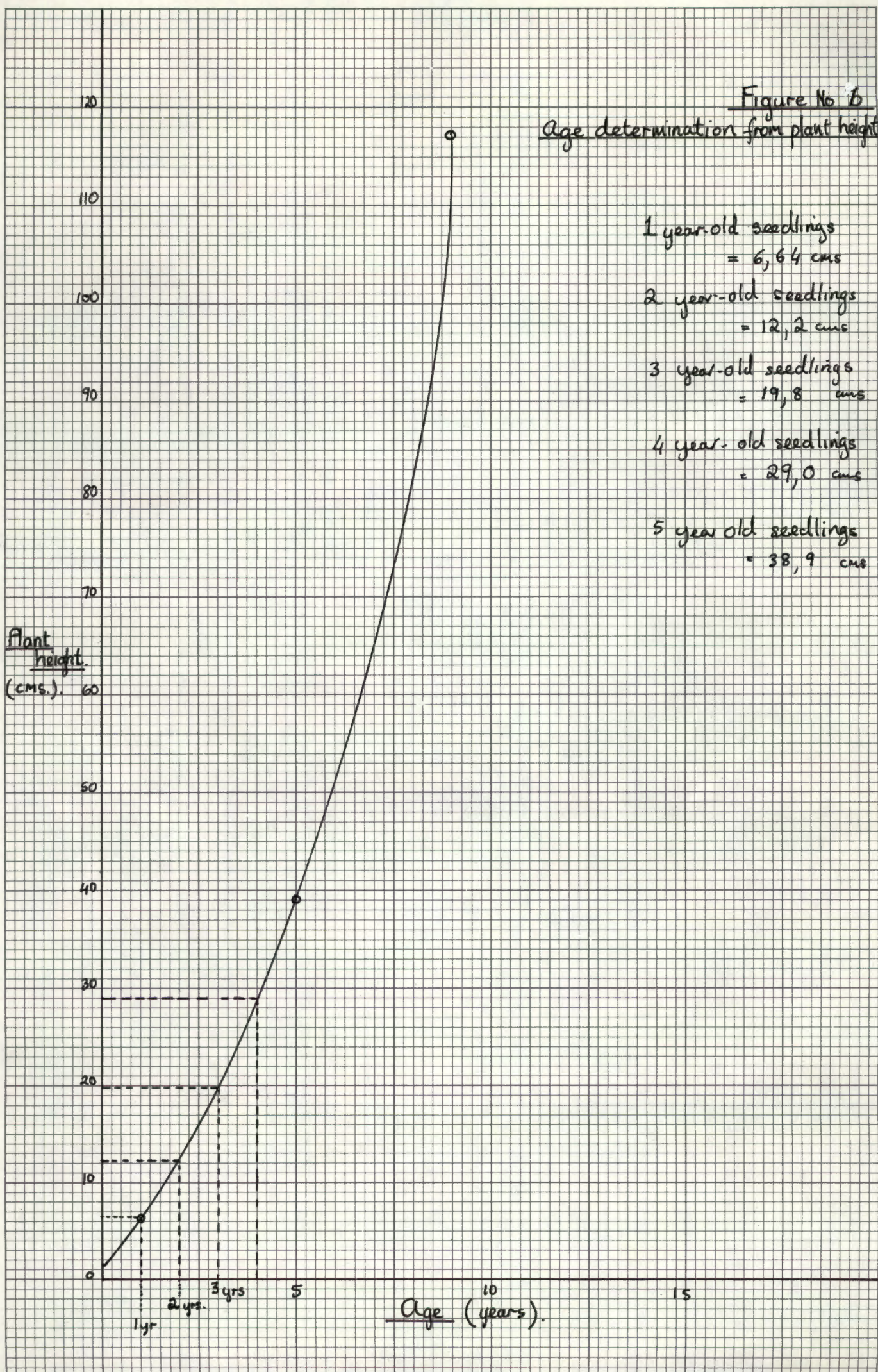
Population 1 (destroyed by fire about 5 years ago) had plants ranging from small seedlings to young mature shrubs. The latter were taken to be five years old and constituted the maximum plant size group of the population; the average height of this group was 38.9cm.

Using those average heights for one-year-old and five-year-old shrubs and assuming the growth curve of Staavia dodii bushes to be approximately linear (up to five years at least), the average height of 2-4 year-old seedlings was postulated (figure 6). The seedling heights (of a 10m x 100 transect or western edge of population 1) formed a continuum from 6.64cm to 38.9cm and thus it was inferred that seeds germinate continuously over a five year period.

Populations 3 and 4 are examples of mature virulent and senescent growth respectively. From transects of these populations it was concluded that the majority of seeds stop germinating about 6 years after a veld fire (that is very few bushes below the average height of 5 year shrubs were recorded in population, and a single seedling was recorded in population 4)

The transect of Population 3 (9 years old shrubs) shows a plant height ranging from 90cm to 130cm, with an average height of 117.54cm. The 20-25 year-old shrubs (transect of population 4) had a average height of 196.35cm. This transect was taken to establish the average height of senescent bushes, and thus only bushes of greater than 160 cm were recorded in the average. The height of these bushes ranged from 163cm to 240cm. A mere 24% of the population was between 75cm and 160cm in height. Apart from the angle seedling, 32cm high, no bushes of less than 75cm occurred.

Figure No 6
Age determination from plant height



- 1 year-old seedlings = 6,64 cms
- 2 year-old seedlings = 12,2 cms
- 3 year-old seedlings = 19,8 cms
- 4 year-old seedlings = 29,0 cms
- 5 year old seedlings = 38,9 cms

10

SEED GERMINATION

Upon observation of the low number of seedlings present in well-established population, the possible mechanisms responsible for free seed germination were investigated. Furthermore, it was noted that fire influenced germination extensively - being responsible for the release of trigger mechanisms and so allowing germination to continue freely, at a level well above that of existing plants in any given population.

A number of laboratory experiments were undertaken with the specific aim of isolating the trigger mechanism. Unfortunately this mechanism has not been isolated as yet, and in spite of sterilization of all equipment by autoclaving or heating to 160°C for 4 hours, no germination occurred. Experimentations included various methods as outlined below.

10.1

Straight Germination

Approximately 100 Staavia dodii seeds were sifted from debris under the shrubs. These seeds were released in the post-flowering season. The seeds were sub-divided into groups of 10 and placed in sterilized petri dishes with sterilized filter paper moistened with sterilized water. The petri dishes were placed in an incubator at 25°C under normal daylight and dark conditions (plate 13). Up till the time of this report no germination had occurred. After a period of 2 weeks the majority of the seeds were completely covered with fungi (plate 14). After some months of incubation a sample number of seeds were sectioned and the embryo's examined microscopically. In a comparison between these incubated seeds, and seeds with zero incubation - no development was observed in the former (plate 17)

10.2

Seeds from the flower heads

As a result of the high level of fungal occurrence, it was decided to use seeds ready for dispersal, but still on the flower heads - so hoping to reduce the fungal infection. The previous experiment was repeated - yielding the same results.

10.3

Imbibition of water

In a further experiment seeds were placed in incubation after an initial 3-week period of imbibing water. This investigation was testing the hypothesis that the seeds possibly needed to reach a certain level of water imbibition before germination proceeded. This observation was made after 4 groups of 10 seeds each were allowed to imbibe water, yielding positive results (figures 8 and 9). Once again 100 seeds were placed in incubation, this time from an initial imbibed state. No germination occurred, fungal infection was rife and embryo development non-existent.

