A FURTHER STUDY OF SECONDARY SUCCESSION ON THE HIGHVELD

by

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DECLARATION

I hereby certify that this thesis entitled " A Further Study of Secondary Succession on the Highveld " is my own work, and has not been submitted for another degree by myself.

Signed:

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CHAPTER I

SECONDARY SUCCESSION

(a) The Nature and Importance of Secondary Succession

The distinction between primary and secondary succession arose soon after development of the concept of plant succession, although the validity of the seperation was doubted by Cowles (1911). The characteristic of primary succession is that it takes place under natural conditions, whereas secondary succession involves changes in vegetation on denuded soils, and is almost always a result of interference by man (Carpenter, 1938). Apart from passing references the only secondary succession considered in this thesis will be that taking place on land that has been cropped or disturbed and subsequently abandoned. For convenience the term 'succession' will be used to denote 'secondary succession', following the example of Davidson (1961).

The study of succession is of considerable practical importance in the world today because of the vast areas of seral vegetation covering the earth's surface. Semple (1952) states that in western United States alone there are 80 million acres of abandoned cropland, an area larger than the Transvaal. Large areas of Africa are also covered with seral vegetation, the 'shifting cultivation' practices of the native populations being the main contributing cause. Semple also states that in most instances the early stages of seral vegetation give low quality feed, and so the areas concerned tend to remain unproductive and in an erosion susceptable state until the arrival of the sub-climax or climax grasses. This process usually takes 30 or more years.

The productivity of these old cultivation lands can be restored by the sowing of an introduced improved or native species after cropping, or by the manipulation of the usual succession.

An example of this latter approach is given by Davidson (1961) who showed how the normal highveld succession was desireably controlled by nitrogen. However the success likely to be achieved in the manipulation of succession is very dependent upon an understanding of the causal factors of succession, and this study reports investigations carried out to help obtain such an understanding.

(b) An Outline of Secondary Succession on the Highveld Sandy Soils

The course of the highveld succession was first described in detail by Rose-Innes (1939), who set up the following stages:-

1. The Ruderal Stage, characterised by annual weeds, under normal conditions mainly dicotyledons such as *Conyza ambigua*.
2. The Primary Grass Stage, characterised by the rhizomatous *Cynodon dactylon* and the bunch grass *Eragrostis curvula*.
3. The Secondary Grass Stage, characterised by the tall growing *Hyparrhenia hirta*.
4. The Grassland Subclimax or Purple Veld, a mixed grassland of about 20 species, e.g., *Tristachya hispida* and *Trachypogon spicatus*.

The primary grass stage usually commences after two years of abandonment, and the secondary grass stage after approximately 10 years. The return of a seral area to subclimax grassland has never been observed, but several workers have suggested this would take place in 30 to 50 years.

Davidson (1961) has split up the primary grass stage into a first grass stage of stoloniferous grasses, and a second grass stage of bunch grasses. Throughout this thesis, however, the classification of Rose-Innes has been followed as observations suggest that there is little or no value in the division of the primary grass stage.

Rose-Innes also postulated that under natural conditions succession will proceed from the grassland subclimax through a Protea Open Woodland to a Scrub Climax. There is still considerable doubt about this further succession, and in this study it will be treated as a 'hypothetical climax' as described by Davidson (1961). The grassland subclimax will be referred to as purple veld throughout this work.

(c) Review of Literature on Secondary Succession

(1) Succession on the South African Highveld

The records of previous workers will be fully discussed in each relevant section, but the following brief outline lists the main research work carried out on this topic.

Murray (1934) outlined the succession and also carried out several root bisect studies, while Rose-Innes (1939) described the succession in detail, performed soil analyses from the various stages, dealt with the reproduction of several species from the sere and also carried out further root bisect studies. At the same time Story (1938) investigated aspects of succession in *Themeda triandra* veld. van Rensburg (1942) gave further information about field aspects of succession, whilst Coetzee (1945) made additional root bisect studies.

Israelstam (1953) compared aerial evaporative power and soil temperature regimes in a fallow and under ruderal vegetation, and investigated the possible effects of the differences on the germination of *Cynodon dactylon* seed. Roux (1954) and Jong and Roux (1955) carried out work on the nitrogen sensitivity of grass seedlings, a study being continued by Roux and Warren (in press). Stiven (1957) studied successional soils with particular reference to available nitrogen. Evidence was also put forward to show that *Trachypogon spicatus* produced an anti-bacterial and a germination inhibiting substance. Davidson (1961) has briefly summarised the results of earlier studies, and has presented field data on the influence of soil fertility on succession.

(2) Succession on other areas.

As far as can be ascertained most investigations of secondary succession have been carried out in the United States. Booth (1941) investigated 106 old fields in Kansas and Oklahoma and described the following typical stages:-

1. A 'weed' stage, lasting approximately two years.
2. An annual grass stage (*Aristida oligantha*), lasting nine to thirteen years.
3. A bunch grass stage which in the oldest field

examined was still dominant, there being no definite signs of invasion by climax prairie. Similar stages in Oklahoma are described by Rice et al (1960). Smith (1940) found that annual weeds and forbs were followed by annual grasses, then by bunch perennials and finally by stoloniferous perennials.

Tomanek et al (1955) investigated the composition of Kansas land last cultivated 33 years ago under ungrazed and moderately grazed conditions. The protected area had 53% of the climax composition and the grazed area only 28%. The main difference was in the occurrence of *Buchloe dactyloides* (a creeping rhizomatous grass similar to *Cynodon dactylon*) which comprised 21% of the cover of all species in the ungrazed area and 61% of the total cover in the grazed area.

Judd and Jackson (1939) described succession in western Nebraska as comprising dicotyledons in the first stage, followed by an annual grass, *Bromus tectorum*, then by a succession of perennial grasses. Judd (1940) found a similar pattern in Montana with one to three years of annuals followed by a mixed annual-perennial pasture, with climax grasses reinvading in eight to ten years, a period much shorter than that usually quoted. The usual period seems to be from 25 to 40 years, as found by Savage and Runyon (1937) on the great plains. Coupland (1952) described a succession in the western Canadian provinces where annual weeds dominat· for the first two ye · ollowed by perennial forbs and short lived grasses and finally by the climax community in 15 to 20 years.

Quaterman (1957) found a slightly different pattern in the central basin of Oklahoma where the cultivated area was originally forrested. Although succession began with weeds (Erigeron sp.), there was only one definite grass stage with Andropogon virginicus being co-dominant from about the fourth to the fifteenth year, after which trees were dominant. Keever (1950) described a varying weed complex in the initial stage of succession in Carolina, and this complex was also followed by Andropogon virginicus which was in turn re-invaded by pine. Evans and Dahl (1955) found that the re-invasion of forests into cleared, cropped and abandoned areas in Michigan was very slow. Piemeisel (1938) described the changing weed complex that follows for at least the first seven years on abandoned lands in the U.S.A. previously under sagebrush (Artemisia tridentata).

