

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.
[1939]

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Thesis.
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INTRODUCTION.

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

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

In order to define the course followed by secondary

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

An appendix has been added dealing with the grass climax in the Southern Transvaal and North Eastern Orange 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 symbols
as in l.v.f - ab. = locally very frequent to abundant

CHAPTER I.

OUTLINE OF MAIN STAGES AND COURSE OF SUCCESSION.

The type of succession outlined here, occurs universally in South Africa upon fallow lands which have been repeatedly 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 the Transvaal and represent a total loss to the farmer of arable 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 a three year's study of a number of fallow lands in all stages of succession, in this area. Information gained in this study has been put together in the lists below. Thus it must be assumed that the plants mentioned in any one particular list will occur upon any one fallow land. However, the fact remains that all the plants mentioned in any one list have been seen upon numerous lands whose ages are approximately the same. For instance, any one of the plants mentioned in the list 1. need not necessarily appear but is likely to appear upon a land in its first year of fallowhood. Notes have been added upon those plants which may frequently occur in a particular community but which are not considered to be true members of it.

Secondary succession in this area can conveniently be 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, but Stages 1. and 6. are as a rule, quite distinct.

1. RUDERAL STAGE.

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

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

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

<u>Nanlenbergia undulata</u> A.D.C.	occ. - f.f.
<u>Walafrida densiflora</u> Rolfe	occ. - f.f. *
<u>Xanthium strumarium</u> Linn.	occ. - v.ab. *
<u>X. spinosum</u> 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 truly belongs to the Grassland Climax Stage and is only found here by reason of the fact that its tuberous 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 truly 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-hammer 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. Walafrida densiflora is found in all stages of succession from the Ruderal Stage to the Grassland Climax. Its true position, however, appears to be the Secondary Grass Stage or in Climax Grassland which is disturbed sufficiently to keep down the heavy choking sedge. 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 longer than two years, very seldom more than three years. The treatment it obtains determines the length of time it will endure. If for example, the community is entirely protected it is likely to last longer than usual. If on the other hand severe trampling occurs ruderal types will quickly disappear and grasses, particularly Cynodon dactylon, will take their 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 the succeeding communities up to and including the Grassland Climax Stage. (See Murray, 1934). The percentage basal 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 that the strain of Cynodon dactylon occurring on the particular area quadrated, had rather an upright habit. It was found that Cynodon dactylon made up 31.77% of the total basal area covered by the vegetation. The figures for mean total basal ~~area~~ 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 competitive 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 Azorella 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:-

<u>Aristida congesta</u> R. & S.	occ. - v.ab. *	1.
<u>Chloris virgata</u> Swartz	occ. - l.f.	1.
<u>Cynodon dactylon</u> Steud.	ab. - v.ab. *	1.
<u>Holcus indica</u> Gaertn.	occ. - l.f.	1.
<u>Eragrostis brizoides</u> Nees.	occ. - f.f.	1.
<u>E. chalcantha</u> Nees.	occ. - v.f. *	1.
<u>E. chloronelas</u> Steud.	occ. - v.ab. *	2.
<u>E. curvula</u> Nees	occ. - v.ab. *	2.
<u>E. guineensis</u> Nees.	occ. - v.ab. *	2.
<u>E. nebulosa</u> Stapf.	occ. - l.v.f.	2.
<u>E. robusta</u> Stent.	occ. - l.v.f.	2.
<u>Perotis indica</u> (Linn.) Kunze.	occ. - l.ab.	2.

<u>Pogonarthria squarrosa</u> (Licht.) Pilg	occ. - f.ab.
<u>Rhynchosytrum repens</u> (Willd.) C.E. Hubb.	occ. - v.ab.
<u>Sporobolus indicus</u> R.Br.	occ. - l.ab.
<u>Tragus berteronianus</u> Schult.	occ. - l.f.
<u>Trichoneura grandiflora</u> Ewan.	occ. - l.f.

Non-grasses:-

<u>Asclepias fruticosa</u> Linn.	occ.
<u>Euryops transvaalensis</u> Klatt.	occ. - l.f.
<u>Helichrysum aureo-nitens</u> Sen.Bip.	occ. - l.v.f.
<u>H. caespititium</u> Sond.	occ.
<u>H. callicomum</u> Harv.	occ. - l.v.f.
<u>Ipomoea bathycolpos</u> Hall.	occ.
<u>I. spp.</u>	occ.
<u>Justicia anagalloides</u> T.Anders.	occ. - f.
<u>Lobelia decipiens</u> Sond.	occ. - l.v.f.
<u>L. rosulata</u> S.Moore	occ. - l.v.f.
<u>Lotononis foliosa</u> Bolus.	occ.
<u>Midorella anomala</u> Steetz.	occ. - l.v.f.
<u>N. hottentotica</u> D.C.	occ. - l.f.f.
<u>Oenothera biennis</u> Linn.	occ. - l.f.f.
<u>Oldenlandia amatymbica</u> Linn.	occ. - l.f.f.
<u>Oxalis setosa</u> E. Mey.	Occ. -
<u>Polargonium ex nitophyllum</u> E.& Z.	v.occ. - l.f.
<u>Senecio venosus</u> Harv.	occ. - l.f.f.
<u>Spermacoce dibrachiate</u> Oliver.	occ. - l.ab.
<u>Stoebe vulgaris</u> Levyns.	occ. - l.ab.
<u>Wahlenbergia undulata</u> A.D.C.	occ.
<u>Malafride densiflora</u> Rolfe	occ. - f.f.
<u>Zinnia pauciflora</u> Linn.	occ.

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

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

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

Eragrostis brizoides and E. chalcantha continue to Grassland Climax Stage and will be discussed under that heading. Suffice it to say that I consider both these grasses to be true members of the Primary Grass Stage; as are also E. chloromelas, E. curvula, E. gummiflua, E. nebulosa and E. robusta. Perotis indica, Pennisetum polystachyon, Sporobolus indicus, Tragus racemosus and Trichoneura grandiglumis are also typical constituents of this veld type. Eleusine repens, on the other hand appears to occur equally frequently in this type and in the Secondary Grass Stage. It is difficult to assign it to one or the other group of plants and I venture no definite statement as to its true position other than to say that it belongs either to the Primary or Secondary Grass Stage. As it is a 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. My figures (1935) show that the total area covered by vegetation only 18.38% represents non-grass types, of which 8.64% consisted of various species of the Cyperaceae. Euryops 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 exist chiefly in this Primary Grass Stage and in locally disturbed areas in Grassland Climax vegetation. Oldenlandia capensis

probably thrives best in this Primary Grass Stage, especially where *Cynodon dactylon* has not gained too great an advantage over other constituents. *Oxalis setosa* - a very small semi-succulent plant - thrives in spaces between tussocks of *Eragrostis*. *Polygonum aconitifolium* 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 separate 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 this 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} Stage. *Spermacoce dibrachiate* 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 constituents.

Wahlenbergia undulata may possibly be a true ruderal type but it most frequently occurs in areas of local disturbance amongst members of higher stages. *Malafria densiflora* 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 5 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 Lasvogelkop (near Johannesburg) and on the Gatsrand, which still support a vegetation consisting almost entirely of Eynodon dactylo. The soil in these cases is pure humus. The kraals have not been used within living memory so that in isolated instances such as this, the Primary Grass Stage may remain in possession 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 or 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 Primary Grass Stage, the dominant grasses of this community are tall, erect, tussock forms. The dominant element, Hyparrhenia, 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 large in extent and allow other less robust members of the community - 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 rusty, brownish tinge, especially apparent in winter months.

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

extermination of some of the smaller species. Intolerant 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 transition, they are very soon crowded out of existence, partly increasing pressure upon available space but also through marked reduction in available light.

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

Grasses:-

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

Non-grasses:-

<u>Calliopsis leptophylla</u> Harv.	occ.
<u>Cassia minuscoides</u> Linn.	occ. - f.f.
<u>Dimorphocassa spectabilis</u> Schltr.	occ.
<u>Eriosema cordatum</u> E. Mey.	v. occ.
<u>E. transvaalensis</u> C.E. Moss (ined.)	v. occ.
<u>Gladiolus crassifolius</u> Baker	v. occ.
<u>Gnidia caffra</u> Naimf.	v. occ.
<u>Helichrysum aureo-vittatum</u> Sch. Bip.	occ. - l.f.

<u>Helichrysum caespititium</u> Sond.	occ.
<u>E. callicomum</u> Harv.	occ. - l.v.f.
<u>E. leiopodium</u> D.C.	v.occ.
<u>Myroxis Rooperi</u> Moore.	v.occ. - occ.
<u>E. rigidula</u> Baker.	v.occ. - occ.
<u>Indigofera hibrida</u> N.E.Br.	v.occ. - occ.
<u>Ipomoea</u> spp.	occ.
<u>Justicia anacardoides</u> T. Anders.	occ. - f.
<u>Lotononis foliosa</u> Bolus.	occ.
<u>Nidorella aromala</u> Stuetz.	v.occ. - l.f.
<u>N. hottentotica</u> D.C.	v.occ.
<u>Oldenlandia amatymbica</u> Linn.	occ. - f.f.
<u>Delargonium aconitophyllum</u> E. & Z.	occ. - l.f.f.
<u>Pentanisia variabilis</u> Harv.	occ.
<u>Stoebe vulgaris</u> Levyns.	occ. - l.ab.
<u>Vernonia Kraussii</u> Sch.Bip.	v.occ.
<u>Walafrida densiflora</u> Rolfs.	f.occ.

The position of Aristida congesta has already been discussed in Paragraph 2. Cymbopogon excavatus is a true member 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 Cymbopogon 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 experimental plots of the CC, DD, EE series at Frankenwald, which have been overgrazed for one and two years respectively and then protected, show this very well indeed. Isolated tussocks of Cymbopogon excavatus and Themeda triandra are very noticeable among the remaining Climax grasses.

Cynodon dactylon, Eragrostis brizoides, E. chalcantha, E. chlorocephala, E. curvula, E. nebulosa, Pogonarthria squarrosa

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

Heteropogon contortus, which according to Murray's figures (1935) occurs very frequently in Climax Grassland in my opinion, a member of this Secondary Grass Stage. Comparisons drawn between list quadrat figures of Scott and Murray (Murray 1934) and those of Glover and Rose Innes (Glover, R. 1937) on the same quadrats strongly support this view. The quadrats were laid out in moderately grazed Po Valley (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 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 hians, T. Rehmanni, Urelytrum squarrosus, Alloteropsis semialata, Andropogon amplexans 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 or 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 mentioned above, in conjunction with the behaviour and true habit of Cymbopogon excavatus, is a grass whose ~~grass~~ form is 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 consequence of local disturbance (e.g. round the edges of termite antbear holes) and moderate overgrazing.

The remaining grass, Schizachyrium semiberbe, occurs very sparsely and appears to prefer such sites as old and rocky outcrops (Glover, l. 1937) Rose Innes, l. 1 to open veld in any stage of succession. However, it occurs in this stage (3) and locally in Climax Grassland sites which show signs of remote disturbance - on old tracks for example. Observations made on old roads show Schizachyrium semiberbe intermingles with such grasses Hyparrhenia ^{hirsuta} and Cymbopogon excavatus - both members of Secondary Grass Stage on fallow lands. For these reasons it has been included in the above list of Secondary Grass 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 leptophylla, Cassia mimusoides, Dimorphotheca spectabilis, Eriosema cordatum, E. transvaalensis, Gladiolus crassifolius, caffra, Helichrysum leiodorum, Hypoxis Rooperi, H. r. Indigofera hybrida and Pentstemon variabilis. Hypoxis Rooperi, H. rigidula and Enidia caffra are all true Grassland members. Callilepis leptophylla, Cassia mimusoides, Dimorphotheca spectabilis and Gladiolus crassifolius are found in slightly disturbed ^{areas} and also, though perhaps not frequently, - in undisturbed Climax Grassland. The first three of these favour ground which has been either picked

or disturbed by grazing animals, while Gleditsia crassifolia appears to thrive better in moister sites, which have suffered a certain degree of disturbance.

Of the remaining plants, Helichrysum caespitosum 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 callicomum 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 is 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 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 numerous 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 Eulafrida densiflora. It has quite frequently been observed growing in undisturbed Climax Grassland but the plants did not appear to be robust or particularly healthy.

GRASSLAND CLIMAX STAGE.

At Frankenwald and over extensive areas of the Highbury 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 foliage does not as a rule stand higher than 1 foot from the ground though the flowering culms reach a height of 3-4 feet. The total basal cover is poor. Murray's figures (1934) show that on the average, it does not exceed 20%, though in some cases it rises to as high as 25% of the total ground surface. The non-grass types, though often conspicuous when in flower, do not form an important part of the community. These plants represent only 0.12% of the total area covered by the vegetation as a whole.

The community when undisturbed, presents an even, homogeneous, unbroken appearance with none of the irregularities of the other communities already described. At Frankenwald it has become known as "Purple Veld", due to its characteristic purple colour during the flowering period. In winter the community assumes a drab, yellowish-brown appearance. The species are frequently very coarse, particularly when prostrate and are often very hairy.

The Purple Veld species are apt to undergo slight change 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 season's growth from choking the plants and seedlings. The spaces between tussocks are kept open and are frequently filled by grasses of a secondary character. Apart from keeping the spaces open, grazing has the effect of giving stoloniferous plants such as Digitaria tricholomaoides, room to extend. Temporary relief from the burden of dead foliage and flowering culms, also provides smaller grasses such as Brachiaria serrata with the opportunity for growth. Burning has the

same general effect but is apt to harm stoloniferous grass. Digitaria tricholaenoides has been observed to suffer from

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

Grasses:-

<u>Alloteropsis senialata</u> Hitchcock.	occ.
<u>Andropogon amplexans</u> Nees.	occ. - f.f.
<u>Brachiaria serrata</u> (Spreng.) Stapf.	occ. - f.
<u>Digitaria tricholaenoides</u> Stapf.	occ. - f.
<u>Diplachne biflora</u> Hack.	occ. - f.f.
<u>Elionurus argenteus</u> Nees.	occ.-f.
<u>Eragrostis trizoides</u> Nees.	occ.
<u>E. chalcantha</u> Nees	occ.-v.f.
<u>Herposcaloa falx</u> (Link.f.) Kunze.	occ. - f.f.
<u>Heteropogon contortus</u> R. & S.	v.occ.
<u>Lophachne digitata</u> Stapf.	l.f.
<u>Loudetia simplex</u> C.E. Hubbard.	v.occ.-l.occ.
<u>Monocymbium seressiforme</u> (Nees) Stapf.	occ.-f.f.
<u>Panicum natalense</u> Hochst.	occ.
<u>Rhynchoselytrum setifolium</u> Choisy.	v.occ.
<u>Sporobolus fimbriatus</u> Nees.	occ.
<u>Themeda triandra</u> Forsk.	l.f.
<u>Trachypogon plumosus</u> Nees.	v.f.-ab.
<u>Tristachya hispida</u> (Thunb.) Schum.	v.f.-ab.
<u>T. Rehmanni</u> Hack. ex Schinz.	occ.
<u>Urelytrum squarrosum</u> Hack.	v.occ.

Non-grasses:-

<u>Acalypha angustata</u> ^{to. Sand} Ba.	
<u>A. caperonioides</u> Baill.	
<u>Albucca pachyclamys</u> Baker.	
<u>Azolepias stellifera</u> Schltr.	

- Asclepias aurea Schlt.
Aster harveyanus Min.
Babiana hypoxea Eusch.
Basium obovatum var. liana N.E.Br.
Berkheya subulata Harv.
Bopusia scabra Presl.
Callilepis leptophylla Harv.
Cassia minusoides Linn.
Clerodendron triphyllum (Harv.) H.A.W. Pears.
Cusumis hirsutis Sond.
Cyanotis nodiflora Kunth.
Cyperus compactus Lam.
C. compactus Lam. var. flavissimus C.B.Cl.
Dianthus moodiensis Williams.
Dicoma anomala Sond.
D. Zeyheri Sond.
Dimorphotheca spectabilis Schltr.
Elephantorrhiza elephantina (Eurch.) Skeels.
Eriosema cordatum E. Mey.
E. transvaalensis C.E. Ross (ined.)
Euphorbia striata Thunb.
E. truncata N.E.Br.
Gazanla pyramida Sond.
Gerbera piloselloides Cass.
Gladiolus crassifolius Baker.
G. edulis Birch.
Gnidia caffra Neimr.
G. capitata Linn.
G. kraussiana Nees.
G. microcephala Nees.
Haplocarpa scaposa Harv.
Hermannia lancifolia Szysz.
Hypericum aethiopicum Thunb.
Hyperis rigidula Baker.
H. Rooperi Robt.
Indigofera hybrida N.E.Br.

Ipomoea bathycolpa Hall.
I. simplex Thunb.
I. spp.
Lobelia decipiens S. Moore.
L. rosulata Sond.
Lotononis foliosa Bolus.
Pachystigma pygmaea
Pelargonium aconitophellum var. angustisectum Kunth.
Pentstemon variabilis Harv.
Peucedanum magalis-montanum Sond.
Polypala boyssinica R.Br.
P. gracilentia Eurttt Davy
Protea hirta Klotzsch.
Raphionacme divaricata Harv.
Scabiosa anthemifolia E. & Z.
Scilla lanceifolia Baker.
S. ovatifolia Baker.
Senecio coronatus Harv.
S. serpa Sond.
S. succosus C.E. Moss.
S. venosus Harv.
Silene oliveriana Burch.
Sphenostylis angustifolia
Striga elegans Benth.
Tephrosia aurantiaca R.G.H. Young.
Tulbaghia leucantha Baker.
Urginea multisetosa Baker.
Vernonia Kraussii Sch.Bip.
V. monocephala Harv.
Malafida 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 biflora, 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 squarrosius is comparatively 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 support this view. Unfortunately no work has yet been done upon root system of this species.

Brachiaria serrata has for a long time been regarded as a true Purple Veld type. Observations in completely protected areas, however, show that it tends to be crowded out of existence by its taller, overbearing associates. Observations made by Altona (Altona 1939) while studying the growth rhythm of Brachiaria serrata in the 1937-38 and 1938-39 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 put forth in the summer of 1938-39, under conditions of complete protection. On the other hand, similar plants growing a few feet away from the latter, in an area which had been burnt but protected from grazing animals, were growing comparatively vigorously. The plants in the burnt area were of course free from the choking burden of taller foliage around them. 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 consists of superficial lateral roots. This seems to indicate that it is a grass which belongs to the earlier stages of true Purple Veld. All true Purple Veld species studied have deep 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 ground

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

Monocymbium cerealisiformae 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.

Tricholaea 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 cerealisiforme which are not so robust as Brachiaris serrata, Rhynchosytrum 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. chaioantha. 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 depression 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. chalcantha 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. chalcantha 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, comes 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 laid 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 level 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 plants 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 it is 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 in Frankenswald and elsewhere. (See Photograph No. 4).

Final conclusive evidence again comes from quadrat analyses. Quoting from the same figures as before, the 1935 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 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 amplexans. 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.

Lophocoma digitata occurs very locally in Purple Veld, usually in slightly wet areas, and is probably 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 triandrus^{confertus and Thunbergii} 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 amplexans, Elionurus argenteus, Harpechloa falx (on moist sites), Panicum natalense, Trachypogon plumosus, Tristachys hispida, T. Rehmanni and Urelytrum squarrosus. (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 effects 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 1934 and 1935.

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 than 3% 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 Gassia 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, Palarzonium acnito-phyllum and Salvia 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 *Helichrysus* 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 *Helichrysus latifolius* in Bow'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 ^{Climax} Grassland Stage. No new grass community invades the Purple Veld or Climax Grassland, and further progression results in a series of trees invading the grassland area.

3. 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, Buikebosrand and Gaterand.

The community typically consists of widely-scattered trees of *Protea caffra* Moism., with a very sparse localised intermingling of *Protea Repullina* Moism. 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
 Field 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 ~~is~~ littered with loose stones
 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 hardest 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
 diabases 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 and are likely to continue to be so. Soils will always be poor and shallow exposed ranges and upper slopes, since the forces of grad 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 part 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*, *Dombeya 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 karroo*.

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.

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

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

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

The invasion of scrub types into Purple Veld, may be begun 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 proximity and availability of supplies of scrub seed; secondly, the presence of termitaria (see Photos Nos 7 & 8) and thirdly the occurrence of a small amount of disturbance such as occasional trampling by oxen, after scrub seed has arrived on an 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 stages. As has been noted by Story (1938) and Rose Innes (1.1937), many plants of the most advanced types have been observed to 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* spp. seeds have been found to germinate and flourish on fallow soils at Frankfort. 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 are heavy, (See Seed Photographs Nos. 15-21) they depend for their distribution upon men, animals and birds. Palatability of scrub fruits is therefore also of great importance, especially with regard to pioneer types. Most of the pioneer species have fruits which are palatable either to man, animals or birds. Amongst these are *Rotunda pallens*, *Adiantum* sp.

Euclea lanceolata, Ehretia hottentotica, Vangueria infausta, Cussonia spicata, Zizyphus mucronata, (See Seed Photograph No.15) Cassine burkeana, (See Seed Photograph No.20) Scaevola Scopolia 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. unguiculata are eaten by natives. Birds are largely responsible for the distribution of Cassine burkeana, Asparagus sp. Rhus spp. Cussonia spicata and possibly, Gynenosporia buxifolia and M. 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 Frankensvald 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 directs 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 latifolia, Cynodon, Grasshopper, 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 1938) 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 area 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 matter 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, find 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 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~~^{due} firstly to seed being available, secondly to the means being present of burying such seed in the soil, thirdly to the protectiveness 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., *Boerhaavia*, *Acacia caffra*, *A. robusta*, *Euclea lanceolata* and *Gymnosporia burifolia*. (See Photos Nos. 7-12) Very frequently, seedlings are found grouped or singly on the sides of termataria, 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 keep away intruders. Seedlings of Boyeria pallens have been observed to grow up through the branches of their Asparagus 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 and disappear completely. The soil becomes covered with a dense 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-increasing area.