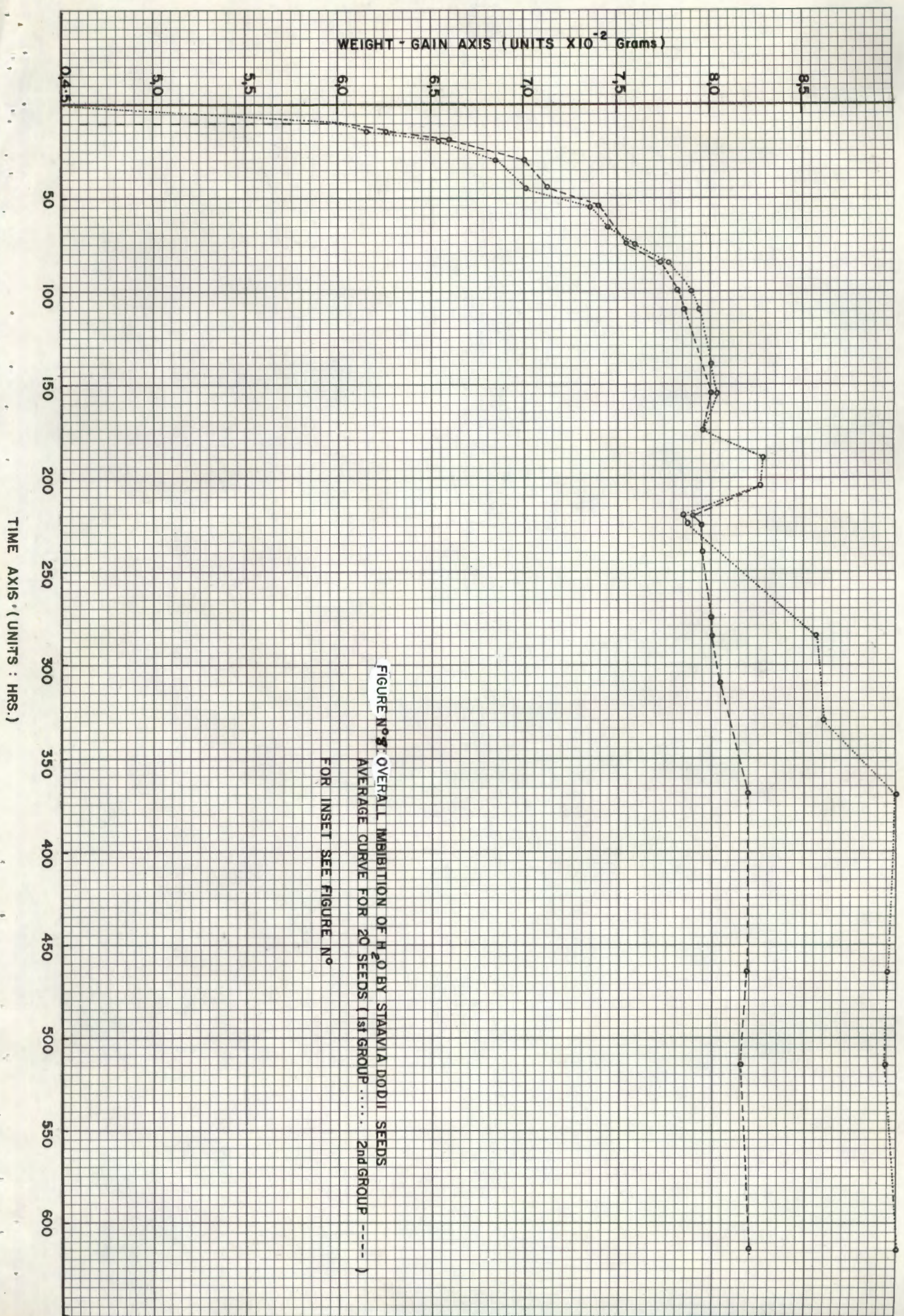
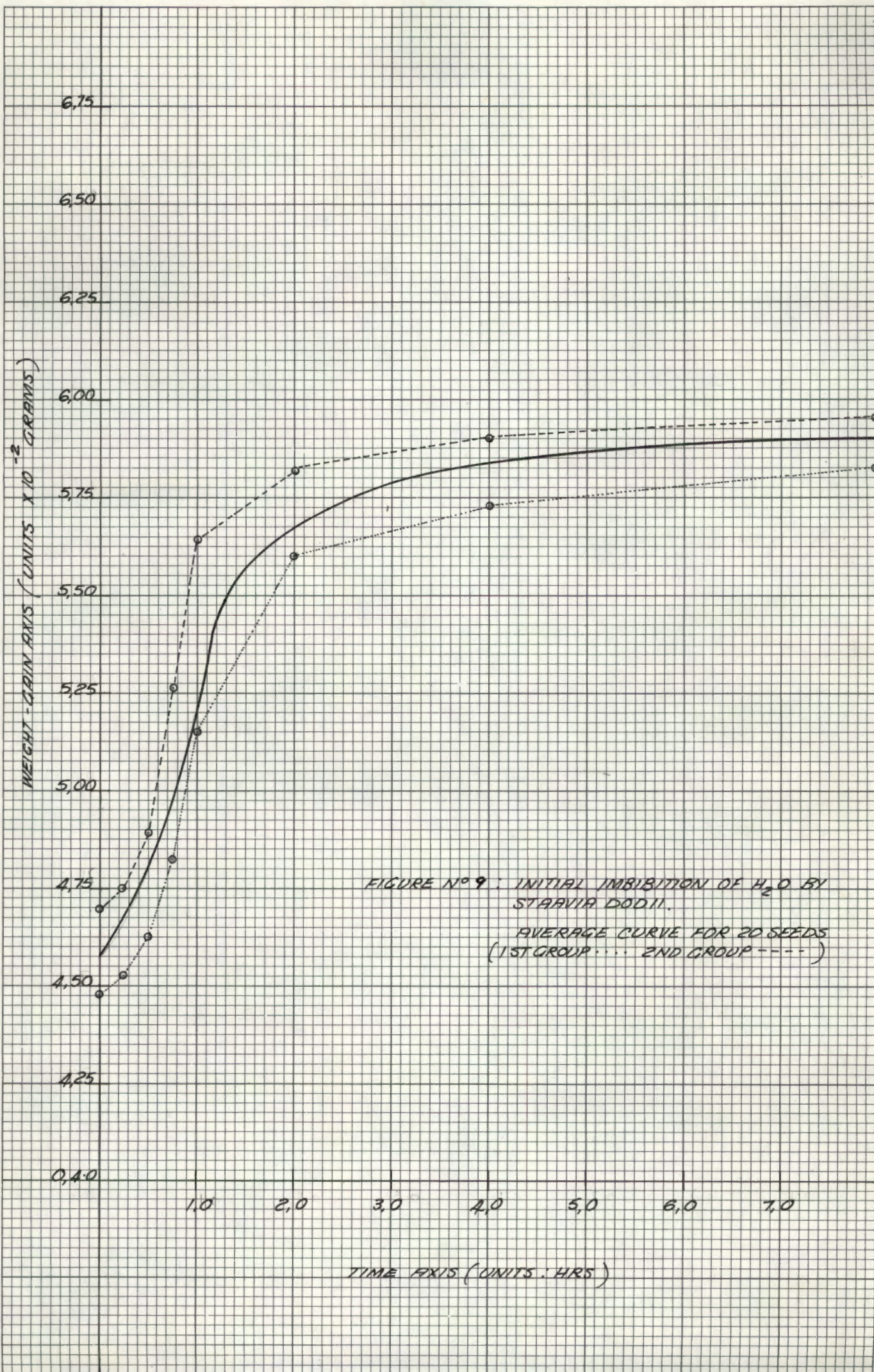


FIGURE N° 2: OVERALL IMBIBITION OF H_2O BY STAAVIA DODII SEEDS
AVERAGE CURVE FOR 20 SEEDS (1st GROUP 2nd GROUP -----)
FOR INSET SEE FIGURE N°

TIME AXIS (UNITS : HRS.)



10.4 Chemical sterilization

From the results of the previous experiments, it was inferred that that the seeds themselves were infected with fungal spores while still on the flower head. Consequently the seeds needed to be sterilized without affecting the embryo. From previous experimentation it was known that concentrated "Gillette's Javel" (which has a concentration of parts per million chlorine) was suited to this purpose. Experiment 10.3 was repeated after soaking 50 seeds in Gillette's Javel for 10 minutes, and another 50 seeds for 20 minutes. The seeds were washed in distilled water and incubated. The only difference in results was that this time initial fungal infection was restricted to the micropyle at the end of the seed, whereas previously it was not restricted to any specific area.

10.5 Leached seeds

All subsequent experiments were carried out on seeds that had been treated with Gillette's Javel. This particular experiment investigated germination in leached in a water contained with a turbulent air stream passing through it continually (plate 15). The rationale behind this was that the seed could possibly contain an inhibiting toxin which delays germination (as has been observed in past experiments on other seeds). After three weeks of leaching and then subsequent incubation - no germination or embryo-development occurred, but about 50% of the seeds were free of fungal growth (plate 14).

10.6 Temperature treatments.

Dry and imbibed seeds were exposed to varying temperature treatments. Both groups were treated with Gillette's Javel, and the imbibed seeds were leached. The temperature treatments (10 seeds for each treatment) were as follows:

- a) Temperature range: 0, 40, 60, 80, 100, 120, 130 and 160°C;
- b) Time period: 5, 10, 15, 20 minutes

Fungal infection was high on dry seeds, but low on imbibed, leached seeds. No germination or embryo-development occurred.

10.7 Scarred testa

The outer testa was scarred with emery paper to improve imbibition, facilitate rapid diffusion of possible toxins and to simulate cracked testa conditions due to fire (plate 16). The seeds were incubated and once again there was no germination or embryo development. Fungal infection was very high.

10.8 Seeds heated with a Fischer burner

At this point it was noted that there was a possibility that heat-treated seeds had not been exposed to sufficiently high temperature, thus seeds were heated on a wire gauze balanced above a Fischer

burner. After 6 - 7 seconds the aril shrunk and tore away from the seed testa, and after a further 3 - 4 seconds intense heating, the testa cracked. Unless a seed was held down with an instrument at the time of the cracking of the testa, it exploded and at times landed 5 m away from the Fischer burner.

This sample was incubated, and although no germination occurred, fungal activity appeared to be absent and slight embryo development took place (plate 18). This embryo enlargement was not attributed to heating since the endosperm cells surrounding the embryo appeared undamaged. Experimentation had proceeded thusfar at the time of writing this report.

10.9 Burning of the seeds with foliage

This experiment was conducted concurrently with experiment 10.8 and it attempted to simulate veld fire conditions by burning foliage (in which seeds had been scattered) in a sterilized asbestos bath containing soil (plate 19). This experiment is still in progress - the seeds in the bath being watered at four-day intervals. No germination has occurred and neither have fungal infection or embryo development been monitored. However, it is hoped that these laboratory conditions, simulating natural conditions fairly closely, will yield positive results.

11 PARASITISM OF GERMINATING SEEDS BY FUNGAL INFECTION

As mentioned previously, fungal infection of germinating seeds was noted to be high. In the initial germination experiment the seeds were obtained from the ground and thus the extensive fungal infections were thought to be contamination from the ground. However, when extensive fungal infection was noted on seeds taken directly from the flower head, the presence of fungal infection was regarded in a more serious light, especially since all equipment had been sterilized. It is clear that

fungus infection occurs at the flower-head level. The glutinous exudation over the surface of the flower would enhance fungal spore trapping from the atmosphere.

Identification of these fungal growths was considered to be important. A sample of infected seeds was placed on Czapek Dox and Potato Dextrose agar medium. Fungal colonies spread from the seeds onto the media. By means of selection and isolation of morphologically different colonies were isolated. Upon microscopic investigation of the samples, identification on a generic level was possible (table 4, plates 20-28)

A soil sample was taken from the soil surrounding the roots of a young *Staavia dodii* plant, and fungal colonies were isolated ^{by means of dilution plate method (plate 29)} and identified (table 5). The fungus, *Daldinia concentrica*, Pyromycetes, was found on a single dead *Staavia dodii* mature shrub.

