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SOME OBSERVATIONS ON THE NATURE AND CAUSES OF SECONDARY SUCCESSION ON CERTAIN AREAS AT FRANKENWALD AND IN THE HIGHVELD OF THE TRANSVAAL.

A thesis submitted in fulfilment of the regulations governing the degree of Master of Science in the University of the Witwatersrand.

1939.
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by

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INTRODUCTION.

The work embodied in this paper is a continuation investigation begun in 1936, which was presented in the of a thesis in part fulfilment of the regulations gove the degree of B.Sc.Hon. in the University of the Witw rand, in February 1937. The work included in that pap consisted for the most part of a mosaic of observation studies made in the field. It was a study of the vari types of secondary succession, due to various initial which are commonly to be seen in the Highveld area of Transvaal.

Once having established the outlines of the main of various types of secondary succession, it was decid confine future work to that type of secondary successi which is at once the most common and the most important South Africa - i.e. succession due to the cultivation virgin veld for purposes of crop production - and to f what factors were responsible for dictating that succes should advance in the particular way it does. We know instance that in succession of this type, the ruderal Tagetes - Datura - etc community which is the first to its appearance, is followed by a Cynodon - Eragrostis stage and that the latter is in its turn ousted by yet seral community in which Hyparrhenia hirta is the domin element. There is, however, no evidence stating why sh should be so. It is true that acceleration of successi either natural or induced, may result in one or more of intermediate stages falling out but, in the main, secon succession follows a comparatively clear-cut line of ad The work which follows was initiated with the object of discovering the factors which are responsible for confi the process of secondary succession to these definite of progression.

In order to define the course followed by secondary

succession upon the ploughed lands in the Highveld a
has been found necessary to repeat a certain amount
ence put forward in 1937. This has been done in ord
provide a basis for discussion of the present work.

An appendix has been added dealing with the gra
climax in the Southern Transvaal and North Eastern O
Free State.

FREQUENCY SYMBOLS USED.

v.ab.	=	very abundant.
ab.	=	abundant.
f.ab.	=	fairly abundant.
v.f.	=	very frequent.
f.	=	frequent.
f.f.	=	fairly frequent.
occ.	=	occasional.
f.occ.	=	fairly occasional.
v.occ.	=	very occasional.
f.r.	=	fairly rare.
r.	=	rare.
v.r.	=	very rare.
l.	=	locally + any symbols above.

There may be various combinations of the above sy
as in l.v.f - ab. = locally very frequent to abundan

C H A P T E R I.

OUTLINE OF MAIN STAGES AND COURSE OF SUCCESSION.

The type of succession outlined here, occurs univers in South Africa upon fallow lands which have been repeate ploughed and cropped for several consecutive years, have seldom if ever been planted to a leguminous crop and have never been fertilised. Such lands cover large areas of t Transvaal and represent a total loss to the farmer of are land and of potentially good pasture.

The plant lists drawn up below do not represent any particular communities I have seen but are the essence of three year's study of a number of fallow lands in all sta of succession, in this area. Information gained in this has been put together in the lists below. Thus it must n be assumed that the plants mentioned in any one particula list will occur upon any one fallow land. However, the f remains that all the plants mentioned in any one list hav been seen upon numerous lands whose ages are approximatel the same. For instance, any one of the plants mentioned in the list 1. need not necessarily appear but is likely appear upon a land in its first year of fallowhood. Note have been added upon those plants which may frequently occur in a particular community but which are not consid to be true members of it.

Secondary succession in this area can conveniently b divided into six main stages of progression:-

1. Ruderal Stage.
2. Primary Grass Stage.
3. Secondary Grass Stage.
4. Grassland Climax Stage.
5. Protea Open Woodland Stage.
6. True Climax - Mixed Scrub Vegetation.

In actual fact, any stage may merge with another, th Stages 1. and 6. are as a rule, quite distinct.

1. RUDERAL STAGE.

The majority of plants in this stage are Dicotyled
though a few grasses occur. Almost all are annuals or
ennials. The community may contain a large number of
different species or may be composed of very few. When
large number of species is present, the appearance of t
community is ragged, due to the varying stature of its
In such communities, the growth is usually semi-succule
nature and vivid green in colour. Where the community
composed of a few members only, it takes on the charact
appearance of the dominant species and is more uniform
appearance - e.g. an even, greyish-white appearance whe
composed of Gnaphalium undulatum. In both cases, thou
owth may be vigorous and dense and foliage very heavy,
total basal cover is very small indeed. The basal area
estimated by the List Quadrat method, (described by Mur
and Glover, 2. 1935) falls between 2% and 6% (cf. van
Rensberg, 1939). The plants rapidly cover a land after
has been allowed to go fallow. The members most frequen
found are marked with an asterisk. The most important
members of this community are:-

Alternanthera repens Steud.	occ. - l.v.ab.
Amaranthus Thunbergii Yog.	Occ. - v ab. *
Argemone mexicana Linn.	occ. - v.ab. *
Asclepias fruticosa Linn.	occ. - ab. *
Bidens pilosa Linn.	occ. - v.ab. *
Chenopodium ambrozoides Linn.	occ. - l.v.f.
C. album Linn.	occ. - l.v.f.
Chloris virgata Swartz.	occ. - v.ab. *
Conyza ambigua - Cesati. Passer & Gibelli.	occ. - v.ab. *
Corrigiola littoralis Linn.	occ.
Cosmos bipinnatus Cav.	l.f. - v.ab. *
Cyperus esculentus Linn.	l.v.f. - v.ab. *
Datura stramonium Linn.	occ. - v.ab. *

Datura tatula Linn.	occ. - v.ab. *
Digitaria horizontalis Willd.	f.f.
Eleusine indica Gaertn.	occ. - v.ab. *
Erigeron canadensis Linn.	occ. - f.ab. *
Euryops transvaalensis Klatt.	occ. - f.
Gnaphalium undulatum Linn.	occ. - v.ab. *
Gomphrena globosa Linn.	occ. - l.v.ab. *
Helichrysum argyrosphaerum D.C.	occ.
H. aureo-nitens Sch. Bip.	occ. - l.ab.
H. caespititium Sond.	occ.
H. callicomum Harv.	occ. - l.f.ab.
Lepidium linoides Thunb.	occ. f.f.
Lobelia decipiens Sond.	occ. - l.ab.
L. rosulata S.Moore.	occ. - l.v.ab.
Lotononis foliosa Bolus.	occ.
Nidorella anomala Steetz.	occ. - l.ab. *
N. hottentotica D.C.	occ. - l.f.
Oenothera biennis Linn.	occ. - f.f. *
Oldenlandia amatymbica (Hochst.) K. Schum.	occ. - f. *
Panicum laevifolium Hack.	occ. - v.f. *
Physalis minima Linn.	occ. - v.f. *
Portulaca oleracea Linn.	occ. - v.f. *
Schkuhria bonariensis H.& V.	occ. - ab. *
Senecio laevigatus Thunb.	occ. - v.f. *
S. venosus Harv.	occ. - l.f.
Setaria sp.	occ. - l.f.ab.
Solanum capense Linn.	occ.
S. sp.	occ.
Spermacoce ditrachiata Oliver.	occ. - v.f. & l.ab. *
Stoebe vulgaris Levyns.	occ. - f.f. *
Tagetes minuta Lam.	occ. - v.ab. *
Tragus berteronianus Schult.	occ. - f.
Tribulus terrestris Linn.	occ. - ab. *
Urochloa helopus Stapf	occ. - f.f.
Ursinea annua Less.	occ. - f.f.

Wahlenbergia undulata A.D.C.	occ. - f.f.
Walafrida densiflora Rolfe	occ. - f.f. *
Xanthium strumarium Linn.	occ. - v.sb. *
X. spinosum Linn.	occ. - v.f. *

Several species mentioned above are not believed to be true members of the Ruderal Stage, although frequently found in it. Euryops transvaalensis truely belongs to the Grassland Climax Stage and is only found here by reason of the fact that its taberous root system is small enough to escape being harrowed out of the land. Helichrysum aureo-nitens is believed to be in its true position in wet or very moist areas within the Grassland Climax Community. This applies also to H. callicomum though it appears to have a wider range of habitat than H. aureo-nitens. Lobelia decipiens and L. rosulata also favour wet areas. Both these appear to be plants of a truely secondary nature since, though they occur in Purple Veld, they appear to do so almost exclusively in the presence of disturbance and surface water. Glover's observations (1937) seem to bear this out. Lotononis foliosa would appear to belong to the Grassland Climax type which suffers moderate disturbance from grazing animals. It is doubtful whether it would survive beneath the heavy top-hamper of undisturbed climax grassland. Oenothera biennis does not compete successfully with a heavy growth of ruderals and is more frequently to be found in the Primary Grass Stage. Senecio venosus appears to be a member of the Grassland Climax which tends to be spread by overgrazing. It is certainly not an important element of the Ruderal Stage.. Stoebe vulgaris has in some cases, been found to occur quite frequently amongst members of the Ruderal Stage. However, it persists long after the death of almost all the other plants in that stage and its rightful position appears to be either in the Primary or Secondary Grass Stage. It has been seen in both. The true position of the grass Tragus berteronianus, would seem to be in the Primary Grass Stage,

rather than in the Ruderal Stage. Melefrida densiflora i found in all stages of succession from the Ruderal Stage the Grassland Climax. Its true position, however, appear to be the Secondary Grass Stage or in Climax Grassland wh is disturbed sufficiently to keep down the heavy choking hamper. Some of the more hardy plants such as Asclepias fruticosa are true members of the Ruderal Stage but are frequently found surviving into the Primary Grass Stage.

The stage as a whole, does not usually last much lon than two years, very seldom more than three years. The treatment it obtains determines the length of time it wil endure. If for example, the community is entirely protec it is likely to last longer than usual. If on the other severe trampling occurs ruderal types will quickly disapp and grasses, particularly Cynodon dactylon, will take the place. (van Rensberg, 1939). Once established, grass vegetation never loses its grip upon the land unless the ground is re-ploughed or cultivated.

2. PRIMARY GRASS STAGE.

The Primary Grass Stage consists mainly of grasses, though various non-grasses appear with them. The non-grasses, however, are not important members of this or of of the succeeding communities up to and including the Gra land Climax Stage. (See Murray, 1934). The percentage ba cover is frequently high, due to the predominance of the prostrate Cynodon dactylon. Murray's figures (1934) show the mean basal cover in this type of veld is about 10.2%. This seems to be very low but is explained by the fact th the strain of Cynodon dactylon occurring on the particula area quadrated, had rather an upright habit. It was foun that Cynodon dactylon made up 31.77% of the total basal area covered by the vegetation. The figures for mean tot basal area of cover would not have been so low if

quadrats had been listed in other areas carrying the same type of vegetation. In contrast to the Ruderal Stage, the majority of the plants are perennials. This fact ensures the comperative stability of the community for a period of several years. The general colour of the type is usually much lighter than in the case of the Grassland Climax Stage. It is generally ragged in appearance, due to the presence of both prostrate creeping forms and erect, tussocky types. If, as sometimes happens, the community contains a high percentage of one species, the presence of shorter grasses such as Eragrostis chalcantha and Cynodon dactylon is masked and the community assumes an even, unbroken appearance - e.g. as in the case of an invasion of Eragrostis curvula whose flowering culms and foliage are carried at a comparatively much higher level than those of Eragrostis chalcantha and Cynodon dactylon. A number of plants found in the Ruderal Stage are still present, though most of these, such as Asclepias fruticosa soon die away.

The most important constituents of this stage have been marked with an asterisk. The order in which succession usually takes place is indicated by the number next to the plant - e.g. No.1 signifies that the plant was the first or among the first to make its appearance.

Grasses:-

Aristida congesta R. & S.	occ. - v.ab. *	1.
Chloris virgata Swartz	occ. - l.f.	1.
Cynodon dactylon Steud.	ab. - v.ab. *	1.
Eleusine indica Gaertn.	occ. - l.f.	1.
Eragrostis brizoides Nees.	occ. - f.f.	1.
E. chalcantha Nees.	occ. - v.f. *	1.
E. chloromelas Steud.	occ. - v.ab. *	2.
E. curvula Nees	occ. - v.ab. *	2.
E. gummiflua Nees.	occ. - v.ab. *	2.
E. nebulosa Stapf.	occ. - l.v.f.	2.
E. robusta Stent.	occ. - l.v.f.	2.
Perotis indica (Linn.) Kuntze.	occ. - l.ab.	2.

Pogonarthria squarrosa (Licht.) Pilg	occ. - f.ab.
Rhyncelytrum repens (Willd.) C.E. Hubb.	occ. - v.ab.
Sporobolus indicus R.Br.	occ. - l.ab.
Tragus berteronianus Schult.	occ. - l.f.
Trichoneura grandiglumis Ehrenb.	occ. - l.f.

Non-grasses:-

Asclepias fruticosa Linn.	occ.
Euryops transvaalensis Klatt.	occ. - l.f.
Helichrysum aureo-nitens Sch.Bip.	occ. - l.v.f.
H. caespititium Sond.	occ.
H. callicomum Harv.	occ. - l.v.f.
Ipomoea bathycolpos Hall, f.	occ.
I. spp.	occ.
Justicia anagalloides T.Anders.	occ. - f.
Lobelia decipiens Sond.	occ. - l.v.f.
L. rosulata S.Moore	occ. - l.v.f.
Lotononis foliosa Bolus.	occ.
Nidorella anomala Steetz.	occ. - l.v.f.
N. hottentotica D.C.	occ. - l.f.f.
Oenothera biennis Linn.	occ. - l.f.f.
Oldenlandia amatymbica Linn.	occ. - l.f.f.
Oxalis setosa E. Mey.	Occ. -
Pelargonium eco nitophyllum E.& Z.	v.occ.- [illegible]
Senecio venosus Harv.	occ. - l.f.f.
Spermacoce dibrachiata Oliver.	occ. - l.ab.
Stoebe vulgaris Levyns.	occ. - l.ab.
Wahlenbergia undulata A.D.C.	occ.
Walafrida densiflora Rolfe	occ. - f.f.
Zinnia pauciflora Linn.	occ.

Many plants noted above do not actually belong to the Primary Grass Stage but have survived from the previous sta These, with the exception of species which continue to flou ish until the Grassland Climax Stage has been reached, are

of little importance and so die away. The following spec fall into this category: Asclepias fruticosa, Cotsaria vi and Eleusine indica.

Though Cynodon dactylon is found in the Secondary Gr Stage, I believe that this stage is its true home. It thrives best on loose exposed soil in the absence of co ion and is essentially a re-claimer of potential "bad la

Eragrostis brizoides and E. chalcantha continue to Grassland Climax Stage and will be discussed under that h ing. Suffice it to say that I consider both these grasse to be true members of the Primary Grass Stage; as are als E. chloromelas, E. curvula, E. gummiflua, E. nebulosa and E. robusta. Perotis indica, Pogonarthria squarrosa, Sporobo indicus, Tragus racemosus and Trichoneura grandiglumis ar also typical constituents of this veld type. Rhynchelytru repens, on the other hand appears to occur equally frequ in this type and in the Secondary Grass Stage. It is difficult to assign it to one or the other group of plant and I venture no definite statement as to its true positi other than to say that it belongs either to the Primary o Secondary Grass Stage. As it is relatively short grass compared with Hyparrhenia hirta, it is probable that it belongs to the Primary Grass Stage. Observations made on low lands in the Hekpoort area indicate that it probably belongs to the Primary Grass Stage.

The non-grasses are all relatively unimportant. Mur figures (1935) show that of the total area covered by veget only 18.38% represents non-grass types, of which 8.64% consisted of various species of the Cyperaceae. Eryops transvaalensis, Helichrysum aureo-nitens, H. callicomum, Lotononis foliosa, Oenothera biennis and Senecio venosus all been dealt with under Paragraph 1.

Nidorella hottentotica and N. anomala appear to exis chiefly in this Primary Grass Stage and in locally distur areas in Grassland Climax vegetation. Oldenlandia amatym

probably thrives best in this Primary Grass Stage, especiall where Cynodon dactylon has not gained too great an advantag over other constituents. Oxalis setosa - a very small semi succulent plant-thrives in spaces between tussocks of Eragrostis. Pelargonium aconitophyllum is quite frequently found in this stage, due to its probable ability to spring up from tuberous roots. A string of tubers is attached to the base of the stem which are likely to give rise to separ new plants. I am in doubt as to which community it really belongs. It thrives well in fallow land but is also found in Climax Grassland, though not to such an extent as in thi stage. It is a true secondary type and though it occurs in the Grassland Climax type, it is probably best placed in the Primary or Secondary Grass Stage. Spermacoce dibrachiata occurs in local abundance in this type. It is difficult to assign it to either the Ruderal Stage or to the Primary Grass Stage. However, it seems doubtful whether it could compete with tall ruderals of dense foliage and may conveniently be put in the Primary Grass Stage, though even here, it tends to colonise only those areas where the ground is comparatively free of Cynodon dactylon - e.g. such areas as very shallow furrows, where slight erosion has occurred.

Stoebe vulgaris seems to belong rightly to the Primary Grass Stage and is most frequently found with its constituen

Wahlenbergia undulata may possibly be a true ruderal type but it most frequently occurs in areas of local disturbance amongst members of higher stages. Walafrida densi flora also seems to fall into the same class as Wahlenbergia Zinnia pauciflora is most frequently found in areas of local disturbance in the Primary Grass Stage.

The Primary Grass Stage described above may endure for a period of time varying approximately between 8 and 30 years, depending upon the nature of the soil upon which it exists and also upon subsequent treatment. For example, areas suffering constant disturbance from grazing animals

would remain under this type of vegetation until such disturbance ceased or diminished in intensity. On the other hand, old native kraals have been observed on Aasvogelkop (near Johannesburg) and on the Gatsrand, which still suppo a vegetation consisting almost entirely of Cynodon dactyl The soil in these cases is pure humus. The kraals have no been used within living memory so that in isolated instan such as this, the Primary Grass Stage may remain in posses of the area for a period lasting up to 100 years - or more

The transition to the Secondary Grass Stage probably takes place gradually, on the average after about twelve fifteen years.

2. SECONDARY GRASS STAGE.

The majority of plants in this stage is grasses though there are actually more species of non-grasses. As before the non-grasses form a very unimportant portion of the community. Unfortunately, I can supply no figures stating the mean basal cover of grasses and non-grasses. It is quite evident, however, that the non-grasses form a very small percentage of the total basal cover.

In marked contrast to the smaller grasses of the Prim Grass Stage, the dominant grasses of this community are t erect, tussock forms. The dominant element, Hyparrhenia h occurs in scattered irregular patches of extremely dense, growth. It has seldom been observed to completely fill a large area. The general appearance is thus very irregular The spaces between the scattered clumps are frequently lar in extent and allow other less robust members of the comm - and also Primary Grass Stage constituents - to obtain a footing. The patches of Hyparrhenia hirta, combined with certain amount of Themeda triandra, give the community a ruddy, brownish tinge, especially apparent in winter month

An immediate result of the invasion of the Primary Gr community by plants of the Secondary Grass Stage, is the

extermination of some of the smaller species. Intoleran grasses such as Aristida congesta frequently disappear before the advance of the Secondary Grass Stage. If, however, they are still present during the period of tra ion, they are very soon crowded out of existence, partly increasing pressure upon available space but also throu marked reduction in available light.

The most important plants in the community have bee marked with an asterisk. The numbers opposite the name give the approximate order of their appearance.

Grasses:-

Aristida congesta R.S.	v.occ.
Cymbopogon excavatus (Hochst.) Stapf.	occ. - f.
Cynodon dactylon Steud.	f. - l.ab.
Eragrostis brizoides Nees.	v.occ.
E. chalcantha Nees.	occ. -l.f.ab.
E. chloromelas Steud.	occ. - l.f.
E. curvula Nees.	occ. - l.f.
E. nebulosa Stapf.	occ. - l.f.f.
Heteropogon contortus Linn.	occ. - l.f.
Hyparrhenia hirta Stapf.	occ. - l.v.ab.
Pogonarthria squarrosa (Licht.) Pilg.	occ.
Rhynchelytrum repens (Willd.)C.E.Hubb.	occ.-l.f.ab.
Schizachyrium semiberbe Nees	v.occ.
Themeda triandra Forsk.	occ - l.f.

Non-grasses:-

Callilepis leptophylla Harv.	occ.
Cassia mimosoides Linn.	occ. - f.f.
Dimorphotheca spectabilis Schltr.	occ.
Eriosema cordatum E.Mey.	v.occ.
E. transvaalensis C.H.Moss (ined.)	v.occ.
Gladiolus crassifolius Baker	v.occ.
Gnidia caffra Meisn.	v.occ.
Helichrysum aureo-nitens Sch.Bip.	occ. - l.f.

Helichrysum caespititium Sond.	occ.
H. cerllicomum Harv.	occ. - l.v.f.
H. leiopodium D.C.	v.occ.
Lyperoxis Rooperi Moore.	v.occ. - occ.
H. rigidula Baker.	v.occ. - occ.
Indigofera bibrida N.E.Br.	v.occ. - occ.
Ipomoea spp.	occ.
Justicia anagalloides T. Anders.	occ. - f.
Lotononis foliosa Bolus.	occ.
Nidorella aromala Stuetz.	v.occ. - l.f.
N. hottentotica D.C.	v.occ.
Oldenlandia amatymbica Linn.	occ. - f.f.
Pelargonium aconitophyllum E.& Z.	occ. - l.f.f.
Pentanisia variabilis Harv.	occ.
Stoeba vulgaris Levyns.	occ. - l.ab.
Vernonia Kraussii Sch.Bip.	v.occ.
Walafrida densiflora Rolfe.	f.occ.

The position of Aristida congesta has already been di cussed in Paragraph 2. Cymbopogon excavatus is a true mem of this stage (3).

A fact which bears out this statement is that when Climax Grassland (which is the next stage in the succession is overgrazed, one of the first grasses to appear is Cymbo pogon excavatus. (If however, overgrazing is too severe, succession is thrown back to the Primary Grass Stage, with Cynodon dactylon dominant.) The appearance of Cymbopogon excavatus in overgrazed natural veld has frequently been noted in experimental areas and in the field. Certain exp mental plots of the CC, DD, EE series at Frankenwald, whic have been overgrazed for one and two years respectively an then protected, show this very well indeed. Isolated tuss of Cymbopogon excavatus and Theveda triandra are very noti able among the remaining Climax grasses.

Cynodon dactylon, Eragrostis brizoides, E. chalcanthe E. chloromelas, E. curvula, E. nebulosa, Pomonarthria squa

and Rhyncelytrum repens are truly members of the Stage 2, but are well represented in the spaces between clumps of Hyparrhenia hirta. Eragrostis brizoides and E. chalcantha are further dealt with under 4.

Heteropogon contortus, which according to Murray's figures (1935) occurs very frequently in Climax Grassland is, in my opinion, a member of this Secondary Grass Stage. Comparisons drawn between list quadrat figures of Scott & Murray (Murray 1934) and those of Glover and Rose Innes (Glover, P. 1937), on the same quadrats, strongly support this view. The quadrats were laid out in moderately grazed Part Veld (see Grassland Climax) in 1933 and were protected from that time onward. The Scott-Murray estimations were made in 1933, the Glover-Rose Innes estimations in 1936. A comparison of the results obtained show a marked decrease in Heteropogon contortus under control conditions, In 20 quadrats the average percentage cover was 1.72% in 1933 and 0.76% in 1936. Heteropogon contortus has thus been reduced by well over half its cover since 1933. The percentage cover in this instance is estimated as a percentage of the total area possible to be covered, not as percentage cover of the area actually covered by vegetation. The figures would have been much higher if calculated on the latter basis. Observations on other completely protected areas fully substantiate the statement put forward above. Heteropogon contortus cannot exist in competition with such rank, tall tussock grasses as Trachypogon plumosus, Tristachya hispida, T. Rehmanni, Urelytrum squarrosum, Alloteropsis semialata, Andropogon amplectens and other true constituents of Climax Grassland, under conditions of complete protection. On the other hand, it thrives in fallow lands in the Secondary Grass stage of succession, provided that it is not situated immediately next to Hyparrhenia hirta. Old fallows in this stage of succession, near the laboratory at Frankenwald, show an abundance of Heteropogon contortus.

Themeda triandra which has already been mention
above, in conjunction with the behaviour and true ha
of Cymbopogon excavatus, is a grass whose grass form
similar to that of Heteropogon contortus and behaves
the same way, though it is not nearly so abundant in
Grassland. It occurs in the latter stage only in con
of local disturbance (e.g. round the edge of termita
antbear holes) and moderate overgrazing.

The remaining grass, Schizachyrium semiarbe, o
very sparsely and appears to prefer such sites as old
and rocky outcrops (Glover, I. 1937) Rose Innes, I.
to open veld in any stage of succession. However, it
occur in this stage (3) and locally in Climax Grassl
sites which show signs of remote disturbance - on old
tracks for example. Observations made on old roads
Schizachyrium semiberbe intermingles with such grasse
Hyparrhenia hirta and Cymbopogon excavatus - both members
Secondary Grass Stage on fallow lands. For these rea
it has been included in the above list of Secondary
Stage plants.

Of the other non-grass species, none can be said
of much importance in the community as a whole. The
noticeable point is the appearance of several species
to the succession, some of which have affinities with
Grassland. Among these species are Callilepis laptop
Cassia mimusoides, Dimorphotheca spectabilis, Erioseu
cordatum, E. transvaalensis, Gladiolus crassifolius,
caffra, Helichrysum leiochodium, Hypoxis Rooperi, H. r
Indigofera hibrida and Pentanisia variabilis. Hypoxi
Rooperi, H. rigidula and Gnidia caffra are all true C
Grassland members. Callilepis laetophylla, Cassia mi
Dimorphotheca spectabilis and Gladiolus crassifolius
found in slightly disturbed areas and also, though perhaps
frequently - in undisturbed Climax Grassland. The fi
three of these favour ground which has been either pl

or disturbed by grazing animals, while Gladiolus crassifolius appears to thrive better in moister sites, which have suffered a certain degree of disturrence.

Of the remaining plants, Helichrysum caespititium seems to have found the limit of its advance. It is a prostrate plant, looking much like a flattened pin-cushion and certainly cannot and does not compete with the tall rank grasses of protected Climax Grassland. Helichrysum aureo-nitens is found in moist sites in Climax Grassland, often in the presence of slight disturbance. Its true position is probably with other plants inhabiting wet areas which have been disturbed. Helichrysum pallicomum does not appear to advance further than this stage in the succession, to which it probably belongs. Justicia anagalloides occurs in Climax Grassland under conditions of moderate disturbance but I believe its true position may be with the members of the Secondary Grass Stage. In a community such as this, it is able to thrive in spaces between patches of Hyparrhenia hirta where the vegetation is not dense enough to kill off its prostrate runners. This also may apply to the species of Ipomoea. I have not investigated the root system of Justicia anagalloides but the Ipomoea species generally have a tuberous root system of very large proportions which would enable the plants to survive in Climax Grassland in conditions of complete protection, for a considerable period of time. I am inclined to doubt, however, whether their long un-rooted runners would be able to maintain the intense struggle for light and existence itself, in competition with the tall rank bunches of Climax grasses. Stoebe vulgaris does occasionally occur in locally disturbed areas in Climax Grassland but the Secondary Grass Stage generally seems to be the limit of its advance. This is also probably true of Gerbera densiflora. It has quite frequently been observed growing in undisturbed Climax Grassland but the plants did not appear to be robust or particularly healthy.

4. GRASSLAND CLIMAX STAGE.

At Frankenwald and over extensive areas of the Highv region, this type of grassveld exists on dry, undulating, country. The community consists largely of an open cover of tall, erect tussocks of grass, in spaces among which are scattered numerous non-grass species. The grass foli does not as a rule stand higher than 1 foot from the grou though the flowering culms reach a height of 3-4 feet. T total basal cover is poor. Burray's figures (1934) show that on the average, it does not exceed 20%, though in so cases it rises to as high as 25% of the total ground surf The non-grass types, though often conspicuous when in fl do not form an important part of the community. These pl represent only 0.12% of the total area covered by the veg ation as a whole.

The community when undisturbed, presents an even, h geneous, unbroken appearance with none of the irregularit of the other communities already described. At Frankenwa it has become known as "Purple Veld", due to its characte tic purple colour during the flowering period. In winter community assumes a drab, yellowish-brown appearance. Th species are frequently very coarse, particularly when pro tected and are often very hairy.

The Purple Veld species are apt to undergo slight ch when the veld is grazed or occasionally burnt. The reason is that grazing and in particular burning, prevent the tussocks from becoming rank and the debris of previous sea growth from choking the plants and seedlings. The spaces between tussocks are kept open and are frequently filled b grasses of a secondary character. Apart from keeping the spaces open, grazing has the effect of giving stoloniferou plants such as *Digitaria tricholaenoides*, room to extend. Temporary relief from the burden of dead foliage and flowe ing culms, also provides smaller grasses such as *Brachiari serrate* with the opportunity for growth. Burning has the

same general effect but is apt to harm stoloniferous gra
Digitaria tricholaenoides has been observed to suffer fr

The most important species occurring in this Grassl
Climax or "Purple Veld" Stage have been listed below. Th
species which are considered to be members of the undistu
Grassland Climax are marked with an asterisk. The approx
order of their appearance is indicated by the numbers opp
the specific names.

Grasses:-

Alloteropsis semialata Hitchcock.	occ.
Andropogon amplectens Nees	occ. - f.f.
Brachiaria serrata (Spreng,)Stapf	occ. - f.
Digitaria tricholaenoides Stapf.	occ. - f.
Diplachne biflora Hack.	occ. - f.f.
Elionurus argenteus Nees.	occ.-f.
Eragrostis brizoides Nees.	occ.
E. chalcantha Nees	occ.-v.f.
Harpechloa falx (Linn.f.)Kuntze.	occ.-l.v.f.
Heteropogon contortus R. & S.	v.occ.
Lophacme digitata Stapf.	l.occ.
Loudetia simplex C.E. Hubbard.	v.occ.-l.oc
Monocymbium ceressiforme (Nees)Stapf.	occ.-f.f.
Panicum natalense Hochst	occ.
Rhyncelytrum setifolium Choiv.	v.occ.
Sporobolus fimbriatus Nees.	occ.
Themeda triandra Forsk.	l.f.
Trachypogon plumosus Nees.	v.f.-ab.
Tristachya hispida (Thunb.)Schum.	v.f.-ab.
T. Rehmanni Hack.ex Schinz.	occ.
Urelytrum squarrosum Hack.	v.occ.

Non-grasses:-

Acalypha angustata. Sond.

A. caperonioides Baill.

Albuca pachyclamys Baker.

Asclepias stellifera Schltr.

Asclepias aurea Schltr.

Aster harveyanus Min.

Babiana hypogea Burch.

Nidium obovatum var. Niana N.E.Br.

Berkheya subulata Harv.

Bopusia scabra Presl.

Callilepis leptophylla Harv.

Cassia mimusoides Linn.

Clerodendron triphyllum (Harv.) H.A.W. Pears.

Cucumis hirsutis Sond.

Cyanotis nodiflora Kunth.

Cyperus compactus Lam.

C. compactus Lam. var. flavissimus C.B.Cl.

Dianthus mooiensis Williams.

Dicoma anomala Sond.

D. Zeyheri Sond.

Dimorphotheca spectabilis Schltr.

Elephantorrhiza elephantina (Burch.) Skeels.

Eriosema cordatum E.Mey.

E. transvaalensis C.E.Moss (ined.)

Euphorbia striata Thunb.

E. truncata N.E.Br.

Gazania pygmaea Sond.

Gerbera piloselloides Cass.

Gladiolus crassifolius Baker.

G. edulis Birch.

Gnidia caffra Neimr.

G. capitata Linn.

G. Kraussiana Meisen.

G. microcephala Meisn.

Haplocarpa scaposa Harv.

Hermannia lancifolia Szysz.

Hypericum aethiopicum Thunb.

Hypoxis rigidula Baker.

H. Rooperi Moore.

Indigofera hibrida N.E.Br.

Ipomoea bathycolpos Hall.

I. simplex Thunb.

I. spp.

Lobelia decipiens E.Moore.

L. rosulata Sond.

Lotononis foliosa Bolus.

Pachystigma pygmaea

Pelargonium aconitophyllum var. angustisectum Dunth.

Pentanisia variabilis Harv.

Peucedanum magalis-montanum Sond.

Polygala boyssinica R.Br.

P. gracilenta Burtt Davy

Protea hirta Klotzch.

Raphionacme divaricata Harv.

Scabiosa anthemifolia E.& Z.

Scilla lanceaefolia Baker.

S. ovatifolia Baker.

Senecio coronatus Harv.

S. serra Sond.

S. succosus C.H.Moss.

S. venosus Harv.

Silene oliveriana Burch.

Sphenostylis angustifolia

Striga elegans Benth.

Tephrosia aurantiaca R.G.N.Young.

Tulbaghia leucantha Baker.

Urginea multisetosa Baker.

Vernonia Braussii Sch.Bip.

V. monocephala Harv.

Walafrida densiflora Rolfe.

Zizyphus zeyheriana Sond.

There is some doubt about the real position of some of the grass species, marked above as true Purple Veld constituents. Diplachne fiflora, though it is found scattered fairly frequently among Purple Veld grasses, is a delicate

leafed plant whose height compared with such species as Trachypogon plumosus and Urelytrum squarrosum is compara small. Nor is it a robust type. For these reasons, it seems likely that it would not exist in competition with robust Purple Veld grasses for any great length of time under conditions of complete protection. The fact that growth in burnt areas is quite vigorous, seems to suppo this view. Unfortunately no work has yet been done upon root system of this species.

Brachiaria serrata has for a long time been regarde a true Purple Veld type. Observations in completely pro tected areas, however, show that it tends to be crowded of existence by its taller, overbearing associates. Obs vations made by Altona (Altona 1939) while studying the growth rythm of Brachiaria serrata in the 1937-38 and 19 seasons, show that several plants of Brachiaria serrata marked for measurement in the summer of 1937-38, showed definite deterioration in the total amount of foliage pu forth in the summer of 1938-39, under conditions of compl protection. On the other hand, similar plants growing a feet away from the latter, in an area which had been burn but protected from grazing animals, were growing compara vigorously. The plants in the burnt area were of course free from the choking burden of taller foliage around th On the other hand, Brachiaria serrata is known to have a large, deep root system (see Chart No. 14) well fitted to compete with those of the other Purple Veld grasses. It will be noted, however, that part of its root system cons of superficial lateral roots. This seems to indicate the it is a grass which belongs to the earlier stages of true Purple Veld. All true Purple Veld species studied have d root systems with no superficial lateral extensions. (See further notes on root system of this species, Chapter "I

Harpechloa falx is frequently found in Purple Veld, I regard it as a slightly atypical constituent on the gro

that it tends to restrict its operations to moist flushes and damp ground.

Monocymbium ceresiiforme is also frequently found in lightly grazed Purple Veld but I am doubtful as to its true position. Observations made on the southern side of the Klipriversberg on shaly, shallow, sloping ground, indicate that it prefers to grow in a more open vegetation on shallow soil. It is also found on moist ground, however. Its range of habitat therefore appears too wide. I have little doubt, however, from the delicate nature of the plant and its comparatively low height, that it would be one of the first grasses to disappear from a Climax Grassland area which was progressing toward the true climax.

Tricholaena setifolia is to be found scattered sparsely through Purple Veld vegetation. It is a fairly small plant, quite low in height. It is one of the less important constituents of this vegetation type and I believe would quickly disappear under conditions of complete protection. Sporobolus fimbriatus would also probably fall into this category.

It would perhaps be unwise to place the plants mentioned in the notes above, into a successional stage by themselves. I feel, however, that several of them could conveniently be classed together as a group of Purple Veld grasses which are likely to be amongst the first to disappear from grassland moving towards the true climax. I consider that Diplachne biflora and Monocymbium ceresiiforme which are not so robust as Brachiaria serrata, Rhynchelytrum setifolium and Sporobolus fimbriatus would disappear first, to be followed at a short interval by the latter three grasses.

Of the remaining grasses, several occur frequently in Purple Veld but are not typical constituents. I shall deal first with Eragrostis brizoides and E. chalcantha. The latter is by far the most widely spread and is the more important of the two. Though Eragrostis brizoides is found in undisturbed Purple Veld, it constitutes considerably less than 2%

of the total vegetal cover (Murray 1934) and quickly disappears as the period of protection increases. Eragrostis chalcantha, however, is more abundant than E. brizoides in protected Purple Veld and is able to hold its own for a longer period of time.

As has been stated, these two grasses are found in all stages of grass succession from the Primary Grass Stage onward. In Purple Veld, they exist in the spaces between tussocks of the tall grasses. (See Photograph 2). Under ordinary grazing conditions these spaces are kept open by the constant disturbance of the grazing animals. Glover (1. 1937) states that "Eragrostis chalcantha really belongs to undisturbed veld (i.e. to undisturbed Purple Veld) but it is also found on ------disturbed veld." This statement is actually a reversal of the facts. It is found in its true position in disturbed areas and is essentially a grass belonging to the lower stages of secondary succession. Its mere presence in Purple Veld is a flag-signal of disturbance slight perhaps, but significant.

Plants of Eragrostis brizoides and especially E. chalcantha, observed occurring on recently ploughed land in the Primary Grass Stage, exhibited vigorous growth and prolific flowering. One year later when the vegetation had thickened and competition had been increased, flowering and growth were depressed in both species. In the third year there was an even further regression in flowering and growth. In undisturbed Purple Veld, plants of both species are generally small, of poor growth, flower very sparsely, (see Photo. No.) and appear to be merely existing at the bare level of subsistence. This evidence is significant.