Rowe (1962) outlined the course of succession on abandoned tobacco lands in Rhodesia. Weeds, such as Tagetes minuta, dominated in the first year, and these in the second year were followed by seral grasses similar to the primary grasses of the highveld sere. Aristida sp. was usually dominant in the third year, but was displaced in the fourth to seventh year by Hyparrhenia sp., which in turn was replaced by woodland. If Aristida and Perotis sp. dominated for longer than seven years, lands had usually been overcropped prior to abandonment.

Nye and Greenland (1960) have summarised the available data on the course and causes of succession in tropical African forests.

The published investigations of succession in South Africa appear to be confined to the studies of the highveld, but Acocks (1955) in a general review refers to "the problem of old fallows which remain for decades, even half a century, at an early or relatively useless stage of succession."

All the studies referred to have dealt with succession on old cultivated land, but similar studies have been carried out on other disturbed or degenerate areas. Langenheim (1956) investigated succession on a subalpine earthflow and Bramble and Ashley (1955) found that rocky spoil areas from open cut mining had trees and shrubs as pioneers, and that herbs only developed where top soil was exposed. Tabor (1962) has suggested that succession can be utilised to maintain a cover on abandoned road cuts and similar areas. Weaver (1954) has described the regeneration of prairie in the midwestern United States after the great droughts and windstorms of the 1920s and 1930s. Shields and Wells (1962) reported that the succession on blast areas of nuclear explosions was the same as that occuring on disturbed areas or outwashes on the surrounding desert vegetation type.

The studies referred to described the pattern of succession in different areas. Fewer investigations have been made about the causes of succession and these will be mentioned in the relevant chapters of this thesis.

Conclusions

From this brief review of literature it appears that secondary succession in grassland usually comprises a ruderal stage, a stage of annual or short lived perennial grasses, followed by a further one or two perennial grass stages, and in most instances by climax prairie. This overall pattern suggests that the main causal factors of secondary succession would be of a universal nature, and would not be special properties of particular species in any one area.

(d) Review of Literature on Plant Competition

As succession is a series of invasions by successful competitors with a consequent partial or complete elimination of the unsuccessful competitors, it is important to briefly consider the subject of plant competition, the most comprehensive reference for this subject being that by Clements et al (1929).

These authors stated that in almost all circumstances two plants do not compete as long as the supply of water and air, nutrients and heat and light are in excess of the needs of both. Brenchley (1919) and Milthorpe (1961) list the same environmental factors with an additional one being the possible harmful effect due to toxic excretions, if such occur.

Competition, then, is a combined need in excess of supply, and competition is only for energy and raw materials and not for indirect factors such as space, wind and humidity.

Clements et al stated that the advantages of a competing species may be summarised in two words, "amount" and "rate". Greater storage in seed or rootstock, more rapid and complete germination, earlier start, more rapid growth of roots and shoots, taller and more branching stems, deeper and more spreading roots, more tillers, larger leaves and more numerous flowers were all mentioned as the "essence of success." Knapp (1961) has given a similar list of properties including seed production and seed dispersal. Clements and Shelford (1939) also comment that "rate and amount of germination often yield an initial advantage difficult to overcome later, and these are related to the number and kind of seeds produced..." Leith (1960) has also mentioned the importance of adaptation and efficiency of dispersal in competitive success.

Clements et al have described several experiments where seeds of annual or biennial ruderals (one species being Oenothera biennis) were sown with perennial grass seed. The ruderals usually dominated in the first year, but in the second or subsequent years the grass became dominant and the grass community prevented both germination and establishment of annuals, and the authors state "annuals and biennials are unable to compete with the climax grasses during the proper season for the latter.

In consequence they never occur in the climax except in disturbed places...."

Experiments carried out with short and tall prairie grasses showed that short grasses could only maintain themselves when tall grasses are kept down by grazing or mowing, but were reduced or eliminated by protection.

Other conclusions reached by Clements et al can be summarised as follows:-

(1) As a stand becomes increasingly dominated by one species, competition decreases, a point restated by Elton (1958).

(2) Competition in grassland is usually for water, light and nutrients playing a secondary role.

(3) Species establishment is the direct outcome of response to the physical factors of a habitat only in open pioneer communities where competition has not begun. In all communities proper, establishment and ecesis are determined as much or more by competition and reaction than by the initial factors themselves.

(4) Competition in a community eventually gives rise to an equilibrium state, but it is a dynamic equilibrium continually changing as new shoots and individuals appear.

(5) Transplant experiments, even when carried out under conditions favourable to the transplant, were rarely successful, emphasising the advantage of the species in possession at that time. It was found to be very difficult for an alien species to to invade and establish in the face of the control exerted by undisturbed occupants.

This last point has been emphasised by many workers. Elton (1958) stated that almost all alien plants in the British Isles live in habitats such as arable land and roadsides which have been disturbed and simplified by man. Few introduced plants had successfully established themselves in natural communities. Piemeisel (1951) reached a similar conclusion from studies on shrubland in the U.S.A. Moore (1959) emphasised this for

Australian communities, and went on to state that aliens which had entered as a result of disturbance are in many cases eliminated if the disturbing factor is removed. Relph (1958) also pointed out that exotics usually only establish under disturbed conditions. Bunting (1960) pointed out that weeds in arable land are, in a sense, adapted to the crop, and when cropping ends it follows that these species are not adapted to living in a closed community.

Increasing numbers of studies are expressing plant competition on a quantitative basis. Harper (1960) and Harper and Gajic (1961) have studied the factors controlling plant numbers and the reaction of plants to increasing density, and replacement series of pot trials are being used to investigate such problems as the effect that altered nutrient levels have on a mixture of two species (van der Bergh and Elberse, 1962).

Competition as experienced by seedlings

Seedlings are usually the weakest stage in the life cycle of a species. Eleven species emerged from sowings by Leigh (1960) into Eragrostis curvula pasture, but all the seedlings died. Leigh attributed this to either soil moisture deficiency or to carbon dioxide levels, although it is difficult to see how the latter could be involved.

Grass seedlings are particularly susceptible to soil moisture deficiency in the seedling stage. Laing (1958) attributed seedling death of grasses to the failure of adventitious roots to develop and to the inability of seminal roots to supply adequate moisture, though Locke and Clarke (1924) found that under their conditions seminal roots of wheat seedlings supplied adequate moisture until adventitious roots developed.

As elongation of the grass mesocotyl places the crown node near the surface, sustained moist conditions are required for adventitious root development from this point. Olmstead (1941) stated that three days of moist conditions are required in the case of Bouteloua curtipendula, and attributed many field seedling deaths to the failure of adventitious root development. Glendening (1941) also found that lack of soil moisture retarded adventitious root development and that soil moisture was the major controlling factor in the establishment of Heteropogon contortus under range conditions. Blake (1935) found that drought was the principal cause of death following the temporary establishment of seedlings, and soil moisture deficiency was also indicated by Champness (1950) as being the major cause of seedling death.