Asparagus sp. is by no means an essential part of the succession in this transition stage. Seedlings of Boyeria pallens, Euclea undulata, E. lanceolata and Gymnosporia buxifolia have frequently been found coming up in open veld. Acacia caffra, A. karroo and A. robusta seedlings more often appear to arise in this manner. (See Photos Nos. 9 & 10). The latter being of a thorny nature are well able to protect themselves from disturbance caused by grazing animals. Acacia robusta seeds appear to be capable of germinating and developing in the most extreme conditions such as are found 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 pioneers though they are not so frequently found as those mentioned above and more often appear after them. The following species fall into this group: Eretia hottentotica and Sceloparia Zeyheri, (see Photo No. 11) Vangueria infausta (usually on rocky outcrops), Gymnosporia polycantha, Cassine burkeana, Chilienthus arboreus, Zizyphus mucronata (see Photo No. 7) and Rhus Queinzii. Hens (1917) speaking of the thornveld vegetation near Maritzburg states that in that area, Acacia

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

Bews (1917) states that in Maritzburg, Chilanthus 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, Chilanthus 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 ^{members} ~~species~~ being on the outside and the older ^{ones} ~~members~~ on the inside ^{of the belt}. The latter appear to be dying out. Within this belt seedlings of Rhus Gueinzii, Acacia caffra and A. erioloba 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, Leonotis martinicensis, Lantana salvifolia, Sansevieria thyrsiflora, Lapeyrouisia oreunta, Asparagus sp. (small), Chyranthes 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 Fig. No. 13) Sarcostemma c.f. viminalis, Helinus ovatus, Plumbago capensis, Becamone Alpinii. I have not observed such plants killing the scrub trees upon which they support themselves as described by Bews in the Maritzburg area.

The final change which takes place in this scrub community type comes with the entrance of such species as Fagara mcalismontana, Brachylaena discolor, Tarchonanthus camphoratus, Celtis rhacnifolia, Olea verrucosa, Doryalis Zeyheri, Dombeya rotundifolia, Heteromorpha arborescens, Maerua triphylla, Pappia capensis, Cassia abyssinica, Pavetta sp., Pittosporum viridiflorum, Electronia mundtiiana, Royena and others. In the scrub vegetation of this area, such species are sparsely scattered throughout, with occasional large aggregations of the more hygrophilous types in the vicinity of rocky outcrops. Although it is quite possible that such 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 Rekepoort, or on undisturbed hills and koppies in Klipriverberg. I feel that the mixed scrub type of vegetation 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 for which have been described above and which are typical of secondary succession on fallow lands in this area. It was decided, however, that one of these communities - the most stable and most abundantly found - would have to be used as a standard of comparison for the remaining three. The reason 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. Areas may differ very widely indeed within a single community and even more so when analyses are made at widely different 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 time widely separated communities, would be quite useless for purposes of comparison. It is the comparative results which are required here.

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

1. Cynodon-Eragrostis-etc. Fallow / Adjacent Purple Veld
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 areas may be compared and assessed.

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

Description of Areas Chosen for Comparison.

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

(a) The fallow area supports a vegetation typical of Primary Grass Stage already described. It consists chiefly of the following species: Cynodon dactylon, Eragrostis curvula, E. chloromelas, E. guineensis, E. chaetanthus and Rhynchoselytrum repens. The land was last ploughed in 1920 and is thus 16 years old. It was, however, an old fallow before that time and was previously last ploughed in 1905. On the second occasion, it was only ploughed once and was then left to grow. No fertiliser has ever been used on it.

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

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

There are no rocky outcrops or seepage lines nearby. Samples 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 clumps of Hyparrhenia hirta scattered irregularly through vegetation consisting chiefly of Cynodon dactylon, Rhynchosistrum repens and Eragrostis spp. In all cases in this area, sampling was carried out only within the clumps of Hyparrhenia. The land is stated to be 29-30 years old and was originally sown to Manna grass upon which cattle were grazed. It is unknown from how long the land was in use. No fertilizer was used.
- (b) The adjacent Purple Veld area was typical of its kind.

3) Both vegetation types are found on the same type of 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 seepage 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 Chilanthus arboreus is locally abundant, otherwise the vegetation can be said to be typical. Samples were taken from the vicinity of a large number of species representative of the area.
- (b) The Purple Veld is typical. An old denuded road runs through the area but this was avoided when samples were taken.

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

1. Moisture.
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 randomized 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 Gunning and Day (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 and holard 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 of 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 using the cylinder itself to scoop out the soil.

40 samples were taken from the Cynodon/Purple Veld
20 samples from each vegetation-type.

30 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 differences 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 Lapparhenia nirta 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.

Substantially!

The suspected presence of an unusually moist area in Purple Veld was verified by the results of analysis.
Conclusions: It is concluded that percentage holard of soils increases at 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 desiccating winds. It may also be due in some measure to decreased run-off. These results agree with those obtained by Story (1933) 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 Veld
- (ii) Hyparrhenia veld " " " " " "
- (iii) Purple Veld soil " " " " " Climax Scrub
- (iv) Purple Veld maintains a comparatively consistent stage

Write clearly 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%, 3.35%, 3.77%, 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 decaying foliage.

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	- 19.30 %

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, consisted of no less than 30 large, well-randomised samples that individual results were remarkably consistent it is possible that the results above is significant. The difference lies in the direction which would be 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 vary quite appreciably.

Conclusions:-

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

4. Soil Maximum Water Retaining Capacity Analyses.

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

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

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

$$\text{e.g. Percentage W.W.R.C.} = \frac{\text{Water retained by saturation}}{\text{Dry soil used}}$$

$\times 100.$

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) W.W.R.C. of Cynodon veld soil is lower than that of Purple Veld soil.
- (ii) W.W.R.C. of Hyparrhenia veld is slightly lower than that of Purple Veld soil.
- (iii) W.W.R.C. of Purple Veld soil is lower than that of Climax Scrub soil.

The results are what were expected and with the possible 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:

W.W.R.C. of soils increases as secondary succession fallow lands advance toward the climax, with the greatest difference existing between W.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 vegetation 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. <i>Cynodon</i> - <i>Eragrostis</i> -etc fallow	= 23 min. 2 sec.
B. Adjoining Purple Veld	= 35 " 6 "
C. <i>Hyparrhenia hirta</i> -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

54.
would still be faster than that for Hyparrhenia veld. The answer to the problem may lie in the inaccuracy 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 figure 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 H.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.
 (ii) Hyparrhenia Veld " " " " " " " "
 (iii) Purple Veld " " " " " Climax Scrub

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 toward 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: Analysis.

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 $\pm 70^{\circ}\text{C.}$, 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 1" 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 Lemmexman (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:-

		<u>Estimations.</u>	
		<u>Dr. Weinmann</u>	<u>Rose Innes.</u>
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	=	4.5	4.5
F. Adjoining Purple Veld	=	4.2	4.3

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.

The results obtained were as follows:-

(* = spoilt determination)

(1) Gynedon veld soil contains more acid than that of Purple
Veld.

(iii) Hypocyanic	"	"	"	"	"	"	"	"
(iii) Purple	"	"	"	"	"	"	"	Glass Cover.
(iv)	"	"	"	"	"	"	"	d. fers considerably in acid content.

It will be seen that the acid content of soils decreases steadily as vegetation approaches the climax. The gradient seems to be fairly smooth 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 is 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 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 Necht Photometer described by Phillips, Scott and Hoggridge (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 W.A.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.

(1) 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 holdard 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 successional 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.R.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.R.C. is not responsible for accelerating succession. Percentage M.W.R.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.R.C. has some small effect upon preparing the way for the invasion of successional 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, bulard and M.W.R.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 these 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. 35) 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 congesta 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,
AND
TIME OF GERMINATION, STRUCTURE AND DOMINANCE
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 nature to the ground. The disseminules were collected from plants existing in areas of which they were typical constituents - e.g. *Aristida longesta* 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 Scott (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 on the same samples of seed and the results were in each case expressed as a percentage of the sample. The results obtained for insect parasitism are as follows. The key to the number 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	Community No.
<i>Trachypogon plumosus</i>	300	39.0	4
<i>Acacia robusta</i>	3026	35.03	5
<i>A. Karroo</i>	2000	23.50	5
<i>A. caffra</i>	4700	17.02	5
<i>Andropogon amplexans</i>	267	12.32	4
<i>Pogonochloa magalis-montana</i>	250	6.80	5
<i>Panicum natalense</i>	250	5.60	4
<i>Urelytrum squarrosum</i>	250	4.40	4
<i>Zizyphus mucronata</i>	550	4.360	5
<i>Aristida congesta</i>	250	4.00	2
<i>Hyparrhenia hirta</i>	250	4.00	3
<i>Themeda triandra</i>	250	3.80	3
<i>Bidens pilosa</i>	275	2.91	1
<i>Eragrostis guineensis</i>	250	2.80	2
<i>Heteropogon contortus</i>	260	1.60	3
<i>Setaria</i> sp.	250	1.60	1
<i>Cymbopogon excavatus</i>	250	0.80	3
<i>Pogonarthria squarrosum</i>	250	0.80	2
<i>Schizachyrium semiterbe</i>	250	0.40	3
<i>Datura stramonium</i>	250	0.40	1
<i>Physalis minima</i>	250	0.40	1
<i>Amaranthus Thunbergii</i>	275	0.36	1

Species	No. dissected	Percentage parasitised	Community No.
<i>Eleusine indica</i>	250	-	1
<i>Sonchus oleraceus</i>	260	-	1
<i>Chloris virgata</i>	250	-	1
<i>Hydrocotyle repens</i>	250	-	2
<i>Cynodon dactylon</i>	300	-	2
<i>Royena pallens</i>	187	-	
<i>Vangueria infausta</i>	250	-	
<i>Tagetes minuta</i>	250	-	1
<i>Tristachya hispida</i>	400	-	4
<i>Cassia burkeana</i>	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, Cassia 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 Aristachya 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 Koyena bailans 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
<i>Themeda triandra</i>	Insect larvae, possibly Chalcids.
<i>Vangueria infausta</i>	Possibly a moth larvae.
<i>Schizachyrium semiberbe</i>	Plant bug and Psocids - found amongst stored seed.
<i>Tristachya hispida</i>	Insect larvae. Possibly Chalcids.
<i>Trachypogon plumosus</i>	Insect larvae. Dipterous or hymenopterous.
<i>Acacia caffra</i>	Bruchidae, Coleoptera - possibly <u>Bruchus</u> sp.
<i>A. robusta</i>	" " " " "
" "	Immature bugs, Lygaeidae or Pyrrhocoridae - found inside the pod, not on seed.
" "	<u>Enaretta acaciaria</u> . Lemnidae, Coleoptera.
<i>Andropogon amplexans</i>	Dipterous larvae, probably Mycetophilidae.

Species.	Parasitised by
<i>Hyparrhenia hirta</i>	Unknown insect larvae.
<i>Eragrostis sagalis-contans</i>	Curculionidae, Coleoptera.
<i>Eragrostis gummiflua</i>	Chirothrips sp. (1) Triptidae. Thysanoptera.
<i>Pogonarthria squarrosa</i>	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:-

<i>Trachypogon plumosus</i>	Syagrus sp. Eumolpidae, Coleoptera.
<i>Andropogon amblectens</i>	
<i>Symbopogon excavatus</i>	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.
<i>Themeda triandra</i>	250	7.60	4
<i>Cassine burleana</i>	310	5.81	5
<i>Urelytrum squarrosam</i>	250	4.00	4
<i>Bidens pilosa</i>	275	2.19	1
<i>Gymnopogon excavatus</i>	250	1.60	3
<i>Myarrhenia hirta</i>	250	0.80	3
<i>Adiropogon amplexans</i>	267	0.37	4
<i>Vangueria inifolia</i>	250	0.20	5
<i>Eleusine indica</i>	250	-	1
<i>Fagara magalis-montana</i>	250	-	5
<i>Schkuhria bonariensis</i>	260	-	1
<i>Schizachyrium semiberbe</i>	250	-	3
<i>Heteropogon contortus</i>	260	-	1
<i>Chloris virgata</i>	250	-	1
<i>Amaranthus Thunbergii</i>	275	-	1
<i>Rhynchosytrum repens</i>	250	-	2
<i>Panicum natelense</i>	250	-	4
<i>Setaria sp.</i>	250	-	1
<i>Cynodon dactylon</i>	300	-	2
<i>Pogonarthria squarrosam</i>	250	-	2
<i>Royena pallens</i>	187	-	5
<i>Aristida congesta</i>	250	-	2
<i>Eragrostia gummiflua</i>	250	-	2
<i>Zizyphus mucronata</i>	275	-	5
<i>Datura stramonium</i>	250	-	1
<i>Physalis minima</i>	250	-	1
<i>Tagetes minuta</i>	250	-	1
<i>Tristachya hispida</i>	400	-	4
<i>Trachypogon plumosus</i>	300	-	4
<i>Azadirachta indica</i>	4700	-	5
<i>A. indica</i>	2000	-	5
<i>A. robusta</i>	3026	-	5

With the exception of Eidens 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 Neerpoort, 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 teliospore 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.
<i>Canium natalense</i>	250	92.80	4
<i>Urcytrum squarrosus</i>	250	86.80	4
<i>Andropogon amplexans</i>	267	80.15	4
<i>Setaria</i> sp.	250	78.00	1
<i>Cymbopogon excavatus</i>	250	76.00	5
<i>Schizanthium semiberbe</i>	250	74.00	3
<i>Eragrostis gummiflua</i>	250	74.00	2
<i>Royena pallens</i>	187	68.98	5
<i>Pagara magalis-montana</i>	250	64.40	5
<i>Hyperbentia hirta</i>	250	64.40	3
<i>Chloris argata</i>	250	58.00	1
<i>Pogonochloa squarrosan</i>	250	57.60	2
<i>Cynodon dactylon</i>	300	56.00	2

Species	No. used.	Percentage undeveloped	Community No.
<i>Trachypogon plumosus</i>	300	52.67	4
<i>Vangueria infausta</i>	250	39.60	5
<i>Amaranthus Thunbergii</i>	275	32.00	1
<i>Cassine burkeana</i>	310	31.29	5
<i>Heteropogon contortus</i>	260	30.00	3
<i>Aristida congesta</i>	250	24.00	2
<i>Themeda triandra</i>	250	17.60	3
<i>Schkuhria bonariensis</i>	260	16.54	1
<i>Rhynchosytrum repens</i>	250	12.40	2
<i>Bidens pilosa</i>	275	5.45	1
<i>Eleusine indica</i>	250	5.20	1
<i>Zizyphus mucronata</i>	275	4.73	5
<i>Tagetes minuta</i>	250	3.60	1
<i>Datura stremonium</i>	250	-	1
<i>Physalis minima</i>	250	-	1
<i>Tristachya hispida</i>	400	-	4
<i>Acacia caffra</i>	4700	-	5
<i>A. karroo</i>	2000	-	5
<i>A. robusta</i>	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 guineiflora* it is certain that some seeds dropped out of the disseminules 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 *Pennisetum squarrosus*. The results for *Boyseniana pallens* are probably inaccurate.

In the case of *Vangueria infausta* and *Boyseniana 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 parasitized seed in this species.

For reasons already mentioned, it is impossible to obtain a true idea of the percentage undeveloped seed in species such as Datura stramonium and Physalis ~~minima~~ ^{peruviana}.

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.
<u>Physalis minima</u>	99.60	1
<u>Datura stramonium</u>	99.60	1
<u>Eleusine indica</u>	96.40	1
<u>Tagetes minuta</u>	94.80	1
<u>Zizyphus</u>	90.99	5

Species	Percentage Good seed.	Community No.
<i>Bidens pilosa</i>	89.45	1
<i>Abundelytrum ^{robens} squarrosum</i>	87.60	2
<i>Schkuhria bonariensis</i>	83.46	1
<i>Acacia caffra</i>	82.98	(5)
A. Karroo	76.50	(5)
<i>Aristida congesta</i>	72.00	2
<i>Themeda triandra</i>	71.20	3
<i>Heteropogon contortus</i>	68.40	3
<i>Amaranthus Thunbergii</i>	68.38	(1)
<i>Acacia robusta</i>	64.97	5
<i>Cassine burkeana</i>	62.90	(5)
<i>Vangueria infausta</i>	58.40	(5)
<i>Cynodon dactylon</i>	44.00	2
<i>Chloris virgata</i>	42.00	1
<i>Pogonarthria squarrosam</i>	41.60	2
<i>Fagara regalis-montana</i>	32.80	(5)
<i>Royena pallens</i>	31.01	(5)
<i>Hyparrhenia hirta</i>	30.90	3
<i>Schizachyrium semiberbe</i>	25.60	3
<i>Eragrostis gummiflua</i>	23.20	2
<i>ymbopogon excavatus</i>	21.60	3
<i>Setaria sp.</i>	20.40	(1)
<i>Tristachya hispida</i>	20.25	4
<i>Trachypogon plumosus</i>	2.33	4
<i>Antropogon asplectens</i>	7.12	4
<i>Abundelytrum squarrosam</i>	4.80	4
<i>Panicum natalense</i>	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 of about thirty species of seed upon fallow soils 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:

$$A T = \frac{\sum g t}{\sum g} \quad \text{where } A T = \text{average time}$$

$\sum$ - "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 gumiflua, caryopses were used in laboratory test instead of disseminules.

Zizyphus fruits were planted instead of seeds. This was done as the number of seeds each fruit contained was known 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
<i>Bidens pilosa</i>	1 day	2.6	96.00	500
<i>Acacia caffra</i>	4 days	11.6	95.00	200
<i>Physalis minima</i>	2 "		93.00	500
<i>Tagetes minuta</i>	2 "	2.6	89.40	500
<i>Ceniza antiqua</i>	2 "	3.0	82.00	500
<i>Acacia robusta</i>	19 "	61.9	77.20	
<i>Heteropogon contortus</i>	2 "	4.4	76.80	500
<i>Rhyndelytrum repens</i>	2 "	4.76	61.00	500
<i>Themeda triandra</i>	3 "	5.0	45.00	500
<i>Vangueria infausta</i>	58 "	61.9	42.00	100
<i>Eragrostis gumiflua</i>	4 "	6.0	28.20	500
<i>Schizachyrium semiberbe</i>	4 "	8.8	27.40	500
<i>Hyparrhenia hirta</i>	2 "	3.1	24.20	500

Species	Time of 1st. Ger- mination	Average time of germin- ation	Percentage germinat- ion	No. of disseminules in test
<i>Cymbopogon excavatus</i>	2 days	3.8 days	18.40	500
<i>Sonchuhria bonariensis</i>	2 "	3.4 "	18.00	500
<i>Gymnosporia buxifolia</i>	8 "	13.3 "	17.00	500
<i>Trachypogon plusosue</i>	3 "	4.5 "	10.00	500
<i>Amaranthus Thunbergii</i>	2 "	7.4 "	8.6 or 22.2	500
<i>Caloris virgata</i>	1 day	2.8 "	7.60	500
<i>Tristachya hispida</i>	3 days	6.0 "	7.29	150
<i>Aristida congesta</i>	4 "	9.2 "	6.80	500
<i>Andropogon amplexans</i>	3 "	6.2 "	4.80	500
<i>Zetaria sp.</i>	4 "	5.9 "	3.80	500
<i>Urelytrum squarrosus</i>	5 "	7.6 "	3.20	500
<i>Eleusine indica</i>	3 "	9.1 "	2.00	500
<i>Rhus Gueinzii</i>	18 "	29.87 "	1.20	500
<i>Gnaphalium undulatum</i>	5 "	7.66 "	0.60	500
<i>Nidorella anomala</i>	11 "	13.0 "	0.60	500
<i>Panicum natalense</i>	14 "	15.0 "	0.20	500
<i>Pogonarthria squarrosa</i>	5 "	6.0 "	0.20	500
<i>Datura stramonium</i>	-	-	0.00	500
<i>Cynodon dactylon</i>	-	-	0.00	500
<i>Fagara sagalis-montana</i>	-	-	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 Sagura megalis-montana and Rhus Guinizii, 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. ger- mination	Average time of germin- ation	Percentage germinat- ion	No. of dissem- inules in test.
<i>Acacia caffra</i>	4 days	11.6	35.0	200
<i>Physalis minima</i>	8 "	10.5	63.0	200
<i>Acacia robusta</i>	19 "	61.9	77.2	136
<i>Schizachyrium semiberbe</i>	8 "	13.7	75.0	400
<i>Eryena pallens</i>	39 "	65.7	71.8	85
<i>Heteropogon contortus</i>	5 "	7.6	65.0	400
<i>Themeda triandra</i>	6 "	12.4	59.5	400
<i>Eleusine indica</i>	6 "	20.7	57.0	400
<i>Bidens pilosa</i>	2 "	6.8	53.7	400
<i>Vangueria infausta</i>	89 "	97.5	42.0	100
<i>Rhynchosytrum repens</i>	7 "	9.5	37.5	400
<i>Amaranthus Thunbergii</i>	5 "	9.6	35.0	200
<i>Caloris virgate</i>	3 "	6.99	32.3	400
<i>Aristida congesta</i>	6 "	7.8	28.5	400
<i>Datura stramonium</i>	19 "	44.5	28.0	200
<i>Cassine burkeana</i>	52 "	64.0	25.0	160

Species	Time of 1st. ger- mination	Average time of germin- ation	Percentage germinat- ion	No. of dissemin- ules in test
<i>Gymnosporia buxifolia</i>	30	49.8	22.0	100
<i>Hyparrhenia hirta</i>	6	10.2	21.0	400
<i>Cymbopogon excavatus</i>	5	6.8	20.5	400
<i>Tagetes minuta</i>	3	6.7	17.0	400
<i>Trachypogon plumosus</i>	7	10.2	14.5	400
<i>Acacia Karroo</i>	8	52.6	12.0	200
<i>Andropogon amplectens</i>	4	7.3	11.5	400
<i>Urelytrum squarrosus</i>	10	15.9	5.0	400
<i>Zizyphus mucronata</i>	136	172.7	4.7	150
<i>Ahus Gueinzii</i>	48	22.5	3.0	200
<i>Pagara magalis- montana</i>	36	69.0	1.0	200
<i>Cynodon dactylon</i>	-	-	-	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, Schizanthus lamarckii, Amaranthus thunbergii, Eleusine indica, Gnaphalium undulatum, Fitorella anomala, Pogonarthria squarrosa and Datura stramonium - which, with one exception, are all members of the ruderal group. Seeds do not develop in about 50% 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 Schizanthus. 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 radicle 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 Fitorella 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.