It will be argued that almost any climax grass, when established upon loose soil in the absence of serious competition, will flourish better than it would in its natural habitat. Trachypogon plumosus for instance, has been observed to do this at Frankenwald, moreover upon the same ploughed

area mentioned in the previous paragraph. The argument breaks down, however, when it can be shown that Trachypogon plumosus in its natural habitat in undisturbed Purple Veld will continue to flourish, whereas E. brizoides and E. chaltha become more and more insignificant as time goes on.

The two grasses in question owe their existence in Purple Veld firstly, to the open structure of the veld which in certain conditions of disturbance allows the intrusion of such foreign elements and secondly, to disturbance causing such spaces to be kept open and available for colonisation to take place. The disturbance is due chiefly to grazing, not necessarily overgrazing - to fire, which removes debris from the spaces even more effectively, or to a combination of these two.

A further point is that the root system of E. chaltha is superficial (see Chart No.8) and more allied to those of secondary grasses than to grasses of the Purple Veld type.

Observations in a plot at Frankenwald which has been protected from grazing and fire since September 1934, show that E. chalcantha is fast disappearing, except where in the vicinity of local disturbance, such as the activities of the harvester termite - Hodotermes natalensis - and the mounds of other termite species, E. brizoides seems to have almost completely disappeared.

The most conclusive evidence in support of the argument above, come from figures of quadrat analyses. These comparative data come from the same sources as those for Heteropogon contortus - mentioned previously. Protection was started on 20 quadrats in 1933. The quadrats were limed in that same year and again in 1936. In 1933 E. chalcantha composed 2.63% of the total ground area. In 1936, however, this figure had fallen to the low percentage of 0.57%. The cover was thus about five times greater in 1933 than in 1936 and this can be attributed solely to the influence of protection.

Digitaria tricholaenoides is another grass which has also been regarded for some time as a true constituent of the Climax Grassland type. The robust nature of its deep-seated root system would seem to support this view. There are several reasons, however, which lead one to doubt the truth of this belief. Turning first to the growth form of the grass, it will be seen that it is prostrate and stoloniferous, with the flowering culms projecting vertically upwards to a height of about 18 inches to 2 feet above the mass of leaves. This in itself leads one to doubt whether it could compete with the rank tussock grass types of undisturbed Purple Veld. Observations in protected plots bear this out. The prostrate mat tends to be crowded out by the taller grasses and the light available to the lowly-situated leaves is considerably cut down. The stolons do not root and the leaves tend to grow vertically rather than horizontally. Furthermore, under light grazing the plant thrives and is able to hold its own under conditions of reduced competition for light and space. Under conditions of moderate overgrazing, not sufficiently severe to cause a complete throw-back of succession to the Primary Grass Stage - Digitaria tricholaenoides spreads and increases its basal cover to an enormous extent, almost to the complete exclusion of true Purple Veld tussock types. This has been observed on large areas of land on Frankenwald and elsewhere. (See Photograph No.4).

Final conclusive evidence again comes from quadrat analyses. Quoting from the same figures as before, the 1936 analyses show that the grass then covered 3.09% of the total ground area, while in 1936 this figure had fallen to 2.09% - a little more than half the previous total. On the strength of these arguments it seems that if Digitaria tricholaenoides is to exist in Purple Veld, it must be under conditions of moderate grazing. Under conditions of complete protection it eventually disappears and leaves the the true Purple Veld types in complete possession of the ground.

Loudetia simplex is a grass which occurs very occasionally in Purple Veld in the Frankenwald area. As stated by Glover (1.1937) it occurs more frequently on rocky outcrops. Further to the North, however, at the Drylands Experimental Station near Pretoria and on Hartley's Estates in the Magaliesberg, Loudetia simplex has been found to be abundant on shallow ground, in the presence of several true Purple Veld species such as Trachypogon plumosus and Andropogon amplectens. It is a tall coarse grass with the same growth habit as the true Purple Veld types. If it occurred in greater abundance in the Frankenwald area it would certainly be one of the last grasses to disappear before the advance of the true Climax.

Lophacme digitata occurs very locally in Purple Veld, usually in slightly wet areas, and is probably a typical of ~~Purple Veld~~. It is of no importance in this type of grass and being of a delicate nature, would soon disappear in protected Purple Veld.

Heteropogon contortus and Themeda triandra have been fully dealt with under the Secondary Grass Stage, to which they belong.

The remaining grasses are considered to be true Purple Veld types, which would be the very last to disappear before the advance of the true climax vegetation. These grasses are Alloteropsis semialata, Andropogon amplectens, Elionurus argenteus, Harpechloa falx (on moist sites), Panicum natalense, Trachypogon plumosus, Tristachys hispida, T. Rehmanni and Urelytrum squarrosum. (See Photograph No.5.) I am a little doubtful as to the validity of placing Elionurus argenteus in this group, since it appears to suffer more from the effect of complete protection than the other grasses named above and grows with correspondingly increased vigour when the veld has been fired. However, as I have little evidence to support or refute this theory, I have included Elionurus argenteus in the group above. A very significant decrease in cover, however, - 6.21%-occurred in protected quadrats between 19[illegible] and 1936.

The non-grass species are so numerous and so sparsely scattered throughout this type of vegetation that it has been impossible to devote much attention to their true position. Apart from this, they form such a very small part of the vegetation as a whole, that such an investigation was not considered to be of great importance. Murray's figures show that these plants, in spite of the relatively large number of species, constitute slightly less then 5% of the total vegetal cover. Some points have been noted, however, which will be included here.

Nearly all the plants mentioned above are capable of raising their flowers and foliage above the general level of duff and grass leaves in undisturbed areas and are thus able to compete with the dense growth of their neighbours, by rising above it. In this connection it has been noted that some of the plants which, when growing in disturbed areas under Primary and Secondary Grass stage plants, maintain a prostrate or semi-prostrate habit, in Purple Veld assume an erect growth form. This is noticeable in the case of Gazania mimusoides.

Some of the plants mentioned above seem to be more at home in disturbed soils than in Purple Veld. This is noticeable in the case of Dimorphotheca spectabilis but information is too scanty to make any definite statement in connection with its place in succession.

Lobelia decipiens, L. rosulata, Pelargonium aconitophyllum and Helichrysum densiflora have been dealt with already.

From a cursory examination of some of the root systems of a few of these plants, it seems that a very high percentage of them are equipped with root systems specially adapted to stand up to the rigours of existence in open grassland, where conditions of drought, fire, grazing and extremes of temperature are common and severe.

Some root systems such as that of Pentanisia variabilis (see Chart No. 18) descend to a remarkable depth for plants

of such small size. They are also inclined to combine extensive deep-seated root systems with large storage organs. Almost every type of underground storage organ can be found amongst these plants. Corms, bulbs, tubers and rhizomes are found in profusion. Other plants such as some of the Helichrysums and Senecio spp. are equipped with large, short succulent roots extending in a dense mass vertically and laterally below the plant. The depth which such fleshy root systems attain is not known but is not likely to be very great. They are almost identical to, but slightly more succulent than those illustrated under Helichrysum latifolium in Bew's "The Grasses and Grasslands of South Africa."

These facts lead one to believe that one of the conditions of existence in Purple Veld for non-grass plants is that they should possess either particularly well-developed root systems or some type of storage organ or a combination of the two.

These notes conclude the outline of secondary succession from the Ruderal Stage to the Grassland (Climax) Stage. As new grasses invade the Purple Veld or Climax Grassland community, and further progression results in a series of trees invading the grassland area.

5. PROTEA OPEN WOODLAND STAGE

The Protea Open Woodland community is one which covers fairly large, though localised areas in the Highveld of the Witwatersrand. Protea spp. are also locally abundant in the vicinity of Pretoria and on the Magaliesberg, Witwatersberg, Suikerbosrand and Gaterand.

The community typically consists of widely-scattered trees of Protea caffra Meisn., with a very sparse localised intermingling of Protea Rompelliae Meisn. The trees may attain a height of 25 feet but generally stand at a height of 15' to 20' and are situated in a ground-level flora of the Purple Veld type. The latter vegetation-type need not be

described again. It is essentially similar to true Purple Veld but is inclined to be more open, a fact which is due to the type of shallow, stony soil on which it usually exists. Other trees are rarely found within the community except in transition zones and are atypical of it.

Protea open woodland is typically found on the crests and higher slopes of mountain ranges and upon the crowns and upper slopes of the low undulating hills, characteristic of the Northern side of the Witwatersrand. The soil in such areas is extremely shallow and, as in the Kagaliesberg and Witwatersberg, the surface is often littered with loose stone and shale-flakes. Such areas are exposed to intense light and the full force of the wind, sun and rain. Temperatures are frequently extreme. The influence of fire on the sparse vegetation, particularly on mountain ridges is severe, though not as severe as on the denser, more inflammable vegetation in low lying plains. Water is apt to drain away with great rapidity. Such conditions demand that vegetation should be of the hardiest type. Glover is also inclined to this view. (Glover, 1, 1937).

This community has been observed growing on almost every possible aspect and upon soils derived from quartzites, shale, diabase, and granite, with a range in altitude from 4,900 to 5,700 feet. Generally speaking, however, the trees seem to favour the southern aspect of mountainous areas. (See Photo No.6).

Protea caffra and P. Roupelliae seem well equipped to live in such an environment. The tough, corky nature of the bark protects the trees to some extent from fire. They are drought resistant and their leaves are well able to stand up to severe frost and intense illumination.

I am inclined to the view that Protea Open Woodland existing on upper mountainous slopes, is a subclimax vegetation. In such areas, it is scarcely possible to conceive of any other type of vegetation succeeding it, since the environment

conditions are rigorous in the extreme end are likely to continue to be so. Soils will always be poor and shallow exposed ranges and upper slopes, since the forces of erosion are continually at work. Meteorological factors, it may be assumed, will remain the same.

Protea Open Woodland existing on low hills and upon slopes which are less steep than those mentioned above, however, is capable of undergoing change and of allowing some of the Scrub Climax Vegetation to enter. Conditions in these areas are less severe than described above and the soil is deeper.

In several instances, Protea Spp. found growing on mountain slopes were found mingled with a number of other tree species. An example of this mixed type of woodland may be seen at Nooitgedacht in the Magaliesberg, on the farm of Mr. Arthur Carey. The area has been fairly well protected from fire. Trees and seedlings of Acacia caffra, Combretum rotundifolia, Zizyphus mucronata and Vangueria infausta are quite frequently found. On the other hand, no Protea spp. seedlings were to be found in the denser Acacia-Other spp. scrub and mixed kloof bush communities nearby. It seems likely, therefore, that in areas where conditions are not too extreme and where the soil is not too shallow, Protea Open Woodland, will eventually give way to a mixed scrub climax vegetation.

6. TRUE CLIMAX MIXED SCRUB VEGETATION.

Relics of the Mixed Scrub Climax Vegetation are to be found locally throughout the Highveld area. The vegetation seldom rises to a height of more than 30 feet and presents a fairly level appearance. It may be very dense indeed when fully protected. Only two important strata are found within the structure of this vegetation type, a tall canopy stratum consisting of the crowns of various tree species and a ground level stratum, consisting of a number of annual herbaceous

plants and perennial geophytes. The colour varies according to the species present and the season of the year. In Spring, the scrub often assumes a vivid, light-green colour where Acacia spp. are dominant, fading to a duller green as the season advances. The presence of large numbers of such constituents as Euclea lanceolata, E. undulata and Chilianthus arboreus may impart a drab grey-green colour to the vegetation. The dominant species are Acacia caffra and Acacia horrida.

The most important members of this type of vegetation are listed below. The names marked with an asterisk indicate the species which are most frequently found. The numbers indicate the order in which the species are likely to appear.

Acacia caffra Willd.	v.f.-ab.	*	1.
A. horrida Hayne. = A. horrida Willd.	v.f.-ab.	*	1.
A. litakunensis Burch.	rare		
A. robusta Burch.	occ.-f.f.		1.
Asparagus aspera Linn.	l.ab.		
Agrimonia Eupatoria Linn.	l.ab.		
Asparagus sp. (large)	occ.		1.
A. spp. (small)	f.		
Bowiea volubilis Harv.	occ.		
Brachylaena discolor D.C.	occ.		1.
Carissa Arduina Lam.			2.
Cassine burkeana Sond.		*	1.
Celtis rhamnifolia Presl.		*	2.
Chilianthus arboreus A.D.C.		*	2.
Cussonia spicata Thunb.			1.
Dombeya rotundifolia Planch.			2.
Dovyalis Zeyheri Harv.			2.
Ehretia hottentotica Burch.		*	1.
Euclea lanceolata E.Mey.		*	1.
E. undulata Thunb.			1.
Fagara Magalis-montana Engl.		*	1.
Grewia flava D.C.			1.

Gymnosporia buxifolia (Linn.)Szysz.		*
G. polyacantha (Sond.) Szysz.		*
Helinus ovatus E.Mey.		
Heteromorpha arborescens Ch. & Schl.		
Hypoestes verticillaris R.Br.		
Lantana salvifolia Jacq.	occ.	
Lapeyrousia cruenta Baker.	v.occ.	
Leucas martinicensis R.Br.	l.ab.	
Maerua triphylla A.Rich.	v.occ.	
Olea verrucosa Link.	occ.-l.f.	*
Osyris abyssinica Hochst.	occ.	
Pappea capensis E. & Z.		
Pavetta sp.	occ.	
Pittosporum viridiflorum Sims.		
Plectronia mundtiana (Ch.& Schl.)Pappe		
Plumbago capensis Thunb.	v.occ.	
Rhoicissus cuneifolia (E.& Z.)Planch.	v.occ.	
Rhus Gueinzii Sond.	f.f.	*
R. cf. mucronata Thunb.	f.	
Royena pallens Thunb.	v.f.	*
R. Wilmsii Guerke.	v.occ.	
Sanseviera thrysiflora Thunb.	v.occ.	
Sarcostemma viminale R.Br.	v.occ.	
Secamone Alpini Schultes.	occ.	
Scolopia Zeyheri Sim.	occ.-f.f.	*
Senecio pentactinus Klatt.	l.v.ab.	
Sida sp.	occ.	
Tarchonanthus camphoratus Linn.	occ.	
Teucrium capense Thunb.	l.v.ab.	
Vangueria edonymoides Schweinf.	occ.	
V. infausta Burch.	occ.-f.f.	*
Zizyphus mucronata Willd.	occ.-v.f.	*

It has been seen from the discussion on the Grassland Climax and Protea Open Woodland stages that the Climax Mix Scrub vegetation may invade either community. I have alre

set down much of the scanty information I have at my dispos in connection with scrub constituents invading Protea Open Woodland.

The invasion of scrub types into Purple Veld, may be be gun by various species mentioned above and the process as compared with invasion of Protea Open Woodland, may be comparatively rapid. The time taken by scrub constituents to advance into open Purple Veld, is governed in a certain degree by various factors. The first of these is the prox mity and availability of supplies of scrub seed; secondly, the presence of termitaria (see Photos Nos 7 & 8) and third the occurrence of a small amount of disturbance such as oc asional trampling by oxen, after scrub seed has arrived on area. The first of the three factors above is perhaps the most important and is one of the biggest influences at work in determining the course of succession in its latter stag As has been noted by Story (1938) and Rose Innes (1.1937), many plants of the most advanced types have been observed grow quite well on the impoverished soils of fallow lands. Artificial re-seeding of old fallow lands has frequently been done with seed of advanced grass species and as Story (1938) points out, almost any plant can be made to act as a pioneer, always excepting such plants as would not grow in virgin soil on these areas. Acacia spps seeds have bee found to germinate and flourish on fallow soils at Franken So too, have grasses of the Purple Veld type.

All the above facts point to the availability and mobility of seed as being of the highest importance. (see Rose Innes 1937.1.). As most of the seeds of scrub types heavy, (See Seed Photographs Nos. 15-21) they depend for t distribution upon man, animals and birds. Palatability of scrub fruits is therefore also of great importance, especi with regard to pioneer types. Most of the pioneer species have fruits which are palatable either to man, animals or birds. Amongst these are Rhoicus pallens, Asparagus sp.

Euclea lanceolata, Ehretia hottentotica, Vangueria infausta, Gussonia spicata, Zizyphus mucronata. (See Seed Photograph No.15) Cassine burkeana. (See Seed Photograph No.20) Cassine Scolopia Zeyheri and Rhus spp.

Fruits of Royena pallens, Vangueria infausta and Ehretia hottentotica are frequently taken by man. Bews (1917) also states that the fruits of Euclea lanceolata and E. undulata are eaten by natives. Birds are largely responsible for the distribution of Cassine burkeana, Asparagus sp. Rhus spp. Gussonia spicata and possibly, Gymnosporia buxifolia and G. polycantha. I have observed baboon faeces containing the fruits of Zizyphus mucronata, in the Witwatersberg. Goats are frequently fed upon the seedpods of Acacia spp. in the bushveld areas, though it is unlikely that many seeds would survive as the pods are usually green when eaten.

With regard to the influence of termitaria on invasion of pioneer types into open grassland, it may be said that their presence is extremely important. I have already drawn attention to this fact (Rose Innes (1.1937). Bews (1917) states that birds flying over the veld naturally alight on the mounds and ---"this doubtless explains why a primary clump of thorn veld species is so often established on the site of an old termites' nest." At Frankenwald a high proportion of tree pioneer species (mostly Royena pallens), now invading the open grassland, are situated on mounds of living termites. The activities of the termites do not seem to harm the roots in any way. This was also noticed at Hekpoort when work on root bisects was in progress. Termite nests were found to be dotted all over the face of the river wall, from the surface to a depth of about 10', in some cases deeper. The roots exposed during the work were all untouched. The termites were fungus-growers but were not specifically determined. Murray (1937) found that roots of grasses were rarely attacked by termites.

In the scrub vegetation at Modderfontein, termites are

numerous, though no count was made to determine the number of nests in any given area. Murray (1938) states that " it will be noticed that as plant succession advances from the first stage (Conyza ambigua, Cynodon, Gnaphalium, etc.) to the Climax Stage (Purple Veld), the number of termite mounds increases." Unfortunately, this investigation was not followed into the scrub-covered areas. I am inclined to believe that the incidence of termite mounds in such areas would be even higher. Apart from their influence upon succession as centres of seed deposition, termitaria probably have a profound influence upon preparing the soil for the advance of succession. For instance it has been found (Murray 19 that the colloid content of termitarium soil is extremely high, as compared with that of the surrounding veld. Soil analyses made at Frankenwald in the Modderfontein scrub also show that the colloid content of soils increases as succession advances. This may be due in some measure to the activities of termites. Though it would be unwise to draw conclusions without a further extensive investigation, it seems possible or even probable, that both the reactions of termites and advancing succession upon the soil, are complementary and that as a result, succession is to some extent enabled to proceed further. In this connection it is interesting to note Murray's statement: "It can be concluded then, that the termites do not increase in abundance as a result of the presence of the actual plants themselves, but they do so as the surrounding conditions are changed by the plants. The writer feels that the most important change is in the texture of the soil. The soil particles appear to be bound together more closely by the root mats of the climax vegetation."

In dealing with the third factor mentioned above, the following point should be noted. Tree seeds deposited upon heavily grassed areas such as Purple Veld, finds themselves in an environment well suited to the growth of seedlings

but, in one respect, poorly adapted to germination requirements. Seeds have little chance of germinating unless, as in the case of numerous grasses, special mechanisms exist for burying the disseminules in the soil. The disseminules of scrub species mentioned above possess no such equipment and the seed must do its best to germinate upon the surface of the soil. This is wellnigh impossible except under conditions of slight disturbance. In areas where occasional grazing takes place, the disseminules may be trampled into the soil by the grazing animals and germination is ensured. In heavily overgrazed areas, it has frequently been noted that there is an extremely rapid invasion of Acacia spp. especially where seed is available nearby. This is due firstly to seed being available, secondly to the means being present of burying such seed in the soil, thirdly to the protection thorniness of the seedlings and lastly to absence of the destructive influence of fire (due to the lack of inflammable grass material in such overstocked areas) upon the young seedlings. Non-thorny types would not fare as well as Acacia spp. and other thorny types, upon heavily grazed areas, where cattle would soon trample them to death. In well-grassed areas, however, under conditions of occasional grazing and absence of fire, it is believed that seedling growth would be promoted, always provided the seeds were already present.

Among the first species to appear in grassland areas are Asparagus sp., Rhoicissus tridentata, Acacia caffra, A. karroo, A. robusta, Euclea lanceolata and Gymnosporia buxifolia. (See Photos Nos. 7-12) Very frequently, seedlings are found grouped or singly on the sides of termitaria, where they have been deposited by birds. (See Photos 7 & 8). In open veld, Asparagus sp. has been noted playing the role of pioneer. (See Photos Nos. 11-12). This may be expected since the juicy red fruits are just the type to be taken by birds. Also, birds frequently make their nests in

bushes of Asparagus sp. which are prickly and likely to ke away intruders. Spe[illegible]ens of Royena pallens have been observed to grow up through the branches of their Asparagu foster-parent and finally smother it. (See Photos Nos. 11 and 12) This has also been noticed in the case of Rhus cf. mucronata and Euclea undulata. (See Photos 11 & 12) The habitat within such scrub-nuclei rapidly undergoes a change. Grasses which were present are soon shaded out an disappear completely. The soil becomes covered with a den litter of rotted leaves which forms a moist bed, well adapted for the germination of seed of succeeding species. New species make their appearance in the scrub-nuclei thus formed and the scrub spreads outward over an ever-increasi area.

Asparagus sp. is by no means an essential part of the succession in this transition stage. Seedlings of Royena pallens, Euclea undulata, E. lanceolate and Gymnosporia buxifolia have frequently been found coming up in open veld Acacia caffra, A. karroo and A. robusta seedlings more oft appear to arise in this manner. (See Photos Nos. 9 & 10). The latter being of a thorny nature are well able to prote themselves from disturbance caused by grazing animals. Acacia robusta seeds appear to be capable of germinating a developing in the most extreme conditions such as are foun on old roads and areas totally denuded by overgrazing and termite activity. (See Photo No. 9).

Other species are also capable of acting as scrub pio though they are not so frequently found as those mentioned above and more often appear after them. The following spe fall into this group: Euretia hottentotica and Scolopia Zeyneri, (see Photo No.11) Vangueria infausta (usually on rocky outcrops), Gymnosporia polyacantha, Cassine burkeana, Chillianthus arboreus, Zizyphus mucronata (see Photo No. 7) and Rhus Queinzii. Rees (1917) speaking of the thornveld vegetation near Maritzburg states that in that area, Acacia

horrida (= A. karroo), Celastrus buxifolius (= Gymnosporia buxifolia), Vangueria infausta and others may act as pioneer though not very frequently.

Bews (1917) states that in Maritzburg, Chilianthus arboreus is not a pioneer but follows immediately after Acacia arabica Willd. var. Kraussiana Benth. which, in that area is the true pioneer. From his description of the Maritzburg thornveld, it is evident that tree succession in the latter area and at Frankenwald are very similar indeed. At Modderfontein near Frankenwald, where the scrub vegetation is quite extensive, Chilianthus arboreus is often found deep within the scrub and does not appear to act as a true pioneer. At Hekpoort in the Witwatersberg, however, there are definite indications that this tree acts as a margin pioneer to dense mixed scrub. A belt of these trees may be seen extending round the edge of a large scrub community, the youngest specimens being on the outside and the older on the inside of the belt. The latter appear to be dying out. Within this belt seedlings of Rhus Gueinzii, Acacia caffra and A. eriadenia Benth. were quite frequently found.

Senecio pentactinus, a tall herb, also seems to act as a scrub-margin pioneer in some instances. This has been noticed on Frankenwald East. The death of the plants in winter brings a heavy fall of dead organic material to the soil.

Soon after the arrival of the first few trees in the grassland, a second stratum of the scrub vegetation makes its appearance. This is the ground-level herbaceous flora of scrub areas. The plants consist chiefly of annual herbs with an intermingling of geophytes. Typical members of this stratum are Hypoestes verticillaris, Teucrium capense, Lemosa Martinicensis, Lantana salvifolia, Sanseviera thyrsiflora, Lapeyrousia oreunta, Asparagus sp. (small), Achyranthes asper, Galinsoga parviflora, Sida sp., Agrimonia eupatoria (in moister areas).

In well protected areas certain climbing plants may make

their appearance, such as Rhoicissus cuneifolia, (see Pho No. 13) Sarcostemma c.f. viminale, Helinus ovatus, Plumba capensis, Secamone alpini. I have not observed such plan killing the scrub trees upon which they support themselve as described by Bews in the Maritzburg area.

The final change which takes place in this scrub cli type comes with the entrance of such species as Fagara megalismontana, Brachylaena discolor, Tarchonanthus camph atus, Celtis rhamnifolia, Olea verrucosa, Doryalis Zeyhe Dombeta rotundifolia, Heteromorpha arborescens, Maerua t phylla, Pappea capensis, Osyris abyssinica, Pavetta sp., Pittosporum viridiflorum, Plectronia mundtiana, Royena hi and others. In the scrub vegetation of this area, such ies are sparsely scattered throughout, with occasional la aggregations of the more hygrophilous types in the vicini of rocky outcrops. Although it is quite possible that su a vegetation would in time, cover most of this area now occupied by grassland, it seems doubtful whether it would ever give way to such a luxuriant type of mixed scrub as found at Hekpoort, or on undisturbed hills and koppies in Klipriversberg. I feel that the mixed scrub type of vege described above may safely be regarded as the true climax of the Frankenwald area. This concludes the observations made upon the course of secondary succession upon fallow lands in the Frankenwald area.

CHAPTER II.

SOME FACTORS DETERMINING THE COURSE OF SUCCESSION.

SECTION A.

A COMPARISON OF THE HABITAT FACTORS OF FOUR TYPICAL COMMUNITIES OCCURRING IN SECONDARY SUCCESSION.

The communities chosen for this investigation, are fo which have been described above and which are typical of secondary succession on fallow lands in this area. It w decided, however, that one of these communities - the mo stable and most abundantly found - would have to be used a standard of comparison for the remaining three. The re for doing this is, that soil is notoriously difficult to analyse when a single figure representing - for instance is required to express the pH of the area as a whole. An ses may differ very widely indeed within a single communi and even more so when analyses are made at widely differe points within that community. Since soil analyses can be expected to differ widely within a single community, then results obtained from totally different and at the same t widely separated communities, would be quite useless for purposes of comparison. It is the comparative results wh are required here.

Purple Veld was finally chosen as the standard since it fills both the requirements mentioned above. The remain three communities were selected so that in each case they were immediately adjacent to an area of typical Purple Ve existing under almost exactly similar conditions. The areas compared are therefore as follows:-

1. Cynodon-Eragrostis-etc. Fallow / Adjacent Purple
2. Hyparrhenia hirta-etc. Fallow / " "
3. Climax Mixed Scrub / " "

The advantage of comparing results under this system

that the results obtained from the standard type may be as a yard stick, against which results from the other ar may be compared and assessed.

The first two of these areas mentioned above, are situated on Frankenwald. The third lies at Modderfonte Unfortunately the soil in the latter area is derived fr types of rock - granite and quartzite, while at Franken the soil is derived purely from granite. This area, ho was the most suitable to be found in the vicinity and n be accepted.

Discription of Areas Chosen for Comparison.

1) Both adjacent types exist on the same soil. Th slope - a very slight one, is the same in each case. T Purple Veld area is on the lower side. There are no ro outcrops or noticeable seepage areas nearby. Samples w taken in each type from a belt 15 yards wide on either s of the line of contact between the two areas.

(a) The fallow area supports a vegetation typical o Primary Grass Stage already described. It consi chiefly of the following species: Cynodon dactyl Eragrostis curvula, E. chloromelas, E. gummiflu E. chalcantha and Rhyncelytrum repens. The la last ploughed in 1920 and is thus 16 years old. was, however, an old fallow before that time wa previously last ploughed in 1915. On the secon occasion, it was only ploughed once and was ple to maize. No fertiliser has ever been used o

(b) The adjacent Purple Veld is slightly atypical i the ground appears to be moister than is usual. (This was borne out by holards). Helichrysum a nitens occurs in small localised patches. These avoided when sampling. The vegetation otherwise consists of typical Purple Veld species.

2) Both vegetation types exist on the same soil an the same general slope. Purple Veld is on the lower si

There are no rocky outcrops or seepage lines nearby. Samp were taken from a belt 15 yards in width, on either side of the line of contact.

(a) The fallow area supports a vegetation typical of the Secondary Grass Stage. It is made up of clump of Hyparrhenia hirta scattered irregularly throug vegetation consisting chiefly of Cynodon dactylon Rhynchelytrum repens and Eragrostis spp. In all c in this area, sampling was carried out only withi the clumps of Hyparrhenia. The land is stated to 29-30 years old and was originally sown to Kennar upon which cattle were grazed. It is unknown fro how long the land was in use. No fertiliser was used

(b) The adjacent Purple Veld area was typical of its kind.

3) Both vegetation types are found on the same type o soil and on the same gentle slope. In this case, however, the line of contact runs up and down the slope, not across as in the case of 1. and 2. There are no outcrops or seep areas apparent in either type. Samples were taken from a belt extending to a distance of 30 yards on either side of the line of contact.

(a) The scrub vegetation has been undisturbed for a long time. Areas occur where Chilianthus arboreus is locally abundant, otherwise the vegetation can said to be typical. Samples were taken from the vicinity of a large number of species representati of the area.

(b) The Purple Veld is typical. An old denuded road r through the area but this was avoided when samples were taken.

Soils of the areas described above were analysed for t following properties:-

1. Polard.

2. Organic Matter Content.

3. Colloid Content.
4. Maximum Water Retaining Capacity.
5. Permeability.
6. Nitrogen Content.
7. pH.

Sampling Methods.

In the case of analyses for Organic Matter Content, Colloid Content, M.W.R.C., and Nitrogen Content a composite sample was taken from each of the six areas involved. This was done in the following manner. Thirty randomised pits were dug to a depth of six inches in each of the six areas. A spadeful of the soil lying between depths of 6" and 8" levels was taken from each pit and placed in a sack. Six very large composite samples, representative of soils lying between depths of 6" and 8" in the six respective areas, were thus obtained. The 6" - 8" layer was chosen firstly, because quartz pebbles are likely to occur below this depth and secondly, because a high proportion of plant roots (excluding those of scrub species) are found in the vicinity of this soil horizon. Thirty samples were thought to be sufficient to give significant results. Each large composite sample weighed about 300 pounds.

In order to obtain a high degree of homogeneity in each composite sample, the soil was mixed in the following way. Each sample was spread out separately upon a concrete mixing floor and thoroughly mixed by two men for about 20 minutes, following the same method which builders use to mix concrete. In order to reduce the size of samples and also to mix them further, a quartering method similar to that described by Cumming and Hay (1934) was used. Each composite sample was thus thoroughly mixed and reduced to a size large enough to provide samples required for the various analyses. Finally, each of the six composite samples was sieved through a 20 mesh-per-inch sieve, thoroughly dried at a temperature of about 70°C., and bottled.

The method of soil sampling used in connection with Holard and pH analyses will be described separately below.

1. Holard Analyses.

Sampling was done in the following manner in each of the six areas. A pit about 8" square was dug to a depth of 8". Soil was then quickly scooped out from the side the pit between the 6" and 8" levels, straight into small metal cylinders. An airtight top was fitted on immediately It was found possible to avoid including small stones in sample, by scraping the soil away in moderately thin layers ing the cylinder itself to scoop out the soil.

40 samples were taken from the Cynodon/Purple Veld

20 samples from each vegetation-type.

80 samples were taken from the Climax Scrub/Purple

40 samples from each vegetation-type.

40 samples were taken from the Hyparrhenia hirta/Purple veld area

20 samples from each vegetation type.

The sampling was done at the end of winter with the purpose of obtaining equal conditions in all 6 areas. Rain fell two days before sampling commenced but the amount (0.07" and 0.01") was so small that it did not penetrate deeper than 3" and the soil at the 6" - 8" depth was unaffected.

The method used for holard determinations was the usual one, whereby holard is expressed as a percentage of the weight of soil used and is calculated as follows:-

$$\text{\% water} = \frac{\text{loss on drying} \times 100}{\text{dry weight of soil used.}}$$

The average holard for the soils in each of the six different areas was as follows:-

A.	Cynodon-Eragrostis etc. Fallow	= 3.70%
B.	Adjoining Purple Veld	= 7.51%
C.	Hyparrhenia hirta etc. Fallow	= 5.50%
D.	Adjoining Purple Veld	= 5.32%

E. Climax Scrub Vegetation = 5.76 %
F. Adjoining Purple Veld = 4.65 %

A statistical analysis of the significance of differen in percentage holard in the three groups showed that:-

(i) The difference between A and B is significant,
(ii) " " " C " D is not significant,
(iii) " " " E " F is significant.

It was expected that Purple Veld would have a higher percentage holard than Hyparrhenia hirta fallow. This was not so but the difference between the two areas is so slight as to be insignificant. I feel that an analysis made over a larger area with a greater number of samples would probably show that Purple Veld actually has a higher percentage holard.

The suspected presence of an unusually moist area in Purple Veld was varified by the results of analysis.

Conclusions: It is concluded that percentage holard of soils increases as secondary succession advances. (See Histogram No.1). This is probably due to an increase in cover in higher successional stages lowering temperatures at the soil surface, increasing relative humidity and decreasing evaporation and the effect of dessicating winds. It may also be due in some measure to decreased run-off. These results agree with those obtained by Story (1938) in fallow lands and Themeda veld.

2. Organic Matter Content Analyses.

Sampling was carried out as described above. Material for analysis was extracted from the composite samples of the six areas described. In order to reduce the possibility of experimental error to a minimum, ten samples were taken for analysis from each of the six composite soil samples. The percentage organic matter content was determined by the usual method of ignition and was expressed thus:

Percentage organic matter content = $\frac{\text{loss on ignition}}{\text{dry weight of soil}}$

Care was taken to thoroughly ignite all crucibles used in the determinations and the soils themselves were ignited for not less than four hours. The average result was calculated for each set of samples. Results were as follows:-

A.	Cynodon-Eragrostis-etc. Fallow	= 3.06 %
B.	Adjoining Purple Veld	= 3.77 %
C.	Hyparrhenia hirta-etc. Fallow	= 3.35 %
D.	Adjoining Purple Veld	= 3.61 %
E.	Climax Scrub Vegetation	= 5.70 %
F.	Adjoining Purple Veld	= 3.88 %

The results show that:

(i) Cynodon veld soil has less organic matter than Purple

(ii) Hyparrhenia veld " " " " " "

(iii) Purple Veld soil " " " " " Climax Scrub

(iv) Purple Veld maintains a comparatively consistent st

I believe that although the differences are small they are significant, especially when this fact is taken into consideration, that the organic matter content of soils in dry open veld in these areas is generally very low. If we take the average of figures for three Purple Veld stages involved, we see that organic matter content increases from Cynodon fallow to Climax Scrub as follows:- 3.06%, 3.36%, 3.75%, 5.70%. As one would expect, the biggest increase takes place between Purple Veld and Climax Scrub.

Conclusions:

There is a slight but clear-cut increase in the percentage organic matter content of soils, consistent with the advance of secondary succession. The biggest increase occurs with the change of grassland to scrub vegetation. (See Histogram No.2). This is probably due to a very slight increase in deposition of organic matter from denser foli

of more advanced successional communities. Also, temperature of the soil is decreased as cover increases and this brings about reduction of incineration of organic matter which is known to occur in cultivated lands. It is probable, too, that less organic matter - existing in the colloidal state - is leached away from the less permeable soils of higher successional stages. (See also Histogram No.5 and analysis results for Paragraph 5). The results tally with those of Story (1938) and Russell (1929) both of whom found a decrease of organic matter in cultivated areas.

3. Soil Colloid Content Analyses.

Sampling was carried out as described above. In order to reduce experimental error to a minimum, ten samples were taken from each composite sample for analysis. The results of individual analyses, however, showed that half this number would have been quite sufficient. Samples of 100 gm. weight were used.

The analytical method used was that of Bouyoucos (1930). The results are expressed as the percentage colloid left in suspension after a soil sample has been specially dispersed and allowed to stand in a special cylinder for a period of 10 minutes. The average figure for each group of determinations was calculated - with the following results:-

A.	Cynodon-Eragrostis-etc. Fallow	= 16.14 %
B.	Adjoining Purple Veld	= 18.92 %
C.	Hyparrhenia hirta-etc. Fallow	= 15.61 %
D	Adjoining Purple Veld	= 16.78 %
E.	Climax Scrub Vegetation	= 24.37 %
F.	Adjoining Purple Veld	= 19.3[illegible] %

From the results above, it will be seen that:-

(i) Cynodon veld soil contains less colloidal matter than that of Purple Veld.

(ii) Hyparrhenia veld soil contains very little less colloidal matter than that of Purple Veld.

(i do not claim that the difference is significant but in view of the facts that the composite sample from which soil was extracted for analysis, consi of no less than 30 large, well-randomised samples that individual results were remarkably consisten it is possible that the result above is signific The difference lies in the direction which would expected.

(iii) Climax Scrub soil has a higher percentage colloid content than Purple Veld soil.

(iv) Colloid content of soil in Purple Veld areas may v quite appreciably.

Conclusions:-

It may be seen from the above figures the percentage colloid content of soils increases with the advance of se dery succession. The biggest difference again lies betw the soils of Purple Veld and Climax Scrub Vegetation. (S Histogram No.3). These results are probably closely re with the increase of organic matter and decrease of perme lity (See results for Paragraphs 2 and 5 and Histograms N 2 and 3.) in vegetation advancing towards the climax. A certain amount of colloidal matter in the soil is presumab organic in origin and this, together with inorganic soil colloids, would tend to be leached out of the highly perme soils encountered in the lower steges of secondary succes on fallow lands.