12

MYCORRHIZA

Endotrophic mycorrhiza (mycor + rhiza = fungus + root) were found to be present on the rooting system of *Staavia dodii* populations (plate 30). These mycorrhiza are of the vesicular-arbuscular type with (aseptate) intracellular hyphal penetration, resulting in a hyphal mass within the root cortical cells (plates 31-34).

The causal organisms probably belong to the ~~Hy~~comycetes. These hyphae pass from cell to cell, or between the cells of the root cortex (plates ³¹₃₂). Within the cells they form coils which, in some cases, fill the lumina. These complex hyphal systems within the cortex are called ^(Plates 33 + 34) "arbuscles." ^ Hyphal branches may become swollen at their apices forming round fungal bodies or "vesicles" (plate 35).

Mycorrhizal associations play an important role in nutrient

Identification of Fungal Infections
parasitic on Staavia dodii seeds.

Colony. Petri. Dish

Classification

- | | |
|-----|--------------------|
| 1. | Penicillium sp. A. |
| 2. | Alternaria tenuis. |
| 3. | Alternaria tenuis. |
| 4. | Paecilomyces sp. |
| 5. | Paecilomyces sp. |
| 6. | Alternaria tenuis. |
| 7. | Alternaria tenuis. |
| 8. | Alternaria tenuis. |
| 9. | Alternaria tenuis. |
| 10. | Aspergillus sp. A. |
| 11. | Alternaria tenuis. |
| 12. | Alternaria tenuis. |
| 13. | Alternaria tenuis. |
| 14. | Penicillium sp. B. |
| 15. | Alternaria tenuis. |
| 16. | Cladosporium sp. |
| 17. | Alternaria tenuis. |
| 18. | Penicillium sp. A. |
| 19. | As. Actinomycete. |
| 20. | Alternaria tenuis. |
| 21. | Alternaria tenuis. |
| 22. | Alternaria tenuis. |
| 23. | Alternaria tenuis. |
| 24. | Penicillium Sp. C. |
| 25. | Penicillium Sp. D. |
| 26. | Penicillium Sp. A. |
| 27. | Cladosporium sp. |

Colony. Petri Dish.

Classification

- | | |
|-----|--------------------|
| 28. | Penicillium Sp. K. |
| 29. | Aspergillus Sp. A. |
| 30. | Sterile mycelium. |
| 31. | Alternaria tenuis. |
| 32. | Fusarium sp. |
| 33. | Fusarium. sp. |
| 34. | Alternaria tenuis. |
| 35. | Bacterium. |

Table 5

Results of the dilution Plate Method of Fungal Isolation, from a soil sample from *Staavia dodii* roots.

<u>Dilution</u>	<u>Fungal sp. present.</u>	<u>No. of Colonies</u>
$\frac{1}{1,000,000}$	Penicillium sp. C.	1.
$\frac{1}{100,000}$	Penicillium sp. C.	4.
$\frac{1}{10,000}$	Penicillium sp. C.	12.
	Aspergillus sp. A.	5.
$\frac{1}{1,000}$	Aspergillus sp. A.	14.
	Penicillium sp. C.	57.
	Penicillium sp. B.	4.
	Penicillium sp. D.	2.
$\frac{1}{100}$	Penicillium sp. C.	± 200 .
	Aspergillus sp. A.	± 80 .

and energy cycling in an ecosystem - these associations resulting in most cases, in enhanced acquisition of soil-nutrients by the plant, and in derivation of host carbohydrates, amino acids and other organic compounds by the fungus. Mycorrhizal fungi, apart from passing on acquired nutrients to the host, may also store certain nutrients within their hyphae. These nutrients become available to the host on the decay of the hyphae. This would be of considerable importance to the *Staavia dodii* plants, since there is a general lack of paucity of soil nutrients in the rocky or shallow-soiled habitat that this species occupies - where root-systems may be reduced in plants growing just above bedrock or between the soil-filled cracks of large boulders above the soil surface.

13 THE STAAVIA DODII & SALTERA SARCOCOLLA COMMUNITY

The Braun-Blanquet method of vegetation description and classification was employed to investigate the Staavia dodii - Saltera sarcocolla community.

13.1 Sites chosen

Thirty-two sites were chosen, 25 from certain *Staavia dodii* populations, and 7 outside the populations. Relevés 1 - 10 occurred within the bands of Population 3, on the fire-break, near Sirkelsvlei. Relevés 11 - 15[^] within population 4 on spot height 361. Relevés 18 - 19 occurred within Population 4, but without *Staavia dodii* being present. Relevé 20 occurred with Population 5, to the east of spot height 299. Relevés 16 and 17 occurred south of spot height 361, between this spot height and Sirkelsvlei. Relevés 21 - 23 occurred within Population 6 at spot height 299. Relevé 24 occurred to the south of spot height 299. Relevés 25 to 28^o occurred within population 7, at spot height 258. Relevés 29 and 30 occurred to the south of spot height 258. Relevés 31 and 32 occurred with population 1, at spot height 262. See plates 38 - 50.
 " Figures 10 - 12 for profiles of relve areas.

13.2 Climate, altitude, distribution and topography

This information is included in sections 1 and 2.

13.3 Geology and soils

At all sample sites the underlying rock was Table Mountain Sandstone. The derived soils are generally sandy and deficient in nutrients.

13.4 Methods

Only perennially identifiable vascular plants were recorded in the sampling procedure. Plot size was finally determined in a totally subjective way. This was decided after the Nested plot method and the method described by Moll and Campbell (in prep.) were found to be unsatisfactory (table 6). The plot size was chosen in such a way so as to include a good coverage of Staavia dodii, since this plant was the focus of the study and subjective selection would ensure that there would be no departure from this community - thus the plot sizes varied.

All environmental data is included at the base of the Phytosociological table. ^(Table 7) Shuffling of the table was done on graph paper. Plot order was arranged in order of possible age of the populations. Species recorded were divided as follows:

i) all species occurring solely within the Staavia dodii - Saltera sarcocolla community and not in relevés 16, 17, 24, 29 and 30 were kept within the first third of the table;

ii) species occurring in the Staavia dodii populations as well as within relevés 16, 17, 24, 29 and 30, but were of some importance to the Staavia dodii populations were used as transitional species;

iii) all species occurring in relevés 16, 17, 24, 29 and 30 were dropped to the bottom quarter of the table;

iv) species common to all the communities were dropped to the bottom of the phytosociological Table, to form a separate group.