Conclusions

This review emphasises that plants only compete for energy and 'raw material' requirements, and points out the difficulties of seedling invasion in a closed and undisturbed community, with particular reference to the role of soil moisture in seedling establishment.

CHAPTER II

EXPERIMENT T6B NORTH

(a) The Outline and Aims of the Experiment

The studies reported in this thesis are centered around experiment T6B North which was laid out to be ready for investigation in the period 1960-1963. For convenience the experiment is hereafter referred to as T6B.

The experiment is on the Frankenwald Field Research Station situated on latitude 26°41'S and longitude 28°06'E at approximately 5,000 feet above sea level. The soils, derived from pre-Witwatersrand old granites, are acid and sandy. The station has a summer dominated rainfall averaging 30 inches a year.

The experiment originally consisted of nine adjacent blocks, each 25 x 150 feet. All blocks were cultivated and cropped in 1950/1951, and the next year eight were cropped, and then seven, with one additional block being left to fallow in each year. In 1957/1958 when seven adjacent blocks had been abandoned an additional block was laid out at the top of the previously marked area, and this was cropped for three seasons (1957/1958 to 1959/1960) before it was abandoned. This gave ten adjacent blocks which had been abandoned from 1951 to 1960.

It should be noted that when this work was being carried out no one at Frankenwald was aware of the shorter cultivation period of the extra block and it had been assumed that the last abandoned block had been cropped for 10 years, and the experiments described in this study were laid out on this assumption.

Unfortunately no record was made of the botanical composition of the area prior to the first ploughing, but from the appearance of the surrounding vegetation and from aerial photographs it may be assumed to have been an 'old fallows' vegetation of such species as *Hyparrhenia hirta*, *Stoebe vulgaris*, *Eragrostis* sp. and *Cynodon dactylon* (confirmed by Davidson, personal communication).

Two points in particular should be noted about this experimental design.

Firstly, there is no 'buffer zone' around the experiment, and the ends of all the plots and the outside edges of the 1959/1960 and 1950/1951 plots were exposed so that they could be influenced by the vegetation along the boundaries.

Secondly, the range of treatments on the soil varied from one year of cropping to nine years of cropping. The only fertilizer used was superphosphate which was applied at each cropping.

An area of purple veld usually grazed or mown lay further down the slope from experiment T6B, and in this area a block of 25 x 150 feet was pegged out approximately 50 yards south-west of the 1950/1951 plot. This area was used for equivalent studies to those carried out on the seral vegetation.

Most studies were confined to four plots, the 1959/1960 plot representing the ruderal stage, the 1956/1957 plot the primary grass stage, the 1950/1951 plot the secondary grass stage and the plot described above in the purple veld or Trachypogon - other species grassland. For convenience these plots will be referred to as the R, E, H and T plots, and these initials will only refer to these particular plots. Also a plot referred to as a 1959 plot, for example, would be that cropped in 1958/1959, hence abandoned in 1959.

These plots were used to measure the environment of the various seral communities growing alongside each other with the same aspect on the same soil type. It had been proposed (Anon, 1959) to measure the following environmental characters:-

Light

Temperature: soil temperature and air temperature beneath the canopy

Humidity: relative humidity and evaporating power of the air

Soil Moisture

Soil Nutrients

After defining the environment of the seral stages it was proposed to measure the tolerance of the dominant species to each of these factors, and possibly to be able to prove "that succession is due to biotic reactions, i.e. that each community produces an environment which is unsuitable for itself and suitable for the next stage in succession."

The final stage of this programme would be the modification of the environment by artificial measures which would make possible the development of any seral stage by providing the microclimate desired.

(b) Experiment T6B in 1961/1962

(1) Analysis of Vegetation

As various measurements of the micro-environment were being taken throughout the growing season, no quantitative analysis of the vegetation was made until late autumn 1962 when the environmental studies were being concluded. Measurements of species basal cover were then taken on the 10 plots of T6B, and the T plot, 500 point quadrats being thrown on each plot using a 10 point frame.

The customary standards were used for the recording of a hit, and in the case of C. dactylon a hit was taken as being any strike on a main runner, as well as counting those hits on a rooted node. Those points which did not strike a plant base were recorded as 'bare' or 'litter'. Litter was defined as a strike on an area where the soil was well protected by living or dead plant material lying close to the ground.

In the R, E, H and T stands measurements of plant density and frequency were taken from 40 throws of a quarter-metre quadrat, and visual observations were made on all plots.

Results

The results of the point quadrat analyses are given in table 1 and the results of the frequency and density determinations, the latter being expressed as plants per sq. metre, are given in table 2. The errors to be expected from using 40 quadrat throws for frequency determinations can be assessed from table A1 in the Appendix.

TABLE 2

SPECIES FREQUENCY AND DENSITY

R, E, H and [illegible] PLOTS

Species	Density (plts/sq.m.) R	E	H	T	Percent Frequency R	E	H	T
Conyza ambigua	10.6	4.7	6.3	-	88	31	48	-
Gnaphalium luteo-album	0.7	14.3	8.2	-	13	68	48	-
Tagetes minuta	52.6	19.5	0.4	-	73	73	5	-
Oenothera biennis	2.1	5.4	0.4	-	28	28	8	-
Ursinia nana	ND	ND	-	-	58	8	-	-
Acanthospermum xanthoides	ND	ND	-	-	78	8	-	-
Senecio sp.	-	-	0.2	-	-	-	3	-
Helichrysum sp.	-	-	1.3	-	-	-	20	-
Bidens schimperi	-	32.1	-	-	-	40	-	-
Misc. dicots	-	-	0.4	-	-	-	10	-
Eragrostis curvula	0.9	2.5	4.3	4.0	13	50	63	20
Paspalum commersonii	0.6	0.7	0.7	-	10	15	13	-
Sporobolus pyramidalis	-	-	0.1	-	-	-	3	-
Setaria pallide-fusca	0.4	-	0.1	-	8	-	3	-
Cynodon dactylon	ND	ND	ND	ND	78	88	70	8
Eragrostis racemosa	0.1	-	--	1.4	3	-	-	28
Hyparrhenia hirta	0.4	-	4.7	0.1	8	-	53	3
Stoebe vulgaris	-	-	1.5	0.1	-	-	25	3
Andropogon amplectans	-	-	-	0.2	-	-	-	5
Cymbopogon excavatus	-	-	-	0.5	-	-	-	10
Monocymbium ceresiiforme	-	-	-	0.1	-	-	-	3
Brachiaria serrata	-	-	-	1.5	-	-	-	25
Heteropogon contortus	-	-	-	5.2	-	-	-	58
Diplachne biflora	-	-	-	1.5	-	-	-	33
Digitaria tricholaenoides	-	-	--	ND	-	-	-	28
Urelytrum squarrosum	-	-	-	0.1	-	-	-	3
Elyonurus argenteus	-	-	-	6.9	-	-	-	60
Tristachya hispida	-	-	-	13.2	-	-	-	85
Trachypogon spicatus	-	-	-	8.5	-	-	-	85

ND = Not determined, counting not possible owing to the habit of the plant, frequency alone recorded.