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, 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 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 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 ^{be} 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 senilbarbe, 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 14. r) Acacia calfra 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 Erythrina 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 Schizanthium semiterre. (See Seed Photograph No. 5.) In the latter instance, the disseminule and the attached sterile spikelet were weighed together. In doubtful instances, however, such as Triphragon plumosa, Andropogon amplexicaulis, Cymbopogon excavatus and others, the sterile spikelet was removed -- if it had not already fallen off -- and the disseminule alone was weighed. From the way in 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 its 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.
<i>Vangueria infausta.</i>	150	3.39000	5
<i>Zizyphus mucronata.</i>	1000	1.40350	5
<i>Acacia robusta.</i>	500	0.16633	5
<i>Royena pallens.</i>	75	0.12912	5
<i>Acacia caffra.</i>	5400	0.04930	5
<i>A. Karroo.</i>	500	0.04066	5
<i>Fagara mangle-montana.</i>	300	0.01914	5
<i>Themeda triandra.</i>	500	0.01244	3
<i>Urolytrum squarrosum.</i>	250	0.01220	4
<i>Rhus Gueinzii.</i>	2000	0.00965	5
<i>Heteropogon contortus.</i>	250	0.00853	3
<i>Datura stramonium.</i>	1000	0.00679	1
<i>Gymnosporia buxifolia</i>	400	0.00540	5
<i>Trachypogon plumosus.</i>	500	0.00535	4
<i>Andropogon amplexans.</i>	500	0.00245	4
<i>Bidens pilosa.</i>	1000	0.00222	1
<i>Schizachyrium semiberbe.</i>	500	0.00189	3
<i>Rhynchosytrum repens.</i>	500	0.00099	2
<i>Hyparrhenia hirta.</i>	250	0.00097	3
<i>Schkuhria bonariensis.</i>	400	0.00088	1
<i>Tagetes minuta.</i>	500	0.00087	1
<i>Eleusine indica.</i>	500	0.00078	1
<i>Cymbopogon exaristatus.</i>	500	0.00058	3
<i>Setaria sp.</i>	500	0.00056	1
<i>Aristida congesta.</i>	500	0.00051	2
<i>Amaranthus Thunbergii.</i>	500	0.00051	1
<i>Chloris virgate.</i>	500	0.00030	1
<i>Panicum natalense.</i>	500	0.00029	4
<i>Conyza ambigua.</i>	500	0.00019	1
<i>Cynodon dactylon.</i>	500	0.00016	2
<i>Pogonarthria squarrosum.</i>	500	0.00008	2
<i>Eragrostis gumiflua.</i>	500	0.00003	2
<i>Nidomella anomala.</i>	500	0.00003	
<i>Graphelium undulatum.</i>	Not weighed - leaflets had fallen off. weight not between Nidomella and Conyza.		

An attempt was made to express the results graphically. 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 disseminules of Purple Veld and those of the Scrub Climax.

Another important result which emerges - though this fact is already well known - is that the species which are able to colonise 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 as *Pogonarthria squarrosa* and *Eragrostis curviflora* 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 mud on animal hooves. But this must be 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 Pidans 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 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).

(1) 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 Photograph No. 13. The mechanism is very efficient and so is the whole process of dispersal. A factor which probably plays some part 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 virgate - 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) : Conate Mechanisms.

Only one species falls legitimately into this group. Aclepias 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 amoigna. 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 described later.

Species which fall into this group are such as Xanthium spinosum, X. strumarium, Combrene globosa (no hooks but the effect is the same), Tragus berteronianus, Taraxacum officinale, Bidens pilosa, and Tribulus terrestris (no hooks). Though the mechanism itself may be an extremely efficient organ of attachment --e.g. as in the disseminule of Xanthium strumarium or Bidens pilosa (See Photograph No. 12) -- dissemination by this means depends upon the variable, casual factor, of the presence of animals or men. It is chiefly for this 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 mechanism 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 which spreads more by creeping stolons than by dispersal 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, Furcraea laxifolia, Scleria
sp., Amaranthus Wimmersii, 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 cumulative
effect of continual ploughing and poor cultivation
upon the reserves of seed in the soil. The seed dep
in the soil increases year by year. When cultivation
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 mobility
and viability of many ruderal species, combined with
the effect of continual ploughing and ^{poor} cultivation,
the root cause of the invasion of fallow land by
these species.

(11) Primary Grass Stage.

Group (a) : Parachute Mechanisms.

These do not actually exist in this stage but
disseminules of Aristida congesta and Rhynchelytrum
repens have been included here for purposes of
convenience. Aristida congesta disseminules are
to a certain extent dispersed by wind. The tripartite
arm is able to support the disseminule quite
well in the air and the seed is light. The disseminule
of Rhynchelytrum repens is covered with short
silky hairs which support it fairly well in the wind
(See Seed Photographs Nos. 4 and 5). Both types are
inefficient, however, as compared with the parachute
of Conyza rubra. 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. The
effects of these organs upon driving the disseminules

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 Phurcalytrum 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 occurred.

Group (b) : Spiked Calluses with Retrose Hairs.

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

Group (c) : Stolons.

A note has been added here upon the dispersal of Gynodon distylon. The disseminules are very light but possess no mechanism to aid dispersal. They are of the same type as that illustrated in Seed Photograph 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 Photograph 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 comparatively immobile by the lack of disper-

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) : Tuntlers.

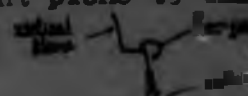
Trichoneura grandiflora falls into this group. The whole flower head breaks off and is rolled over the veld by the wind. The presence of tall grasses, however, may render the apparatus immobile. It is probably quite an efficient means of dispersal in areas where grass is short. The disseminules break 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.

(11) Secondary Grass Stage.Group (a) : Spiked Callus with Barbed Hairs.

All the grass species in this stage can be said to fall into this single group. In the case of Tripsacis triopis 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 Euphorbia hirta and Cymbopogon excavatus is only very moderately efficient as an attachment mechanism. In Schizachyrium paniculata, 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 the other 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 swn of Scirpus americanus 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 Thymus triandra and Heteropogon contortus differ slightly from those above and tend to be straighter. The effect, however, is the same.

Conclusions. (See Also Seed Photograph No. 1.)

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

(iv) Purple Vale or Grassland Climax Stage.

Group (a) : Spiked Callus with Entrance Hairs.

Trachypogon plumosus (See Seed Photograph No. 1) and Tripsaccha hispida are members of this group. The disseminule of T. hispida is very like that of Thymus triandra (See Seed Photograph No. 2.). The callus in both cases is an efficient organ of attachment but is not as efficient as that of Thymus triandra. Uralytrum squarrosus may be included in this group. Its callus as an attachment mechanism is, however, quite inefficient. The hairs are too weak and the callus blunt to allow of attachment. (See Seed Photograph 3). Monocymbium cerealiforme may also be included. The callus is relatively inefficient but the swn revolves well.

It is possible that the awns aid penetration of the soil to some extent in the case of Trachypogon plumosus, Tripsaccha hispida and Monocymbium cerealiforme. The swn of Uralytrum squarrosus scarcely does at all.

Group (b) : Lamiaceae.

Diplazium biflorum, Harpechloa falx, Panicum natalense (See Seed Photograph No.7), Alloternstroemia semialata, Distertia trichosperma, and Brachiaria 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 Bovina 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 as Acacia robusta and Zizyphus mucronata respectively,

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is likely that disseminules of scrub species 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. Ruderal 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 2.)

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 Coryza 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 area, 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 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, Brachiaria ab-undantia, Cymbopogon excavatus, Themeda triandra, Digitaria tricholamoides, Brachiaria serrata, Elymus aeneus and Tristachya Rohmanni and Bunting's work on Pennisetum 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 print. 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 Nakpoort 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.(1) Cynodon dactylon.

The taproot is distinct but much reduced in

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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.

(11) Taraxacum minima-

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 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 dissect 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 lateral roots given off. Some of these traverse horizontal 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 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 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 12" 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 "oukkip" 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 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 develops 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) Bracharia 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 Rehmanii, Urelytrum squarrosus 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 lateral

roots seems to indicate that it is likely to belong to a stage in succession which immediately precedes the stage containing the ultimate members of the Grassland Climax Stage. This indication is backed by results of 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, the large roots were broken. In the main, however, the roots tend to descend directly to comparatively deep levels where maximum division occurs. This is usually in the 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 roots. No superficial laterals of any importance are developed. The terminations of the deep roots are finely-branched and draw upon deep-seated water supplies.

Conclusions.

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

(xvii) Tristachya Reimanni.

Scarcely any superficial lateral roots are developed. Almost all roots penetrate to comparatively deep soil levels, though they appear to give off fine rootlets all the way down. The plant depends 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 water.

(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 Class

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 is 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. The 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 species.

6. Climax Scrub Vegetation.

The bisects were done on the eroded river walls of the Mekoport River in the Mago 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 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 roots

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assume its functions. This tree was probably about 12 years old.

Conclusions.

The superficial lateral roots of young Acacia Karroo trees are very well developed. These intercept water percolating down from the soil surface. The taproot is also very well developed and contacts very deeply-situated water supplies. The system as a whole 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 seen 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 taproot to its full extent in the one instance. The system is similar to that of Acacia Karroo in that it possesses both superficial laterals and a very deep taproot. The laterals may extend for quite large distances and 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. Vegetative reproduction is to some extent responsible for its rapid spreading. It is concluded from this evidence that the tree is well suited to colonise open grassland.

(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 rhannifolia.

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 preceding 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 rhannifolia. 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 rhombifolia 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 *Brachiaris* 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 two 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 three 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 111.CONCLUSIONS.SECTION A. : CHAPTER 1.

It was concluded from the results obtained in this portion of the work that soils &c 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 11.

Conclusions drawn from results given in this section are that the factors of mobility and viability of seed (which can be said to 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 11.

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 once secondary succession as studied in this work.

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.

APPENDIXTHE 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. Trachypogon plumosus (= T. polymorphus var. capensis), Urelytrum squarrosus 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 cerasiiforme, Panicum natalense, Andropogon schirensis, Harpachloa 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, Bethul, Cedarfont, 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.

Transsect 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 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 '28.
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. 10 & 11.) (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 Egg 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 West 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 possible Purple Veld may at one time have covered a much greater area than it does today, that it might possibly have filled the present semicircular, saucer-rim distribution and that it is quite possible that Themeda triandra veld is seral in character, merely a subclimax stage to the Purple Veld Climax.

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

A. caffra Willd.
A. eriadenia Benth.
A. Karroo Hayne (= *A. horrida* Willd.)
A. litakumensis Burch.
A. robusta Burch.
Acalypha angustata Sond.
A. caperonioides Baill.
Achyranthes aspera Linn.
Agrimonia eupatoria Linn.
Albucca pachyclanys Baker.
Alloteropsis semialata Hitch.
Alternanthera repens Stend.
Amaranthus Thunbergii Vog.
Andropogon amplexans 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.
Bacium obovatum var. *hians* N.E.Br.
Berkheya subulata Harv.
Bidens pilosa Linn.
Bopusia scabra Presl.
Bowisa volubilis Harv.
Brachiaria serrata (Spreng.) Stapf.
Brachyleena discolor D.C.
Callilepis leptophylla Harv.
Carissa arduina Lam.
Cassia minusoides Linn.

- Chenopodium ambrosioides* 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.
Doryalis Zeyheri Harv.
Ehretia hottentotica Burch.
Elephantorrhiza elephantina (Burch) Skeels.
Eleusine indica Gaertn.
Elionurus argenteus Nees.
Eragrostis brisoides Nees.
E. ^{chalcantha} chalcantha Nees.
E. chloromelas Steud.
E. curvula Nees.
E. gummiflua Nees.

- Eragrostis nebulosa* Stapf.
E. robusta Stent.
Erigeron canadensis Linn.
Eriosema cordatum E.Hey.
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 Keimr.
G. capitata Linn.
G. kraussiana Nelson.
G. microcephala Nelson.
Gomphrena globosa Linn.
Grewia flava D.C.
Gymnosporia buxifolia (Linn.) Szysz.
G. polycantha (Sond) Szysz.
Haplocarpa scaposa Harv.
Harpechloa fatx (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.

- Hyperbentia hirta* Stapf.
Hypericum aethiopicum Thunb.
Hypoestes verticillaris R.Br.
Hypoxis rigidula Baker.
H. Hooperi Moore.
Indigofera hybrida R.Br.
Iponoea bathycaulpos Hall.
I. simplex Thunb.
I. sp.
Justicia anagalloides T.Anders.
Kiggelaria africana Linn.
Lantana salvifolia Jacq.
Laportea eruenta Baker.
Lepidium lineoides Thunb.
Leucas martinicensis R.Br.
Lebelia decipiens S.Moore.
L. regulata Send.
Lophoceros digitata Stapf.
Londesia simplex C.E. Hubbard.
Lotononis foliosa Delus.
Marrum triphylla A.Rich.
Mossymbium cerasiiforme (Nees) Stapf.
Niderella anomala Steetz.
N. hottentotica D.C.
Oenothera biennis Linn.
Olea verrucosa Link.
Oldenlandia austynbica (Hochst) E.Schum.
Oxyris abyssinica Hochst.
Oxalis setosa E.Mey.
Pachystigma pygmaea
Panicum celeratum Linn.
P. laevifolium Hack.
P. natalense Hochst.
Pappus capensis E. & Z.
Parvella sp.
Pelargonium acuminatophyllum E. & Z.

- Pelargonium aconitophyllum* var *angustisectum* Kunth.
Pentanisia variabilis Harv.
Perotis indica (Linn Kuntze)
Peucedanum magalis-montanum Sond.
Physalis minima Linn.
Pittosporum viridiflorum Sims.
Plectronia mundtiana (Ch. & Chl.) Pappe.
Plumbago capensis Thunb.
Pogonarthria squarrosa (Licht) Pilg.
Polvgala abyssinica R.Br.
P. gracilentia Burt Davy.
Portulaca oleracea Linn.
Protea caffra Meisn.
P. hirta Klotzch.
P. Rouppelliae Meisn.
Raphionacme divaricata Harv.
Ravenelia MacOwaniana Pazschke.
Rhoicissus cuneifolia (E. & Z) Blanch.
Rhus Gueinzii Sond.
R. c.f. mucronata Thunb.
Rhyncelytrum repens (Willd) C.E. Hubb.
~~*R. setifolium* Choisy.~~
Royena pallens Thunb.
R. Wilmsii Querke.
Sansevieria thyrsiflora Thunb.
Sarcostemma viminalis 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 gibbachiata* Oliver.
- Sphenostylis angustifolia* Sond.
- Sporobolus fimbriatus* Nees.
- S. indicus* R.Br.
- Stiburus alopecuroides* (Hack) Stapf.
- Stoete vulgaris* Levyns.
- Striga elegans* Benth.
- Tagetes minuta* Lam.
- Tarchonanthus camphoratus* Linn.
- Tephrosia auriantiaea* R.G.W.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.
- Utrum squarrosus* Hack.
- Urginea multisetosa* Baker.
- Urochloa helopus* Stapf.
- Ursinea annua* Less.
- Vangueria euonymoides* Schweinf.
- V. infausta* Burch.
- V. Kraussii* Sch Bip.
- V. monocephala* Harv.
- Wolffia uncalata* A.D.C.

Walafridea densiflora Rolfe.

Xanthium spinosum Linn.

X. strumarium Linn.

Zinnia pauciflora Linn.

Zizyphus mucronata Willd.

Z. zeyheriana Sond.

141
Walafrida densiflora Rolfe.

Xanthium spinosum Linn.

X. strumarium Linn.

Zinnia pauciflora Linn.

Zizyphus mucronata Willd.

Z. zeyheriana Sond.

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I should like to acknowledge my indebtedness in the first instance to D. R. John Phillips for his guidance of this work and for his continued interest and constructive criticism.

I have to thank the Secretary for Agriculture, Dr. I.B. Pole Evans - Head of the Division of Plant Industry and Mr. Rowland - Senior Pasture Research Officer, for authority to accompany the Pasture Research Officer, Leeuwkuil Research Station, on an extensive motor survey tour of the central Free State and South Western Transvaal; Mr. Rowland and Pasture Research Officers for the loan of apparatus, Dr. E.P. Phillips of the National Herbarium for determination of plant species and Mr. Munro of the Section of Entomology, Division of Plant Industry, for determination of insect species.

Mr. Gilliland has assisted me with information on the Drakensberg area and Dr. Weinmann with advice and analytical work in the laboratory.

Mr. Story has provided me with information on the Vereeniging vegetation types. One of the histograms reproduced here is his work.

My thanks are due to Mr. Palf of the University Photographic Department for his valuable work on the seed photography and to Mr. Allison for assistance in photographing root bisects. Mr. Davidson gave me much valuable help with work on root bisects, seed germination and parasitism.

Mr. van Rensburg placed the results of his quadrat analyses at my disposal and helped to draw up the graphs. Mr. Dickinson also assisted with graphical work.

Mr. Altona provided me with information on certain grass species. Mr. Murray has placed his root bisect charts at my disposal.

Miss Murray assisted me with work on belt transects and has given much help with statistical analyses and preparing the graphs and plant lists for this paper.

Finally I should like to express my sincere thanks to Mr. Hume for the typing and final preparation of this paper.

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, GRAPHIST
ROOT BISECT CHARTS AND PHOTOGRAPHS.

(To accompany the above thesis.)

H. K. H. H. H.

PHOTOGRAPH.

Photograph No. 1.

Recently ploughed fallow. Note colonization
tion by *Cyperus esculentus* runners - very
abundant here. Also one or two plants
of *Gonysa ambigua* and *Erigeron annuus*.



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. 3.

Two *Eragrostis chaetantha* 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. *Prolytrum*
squarrosus, *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.
Zizyphus zeyheriana growing on the mound
and Z. mucronata seedling just beyond.
Note zone of Vernonia Kraussii (in flower)
round the termitarium.



Photograph No. 8.

Termitaria. Invasion of scrub species.
In foreground, termitarium with *Cynodon*
dactylon in centre and a number of
Gymnosporia burkeana 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 ~~the~~ and deruded
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 hettentotica*, somewhat lower than the *Euclea*. Seedlings of *Scoroptia Zeyheri* also occurred here with *Lantana salvifolia*.



Photograph No. 12.

Invasion of scrub species. Text to figure:
Asparagus sp. protruding from a small speci-
men of Rhus v.f. mucronata which is growing
up and choking the latter. *Rayana pallens*
in background.



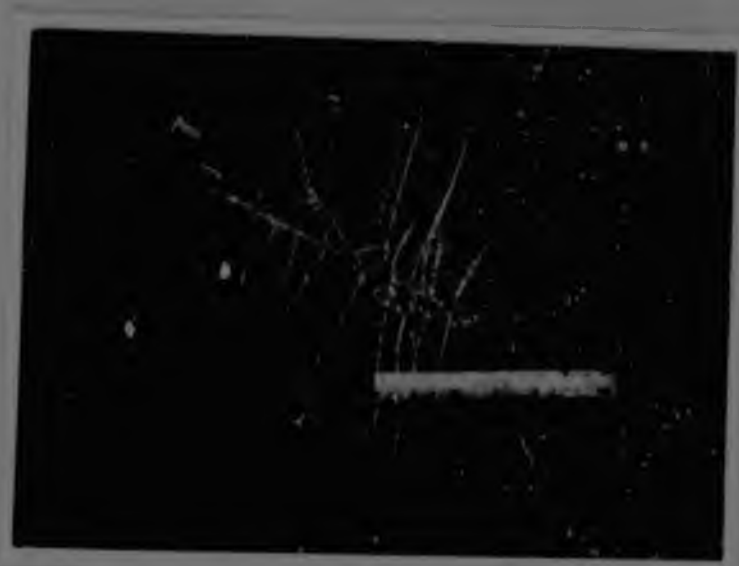
Photograph No. 13.

Rhoicissus cuneifolia spreading over ~~*****~~
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 *Zizyphus mucronata*. Root activity is intense in superficial soils in scrub areas.



Photograph No. 18.

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.



REED PHOTOGRAPH

Fig. 1. Trachypogon plumosus.

Dispersal of *Trachypogon plumosus*. Note
long twisted arm, twice bent. Note also
spiked callus with stiff retrose hairs.

Millimetre scale.

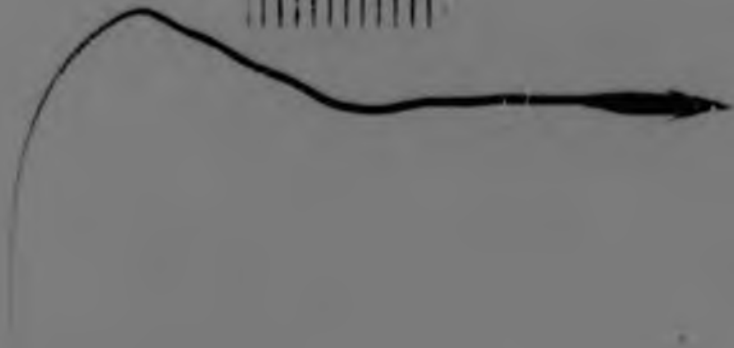
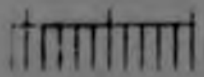
Head Photograph No. 2.

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

Millimetre scale.



2



Seed Photograph No. 1.

Disseminule of *Urolytrum squarrosu*. Note
very blunt callus with few weak hairs,
straight untwisted awn with no bends.

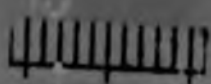
Millimetre scale.

Leaf Photograph No. 4.

Diagram of *Aristida congesta*. Note
tripartite, twisted awn and spinous 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.

Disseminule of *Panicum natalense*. Note complete absence of any dispersal mechanisms.

Millimetre scale.



Seed Photograph No. 3.