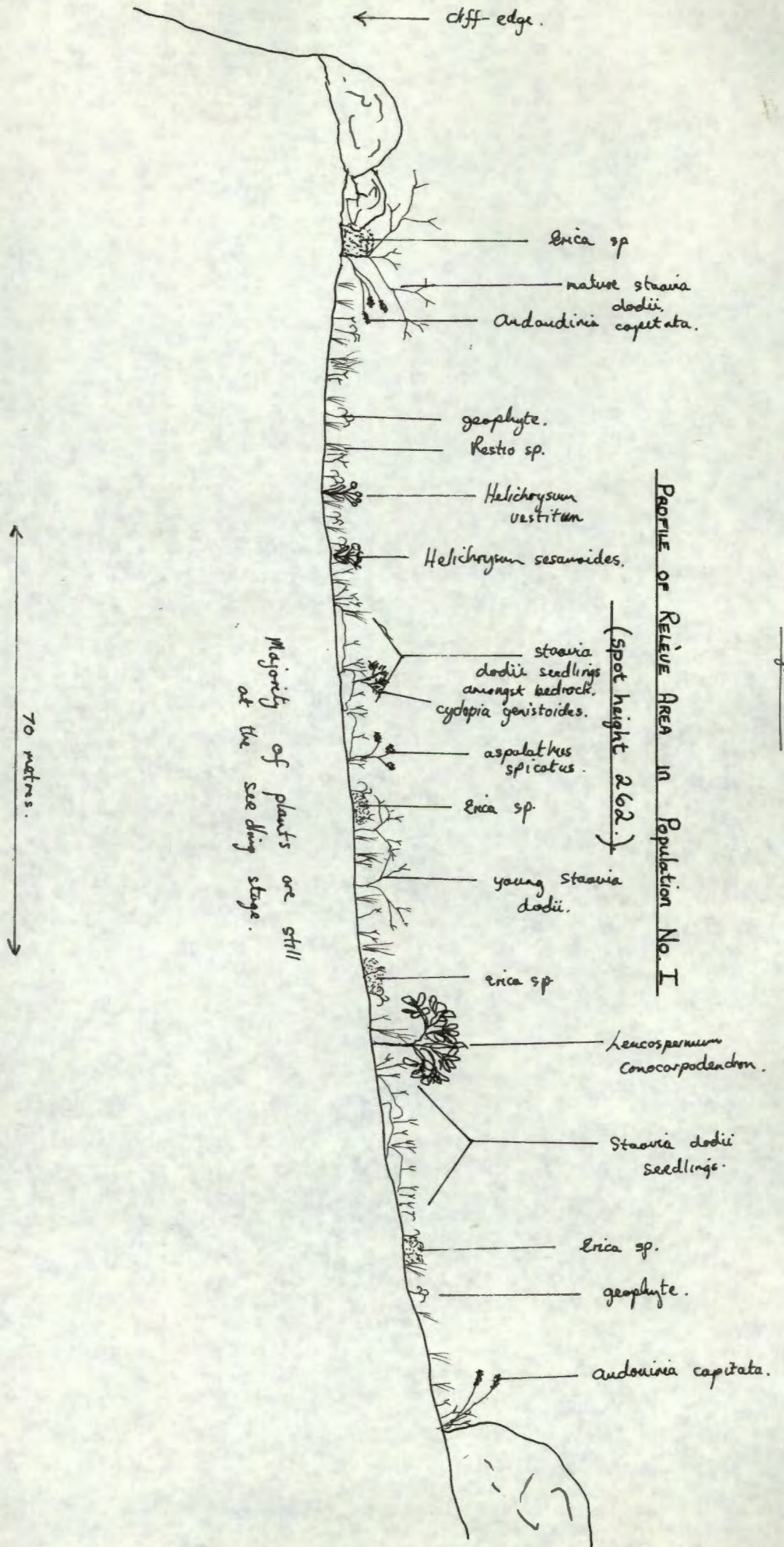
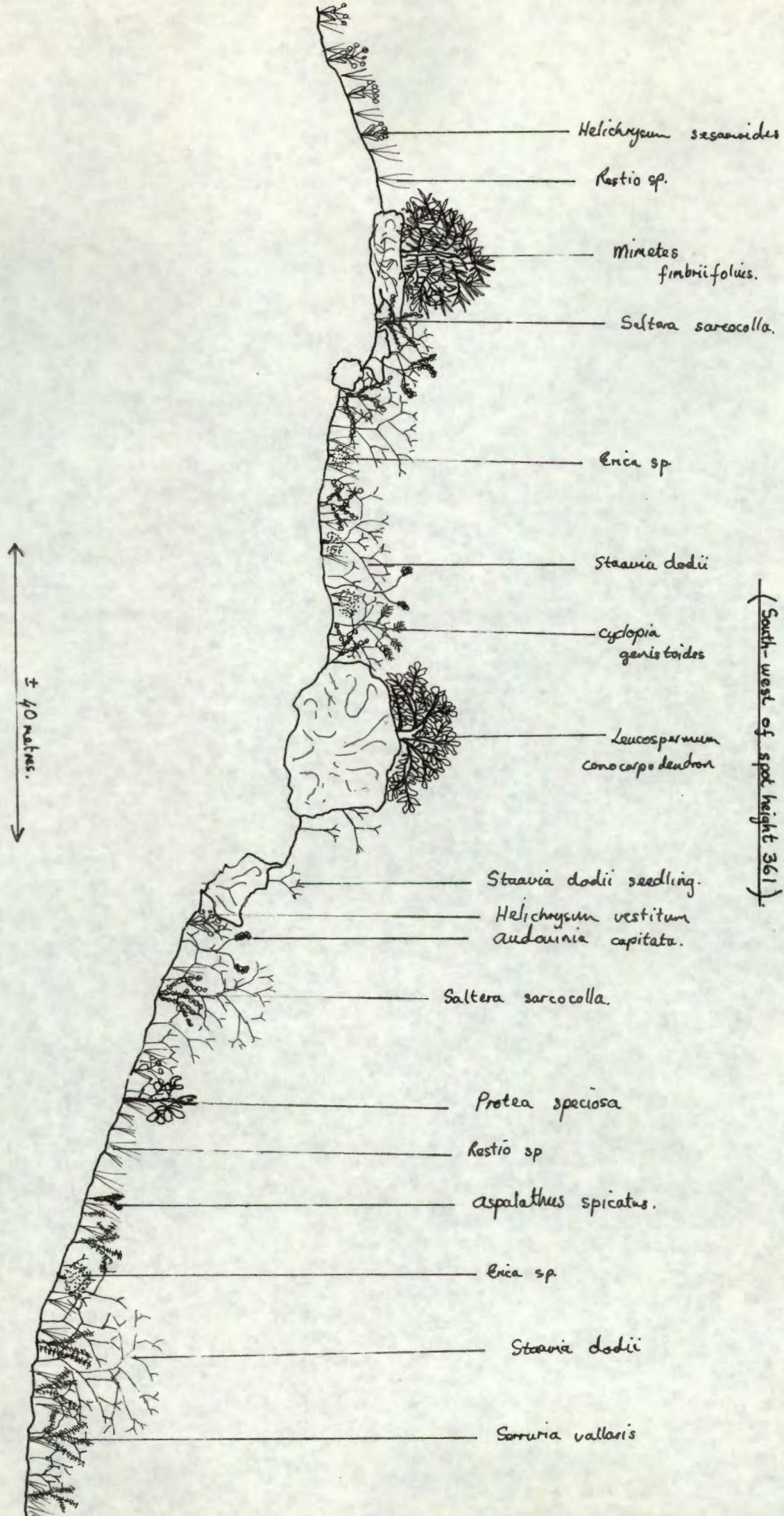


Figure 10



± 40 metres.

Helichrysum sesamoides

Restio sp.

Mimetes fimbriifolius.

Saltera sarcocolla.

Erica sp

Staavia dodii

cyclopia genistoides

Leucosparnum conocarpodendron

Staavia dodii seedling.

Helichrysum vestitum
audouinia capitata.

Saltera sarcocolla.

Protea speciosa

Restio sp

aspalathus spicatus.

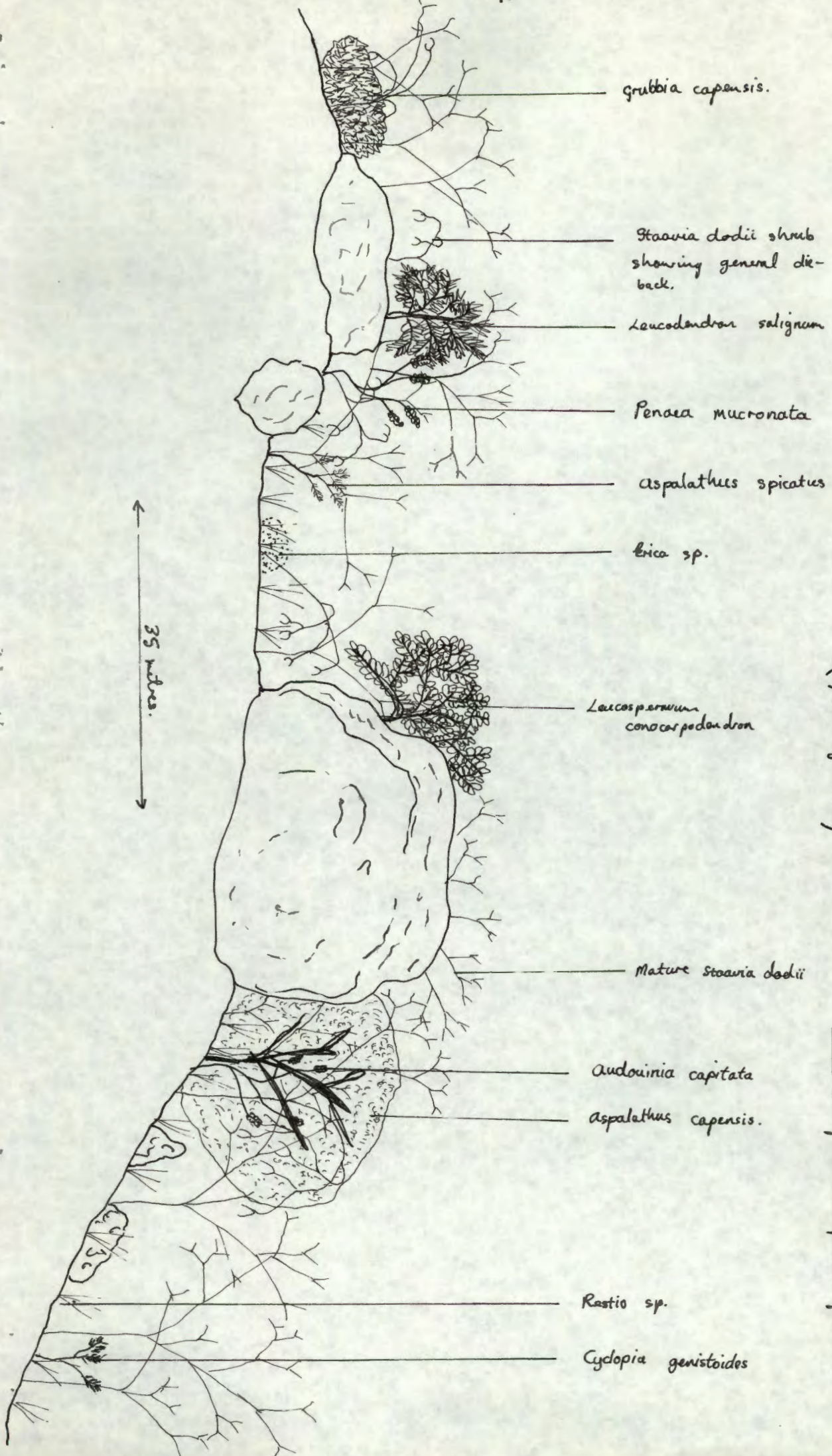
Erica sp

Staavia dodii

Serruria vallis

PROFILE OF RELIEF AREA IN POPULATION No. III
(South-west of spot height 361).

Figure II



35 miles.

Grubbia capensis.

Stoaia dodii shrub showing general die-back.

Leucodendron salignum

Penea mucronata

Aspalathus spicatus

Erica sp.

Leucospermum conocarpodendron

Mature Stoaia dodii

Audouinia capitata

Aspalathus capensis.

Rastio sp.

Cyclopia genistoides

PROFILE OF RELIEF AREA IN Population No. IV - (spot height 361.)

To show some of the more important species present.

Figure 12.

Table No. 6.NESTED PLOT METHOD

Area of Sample.		No. of Species
1.	1 m ²	17 sp.
2.	2 m ²	21 sp.
3.	4 m ²	24 sp.
4.	8 m ²	34 sp.
5.	16 m ²	39 sp.
6.	32 m ²	47 sp.
7.	64 m ²	53 sp.
8.	128 m ²	59 sp.

Total Population Area : 65.

13.5 Communities

The two communities formed by relevés 16 and 17, and 24, 29 and 30 will not be discussed.