Throughout this thesis <u>Conyza ambigua</u> covers both this species and <u>Erigeron canadensis</u>, as seperation of these species in the field proved to be very difficult, or impossible in the case of plants without seed heads.

TABLE 1

PERCENTAGE BASAL COVER

500 point quadrats in each plot

Cover	Plot 1960	1959	1958	1957	1956	1955	1954	1953	1952	1951	T
Bare ground	83.6	82.2	62.8	30.6	21.8	1.0	5.8	5.8	18.8	14.6	11.6
Litter	8.2	11.2	27.8	49.4	61.2	83.8	82.2	79.4	70.0	74.8	68.2
Total non basal cover	91.8	93.4	90.6	80.0	83.0	84.8	88.0	85.2	88.8	89.4	79.8
Acanthospermum xanthoides	1.4	2.0	1.0	-	-	-	-	-	-	-	-
Oenothera biennis	0.4	0.2	0.6	-	1.0	0.2	0.2	0.4	-	-	-
Other ruderal dicots	-	0.4	0.8	0.4	0.2	0.2	0.4	0.4	0.2	0.4	-
Cynodon dactylon	6.0	0.4	2.2	14.8	11.0	11.4	7.2	8.4	2.2	3.6	-
Eragrostis curvula	0.4	3.6	3.0	4.4	4.0	1.6	2.4	3.4	5.2	2.6	2.0
Hyparrhenia hirta	-	-	-	-	-	0.4	1.0	0.8	0.8	3.2	-
Other seral grasses	-	-	1.6	0.4	0.8	1.4	0.8	1.4	2.4	0.4	0.6
Stoebe vulgaris	-	-	0.2	-	-	-	-	-	0.4	0.4	-
Tristachya hispida	-	-	-	-	-	-	-	-	-	-	6.8
Trachypogon spicatus	-	-	-	-	-	-	-	-	-	-	3.8
Other purple veld grasses	-	-	-	-	-	-	-	-	-	-	7.0
Total plant basal cover	8.2	6.6	9.4	20.0	17.0	15.2	12.0	14.8	11.2	10.6	20.2

In figure 1 the percentage basal cover of all species, percentage bare ground and percentage litter for all the plots have been depicted in graphical form, and other graphs illustrate the change in basal cover of C. dactylon, E. curvula and H. hirta with an increasing period of revegetation, the figures for the T plot being shown as zero years of cultivation.

Brief descriptions of the T6B and T plots as at the 1961/1962 season are given below, and throughout these descriptions and thereafter Cynodon will refer only to C. dactylon, Eragrostis to E. curvula, Hyparrhenia to H. hirta, and Trachypogon to Trachypogon spicatus.

1960 (R) plot: Much bare ground, Eragrostis scattered with many tussocks from 1960/1961 season; good growth of Cynodon in past and present season, many runners from bordering vegetation on N.E. or long boundary; approximate count of Hyparrhenia 34 plants, smallish, mainly from past season; scattered Paspalum commersonii through this plot and all to 1951; very scattered Eragrostis racemosa.

1959: Much bare ground; more Eragrostis than 1960 plot, in good health; less Cynodon than 1960 plot; approx. count of Hyparrhenia 21 plants, some large; Tagetes minuta growth best near Tatra sp. (rodent) burrows, noted also in 1960 plot; rare to very rare Pogonarthria squarrosa, Andropogon eucomus, Aristida congesta and E. racemosa.

1958: Much bare ground, but less than 1959 plot. Eragrostis still healthy but increasing proportion of dead material; slight increase in Cynodon; approx. Hyparrhenia count 18, most tussocks large; rarer species as for 1959 plot: with 1957 and 1956 plots has highest Oenothera biennis density.

1957 (E): Little bare ground - applies for remaining plots; big increase of Cynodon in fair condition; Eragrostis in very poor condition where Cynodon plentiful, otherwise in fair health; approx. Hyparrhenia count 7, all large; thick Gnaphalium luteo-album, mainly associated with Cynodon.

BETWEEN PAGE 16 and 17 SEE 35MM FICHE

1956: Cynodon often very thick, fair to poor condition; Eragrostis poor, almost all dead in dense Cynodon areas; approx. Hyparrhenia count 40, with few small bushes.

1955: Cynodon the main grass, fair to poor condition, Eragrostis very poor, mostly dead; estimated Hyparrhenia count over 100.

1954: Cynodon and Eragrostis as for 1955 plot; further increase in Hyparrhenia with some old tussocks; 2 apparently spreading clumps of Cymbopogon excavatus - only ones in T6B, each clump quite distinct, no special environmental characteristics noted.

1953: Cynodon dominant where Hyparrhenia absent; Eragrostis poor; slightly larger number of live Hyparrhenia than 1954 plot, but more dead material.

1952: Cynodon and Eragrostis both in poor condition; greater number of dead Hyparrhenia tussocks which in all plots tend to be at the S.E. end. An area of Stoebe vulgaris in N.W. corner continuous with a similar area outside.

1951 (H): Further decrease in Eragrostis and Cynodon; many more live and dead Hyparrhenia tussocks, alive in centre of plot, dead in the S.E. end, with the N.W. covered by Stoebe vulgaris.

All the plots from 1960 to 1951 had varying amounts of annual weeds, mainly Conyza ambigua, Gnaphalium luteo-album, Tagetes minuta, and Bidens schimperi. Acanthospermum xanthoides and Ursinia nana were common in the recently abandoned plots. At the beginning of the season dead stalks from the 1960/1961 ruderals were noticeable but these soon flattened out.

Purple Veld Plot (T):

Typical purple veld over most of the plot except for an area of small and low Eragrostis tussocks in one corner of the plot.

Photographic Record

Plates 1 to 9 further illustrate the characteristics of these experimental plots, and reference can be made to plates 11, 13 and 15 which also illustrate various features of the plots.

Discussion

Reference will be made to the botanical analysis and description of the plots in several of the following chapters, but the following points will be noted now and their importance discussed later on.

(1) There were no annual ruderals growing in purple veld, even though a small number of ruderal seedlings were present in the veld at the start of the season (as shown in the following section). In contrast to this ruderals were abundant in the T6B plots.