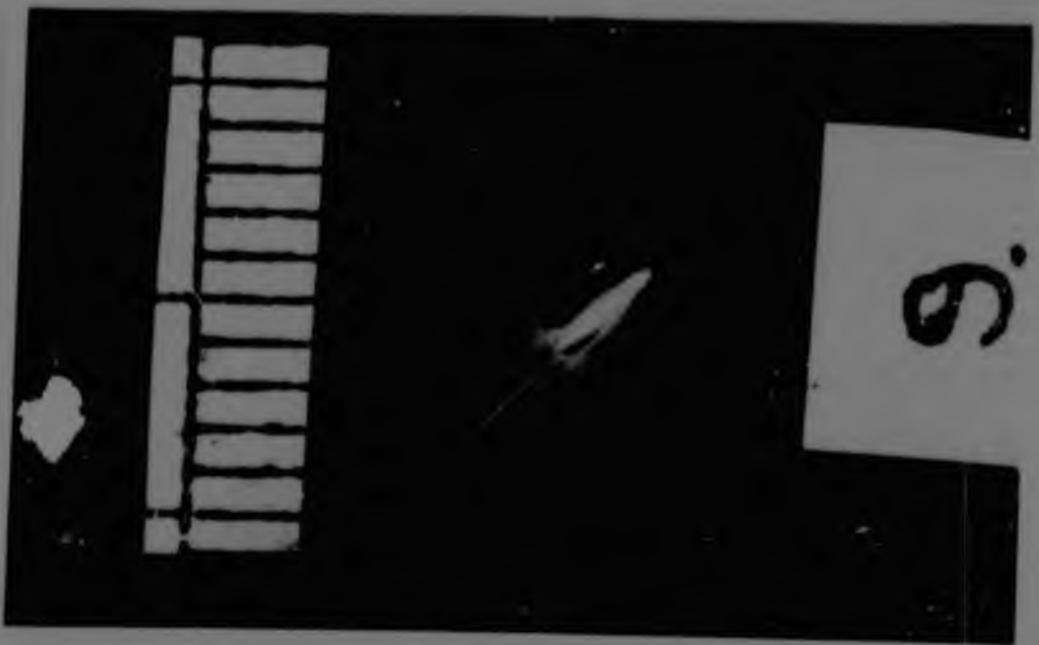
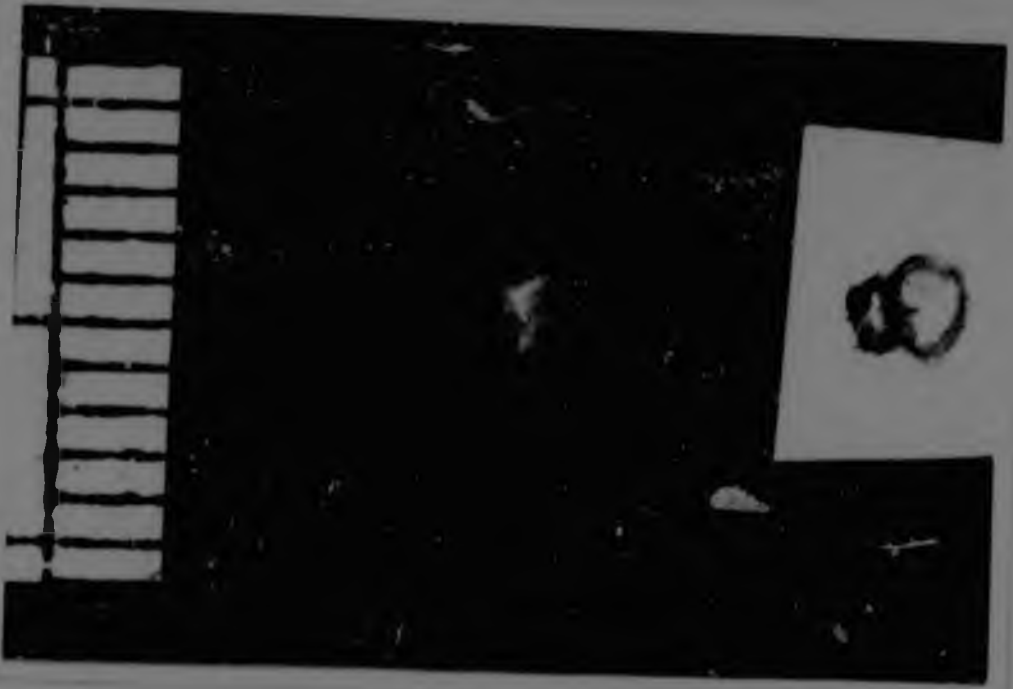
Elaeagnus of Rhynchospora repens. Note
long filay hairs covering glumes.

Millimetre scale.

Seed Photograph No. 9.

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

Millimetre scale.



Real Photograph No. 10.

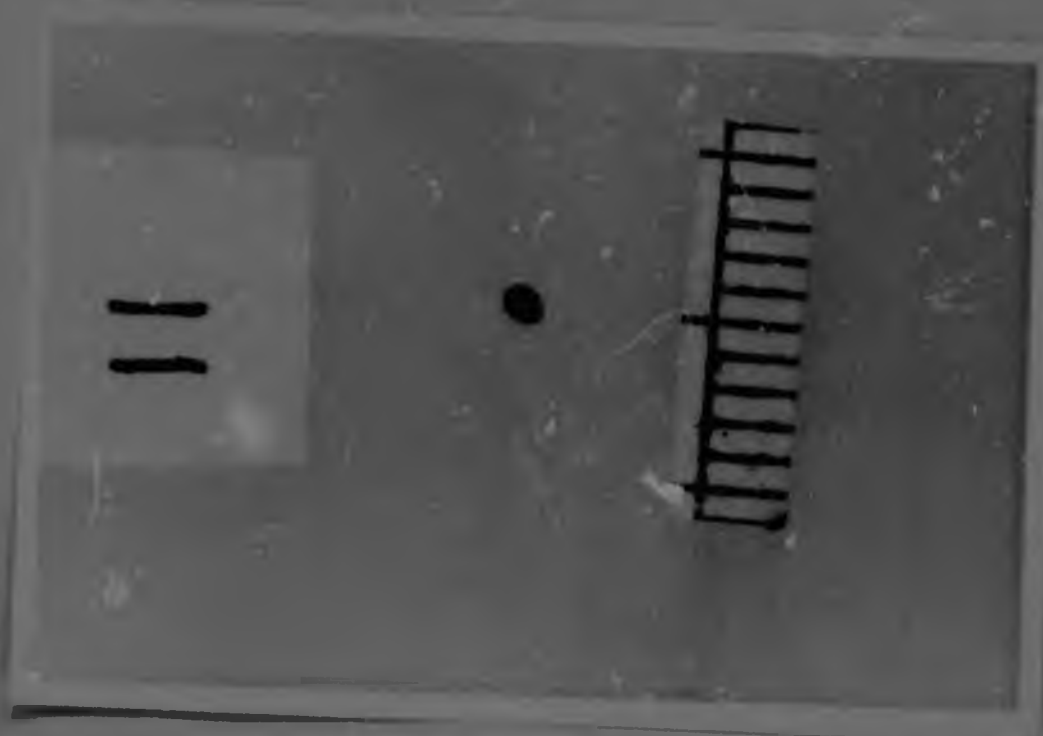
Disseminule of *Pogonarthria squarrosa*. Note
complete absence of any dispersal mechanism.

Millimetre scale.

Seed Photograph No. 11.

Seed of *Amaranthus Faunbergii*. Note size
and absence of any dispersal mechanisms.

Millimetre scale.



Real Photograph No. 12.

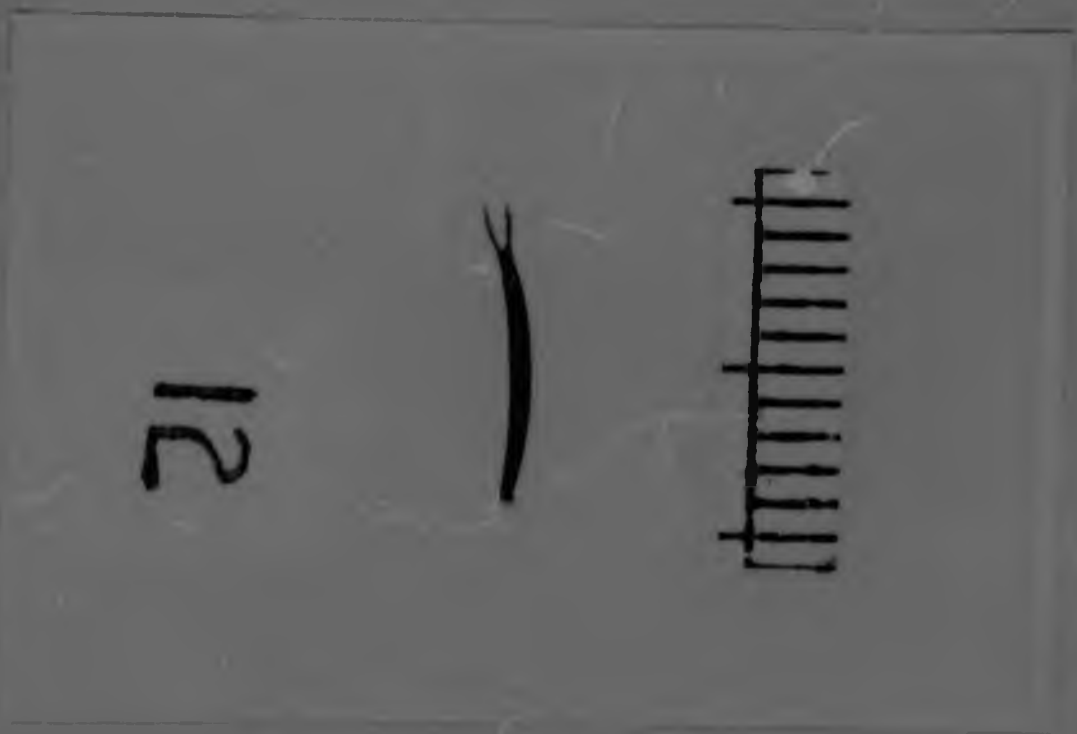
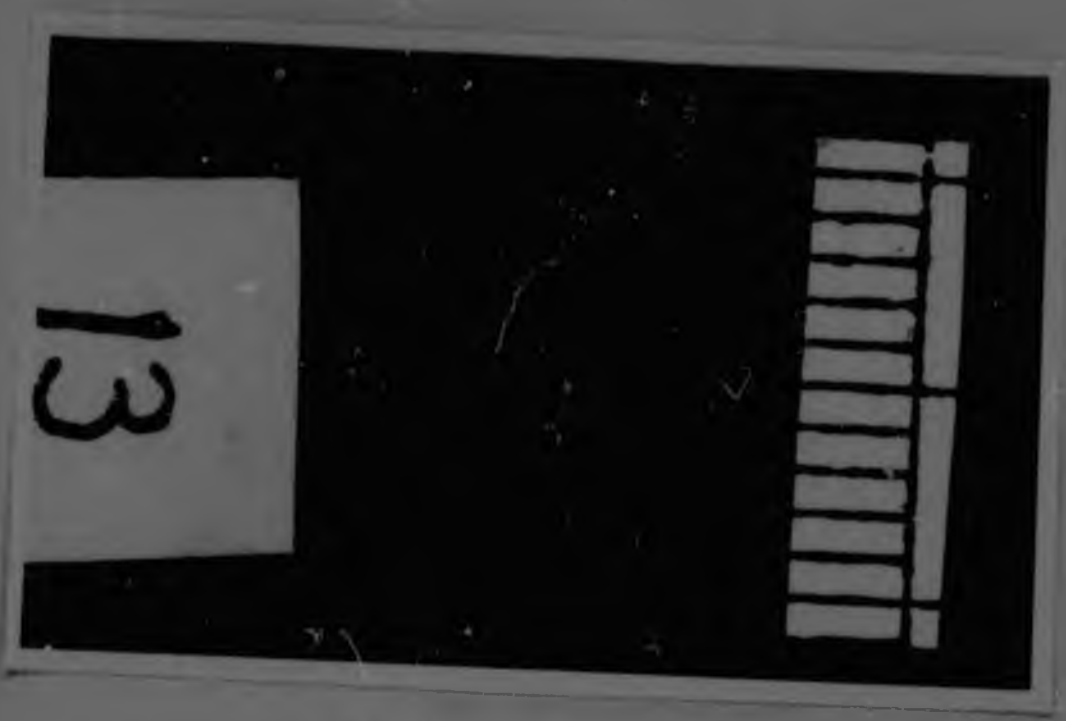
Disseminule of *Bidens pilosa*. Note barbs
at one end which aid in dispersal.

Millimetre scale.

Field Photograph No. 13.

Disseminule of *Conyza rubra*. Note para-
chute-like jappus.

Millimetre scale.



Seed Photograph No. 14.

Seed of *Datura stramonium*. Note absence
of dispersal mechanism.

Millimetre scale.

Seed Photograph No. 15.

Fruit (disseminule) of *Isopyrus macrocarpa*.

Note large size, lack of diapycnal mechanism,
and fleshy character.

Millimetre scale.

1111111111



14

1111111111



15

Seed Photograph No. 16.

Seed of *Asucia 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.

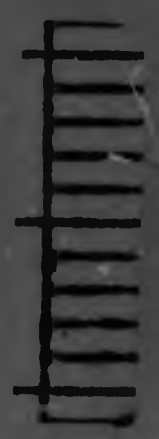
17



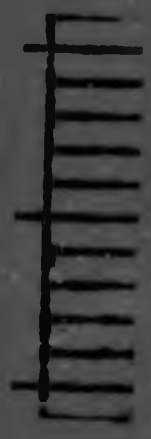
16



17



16



Seed Photograph No. 15.

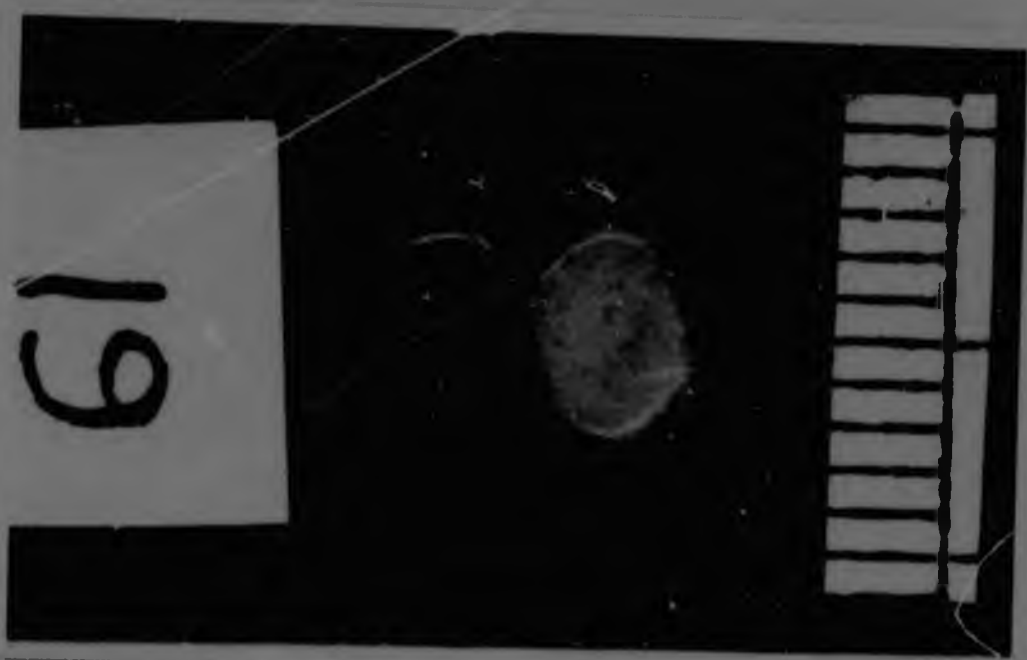
Fruit of *Vangueria infausta*. Note large
size, fleshy character and lack of dispersal
mechanisms.

Millimetre scale.

Leaf Photograph No. 13.

Fruit of *Rhus Gueinzii*. Note absence of
dispersal mechanisms.

Millimetre scale.



Seed Photograph No. 20.

Fruit of *Cuscuta burkeana*. Note fleshy
character, comparatively large size and absence
of dispersal mechanism.

Millimetre scale.

Seed Photograph No. 21.

Dehiscing fruit of *Fagaria sagalis-montana* with
seed. Note comparatively small seed and
absence of mechanisms.

Millimetre scale.



21



20



21



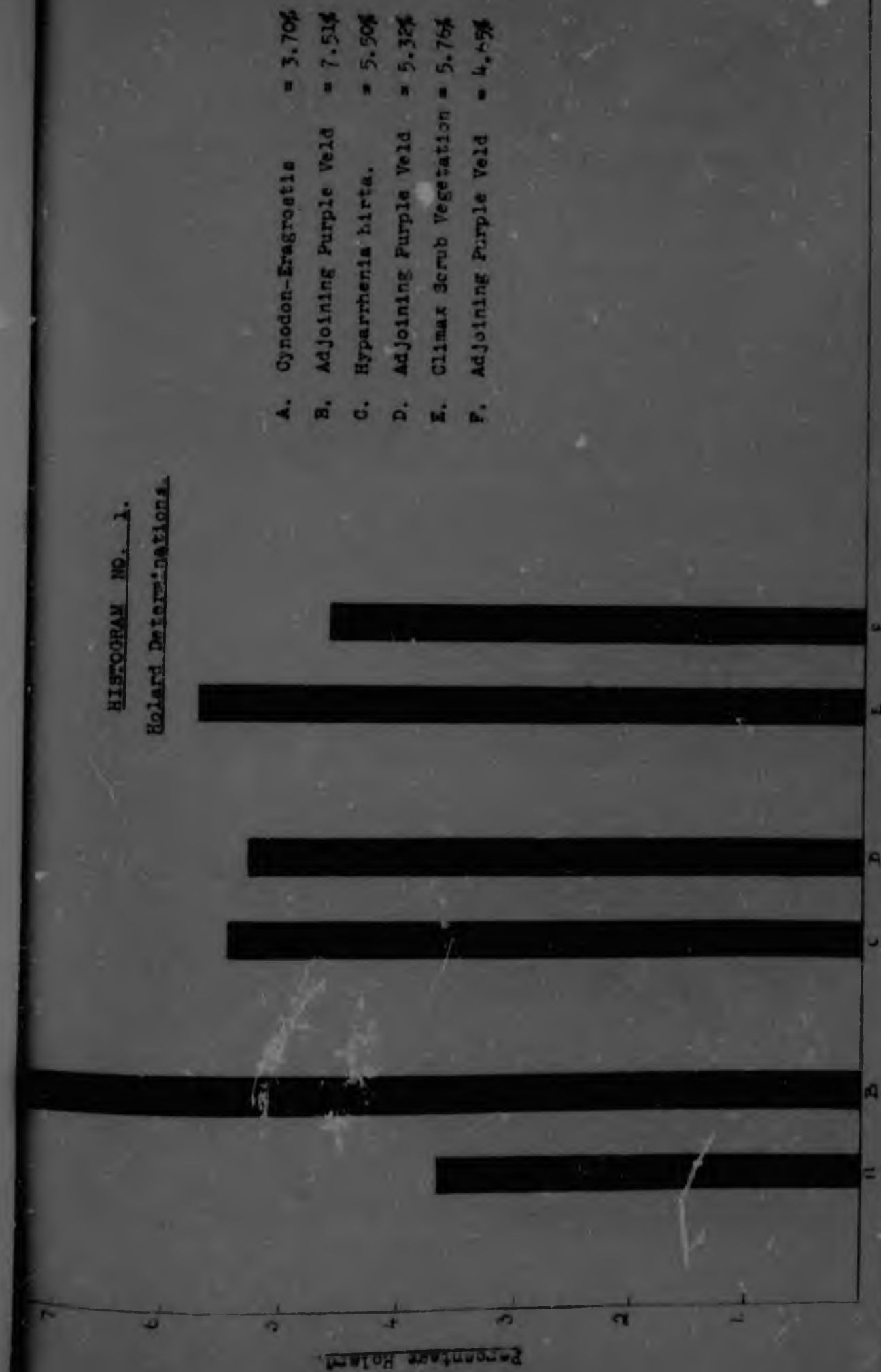
20

1. The first step is to identify the problem.
 2. The second step is to define the problem.
 3. The third step is to analyze the problem.
 4. The fourth step is to develop a solution.
 5. The fifth step is to implement the solution.
 6. The sixth step is to evaluate the solution.

HISTOGRAMS AND GRAPHS.

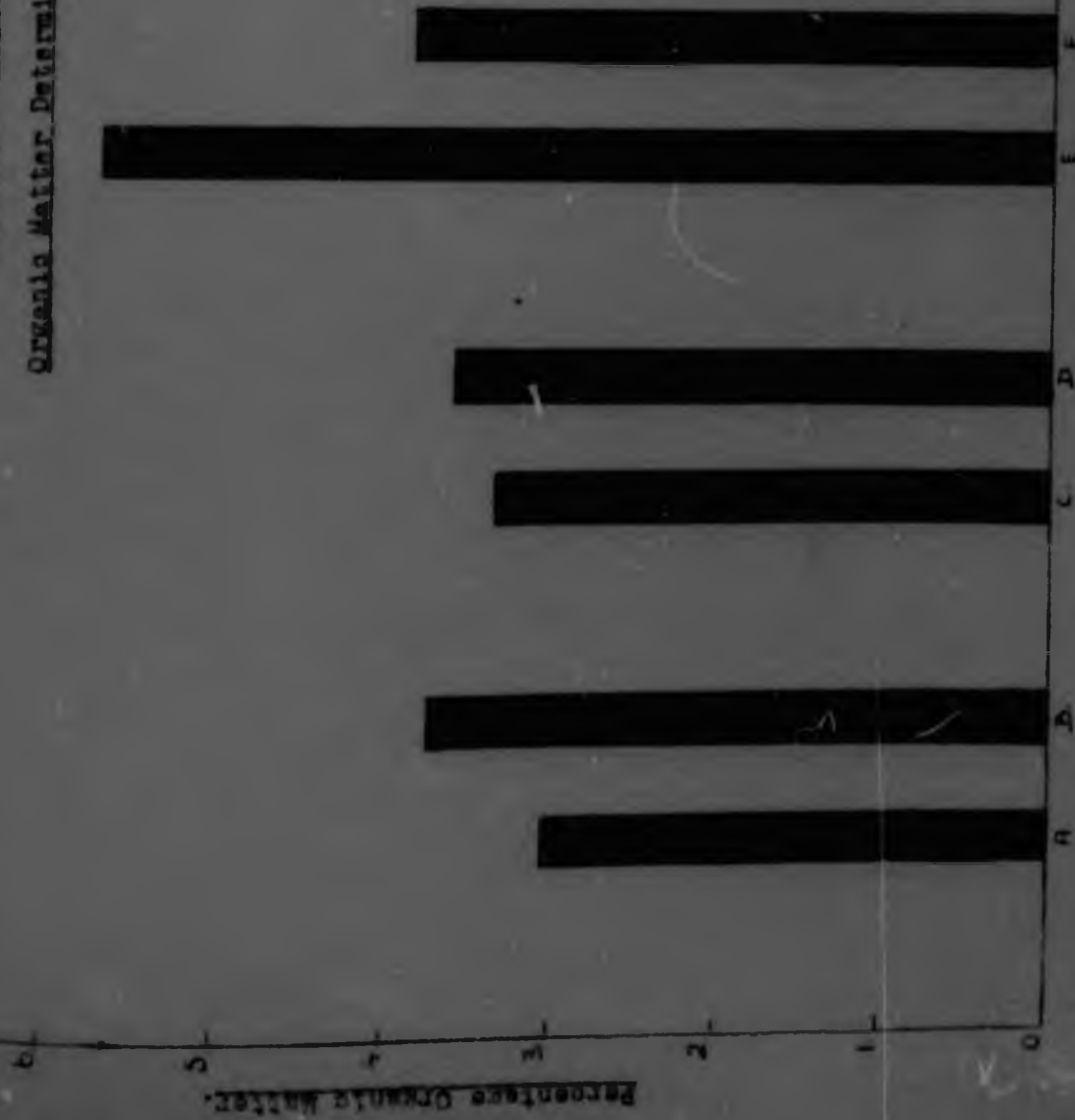
HISTOGRAM NO. 1.