13.5.1 The Staavia dodii - Saltera sarcocolla community
(see Table 7)

As can be seen from the phytosociological table, this community can be subdivided into 5 subcommunities on the basis of age/species diversity criteria. Diversity decreases with increasing age of the population species. Important differential species throughout the community are: Staavia dodii, Saltera Sarcocolla, Leucospermum conocarpodendron, Mimetes frimbriifolius, Pentaschistus sp (as yet unidentified), Audouina capitata, Erica corifolia, Helichrysum sesamoides, Asparagus capensis, Adenandra villosa ssp sonderi, Cyclopia genistoides and Amphitalea ericifolia.

All the populations were free from alien vegetation encroachment. Plates 38-50 give a general idea of the population structure.

14

A THEORY ON THE ROLE OF FIRE IN SEED GERMINATION AND
SEEDLING DISTRIBUTION

This theory incorporates the postulate that those seeds which germinate and give rise to seedlings are seeds which are burnt by a veld fire while still on the flower head. At any given time towards the end of the flowering season there may be 2 or 3 exposed seeds on the flower head. During this period (November) there is a comparatively strong possibility of a veld fire occurring - this possibility increasing in early December.

In laboratory experiments (10.8) it was found that high temperatures are required to facilitate cracking of

the testa. Similarly, seeds at a height above the ground would be in the hottest region of a veld fire, that is just above the level of the flames. A further result of laboratory experiment 10.8 was the observation that the rupturing of the testa yields sufficient explosive force so as to propel the seed for a distance of 5 m. In the event of a veld fire there are additional factors which could be instrumental in transporting the seed away from the original plant i.e. thermal and convective currents set up as a result of the fire. This offers a possible explanation for the observed trend in the population area being greater after fires; whether seedlings which germinate in areas further afield will survive or not is a debatable point.

Furthermore, the observed pattern of dispersed seeds supports the hypothesis of explosive seed projection. In burnt out populations the seedlings are found in a ring having a radius of approximately 2.5 m from the mature parent shrub. By way of contrast, seed dispersal in mature unburnt populations is high under and in the immediate vicinity of the parent plant.

In the germination experiments the only truly effective means of sterilizing the seeds was by means of a Fischer burner. An important conclusion was that the seeds on the flower heads were infected with fungal spores. It is apparent that veld fires could serve the purpose of sterilizing the seed testas as well as the ground. Thus the seed would be able to germinate under sterile conditions once the germination trigger mechanism has been released.

Contrary to a suggestion that seeds from past flowering seasons lying on the ground, will germinate after a fire, is the fact that from a large sample of ^{old} seeds collected amongst rotting debris and foliage, most were found to be hollow - the contents having been devoured by the fungi present. Since fungal infections are present while the seed is still on the flower head, fungi will start to

develop as soon as the seed hits the ground and favourable conditions for fungal growth are encountered. Thus the only really viable seeds at any one given time are those in the flower head and open to the atmosphere i.e. able to explode out of the carpel on heating. Since each flower head has 2 to 3 seeds at any one time, and a mature bush has a large number of flower heads, a possible reason for the very rapid expansion of a mature population after a fire, exists, i.e. favourable germination conditions for many viable seeds exist.

The possible importance of fire to the Staavia dodii populations has been outlined. However the danger does not lie in too infrequent burning of the population (within limits as mentioned earlier), but rather in too frequent burning. This is especially important when considering the fact the seedlings continue to germinate for a five to six year period after a fire (although how this occurs over such a long period without fungal infection is not known). At five years few seedlings are flowering and so the number of germinating seeds will decrease drastically. However, it is unlikely that the same are will be burnt twice within a 5-year period due to the sparseness of the vegetation.

What possible advantage would mass germination once in 15 to 20 years affords to Staavis dodii?

A number of points may be put forward:-

a) mass seedling production at any one given time does not favour regular predation by animal forms - the irregularity of occurrence not forming a steady source supply;

b) owing to the high predation on Staavia dodii seeds by fungal infection (experimentally verified), it is advantageous to have mass seed germination when fungal presence is at an absolute minimum i.e. after a fire. Future fungal infection will be a result of the influx of fungal spores from unburnt marginal areas and spore dissipation from the atmosphere;

c) as a result of mass germination after a fire, most shrubs in population will be of the same age - thus resulting in every available niche being filled by mature flowering shrubs. In the event of fire, maximum seed germination occurs since there is maximum seed availability;

d) mass germination results in intraspecific competition for a restricted availability of niche. Consequently, only superior seedlings survive.

CONCLUSION

As a result of the limited time and resources available for a report of this nature, many of the conclusions are speculative - based on facts which might well have been misinterpreted. Nevertheless, a number of interesting and enlightening facts have come to the fore. Amongst these particular emphasis has been placed on seed dispersal and germination, fungal infection and the general adaptations to fire.

The association between these is complex; there is a high degree of predation of seeds by fungal infection and the general adaptations to fire are used as a form of survival. Further understanding of these mechanisms in Staavia dodii may lead to a better understanding and knowlege of the adaptations to fire found in Fynbos in general. Once again this is particularly important when seen in the light of possible burning programmes as well as unintentional fires.

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Plate I



Plate 2



Plate 3.



Plate 4.



Plate 5.



Plate 6.



Plate 7



Plate 8



Plate 9.



Plate 10



Note yellow flowering Aspalathus capensis.

Plate 11.



Plate 12.



Note the Bumble-bee visiting the flower
in the centre of the photograph.

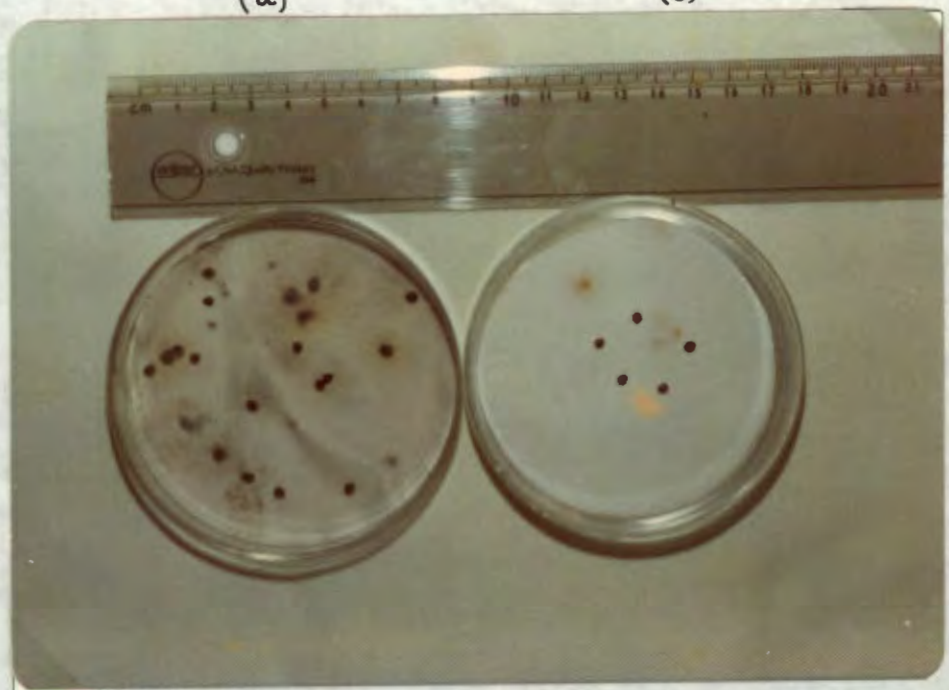
Plate 13.



Plate 14.

(a)

(b)



- a) - note seeds are extensively covered by fungal infection.
b) - seeds which have undergone leaching are noticeably free of fungal infection.

Plate 15.

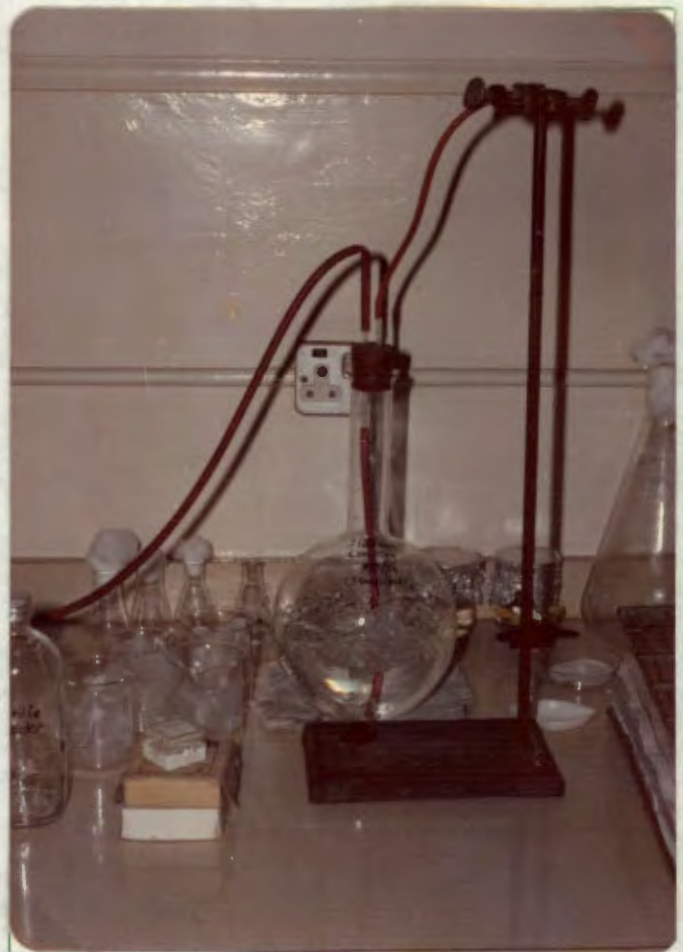


Plate 16



Note the yellow-brown colour of the filter-paper
This is due to carbohydrate leakage from the
site of scarring.

Plate 17.