4. Soil Maximum Water Retaining Capacity Analyses.

The soil was sampled in the same way described above The usual laboratory method was used for determination of M.W.R.C. It may be argued that the field method would yi more accurate results. In this case, however, the attain of a high degree of accuracy in a large number of individ determinations in the field was not so desirable as a ear of easily determined, reasonably sound results which woul

used for purposes of comparison. The time and labour in
in carrying out a large number of determinations in the
field therefore did not appear to be justified. The res
obtained by the laboratory method have proved quite adeq
for the purpose of comparing the M.W.R.C. of soils in th
various areas under discussion.

Five determinations were made on soil extracted fro
each of the six composite samples. The average figure w
calculated from each set of five examples. M.W.R.C. was
taken to mean the amount of water capable of being abso
by the soil, expressed as a percentage of the dry fine s

e.g. Percentage M.W.R.C. = $\frac{\text{Water obtained by saturate}}{\text{Dry soil used}}$

~~x 100~~.

The results obtained are as follows:-

A.	Cynodon-Eragrostis-etc. Fallow	- 28.92 %
B.	Adjoining Purple Veld	- 34.31 %
C.	Hyparrhenia hirta-etc. Fallow	- 33.06 %
D.	Adjoining Purple Veld	- 33.76 %
E.	Climax Scrub Vegetation	- 43.80 %
F.	Adjoining Purple Veld	- 34.25 %

It will be seen from the above results:-

(i) M.W.R.C. of Cynodon veld soil is lower than that o
Purple Veld soil.

(ii) M.W.R.C. of Hyparrhenia veld is slightly lower tha
that of Purple Veld soil.

(iii) M.W.R.C. of Purple Veld soil is lower than that of
Climax Scrub soil.

The results are what were expected and with the pos
exception of those for Hyparrhenia and Adjoining Purple
all appear to be significant. As before, the difference
between Purple Veld and Scrub soils is the greatest.

Conclusions:

M.W.R.C. of soils increases as secondary succession
fallow lands advances toward the climax, with the lowes
difference existing between M.W.R.C. of Purple Veld and

Climax Scrub soils. (See Histogram No.4). These results are probably closely correlated with the increase of organic matter and colloid content of soils upon areas whose vegetatio is advancing toward the climax. (See Paragraph 3 and Histogram No.3). Colloidal particles have the power of adsorbing water and when the colloidal content of a soil is high, more water will be retained. These results may also be closely correlated with those for permeability. (See Paragraph 5 and Histogram No.5). The permeability of Climax Scrub soils is extremely low and that of Cynodon veld soils,high. This is probably partly due to high M.W.R.C., colloid content and organic matter content of Climax Scrub soils and low M.W.R.C. organic matter and colloid content of Cynodon veld soils. (See Paragraphs 2 and 3 and Histograms Nos. 2 and 3). These results do not agree with those of Story (1938), who found that M.W.R.C. of fallow soils was higher than that of Themeda veld soils.

5. Soil Permeability Tests.

Since Story (1938) had described the difficulty of using the Flory method (Flory 1936), it was decided to use the method described by Burger (1923). The steel cylinders used were in each case beaten into the soil by laying a block of wood evenly across the rim and driving it in by blows from a 15 lb. hammer. All the tests were made upon the six different areas during a single day. In the case of scrub soils several tests were not concluded as the water in the cylinders had not reached ground level by long after nightfall. The soil beneath the cylinders was dug out after they had been extracted but nothing was found which could have impeded percolation in any way. In these cases the time when the cylinders were extracted was noted and regarded as the total time taken for the water to disappear. If I had been able to conclude these tests, the results would have been even more significant than as stated below.

Thirty tests were made in Cynodon veld soil and a similar number upon adjoining Purple Veld soil. Twenty-two tests were made on Hyparrhenia veld soil and twenty-one upon adjoining Purple Veld soil. Twenty-three tests were made upon scrub soil and a similar number upon the adjoining Purple Veld soil. No rain had fallen for several days and none fell while work was in progress. The tests in all cases were made upon the top 4 inches of soil. The average time taken for the water to percolate was calculated from each set of tests and the results are as follows:-

A.	Cynodon-Eragrostis-etc fallow	= 23 min.	2 sec.
B.	Adjoining Purple Veld	= 35 "	6 "
C.	Hyparrhenia hirta-etc. fallow	= 16 "	51 "
D.	Adjoining Purple Veld	= 31 "	15 "
E.	Climax Scrub Vegetation	=114 "	24 "
F.	Adjoining Purple Veld	= 39 "	29 "

The differences in the above results were statistically examined in order to discover if they were significant. It was found that the differences between A and B, C and D and E and F, were all significant. The summarised results of these tests are as follows.-

(i) Percolation-rate is faster in Cynodon veld soil than in Purple Veld soil.

(ii) Percolation-rate is faster in Hyparrhenia veld soil than in Purple Veld soil.

(iii) Percolation-rate is faster in Purple Veld soil than in Climax Scrub soil.

(iv) Percolation-rate is fairly consistent in Purple veld soils.

I can offer no explanation why the rate of percolation in Hyparrhenia veld soils should be faster than in Cynodon veld soils. There is also a slight difference in the Purple Veld standard for these two areas but it is not big enough to make any large difference to the facts. Even if the two fallow veld figures were proportionately adjusted to the Purple Veld figures, the percolation rate for Cynodon veld

would still be faster than that for Hyparrhenia veld. The answer to the problem may lie in the inaccuracies of the method or in localised atypical soil conditions. It was expected that the percolation rate for Hyparrhenia veld soil would have been slightly slower than that for Cynodon veld soil. Apart from this presumed defect in results, the figures still show a tendency for percolation rate to increase as succession advances toward the climax.

Conclusions:

In spite of the fact that percolation takes longer in Cynodon veld soil than it does in Hyparrhenia veld soil, it is concluded that the rate of percolation in soils increases - or permeability decreases - as secondary succession on fallow lands advances toward the climax. (See Histogram No.5). It is probable that this finding is closely correlated with the fact that colloid content, organic matter content and percentage M.M.R.C. of soils all increase as secondary succession advances toward the climax. (See Paragraphs Nos. 2, 3 and 4 and Histograms Nos. 2, 3 and 4). Reasons for making this statement have been discussed in previous paragraphs. The results obtained in these tests agree with those obtained by Story(1938) upon fallow lands and Themeda veld in the Vereeniging district.

6. Soil Nitrogen Content Analyses.

The method of sampling employed has already been described. Samples for analysis were taken from six composite samples representing the six areas previously described. The standard Kjeldahl method was used for determining the nitrogen content of these soils. A catalyst, consisting of a mixture of 9 parts of K_2SO_4 to 1 part $CuSO_4$, was used to aid digestion. The results given, express the percentage nitrogen present in the soil. Three samples from each of the six composite samples were taken for analysis and the average result was calculated for each set of analyses. The results were as follows:-

A. Cynodon-Eragrostis-etc fallow = 0.0716 %
B. Adjoining Purple Veld = 0.1008 %

C. Hyparrhenia hirta-etc. fallow = 0.0939 %
D. Adjoining Purple Veld = 0.1154 %

E. Climax Scrub Vegetation = 0.1467 %
F. Adjoining Purple Veld = 0.1256 %

The results above show that:-

(i) Cynodon veld soil contains less nitrogen than Purple Veld.soil

(ii) Hyparrhenia Veld " " " " " " " "

(iii) Purple Veld " " " " " Climax Scrub soil

It will be seen that there is a distinct increase in soil nitrogen as secondary succession advances toward the climax. The gradient is smooth but there is a much larger increase in percentage nitrogen between Purple Veld and Climax Scrub than any in the other two areas.

Conclusions:

The percentage of nitrogen in the soil increases as secondary succession on fallow lands advances towrad the climax. The greatest increase appears between the last two successional stages, Purple Veld and Climax Scrub. (See Histogram No.6). This result is what was expected. The increase in soil nitrogen with the advance of succession may be due in some measure to an increased deposition of organic matter occasioned by the increase in vegetal cover. As has already been stated in the discussion on the Climax Scrub type, it may also be due to the presence of a high proportion of termitaria in soils of the higher stages of succession. Murray (1938) points out that though the nitrogen content of soil composing termitaria is nearly double that of the surrounding soils, the nitrogen is unavailable to plants while the termites are alive but is probably liberated when such termitaria disintegrate and become oxidised.

7. pH and Titration Acidity of Soils: Analyses.

As pH of soils may change when soils are stored, samples extracted from the composite samples could not be used for these determinations. A series of six small composite samples (one composite sample from each area) were taken by means of a soil-borer. A total of 30 small samples were taken from each of the six areas described and these were thoroughly mixed together, dried at ± 70°C., and sieved to form the six composite samples. When extracting each individual sample, the borer was thrust into the soil to a depth of 8". Each sample consisted of that portion of the soil-core lying between the 0" and 8" marks. Determinations were carried out well within 24 hours of the conclusion of the sampling.

An attempt was made to determine the pH of the six samples by using the indicator method with Merck's Universal Indicator. Accuracy of ± 0.25 pH is claimed for this method and this was thought to be quite sufficient for comparative purposes.

100 grams of soil was taken for analysis from each of the six small composite samples and placed in separate flasks to which were added 150 cc. KCl solution. The flasks were stoppered and shaken vigorously for 1 hour, after which the solutions were filtered off into Erlenmeyer flasks. The method of extraction is the same as that described by Lemmermann (1924). 8 cc. of each solution was then pipetted out into a white porcelain dish to which was added 2 drops of the indicator. The colours of the samples were compared with the standard colours on the colour-card provided. Estimations were done by two workers, working independently. In all 6 cases estimations were found to agree within 0.2 pH. Results were as follows:-

	Estimations.	
	Dr. Weimann	Rose Innes.
A. Cynodon-Eragrostis fallow	pH 4.2	pH 4.3
B. Adjoining Purple Veld	4.4	4.4
C. Hyperrhenia hirta fallow	4.3	4.3
D. Adjoining Purple Veld	4.4	4.3
E. Climax Scrub Vegetation	4.6	4.5
F. Adjoining Purple Veld	4.2	4.3

On consultation it was agreed that 4.6 would represent a better determination for E. Except in the case of E., whose pH was significantly higher than that of the remaining samples, the results appeared to be very inconclusive. It was therefore decided to determine the titration acidity of the soils of the various areas (using the same solutions as prepared for the estimation of pH) in order to obtain a check on the pH results. The reference to the method is given by Weissmann (1926).

The solutions obtained from the extraction were titrated against 1/50 N NaOH solution and the results were expressed in terms of ccs. of 1/10 N NaOH. Measured titration acidity includes also the so-called "exchange acidity", i.e. the acid due to hydrolysis of iron and aluminium salts liberated by base exchange through reaction with KCl.

Two separate sets of titrations were made, the first with 100 cc. of solution, the second with 50 cc. The latter was found to give a much clearer indication of the end-point. The results obtained by this method were found to be perfectly satisfactory for purposes of comparison.

The results obtained were as follows:-

	Set I.	Set II (x 2)	Average
A. Cynodon-Eragrostis-etc fallow	2.28	2.19	2.24
B. Adjoining Purple Veld	1.95	2.05	2.00
C. Hyparrhenia hirta-etc, fallow	2.45	2.59	2.52
D. Adjoining Purple Veld	1.62	1.70	1.66
E. Climax Scrub Vegetation	0.24*	0.19	0.19
F. Adjoining Purple Veld	2.31	2.45	2.38

(* = spoilt determination)

Determination E. for Set I was spoilt. The results show that:-

(i) Cynodon veld soil contains more acid than that of Purple Veld.

(ii) Hyparrhenia " " " " " " " " "

(iii) Purple " " " " " " " " Climax Scrub.

(iv) " " " " differs considerably in acid content.

It will be seen that the acid content of soils decreases steadily as vegetation approaches the climax. The gradient seem to be fairly smooths but a big difference occurs between Purple Veld and Climax Scrub communities. These results agree well with those of Story (1938) who found that the pH of fallow soils in the Vereeniging area are consistently lower than pH of natural veld soils.

Conclusions:

It is concluded from these results that soil alkalinity increases - or soil acidity decreases - as secondary succession upon fallow lands advances toward the climax. (See Histogram No.7). There is a clear-cut gradient. It is concluded that on the basis of these results and those obtained by Story (1938) at Vereeniging, pH values fall in soils which undergo cultivation and that this is probably due to leaching taking place in the highly permeable soils of fallow lands. (See Paragraph 5 and Histogram No.5).

This concludes the investigation into soil habitat factors in various stages of succession. It was found impossible to carry out an analysis of the aerial habitat factors in these areas owing to the high degree of replication of instruments and workers necessary for such an investigation. Certain conclusions, however, have been drawn from results obtained by Story (1938) in his comparative investigation of the habitat factors on fallow lands and natural veld in the Vereeniging district.

B. Evaporating Power of the Air and Evaporativity.

Story states that on the basis of daily readings from Livingston-Thone atmometers (Livingston 1915, 1935. Thone 1924) all readings on black and white atmometers showed a much greater value in fallows than in the edge veld. He concludes that this is due to the lack of cover and consequently to increased insolation in fallow soils and the increased effect of wind on poorly covered areas.

It is highly probable that readings of this type on the areas included in my investigations would give similar results and that they would indicate a decrease in evaporation from soils as secondary succession on fallow lands advanced toward the climax. Climax Scrub, which in summer has two fairly well-defined vegetal strata - the canopy stratum protecting the soil from great insolation and the herbaceous ground-level stratum protecting the soil from the effect of wind - would probably show a much greater reduction in evaporation than any other area.

9. Light.

Story's results, obtained from readings of the Eder Hecht Photometer described by Phillips, Scots and Hoagridge (1931) and the Weston Cell, show that the values for natural Themeda veld were roughly half as high as those for fallow lands in the Vereeniging area. I feel that if readings of this nature were carried out in the vegetation types investigated here, the results would show a steady decrease in light intensity as succession advanced toward the climax. This is obvious from the nature of the changes occurring in the cover. The biggest difference would definitely occur between the Purple Veld and Scrub Climax vegetations.

10. Humidity.

Story's results - obtained from hygro-thermograph readings, showed that fallows were found to be on the average drier by about 10% throughout the year. It is expected that similar results would be obtained in the areas investigated here and that humidity would increase as secondary succession advances towards the climax.

Summarised Findings on Chapter I, Section A.

(i) Percentage holard of soils increases as secondary succession advances.

(ii) Percentage organic matter increases as secondary succession advances.

(iii) Percentage colloid content increases as secondary succession advances.

(iv) Percentage M.W.H.C. of soils increases as secondary succession advances.

(v) Permeability of soils decreases as secondary succession advances.

(vi) Percentage nitrogen content of soils increases as secondary succession advances.

(vii) Acidity of soils decreases as secondary succession advances.

Observations based on the results obtained by Story (1938) in the Vereeniging district, show that it is likely that:-

(viii) Evaporation from soils decreases as secondary succession advances toward the climax.

(ix) Light intensity under foliage decreases as secondary succession advances toward the climax.

(x) Humidity under foliage increases as secondary succession advances toward the climax.

Final Conclusions on Chapter I, Section A.

(i) Increases in cover and holard, consistent with advancing succession, appear to be interdependent and intimately related to decrease in evaporation from the soil. It is probable that the increase in holard is to some extent responsible for the invasion of species of a more hygrophilous type. Observations in the field, however, show that many advanced species such as Trachypogon plumosus once having established themselves upon fallow soils, will thrive in those areas. (See Story, 1938; Rose Innes, 1, 1937). This fact

seems to belie the probability stated above. The importance of high percentage hoisard in more advanced stages, however, may lie in increasing the chances of survival of plants in the most critical stage of their existence - i.e. immediately after germination and before their roots have been able to reach a constant supply of water.

(ii) The organic matter content of soils increases as succession advances. This fact does not cause succession to advance but is rather a result of advance in succession. It may of course, prepare the way to some small extent for the invasion of species belonging to higher stages, but it is not believed to be such an important factor in causing an acceleration in the advance of succession as might be supposed. Increased organic matter content of soils manifests itself chiefly in increased plant growth. Numerous experiments conducted on Government experimental stations bear this out. Generally speaking, however, the organic matter content of soils in this area is so small that such minute increases as have been recorded in the results would bring about little difference in growth and consequently very little difference in accelerating the advance of succession.

(iii) Increases in colloidal matter in the soil are relatively small and at most, do not, according to these results, vary by more than 4% between Cynodon veld and Purple Veld soils. It is not wholly true to say that increasing colloidal content of the soil is responsible for accelerating the advance of succession. The soil colloids increase as a result of increased cover, greater deposition of organic matter and reduction of permeability due to the binding operations of roots. It is concluded therefore that although an increase in soil colloids may in some measure prepare the way for the invasion of successionally higher plant types, it does not have any marked effect upon increasing the rate

of advance of succession. This seems all the more obvious when it is observed that the increase in soil colloids is not more than 4% between fallow soil and soils of climax grassland. Further, from observations in the field and re-seeding experiments, it seems likely that if grasses of more advanced stages could be successfully established upon fallow soils of comparatively low colloid content, they would thrive almost as well if not just as well as they would thrive upon virgin soils of slightly higher colloid content. The same is also probably true of organic matter content of soil.

(iv) The percentage M.W.H.C. of soils has been shown to increase by as little as 5% - 6% between soils of the Primary Grass Stage and those of Climax Grassland. The big increase - as also in the case of other soil constituents - has been shown to take place between climax grassland and Scrub, which from the point of view of pasture farming, is unimportant. Increase in percentage M.W.H.C. is not responsible for accelerating succession. Percentage M.W.H.C. increases with increase in organic matter and colloid and decrease in permeability, all of which change as a result of increasing cover - due to advancing succession. Increased percentage M.W.H.C. has some small effect upon preparing the way for the invasion of successionally higher types but increases are so small that it is unlikely that this results in any significant acceleration of succession.

(v) Well-defined differences appear in the percolation rate of soils in fallows and Purple Veld. This factor may have an appreciable effect upon succession, in that several other factors are affected by it - e.g. soil salts and pH, organic matter and colloid content and also indirectly, holard and M.W.H.C. This factor therefore may be of quite appreciable importance in that its effects represent the sum of the effects of the factors mentioned above. Until

permeability is reduced by increased root penetration and consequent binding of the soil, the soil has little chance of regaining its lost reserves of organic matter, colloids, and mineral salts.

(vi) The increase of nitrogen content between fallow soils and Purple Veld soils was observed to be very small indeed - a difference of only 0.054%. This increase is due almost wholly to increased deposition of organic matter as a result of increased foliage. The minute increase in nitrogen in the soil which manifests itself chiefly in increased plant growth can hardly be considered responsible for any very appreciable acceleration of succession.

(vii) The relatively high acidity of fallow soils is considered to be due to the high permeability of those soils and consequent leaching out of alkaline mineral salts. (It will be noticed that high acidity and high permeability are closely related in the results given in Paragraphs 7 and 5). Acidity would therefore appear to some extent to be an expression of permeability and decreased permeability is due solely to increase in root penetration. This decreasing acidity seems to be indirectly dependent upon advance in succession, not the reverse. As in other cases, however, decreasing soil acidity may to some extent pave the way for an invasion of advanced types.

(viii) On the basis of Story's observations, it can be seen that the density of plant cover has a big effect on evaporation, which is another instance of increase of vegetal cover affecting habitat conditions. Decreased soil evaporation must have a direct result upon holard and indirectly paves the way for invasion of higher types.

(ix) From many field observations made in 1937 (Rose Innes 1, 1937, p. 33) and since, and from the results obtained

by Story (1938) on screening experiments, it is concluded that certain plants of the primary stages of secondary succession have no chance of surviving any appreciable decrease in intensity of illumination. Decreases in light intensity occasioned by increased foliage in an advancing succession, appear to be largely responsible for causing the disappearance of several species of the Primary Grass Stage - e.g. Aristida conneata and Eragrostis curvula. Cynodon dactylon, however, exhibits extreme tolerance. (See Story 1938). Decreased light is again a direct result of an increasing density of foliage in an advancing succession.

(x) Increased humidity in well-covered areas is noted by Story (1938). This is again a result of changes taking place in the vegetal cover of the earth.

In conclusion I should say that although none of the investigations above point to any one factor having an appreciable effect upon accelerating succession, the total effect of these factors upon vegetation and soil which has advanced a little way from the ruderal stage, is probably to prepare the soil in some slight degree for the invasion of more advanced species. The effect of these factors is by no means all-important in promoting the advance of succession. The habitat factors outlined above (and applied to this type of succession in particular) do not demand that any one community should remain more or less static until such time as certain soil deficiencies have been made good - although this must be a contributory cause to certain successional stages remaining more or less stationary for considerable periods of time. The important points in connection with the acceleration of succession appear rather to be bound up with such problems as root development, seed viability, parasitism and non-development of seed, seed weight, time of germination, availability and mobility of seed and related problems. These points are dealt with in Sections B and C below.

SECTION B.

DISSEMINULES: THE INFLUENCE OF PARASITISM, WEIGHT, TIME OF GERMINATION, STRUCTURE AND DORMANCY UPON SUCCESSION.

The heavy insect infestation of certain samples of Acacia seed collected for the purpose of carrying out germination tests, led me to investigate the problem of non-development and parasitism of seed in over 30 commonly found species in all stages of succession, and the effects of these factors upon germination and ultimately upon secondary succession.

1. Non-development, Parasitism by Insects and Fungus: the Effects on Seed Germination.

The disseminules were in all cases collected in the 1937-38 season at a time when they were ready to fall naturally to the ground. The disseminules were collected from plants existing in areas of which they were typical constituents - e.g. Aristida congesta disseminules were collected from the Primary Grass Stage, those of Trachypogon plumosus from Purple Veld and so on. In a few cases, for example that of Acacia robusta, disseminules were not collected on Frankenwald itself owing to the lack of members of that species. In such instances, however, the disseminules were collected from sites as near to Frankenwald as possible. This was done because of the fact that environmental conditions, particularly meteorological ones, are known to have an effect upon germination. This point has been mentioned by Kidd and West (1918 & 1919), though their attention was devoted mainly to the effect of environmental conditions upon seedlings of the next generation.

In making this investigation the seed samples used were all of sufficient size to obviate statistical errors. The

counts made for non-development and parasitism were made u
the same samples of seed and the results were in each case
expressed as a percentage of the sample. The results obta
for insect parasitism are as follows. The key to the Numb
of the Communities in which these plants occur is:

1 = Ruderal Stage.

2 = Cynodon-Eragrostis-Aristida-etc. Stage.

3 = Hyparrhenia-Themeda-Cymbopogon-etc. Stage.

4 = Purple Veld Stage.

5 = Climax Scrub.

Species	No. dissected	Percentage parasitised	Communit No.
Trachypogon plumosus	300	39.0	4
Acacia robusta	3026	35.03	5
A. karroo	2000	23.50	5
A. caffra	4700	17.02	5
Andropogon amplectens	267	12.32	4
Fagara magalis-montan	250	6.80	5
Panicum natalense	250	5.60	4
Urelytrum squarrosum	250	4.40	4
Zizyphus mucronata	250	4.360	5
Aristida congesta	250	4.00	2
Hyparrhenia hirta	250	4.00	3
Themeda triandra	250	3.60	3
Bidens pilosa	275	2.91	1
Eragrostis gummiflua	250	2.80	2
Heteropogon contortus	260	1.60	3
Setaria sp.	250	1.60	1
Cymbopogon excavatus	250	0.80	3
Pogonarthria squarrosa	250	0.80	2
Schizachyrium semiberbe	250	0.40	3
Datura stramonium	250	0.40	1
Physalis minima	250	0.40	1
Amaranthus Thuntergii	275	0.36	1

Species	No. dissected	Percentage parasitised	Community No.
Eleusine indica	250	-	1
Sohkuhria bonariensis	260	-	1
Chloris virgata	250	-	1
Rhynchelytrum repens	250	-	2
Cynodon dactylon	300	-	2
Royena pallens	187	-	
Vangueria infausta	250	-	
Tagetes minuta	250	-	1
Tristachya hispida	400	-	4
Cassine burkeana	310	-	

The results show a general tendency for percentage insect parasitism to increase with the advance of succession. The percentage of seed destroyed is highest in species which belong to the climax scrub or climax grassland vegetation. There are some exceptions to this statement. For instance, Aristida congesta and Bidens pilosa occur relatively high on the scale although they are members of the lower stages of succession. On the other hand, Vangueria infausta, Cassine burkeana and Royena pallens (see note) which are Scrub Climax members are placed at the bottom of the scale.

There are unfortunately several inaccuracies in these figures. This is largely due to the fact that this investigation had not been planned when the seed was picked, with the result that diseased pods and fruits were not picked. In the case of the grasses, however, (with the exception of Tristachya hispida) this made no difference to the results because diseased and good seeds are almost indistinguishable. Furthermore, in the case of a species such as Physalis minima, it is scarcely possible to assess the amount of damage due to insects for this reason, that if the seed is attacked at all, it is attacked within the fleshy fruit. No such fruits

were picked. Loss of seed in the case of this species is likely to be due to the fruits being swallowed whole by birds and animals - though in the case of animals, some seed may survive digestion. The figure for Royena pallens is incorrect. The fruits were badly parasitised and many seeds had entirely disappeared. This may have been due either to insects or non-development, more likely to the former. The figure given in the results only represents the quantity of seed definitely known to be parasitised. Panicum natalense was picked too soon. There were very few seeds and insects were found only in the flowers. The figure for Tristachya hispida is incorrect. The seeds were specially selected, NOT indiscriminately collected as in the other cases. From observation it is known that percentage parasitism is high.

Although specimens were kept of all parasites found, it was only possible to determine a very few of these chiefly because many of the parasites were in the larval form. Determinations made are as follows:-

Species.	Parasitised By
Themeda triandra	Insect larvae, possibly Chalcids.
Vangueria infausta	Possibly a moth larvae.
Schizachyrium semiberbe	Plant bug and Psocids - found amongst stored seed.
Tristachya hispida	Insect larvae. Possibly Chalc
Trachypogon plumosus	Insect larvae. Dipterous or hymenopterous.
Acacia Saffra	Bruchidae, Coleoptera - possibl Bruchus sp.
A, robusta	" " " " "
" "	Immature bugs, Lygaeidae or Pyrrhocoridae - found inside the pod, not on seed.
" "	Enaretta sociaria. Lamiidae, Coleoptera.
Andropogon amplectens	Dipterous larvae, probably Mycetophilidae.

Species.	Parasitised by
Hyparrhenia hirta	Unknown insect larvae.
Pagara magalis-montana	Curculionidae, Coleoptera.
Eragrostis gummiflua	Chirothrips sp.(1) Tripidae. Thysanoptera.
Pogonarthria squarrosa	Chirothrips sp.(2) " "

Apart from the above list, beetles have this season been observed eating the flowers of certain grass species. These insects were determined as follows:-

Trachypogon plumosus	Syagrus sp. Rumolpidae, Coleoptera.
Andropogon amplectens	
Cymbopogon excavatus	Chrysomelidae, Coleoptera.

On the basis of these results and on field observations, it is concluded that the percentage parasitism of seeds increases as secondary succession advances toward the climax. It is expected that parasitism of seed in typical, well-protected and heavily-wooded scrub areas, would be very high indeed. It is further concluded that this factor in some instances exercises an appreciable influence upon shaping the course of secondary succession. When one considers that a grass such as Trachypogon plumosus loses 39% of the seed it produces and Eleusine indica loses no seed at all, it can be partly understood why some grasses are able to gain a footing upon fallow lands to the exclusion of others. Parasitism and loss of seed should be correlated with the total amount of seed produced by each plant. Unfortunately no work has been done in this connection.

In order to obtain a complete and reliable analysis of the problem of parasitism and non-development of seed and its reaction upon succession, it would be necessary to obtain some estimate of the amount of seed likely to be produced by each plant taking part in the succession. The work would be laborious and in some cases it would be impossible to estimate the average number of seeds produced per plant, but I feel that this line of research is one which could be investigated to advantage.

Fungus Parasitised.

Species	No. dissected	Percentage parasitised	Community no.
Themeda triandra	250	7.60	4
Cassine burmeana	310	5.81	5
Urelytrum squarrosum	250	4.00	4
Bidens pilosa	275	2.19	1
Cymbopogon excavatus	250	1.60	3
Hyparrhenia hirta	250	0.80	3
Andropogon amplectens	267	0.37	4
Vangueria infausta	250	0.20	5
Eleusine indica	250	-	1
Fagara magalis-montana	250	-	5
Schkuhria bonariensis	260	-	1
Schizachyrium semiberbe	250	-	3
Heteropogon contortus	260	-	1
Chloris virgata	250	-	1
Amaranthus Thunbergii	275	-	1
Rhynchelytrum repens	250	-	2
Panicum natalense	250	-	4
Setaria sp.	250	-	1
Cynodon dactylon	300	-	2
Pogonarthria squarrosa	250	-	2
Royena pallens	187	-	5
Aristida congesta	250	-	2
Eragrostis gummiflua	250	-	2
Zizyphus mucronata	275	-	5
Datura stramonium	250	-	1
Physalis minima	250	-	1
Tagetes minuta	250	-	1
Tristachya hispida	400	-	4
Trachypogon plumosus	300	-	4
Acacia caffra	4700	-	5
A. Karroo	2000	-	5
A. robusta	3026	-	5

With the exception of Bidens pilosa, fungus appears to confine itself to seeds of plants which occur relatively high in the succession. It must be noted that the seeds used as material for dissection had been stored for nearly a year and traces of fungus infestation may have disappeared before the seeds were examined. In spite of this however, it appears that infestation of seeds by fungus is responsible for destruction of only a very small percentage of seed produced. In heavily-wooded, protected areas, such as the riverine scrub at Nelspoort, it is possible that the percentage fungus parasitism of seed will increase. In this connection, it is interesting to note that the fungus Ravenelia MacOwaniana Pazschke is quite frequently found in the aecidial stage on pods of Acacia karroo. (The teulemtospore stage is found on the leaves).

I conclude that this type of parasitism is thus unlikely to have any effect upon determining the course of succession. The same inaccuracies apply to these figures as are mentioned above.

Undeveloped Seed.

Species	No. used	Percentage undeveloped	Community No.
Panicum natalense	250	92.80	4
Urelytrum squarrosum	250	86.80	4
Andropogon amplectens	267	80.15	4
Setaria sp.	250	78.00	1
Cymbopogon excavatus	250	76.00	5
Schizachyrium semiberbe	250	74.00	3
Eragrostis gummiflua	250	74.00	2
Royena pallens	187	68.98	5
Pagara magalis-montana	250	64.40	5
Hyparrhenia hirta	250	64.40	3
Chloris virgata	250	58.00	1
Pogonarthria squarrosa	250	57.60	2
Cynodon dactylon	300	56.00	2

Species	No. used.	Percentage undeveloped	Community No.
Trachypogon plumosus	300	52.67	4
Vangueria infausta	250	39.60	5
Amaranthus Thunbergii	275	32.00	1
Cassine burkeana	310	31.29	5
Heteropogon contortus	260	30.00	3
Aristida congesta	250	24.00	2
Themeda triandra	250	17.60	3
Schkuhria bonariensis	260	16.54	1
Rhyncelytrum repens	250	12.40	2
Bidens pilosa	275	5.45	1
Eleusine indica	250	5.20	1
Zizyphus mucronata	275	4.73	5
Tagetes minuta	250	3.60	1
Datura stramonium	250	-	1
Physalis minima	250	-	1
Tristachya hispida	400	-	4
Acacia caffra	4700	-	5
A. karroo	2000	-	5
A. robusta	3026	-	5

Inaccuracies again occur in these results, partly due to reasons already mentioned, partly to other causes.

Panicum and Setaria seed must have been collected too early which accounts for the very high percentage of undeveloped seed.

In the case of Eragrostis gummiflua it is certain that some seeds dropped out of the dissemules before they were dissected. The result is that this grass is shown rather too high on the scale. It is possible that this also happened to seed of Pogonarthria squarrosa. The results for Hoyena pallens are probably inaccurate.

In the case of Vangueria infausta and Hoyena pallens, the number of seeds actually found in the fruits was

subtracted from the greatest number of seeds that could possibly be produced, to give the percentage undeveloped seed.

When collecting seed of Amaranthus Thunbergii, it was found to be difficult to prevent immature seed being included in the sample. This fact probably accounts for the high percentage of undeveloped seed.

The results for Acacia caffra, A. karroo and A. robusta are incorrect. This is because the seeds were not counted out of the pods, so that undeveloped seed could not be counted From other observations, however, it has been noted that in all three cases undeveloped seeds do occur. It is not thought that undeveloped seeds form a very high percentage of the total in these three species.

The results for Tristachya hispida are incorrect. The seed was collected very late, when most of it had already been shed. It was therefore selected - NOT indiscriminately collected. Observations made during the last two seasons show that there is a high percentage of undeveloped and parasitised seed in this species.

For reasons already mentioned, it is impossible to obtain a true idea of the percentage undeveloped seed in [illegible] species such as Datura stramonium and Physalis [illegible].

The figures are very mixed indeed and do not give any conclusive results.

When the three factors dealt with above are added together, their total effect upon individual species, expressed as the percentage of potentially viable seed released, is as follows:-

Species	Percentage of good seed.	Community No.
Physalis minima	99.60	1
Datura stramonium	99.60	1
Eleusine indica	96.40	1
Tagetes minuta	94.80	1
Zizyphus	90.99	5

Species	Percentage good seed.	Community No.
Bidens pilosa	89.45	1
Rhyncelytrum repens	87.60	2
Schkuhria bonariensis	83.46	1
Acacia caffra	82.98	(5)
A. Karroo	76.50	(5)
Aristida congesta	72.00	2
Themeda triandra	71.20	3
Heteropogon contortus	68.40	3
Amaranthus Thunbergii	68.38	(1)
Acacia robusta	64.97	5
Cassine burkeana	62.90	(5)
Vangueria infausta	58.40	(5)
Cynodon dactylon	44.00	2
Chloris virgata	42.00	1
Pogonarthria squarrosa	41.60	2
Fagara regalis-montana	32.80	(5)
Royena pallens	31.01	(5)
Hyparrhenia hirta	30.80	3
Schizachyrium semiberbe	25.60	3
Eragrostis gummiflua	23.20	2
Cymbopogon excavatus	21.60	3
Setaria sp.	20.40	(1)
Tristachya hispida	20.25	4
Trachypogon plumosus	8.33	4
Andropogon amplectens	7.12	4
Rhelytrum squarrosum	4.80	4
Panicum natalense	1.60	(4)

The above results do not appear to be conclusive, one way or the other. If, however, all faulty determinations and figures for scrub constituents are omitted, definite indications appear. I have omitted scrub constituents for the reason that they possess a very wide variety of fruits as compared with those of grasses. This fact is probably

the cause of irregularity of the figures above and in preceding tables. Furthermore, it is the grassland communities which are the most important from the point of view of acceleration of succession.

It will be seen from the adjusted results that there is a strong tendency for the ruderal and primary grass stage constituents to escape the attentions of seed parasites and to produce large quantities of potentially viable seed. On the other hand, the Purple Veld grasses at the opposite end of the scale suffer very heavily indeed, many seeds do not develop and the net result is shown in the production of a very small quantity of potentially viable seed.

Conclusions:

On the strength of this evidence it seems clear that the factors of parasitism and non-development of seed are capable of playing quite an important part in shaping the course of secondary succession, though the factors which are intimately connected with these have yet to be investigated. The most important of these is the investigation of differential seed - production of the various species taking part in the succession. It seems perfectly clear from the evidence above, however, that a grass such as Trachypogon plumosus cannot hope to compete with say, Eleusine indica on fallow ground - always presuming the number of seeds present to be the same. In conclusion I should add that factors such as these are likely to be considerably more important in determining the lines along which succession shall proceed, than the factors outlined under Section A.

2. Germination Tests : Viability and Time of Germination: Influence upon Succession.

Germination tests were carried out in three different ways with a view to discovering if any difference in the results was likely to be obtained from tests made in the

laboratory and in natural conditions in the field.

A large field germination experiment was designed to test out the viability or about thirty species of seed upon fallow soil, and upon virgin soil, denuded and not denuded. About 10 species had been planted when it was observed that so much disturbance has been caused by termites, cutworms and other seedling parasites that the results had been rendered useless. The experiment was abandoned. As a substitute, however, an experiment was designed with seeds planted in nursery tins.

(1) Laboratory Tests:

Disseminules of over 30 species were tested out for viability. At the same time a note was kept of the time of germination. Both time of germination and viability were thought to be likely to have an effect upon succession.

The tests were made in Petri dishes at room temperature in the laboratory. The dishes contained one thickness of filter paper and were kept constantly wet with tank water. The tests began in the middle of December 1938, on material which had been collected as described at the beginning of section B. The samples tested were large enough to avoid statistical errors. The average time of germination of the disseminules was calculated on the formula of Bunting (1938). The formula is:

$$\Delta T = \frac{\Sigma gt}{\Sigma g}$$

where ΔT = average time

Σ = "the sum of"

g = the number of seeds germinating on any one day.

t = the number of that day from the beginning of the test.

No selection of disseminules was made as it was desired to ascertain the percentage of disseminules produced, which is likely to germinate. This work therefore differs fundamentally from that of Barenbrug (1934). In the laboratory tests

the awns were removed from grass species in order to facilitate fitting the disseminules into the Petri-dishes. In nursery tests the disseminules were planted just as they fall to the ground. Exceptions to this rule were made in the case of Vangueria infausta and Royena pallens because it was impossible to say how many seeds the disseminules contained. Seeds were planted in these two cases. In the case of Eragrostis gummiflua, caryopses were used in laboratory test instead of disseminules.