Holard Determinations



HISTOGRAM NO. 2.

Orkenia Matter Determinations.



- A. Cynodon-Eragrostis Veld = 3.06%
- B. Adjoining Purple Veld = 3.77%
- C. Hyparrhenia hirta Veld = 3.36%
- D. Adjoining Purple Veld = 3.61%
- E. Climax Scrub Vegetation = 5.70%
- F. Adjoining Purple Veld = 3.89%

HISTOGRAM NO. 1.

Colloid Analysis.



- 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%

Percentage M.W.R.C.

30
40
50
60
70
80

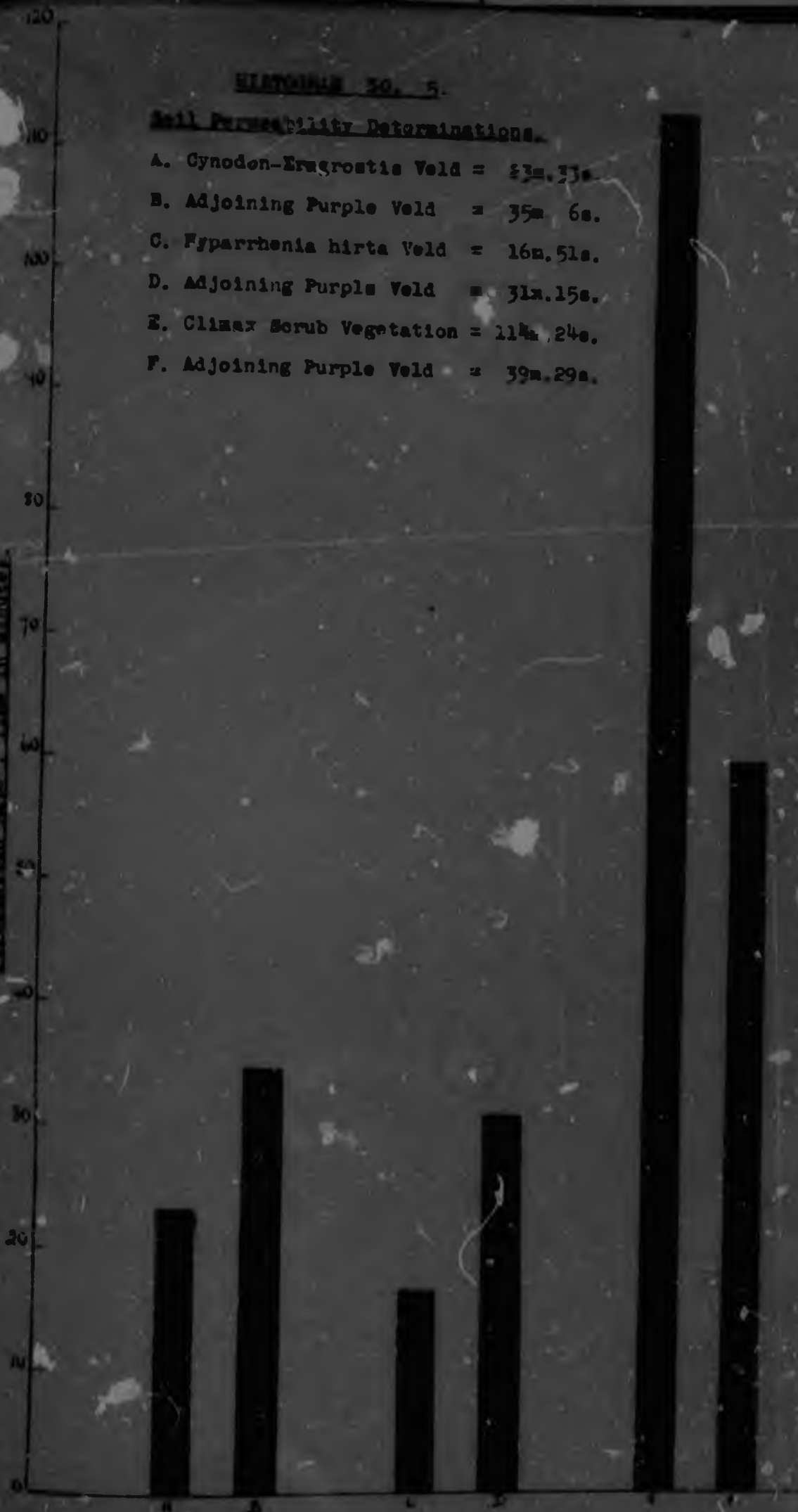


TABLE 30. 5.

Soil Permeability Determinations.

- A. Cynodon-Eragrostis Veld = 23m. 33s.
- B. Adjoining Purple Veld = 35m. 6s.
- C. Eyparrhenia hirta Veld = 16m. 51s.
- D. Adjoining Purple Veld = 31m. 15s.
- E. Climax Scrub Vegetation = 11m. 24s.
- F. Adjoining Purple Veld = 39m. 29s.

Percolation Rate 1 Time in Minutes.



HISTOGRAM NO. 6.

Nitrogen Determinations.

0.15

0.10

0.05

0.00

Percentage Nitrogen.



- 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 cc. of $\frac{1}{10}$ N. NaOH.



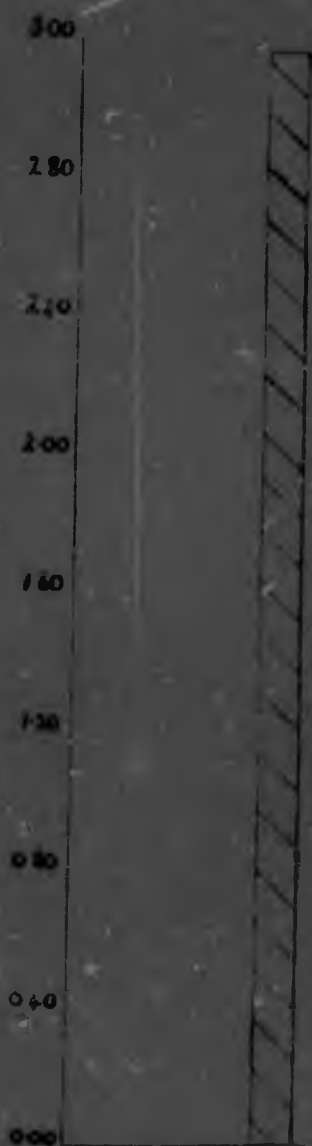
- A. Cynodon-Eragrostis Veld = 2.24
- B. Adjoining Purple Veld = 2.00
- C. Hyparrhenia hirta Veld = 2.52
- D. Adjoining Purple Veld = 1.66
- E. Climax Scrub Vegetation = 0.19
- F. Adjoining Purple Veld = 2.38

HISTOGRAM NO. 11

Belt Transect Figures Effect of
Burning on Flowering of Trachypogon
plumosus

Average number of flower-heads
per plant

1 - Protected Vekt - since 1934
2 - Burnt annually in October
Since 1934



HISTOGRAM NO. 9.

Belt Transect figures. Effect of Burning on
Flowering in *Trachypogon plumosus*.

Average number of flower-heads
per plant.



HISTOGRAM NO. 20.

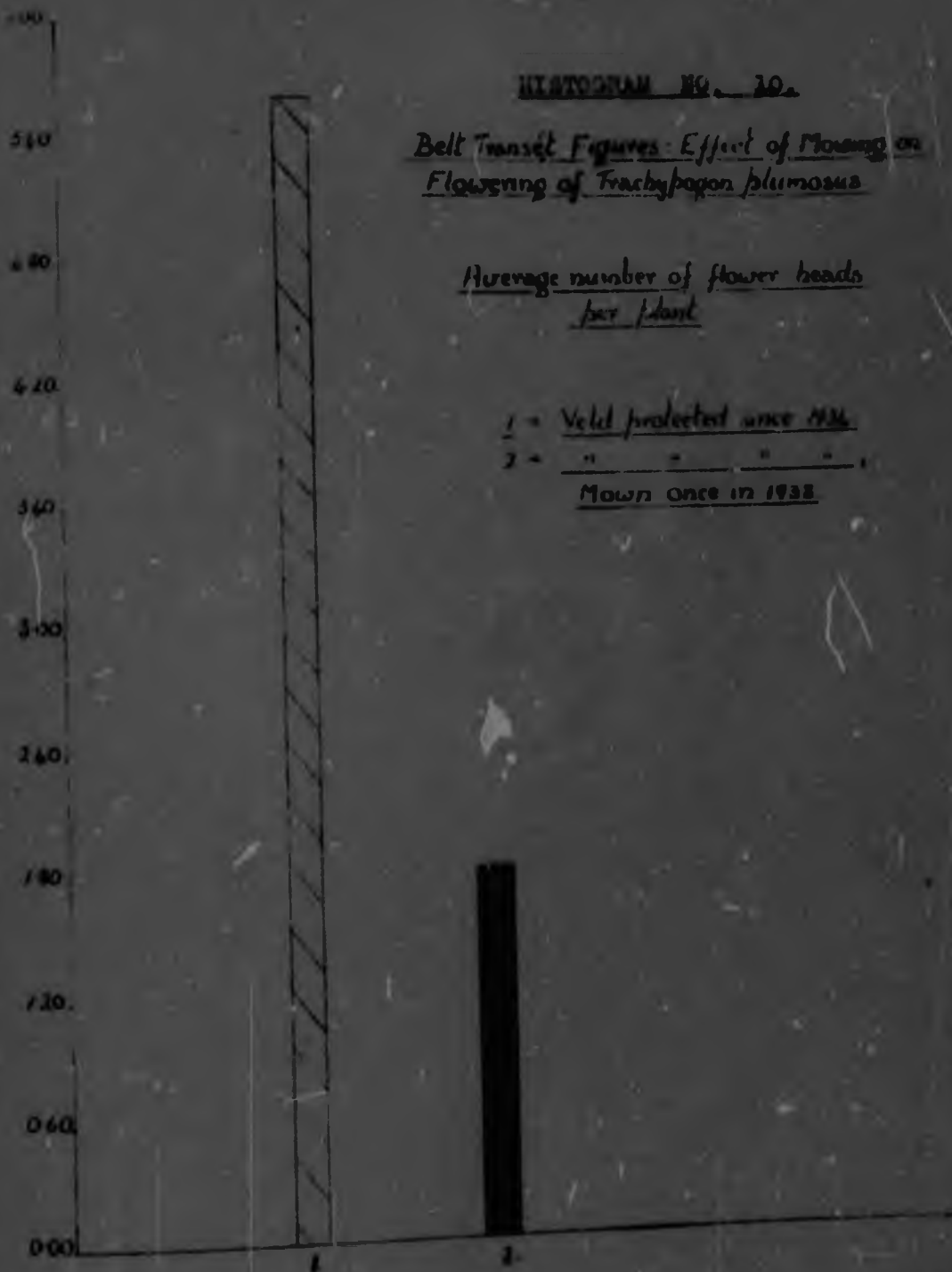
Belt Transect Figures - Effect of Mowing on
Flowering of *Trachypogon plumosus*

Average number of flower heads
per plant

1 = Vegetation protected since 1936

2 = " " " " " "

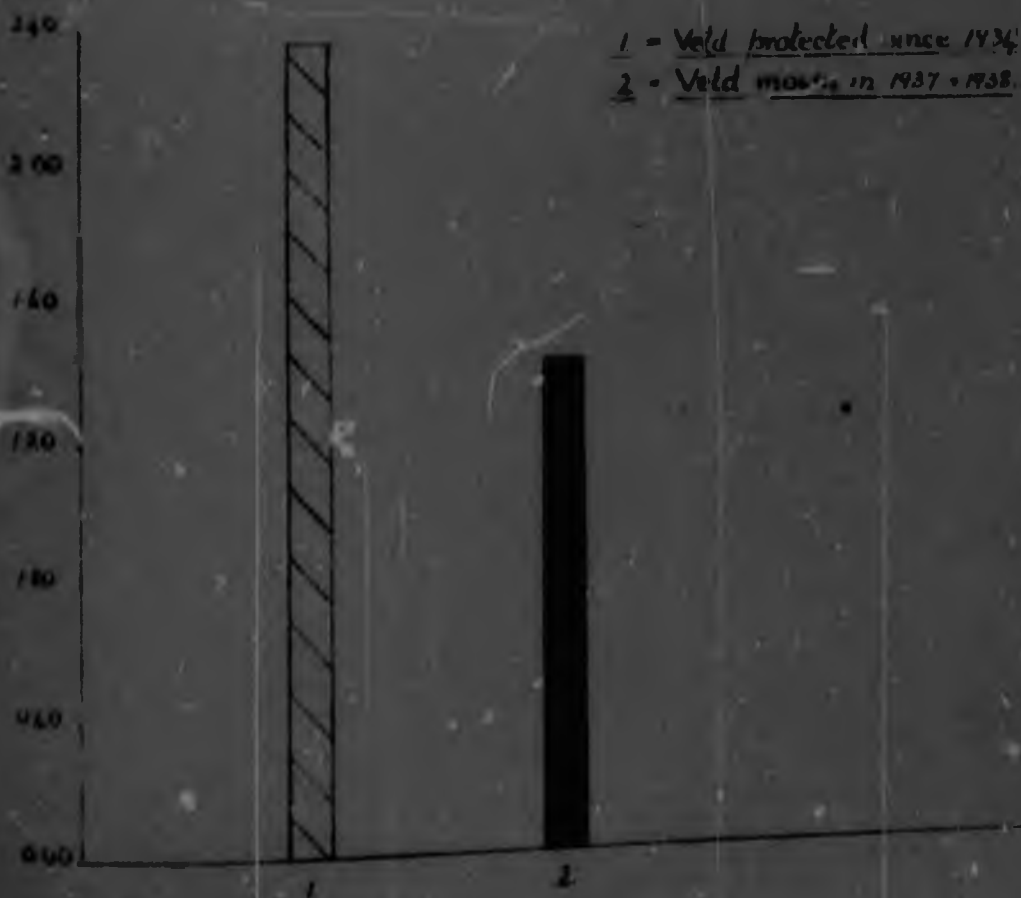
Mown once in 1938



HISTOGRAM NO. 33

Delt Transect Figures Effect of Mowing
on flowering of *Trachypogon plumosus*

Average number of flower heads
per plant



HISTOGRAM NO. 11.

Belt Transect Figures Effect of Mowing
on flowering of Trachypogon blattaris

Average number of flower heads
per plant.

240

200

160

120

80

40

0-00



1 - Veld protected since 1934

2 - Veld mown in 1937-1938

MEMORANDUM NO. 32.

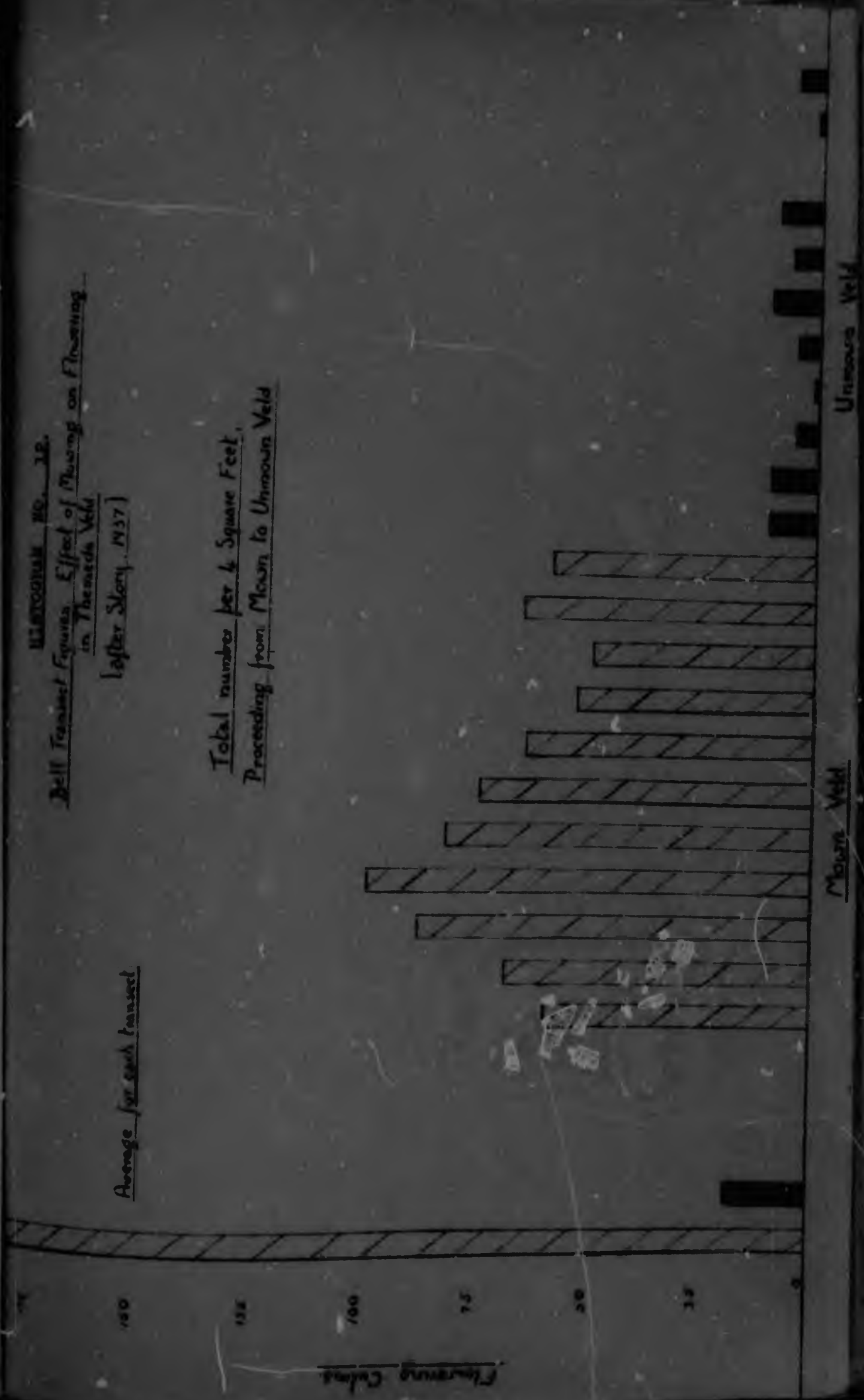
Bell Tractant Figures. Effect of Mowing on Flooding
in Phenatda Veld

(after Story, 1937)

Average for each transect

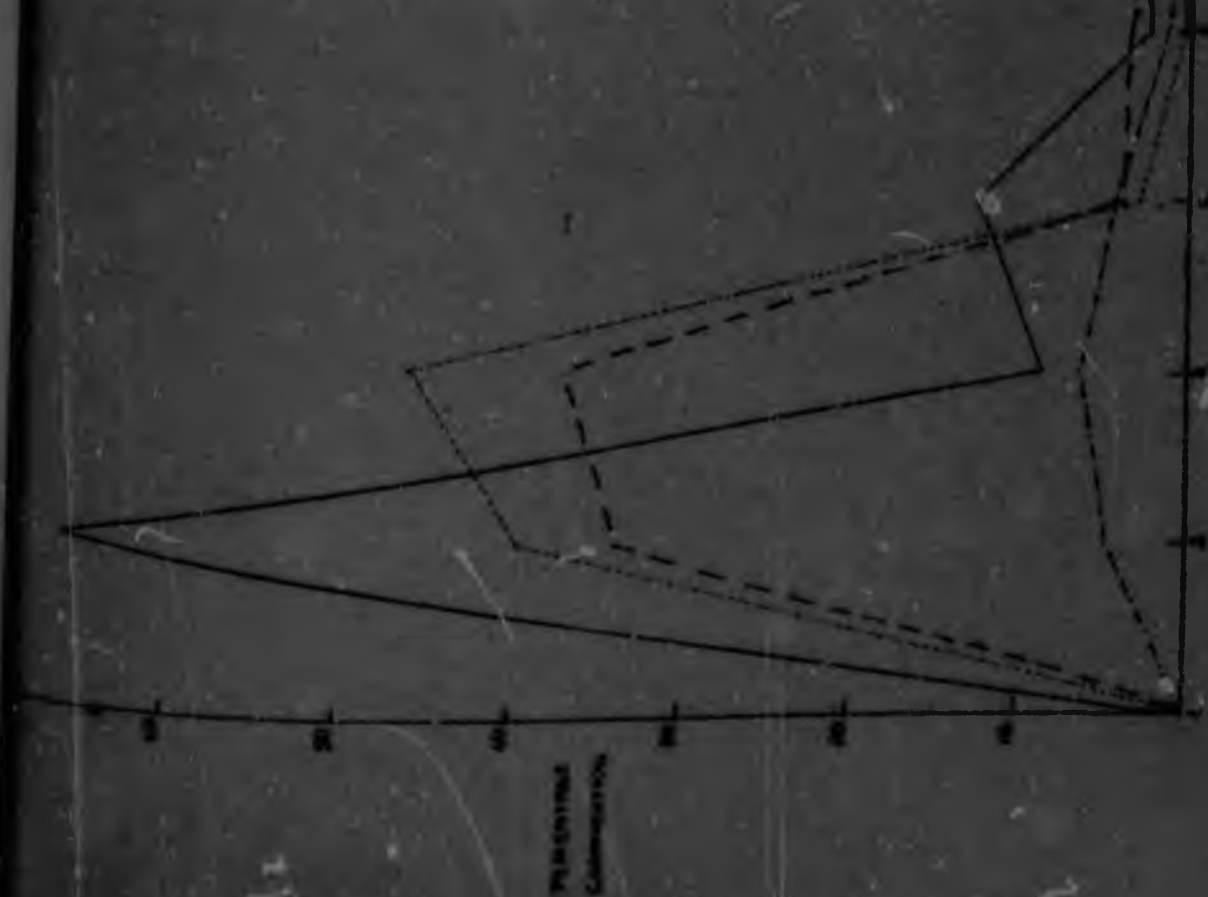
Total number per 4 Square Feet,
Proceeding from Mown to Unmown Veld