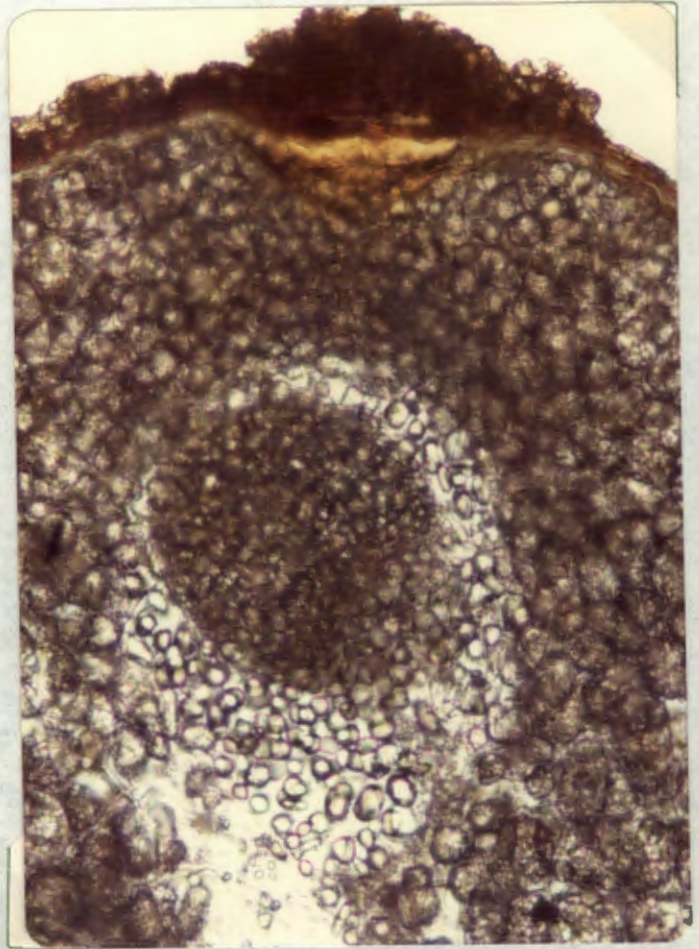


Plate 18

Note the damage to the endosperm by the heat, but no damage to the embryo is obvious.

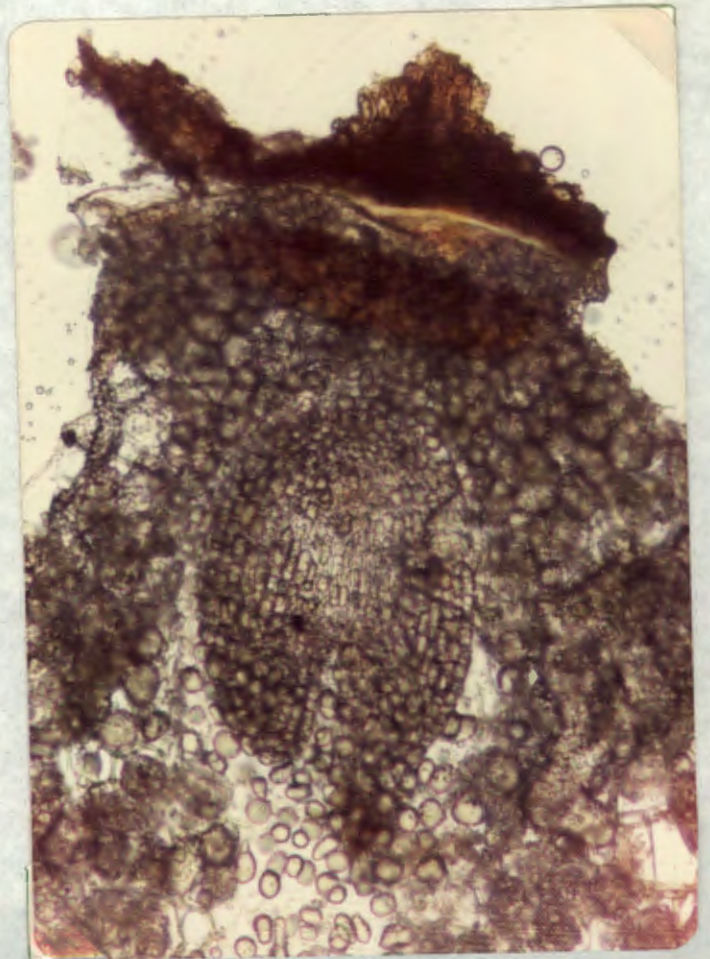


Plate 19.



Plate 20.
Penicillium sp. A.

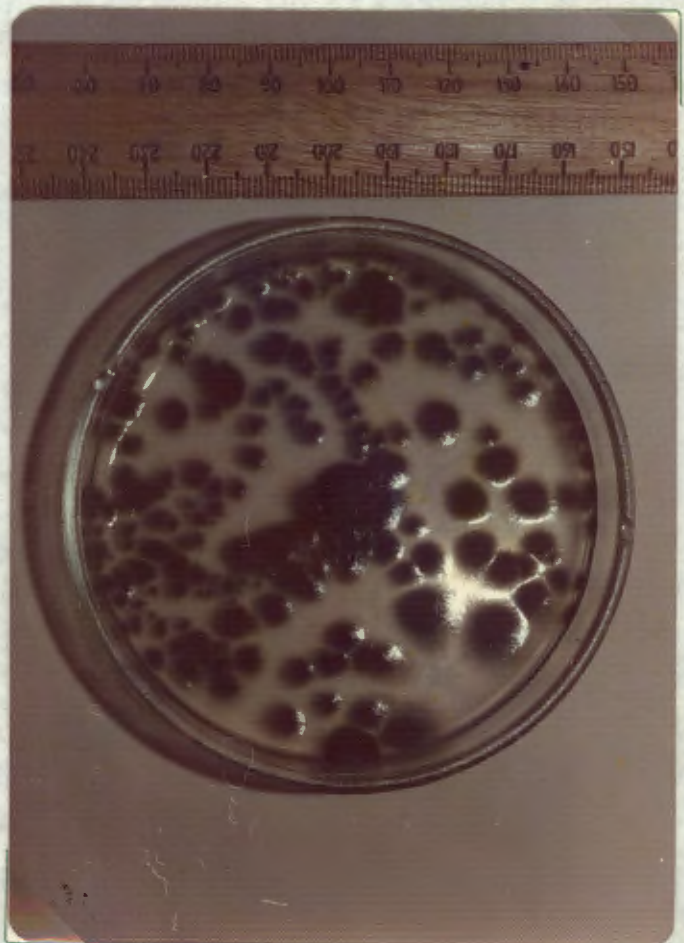


Plate 21
Aspergillus sp. A.

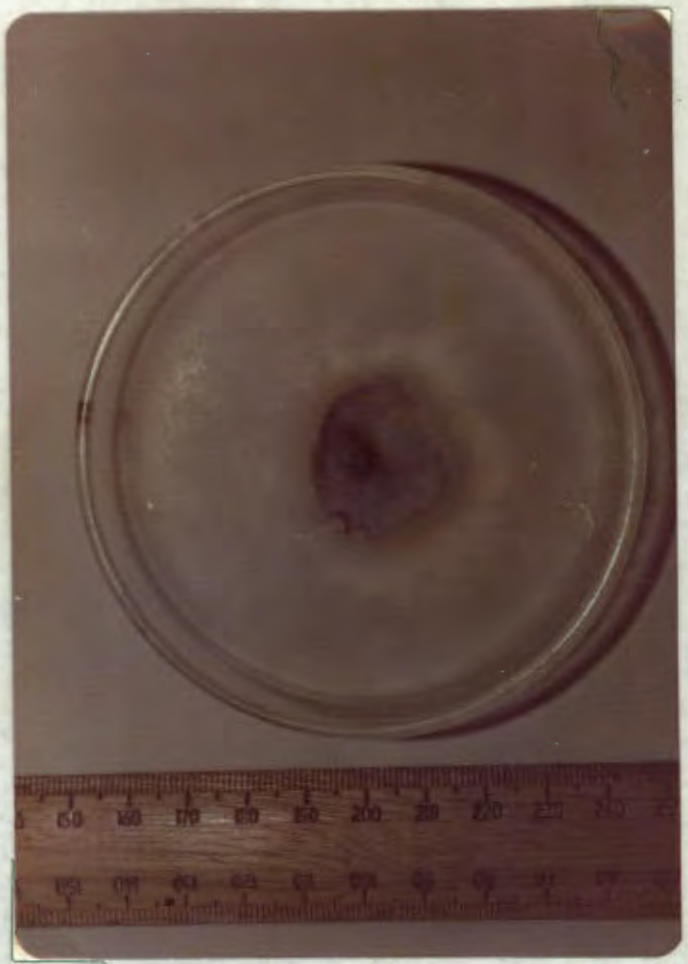


Plate 22
Cladosporium sp.



Plate 23
Penicillium sp. B.



Plate 24.
Paecilomyces sp. ?

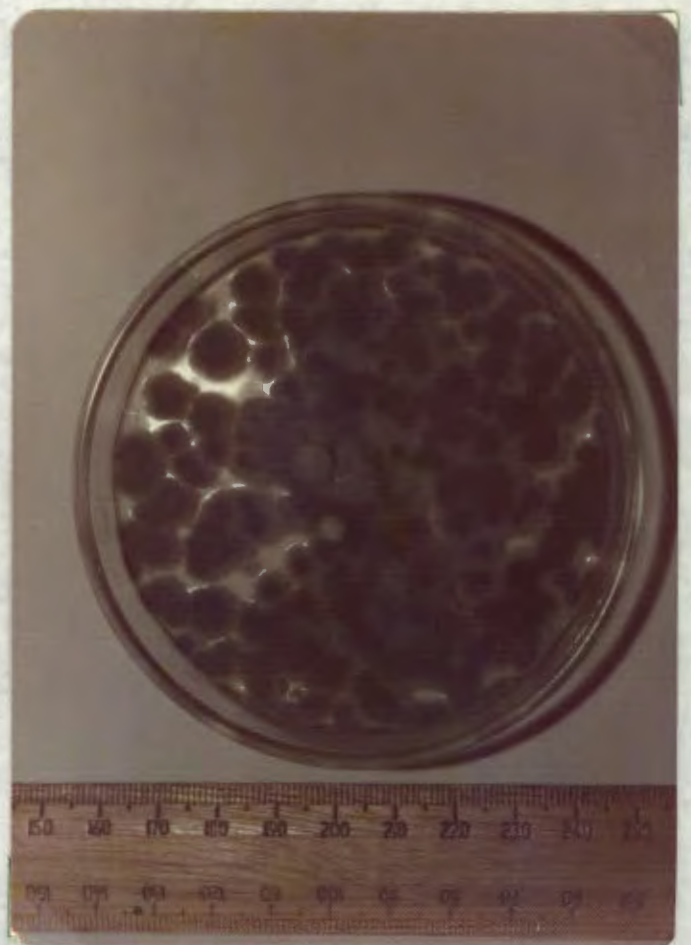


Plate 25
Alternaria tenuis.