(2) There was a decrease in the health of Eragrostis plants as the age of the plots increased, with a particularly large number of dead individuals in the 1953 and 1954 plots. In the 1956 and 1957 plots the growth of Cynodon was much denser around the poor Eragrostis tussocks than the healthy ones; the encroachment of Cynodon did not appear to be the cause of the poor Eragrostis tussocks, but probably paralleled the increasing unhealthiness of the Eragrostis.

(3) There was a marked decrease in the cover of Cynodon in the 1959 plot as compared with the 1960 plot. This was attributed to the outgrowth of this species from the 1960 plot boundary, not to any limiting factor of the 1959 plot.

(4) In the 1960 plot there were more Hyparrhenia plants than in the 1959, 1958 and 1957 plots. Most of the plants counted were from the 1960/1961 season, the first year of abandonment, and the establishment was often on areas which, as far as can be judged from thepresence of dead ruderal stems of that season, would have offered little protection and shelter. The areas with the greatest concentration of young Hyparrhenia were close to the boundary of the plot where dense Hyparrhenia was growing. In the 1959, 1958 and 1957 plots, although there were fewer Hyparrhenia plants

they were very vigorous and in much better condition than those in the 1954 to 1951 plots.

The many dead tussocks in the early plots, especially in the 1951 plot, suggest that many Hyparrhenia plants established in the first years of abandonment in order for the tussocks to have reached such a size before dying off prior to the 1961/1962 season.

The degeneration and death of ungrazed Eragrostis and Hyparrhenia tussocks has a parallel in the similar degeneration of ungrazed purple veld (shown to some extent in plate 21) - though it seems that a longer period of time is required before purple veld tussocks die than is the case for the seral grasses.

Donald (1961) has suggested that the degeneration of ungrazed or unmown grassland is a result of an accumulation of leaf material with a consequent Leaf Area Index such that respiration demands equal or exceed energy gains from photosynthesis.

Conclusions

Experiment T6B has been described, and results presented of botanical analyses carried out in 1962. The succession on these plots has, as a general rule, followed the expected course, but several points have been noted in the discussion.

(2) The Establishment and Growth of Ruderals

i. Early spring establishment counts

Methods

It was noted in late August 1961 that there were considerable numbers of small dicotyledonous seedlings throughout experiment T6B as a result of isolated winter rainfalls. Consequently seedling counts were taken on the 31st August using 30 throws of a 350 sq. cm quadrat in each of the A, E, H and T stands. At the same time five samples of 0-3 inch soil were taken from each stand, and the moisture content determined as percentage of dry soil.

Results

The number of seedlings per square metre, the soil moisture percentages and the wilting point soil moisture percentages (from chapter III) for the four stands are given in table 3.

TABLE 3

SEEDLING COUNTS IN FOUR COMMUNITIES

	Community			
	R	E	H	T
Seedlings per sq. metre	123	545	952	12
Soil moisture %	3.1	3.4	5.8	5.2
pF 4.2 moisture % (wilting point)	4.4	4.7	5.9	5.9

The variation between the counts within each stand was considerable and this is illustrated in table 4 which shows the number of quadrats, out of the 30 thrown in each stand, in which various levels of seedling density were recorded.

TABLE 4

DISTRIBUTION OF SEEDLINGS IN FOUR COMMUNITIES

No. of seedlings per quadrat	No. of quadrats in each community			
	R	E	H	T
0	8	5	2	22
1 - 10	18	14	3	8
11 - 20	3	3	7	-
21 - 30	1	1	5	-
31 - 40	-	1	3	-
41 - 50	-	1	3	-
51 - 60	-	3	1	-
61 - 70	-	1	1	-
71 - 80	-	-	3	-
81 - 90	-	1	1	-
91 - 100	-	-	1	-
Total no. quadrats	30	30	30	30

Discussion

The results in tables 3 and 4 clearly show the low seedling density recorded in the T plot. Although the soil moisture samples were taken after establishment had taken place it would appear that the low seedling numbers cannot be solely attributed to an excessively high moisture tension in the T plot as compared with the other three plots. As there were no dead stalks of ruderals from past seasons in this plot it is obvious that there must be some factor or factors limiting the growth of ruderals.

The seedling establishment in the R plot was lower than in the E or H plots, the main period of germination in the R plot being after the opening seasonal rains at the end of October. This low establishment is largely attributed to the faster rate of drying out of the bare surface soil of the R plot as compared with the protected surface of the other plots. In the R, E and H stands the highest seedling counts were recorded in sheltered and protected areas.

Later visual observations indicated a considerable mortality of these seedlings in all plots, with complete seedling death in the T plot. This mortality is almost certainly due to the higher moisture tension levels in the soils as the perennial grasses began to come away in September with the higher soil temperature, the limiting nature of which has been demonstrated for E. curvula (Leigh, 1960) and T. spicatus (Davidson, unpublished). This moisture stress would be expected to be greatest in the T plot as the early perennial grass growth in this plot was much more vigorous than on the protected E and H plots. Competition for water has been suggested as the reason for the failure of annuals to compete with vigorous perennial grass in Carolina (Keever, 1950).

ii Growth of ruderals

The seedlings which established from winter rains were mainly Conyza ambigua and Gnapthalium luteo-album and almost no Bidens sp. or Tagetes minuta established until the November rains. Even so the growth of these last mentioned species was very poor, and this is illustrated by measurements made of the height and weight of Tagetes and Conyza plants from the R plot in early December and from the R and H plots in mid-February. To avoid interference with the micro-environment studies the samplings were limited to 10 plants, selected at random.

TABLE 5

SAMPLING DATA FOR THE GROWTH OF RUDERALS - 1961/1962

Date & Stand	Tagetes minuta (R) 7/12	(R) 15/2	(H) 15/2	Conyza ambigua (R) 7/12	(R) 15/2	(H) 15/2
Mean height (ins)	1.2	2.7	7.8	10.2	33	39
Fresh weight (gms)	0.1	0.1	0.6	10.4	32	38

Results and Discussion

The results of the sampling, given in table 5, clearly illustrate the much greater bulk production and height of the Conyza plants, and also illustrate that the Tagetes in the H stand grew better than Tagetes in the R stand. Visual observation indicated that Tagetes growth in the E stand was similar to that in the H stand. Observations also indicated that the differences in Tagetes growth between the stands was not related to different seedling densities.

Examination of a number of stands also suggested that although Tagetes and Conyza grew equally well in cropped land, Tagetes and Bidens sp. seldom grew as well as Conyza on abandoned land. Tagetes is very rarely found in completely protected purple veld, a condition which allows considerable Conyza growth (plate 21).

Conclusions

Following scattered winter rains there was an abundant germination of annuals in the R, E, and H stands, but germination was rare in the T plot. There was considerable mortality among seedlings, especially of those in the T stand. Surviving seedlings grew better in the H stand than in the R stand.