Flooding Cycles



GRAPH NO. 3

Eucalyptus nitens
 Carpinus
 Thalictrum
 Scilla
 Scilla



Results of Plant Tests

BLANK NO. 2

SECTION COASTLINE
WATER
LAND
CONTINENTAL SHELF

PERCENTAGE
CONCENTRATION



SECTION OF THE COASTLINE

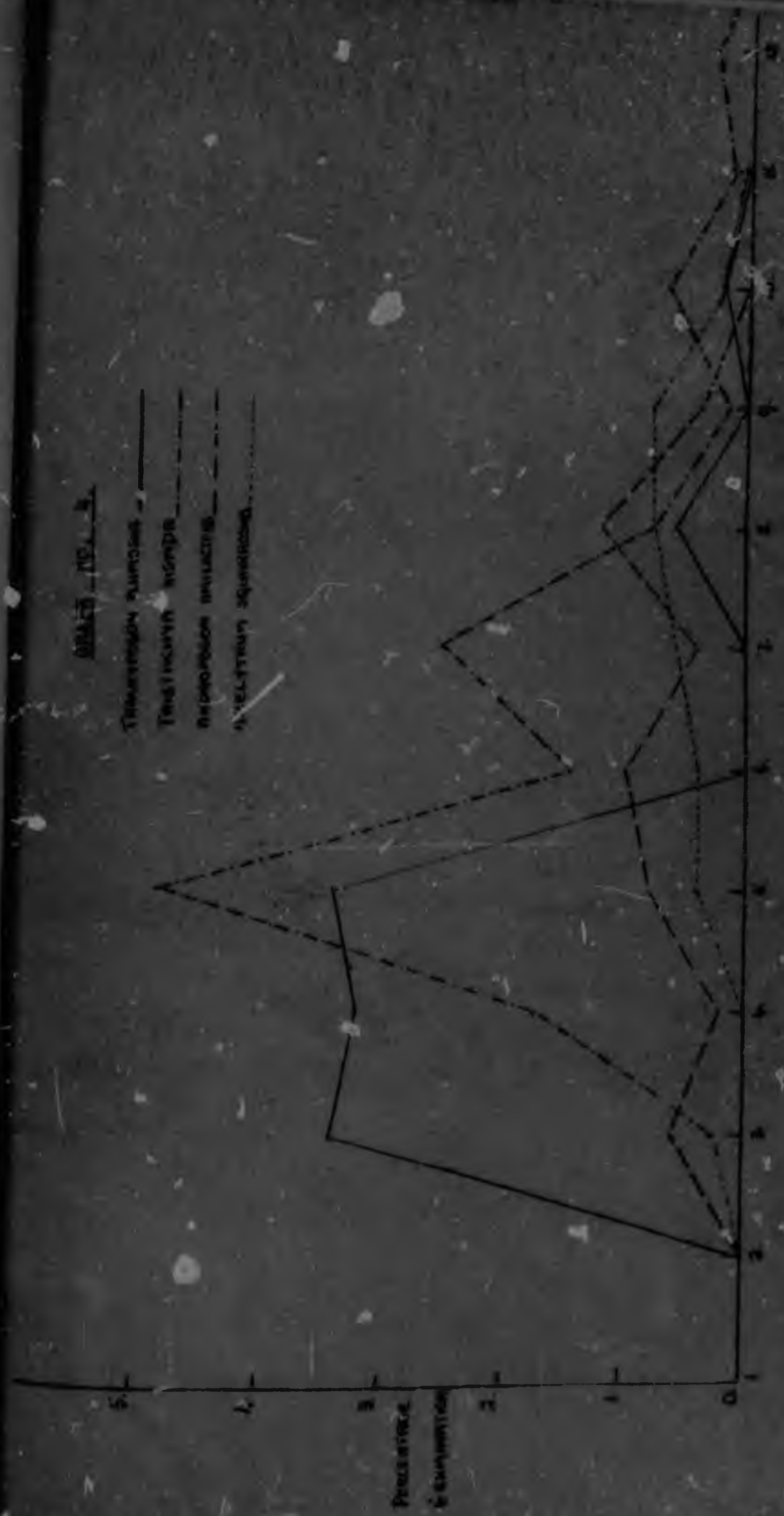
GRAPH NO. 3.

MYRMELEON NIGER ---
 TETRAPODON CONTORTUS ---
 CYNODON F. ---



GRAPH NO. 3

- THYMUS PRAECOX
- TRIFOLIUM VIOLEACEUM
- TRIFOLIUM PRATENSE
- TRIFOLIUM ALBUM
- TRIFOLIUM HYDRUNGUM



FOR GRAPH NO.S.

PLEASE SEE LAST
FICHE

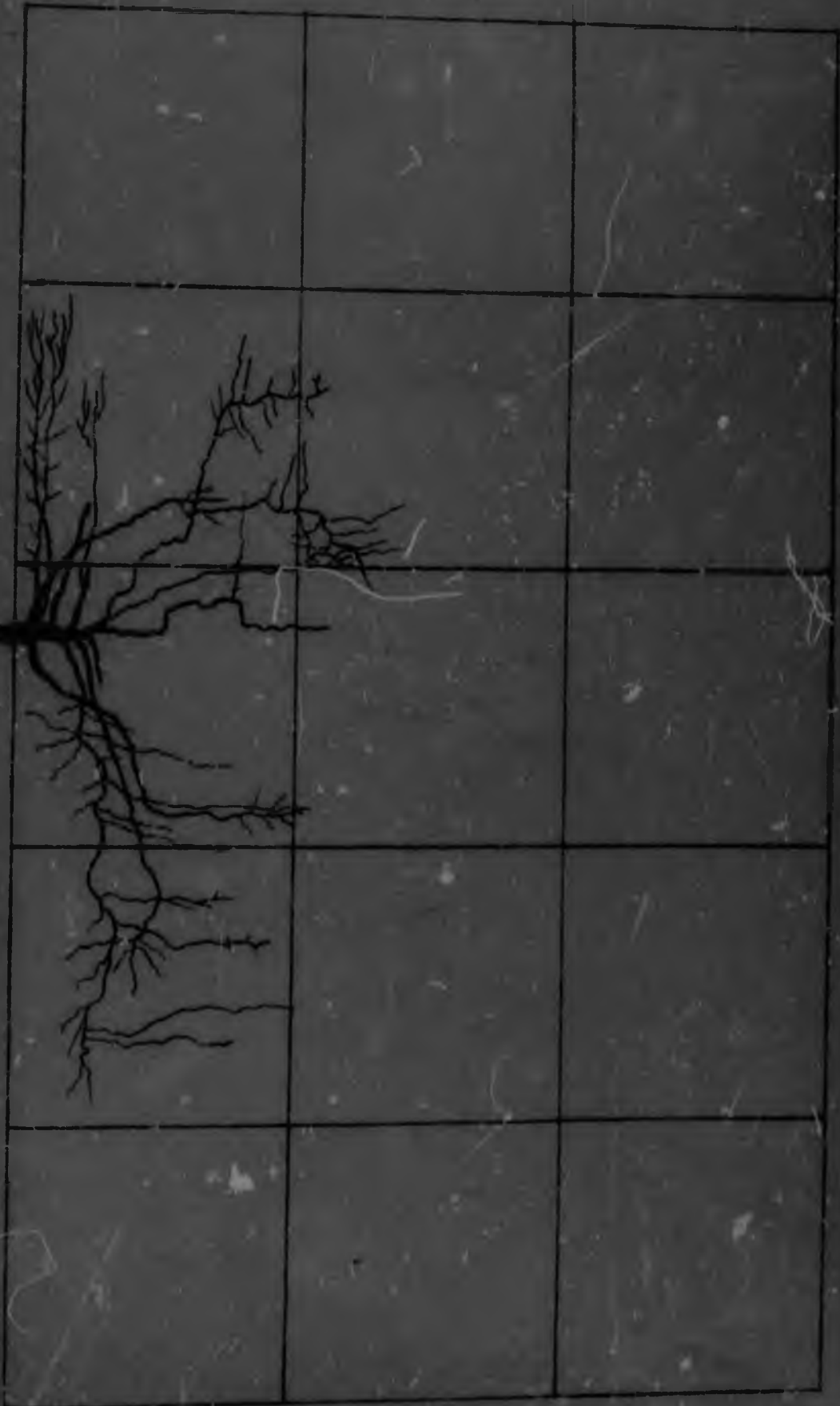
ROOT DIRECT CHARTS AND PHOTOGRAPHS.

FOR CHART NO. I.

SEE LAST FICHE

Chart No. 2

Tegader munda 4/1/12 Scale: 1"=1'



Lower, dark, sand, 13

Dark sandstone and 14

Gravel, clayey, and 15

Occasional quartz, 16
bedded with 17

Quartz, feldspar 18
distributed in 19

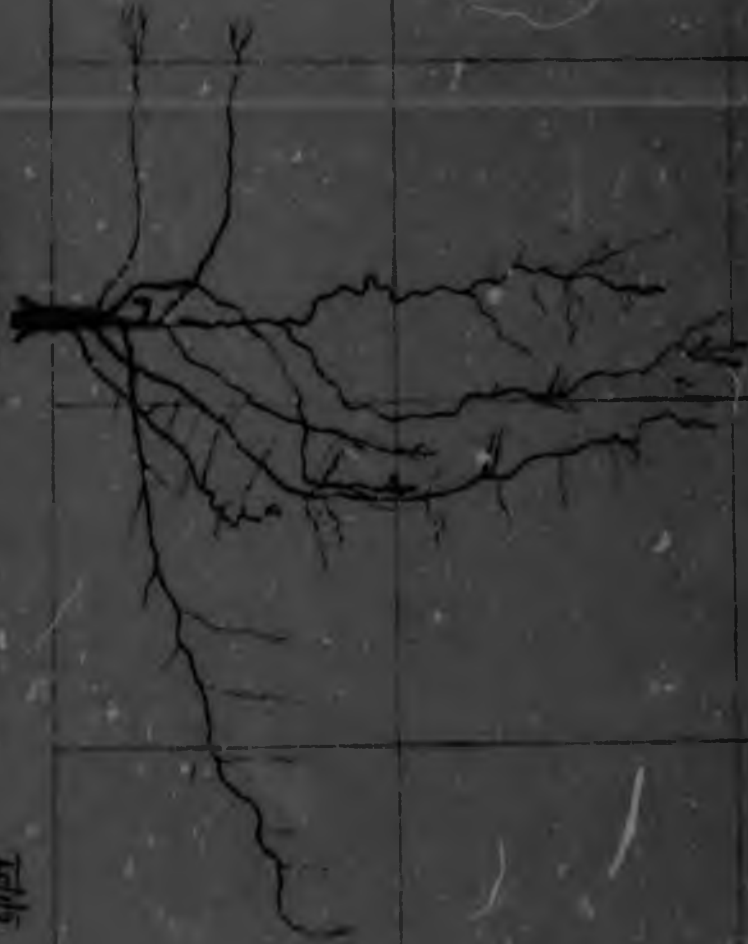
Volcanic

Xanthium strumarium

4/1/54

Chart No. 3

Scale: 1" = 6"



Amaranthus Thunbergii 12/12/38

Chart No. 4

Scale: 1" = 1'



Leaves, stem and

flowers, yellowish soil

Quartz pebbles in
yellowish soil

Dubium stramonium 24/6/50

Quart No. 61
Scale: 1" = 6"



Loose dark
well-aerated soil

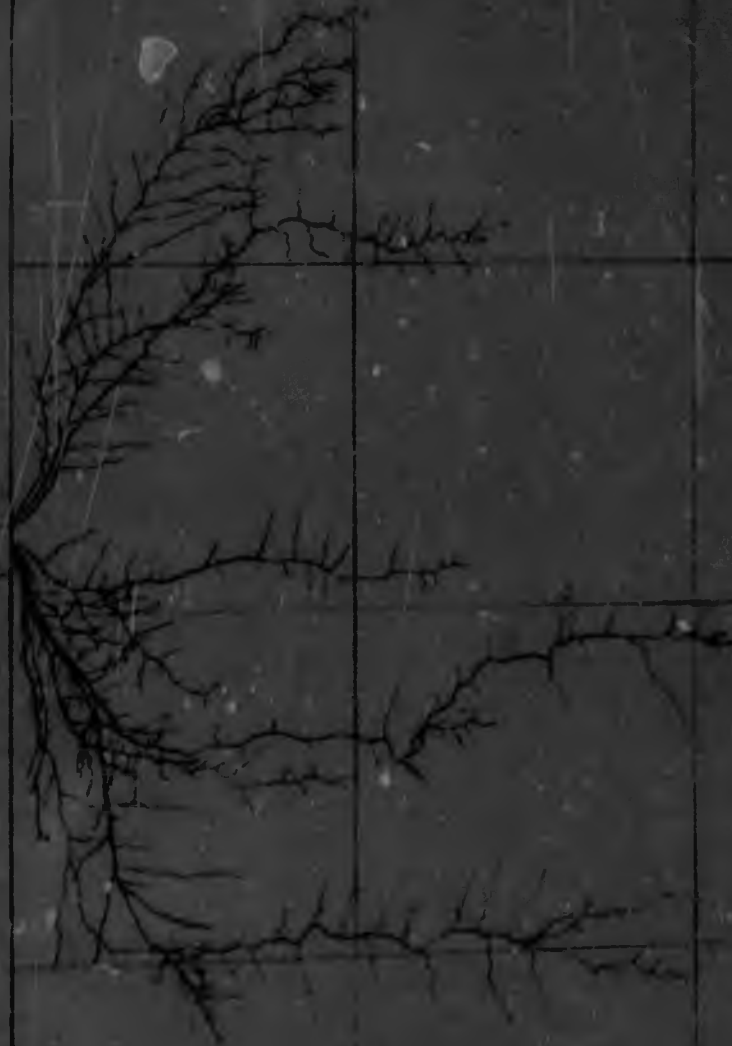
Grey soil

Quartz pebbles
in grey rather
clayey soil

Hard yellow
sandstone
pebbles

Pinus virginiana Mill.

Scale 1" = 6'



Leaves still on tree
about 25%

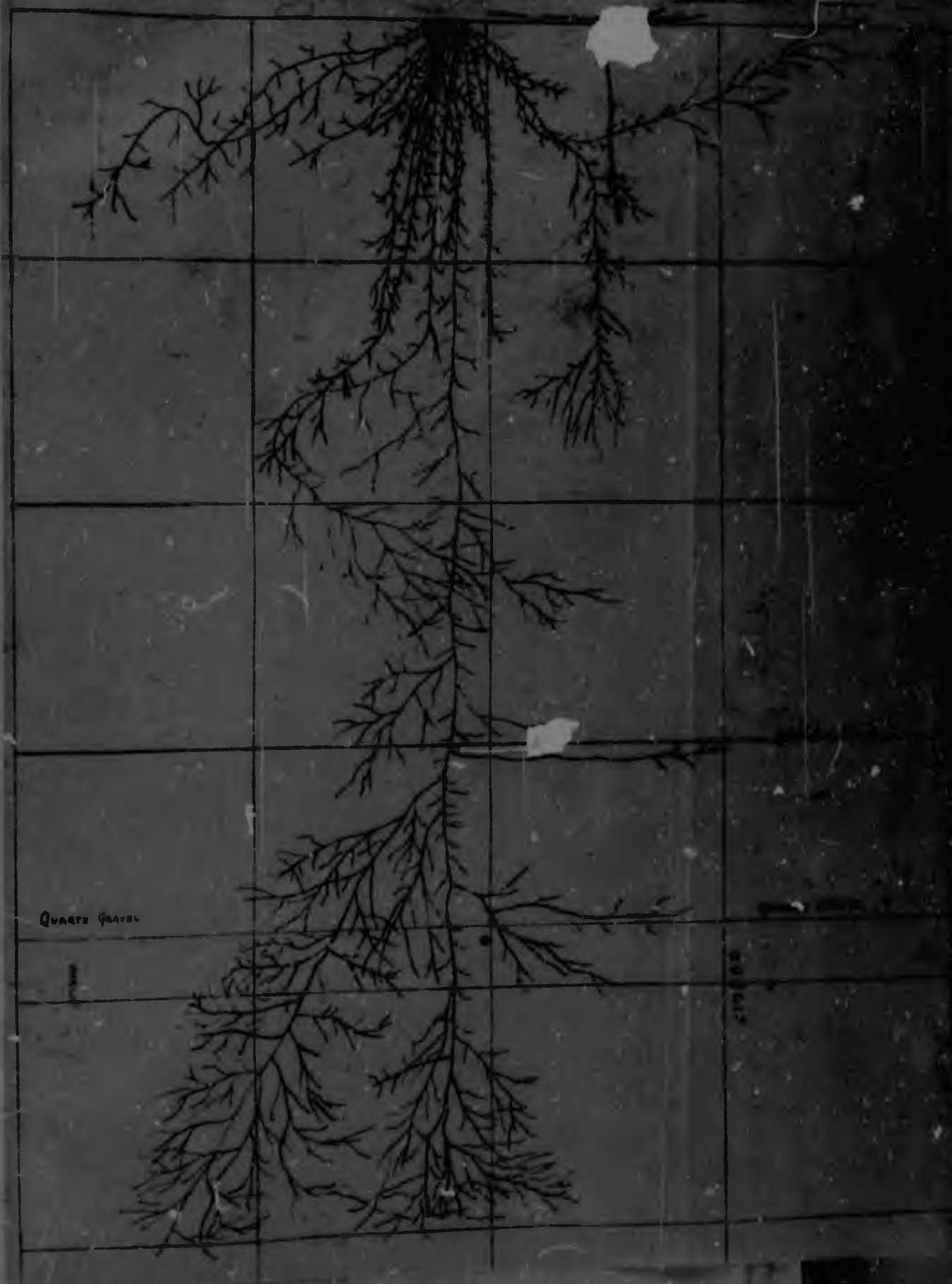
Soft, brownish red

Many leaves
still on tree

Quaternary Section

R. 1. 1

Chart No. 7



Quaternary Section

Quaternary Section

ERAGROSTIS

CHARANTHA

R.B. 5

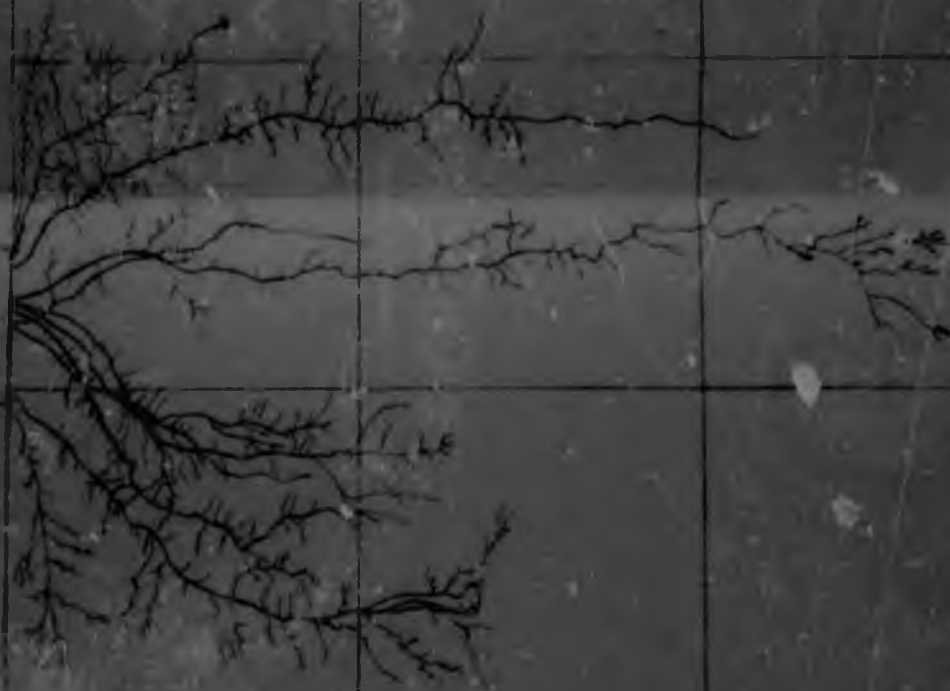
Chart No. 8



Chart No 9.

the chloromela, 20/1/18

Scale: 1" = 6"