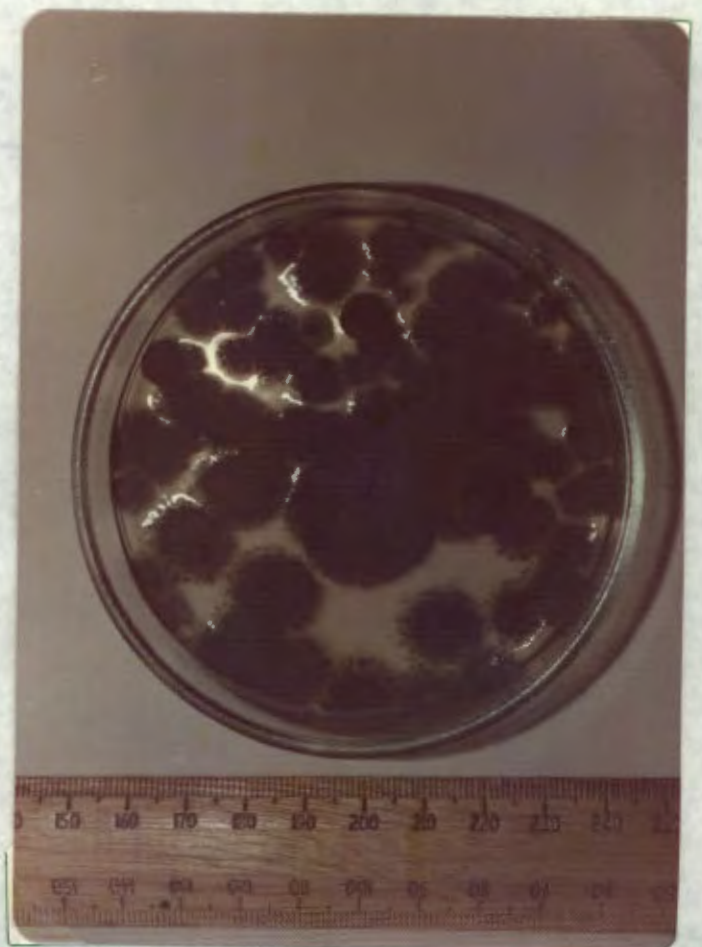
Plate 26.
Fusarium sp.

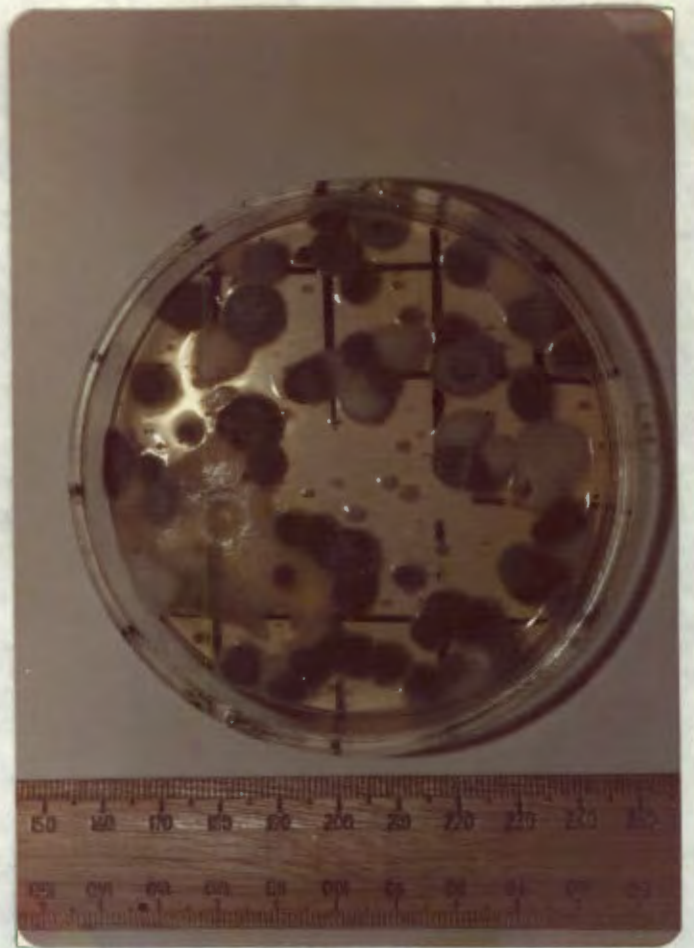


Plate 27
Penicillium sp. C.



Plate 28
Penicillium sp. D

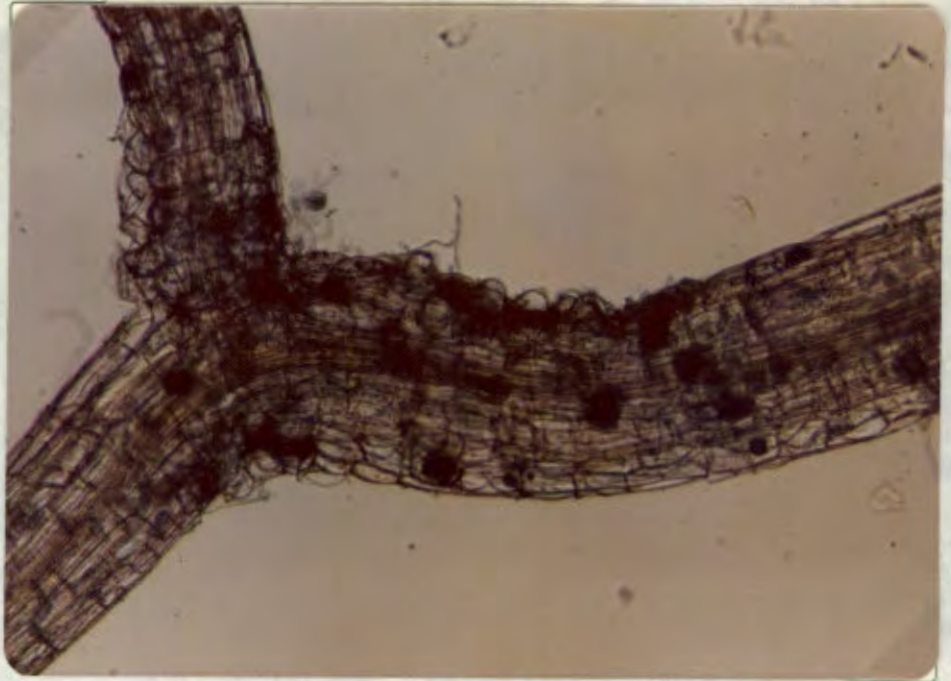




Sample of the Dilution Plate
Method of fungal isolation.
Plate 29

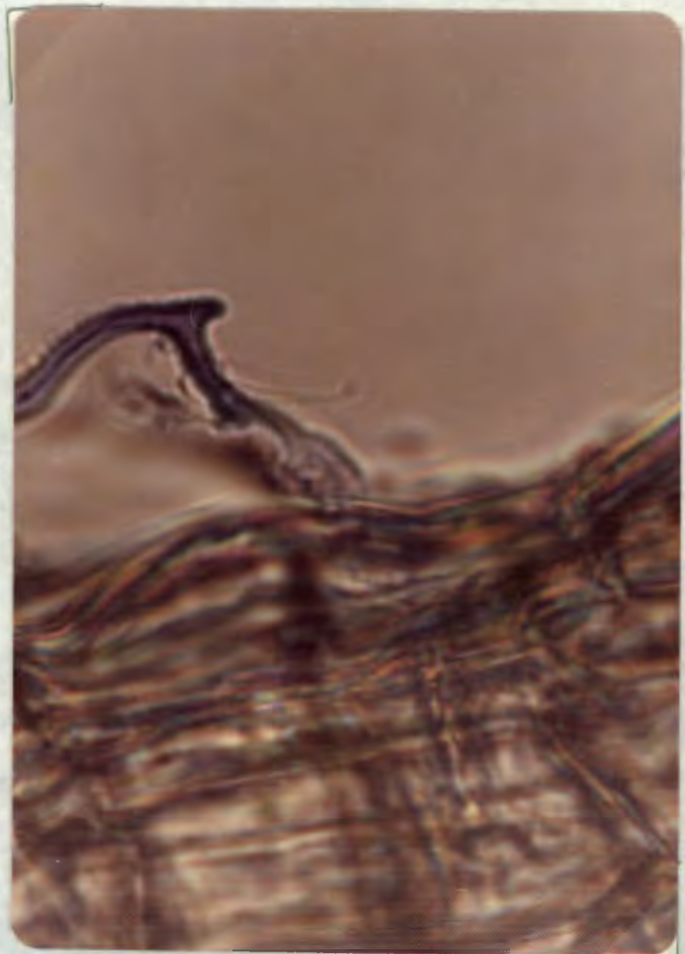
Light colonies - *Aspergillus* sp.
Dark colonies - *Penicillium* sp. C.