CHAPTER III

THE PHYSICAL ENVIRONMENT OF AIR AND SOIL IN RELATION TO SECONDARY SUCCESSION

(a) Light Intensity

In the review of competition in chapter I it was noted that light is one of the main factors in plant competition, and that competition for light was generally of less importance in grassland than competition for soil moisture (Clements et al, 1929).

The major role of light is in regard to requirements for photosynthesis, but light can also be involved in the germination requirements of seeds, and daylength is important in the photoperiod requirements for flowering.

Many studies have been made of light intensity in forests, e.g., Ashton (1958), and a range of results are listed by Shirley (1945). Cooper (1961) studied light intensity under a range of life forms, but most of the work in grasslands has been carried out in connection with Leaf Area Index investigations, e.g., Stern (1962).

Story (1938) by use of the Eder-Hecht photometer showed that the light intensity at ground level in Themeda veld was approximately half that in seral vegetation, and this was confirmed in one set of measurements with a photo-electric cell. Some measurements were also taken with a photo-electric cell in purple veld at Frankenwald (undated, unsigned file record) and although mainly concerned with the passage of different wave lengths through leaves, it was noted that it was quite common to find light intensities under tussocks of 10% or less. No records dealing with succession and light intensity have been located other than those of Story.

Matheson (1939) had used purple veld when comparing light measuring instruments, but gave no details about the actual light conditions in the veld.

It can be misleading to place too much emphasis upon the 'mean' light intensity under vegetation, as the mean is generally made up of a large proportion of low readings and a small proportion of high readings, usually due to 'sunflecks' through the vegetation. The importance of these sunflecks has been discussed by Evans (1939) and briefly by Stern (1962).

Daubenmire (1959) lists different species as having different compensation points (the point of lowest light intensity where a species can maintain itself, and photosynthesis is sufficient to offset respiration), but Blackman and Wilson (1951) suggest that there is little difference in the compensation point between sun and shade plants, although shade plants have an optimum growth rate at lower light intensities than sun plants. These differences between the optimum light intensity levels were more dependent on changes in Leaf Area Ratio rather than on differences in Net Assimilation Rate.

Methods

There are many methods of measuring light intensity, and these have been discussed by Matheson (1936) and Daubenmire (1959). The instrument used in the investigations described was a Weston photometer with a selenium receptor cell. The scale readings on the instrument only went to 250 foot candles, but readings of full sunlight (10,000 to 12,000 foot candles) were brought on to the scale by incorporation of resistances between the receptor cell and the meter. The method of calibration of the scale readings is described in part two of the Appendix.

As recommended and used by almost all authorities (e.g., Evans, 1939) an opal glass filter was placed over the receptor cell. Consequently light intensities were recorded as a percentage of full sunlight and not as absolute values, but this method of recording is often preferred (Daubenmire, 1959). Daubenmire suggested that the days for recording either be comparatively cloudless or have a uniform overcast sky, the latter being preferable as over heating of the receptor cell is evoided. Uniform overcast skies, however, are uncommon in the highveld and so all but two sets of meaurements were carried out in cloudless conditions.

It is very difficult to insert the cell into vegetation without concious or subconcious selection of sites. Daubenmire stated that some workers, in order to obtain a satisfactory value for average light intensity under vegetation, have directed the sensitive element of the light meter upwards and placed it successively at equal intervals along a tape, taking an average of readings made in the open at the beginning and the end of the series as a basis for comparison. In the investigations described it was necessary to kneel down and place the meter and resistance box on the ground before inserting the cell into the vegetation and taking the reading.

The procedure adopted was that six sites were chosen at random within each stage, the studies being carried out on the R, E, H and T plots. At each site six measurements of light intensity were made at equal intervals around the circumference of a 'circle' of diameter six feet, and it was found that only on extremely rare occasions did the plant growth controlling the reading at one point have any effect at the next measuring point. Measurements of full sunlight were taken at the beginning and the end of each set of six readings, and so the average light intensity as percent of full sunlight in each stand was recorded from 36 readings (6 sets of 6) and 12 control readings (6 sets of 2). All readings were taken over the noonday period, and care was taken that the sensitive cell was covered except when readings were being taken.

Throughout the growing season measurements were taken on seven occasions at the half inch level above the soil surface, and on four occasions at the four inch level. Measurements in the H plot were confined to the Hyparrhenia portion of the plot as were all measurements recorded in this and other chapters.

Results

Table 6 lists the reductions of full sunlight intensity recorded in the four stands at both the half and four inch levels for each occasion when measurements were made.

TABLE 6

FIELD LIGHT INTENSITY MEASUREMENTS

Full Sunlight as 100

(a) At the ½ inch level.

Date	Conditions	Stand R	E	H	T
8/11/1961	Cloudy	72	31	22	23
30/11/1961	Sunny	70	24	19	25
19/12/1961	"	64	19	21	23
24/ 1/1962	"	68	27	20	25
21/2/1962	"	70	27	20	18
21/3/1962	"	54	20	16	17
5/5/1962	"	60	18	21	15
Mean		65	24	20	21

(b) At the 4 inch level

Date	Conditions	Stand R	E	H	T
28/2/1962	Sunny	82	63	48	79
13/3/1962	Cloudy	72	31	25	56
6/4/1962	Sunny	75	52	47	61
25/5/1962	Sunny	75	53	45	60
Mean		76	50	41	64

The results are also expressed on a frequency basis, as recommended by Daubenmire (1959), where the number of readings within each 10% level of light intensity are expressed as the percentage of all readings taken. Thus the resulting histograms are based on 252 (7 x 36) readings at the half inch level in each stand for figure 2, and 144 (4 x 36) readings at four inches in each stand for figure 3. The values on which the histograms are based are given in table A2 in the Appendix.

Discussion

The results in figure 2 show there is a marked similarity between the frequencies of the different light intensities at the half inch level in the three grass stages, as compared with the completely different distribution of light intensity within the R stage.

In the measurements at four inches there is a much greater proportion of high intensity readings in the T stand than in the E and H stands, this difference being due to the short habit of the purple veld grassland. Similarly in section (b) of this chapter a large change in the evaporating power of the air at two levels within purple veld grassland is demonstr[illegible]. The greater shading effect of the taller Hyparrhenia is also shown in figure 3.

From visual observation of other stands of the various successional stages it would appear that these measurements would be representative of most of the equivalent ungrazed stages, though a more vigorous and taller growing ruderal stage would probably give greater reductions in light intensity by the end of the season.

Assuming that soil moisture and nutrients are freely available the differences in light intensity within the four stages could have three direct effects as follows.

(1) Stands could have such a high light intensity at the soil surface that seedling establishment may be severely hampered, as postulated for Stoebe vulgaris by Lecatsas (1961).

(2) Stands may have such a low light intensity at the ground surface that seedlings could not, on their own resources, reach a height where there is sufficient light intensity to maintain their growth.

BETWEEN PAGE 27 and 28 SEE MM FICHE

(3) The shading effect of the tall species could severely handicap the shorter species in their growth.