Ziziphus fruits were planted instead of seeds. This was done as the number of seeds each fruit contained was know to be two. Parasitism could also be discounted as a likely loss of seed.

The results obtained from these tests are tabled below in order of their percentage germination.

Species	Time of 1st. Germination	Average time of germination.	Percentage germination.	No. of disseminules in test
Bidens pilosa	1 day	2.6	96.00	500
Acacia caffra	4 days	11.6	95.00	200
Physalis minima	2 "		93.00	500
Tagetes minuta	2 "	2.6	89.40	500
Oryza ambiqua	2 "	3.0	82.00	500
Acacia robusta	19 "	61.9	77.20	
Heteropogon contortus	2 "	4.4	76.80	500
Rhyncelytrum repens	2 "	4.76	61.00	500
Themeda triandra	3 "	5.0	45.00	500
Vangueria infausta	58 "	61.9	42.00	100
Eragrostis gummiflua	4 "	6 0	28.20	500
Schizachyrium semiberbe	4 "	8.8	27.40	500
Hyparrhenia hirta	3 "	3.1	24.20	500

Species	Time of 1st. Germination	Average time of germination	Percentage germination	No. of disseminules in test
Cymbopogon excavatus	2 days	3.8 days	18.40	500
Sohkuhria bonariensis	2 "	3.4 "	18.00	500
Gymnosporia buxifolia	8 "	13.3 "	17.00	500
Trachypogon plumosus	3 "	4.3 "	10.00	500
Amaranthus Thunbergii	2 "	7.4 "	8.6 or 22.2	500
Chloris virgata	1 day	2.8 "	7.60	500
Tristachya hispida	3 days	6.0 "	7.29	150
Aristida congesta	4 "	9.2 "	6.80	500
Andropogon amplectens	3 "	6.2 "	4.80	500
Setaria sp.	4 "	5.9 "	3.80	500
Urelytrum squarrosum	5 "	7.6 "	3.20	500
Eleusine indica	3 "	9.1 "	2.00	500
Rhus Gueinzii	18 "	29.87 "	1.20	500
Gnaphalium undulatum	5 "	7.66 "	0.60	500
Nidorella anomala	11 "	13.0 "	0.60	500
Panicum natalense	14 "	15.0 "	0.20	500
Pogonarthria squarrosa	6	6.0 "	0.20	500
Datura stramonium	-	- "	0.00	500
Cynodon dactylon	-	- "	0.00	500
Fagara magalismontana	-	- "	0.00	500

An attempt to test out seeds of Tangueria infausta was abandoned on account of extremely heavy fungus infestation. On the strength of experience gained from this test and those

on Fagara magalis-montana and Rhus Guoinzii, it was decided to take the results for scrub species from nursery tests as likely to be more accurate.

The results above will be discussed together with those for nursery tests which are given below. In nursery tests the disseminules were planted in tins at a depth consistent with their size. ~~of the species~~. The soil was not treated in any way. Small stones were placed at the bottom of each tin to facilitate drainage. The tins were watered regularly except when the weather was rainy. They were exposed to sunlight and rain. It is unfortunate that these tests were not fully concluded, some of the species being omitted. The results are as follows:-

Species	Time of 1st. germination	Average time of germination	Percentage germination	No. of disseminules in test.
Acacia caffra	4 days	11.6	95.0	200
Physalis minima	8 "	10.5	83.0	200
Acacia robusta	19 "	61.9	77.2	136
Schizachyrium semiberbe	8 "	13.7	75.0	400
Royena pallens	39 "	65.7	71.8	85
Heteropogon contortus	5 "	7.6	65.0	400
Themeda triandra	6 "	12.4	59.5	400
Eleusine indica	6 "	20.7	57.0	400
Bidens pilosa	2 "	6.8	53.7	400
Vangueria infausta	89 "	97.5	42.0	100
Rhynchelytrum repens	7 "	9.5	37.5	400
Amaranthus Thunbergii	5 "	9.6	35.0	200
Chloris virgata	3 "	6.99	32.8	400
Aristida congesta	6 "	7.8	28.5	400
Datura stramonium	19 "	44.5	28.0	200
Cassine burkeana	52 "	64.0	25.0	160

Species	Time of 1st. Germination	Average time of germination	Percentage germination	No. of disseminules in test
Gymnosporia buxifolia	30	49.8	22.0	100
Hyparrhenia hirta	6	10.2	21.0	400
Cymbopogon excavatus	5	6.8	20.5	400
Tagetes minuta	3	6.7	17.0	400
Trachypogon plumosus	7	10.2	14.5	400
Acacia karroo	8	52.6	12.0	200
Andropogon amplectens	4	7.3	11.5	400
Urelytrum squarrosum	10	15.9	5.0	400
Zizyphus mucronata	136	172.7	4.7	150
Rhus Gueinzii	48	22.5	3.0	200
Fagara magalismontana	36	69.0	1.0	200
Cynodon dactylon	-	-	-	400

Apart from certain inaccuracies which are known to exist, a number of the disseminules tested gave results which are very difficult to understand.

The figures given for the scrub species are slightly inaccurate because these were taken from the nursery results. This had to be done because of heavy fungus infestation in laboratory conditions. The average time of germination in these cases therefore, ought to be about 1 day shorter. This correction, however, would make little difference to the results. Other inaccuracies occur in the case of Panicum natalense and possibly Setaria sp. These have already been explained. The graphs were based on the results of laboratory tests since these were thought to be more accurate

than those for the nursery.

The results which are difficult to interpret are those for Chloris virgata, Schkuhria bonariensis, Amaranthus Thunbergii, Eleusine indica, Gnaphalium undulatum, Fibrella anomala, Pogonarthria squarrosa and Datura stramonium - which, with one exception, are all members of the ruderal flora. Seeds do not develop in about 58% of Chloris virgata disseminules. But even this large figure does not account for the 51% which have not germinated. In the nursery, the percentage germination rose to 32% which is a much truer reflection of its capacities. The difference may be due to higher temperature in the soil. The estimations for parasitism and non-development of seed only account for a possible 16% loss of seed in the case of Schkuhria. Its failure to germinate may be due to conditions of temperature or to dormancy. In the case of Amaranthus Thunbergii it was noticed that many of the seeds split open but did not produce radicles or plumules. These were counted as possible germinations. (See figures above). Even though non-development of seed accounts for a loss of about 12%, the germinations results still appear to be low. This is borne out by the nursery results where germination was 35%. The effect of temperature possibly has much to do with this difference. Eleusine indica germinated well in soil but very badly in the laboratory. The difference recorded is 55%. Gnaphalium undulatum also germinated very badly in the laboratory, but in this case there are no comparative figures for the nursery experiment. The same can be said of Fibrella anomala and Pogonarthria squarrosa. Of 500 Datura seeds tested in the laboratory, not one germinated. In the nursery, however, there was a germination of 28%.

In all the above cases I feel that temperature plays an important part and also possibly, a tendency to dormancy, in some species. The latter is probably true of Datura stramonium.

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The results which are difficult to interpret are those for Chloris virgata, Schkuhria bonariensis, Amaranthus Thunbergii, Eleusine indica, Gnaphalium undulatum, Sidorella anomala, Pogonarthria squarrosa and Datura stramonium - which, with one exception, are all members of the Ruderal Stage. Seeds do not develop in about 58% of Chloris virgata dissemirules. But even this large figure does not account for the 5% which have not germinated. In the nursery, the percentage germination rose to 32% which is a much truer reflection of its capacities. The difference may be due to higher temperature in the soil. The estimations for parasitism and non-development of seed only account for a possible 16% loss of seed in the case of Schkuhria. Its failure to germinate may be due to conditions of temperature or to dormancy. In the case of Amaranthus Thunbergii it was noticed that many of the seeds split open but did not produce radicles or plumules. These were counted as possible germinations. (See figures above). Even though non-development of seed accounts for a loss of about 32%, the germination results still appear to be low. This is borne out by the nursery results where germination was 35%. The effect of temperature possibly has much to do with this difference. Eleusine indica germinated well in soil but very badly in the laboratory. The difference recorded is 55%. Gnaphalium undulatum also germinated very badly in the laboratory, but in this case there are no comparative figures for the nursery experiment. The same can be said of Sidorella anomala and Pogonarthria squarrosa. Of 500 Datura seeds tested in the laboratory, not one germinated. In the nursery, however, there was a germination of 28%.

In all the above cases I feel that temperature plays an important part and also possibly, a tendency to dormancy, in some species. The latter is probably true of Datura stramonium.

With the exception of the species discussed here, it seems clear that as a rule, ruderal species have a very high percentage germination and that Purple Veld species have a low percentage germination. The latter is to some extent a reflection of parasitism and non-development of seed. The three Secondary Grass Stage species, Schizachyrium semibarbe, Hyparrhenia hirta and Cymbopogon excavatus are grouped together between the two extremes. Themeda triandra and Heteropogon contortus both have a much higher germination figure but not nearly so high as in ruderal species such as Bidens pilosa.

Primary Grass Stage species are not well grouped. Aristida congesta has been thought to germinate badly. Laboratory tests showed that germination was very poor but from the results of nursery tests, it would seem that the grass would germinate quite well in the field. The production of a very large quantity of disseminules counteracts the tendency for rather low germination capacity. The other species tested seem to be scattered about on the scale.

The time of germination is probably best studied from the graphs. In Graph No. 1, it will be seen that all species - with the exception of Schkuhria, a bad example - germinate on the first day and reach the peak or near the peak of their germination rate within the first two days of planting. In Graph No. 2, none of the species germinate within the first day and only reach the peak germination rate at about the fourth day. The results shown on Graph No. 3, show that the Secondary Grass Stage species do not reach peak germination rate until the third or slightly after the third day. They tend to start germinating within the first 24 hours but the percentage germination is very low during that period. In Graph No. 4, it will be seen that Purple Veld species are much slower to germinate than species already described. Germination only begins within the 48 hour period and the peak rate of germination lies between 4 and 5 days - this in the case of Trachypogon and Aristachya. The remaining two grasses have no definite peak

and germination is spread out over a longer period. Scrub constituents show a much greater lag in reaching peak germination than any of the species so far described. (See Graph No. 7) Acacia caffra reaches its highest rate of germination on the tenth day, though germination started on the first day. In this species germination is concluded before that of Vangueria has begun. The other species all tend to germinate slowly and continually. This is more than likely due to their harder and thicker seed coats. The results for Acacia Karroo, I suspect are not correct, though I can put forward no argument in support of this.

From these results it can be seen that as succession advances, there is a tendency for germination to begin later and to be spread out over longer and longer periods of time.

Final Conclusions on Paragraph 2: Viability and Time of Germination.

I conclude from these results that percentage germination and germination rate tend to fall and that the average time of germination tends to increase as succession moves forward. In the case of percentage germination, parasitism and non-development of seed is of course reflected in the results. As regards the average time of germination, the increase in the case of scrub types must be due to the increased hardness and thickness of seed coats and fruit walls.

It can clearly be seen that these tendencies are bound to have an important effect upon influencing the course of succession. The fact that ruderal species have a higher percentage germination and start germinating before advanced species means that the latter are certain to lose the race for water. Once ruderal species have consolidated their position upon a fallow land - and they are easily able to do this by reason of their quick germination and faster growth - the web of superficial roots formed is so great as to exclude most other species altogether.

3. Average Weights of Disseminules.

This investigation into the weights of disseminules of the most commonly found species in this type of succession, was carried out with a view to estimating the mobility of the species concerned and the influence of this factor upon the course of succession.

Except in three cases where disseminules were scarce, the samples weighed did not contain less than 250 individuals. In most cases, the samples contained 500 or more disseminules.

Wherever possible, the disseminules were weighed in the form in which they usually fall to the ground. Thus the dried fruits of Vangueria infausta and Zizyphus mucronata were weighed. In the case of Eovena pallens, however, the seeds were weighed as fruits were too scarce to form a representative sample.

Many grasses have alternately-placed male and female spikelets upon the flowering head. It is possible that in some cases the two fall to the ground together - as is found in Schizachyrium semiterbe. (See Seed Photograph No. 6.) In the latter instance, the disseminule and the attached sterile spikelet were weighed together. In doubtful instances, however, such as Trachypogon plumosus, Andropogon amplectens, Cymbopogon excavatus and others, the sterile spikelet was removed -- if it had not already fallen off -- and the disseminule alone was weighed. From the ease with which the sterile spikelets could be detached, it was concluded that the two did not generally fall to the ground together. Disseminules equipped with awns were weighed complete.

As it was not possible to tell whether a disseminule contained seed or not -- without se dissection and consequent destruction -- no discrimination was exercised when making up samples for weighing. The weights tabled below therefore represent the average weight of disseminules, some of which are empty.

The results obtained were arranged in order of the average weight per single disseminule, as follows :-

Species.	Number Weighed.	Average wt, in grams.	Community.
Vangueria infausta.	150	3.39000	5
Zizyphus mucronata.	1000	1.40350	5
Acacia robusta.	500	0.16633	5
Royena pallens.	75	0.12912	5
Acacia caffra.	5400	0.04930	5
A. Karroo.	500	0.04066	5
Fagara capensis-montana.	300	0.01914	5
Themeda triandra.	500	0.01244	3
Urelytrum squarrosum.	250	0.01220	4
Rhus Gueinzii.	2000	0.00965	5
Heteropogon contortus.	250	0.00353	3
Datura stramonium.	1000	0.00679	1
Gymnosporia buxifolia	400	0.00540	5
Trachypogon plumosus.	500	0.00535	4
Andropogon amplectens.	500	0.00245	4
Bidens pilosa.	1000	0.00222	1
Schizachyrium semiberbe.	500	0.00189	3
Rhynchelytrum repens.	500	0.00099	2
Hyparrhenia hirta.	250	0.00097	3
Schkuhria bonariensis.	400	0.00088	1
Tagetes minuta.	500	0.00087	1
Eleusine indica.	500	0.00078	1
Cymbopogon excavatus.	500	0.00058	3
Setaria sp.	500	0.00056	1
Aristida congesta.	500	0.00051	2
Amaranthus Thunbergii.	500	0.00051	1
Chloris virgata.	500	0.00030	1
Panicum natalense.	500	0.00029	4
Conyza amoigua.	500	0.00019	1
Cynodon dactylon.	500	0.00016	2
Pogonarthria squarrosa.	500	0.00008	2
Eragrostis gummiflua.	500	0.00008	2
Nidorella anomala.	500	0.00003	1
Gnaphalium undulatum.	Not weighed - [illegible] weight between Nidorella and Conyza		

An attempt was made to express the results grechically. A graph, however, does little more than show the immense increase in weight of the disseminules between Climax Grassland and Climax Scrub.

Two of the figures given above are inaccurate. The figure for Royena pallens represents seed-weight, not disseminule weight- which would be very much greater. The figure for Panicum natalense is not correct. It was previously discovered that over 99% of the disseminules did not contain seed. It was believed that this was not a natural state but that the disseminules had probably been gathered too early.

When the above results are carefully considered it will be seen that, generally speaking, disseminule weight increases fairly consistently with the advance of succession. There is a comparatively enormous increase in weight between the disseminul of Purple Veld and those of the Scrub Climax.

Another important result which emerges - though this fact already well known - is that the species which are able to colon ise denuded fallows quickest are those which have the lightest disseminules and possess mechanisms which aid in dispersal. The most important of these are such species as Conyza ambigua and Gnaphalium undulatum whose dispersal depends upon wind — a factor which is almost constantly in operation.

The only facts which prevent such species as Pogonarthria squarrosa and Eragrostis curvifiua from colonising to the same extent as the species mentioned above, is that their disseminules possess no mechanisms to aid in dispersal. They are thus rendered comparatively immobile and are forced to depend for dispersal upon a slow process of gradually marching forward, plant by plant. Some disseminules may occasionally be picked up in rainy weather on the mud on animal hooves. But this must a rather rare occurrence.

Some species which are commonly found on fallow lands possess dispersal mechanisms depending upon attachment to passing animals. Though the attachment organs may be very efficient

indeed, as in the case of Bidens pilosa , the disseminules have a chance of being widely dispersed unless animals are active in the vicinity.

Conclusions.

Weight of disseminules tends to increase with the advance of succession. The heaviest disseminules are produced by the constituent species of Climax Scrub Vegetation. The disseminule-weight factor is of great importance in shaping the course of secondary succession in its earliest stages, especially upon recently ploughed areas. The influence of this factor decreases rapidly as succession advances, due chiefly to the fact that though disseminules may be light , they possess no organs to aid in dispersal. In the latter stages of succession the disseminule-weight factor exerts a negative influence upon acceleration of succession. The factor is only of importance when combined with the occurrence of mechanisms aiding dispersal. These two properties are combined in the disseminule of Conyza ambigua. Its importance as a colonising species becomes even greater when it is realised that the seed is highly viable.

4. Disseminule Structure : Mechanisms aiding Germination and Dissemination ; Effects upon Secondary Succession.

The disseminule structure of a number of the most important species occurring in this type of succession have been described in the order in which the species make their appearance. The names of many of the mechanisms have been taken from Weaver & Clements (1929).

(i) Ruderal Stage.

Group (a): Parachute Mechanisms.

Conyza ambigua, Nidorella anomala, Erigeron canadensis and Gnaphalium undulatum fall into this group. The disseminules are capable of drifting on air currents for long periods and great distances. They are extremely light and

and are borne on the wind by the Pappus parachute apparatus shown in Seed Photograpg No. 13. The mechanism is very efficient and so is the whole process of dispersal. An factor which probably plays some part in in the dissemination of such disseminules, is that there is usually an up-draught of warm air from the surface of fallow lands. This would tend to carry the disseminules upward to levels where lateral air currents are operating. It should be noted in this connection that the plants mentioned are all tall. This is another factor which aids dispersal.

A grass which might be mentioned in this group is Chloris virgata - though it does not possess a true parachute. The hairs upon the disseminule , however, act fairly efficiently. The plant is semi-prostrate in form and its habit must considerably reduce the dispersal of its disseminules. (See Seed Photograph No. 9)

The parachute mechanism also plays a slight part in burying the disseminule in the soil. It is so shaped as to allow the disseminule to move in one direction only, as shown here :-  It was found almost impossible to push such disseminules along a flat surface in the opposite direction to the arrow shown in the diagram. This fact may help slightly to bury the disseminule in the soil. Apart from this the disseminules are so small that a few particles of soil are sufficient to cover them.

Group (b) : Comate Mechanisms.

Only one species falls legitimately into this group. Asclepias fruticosa liberates disseminules equipped with long silky hairs which are very effective in maintaining them in the air. It is very doubtful whether the presence of these hairs aid the

disseminule to enter the soil. The hairs are more filmy, laxer and longer than those composing the pappus of Conyza amoigua. The plant is tall. This undoubtedly aids dissemination.

Group (c) : Hooked Mechanisms.

This group does not include pointed callus equipped with retrorse hairs. These will be desc ed later.

ee Species which fall into this group are s as Xanthium spinosum, X. strumarium. Combrena sloposa (no hooks but the effect is the same), Tragus berteronianus, Tagetes minuta, Bidens pilosa, and Tribulus terrestris (no hooks). Thou the mechanism itself may be an extremely efficie organ of attachment --e.g. as in the disseminul of Xanthium strumarium or Bidens pilosa (See Se Photograph No. 12) -- dissemination by this mea depends upon the variable, casual factor, of the presence of animals or man. It is chiefly for t reason that these plants do not colonise new fallow lands as quickly and completely as the species mentioned in Group (a).

It seems fairly certain that the mechani of species in this group have little if any effect upon disseminule penetration of the soil.

Group (d) : Stolons.

A note is included here upon a plant whi spreads more by creeping stolons than by dispe sal of seed. Cyperus esculentus is frequently found in great abundance in fallow lands. (See photograph No. 1.) The seeds were not tested.

Group (e) : Immobile Disseminules.

It may be wondered why such typical fallow land plants as Eleusine indica, Datura

stramonium, D. tatula, Panicum laevifolium, Setari
sp., Amaranthus Thunbergii, whose disseminules are
almost all immobile, are able to colonise fallow
lands to the extent they do. (See Seed Photographs
Nos. 10, 11, 14). This is due solely to the cumula-
effect of continual ploughing and poor cultivation
upon the reserves of seed in the soil. The seed de
in the soil increases year by year. When cultivati
ceases, an enormous number of these seeds have the
opportunity to germinate and to grow undisturbed.
Fallow lands are very quickly covered in this way.

Conclusions.

It is concluded that the high degree of mobi
and viablity of many ruderal species, combined wi
the effect of continual ploughing and/poor cultivation,
the root cause of the invasion of fallow land by
these species.

(ii) Primary Grass stage.

Group (a) : Parachute Mechanisms.

These do not actually exist in this stage bu
disseminules of Aristida congesta and Rhyncelytrum
repens have been included here for purposes of
convenience. Aristida congesta disseminules are
to a certain extent dispersed by wind. The tripar
ite awn is able to support the disseminule quite
well in the air and the seed is light. The dissem-
inule of Rhyncelytrum repens is covered with short
silky hairs which support it fairly well in the wi
(See Seed Photographs Nos. 4 and 5). Both types ar
inefficient, however, as compared with the parachu
of Conyza ambigua. The plants are also rather low
the ground and warm up-currents of air are not so
prevalent in better covered areas such as this. T
effects of these organs upon driving the dissemin

into the soil are quite different. The awn of Aristida congesta revolves quite well but it does not tend to push the disseminule forward as in the case of Hyparrhenia hirta. It is supposed to operate in the same way as an auger but it is difficult to see how it could do this unless the disseminule dropped vertically into the ground. The presence of the awn in Aristida and the hairs in Rhynchelytrum demand that the disseminule shall be moved in one direction only once it has reached the ground. This may aid a little in penetration of the soil. The spiked callus of Aristida would certainly hold the disseminule in the ground after penetration had occured.

Group (b) ; Spiked Calluses with Retrorse Hairs.

Aristida congesta also falls into this group. (See Seed Photograph No. 4). The mechanism is very efficient but necessarily depends upon animal activi for dispersal. The species is doubly sure of dispers as its disseminules are dispersed both by wind and by animals.

Group (c) ; Stolons.

A note has been added here upon the dispersal of Cynodon dactylon. The disseminules are very light but possess no mechanisms to aid dispersal. They ar of the same type as that illustrated in Seed Photogr No. 10. Also, the seed appears to be sterile. This was concluded from the results of germination tests. (The seed can and does germinate, however. See Photo- graph No.15). The plant probably spreads most by very rapid penetration of the soil by stolons. This note has been included for sake of convenience.

Group (d) ; Immobile Disseminules.

Most of the species of this stage have been rendered comperatively immobile by the lack of dispe-

sal mechanisms upon their disseminules. This is partly compensated for in some cases, by the very high output of seed. Species falling into this group are Eragrostis spp. -- as mentioned in the list, Pogonarthria squarrosa, Perotis indica, Sporobolus indicus. The disseminules of Eragrostis spp. and Pogonarthria squarrosa fall into a group whose disseminules are similar to those illustrated in Seed Photograph No. 10. These species all appear to spread by a process of slow invasion. The disseminules are light enough to be carried a few yards in a high wind. In most cases the disseminules are small and are easily covered by particles of soil in rainy weather. This probably accounts for their high germination in field conditions. Cynodon dactylon which may also be put in this group spreads chiefly by means of stolons. Story (1937) records that the seed of this species germinates in the field. It is possible that they are dormant for a period or that they require frosty conditions before they will germinate.

Group (c) : Tumblers.

Trichoneura grandiglumis falls into this group. The whole flower head breaks off and is rolled over the veld by the wind. The presence of tall grasses, however, may render the apparatus immobile. It is probably quite an efficient means of dispersal in areas where grass is short. The disseminules break off the flower-head as it rolls along. (See Seed Photograph No. 14.)

Conclusions.

The community as a whole has a low degree of mobility as compared with the Ruderal Stage. One of its members overcomes this to a certain extent by spreading vegetatively.

(iii) Secondary Grass Stage.

Group (a) : Sulked Callus with Retrorse Hairs.

All the grass species in this stage can be said to fall into this single group. In the case of Tremeda triandra and Heteropogon contortus, the callus is so efficient an organ of attachment that it has been known to pierce the hide of sheep. (See Seed Photograph No. 2.) The callus in Hyparrhenia hirta and Cymbopogon excavatus is only very moderately efficient as an attachment mechanism. In Schizachyrium semiberbe, the callus is totally inefficient. (See Seed Photograph No. 6.). In no case does the awn assist in dispersal of the disseminules. All species are relatively immobile.

As far as these mechanisms aid penetration of the soil, it can be said that they are fairly efficient. Both callus and awn take part in the process. The awns of the latter three grasses are very similar. Frequently two bends can be noticed in the awns, both right angled or nearly so. One of these however, is in a different plane to that of the disseminule. (See diagram) 
The awn revolves quite rapidly with increase or decrease in humidity. The right angle bends in the awn ensure that movement is imparted to the disseminule in two directions, firstly a vertical oscillatory movement and secondly a forward-thrusting movement. If the callus remains upon the ground the two movements combined tend to thrust it into the ground. Once embedded, the callus remains in the soil like a barb. The awn continues its movements almost indefinitely.

Although the awn of Schizachyrium semiberbe revolves quite vigorously, it has little effect on thrusting the disseminule into the soil because the callus is too blunt to enter easily. (See Seed Photograph No. 5.)

The awns of Themeda triandra and Heteropogon contortus differ slightly from those above and tend be straighter. The effect, however, is the same.

Conclusions. (See Plan Seed Photograph No. 2.)

It is concluded that this community possesses even lower degree of mobility than the Primary Grass Stage. The hygroscopic movements of the awns probabl have an appreciable effect upon germination in cert species.

(iv) Purple Veld or Grassland Climax Stage.

Group (a) : Spiked Callus with Retrorse Hairs.

Trachypogon plumosus (See Seed Photograph No. and Tristachya hispida are members of this group. T disseminule of T. hispida is very like that of Them triandra (See Seed Photograph No. 2.). The callus i both cases is an efficient organ of attachment but is not as efficient as that of Themeda triandra. Ur lytrum squarrosum may be included in this group. Th callus as an attachment mechanism is, however, quit inefficient. The hairs are too weak and the callus blunt to allow of attachment. (See Seed Photograph 3). Monocymbium ceresiiforme may also be included. The callus is relatively inefficient but the awn revolves well.

It is possible that the awns aid penetration of the soil to some extent in the case of Trachypo plumosus, Tristachya hispida and Monocymbium ceres forme. The awn of Urelytrum squarrosum scarcely mo at all..

Group (b) ; Immobile.

Diplachne biflora, Harpechloa falx, Panicum natalense (See Seed Photograph No.7), Alloteropsis semialata, Digitaria trichoglumoides, and Eragrostis serrata all have disseminules which fall direct to the ground. They have no mechanisms to aid either dispersal or penetration of the soil.

Conclusions.

I conclude that the Purple Veld type has the lowest mobility of all the communities mentioned so far. The community contains only two species which are capable of movement by attachment. Of these two Trachypogon plumosus need scarcely be considered on account of the fact that only about 10% of its seeds are capable of germination.

(v) Climax Scrub Vegetation.

The disseminules of scrub constituents are comparatively very heavy and with rare exceptions, possess no mechanisms which aid in dispersal. (See Seed Photographs Nos. 15 - 21). On the other hand, many species produce fruits which are palatable to birds, animals and man. Reliance is placed upon this fact alone for dispersal of the disseminules. These may be in the form of fleshy fruits as in the case of Royena pallens and others. An account has already been given in Chapter 1., Paragraph 6., of the species whose disseminules are most frequently dispersed in this way.

In none of the species studied do the seeds or fruits possess mechanisms to aid in the penetration of the soil surface. The process of dispersal is at best , very inefficient. On account of the particularly thick seed-coats and fruit walls of species such Acacia robusta and Zizyphus mucronata respectively,

is likely that disseminules of scrub species re are capable of lying on the ground , exposed to all conditions of weather for long periods without harm. They may in this way, eventually become covered with soil and germinate.

Conclusions.

I conclude that Climax Scrub is by far the most immobile of all the communities in this area, which accounts to some extent, for its very slow invasion of grassland areas.

Final Conclusions on Paragraph 4. ; Disseminule Structure.

It seems safe to conclude that a definite gradient of mobility exists in the various plant communities taking part in secondary succession on fallow lands in this area. The most highly mobile species are constituents of the Ruderal Stage, while the most immobile species are found in Climax Scrub Vegetation. Scrub types, however, frequently possess palatable fruits which offset to some extent, the lack of mechanisms for dispersal. The mobility of disseminules of the Ruderal species is due to their lightness and to specially adapted dispersal mechanisms. Generally speaking there is a decrease in the number of the species equipped with these mechanisms and a decrease in the efficiency of the mechanisms themselves , the further succession advances from the earlier stages.

I conclude that the comparatively high incidence of dispersal mechanisms in ruderal types, plays a most important part in shaping the course of secondary succession. This is especially true of the earliest stages, and can be applied in a negative sense to the more advanced stages also. No attention has been paid in this investigation to non-grass species, for the reason that these types are of very little importance as members of the various units. (See quadrat figures quoted in Chapter ...

In a thesis I submitted in 1937, (Rose Innes, I., 1937.) I stressed the importance of the availability of seed as an influence upon shaping the course of succession. The results

given here are of a more specific nature. It can now be understood why species such as Conyza ambigua will almost always be available to invade fallows and why Datura stramonium for instance, will only invade areas which have been well worked and possibly, poorly cultivated. It can be seen too, why scrub constituents must necessarily take such a long time to colonise grassland areas.

Final Conclusions on Section B., Chapter II. ; Disseminules. Summary.

1. The percentage fungus and insect parasitism of seed tends to increase as succession advances. This influences succession in that ruderal species shed far greater quantities of seed than the more advanced species. They are thus able to occupy an areas, almost to the total exclusion of higher types. Fungus parasitism is relatively unimportant.

Non-development of seed accounts for great losses , especially amongst the wind-pollinated grasses. The results obtained here are not conclusive and do not permit me to make any definite statement as to likely influences upon succession.

2. Percentage germination and rate of germination tend to fall , while the average time of germination tends to increase as succession moves forward. This is bound to have an appreciable effect upon succession.

3. Weight of disseminules increases with the advance of succession. This has a direct influence upon mobility of disseminules and upon the early stages of succession.

4. Mobility of disseminules decreases as succession advances. This is partly due to a decrease in the species equipped with seed dispersal mechanisms and to a decrease in the efficiency of the mechanisms themselves. This has a direct influence upon succession, especially in the earliest stages.

I conclude that the total effects of parasitism and non-development of seed are reflected in the percentage germination figures. The factors of disseminule weight and the presence of

dispersal mechanisms are reflected in the mobility of disseminules. The two most important factors therefore, are viability and mobility of disseminules. Of these two, mobility (which in practice is essentially the same as availability) assumes the most importance. It is perfectly clear that the factors mentioned above are of great importance in influencing the course of succession, far more so than soil habitat factors.

Mobility is the first factor to operate in bringing seed to fallow soils. After deposition, the factors of viability and average time of germination assume control. The factor of root habit then comes into prominence. This is dealt with in Section-C. below.

SECTION C.

ROOT HABITS : EFFECTS UPON SUCCESSION.

The work was carried out upon the more important species found in all stages of this type of succession. The investigation aims at ascertaining whether root systems of plants have any effect upon influencing secondary succession. The technique employed in the case of all grasses and ruderal plants was that of Murray and Glover (1935). A new technique was used for charting tree root bisects. The species selected for this work were all found in their true communities. The soil types varied somewhat. A record was made of this.

The root bisect work of Murray and Glover on Cynodon dactylon, Eragrostis chloromelas, Cymbopogon excavatus, Themeda triandra, Digitaria tricholaenoides, Brachiaria serrata, Eliosurus argenteus and Tristachya Rehmanni and Bunting's work on Pentaschistis variabilis has been included here.

With regard to the root bisect work on trees, a new method had to be adopted. An attempt was first made upon a specimen of Acacia Karroo, to employ the Murray-Glover method but this was found to be laborious and where the working face had bulges or recesses, it was found to be inaccurate. (See Root Bisect No. 20) It was therefore decided to make use of the camera in charting the roots. The latter were first fully exposed by digging away the soil from the working face. The roots were then painted white and the whole bisect was photographed with a metre stick as a standard of comparison. A scale was finally ruled onto the photographic prints. A photograph of the Murray-Glover method is included with the tree photographic charts.

The work was carried out on eroded river banks in the Nelspoort region during January 1939. The charts and photographs have been placed in sequence of communities and will be discussed in that order.

1. Ruderal Stage.

(i) Conyza pubigena.

The taproot is distinct but much reduced in

also after the first 4" penetration. It descended in this case to a point just below the water table where a good deal of branching took place. The ends of the ultimate rootlets were thickened. Fine rootlets were given off all the way down but these were neither long nor numerous.

Strong superficial laterals are given off from the taproot in the first 4" of penetration. These extend horizontally for a comparatively long way. A large number of rootlets are given off. Some extend upwards towards and finally run parallel to the surface, the others descend to a fair depth (unfortunately all were broken on this bisect) on the lower side and permeate every cubic inch of soil for quite a distance below their parent laterals.

Conclusions.

It is concluded that the plant taps water supplies in two regions, the surface area and a much deeper area. In the first case roots radiate from the plant and penetrate the surface soil in every direction. A thick web is thus formed which is able to absorb water from the slightest fall of rain. In the second case the roots are in contact with the permanent water supply and are thus able to support the plant when other supplies fail.

(ii) Tagetes minuta.

The taproot only exists as such in the first 3" to 4" penetrated from the surface. After this level it is so reduced in size as to be no bigger than some of the rootlets given off from the lateral roots. It does not appear to have an important function in the adult plant. It may, however, develop in time of drought. Laterals big and small are given off in the first few inches of soil below the surface. These form a form a web of extreme density, for a radius of a few inches about the base of

the stem. Beyond this the laterals go out more-or-less horizontally. The number of rootlets given off does not seem to be at all large as compared with Conyza ambigua or Datura stramonium. The bisect was made in the same pit as that for Xanthium strumarium but the roots did not penetrate to nearly such a depth although the soil was the same. The plant was well grown.

Conclusion.

The plant appears to rely upon big lateral roots for its supplies of water. It would be able to make use of the smallest fall of rain. The taproot does not develop as well as in Conyza ambigua which would therefore seem to be better equipped for withstanding a drought.

(iii) Xanthium strumarium.

As in the previous cases, the taproot becomes much reduced after penetrating a few inches from the surface. This is again due to the large number of big lateral roots given off. Some of these traverse horisontal levels but others seem to draw supplies of water from the same area as the taproot itself. The ends of all deep roots are thickened and finely branched. The big horizontal laterals give off a fair number of rootlets but not nearly so many as in species already discussed.

Conclusions.

The roots tap two areas - the surface area and the area of permanent water supply. The roots descending to deep supplies seem to be more numerous than those in the surface area. The plant would probably withstand drought very well and would also extract much water from the surface area.

(iv) Datura stramonium.

As before, the taproot diminishes abruptly in size within the first few inches penetrated. It does

not lose its identity but sends off many finely-branched rootlets of the type marked 3. on the chart, which also descend to the deep area. Very big lateral of the type marked 2. are given off just below the surface and penetrate horizontally for comparatively big distances. Sometimes they turn and dip vertically as in the case of 4. The superficial laterals give off an immense number of rootlets of the type 5. which must completely fill the area from the taproot to the extremities of the laterals, to a depth of abo about 1'9". Some of the lateral rootlets penetrate horizontally as in the case of 6. Occasionally, deep-seated laterals are given off at a depth of about 6", as in the case of 8. Many finely-branched rootlets given off from the thickest part of the taproot descend vertically as illustrated by 7.

Conclusions.

I conclude that this root system is the most efficient of all the ruderal species studied. The superficial lateral roots seem to combine the functions of horizontal laterals and deep-seated verticals. The soil affected by the plant must contain an enormous mass of roots. The system is extremely efficient.

Final Conclusions on Paragraph 1. : Ruderal Stage.

The root systems of the ruderal plants studied are all of one type. In all cases two soil areas are affected, the surface soil and the soil below the stem in the region of permanent water supply. The type of system is extremely efficient as two sources of water supply are tapped. The plants are able to utilise moisture from the slightest fall of rain and also from the deeper, more permanent supplies during drought periods. This is to be expected in plants of this type which which have only one season at their disposal in which they must complete their whole life cycle. A strong , finely-divided and widespread

system is essential to such plants.

It is concluded that plants having deep-seated root systems would have little chance of survival, firstly because of the blanketing effect of matted laterals above them, and secondly because of the choking effect of the fine verticals around them and lastly to a certain amount of reduction in the permanent water supply.

2. Primary Grass Stage.

(vi) Aristida congesta.

There are no extensive laterals nor any deep vertical roots. The 0"-12" layer of soil seems to contain the majority of roots which are finely branched and spread very well indeed. The greatest concentration of root-endings probably occurs in the 6" level.

Conclusions.

The plant seems best equipped for absorbing water from the upper layers of the soil where the roots are most abundant and finely divided.

(vii) Cynodon dactylon.

The root system penetrates both the surface and deeper areas. The branching of the whole system seems to be very well developed, particularly at the surface and deep down. The system must be very efficient.

Conclusions.

I conclude that this type of root system is one which would bar the entry of such types which are wholly dependant upon deeply situated water supplies, for reasons explained in Paragraph 1.