Loam dark
well mixed
soil

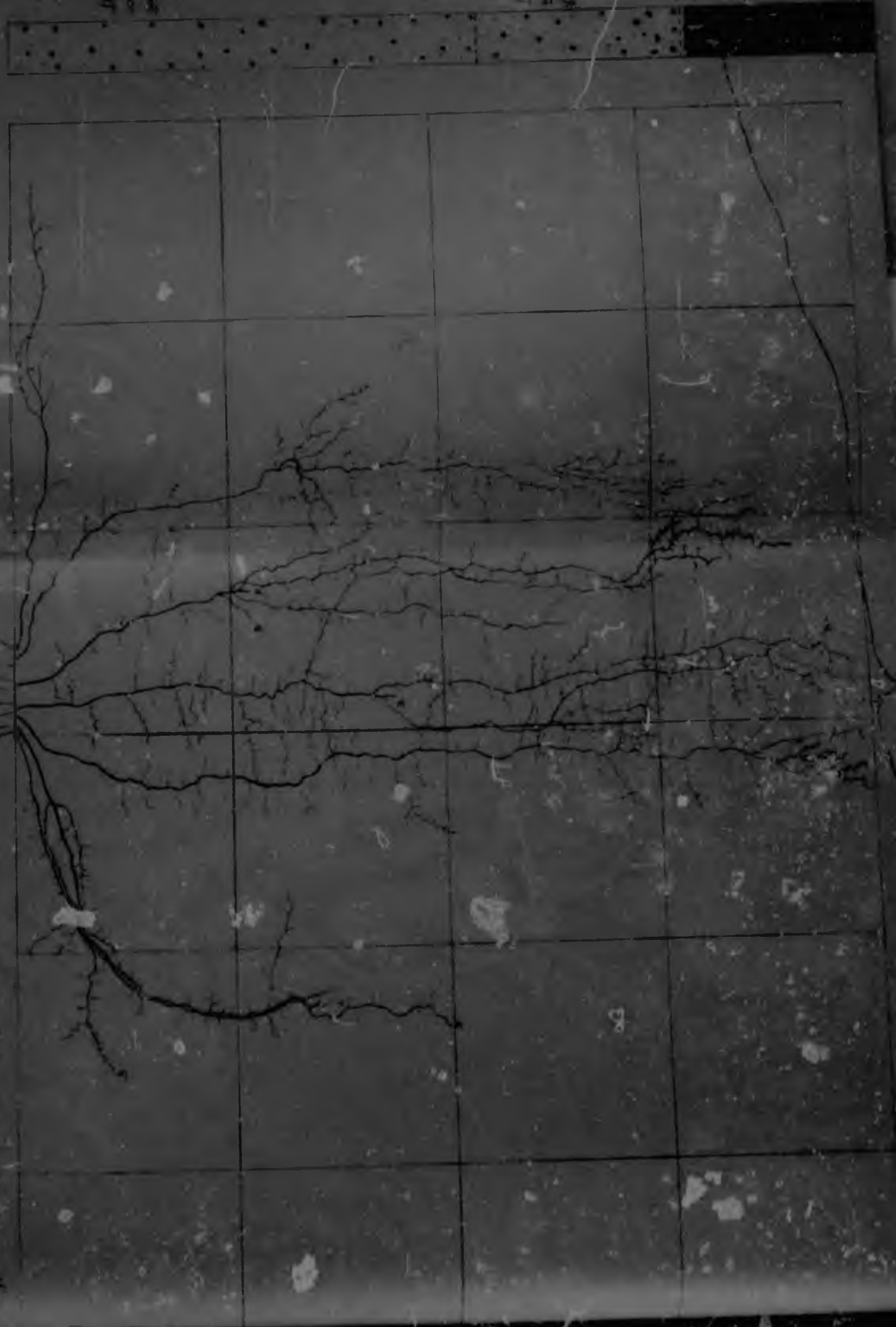
Lighter-colored
fairly soft soil

Light-colored
very fine soil
well mixed
quartz

Hesperomys hirta 4/12/00

Chart No. 10

Scale 1" = 1/2 mi



Card No. 11

R.O. 3. Sub. 11. *Symphyga*

4/11/55



yellowish ↑

green ↑

Themeda triandra

28/4/35

Chart No 12

Scale: 1:1



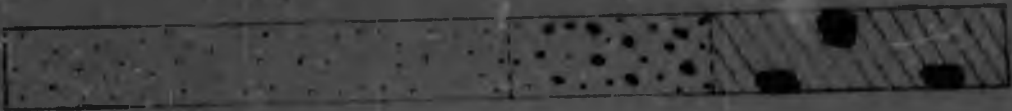
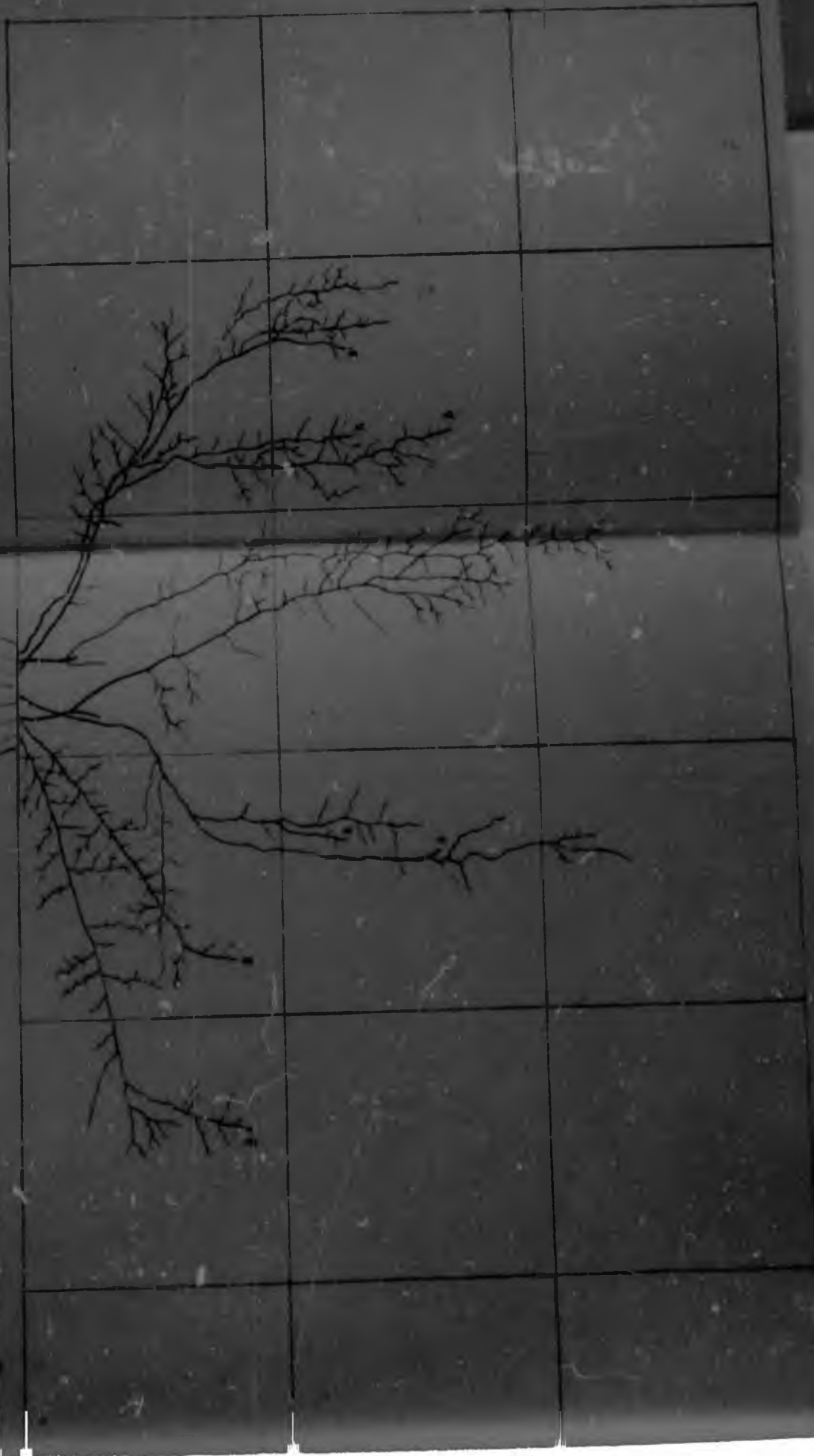
CHART NO. 14 SEE

LAST FICHE

Chart No 15

21/1/51

Scale: 1" = 6"



Dumfries compact
sand

Quartzite

Granite - 100
feet
in place
along
south-east

Diptera *Trichostema*

1933

Chart No. 10

Scale

200 ft

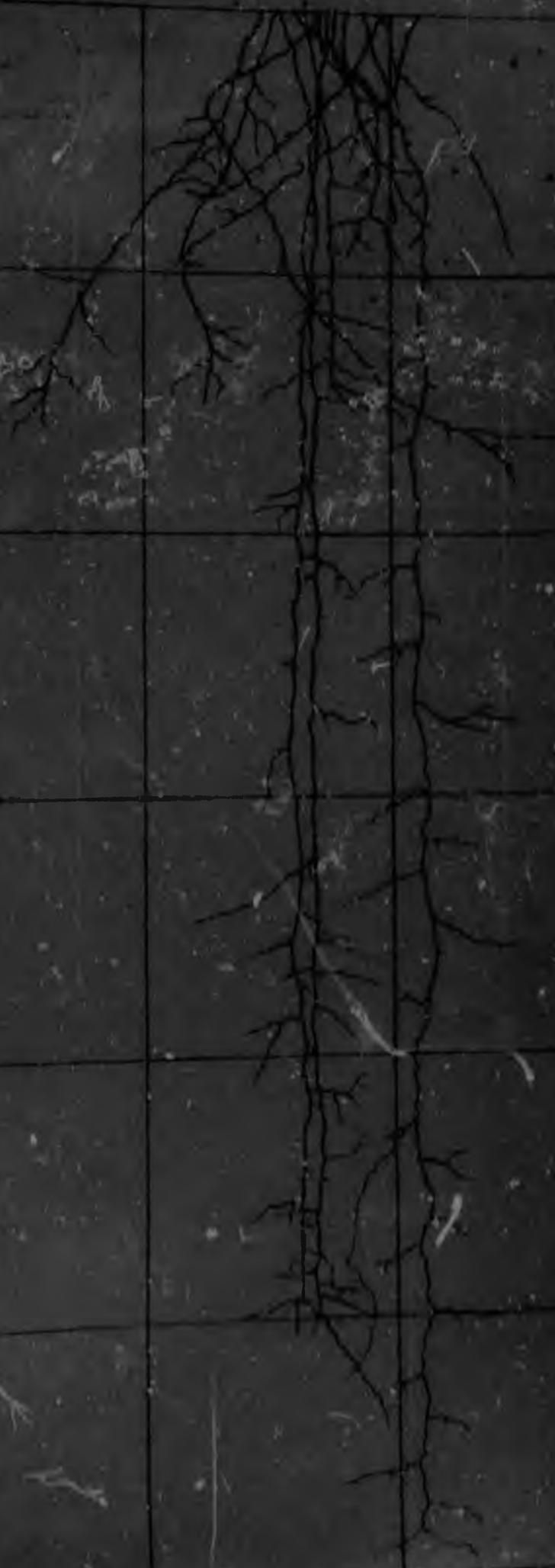


Chart No. 6

RB4

ELYONURUS ARGENTEUS



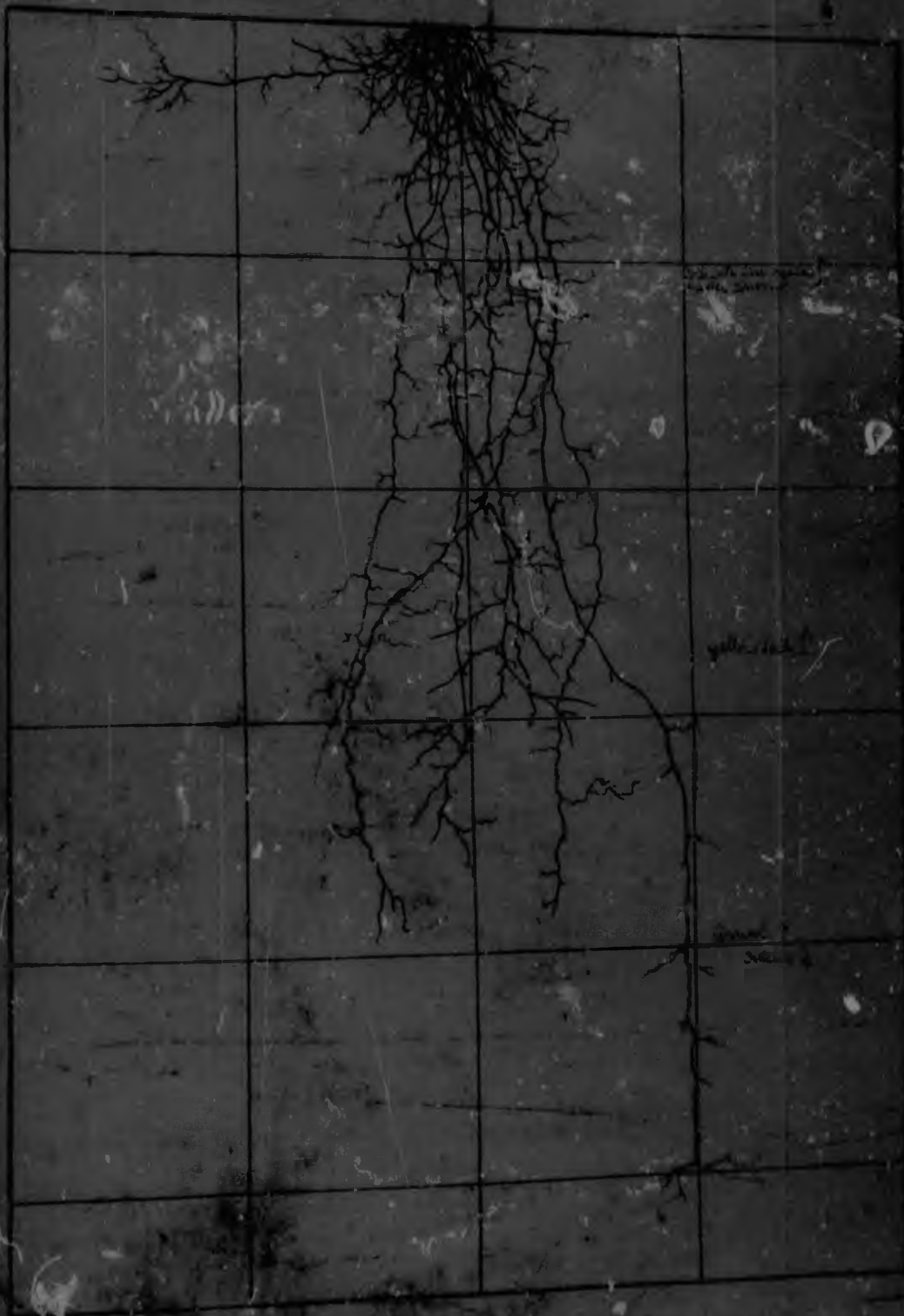
TRISTACHYA

REHMANNII

2-3

Q. 15. 11

SH. 15. 11



Waller

Small root system
in the center

yellowish

Small

Chart No. 11

4/12/16

Scale 1:100



Root Bases. (See Chart No. 3.)

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



Root Masses. No. 20.

Acaela 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 System. No. 51.

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.



East Manat, No. 22.

Colvin rhacrifolia. 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.



East Block. No. 23.

Euclea lanceolata. Scale divisions = 1 metre.

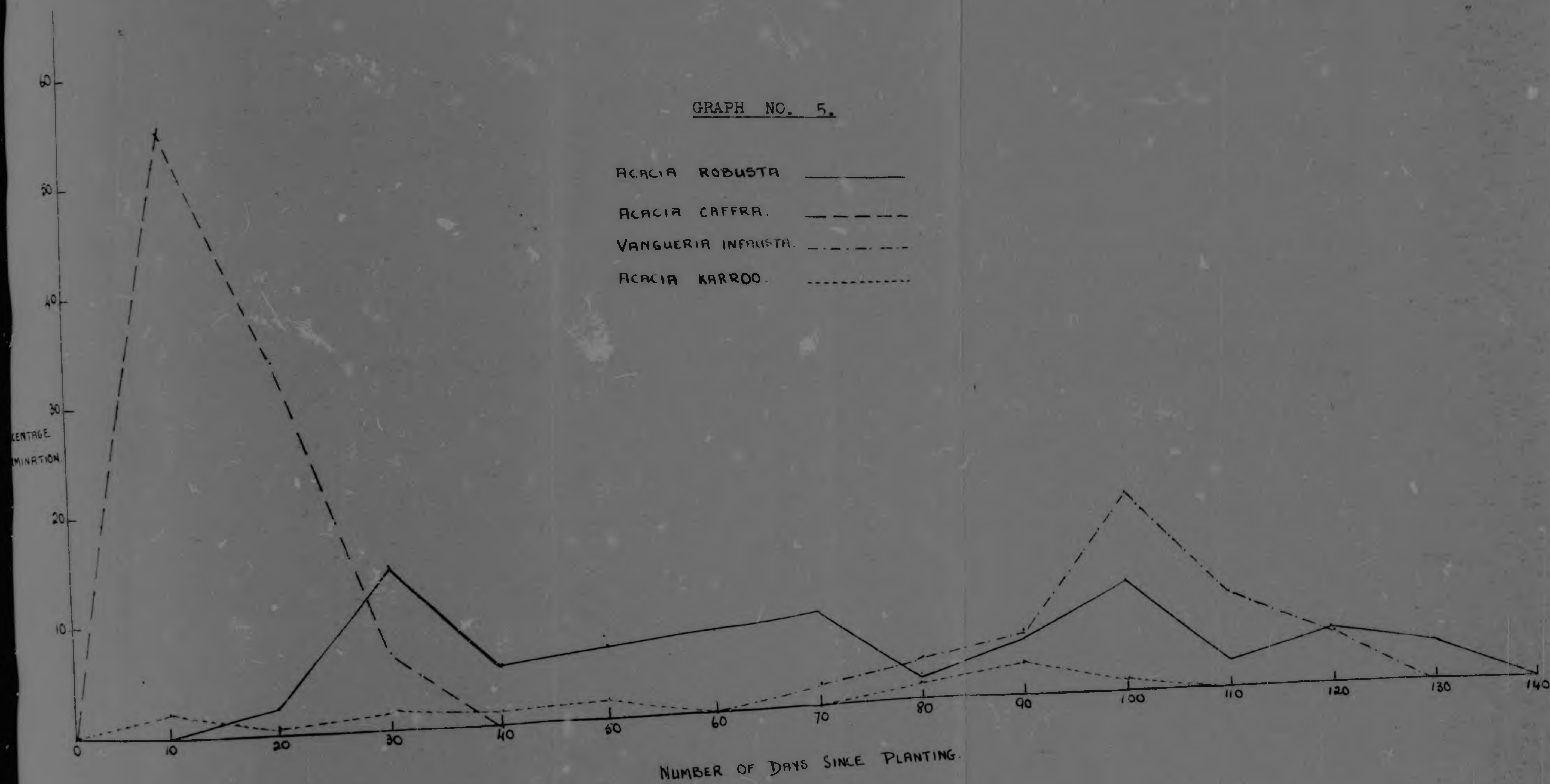
Note: a few superficial laterals and many
deeply-penetrating vertical roots. No main lateral

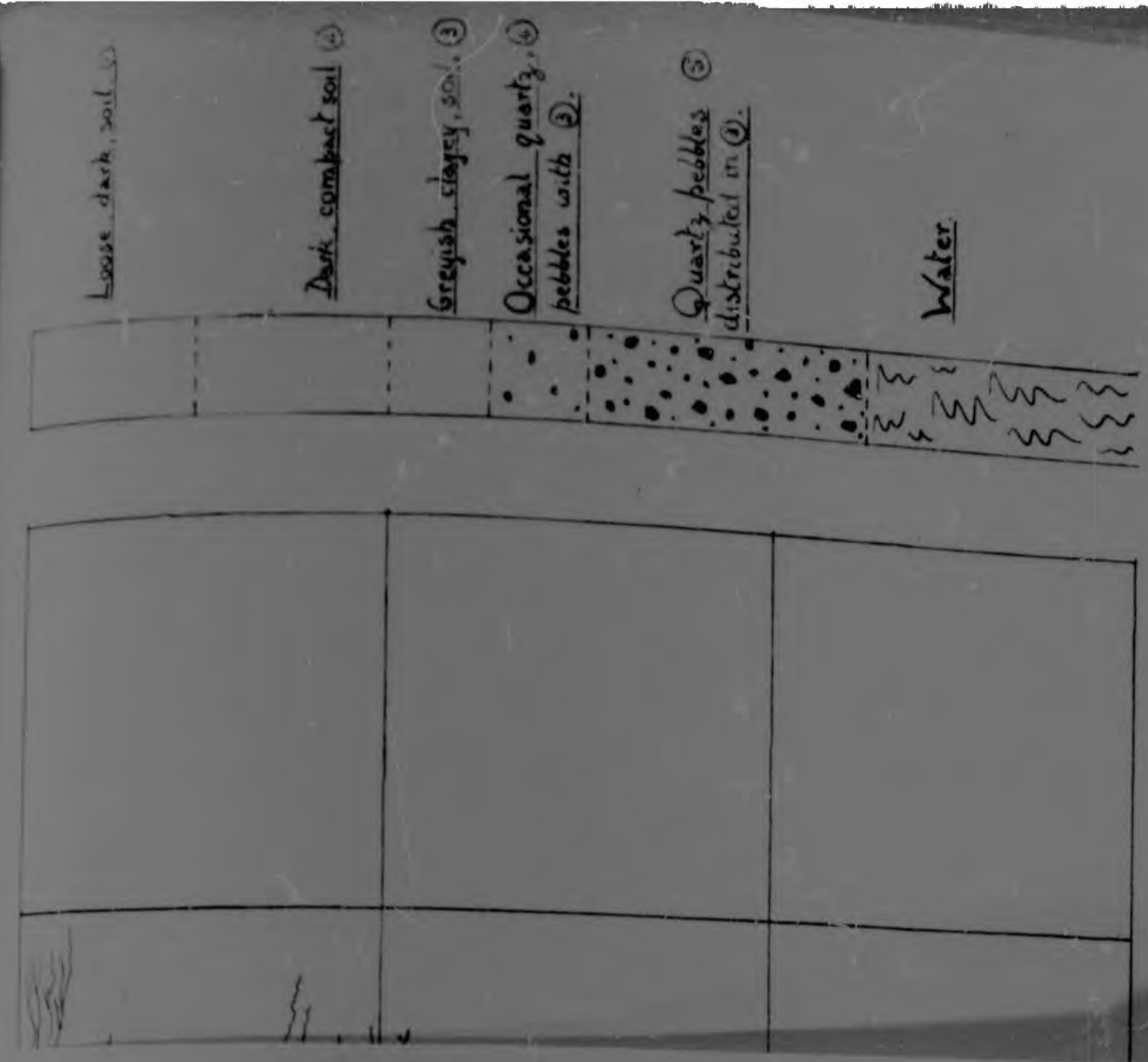


Spot Blight. No. 24.