The first two possible reactions will be discussed in chapter VII after the results of a seedling growth trial have been presented.

From results given by Story (1938) and the compensation points listed by Daubenmire (1959) a figure of 30% full sunlight could be taken as that likely to greatly reduce or to cease mature plant growth. From the four inch measurements it can be seen that only 2, 20, 33 and 13% of sites in the R, E, H and T stands have below 30% of full sunlight at any one time. This suggests that there would be few sites in these stands where mature plants, presumeably at a height of above four inches, could not maintain themselves. The only plant that does not rise far above four inches is Cynodon dactylon, which has the ability to grow in light intensities of well below 30% full sunlight (Story, 1938). It is therefore suggested that the light intensity in these stands is not so limiting that it would, by itself, prevent the growth of mature plants, but it is possible that reduced light intensities could so handicap a plant that it would die under other competition pressures, i.e., for water.

However figures such as these which are for a stand can never give a complete picture. A pasture of Eragrostis with very scattered Hyparrhenia could have the same mean values and frequency distributions of light intensity at various heights as a pasture of pure Eragrostis; yet in the first case the few Hyparrhenia plants present could exert a significant shading effect upon the nearby Eragrostis plants with which they would be competing. For this reason it is suggested that any further studies of light intensity in relation to secondary succession be based on detailed analyses of light intensity within various species interactions as they occur in the field.

Conclusions

It has been shown that the light intensity at the half inch level above ground in the four vegetation types studied was, in order of decreasing intensity, $R \gg E \geqslant H - T$. At the four inch level the order is $R > T \gg E > H$, and the changes between the two levels are attributed to the life forms involved. It has been concluded that reduced light intensity would hardly ever be the sole cause of death of a mature plant, but could make plants more susceptable to death by competition from other causes.

(b) Evaporative Power of the Air

(1) Livingstone Atmometers

The direct measurement of factors which influence plant transpiration, e.g., wind, solar radiation, air temperature and relative humidity, is very difficult, especially in a grassland community. Therefore over the last sixty years ecologists have found it convenient to avoid many of the problems associated with the measurement of these factors by determining the 'evaporative power of the air'. There are several devices for measuring this factor, and they are fully discussed by Livingstone (1935), but it is important to keep in mind that there is usually variation between the different types of atmometers when used under different conditions. When it is further considered that the 'evaporative power of the air' is not an absolute measurement, it is obvious that atmometers are not suitable for highly critical work, and so are often regarded with suspicion by meteorologists.

However to the plant ecologist who is trying to sort out gross differences between the evaporative stress of the air within different plant communities atmometers are a very useful tool, because, as expressed by Daubenmire (1959) 'measurements of the evaporative power of the air are very important because they

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However to the plant ecologist who is trying to sort out gross differences between the evaporative stress of the air within different plant communities atmometers are a very useful tool, because, as expressed by Daubenmire (1959) 'measurements of the evaporative power of the air are very important because they integrate the influences of all the strictly atmospheric factors that promote evapotranspiration from the soil, and most of the factors that affect transpiration." Middleton (1943) in his book "Meteorological Instruments" adopts a view similar to the one given above, namely, that atmometers are a useful instrument provided both their advantages and limitations are recognised.

The relationship of evaporation from Livingstone atmometers to the environmental factors of vapour pressure deficit and wind velocity have been determined by Kucera (1955), and Halkias et at (1955) found that evaporation from Livingstone atmometers and a U.S.A. class A evaporation pan were strongly correlated (r = 0.98), whilst Harrold and Dreibelbis (1958) found a consistent relationship between evaporation as measured from an atmometer and from an evaporation pan. Matheson (1937) demonstrated a very close relationship between the relative day to day readings of a Piche evaporimeter and a Livingstone atmometer.

Livingstone atmometers were used to study the differences in evaporating power of the air in the various stages of succession on sand dunes by Fuller (1911), and have been used in the study of relationships between plant form and microclimate by Cooper (1961). Other examples of studies where atmometers have been used to demonstrate differences in evaporative power between different communities are those of Rice (1960, 1962). The studies of Cooper and Rice are of interest in that they demonstrate the similar relationship of atmometer readings within different communities to the corresponding humidity and wind speed measurements.

Methods

The atmometers, mounted in the manner described and illustrated by Daubenmire (1959), except in that the Livingstone-Thone valves were mounted at the bottom of the uptake tube, were exposed in experiment T6B over the 1961/1962 growing season. The distilled water storage bottles were placed in containers sunk below ground level, as done by other workers, so that the porous cups were approximately eight inches above ground level. Hence the cups were below the main transpiring level of Hyparrhenia leaves and some of the ruderals, were slightly below the corresponding level of Eragrostis leaves and were slightly above the corresponding level of Cynodon and the grasses in the T plot. Plate 10 illustrates the manner in which the cups were mounted, and Plate 11 shows one of the cups in position in the 1957 (E) plot.

Owing to the time taken to get the available cups cleaned, checked and mounted, and to the use of the cups in the washing experiment (Appendix, part three), the full number of cups was not operating until January. Two cups were placed out in the R, E, H and T stands in October, three cups in each stand in November, with two additional cups being exposed during December in clearings of six yards by six yards which were clipped to the one inch level, as shown in Plate 12. Four cups were placed in each of the five stations from January to May, when frost incidence caused the cups to be withdrawn. The usage of four cups in each stand compares favourably with the number used by workers in the references consulted. The atmometers were removed, cleaned and washed at fortnightly intervals, and if the cotton wool of the valves was becoming effected by algal growth it was replaced. The cups were washed in the field at approximately weekly intervals as evidence presented in the Appendix (part three) show that more frequent washing of atmometers is not required.

Readings, made by regular weighing of the atmometer assemblies, were made at intervals of every two or three days over the summer months, lengthening to seven days in autumn. Calibration checks of the atmometers were made throughout the growing season, the later checks being made against two newly purchased and calibrated cups made by the only manufacturer. By means of the coefficients obtained from these calibration checks the corrected figures can be compared with those obtained by all previous users of Livingstone atmometers. Removal of the atmometers for cleaning and calibration checks meant that approximately three days readings were lost every month.

Results

The mean monthly loss of water, expressed as cc per day, from each stand is given in table 7, and the detailed data in table A3 in the Appendix. Figure 4 is a histogram where the readings for the R, E, H and T stands from November to March are given as an average evaporation loss in cc per day.