(viii) Eragrostis chalcantha.

The root system penetrates the surface levels almost entirely in the form of a highly-branched sponge or mat. The surface laterals may sometimes dip downward but do not penetrate very far. Essentially a surface feeder.

Conclusions.

Conclusions.

The dense mat of roots occurs almost exclusively in the surface levels of the soil. The plant must depend almost entirely upon surface water for its existence.

(ix) Eragrostis chloromelas.

Excessive branching takes place in the upper 18" of soil and is most marked at the 6" level. There are no extensive laterals though one or two small ones occur. Some of the roots may extend to the 3' level. The extremities are thickened. This chart may not be exactly true to type as termites were active in the area. But no roots had been damaged.

Conclusions.

The plant would appear to rely upon the extensive branching in the upper soil level than upon deep roots for its supplies of water.

Final Conclusions on Paragraph 2. ; Primary Grass Stage.

A greater variety of root systems is found in this stage than in the Ruderal Stage. Cynodon dactylon spreads very widely throughout the superficial and deeper soils. On the whole, however the root systems described tend to restrict their activities to the superficial soils than to deeper soils. This fact is likely to exclude for some time, those grasses whose maximum root activity is confined to deeper soils.

3. Secondary Grass Stage.

(x) Hyparrhenia hirta.

The lateral superficial roots are moderately well developed. Extensive branching of the main roots occurs from about the 6" level right to the ends. The roots penetrated the bed of "ouklip" through clay pipes and were apparently only prevented from going further by the bed of solid granite shown in the chart. The terminations of the roots were thickened.

Some roots(marked D) had died but their function was taken over by the laterals near the dead portions. Roots marked B. were broken.

Conclusions.

I conclude that this vigorous root system obtains the greater part of its water supply from deep levels but it is also able to obtain surface water through its superficial root system. It seems that the plant would be very difficult to replace.

(xi) Cymbopogon excavatus.

Like Themeda triandra, this grass has a very well developed system of superficial lateral roots. None of the roots penetrate to any appreciable depth.

Conclusions.

I conclude that Cymbopogon excavatus relies almost entirely upon finely-branched superficial laterals for absorption of water. The grass would tend to cut off supplies of water to other grasses having deeper-penetrating root systems.

(xii) Themeda triandra.

This plant has a root system much like that of Cymbopogon excavatus -- well developed superficial laterals, with occasional shallow vertical roots.

Conclusions.

As for (xi).

Final Conclusions for Paragraph 3. : Secondary Grass Stage.

There is a greater variety of root systems in this stage than in the Ruderal Stage. Two of the grasses possess superficial lateral systems with occasional deep roots, while the third has both superficial laterals and deeply-penetrating roots. I am inclined for this this reason to believe that Hyparrhenia hirta occupies a higher place in succession than either Cymbopogon excavatus or Themeda triandra. On the whole, it may be said that Purple Veld constituents, whose roots are generally penetrate to a

much greater depth than do those of the Secondary Grass Stage, are to some appreciable extent prevented from invading areas colonised by these grasses.

4. Purple Veld or Climax Grassland Stage.

(xiii) Digitaria tricholaenoides.

This root system scarcely developes any superficial laterals. The majority of roots descend direct to the low level of about 3'. The plant must therefore draw its water supply almost wholly from deep seated areas, scarcely any from the superficial soils.

Conclusions.

The root system is deep-seated and possesses superficial laterals. This accounts for its place in Purple Veld. It could not hope to compete with grasses whose systems are mainly superficially placed. Much of the water percolating down after rain would be absorbed by the upper superficial roots and those of Digitaria tricholaenoides would be starved.

(xiv) Brachiaria serrata.

The root system is similar to that of Digitaria tricholaenoides but possesses in addition, a well defined system of superficial laterals. It is somewhat difficult to account for this fact in a Purple Veld grass. It may, however, indicate that the grass belongs to a stage immediately preceding that in which Tristachya Rehmannii, Urelytrum squarrosum and such grasses make their appearance. This theory seems to be well borne out by the quadrat figures already quoted.

Conclusions. The plant possesses both superficial lateral and deep seated vertical roots. It is equipped to take its place in a community of deep rooted grasses. The presence of superficial laterals

roots seems to indicate that it is likely to belong a stage in succession which immediately precedes th containing the ultimate members of the Grassland Climax Stage. This indication is backed by results quadrat analyses.

(xv) Tristachya hispida.

No superficial lateral roots are developed. Some roots extend diagonally for some distance from the surface, then penetrate vertically. Unfortunately, s large roots were broken. In the main, however, the y tend to descend directly to comparatively deep level where maximum division occurs. This is usually in th second foot of soil.

Conclusions.

Tristachya hispida draws its water supply chief from deeper soil levels where maximum root activity occurs.

(xvi) Elionurus argenteus.

This grass also possesses deeply-penetrating ma No superficial laterals of any importance are develo The terminations of the deep roots are finely-branch and draw upon deep-seated water supplies.

Conclusions.

It is concluded that this grass depends almost entirely upon deep root penetration for its supplies water. Maximum root activity occurs at deeper levels.

(xvii) Tristachya Rehmanni.

Scarcely any superficial lateral roots are develo -ed. Almost all roots penetrate to comparatively deep soil levels, though they appear to give off fine rootlets all the way down. The plant depend chiefly upon deep root penetration for its water supplies.

Conclusions.

The root system is finely branched. No important

superficial lateral roots are produced. The majority of roots descend direct to deeper soils. Some roots descend diagonally from the surface but these ultimately dip vertically down. A lot of branching occurs in the second 6" of soil but not quite so much at the terminations. The plant , however, was a little on the young side, which may account for this. Root terminations are generally thickened.

Conclusions.

The root system penetrates fairly deeply and appears to draw upon deeply situated supplies of wat

(xix) Pentanisia variabilis.

The bisect chart of this non-grass plant has been included to show the type of system which may be expected to occur in these members of the Purple Veld community. There is a large tapering storage organ immediately below the soil surface. This gives way to a taproot which forks at about the 2'5" level. One fork continues descending vertically to a depth of almost 5'6" -- which is a far greater depth than is ever reached by grass roots. In the last 2'6" of penetration the taproot gives off sparsely-branched laterals which do not extend far.

Conclusions.

It seems that the roots of non-grass species may be expected to descend to far deeper levels than those ever attained by grass roots. The presence of enlarged storage organs is well known in many non-grass species. This fact is well illustrated here.

Final Conclusions on Paragraph 4. : Purple Veld or Grassland Clim

The constituent members studied all possess root systems which penetrate to comparatively deep soil levels from which they draw their supplies of water. In only one case (Brachiaria serrata) need there be any modification of this statement. In this instance the plant was also provided with a system of superficial laterals. This seems to indicate that the plant does not belong to the

ultimate stages of the Grassland Climax community, though it i capable of competing for water at the same deep level. (see also statements made in this connection in Chapter 1, Paragraph 4.)

The fact that this type of grassland is open and contains spaces between its various constituents, allows the intrusion of small plants provided with small superficial root systems. Such plants as Eragrostis chalcantha are able to obtain enough water from the un-tapped superficial supplies to keep them alive. Their root systems never come into competition with the deeply-situated ones of the true Purple Veld species. Complete protection of Purple Veld, however, causes an increase of tall rank foliage which operates to exclude small plants such as this.

5. Protea Open Woodland Stage.

No bisects were made of roots of any of the Protea spec

6. Climax Scrub Vegetation.

The bisects were done on the eroded river walls of the Mokpoort River in the Mega Witwatersberg. The technique employed has already been described.

(xx) Acacia Karroo.

The Murray-Glover technique was employed in this case alone. The grill is composed of 3' x 3' squares. The tree shows an extremely well-developed system of lateral roots which are mostly superficial. The roots extend for over 7 yds. on each side of the stem and branch well. The superficial laterals sometimes dip vertically at the end of their lateral extension. These probably assume the functions the functions of the taproot when the tree becomes older and increases its spread of roots. This was observed in older specimens whose roots had been exposed by erosion. The taproot in this case was broken. It probably descended to the level of the water which is about 25' from the soil surface. In older trees the taproot tends to decrease in importance and the lateral root

assume its funtions. This tree was probably about 18 years old.

Conclusions.

The superficial lateral roots of young Acacia Karroo trees are very well developed. These intercep water percolating down from the soil surface. The ta root is also very well developed and contacts very deeply-situated water supplies. The system as a whol is therefore most efficient. It is much like that of ruderal plants but operates on a much greater scale. It is concluded that the tree is well equipped to colonise open grasslands.

Note. From observations made in this area, it was se that the root system of Acacia caffra was essentially similar to that of A. Karroo.

(xxi) Gymnosporia buxifolia.

The root systems of two trees are shown here, as it was found to be impossible to follow out the tap to its full extent in the one instance. The system i similar to that of Acacia Karroo in that it possess both superficial laterals and a very deep taproot. T The laterals may extend for quite large distances an give off numbers of new trees. The tree thus has a marked tendency to produce new trees by vegetative means. Five stems can be seen emerging on the soil surface. The taproot extended almost to the water 's edge -- a distance of between 6 and 7 metres.

Conclusions.

The root system is very efficient and taps both superficial and deeply-situated water supplies. Vege tative reproduction is to some extent responsible fo its rapid spreading. It is concluded from this evide that the tree is well suited to colonise open grassl

(xxii) Euclea lanceolata.

The spread of superficial laterals is small and

and these roots are not numerous. There is no main taproot. A large number of roots descend to very deep levels -- in this case to a maximum of about 6.3 metres.

Conclusions.

It is concluded from these observations that the tree is probably placed higher in the succession than either Gymnosporia buxifolia or Acacia Karroo. The superficial lateral roots of these species would tend to intercept water percolating down to deep-seated roots such as those of Euclea lanceolata.

(xxiii) Celtis rhamnifolia.

This tree, like Acacia Karroo and Gymnosporia buxifolia , also has extensive lateral roots and a deeply-penetrating taproot. In the case illustrated, further penetration of the taproot was impeded by the presence of an impenetrable layer of stones. Exposed roots have the capacity for producing new stems. (See Photograph No. 46.)

Conclusions.

This tree also possesses an efficient root system. Water supplies are drawn from superficial and deep levels. It does not appear to be as hardy as the preceeding types. This is probably why it does not colonise grassland to any appreciable extent.

(xxiv) Olea verrucosa.

This species has a fairly well developed superficial lateral system and a large number of roots which descend to deep levels. It appears to be much the same as Euclea lanceolata.

Conclusions.

It is concluded on these grounds that the tree probably belongs to a higher stage of the succession than Acacia Karroo, Gymnosporia buxifolia and Celtis rhamnifolia. The fact that it is an exceedingly slow-growing tree gives weight to this theory.

Final Conclusions on Paragraph 6. : Climax Scrub Vegetation.

It is concluded that the roots of Climax Scrub Stage constituents studied, permeate a very large cubic capacity of soil. In pioneer species, the roots in each case seem to be of two kinds superficial laterals and a very deep taproot. These systems bear a marked resemblance to those of ruderal types. The trees are able to make use of superficial water percolating through the soil after rains and also of deeply situated supplies. Acacia Karroo, Gymnosporia buxifolia, Celtis rhamnifolia fall into this group.

Species which tend to appear after the pioneers do not rely to any great extent upon lateral superficial roots for their supplies of water. There is no main taproot but a large number of roots descend vertically and contact the deeply-situated supplies. It appears that species such as Euclea lanceolata and Olea verrucosa would tend to occupy a higher place in the succession than do the species mentioned above.

The lateral systems of pioneer species form a very closely woven web of superficial roots which bind the soil very closely indeed. The root activity in superficial soils in scrub areas is intense. (See Photograph No.17).

Final Conclusions on Section C., Chapter 11. : Root Habits. Summary.

(1)The root systems of the ruderal plants studied are of one type. They have very extensive superficial lateral systems and also rely to some extent upon their taproots contacting more permanent water supplies. Almost every cubic inch of soil in the immediate vicinity is crammed with roots.

2. A greater variety of root systems is found in the Primary Grass Stage. On the whole, the systems of the species described tend to be most active in superficial soils.

3. Root systems investigated in the Secondary Grass Stage are in some cases almost entirely superficial. In one case there is vigorous development of deep roots combined with moderate development of superficial laterals. The presence of very deep roots and superficial laterals in Hyparrhenia hirta seems to suggest that

it is a transition type between plants having deep and shallow systems.

4. With one exception, the Purple Veld species studied deeply-penetrating root systems. The exception is Brachiaria which has been fully discussed above.

5. No bisects were made of roots of Protea spp.

6. The root systems studied in the Climax Scrub Vegetation show that at least two kinds exist, the one type probably preceding the other in succession. The first type of system possesses very extensive superficial laterals combined with a very deeply-penetrating taproot. The second type has poorly developed laterals but a large number of roots descend vertically to deep situated water supplies.

It is finally concluded from these results that, as secondary succession advances towards the Grassland Climax, the horizontal superficial type of root system gradually gives way to the deep penetrating, vertical type. With the advance of Climax Scrub species, however, the process appears to be repeated. The pioneer scrub species have root systems essentially similar to ruderal species, while those following them have root systems more like those of Purple Veld species. Thus when succession is viewed from this angle, it is seen to contain <u>two</u> pioneer stages, the first upon denuded ground, the second upon open grassland. The process in both cases is essentially similar but appears to be somewhat telescoped in the latter instance. Looking at the more visible aspects of succession, it can be seen that the two processes -- invasion of totally denuded fallows and of open grassveld -- are very similar.

The most important conclusion to be drawn from these results is that the influence of root habit upon succession determines to a large extent, the course which it follows. It can be seen that the root systems of the ruderals immediately prevent the invasion of deep-rooted plants by reason of their superficiality. All supplies of water percolating down through the soil after rains are likely to be absorbed before they can reach deeply-situated

roots. It may be argued that such roots could exist solely upon supplies of water obtained at deep levels. They possibly could do so, but that is not the important point. The crucial stage in the life of any plant is during the period in which it is struggling to establish itself. Seedlings of deep-rooted species cannot hope to establish themselves in conditions of intense superficial root competition as is found in the Ruderal Stage.

The root systems of members of the Primary and Secondary Grass Stages must act in much the same way but not to the same extent. The superficial root systems of the first these stages succession are therefore largely responsible for excluding Purple Veld species. The transition from shallow to deep root systems seems to take place in the Secondary Grass Stage where Cynodon dactylon is being killed by pressure of other species by decreased illumination, and where Hyparrhenia hirta sends down a vigorous system of deep roots.

CHAPTER III.

CONCLUSIONS.

SECTION A. : CHAPTER I.

It was concluded from the results obtained in this portion of the work that soils de conditions do not materially alter the rate or shape the course of succession. Succession influences soil conditions -- not the reverse. The advances occurring simultaneously in plant succession and in soils may be said to be complementary to one another , in that soil-changes initiated by changes in succession, prepare the way to some extent for the invasion of new species. These advances therefore are interdependent but, the initial change is always found in succession, not in soils.

SECTION B. : CHAPTER II.

Conclusions drawn from results given in this section show that the factors of mobility and viability of seed (which combine and reflect the influence of several other factors) are extremely important and influence the course of succession to a very marked degree. The influence of these factors is far greater than that of habitat factors of the soil.

SECTION C. : CHAPTER II.

Results given in this section show that the root habits of plant species play an important part in shaping the course of secondary succession. This is particularly evident in the first three stages where a predominance of shallow lateral root systems exclude such species as have well-developed, deeply-penetrating root systems.

The final conclusions I have to make upon this work are that the mobility, viability and availability of disseminules are the most important factors in operation , that root habits have an important effect upon succession once the disseminules have been deposited and lastly , that the habitat factors of the soil are of comparatively little importance in influencing either the course or the velocity of even secondary succession as studied in this area.

These factors all operate positively and usually to a very marked extent, in the first two stages of succession. Their influence in the latter stages of succession is of a negative type.

APPENDIX.

THE GRASSLAND CLIMAX OF THE SOUTHERN TRANSVAAL AND NORTH-EASTERN ORANGE FREE STATE.

I have included a few notes in this appendix which may help to clarify the position with regard to the true grassland climax of the Southern Transvaal and North-eastern Free State.

Bews (1918) mentions that Purple Veld species (as described here) are common in the Witwatersrand-Pretoria area -- e.g. Andropogon plumosus (=T. polymorphous var. capensis), Urelytrum agropyroides and Elionurus argenteus -- but does not make any definite statement as to their place in succession. Pole Evans (1937) states that the Purple Veld species (as described here) cover large areas in this region. The exact area covered is demarcated as "Mixed Grassveld" on his Vegetation Map of South Africa. Pole Evans also states that certain Purple Veld species such as Elionurus argenteus, Digitaria tricholaenoides, Monocymbium ceresiiforme, Panicum natalense, Andropogon schirensis, Harpechloa capensis (= H. falx) are frequently found associated with typical Themeda triandra veld of the Free State "Short Grassveld", especially on poor soils. But he does not mention Trachypogon plumosus -- which I regard as the criterion of this Purple Veld type -- in this connection. The scope of Pole Evans' paper does not include discussion on the position of these grasses in succession. Adamson in a communication as recent as 1938 , however, implies that in typical undisturbed grassveld in the Southern Transvaal and portions of the Orange Free State and Natal, the climax consists of Themeda triandra. This implication is most misleading and certainly in part, incorrect. As has already been pointed out by several workers the climax grassland of this area consists chiefly of the Purple Veld species described here.

As a result of observations made on expeditions into the Short Grassveld area outlined by Pole Evans (1937), numerous small communities of Purple Veld species have been located and studied. These occurred principally in the vicinity of Petrus Steyn, Bethal, Cedarmont, Val and along the Standerton-Vrede

road. In almost all cases these communities were observed upon poor soils or rocky areas. (c.f. Pole Evans).

It is an undisputed fact that very large areas of this Short Grass Veld have either been ploughed or overstocked. Before the colonisation of the area by European farmers, the country supported a very large population of herbivorous game animals.

It seems possible that Purple Veld species may at one time have been far more frequent than they are today and that their disappearance is largely due to the types of disturbance mentioned above and in particular to disturbance caused by the farming population. The results of some experiments carried out at Frankenwald on Trachypogon plumosus lend some support to this theory. The experiments are described below.

Transect belts were marked out in contiguous Purple Veld areas which had received different treatments. The belts measured 20 x 1 sq. yds. Counts were made of the flowering heads and of the plants of Trachypogon plumosus in each belt . The average number of heads per plant was then calculated. The areas analysed were as follows :-

1. Purple Veld protected since '34 / P.V. Burnt annually since '34
2. " " " " " / " " once in 1937.
3. " " " " " / " mown once in 1938.
4. " " " " " / " " in 1937 and 1938

In 1. it was found that the number of flower heads had been greatly reduced as a result of burning. In 2. the result was the same but the effect was more marked. (See Photographs Nos. 18 - 19.) (see Histograms Nos. 8 & 9.

In 3. and 4. the effect was similar to that in the burnt areas but was not so marked. (See histograms Nos. 10 & 11). Unfortunately there was no available unfertilised grazed area which could be similarly analysed for comparison. Observations on grazed veld, however, show that seeding in Trachypogon plumosus is directly affected and inhibited. This is in large measure due to the fact that it is a very late-flowering grass. Grazing defers flowering and even if the veld is protected towards the end of the season, the flowers appear very late and

and tend to be killed by the first frosts. Cook (1938) states that fire defers flowering in the case of Tristachya hispida.

In direct contrast to these results for Trachypogon plumosus, Story (1938) states that mowing and grazing promote flowering to a great extent in the case of Themeda triandra and that conversely, protection kills these plants. (See Histogram No. 12) No observations were made by Story upon the effect of fire upon Themeda triandra but it seems likely that seeding would be inhibited thereby. Cook (1938) , however, reports an increase of Themeda triandra in annually burnt plots. It should be noted that Themeda triandra flowers much earlier than Trachypogon plumosus and is not affected by frost during the flowering period.

On the basis of these results it seems likely that disturbance (excepting fire, ploughing and violent overgrazing) has the effect of increasing flowering in Themeda triandra and decreasing it in Trachypogon plumosus. with consequent results upon the stability of the two types of veld. These results seem to support the theory that has been put forward above.

Observations made in the Drakensberg area at Mont aux Sources by Gilliland (1938) and on the Little Berg near Cathkin Peak by myself in 1937, indicate that Themeda triandra growing there is a seral type in the grassland areas and that the climax is probably a Trachypogon-Tristachya type. In the Cathkin Peak area it was observed that burning had a definitely detrimental effect on flowering in Trachypogon plumosus. This has since again been observed by West (1938). In the latter area, Trachypogon plumosus is dominant in a Trachypogon-Tristachya-Stiburus community. It is possible that annual burning of this grassveld type would have the effect of increasing the cover of Themeda triandra.

Trachypogon plumosus, the most characteristic of Purple Veld grasses, occurs largely at high altitudes. It is distributed with its associates as along the rim of a saucer, from a point a few miles East of Lichtenburg (observed in 1938) , along the Witwatersrand to Middelburg (observed in 1938) and probably further, and thence in scattered patches to the Drakensberg where it is abund-

ANT. Though the appearance of the community may change
the constituent species are usually the same.

I conclude from the notes above that it is possib
Purple Veld may at one time have covered a much greater
it does today, that it might possibly have filled the b
present semicircular, saucer-rim distribution and that
quite possible that Themeda triandra veld is seral in c
merely a subclimax stage to the Purple Veld Climax .

Further field observation should make it clear wh
theory is correct or not.

A. caffra Willd.

A. oriadenia Benth.

A. Karroo Hayne(= A. horrida Willd.)

A. litakunensis Burch.

A. robusta Burch.

Acalypha angustata Sond.

A. caperonioides Baill.

Achyranthes aspera Linn.

Agrimonia eupatoria Linn.

Albuca pachyclamys Baker.

Alloteropsis semialata Hitch.

Alternanthera repens Stend.

Amaranthus Thunbergii Moq.

Andropogon amplectens Nees.

Argemone mexicana Linn.

Aristida congesta R.& S.

Asclepias aurea Schltr.

A. fruticosa Linn.

A. stellifera Schltr.

Asparagus sp.

Aster harveyanus Min.

Babiana hypogea Burch.

Becium obovatum var. hians N.E.Br.

Berkheya subulata Harv.

Bidens pilosa Linn.

Bopusia scabra Presl.

Bowiea volubilis Harv.

Brachiaria serrata (Sprengl) Stapf.

Brachylaena discolor D.C.

Callilepis leptophylla Harv.

Carissa arduina Lam.

Cassia mimusoides Linn.

Chenopodium ambrozoides Linn.

C. album Linn.

Chilianthus arboreus A.DC.

Chloris virgata Swartz.

Clerodendron triphyllum (Harv.) H.H.W.Pears.

Conyza ambigua - Cesati, Passer & Gibelli.

Corrigiola littoralis Linn.

Cosmos bipinnatus Cav.

Cucumis hirsutis Sond.

Cussonia spicata Thumb.

Cyanotis nodiflora Kunth.

Cymbopogon excavatus (Hochst) Stapf.

Cynodon dactylon Steud.

Cyperus compactus Lam.

C. compactus Lam. var flavissimus C.B. & Cl.

C. esculentus Linn.

Datura stramonium Linn.

D. tatula Linn.

Dianthus mooiensis Williams.

Dicoma anomala Sond.

D. Zeyheri Sond.

Digitaria horizontalis Willd.

D. tricholaenoides Stapf.

Dimorphotheca spectabilis Schltr.

Diplachne biflora Hack.

Dombeya rotundifolia Planch.

Dovyalis Zeyheri Harv.

Ehretia hottentotica Burch.

Elephantorrhiza elephantina (Burch) Skeels.

Eleusine indica Gaertn.

Elionurus argenteus Nees.

Eragrostis brisoidas Nees.

E. chaetantha Nees.

E. chloromelas Steud.

E. curvula Nees.

E. gummiflua Nees.

Eragrostis nebulosa Stapf.

E. robusta Stent.

Erigeron canadensis Linn.

Eriosema cordatum E.Mey.

E. transvaalensis C.E.Moss.(ined)

Euclea lanceolata E.Mey.

E. undulata Thunb.

Euphorbia striata Thunb.

E. truncata N.E.Br.

Euryops transvaalensis Klatt.

Fagara magalis-montana Engl.

Galinsoga parviflora Pav.

Gazania pygmaea Sond.

Gerbera piloselloides Cass.

Gladiolus crassifolius Baker.

G. edulis Birch.

Gnaphalium undulatum Linn.

Gnidia caffra Meisr.

G. capitata Linn.

G. kraussiana Meisn.

G. microcephala Meisn.

Gomphrena globosa Linn.

Grewia flava D.C.

Gymnosporia buxifolia (Linn) Szysz.

G. polycantha (Sond) Szysz.

Haplocarpa scaposa Harv.

Harpechloa falx (Linn) F.Kuntze.

Helichrysum argyrosphaerum D.C.

H. aureo-nitens Sch.Bp.

H. caespititium Sond.

H. callicomum Harv.

Helinus ovatus E.Mey.

Hermannia lancifolia Szysz.

Heteromorpha arborescens Scham.Schlt.

Heteropogon contortus (Linn) R.& S.

Hyperrhenia hirta Stapf.

Hypericum aethiopicum Thunb.

Hypoestes verticillaris R.Br.

Hypoxis rigidula Baker.

H. Rooperi Moore.

Indigofera hibrida E.E.Pr.

Ipomoea bathycolpos Hall.

I. simplex Thunb.

I. sp.

Justicia anagalloides T.Anders.

Kiggelaria africana Linn.

Lantana salvifolia Jacq.

Lapeyrensia cruenta Baker.

Lepidium linoides Thunb.

Leucas mentinicensis R.Br.

Lobelia decipiens S.Moore.

L. reculata Sond.

Lophaene digitata Stapf.

Londetia simplex C.E.Hubbard.

Lotononis foliosa Bolus.

Maerua triphylla A.Rich.

Monocymbium ceresiiforma (Nees) Stapf.

Nidorella anomala Stoetz.

N. hottentotica D.C.

Oenothera biennis Linn.

Olea verrucosa Link.

Oldenlandia amatymbica (Hochst) K.Schum.

Osyris abyssinica Hochst.

Oxalis setosa E.Mey.

Pachystigma pygmaea

Panicum coloratum Linn.

P. laevifolium Hack.

P. natalense Hochst.

Pappea capensis E.& Z.

Pavetta sp.

Pelargonium aconitophyllum E.& Z.

Pelargonium acomitophyllum var angustisectum Kunth.

Pentanisia variabilis Harv.

Perotis indica (Linn Kuntze)

Peucedanum magalis-montanum Sond.

Physalis minima Linn.

Pittosporum viridiflorum Simms.

Plectronia mundtiana (Ch.& Chl.) Pappe.

Plumbago capensis Thunb.

Pogonarthria squarrosa (Licht) Pilg.

Polygala abyssinica R.Br.

P. gracilenta Burtt Davy.

Portulaca oleracea Linn.

Protea caffra Meisn.

P. hirta Klotzch.

P. Rouppelliae Meisn.

Raphionacme divaricata Harv.

Ravenelia MacOwaniana Pazschke.

Rhoicissus cuneifolia (E.& Z) Planch.

Rhus Gueinzii Sond.

R. c.f.mucronata Thunb.

Rhynchelytrum repens (Willd) C.E.Hubb.

R. setifolium Cheiv.

Royena pallens Thunb.

R. Wilmsii Guerke.

Sanseviera thyrsiflora Thunb.

Sarcostemma viminale R.Br.

Scabiosa anthemifolia E.& Z.

Schizachyrium semiberbe Nees.

Schkuhria bonariensis H.& V.

Scilla lanceaefolia Baker.

S. ovatifolia Baker.

Scolopia Zeyheri Sim.

Secamone Alpini Schultes.

Senecio coronatus Harv.

S. laevigatus Thunb.

S. pentactinus Klatt.

Senecio serra Sond.

S. succosus C.E.Moss.

S. venosus Harv.

Setaria sp.

Sida sp.

Silene oliveriana Burch.

Solanum capense Linn.

Spermacoce dibrachiata Oliver.

Sphenostylis angustifolia Sond.

Sporobolus fimbriatus Nees.

S. indicus R.Br.

Stiburus alopecuroides (Hack) Stapf.

Stoebe vulgaris Levyns.

Striga elegans Benth.

Tagetes minuta Lam.

Tarchonanthus camphoratus Linn.

Tephrosia auriantiaca R.G.N.Young.

Teucrium capense Thunb.

Themeda triandra Forsk.

Trachypogon plumosus Nees.

Tragus berteronianus Schult.

Tribulus terrestris Linn.

Tricholaena setifolia Stapf.

Trichoneura grandiglumis Ekman.

Tristachy hispida (Thunb) Schum.

T. Rehmanni Hack. ex. Schinz.

Tulbaghia leucantha Baker.

T[illegible]ytrum squarrosum Hack.

Urginea multisetosa Baker.

Urochloa helopus Stapf.

Ursinea annua Less.

Vangueria euonymoides Schweinf.

V. infausta Burch.

Vernonia

V. Kraussii Sch Bip.

V. monocephala Harv.

Wahlenbergia undulata A.D.C.

Walafrida densiflora Rolfe.

Xanthium spinosum Linn.

X. strumarium Linn.

Zinnia pauciflora Linn.

Zizyphus mucronata Willd.

Z. zeyheriana Sond.

Walafrida densiflora Rolfe.

Xanthium spinosum Linn.

X. strumarium Linn.

Zinnia pauciflora Linn.

Zizyphus mucronata Willd.

Z. zeyheriana Sond.

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SOME OBSERVATIONS ON THE NATURE AND CAUSES OF SECONDARY SUCCESSION ON CERTAIN AREAS AT FRANKENWALD AND IN THE HIGHVELD OF THE TRANSVAAL.

PHOTOGRAPHS, SEED-PHOTOGRAPHS, HISTOGRAMS, GRAPHS, ROOT BISECT CHARTS AND PHOTOGRAPHS.

(To accompany the above thesis.)

H. Trevor Jones.

PHOTOGRAPHS.

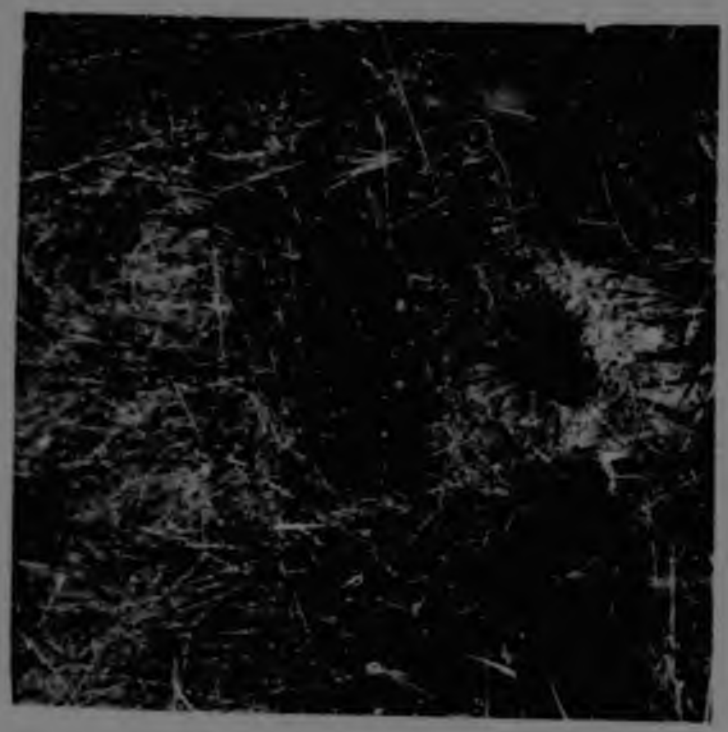
Photograph No. 1.

Recently ploughed fallow. Note colonisation by Cyperus esculentus runners - very abundant here. Also one or two plants of Conyza ambigua and Erigeron [illegible]sis.



Photograph No. 2.

Eragrostis chalcantha as found in Purple Veld. Note the small size of the plant and the space between the large tussocks, in which it occurs.



Photograph No.).

Two Eragrostis chalcantha plants. The small one is from Purple Veld, the large one from fallow land. Note the great difference in growth and flowering.



Photograph No. 4.

Spread of Digitaria trichelaenoides due to moderately heavy grazing. Note the prostrate habit and high cover.



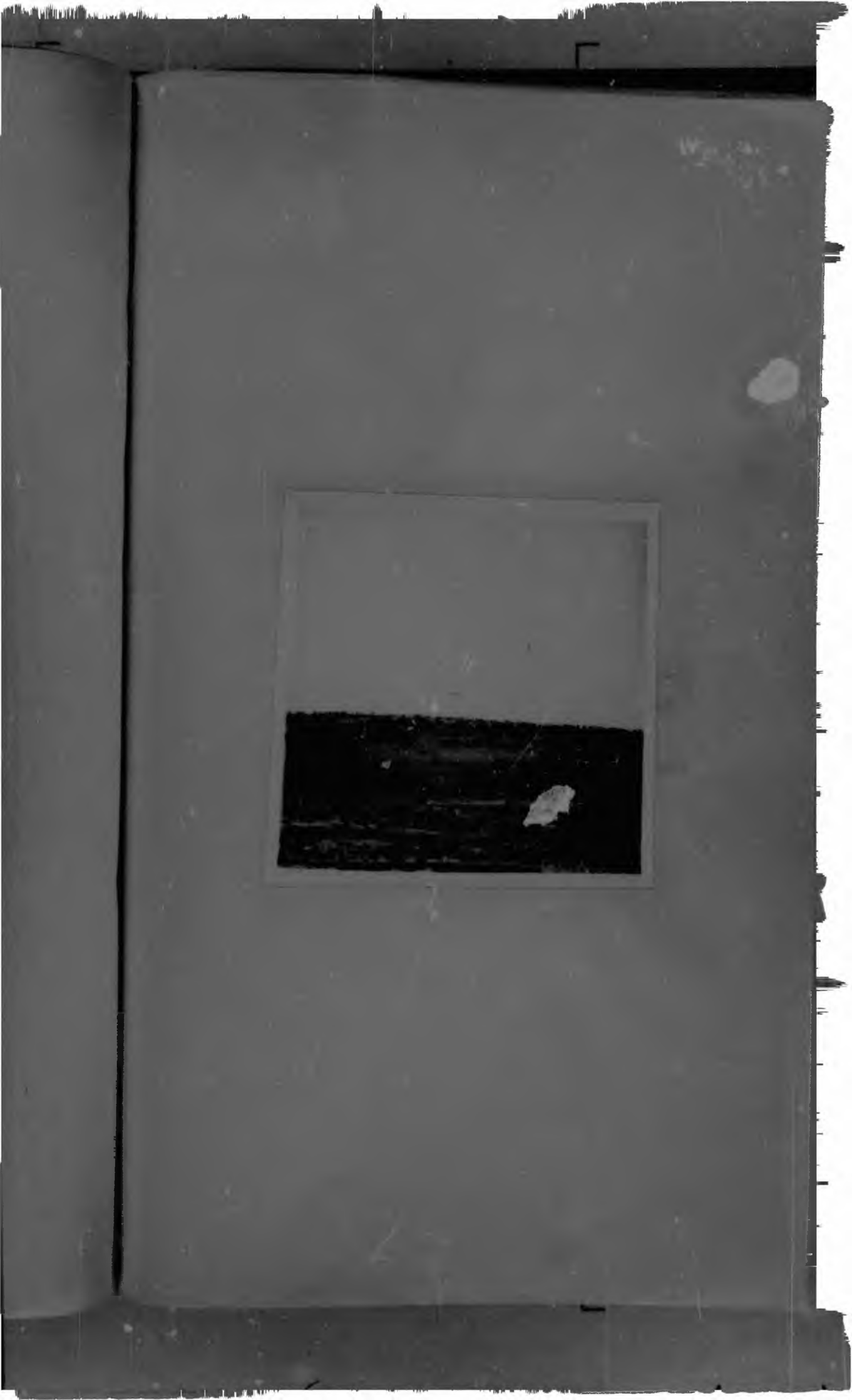
Photograph No. 5.

Plot protected for 30 years. Note extreme rankness of growth. Pralytrum squarrosum, Loudetia simplex and Trachypogon plumosus. Note deposit of dead leaves at the feet of figure.



Photograph No. 6.

Protea caffra Open Woodland near Roberts Heights. Growing almost exclusively on the Southern aspect - shown here. Note tendency for this vegetation type to cling to higher ground only.



Photograph No. 7.

Termitarium. Invasion of scrub species. Ziziphus zeyheriana growing on the mound and Z. mucronata seedling just beyond. Note zone of Vernonia Krausii (in flower) round the termitarium.



Photograph No. 6.

Termitaria. Invasion of scrub species. In foreground, termitarium with Cynodon dactylon in centre and a number of Gymnosporia buxifolia seedlings next to it. In background, Royena pallens tree on termitarium.



Photograph No. 9.

Invasion of scrub species. Acacia robusta and many seedlings growing on [illegible] and denuded by Hodotermes and sheep.



Photograph No. 10.

Invasion of scrub species. Acacia Karroo seedling in foreground which has grown from seed deposited by the large tree in background.



Photograph No. 11.

Pioneer Euclea lanceolata. Note remains of Asparagus sp. protruding from the tree-clump, immediately behind figure and near the ground. On the left is a specimen of Ehretia hottentotica, somewhat lower than the Euclea. Seedlings of Scolopia Zeyheri also occurred here with Lantana salvifolia.



Photograph No. 12.

Invasion of scrub species. Next to figure: Asparagus sp. protruding from a small specimen of Rhus e.f. emarginata which is growing up and choking the latter. Reyena pallens in background.