Plate 30.



Surface view of a fine root of *Staavia dodii* showing Mycorrhizal infection.

Plate 31



Showing penetration of hypha into root epidermis, from external medium.

Plate 32.

Penetration of a forked hypha into a pair of adjacent cortical cells.

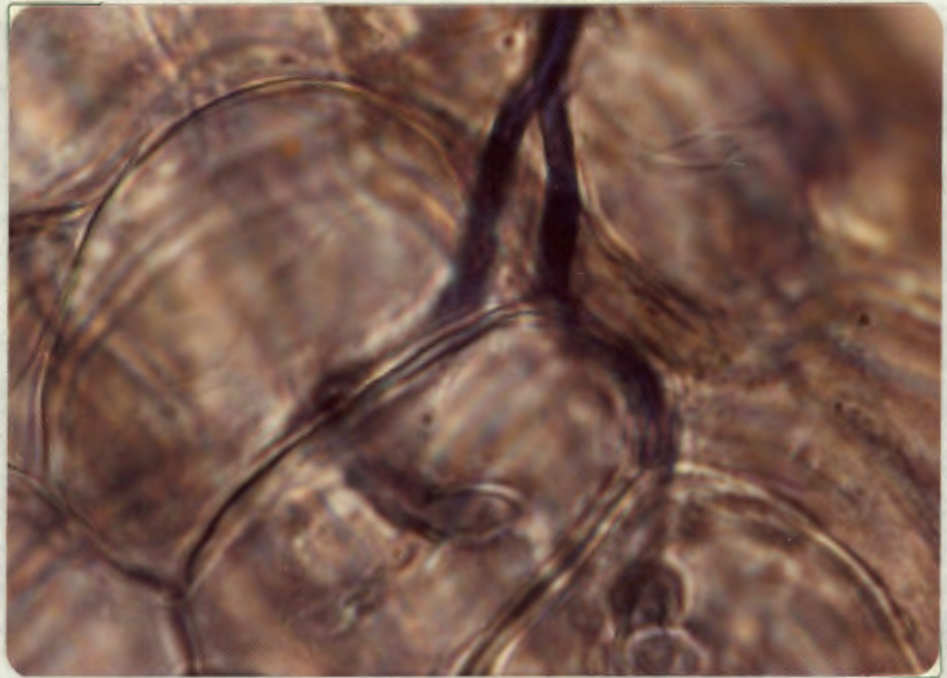
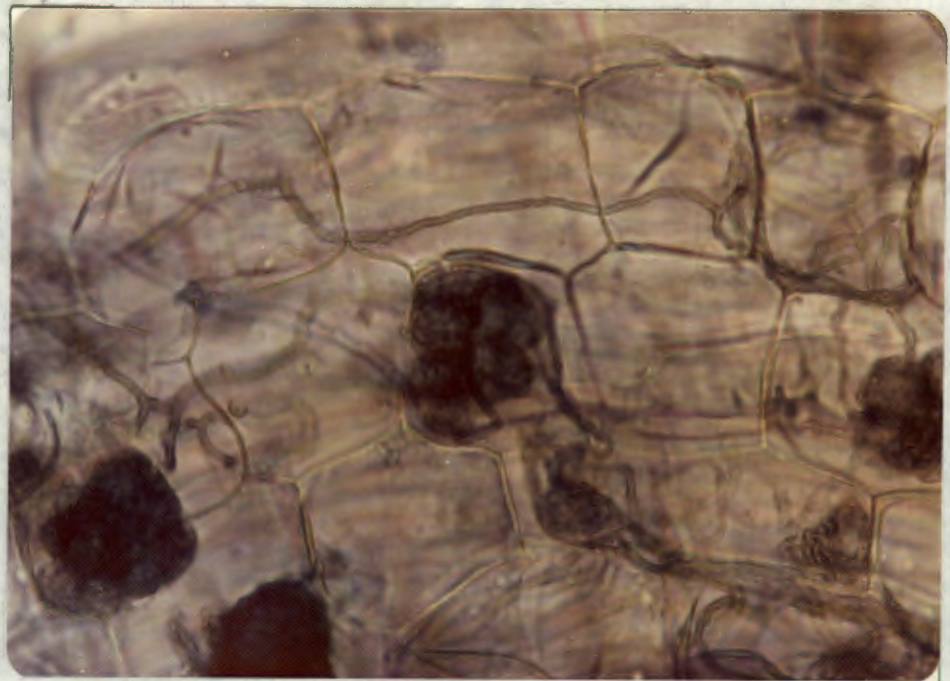


Plate 33.



Note hyphal presence as well as cortical 'arbuscles'.

Plate 34

Well developed arbuscule, completely filling a cortex cell lumen.

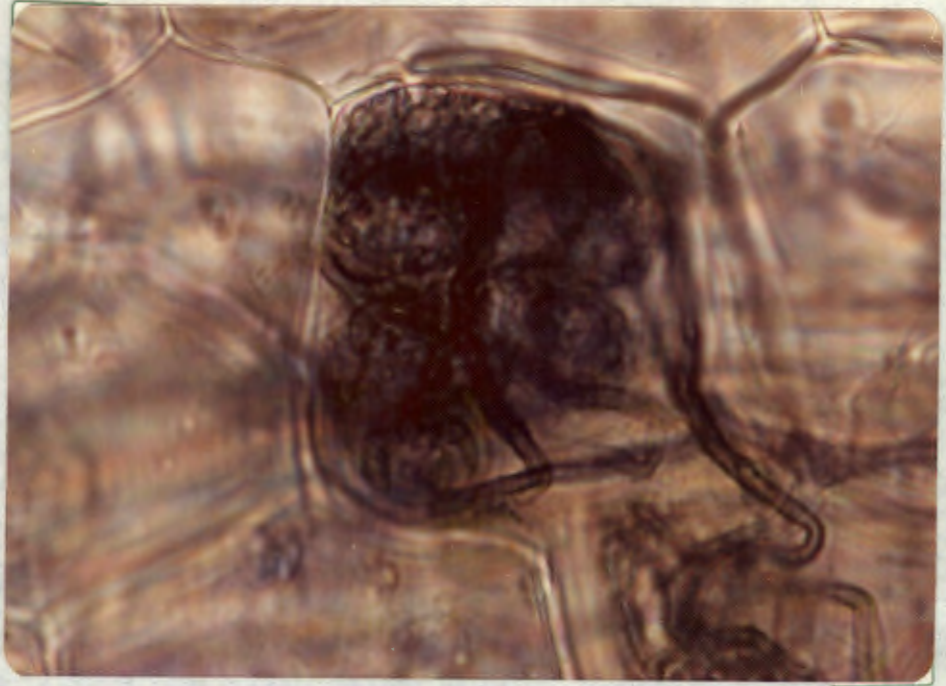


Plate 35.

Group of vesicles protruding from the root epidermis.

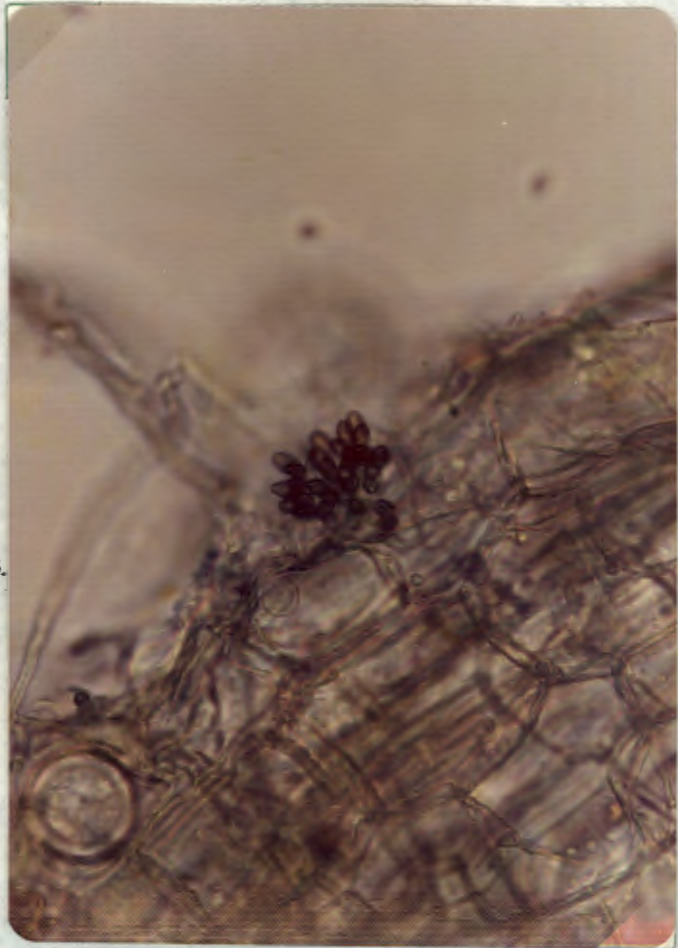


PLATE 38



Population 1. Unburnt section along
edge of cliff

PLATE 39



Population 1 - unburnt section

PLATE 40



Population 2

PLATE 41



Population 3

PLATE 42



Population 3 : Note Audouina capitata protruding
above Staavia dodii shrub

PLATE 43



Population 3 : Note Saltera sarcocolla growing
profusely amongst rocks

PLATE 44



Population 4: Note senescent growth

PLATE 45



Population 4 - southwards. Note senescent growth

PLATE 36



Population 1 - burnt section

PLATE 37



Population 8 - burnt section

PLATE 46



Population 4: Note light coloured Grubbia copensis in centre

PLATE 47



Population 8 : Note rocky terrain

PLATE 48



Population 8: Note fire destruction; burnt remains of Staavia dodii shrubs in foreground

PLATE 49



Population 8 transect area for study of study of seedling distribution

PLATE 50



Area from which relevés 16, 17, 24, 29 and 30
were taken