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



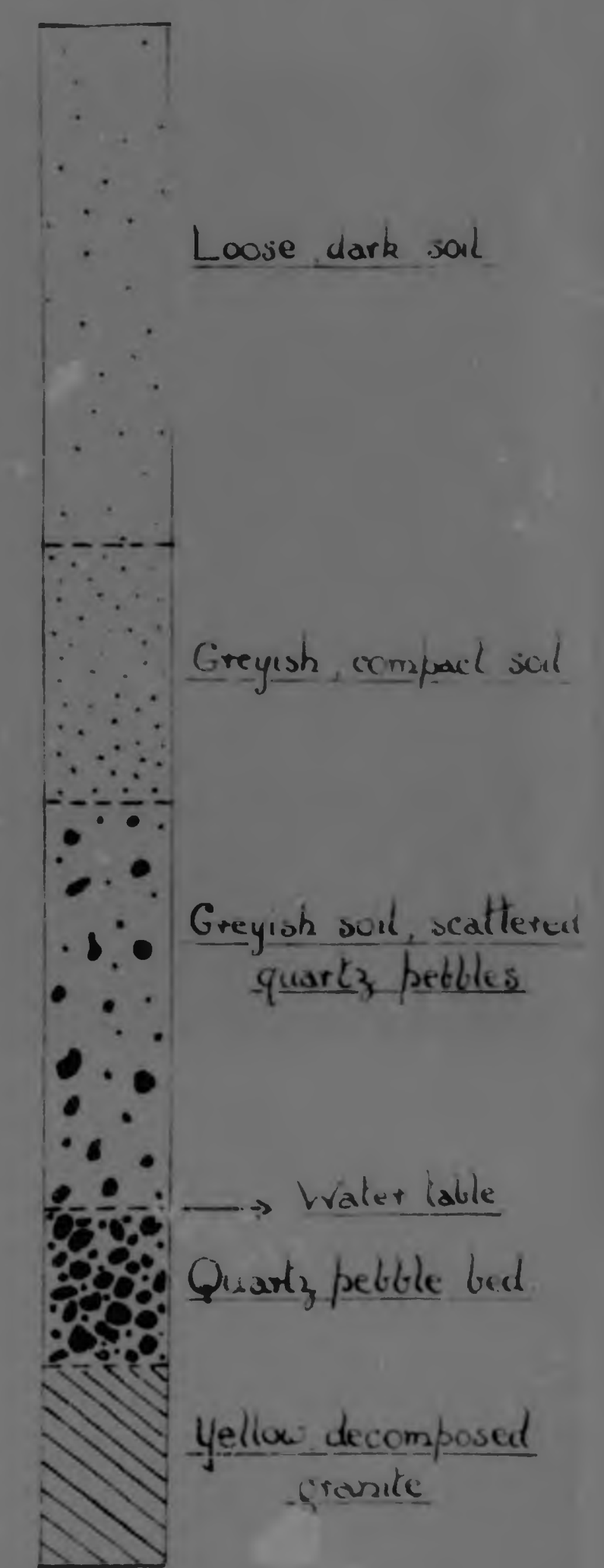
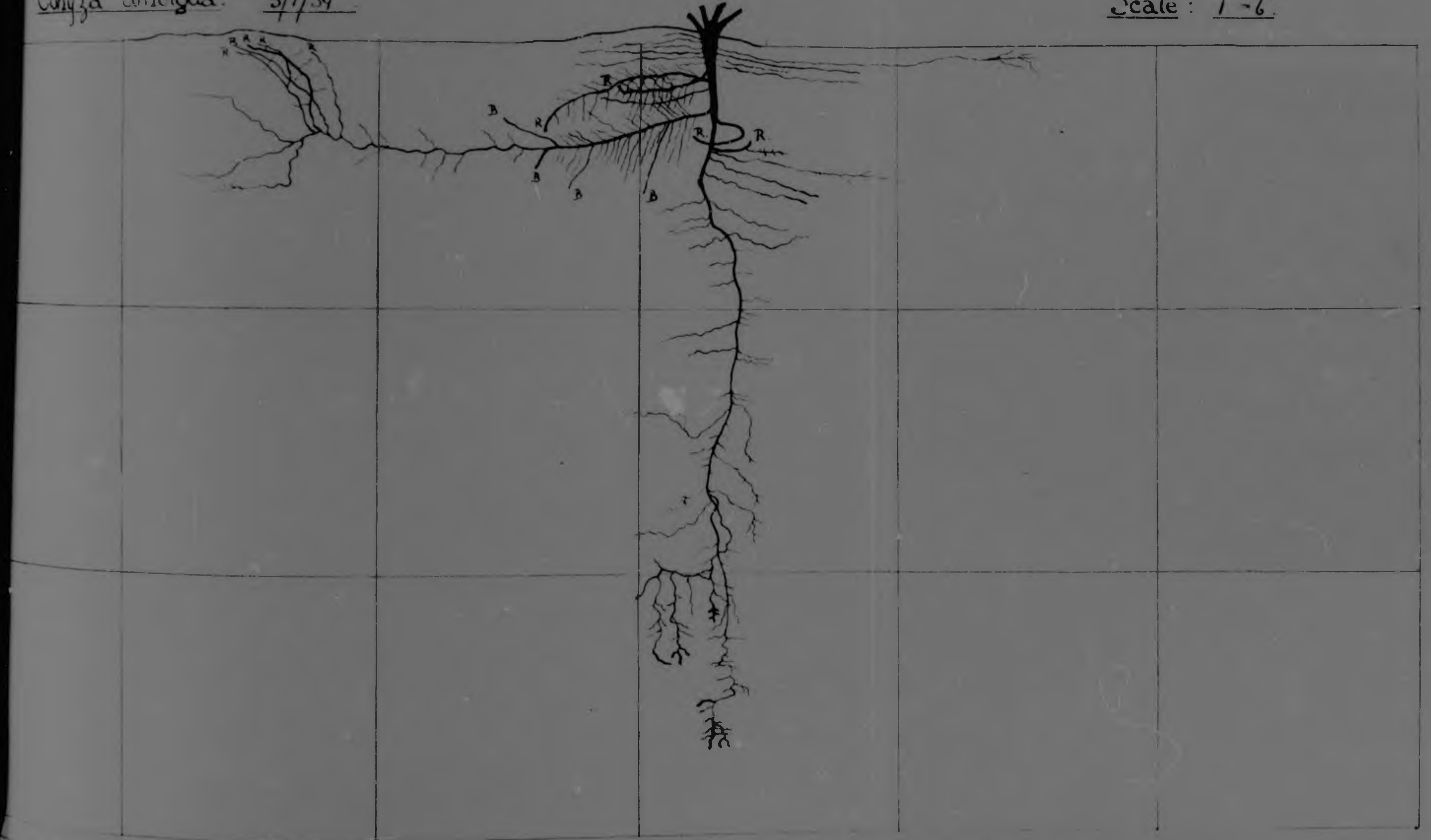




Conyza ambigua 5/1/39

Chart No. 1.

Scale: 1"=6"



TRISTACHYA

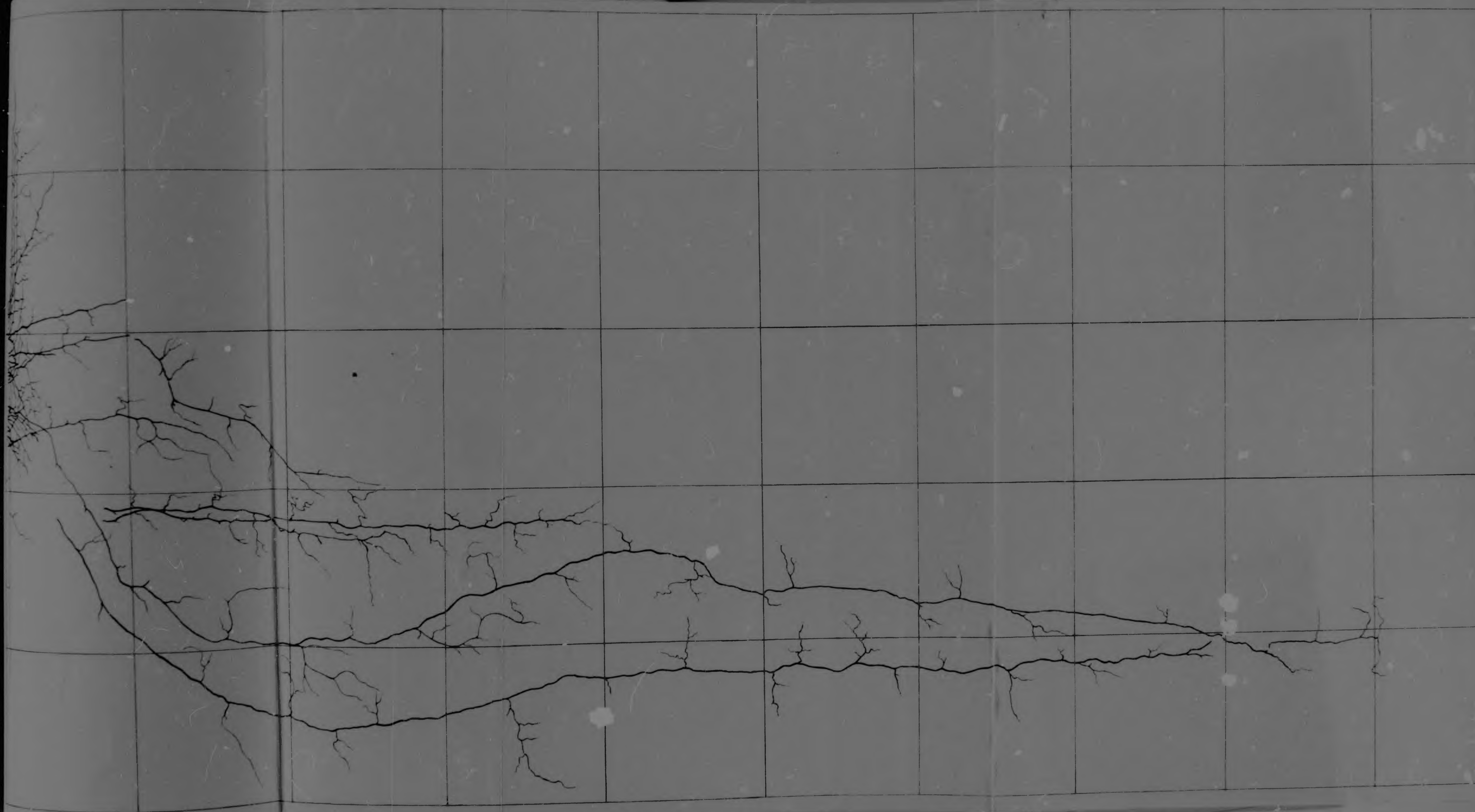
REH/

Chart No.

Chart

ELYONURUS

RB4



TRISTACHYA

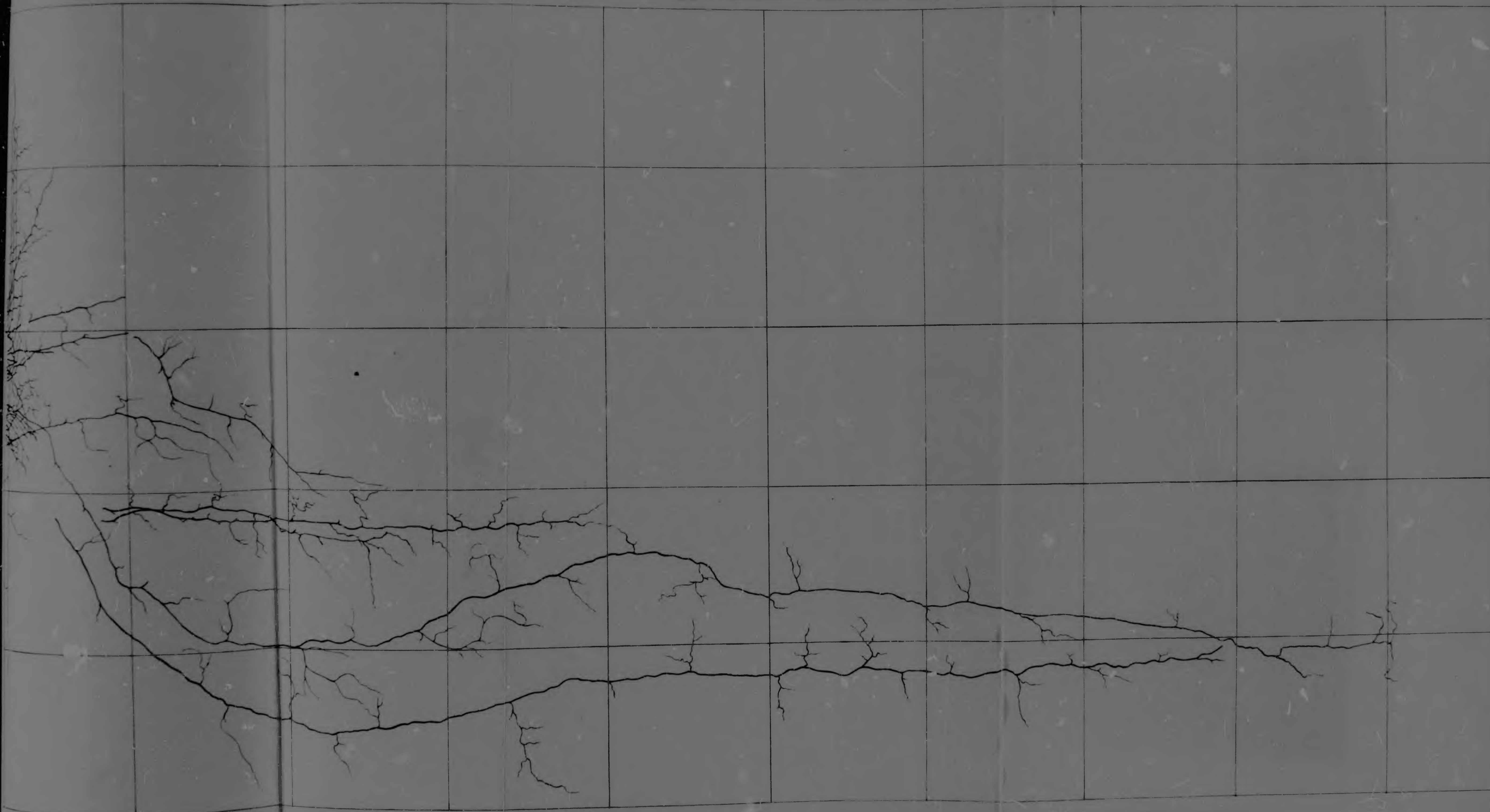
REH/

Chart No.

Chart

ELYONURUS

RB4

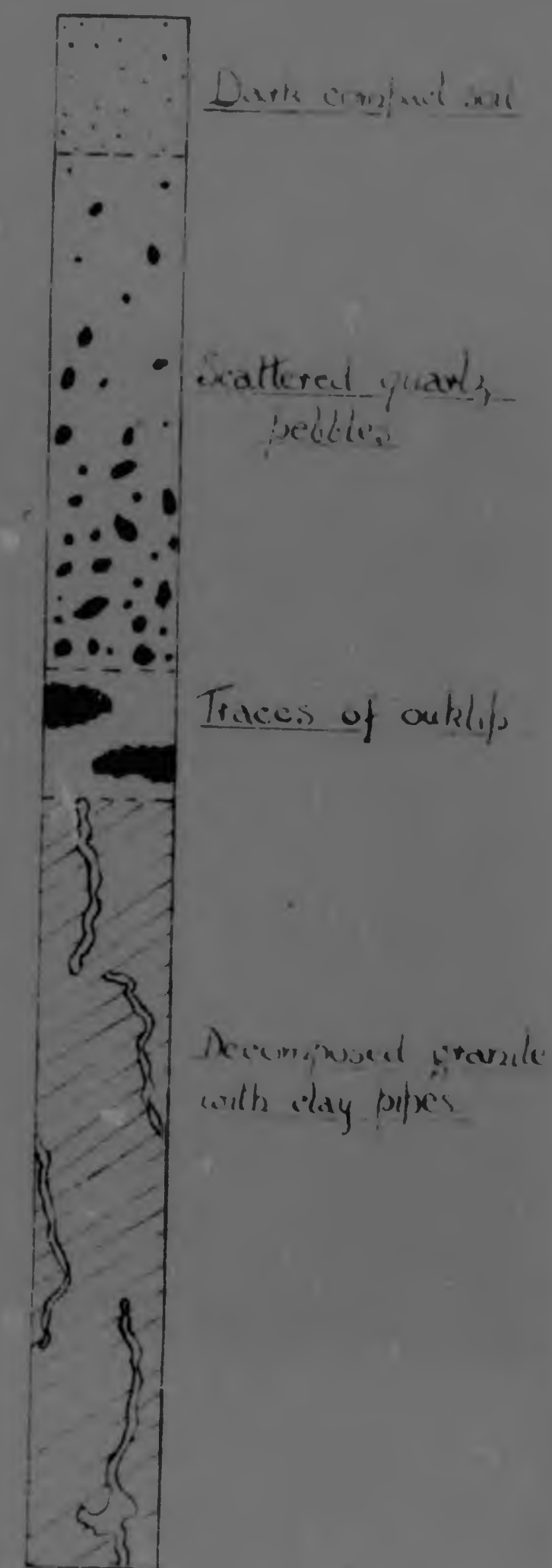
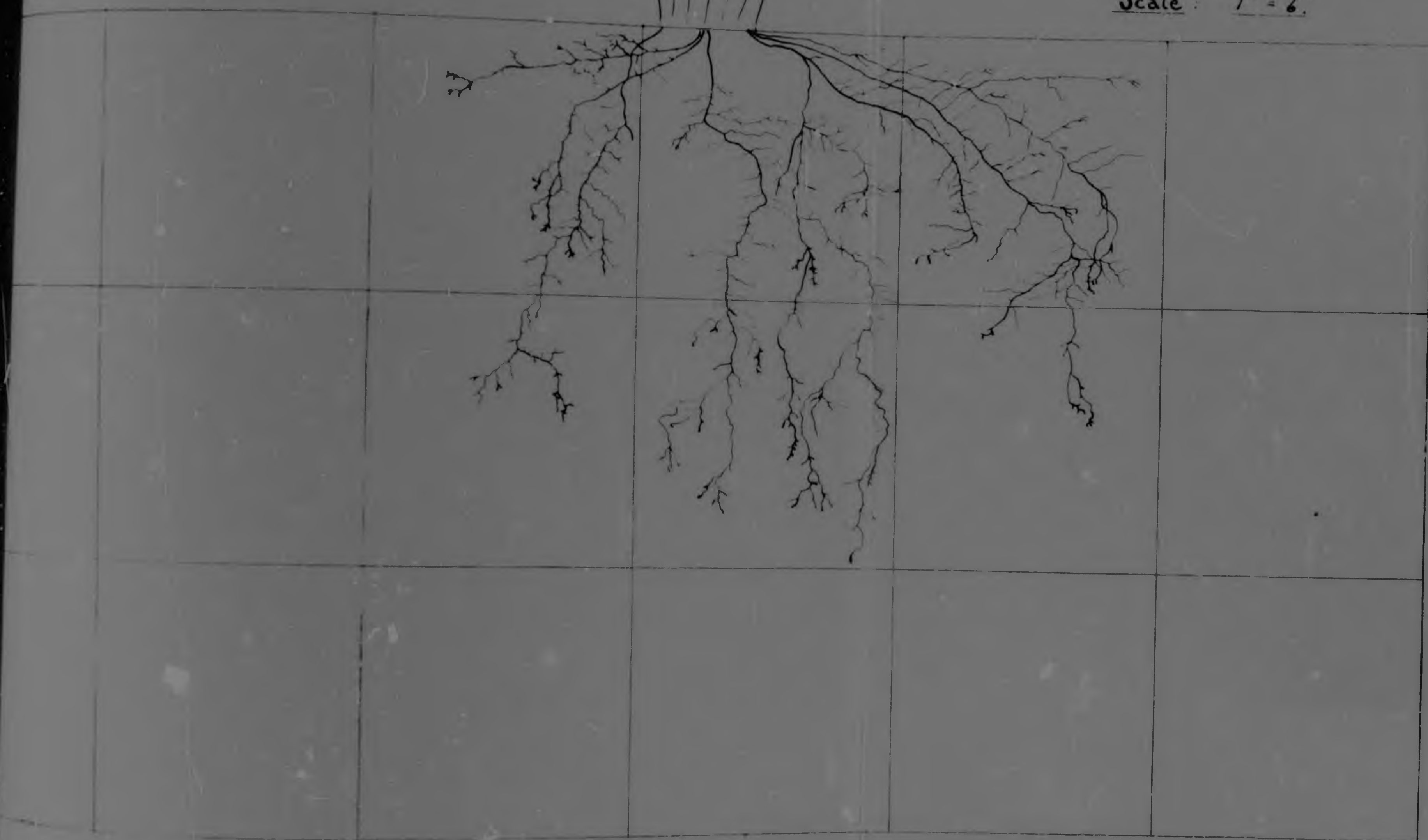


1113-1-1

Alouatta plumbeus 6/12/13

Chart No. 18.

Scale: 1" = 6"

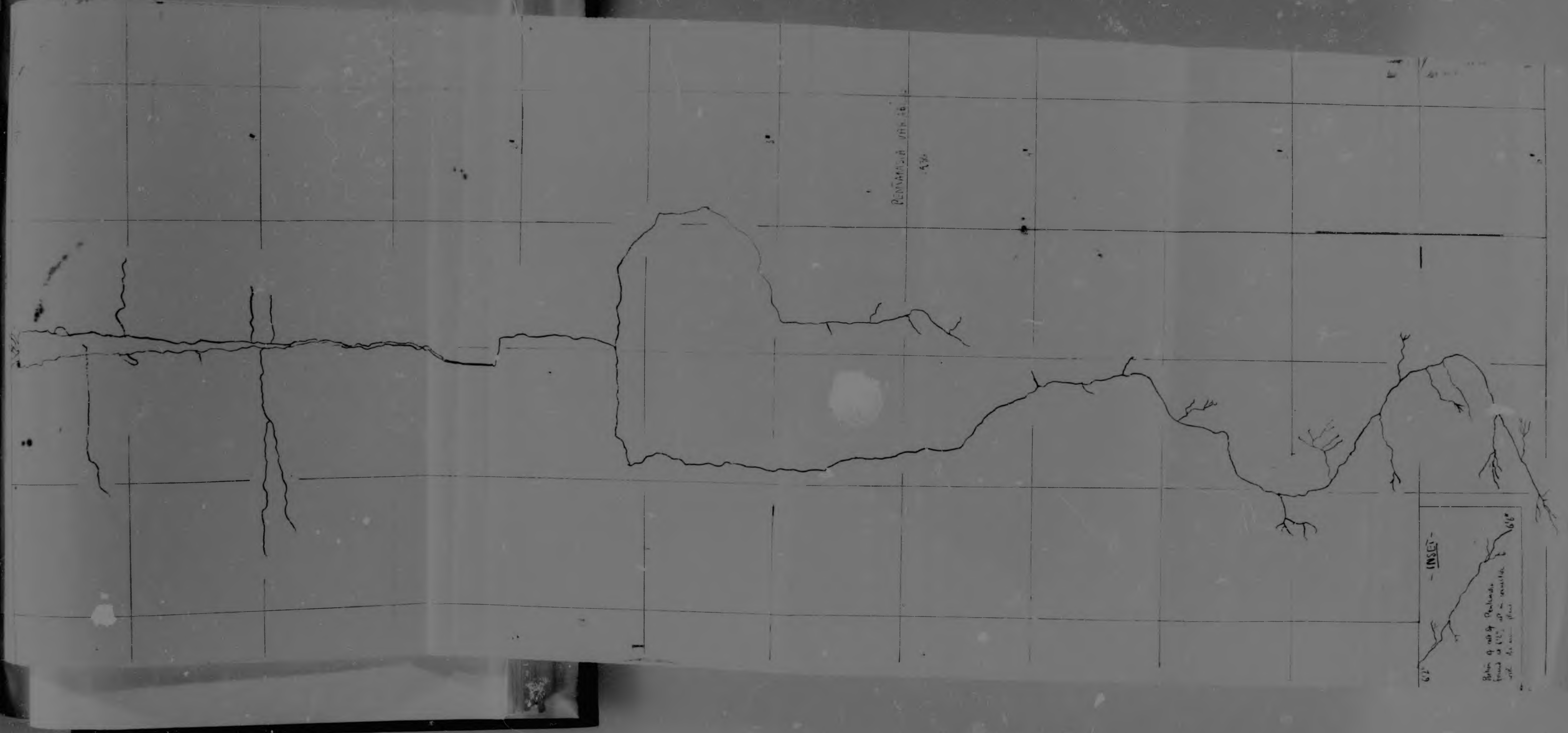


Dark original soil

Scattered quartz pebbles

Traces of outcrop

Decomposed granite with clay pipes



Author Rose-Innes R

Name of thesis Some observations on the nature and causes of secondary succession on certain areas at Frankenwald and in the Highveld of the Transvaal 1939

PUBLISHER:

University of the Witwatersrand, Johannesburg

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