Photograph No. 13.

Rhoicissus cuneifolia spreading over [illegible] of the Climax Scrub Vegetation in the Klipriversberg area.



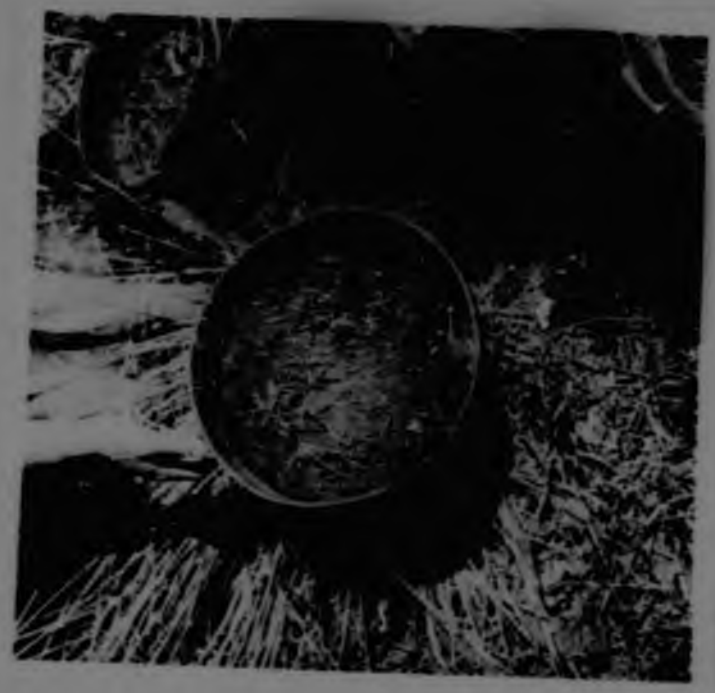
Photograph No. 14.

Seed-head of Trichoneura grandiglumis. The disseminules of this species are dispersed by the entire seed-head being rolled over the veld by the wind.



Photograph No. 15

Germination of Cynodon dactylon seed. The tin was planted with fruits of Zizyphus mucronata, in ordinary veld soil. The Cynodon seedlings came up with a number of weed seedlings.



Photograph No. 16.

Exposed root of Celtis rhamnifolia showing development of shoots. The effect is especially important in eroded riverine areas where trees developing vegetatively are able to bind the soil against further erosion.



Photograph No. 17.

Exposed web of roots of the superficial lateral systems of Acacia Karroo, Celtis rhamnifolia and possibly Ziziphus mucronata. Root activity is intense in superficial soils in scrub areas.



Photograph No. 16.

Effect of fire on flowering of Trachypogon plumosus. A fire-break in Purple Veld. Note heavy flowering on unburnt portion on left - mostly flowering culms of Trachypogon plumosus - and very sparse flowering in burnt strip.



Photograph No. 19.

Effect of mowing on flowering of Trachypogon plumosus. Note heavy flowering in un-mown Purple Veld and sparse flowering in mown area.



[illegible] PHOTOGRAPHS.

Text Photograph No. 1.

Diaspeminule of Trachypogon plumosus. Note long twisted awn, twice bent. Note also spiked callus with stiff retrorse hairs.

Millimetre scale.

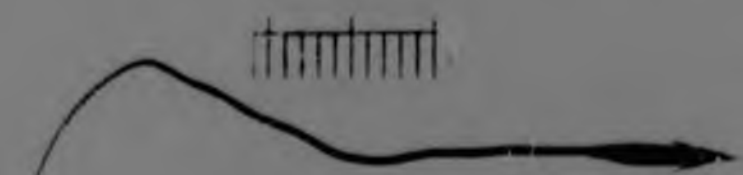
Seed Photograph No. 2.

Dissominule of Themeda triandra. Note very sharp spiked callus with retrorse hairs and long twisted awn, bent in two places.

Millimetre scale.



2.



Semi Photograph No. 1.

Dissemimule of Urelytrum squarrosum. Note very blunt callus with few weak hairs, straight untwisted awn with no bends.

Millimetre scale.

Key Photograph No. 4.

Dissections of Aristida congesta. Note tripartite, twisted awn and spikelet callus with setaceous hairs.

Millimetre scale.

3



4



Seed Photograph No. 6.

Disseminule of Schizachyrium semiberbe. Note bluntly-pointed callus with short weak retrorse hairs, weak awn and sterile floret.

Millimetre scale.

Seed Photograph No. 7.

Dissominule of Panicum natalense. Note complete absence of any dispersal mechanisms.

Millimetre scale.


7


6.

Seed Photograph No. 3.

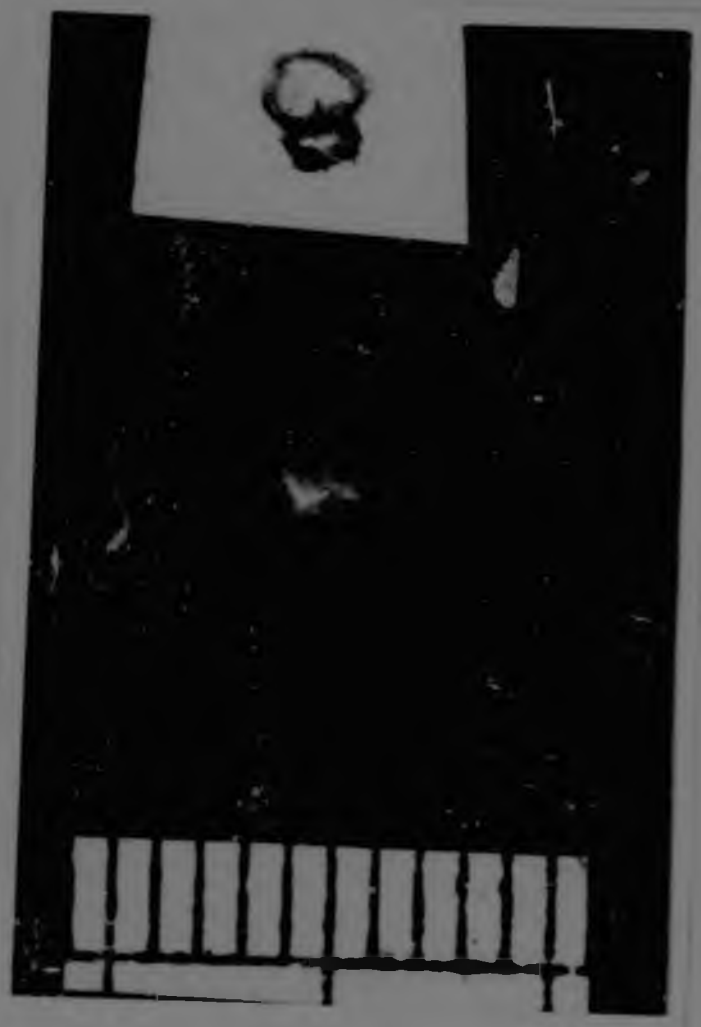
Disseminule of Rhynsoletrum repens. Note long filmy hairs covering glumes.

Millimetre scale.

Seed Photograph No. 9.

Disseminule of Chloris virgata. Note fairly well-developed hairs on upper edge of glumes.

Millimetre scale.





Micro Photograph No. 10.

Disseminule of Pogonarthria squarrosa. Note complete absence of any dispersal mechanisms.

Millimetre scale.

Seed Photograph No. 11.

Seed of Amaranthus Paunbergii. Note size and absence of any dispersal mechanisms.

Millimetre scale.



11



10

Real Photograph No. 12.

Disseminule of Bidens pilosa. Note barbs at one end which aid in dissemeal.

Millimetre scale.

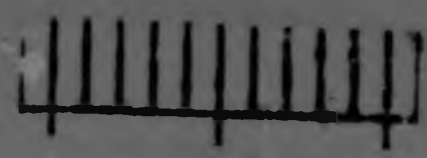
Seed Photograph No. 13.

Dissceminule of Conyza ambigua. Note para-
chute-like pappus.

Millimetre scale.



13



12

Seed Photograph No. 14.

Seed of Datura stramonium. Note absence of dispersal mechanisms.

Millimetre scale.

Seed Photograph No. 15.

Fruit (disseminule) of Zizyphus mucronata.
Note large size, lack of dispersal mechanisms,
and fleshy character.

Millimetre scale.



15



14

Seed Photograph No. 16.

Seed of Acacia robusta. Note lack of dispersal mechanisms and large size.

Millimetre scale.

Seed Photograph No. 17.

Seed of Acacia saligna. Note lack of dispersal mechanisms.

Millimetre scale.

17

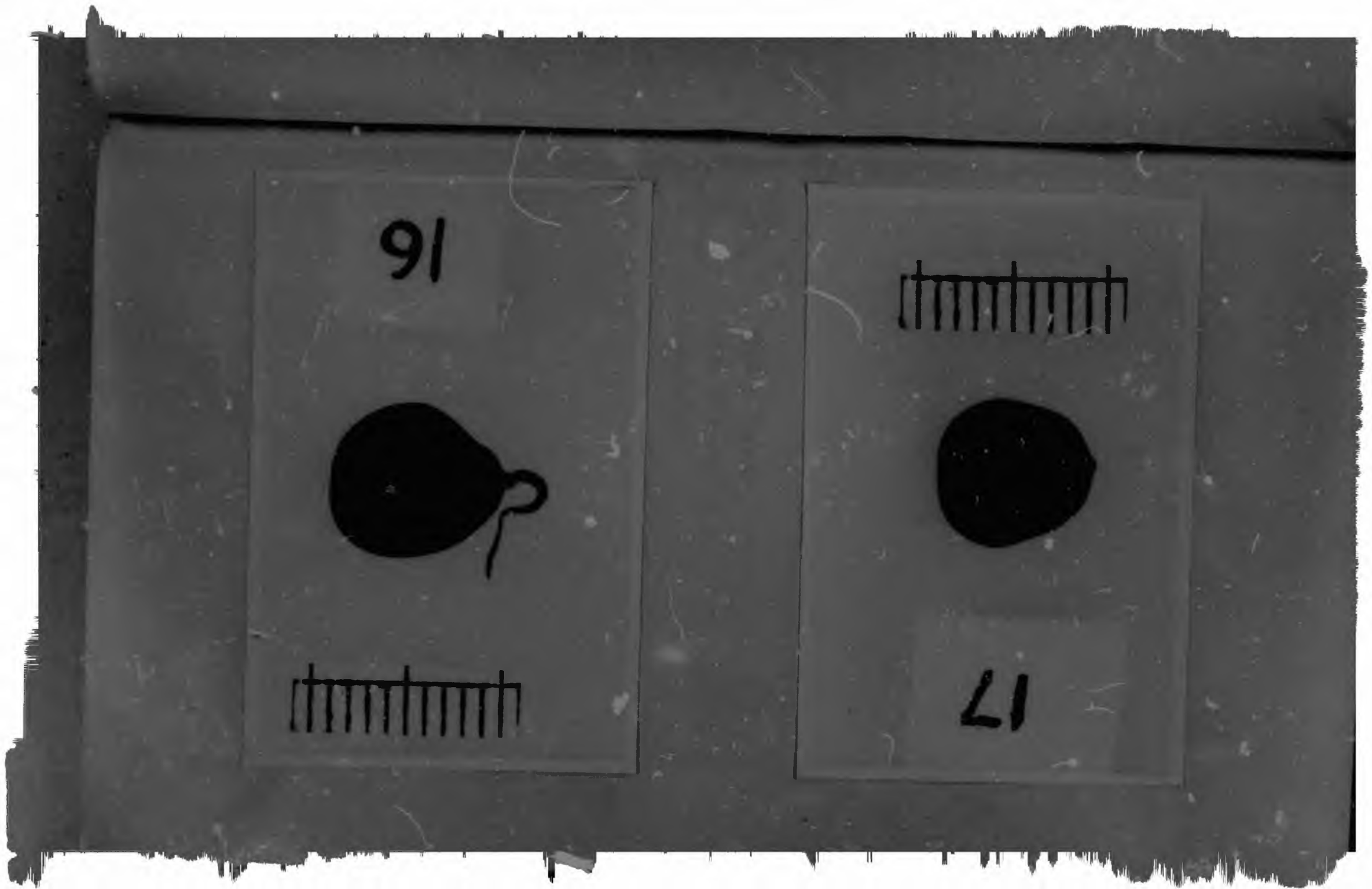








16


91
17

Spod Photograph No. 15.

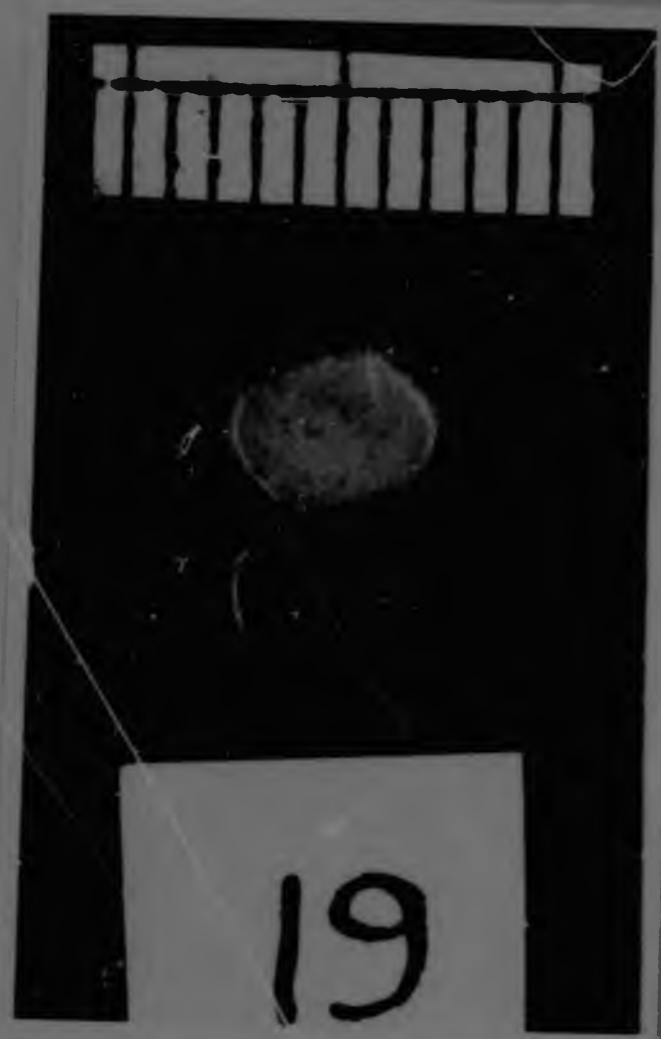
Fruit of Vangueria infausta. Note large size, fleshy character and lack of dispersal mechanisms.

Millimetre scale.

Ref Photograph No. 12.

Fruit of Rhus Gueinzii. Note absence of dispersal mechanisms.

Millimetre scale.



19



18

Seed Photograph No. 22.

Fruit of Guazuma burkeana. Note fleshy character, comparatively large size and absence of dispersal mechanisms.

Millimetre scale.

Seed Photograph No. 21.

Dehiscing fruit of Fagara angalis-montana with seed. Note comparatively small seed and absence of mechanisms.

Millimetre scale.



21



20



21

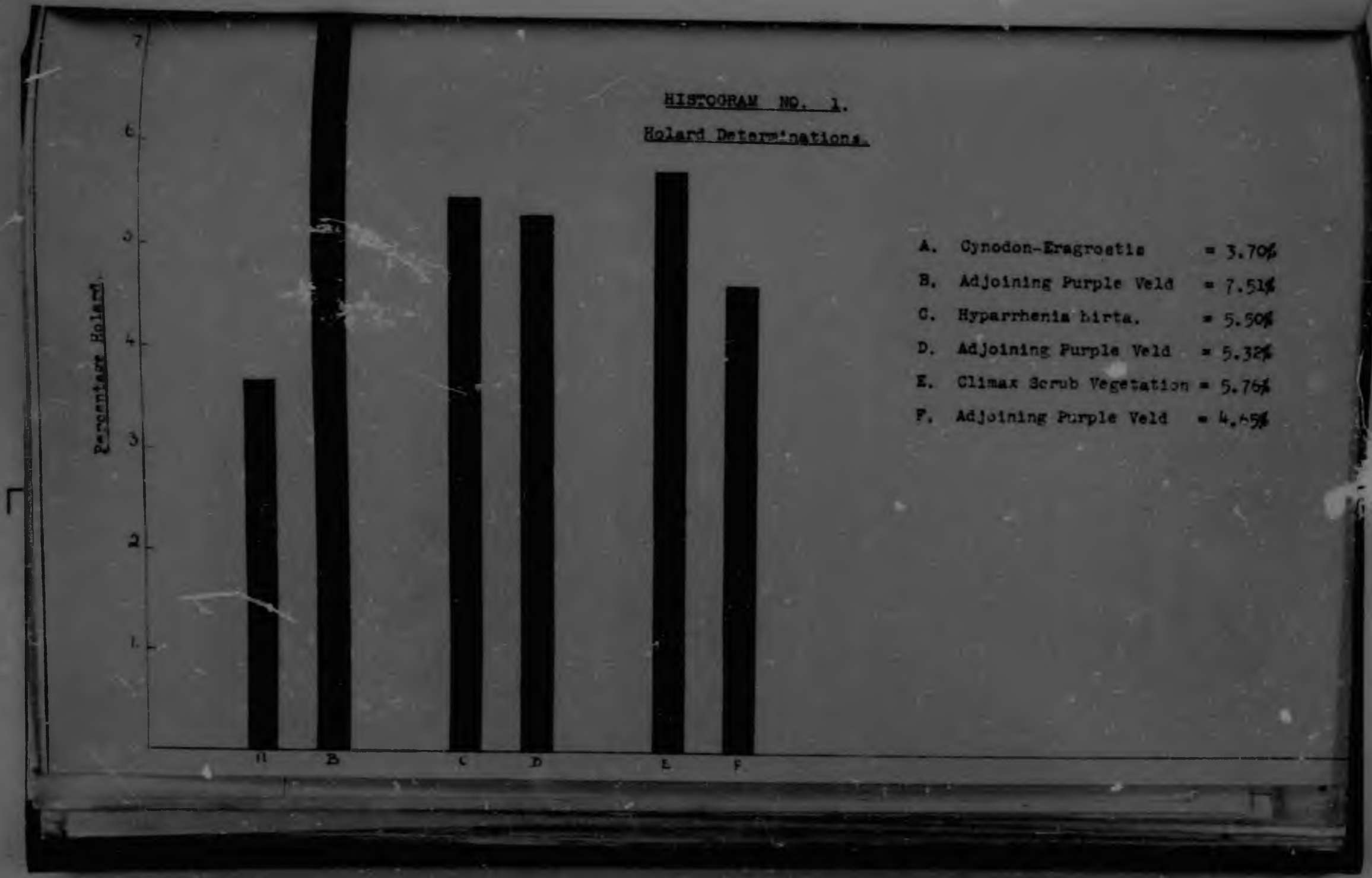


20

HISTOGRAMS AND GRAPHS.

HISTOGRAM NO. 1.

Holard Determinations.



A. Cynodon-Eragrostis = 3.70%

B. Adjoining Purple Veld = 7.51%

C. Hyparrhenia hirta. = 5.50%

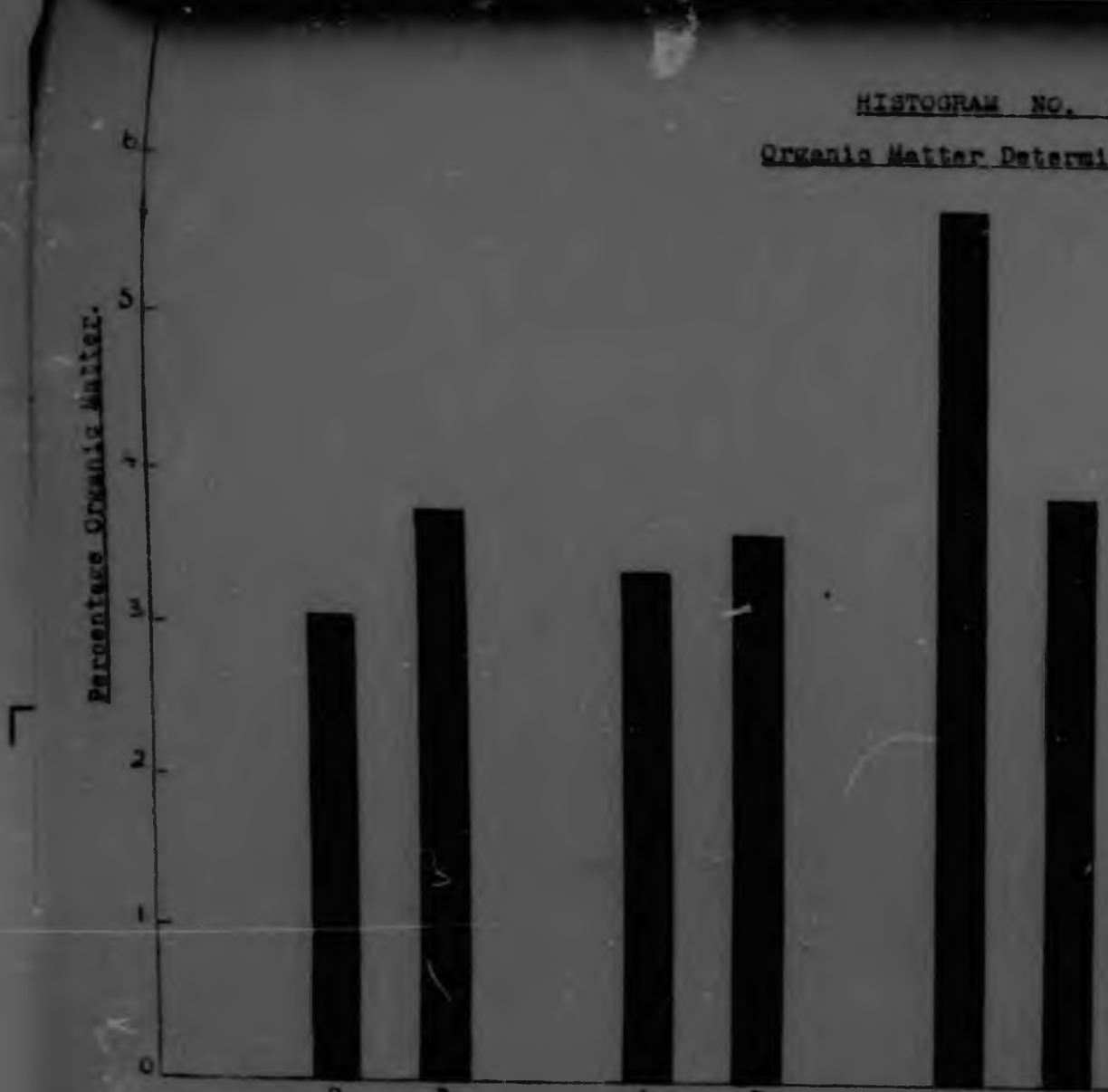
D. Adjoining Purple Veld = 5.32%

E. Climax Scrub Vegetation = 5.76%

F. Adjoining Purple Veld = 4.65%

HISTOGRAM NO. 2.

Organic Matter Determinations.



A. Cynodon-Eragrostis Veld = 3.06%

B. Adjoining Purple Veld = 3.77%

C. Hyparrhenia hirta Veld = 3.36%

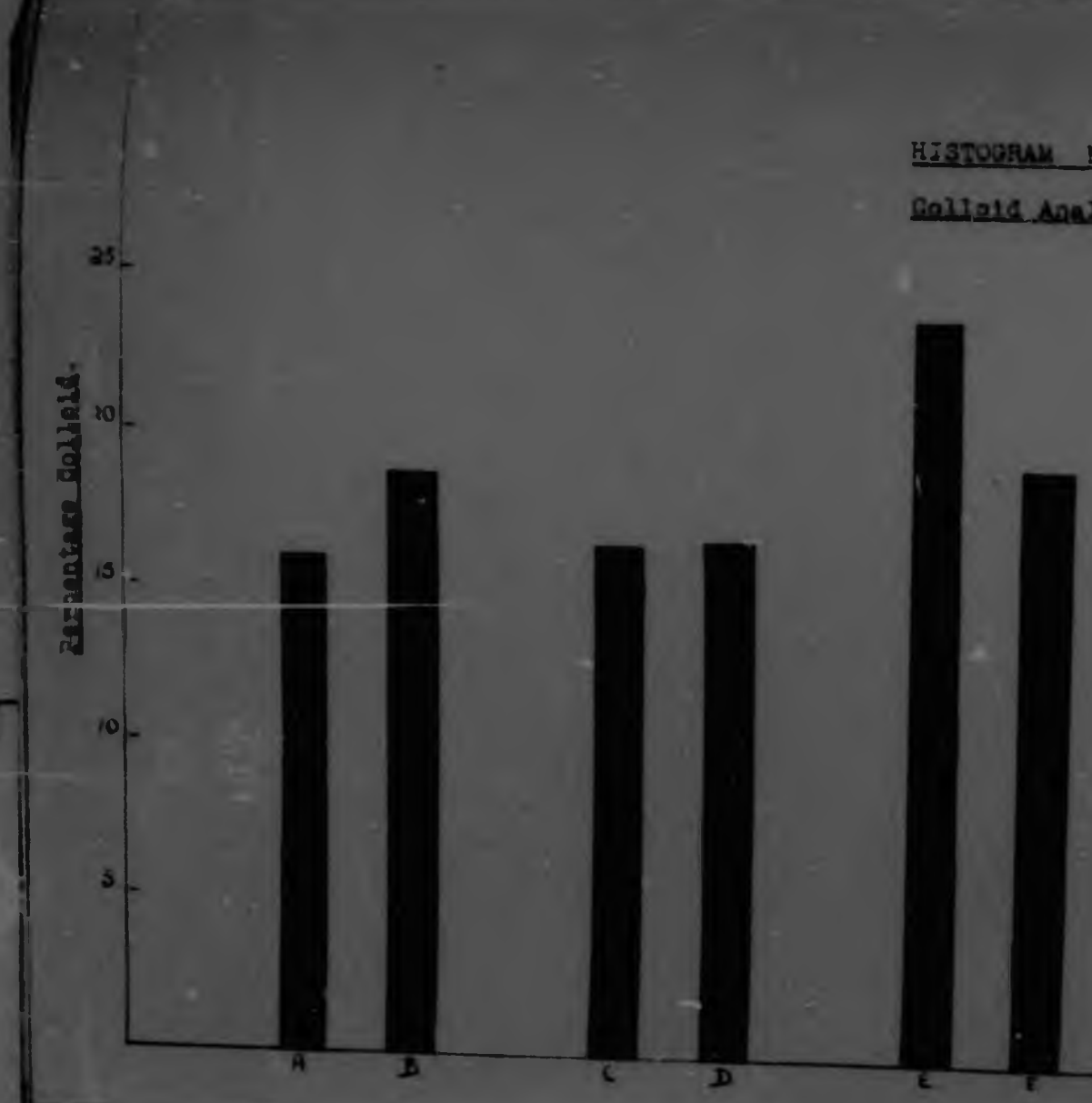
D. Aljoining Purple Veld = 3.61%

E. Climax Scrub Vegetation = 5.70%

F. Adjoining Purple Veld = 3.88%

HISTOGRAM NO. 3.

Colloid Analyses.



A. Cynodon-Eragrostis Veld = 16.14%

B. Adjoining Purple Veld = 16.92%

C. Hyparrhenia hirta Veld = 16.61%

D. Adjoining Purple Veld = 16.78%

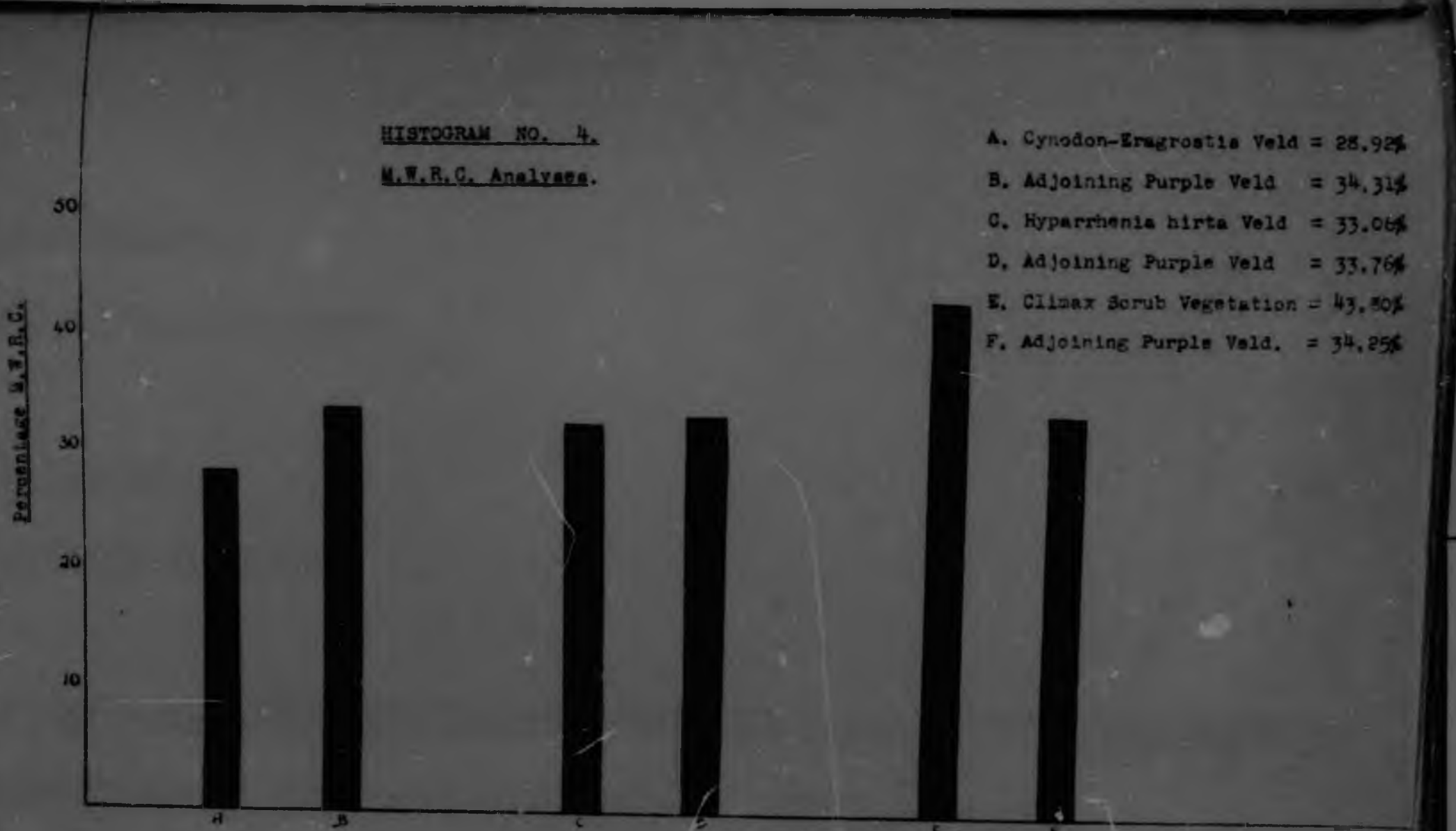
E. Climax Scrub Vegetation = 24.37%

F. Adjoining Purple Veld = 19.36%

HISTOGRAM NO. 4.

M.W.R.C. Analyses.

A. Cynodon-Eragrostis Veld = 28.92%
B. Adjoining Purple Veld = 34.31%
C. Hyparrhenia hirta Veld = 33.06%
D. Adjoining Purple Veld = 33.76%
E. Climax Scrub Vegetation = 43.80%
F. Adjoining Purple Veld. = 34.25%



HISTOGRAM NO. 5.

Soil Permeability Determinations.

A. Cynodon-Eragrostis Veld = 43m.33s.

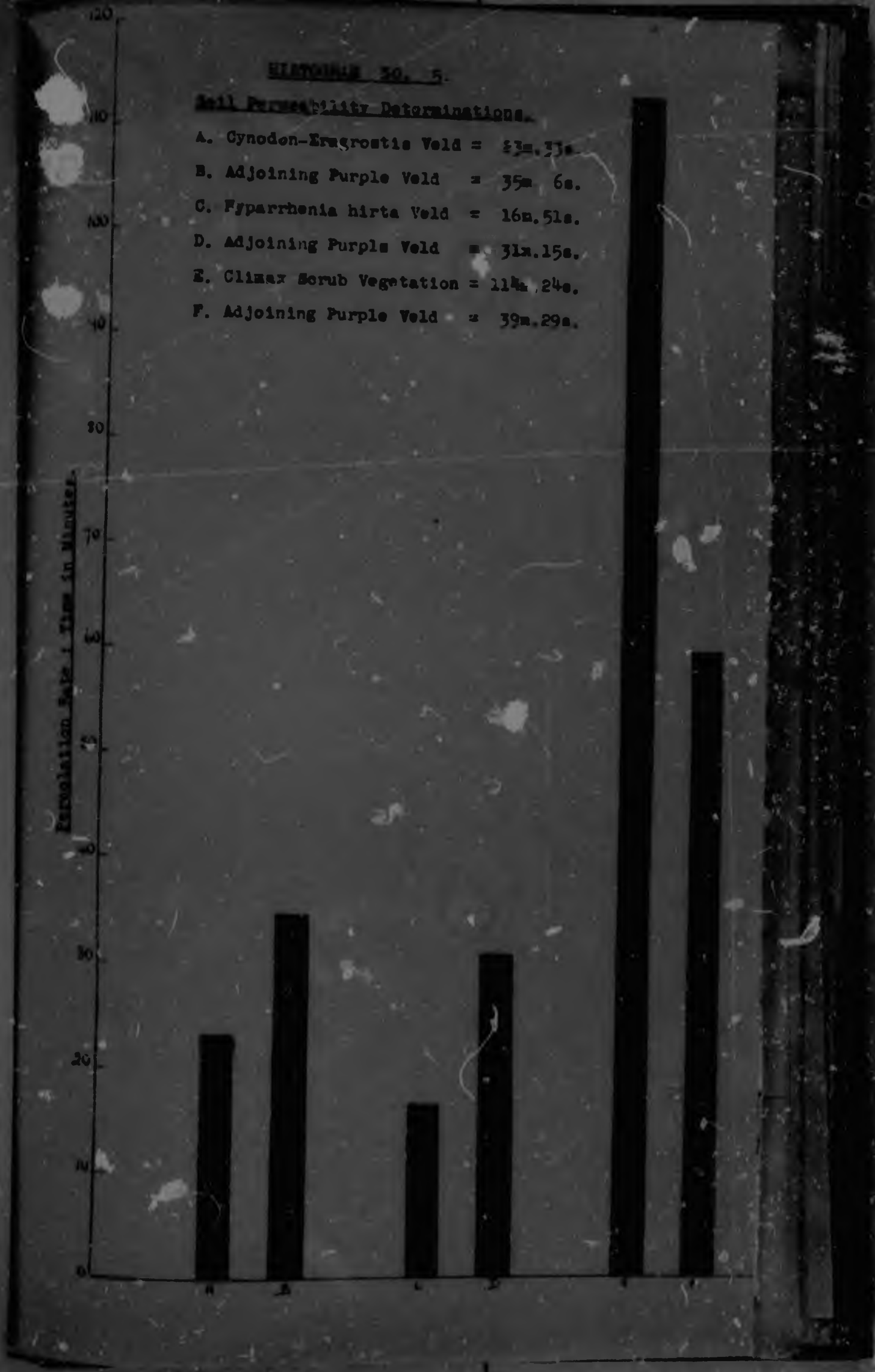
B. Adjoining Purple Veld = 35m. 6s.

C. Hyparrhenia hirta Veld = 16m.51s.

D. Adjoining Purple Veld = 31m.15s.

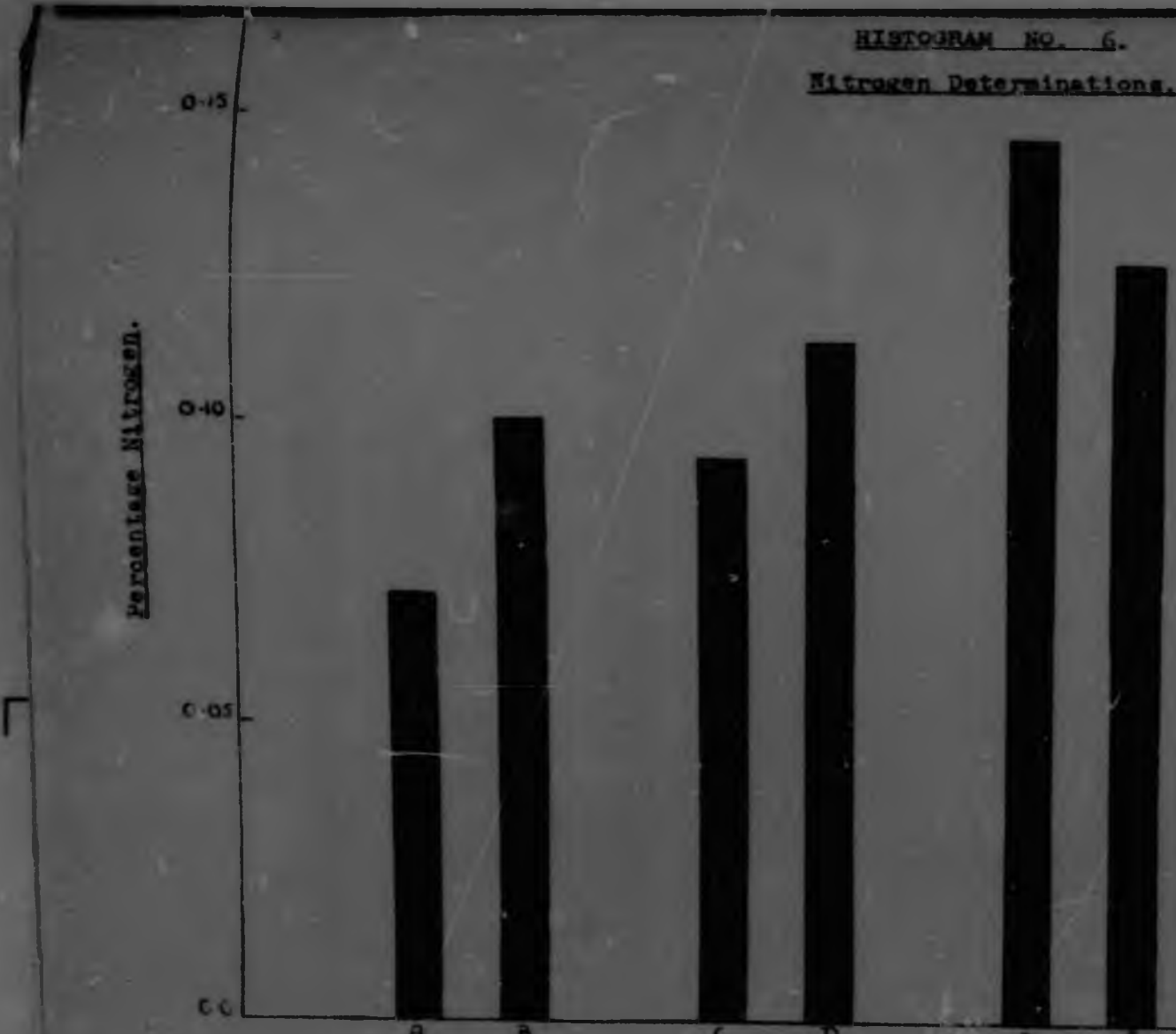
E. Climax Scrub Vegetation = 114m.24s.

F. Adjoining Purple Veld = 39m.29s.



HISTOGRAM NO. 6.

Nitrogen Determinations.



A. Cynodon-Eragrostis Veld = 0.0716%

B. Adjoining Purple Veld = 0.1008%

C. Hyparrhenia hirta Veld = 0.0939%

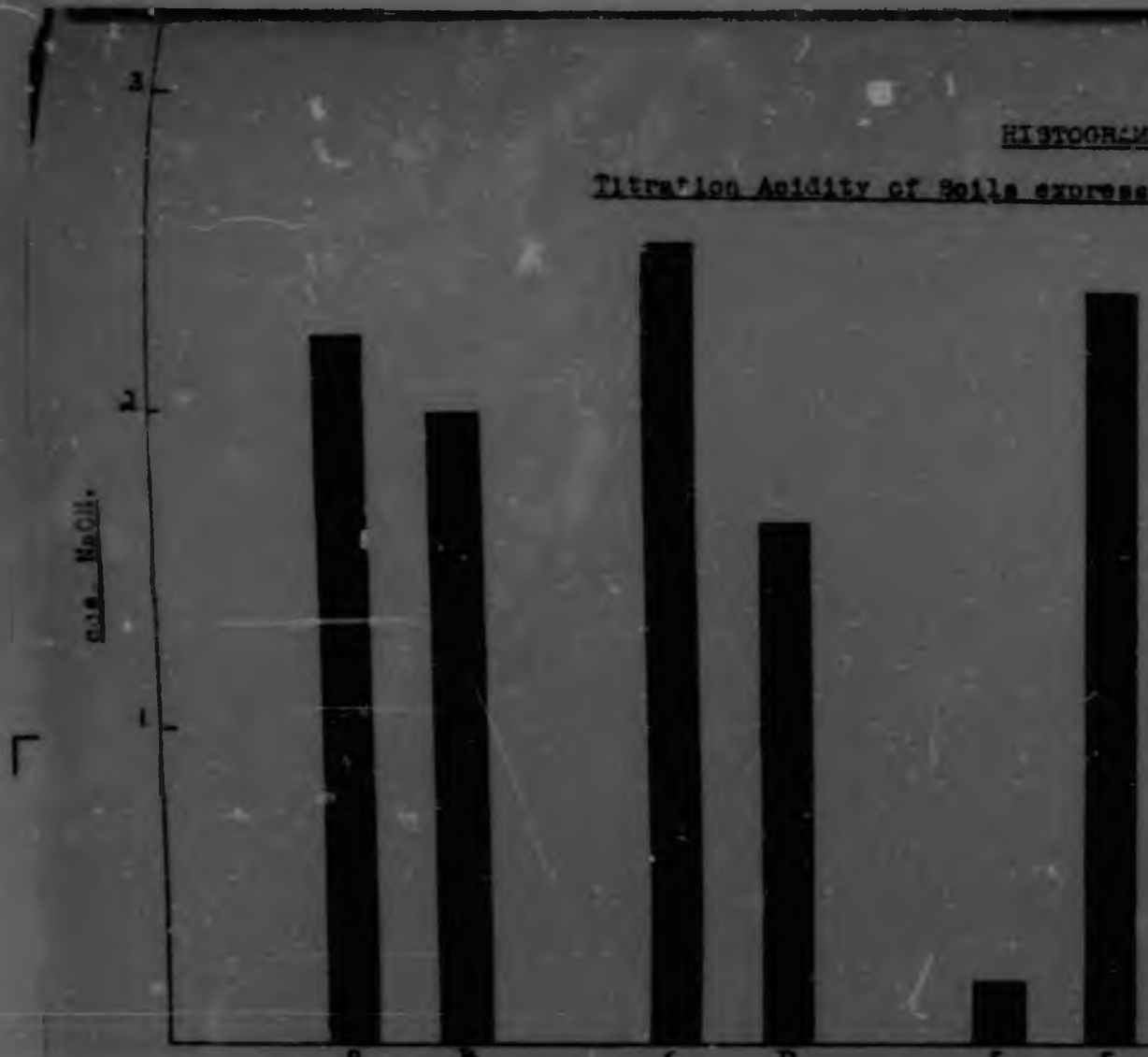
D. Adjoining Purple Veld = 0.1154%

E. Climax Scrub Vegetation = 0.1467%

F. Adjoining Purple Veld = 0.1256%

HISTOGRAM NO. 7.

Titration Acidity of Soils expressed in terms of ccs. of $\frac{1}{10}$ N. NaOH.

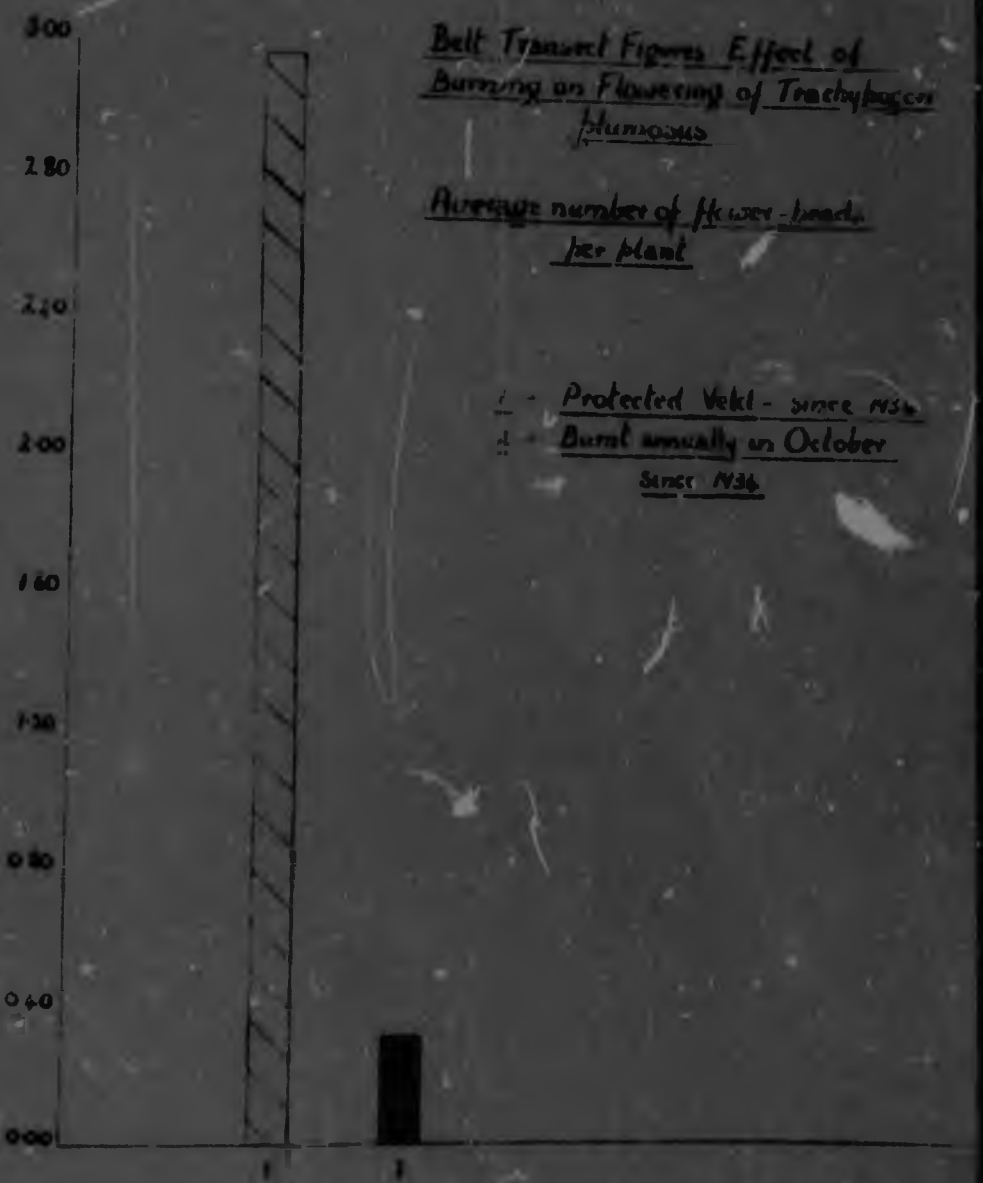


A. Cynodon-Eragrostis Veld = 2.24
B. Adjoining Purple Veld = 2.00
C. Hyparrhenia hirta Veld = 2.52
D. Adjoining Purple Veld = 1.66
E. Climax Scrub Vegetation = 0.14
F. Adjoining Purple Veld = 2.38

HISTOGRAM No. 11.

Belt Transect Figures Effect of Burning on Flowering of Trachypogon plumosus

Average number of flower-heads per plant



1 - Protected Veld - since 1934
2 - Burnt annually in October since 1934

HISTOGRAM NO. 9.

Bell Transect figures. Effect of Burning on Flowering in Trachypogon plumosus.

Average number of flower-heads per plant.



1 - Protected Veld
2 - Veld burned over

HISTOGRAM NO. 30.

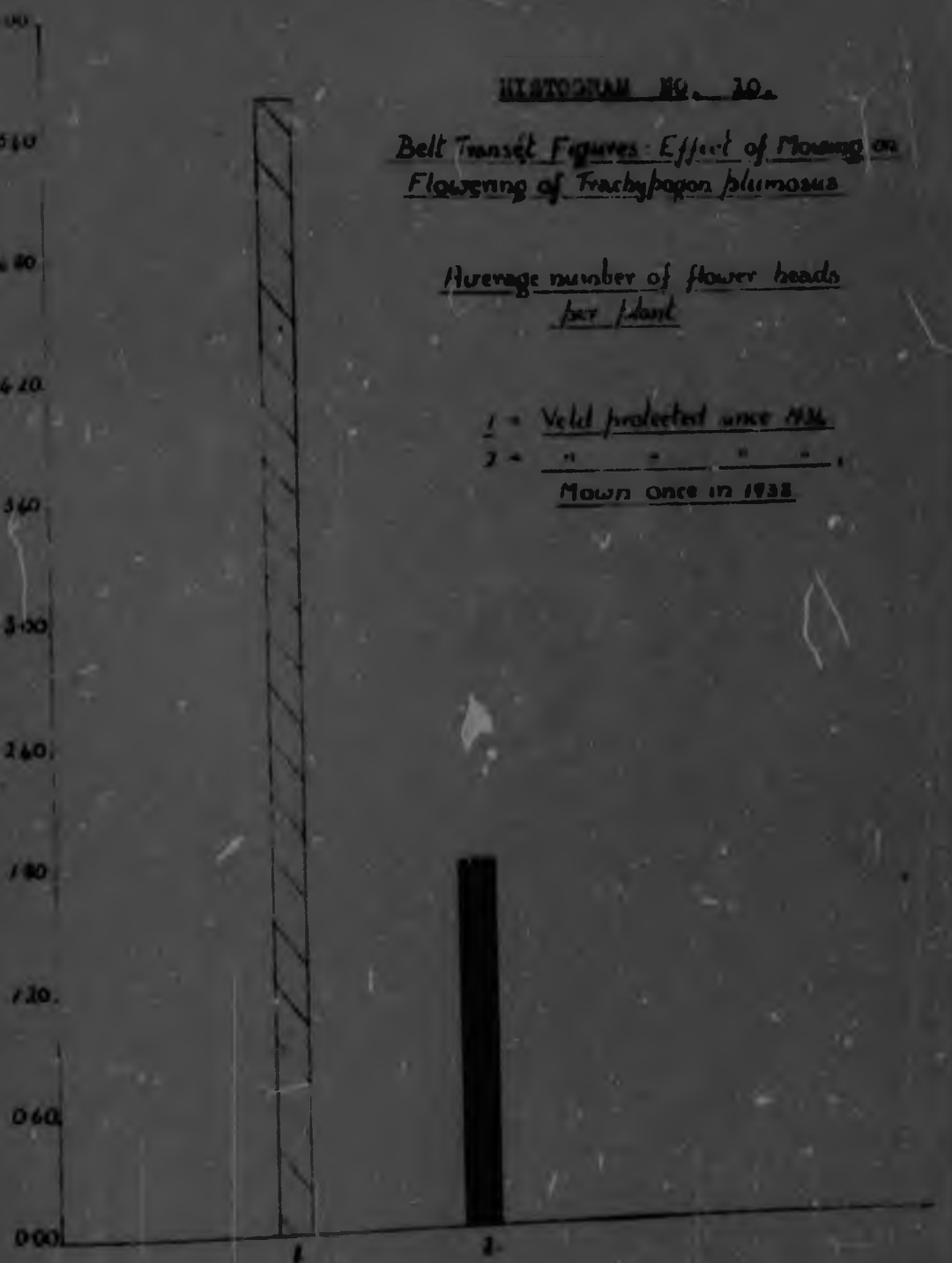
Belt Transect Figures: Effect of Mowing on Flowering of Trachypogon plumosus

Average number of flower heads per plant

1 = Veld protected since 1934

2 = " " " "

Mown once in 1938

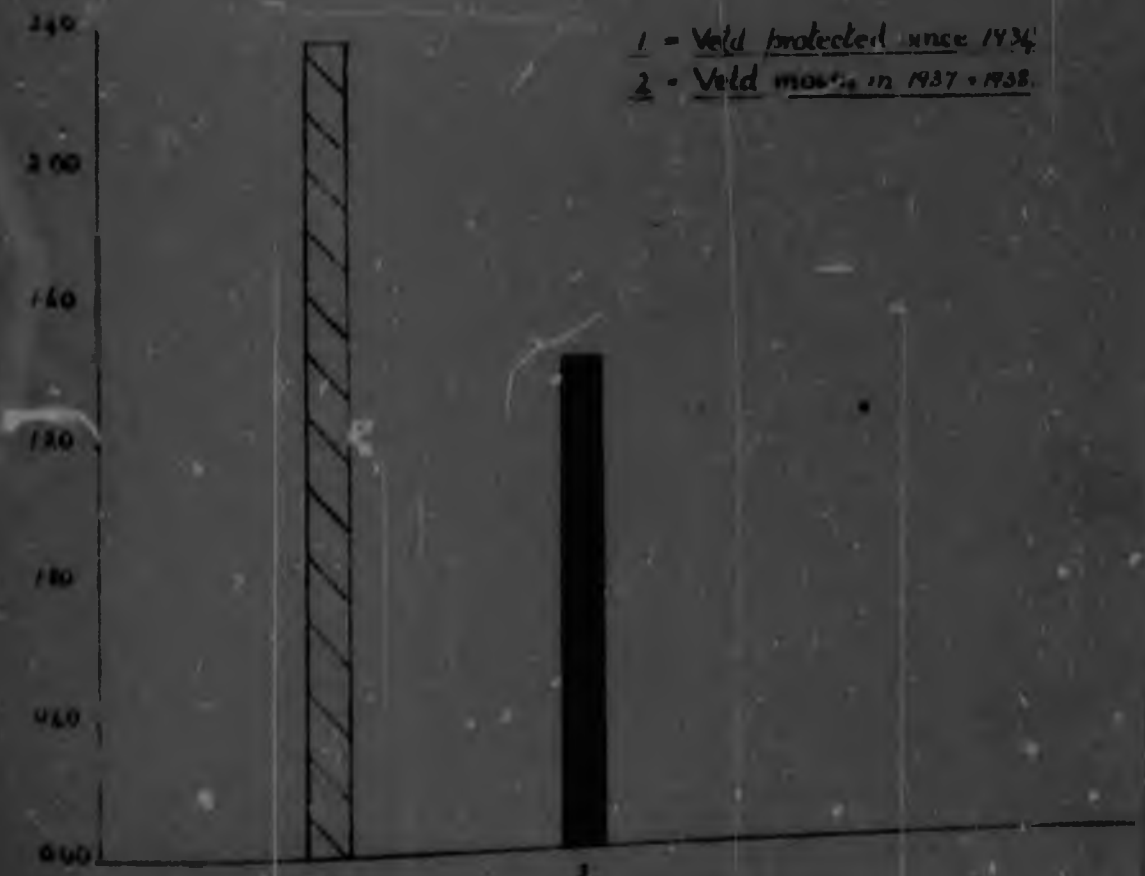


HISTOGRAM NO. 11.

Belt Transect Figures Effect of Mowing on flowering of Tragopogon pluriseus

Average number of flower heads per plant.

1 = Veld protected since 1934
2 = Veld mown in 1937 + 1938.



HISTOGRAM NO. 11.

Belt Transect Figures. Effect of Mowing on flowering of Trachypogon plumosus

Average number of flower heads per plant.

1 = Veld protected since 1934

2 = Veld mown in 1937 + 1938

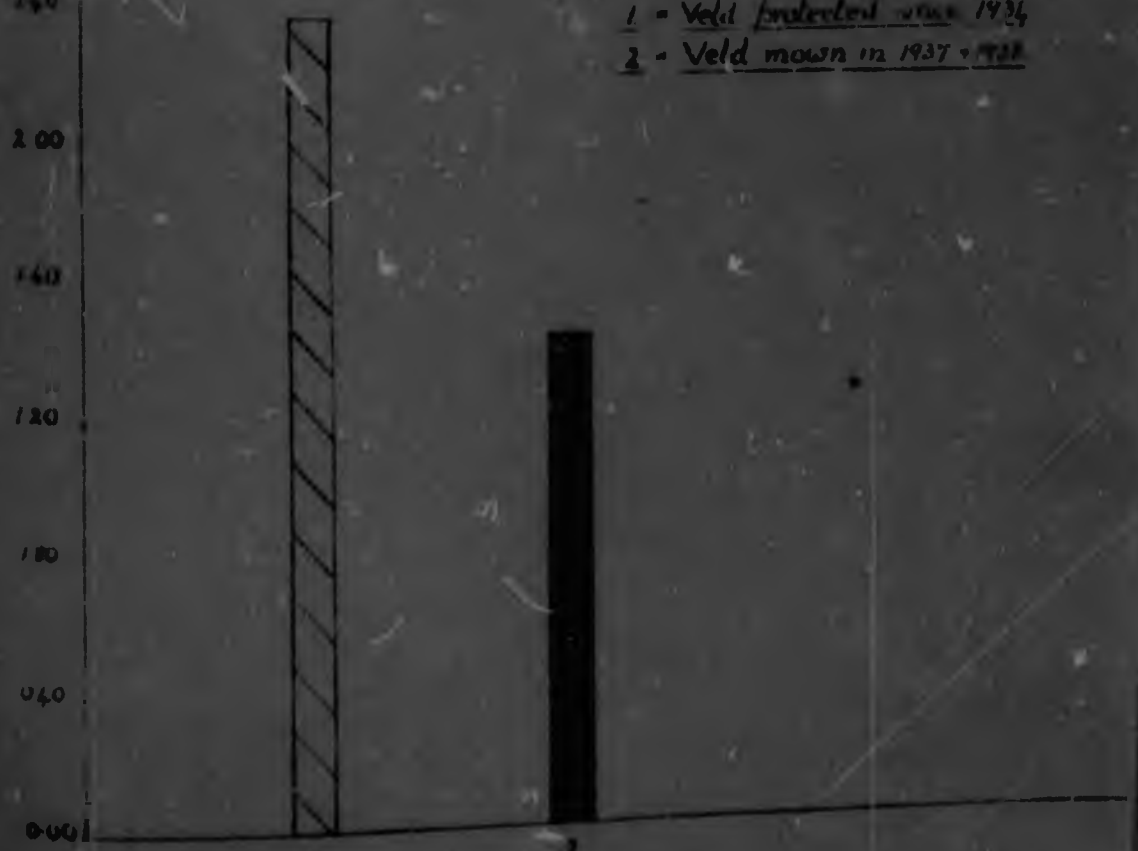


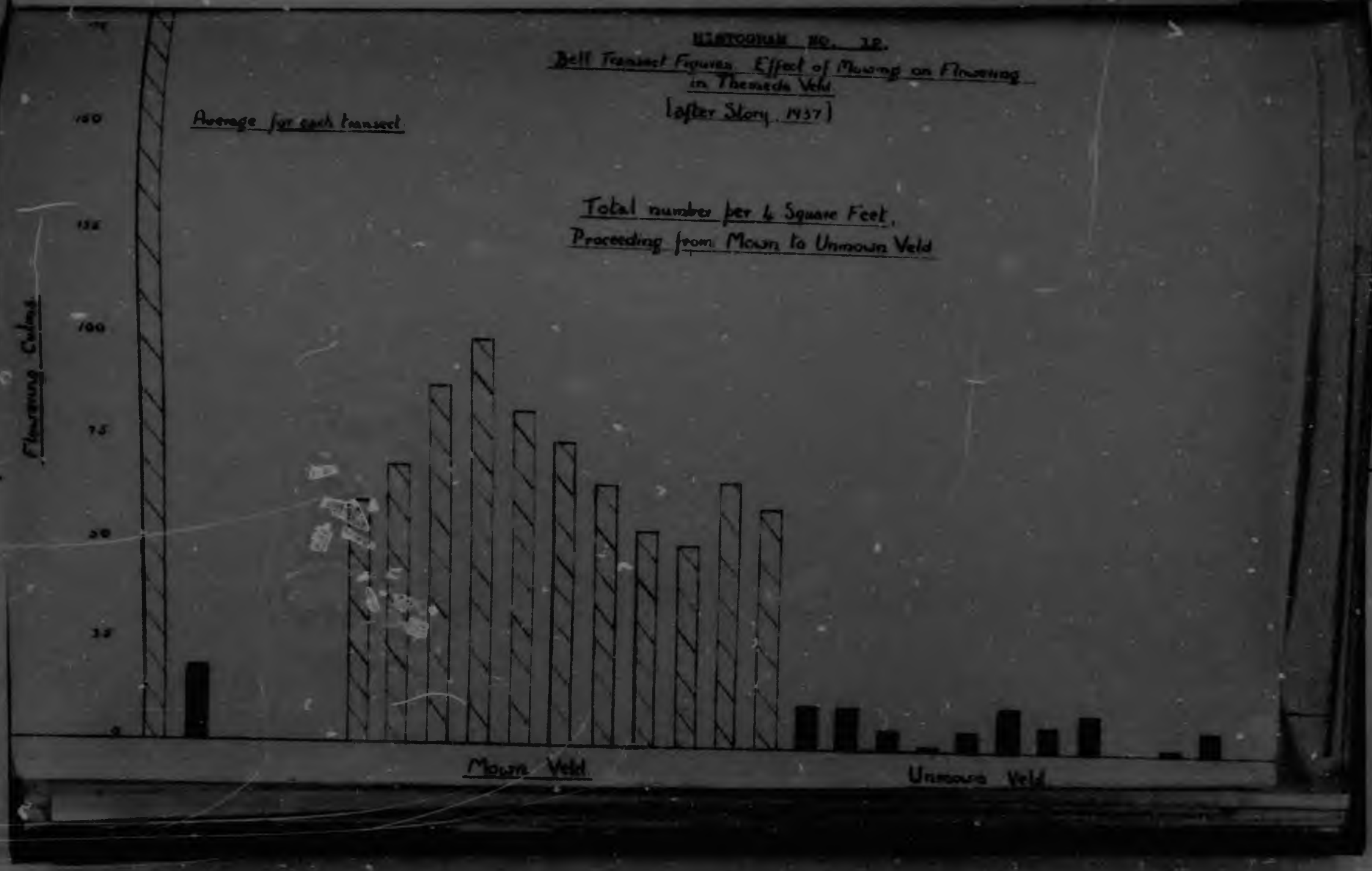
DIAGRAM NO. 12.

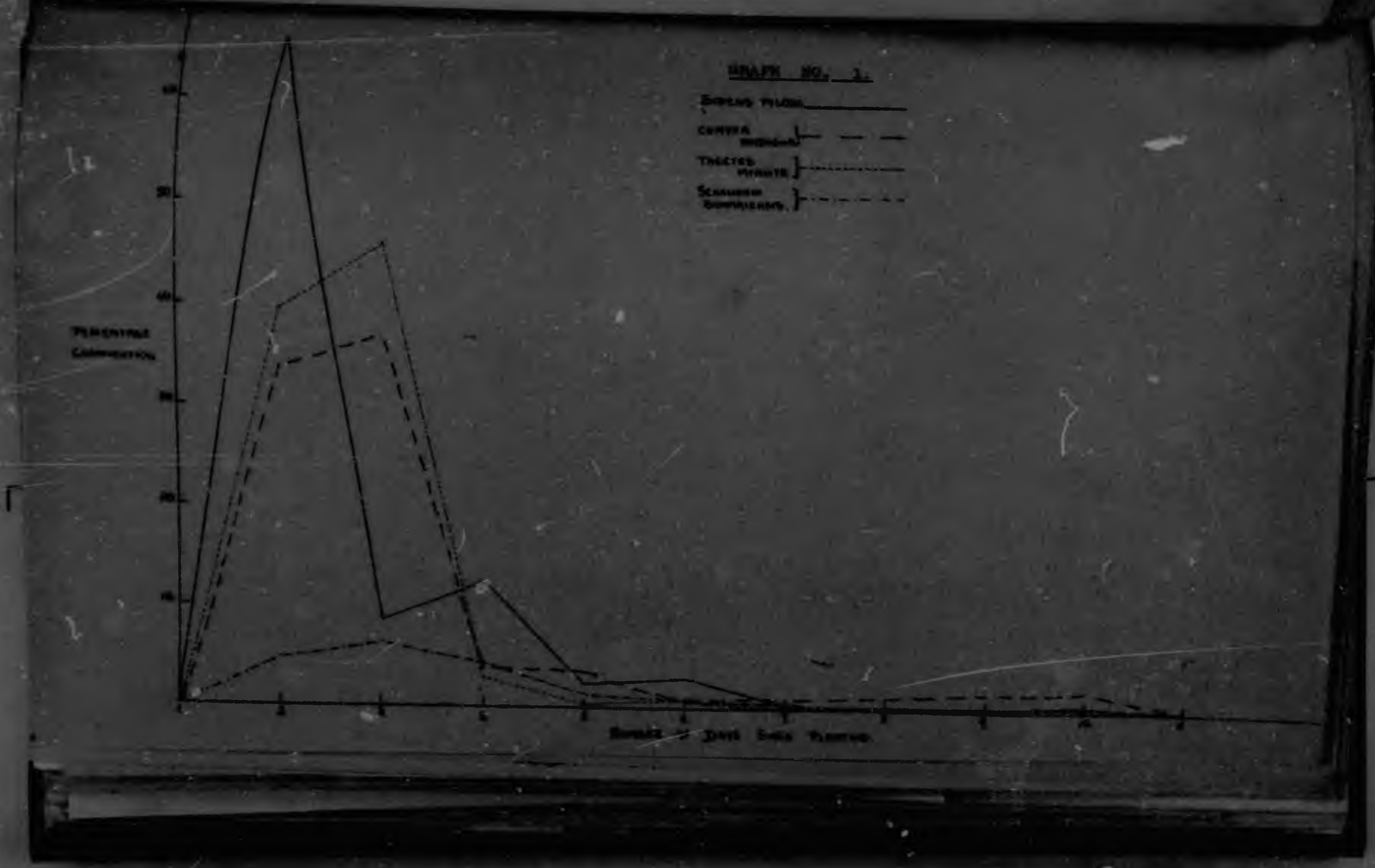
Bell Transect Figures. Effect of Mowing on Flowering in Thesseda Veld

(after Story. 1937)

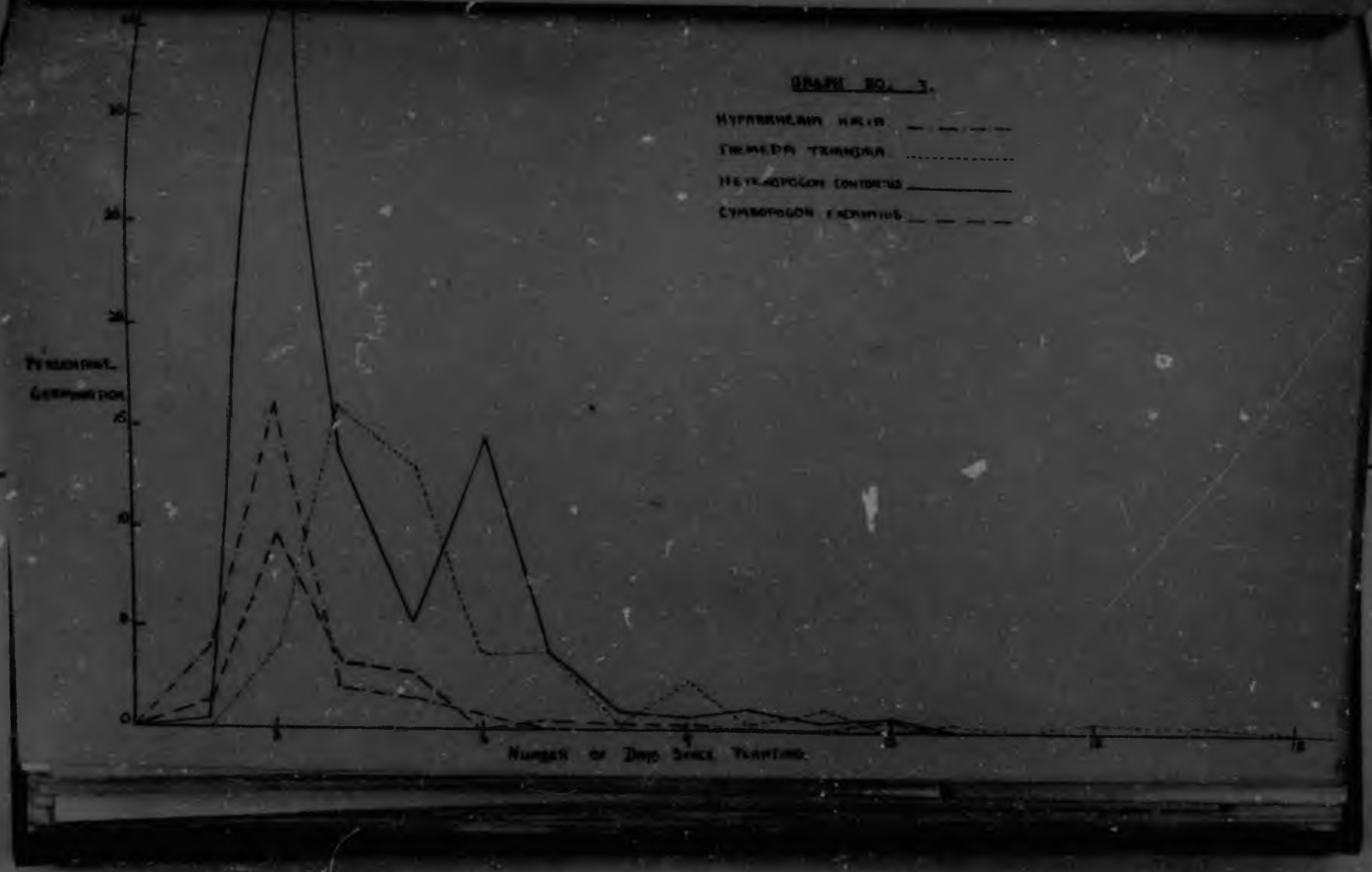
Average for each transect

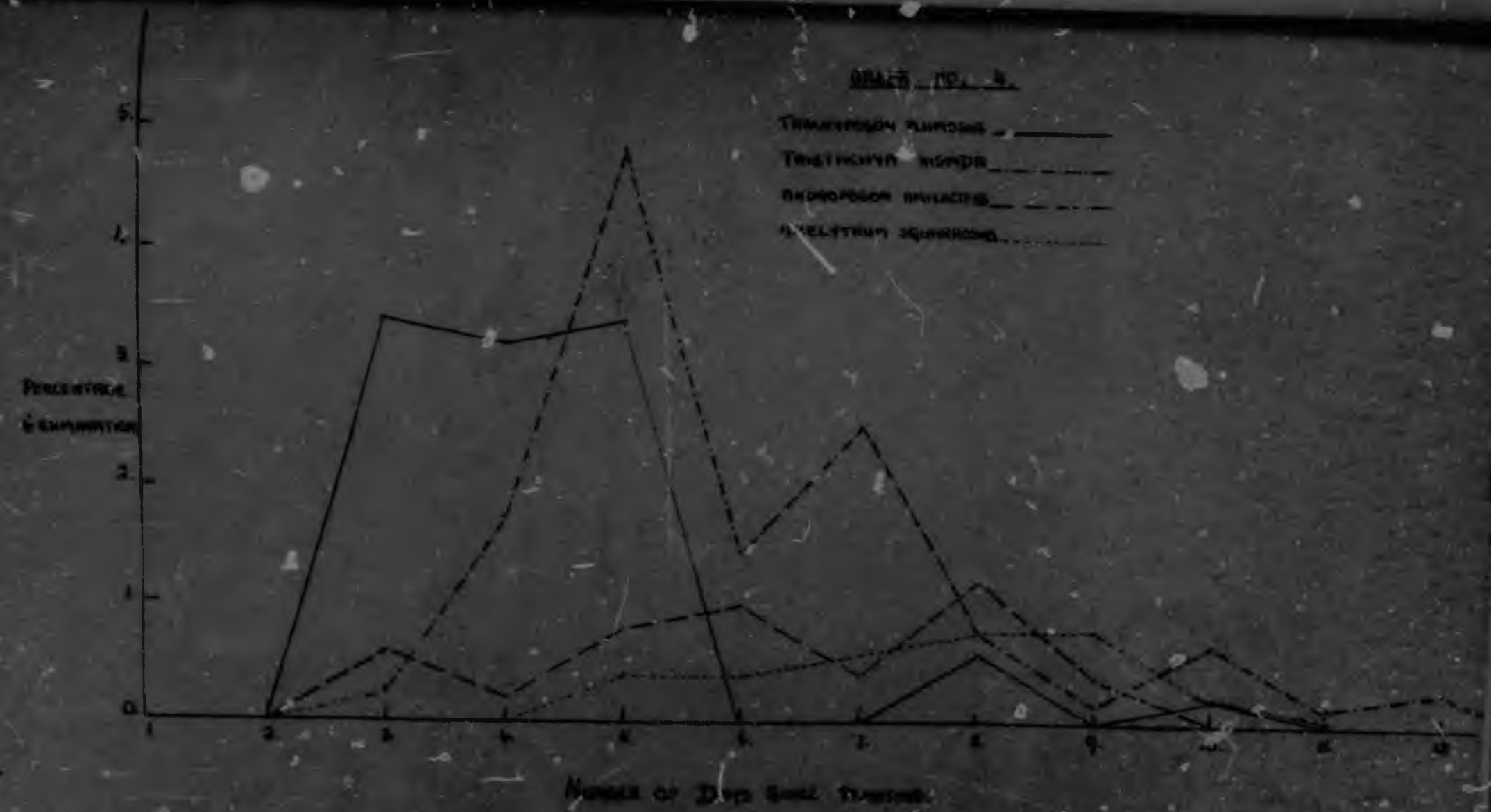
Total number per 4 Square Feet,
Proceeding from Mown to Unmown Veld




GRAPH NO. 1.
Bidens Pilosa
Convex Bidens
Tracted Minute
Schaumann Bonnrichens
Percentage Composition
Number of Days Since Planting


PERCENTAGE


GRAPH NO. 3.
HYPARRHENIA HIRTA
THEMEDA TRIANDRA
HETEROPOGON CONTORTUS
CYMBOPOGON EXCAVATUS
PERCENTAGE GERMINATION
NUMBER OF DAYS SINCE PLANTING
0
10
20
30
40
2
4
6
8
10
12
14


GRAPH NO. 4.
TRAGOPOGON PLUMOSUS
TRISTICHYA HISPIDA
ANDROPOGON AMILACEUS
ELYTRUM SQUARROSUS
PERCENTAGE
EXAMINATION
NUMBER OF DAYS SINCE PLANTING
0
1
2
3
4
5
6
7
8
9
10
11
12

FOR GRAPH NO.S.

PLEASE SEE LAST

FICHE

ROOT DIRECT CHARTS AND PHOTOGRAPHS.

FOR CHART NO. I.

SEE LAST FICHE

Tepetes minuta 4/1/22 Scale: 5-6'

Chart No. 2




Xanthium strumarium 6/1/34
Chart No. 5.
Scale: 1" = 6'
Dark loose soil
Compact gravel soil
Quartz pebbles
Water table

Chart No 4.

Amaranthus Thunbergii 15/12/38

Scale: 1"=1'



Loose dark soil

Harder yellowish soil

Quartz pebbles in yellowish soil




Scale 1" = 6'
Loose well
dark soil

Chart No. 7



ERAGROSTIS

CHARANTHA

R B 5

Chart No 8



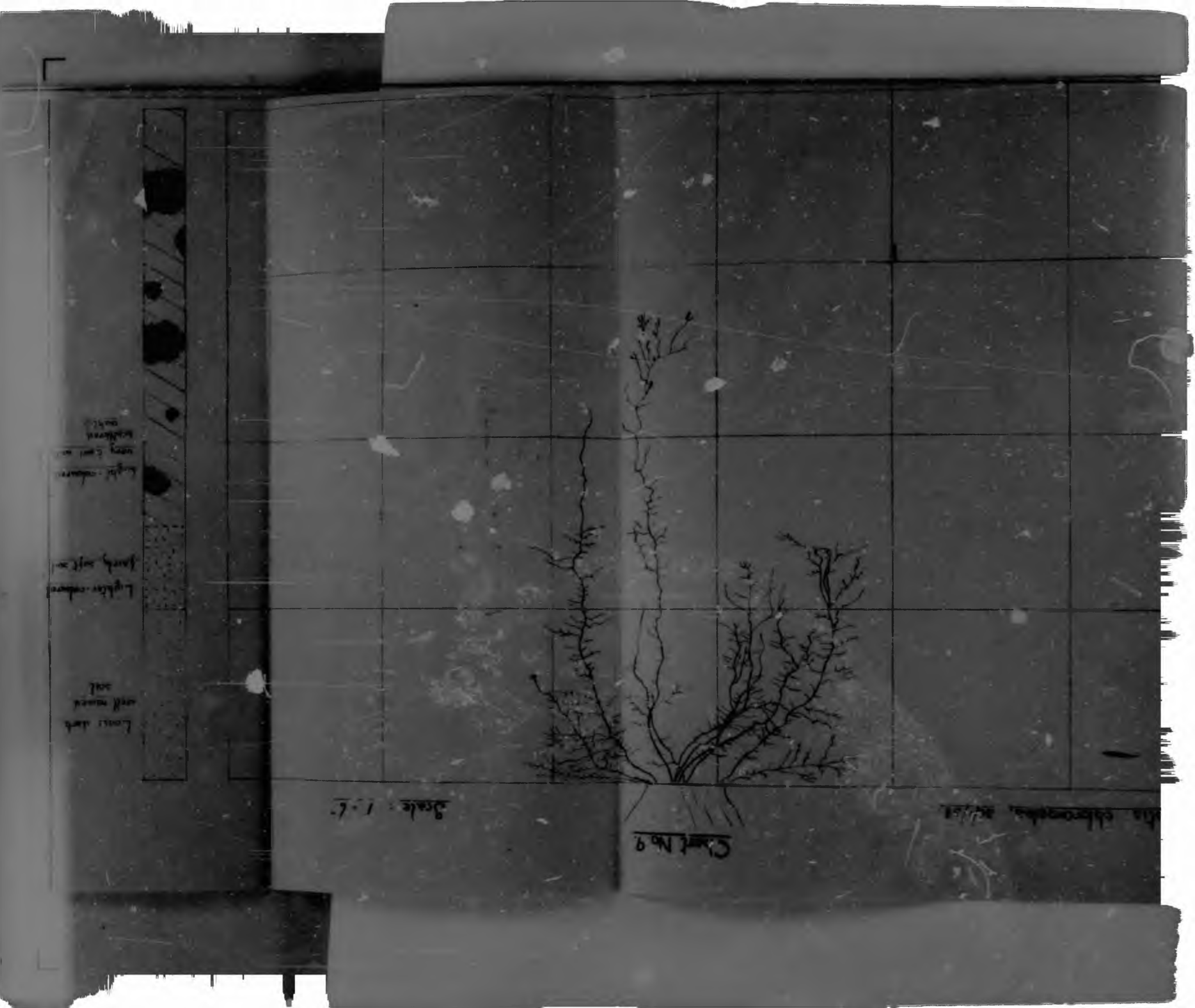



Chart No. 10
Hypermenia hirta
Scale
Dark sandy
with very
small gravel
pebbles
Hard yellow
with very
gravel
Dublip
clay
Solid granite




Themeda triandra
28/11/33.
Chart No. 12

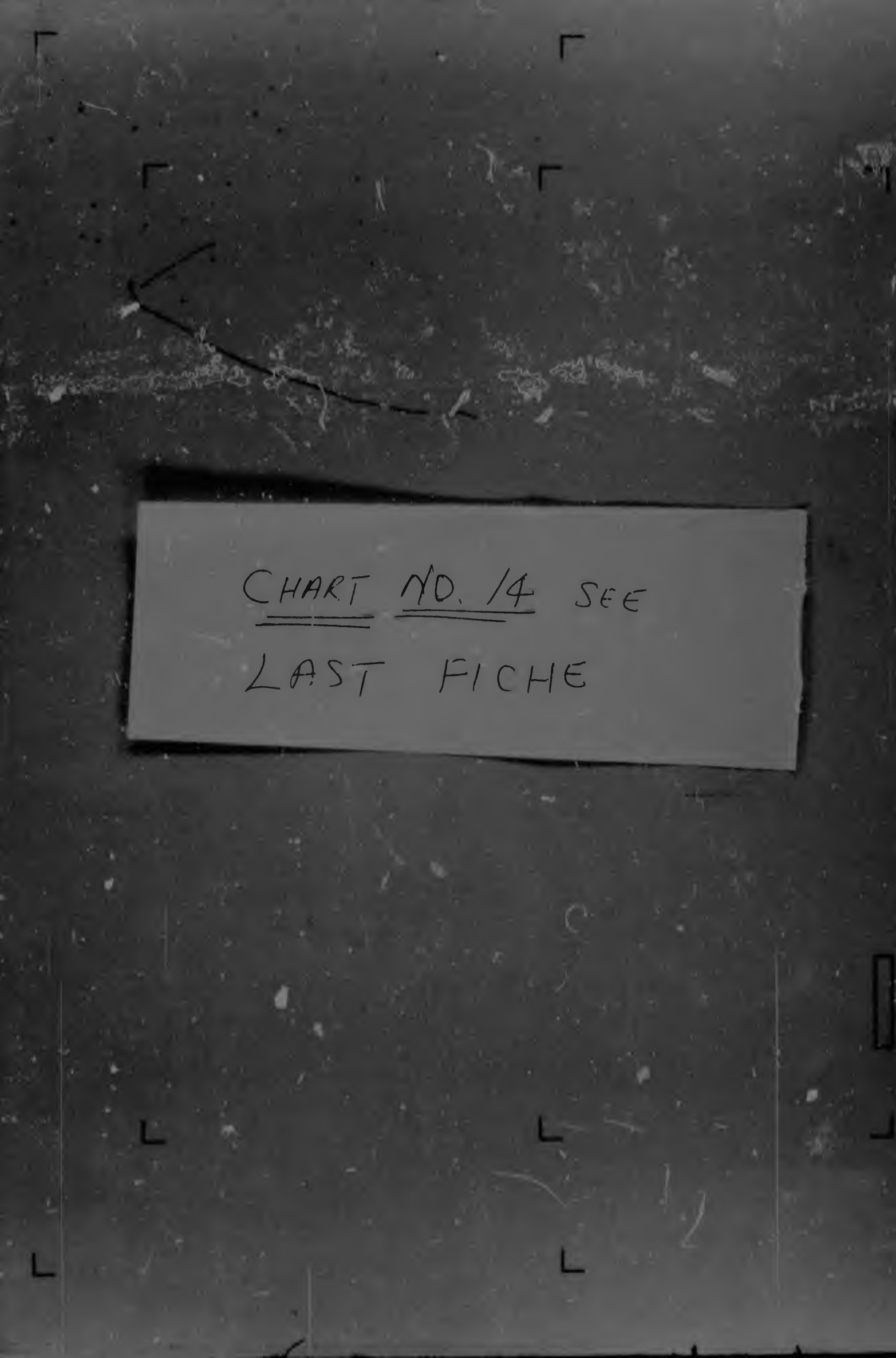


CHART NO. 14 SEE
LAST FICHE

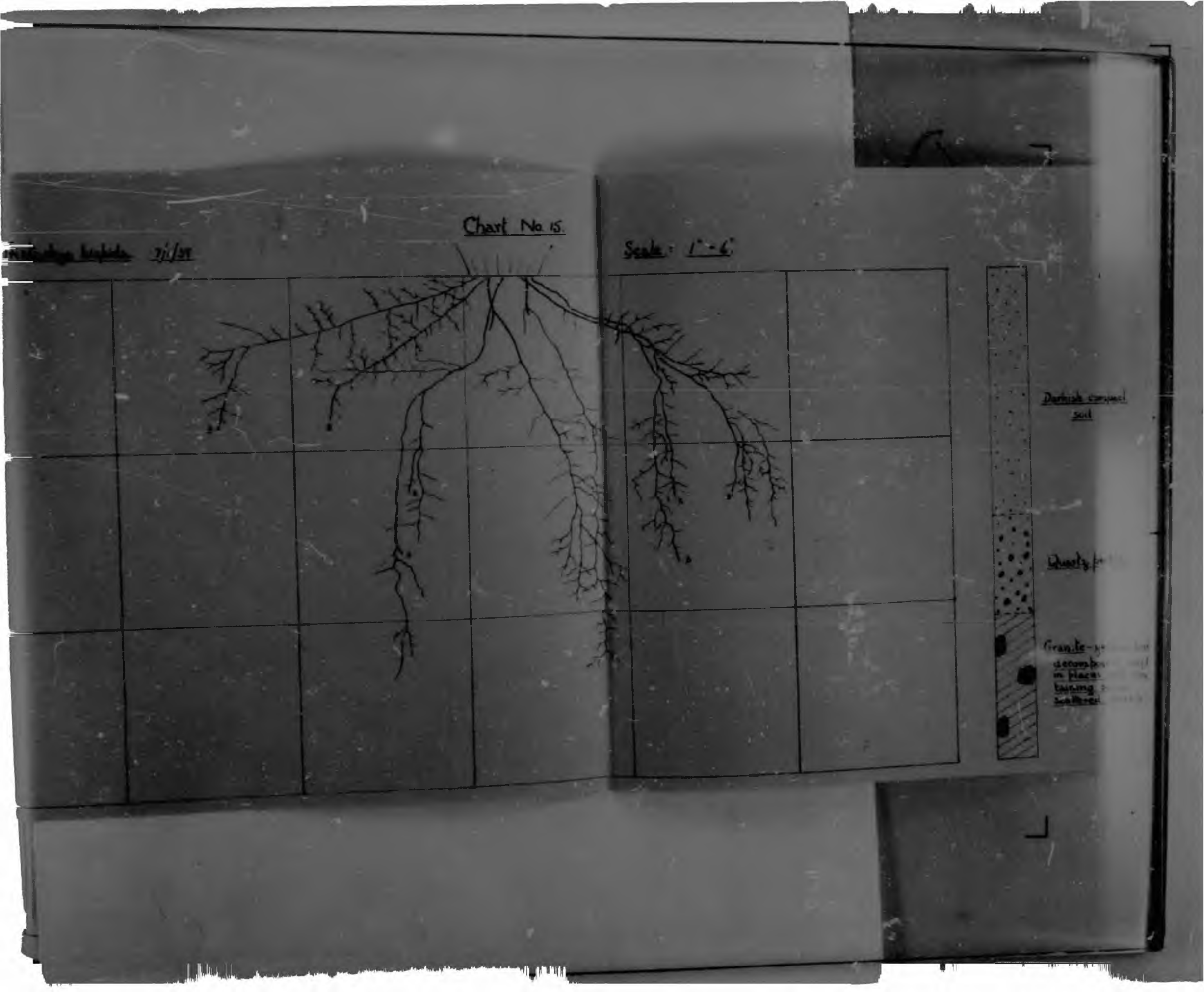


Chart No. 15.
Scale: 1" = 6'
Darkish compact soil
Quartz
Granite
in places
tuning
scattered

Digitaria [illegible] 1933 Chart No. 12. Scale [illegible]



Chart No. 6

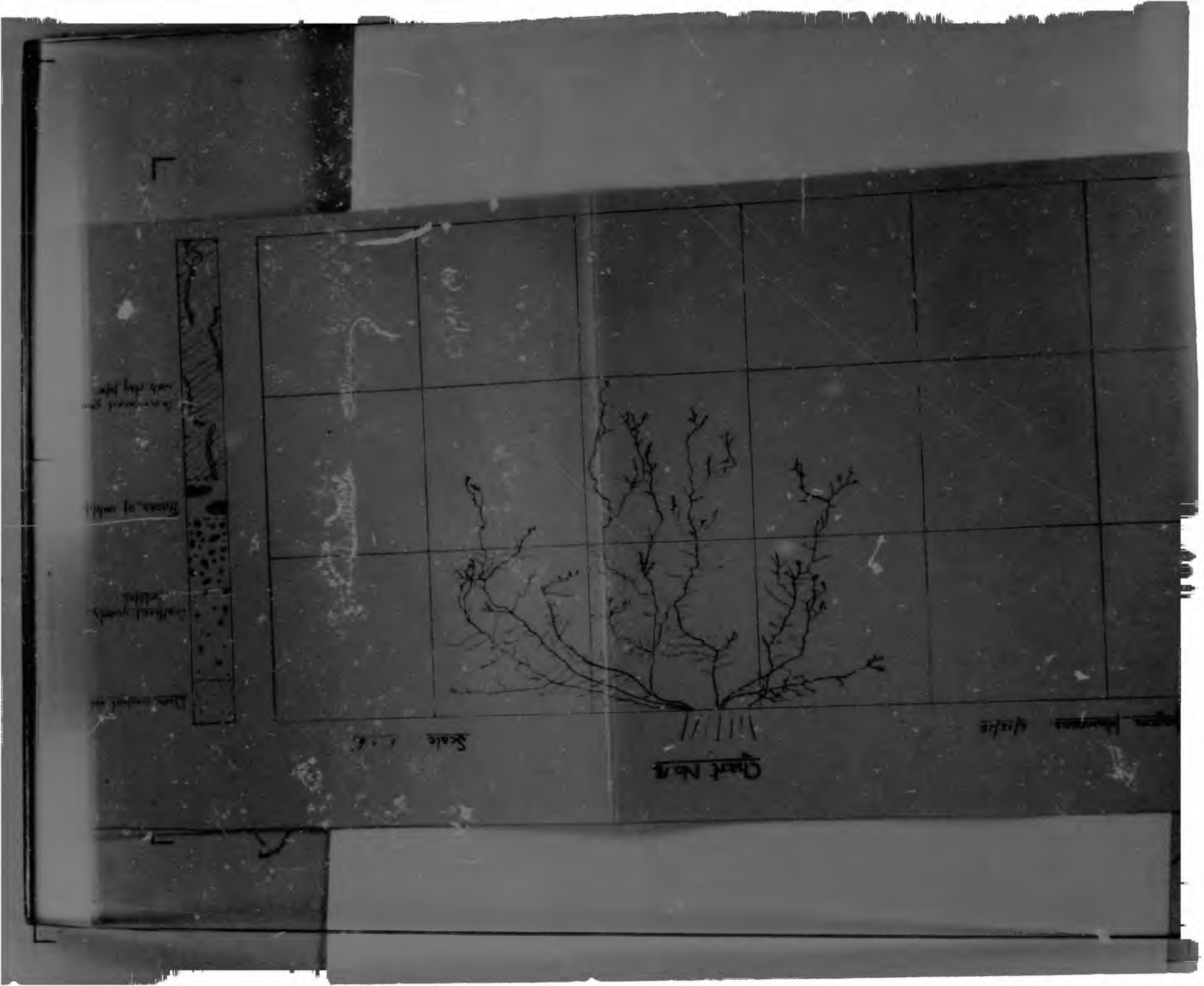
RB4

ELYONURUS ARGENTEUS



TRISTACHYA REHMANNII





Root Disease. (See Chart No. 3.)

Photograph illustrating the method of Murray and Glover (1935), used to expose and chart the roots. The plant is Xanthium strumarium. The grill is composed of 6" squares.



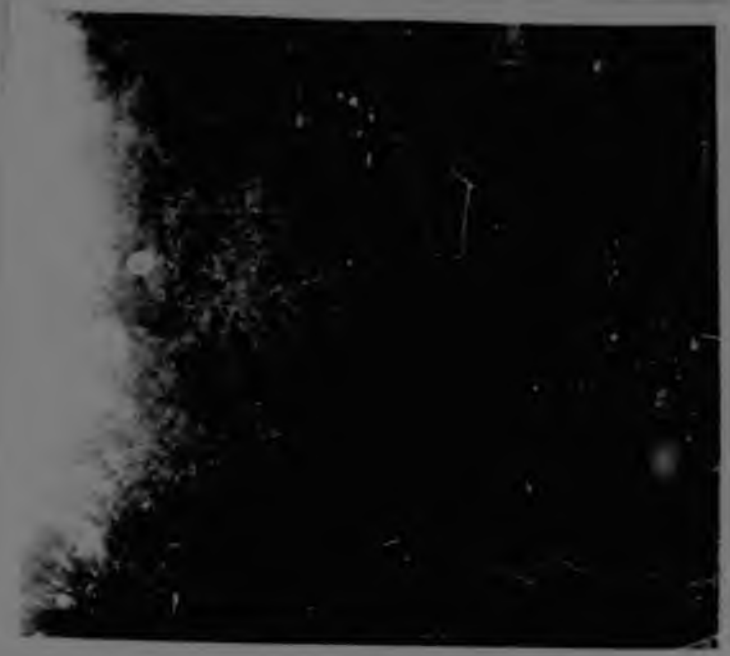
Root Diagram No. 20.

Acacia Karroo. Grill = 3' x 3' squares. Note extensive superficial lateral system and deep taproot. Superficial laterals on the right dip vertically downwards at the end of their lateral extension.



Root Diagram. No. 21.

Gymnosporia buxifolia. Scale divisions = 1 metre. Two trees shown. Taproot on left followed to its extremity. Note well-developed superficial lateral system of tree on the right. Note also the five roots emerging as small trees on the surface.



Root Model No. 22.

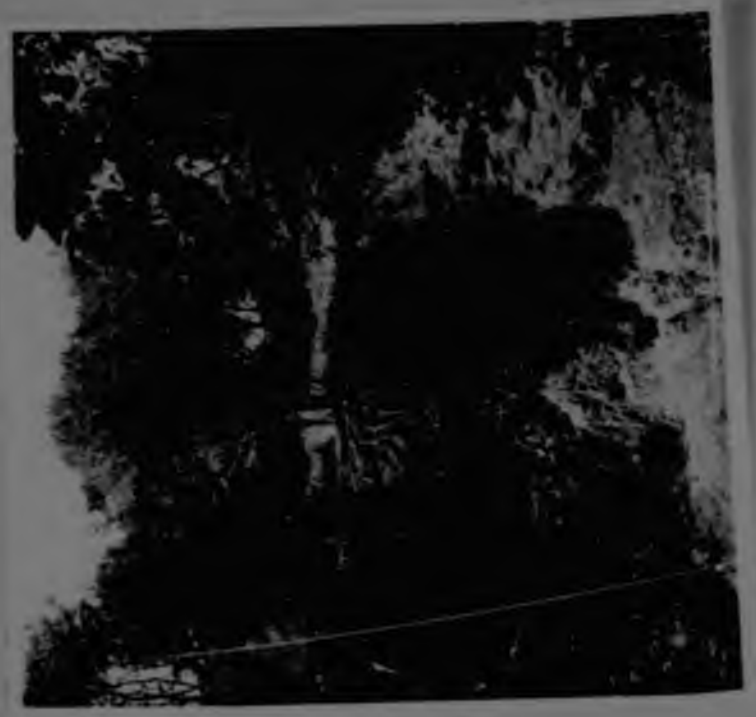
Celtis rhamnifolia. Scale divisions = 1 metre. Note deep taproot turning to the right along alluvial stone deposit. Note also well-developed system of superficial lateral roots on left.



Root Diagram. No. 53.

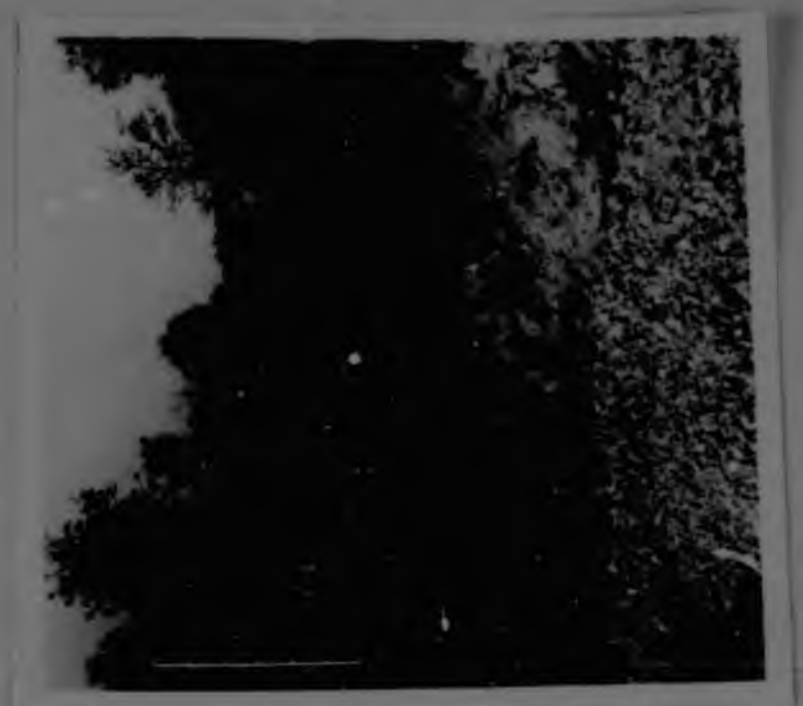
Euclea lanceolata. Scale divisions = 1 metre.

Note: a few superficial laterals and many deeply-penetrating vertical roots. No main tap-root



Root Digest. No. 24.

Olea verrucosa. Scale divisions = 1 metre. Note two superficial laterals extending to the left and large number of deep-rooted vertical roots. No main taproot.



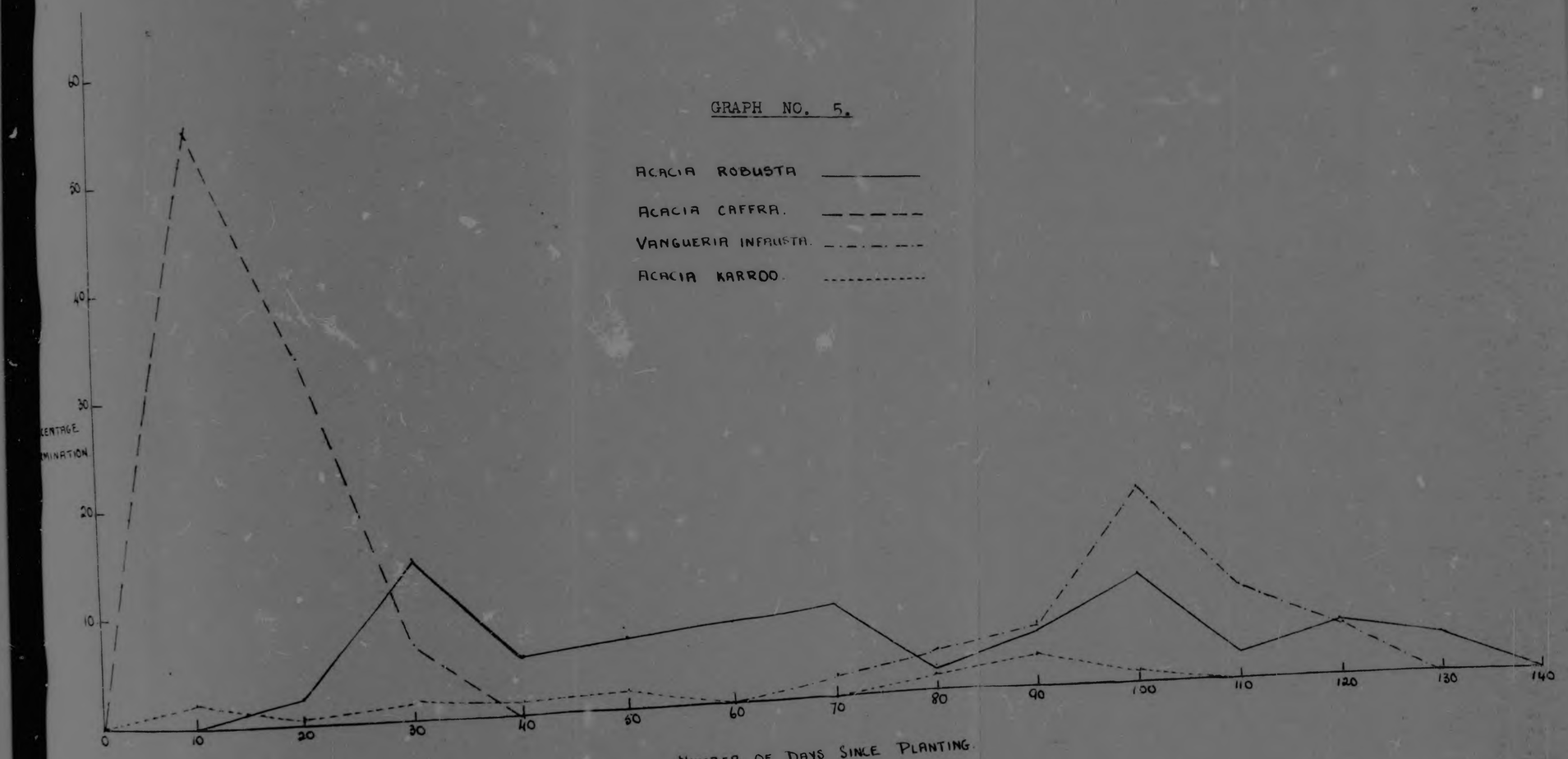
GRAPH NO. 5.

ACACIA ROBUSTA _____

ACACIA CAFFRA. _ _ _ _ _

VANGUERIA INFAUSTA. _ . _ . _ .

ACACIA KARROO. ----------



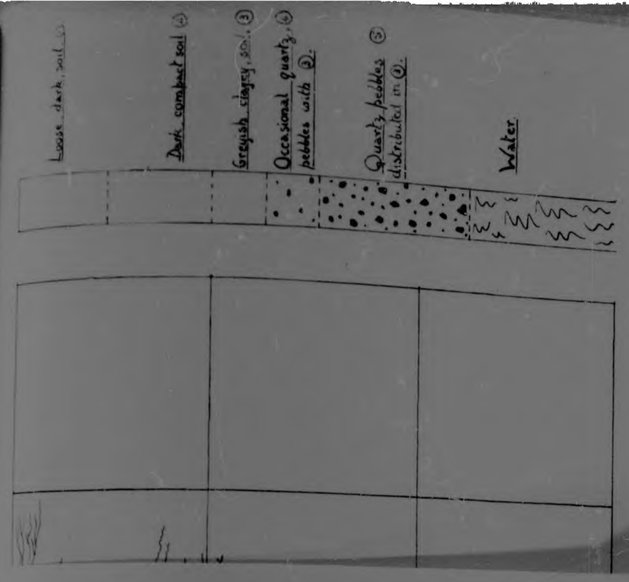
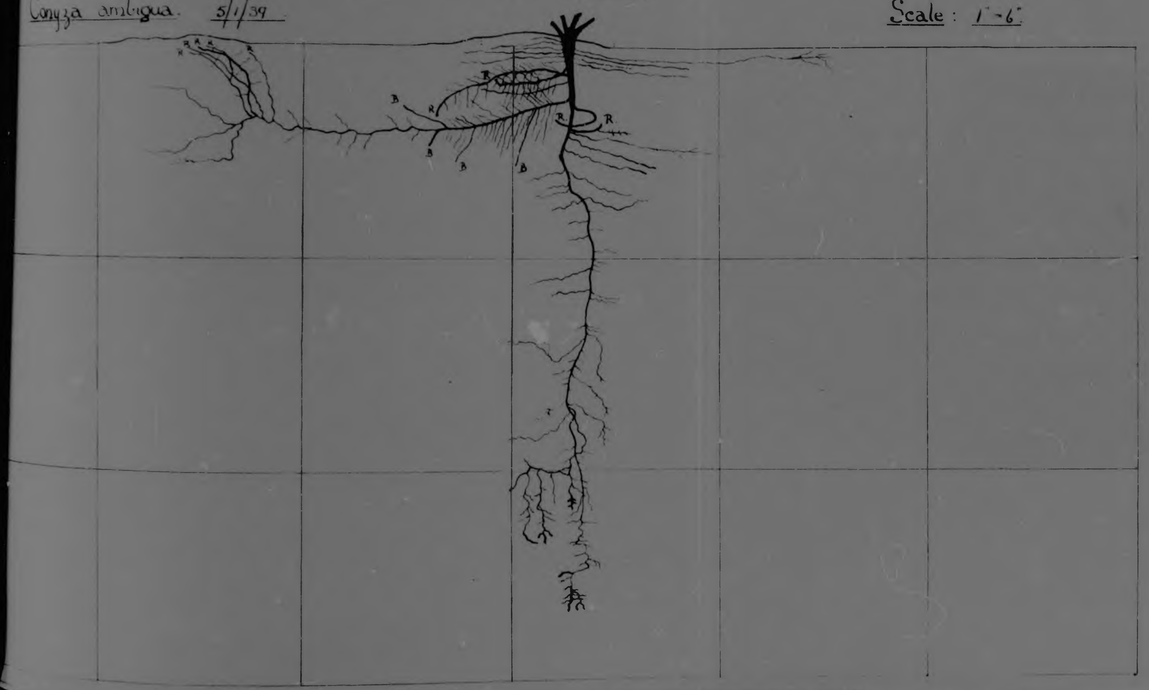
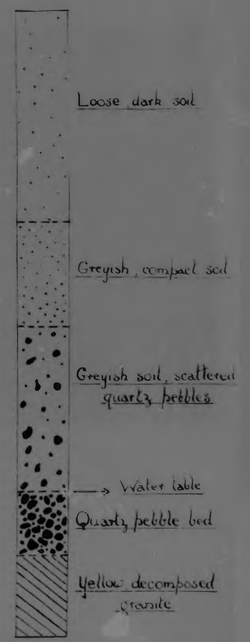


Chart No. 1.

Conyza ambigua. 5/1/39

Scale: 1"-6"





TRISTACHYA REH

Chart No.

Chart

ELYONURUS

RB4

TRISTACHYA REH

Chart No.

Chart

ELYONURUS

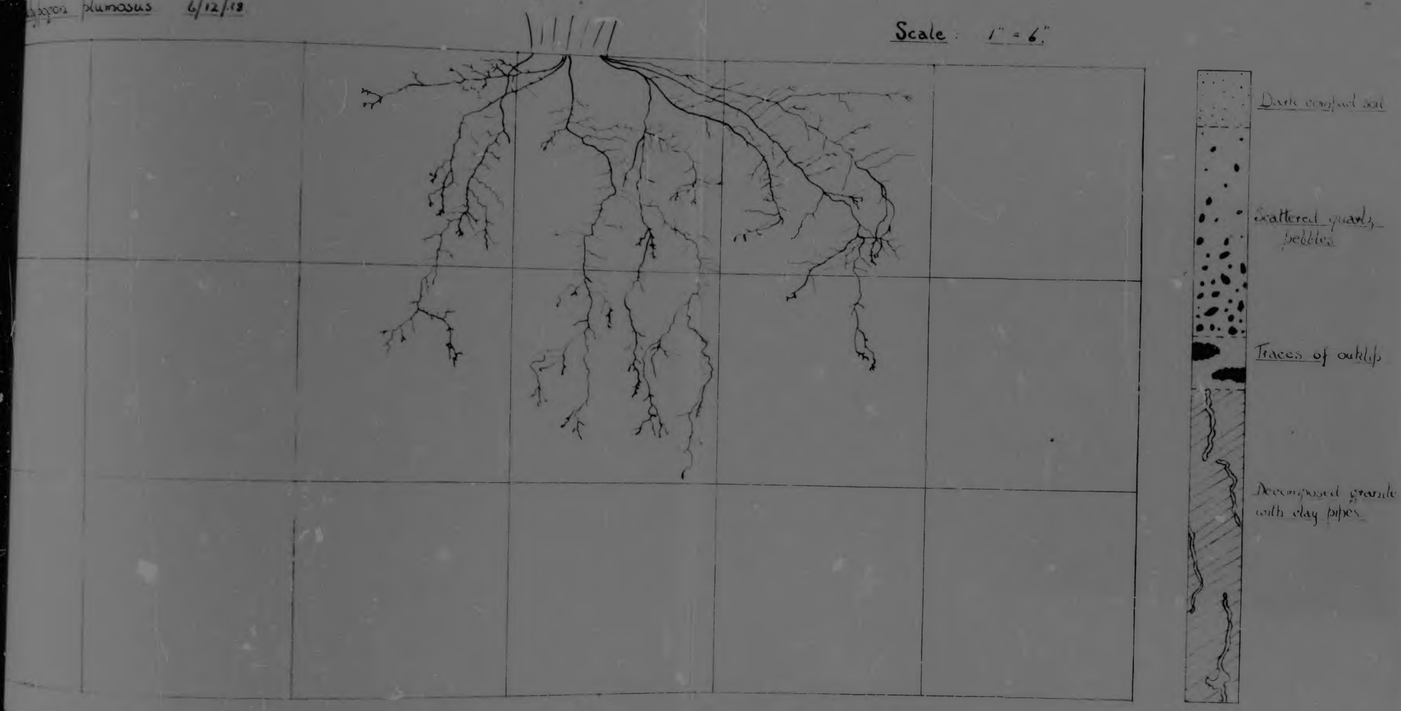
RB4

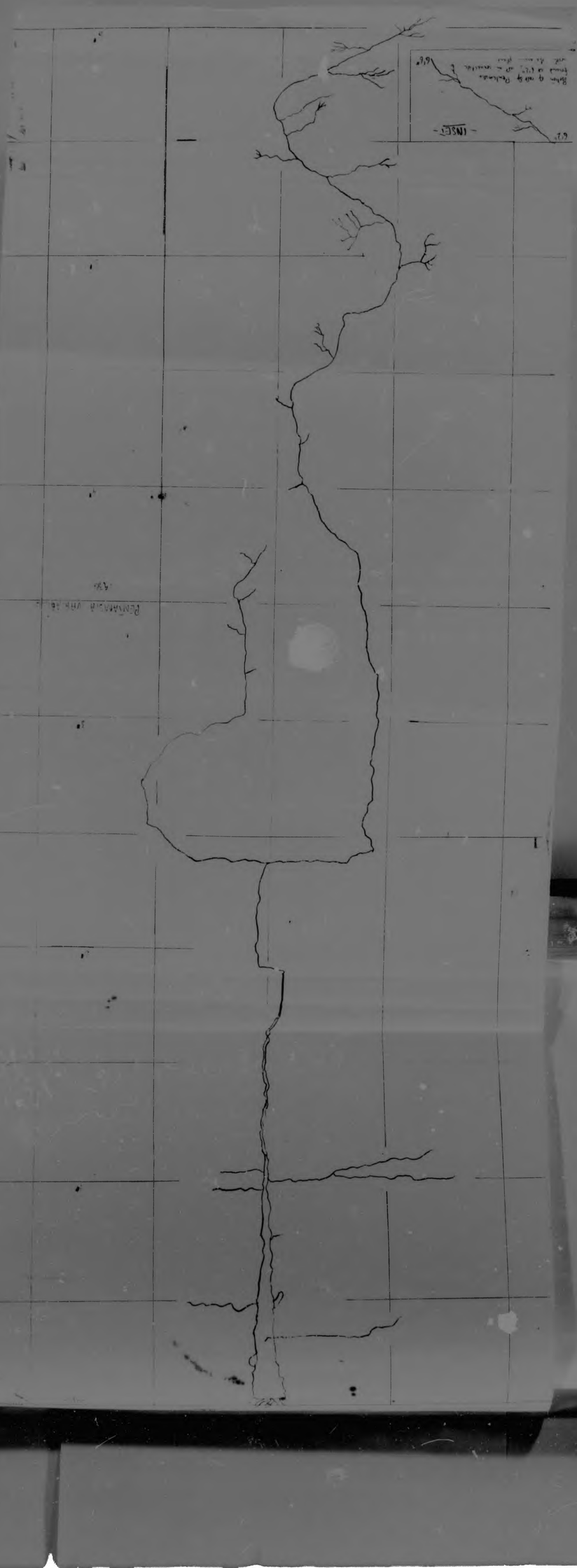


Chart No. 18.

...pogon plumosus 6/12/18

Scale: 1" = 6"





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