Discussion

The values for the evaporation losses are of the order to be expected under these conditions. Under more temperate conditions in America Cooper (1961), for example, recorded six monthly averages over the summer period from 8.5 to 13.0 cc per day in various vegetation types, and Fuller (1911) recorded a maximum average loss over summer of 21 cc per day in the most exposed association studied. On the highveld Israelstam (1953) showed that evaporation losses in a ruderal stand were consistently about 80% of those over bare ground. The only figures available for the average evaporation over 24 hours were 54 and 68 cc per day for the ruderal and fallow stages in October, and 29 and 36 cc per day respectively in November. Story (1938) compared the evaporative power in seral vegetation and climax Themeda veld and found the average monthly evaporation over the year ranged from 9.6 to 20.8 cc per day for the veld, and 11.3 to 32.8 cc per day for the seral stage. The yearly evaporation for the veld was 75% of that of the seral stage, but there was considerable variation in this figure from month to month.

TABLE 7

MONTHLY EVAPORATION FROM LIVINGSTONE ATMOMETERS

IN CC PER DAY

Month	Stand				
	R	E	H	T	Cleared
October	47	36	30	46	-
November	23	18	17	26	-
December	22	15	19	21	26
January	24	17	17	23	28
February	22	15	14	23	26
March	22	16	16	24	26
April	19	13	14	22	21
May	18	14	14	20	19
Mean November-March	23	16	16	23	27 x

x = December - March readings

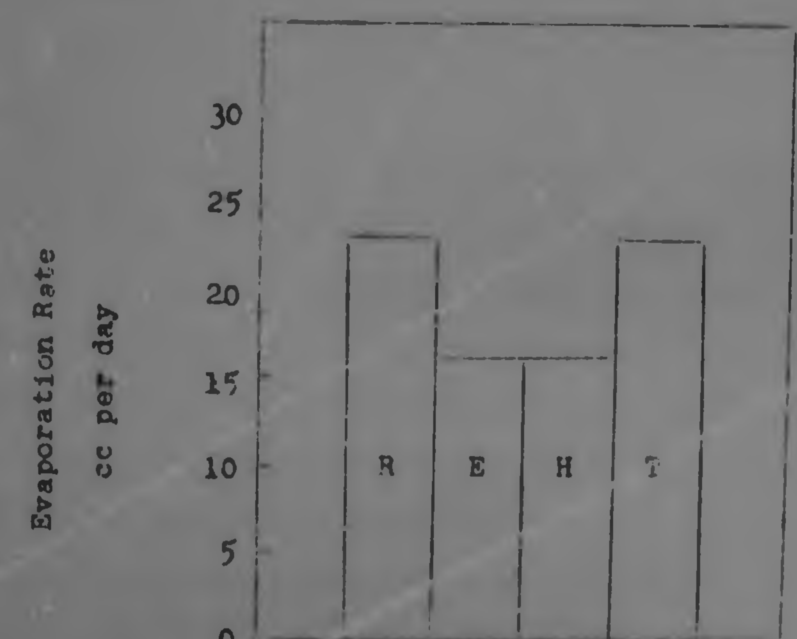


Fig. 4 Average evaporation from November to March for the R, E, H & T stands. Evaporation in cc per day

The evaporation rates recorded in October 1961 were very much higher than those recorded in any of the following months, as was the case in the figures of Israelstam quoted above. This is attributed to the dryness of the atmosphere before the onset of rains and to the windier conditions which prevailed during this period. (The climatic conditions during the 1961/1962 growing season are described in part seven of the Appendix). Evaporation losses did not vary to any appreciable extent over the remainder of the growth period, but fell away slightly with the onset of autumn. The slight lowering of evaporation loss in autumn was in no way a true reflection of the greater falling off in plant growth.

The relationship between the four successional stages can be summarised in the following way, listing stands in terms of decreasing evaporation:-

$$T = R > E = H$$

If the records for the cleared areas are considered with those from the T and R stands it appears that there is a general change in relative values as follows; C.A. > R > T (Dec, Jan.) to C.A. > T > R (Feb, Mar.) to T > C.A. > R (Apr, May). As the main protection in the R plot was comprised of <u>Conyza ambigua</u>, which does not run to head until mid summer, it is understandable that the R > T of December/January changed to T > R thereafter - though the November results do not follow this pattern.

It is however far more difficult to explain the very consistent reversal of C.A. > T to T > C.A. which took place in April. There was a definite lowering of height of the leaf layer in the T plot over this period, so T would be expected to become close to C.A., but this does not explain the change to T > C.A. The only reasonable explanation would appear to be that the slightly different situation of the T plot, which was surrounded by low purple veld, was sufficient at this time to bring about slightly higher evaporation losses than those recorded in the areas cleared among taller vegetation further up the slope.

From consideration of the variation in structure, composition and density of the various seral areas observed, it is suggested that in ungrazed pasture the general pattern of summer evaporation at the eight inch level, in order of decreasing evaporation, would be

Trachypogon $\gtreqless$ Ruderal $\geqslant$ Eragrostis $\geqslant$ Hyparrhenia

However when the small differences between the four stands studied are viewed in relation to the equally small differences observed by Israelstam and Story, and to the much greater range recorded by other workers, e.g. Rice (1960), it is suggested that the differences in aerial evaporative power will not be a causal factor in succession. Reference to the investigations where evaporative power has been recorded in conjunction with wind speed, humidity and air temperature, e.g., Cooper (1961), Rice (1962), indicates that there will be no critical differences in these factors between the four communities studied at this particular height.

Different ratios of evaporative power would be expected in the air layers within one or two inches of the soil surface, and it is possible that these differences may be important in regard to seedling establishment and persistance.

Conclusions

In the R, E, H and T communities investigated, the E and H communities offered the greatest protection against evaporation loss from Livingstone atmometers at eight inches above ground level, and the R and T communities offered less protection. However the differences involved were small, and from consideration of all the factors involved it is suggested that differences between the four stages in evaporative power at this height and presumably in air temperature, humidity, and wind speed, are not causal factors of the highveld secondary succession.

(2) Soil Point Cones

In addition to measuring the evaporative power of the air at eight inches above ground level, it was considered desirable to measure this factor at the immediate ground level in the environment of germinating and establishing seedlings. Livingstone atmometers cannot be operated so close to the ground, and insufficient Piche atmometers were available, and in any case these instruments were difficult to use in dense grass or litter. It was therefore decided to use Soil Point Cones, described by Livingstone (1935), as evaporimeters. The decision to use another [illegible]n of evaporimeter was taken reluctantly, but tests outline[illegible] [illegible]etail in part four of the Appendix demonstrated that evaporati[illegible] [illegible]osses from Piche evaporimeters and points were in a const[illegible] [illegible]io, and hence the ratio between points and Livingstone atmometers would also be in a constant ratio (Matheson, 1937). Plate 13 shows one of the points operating in the R stand. The pre-soaked points were filled with 5 cc of water, evaporation was allowed to take place through the porous band marked 'P' in plate 13, and after a suitable length of time the remaining water was measured and the 'evaporation rate' calculated.

Methods

Measurements of evaporation losses from soil points were made in the R, E, H and T stands. The runs were always carried out during daylight hours, the length of time varying with the evaporation rate. Four points were exposed in each stand, and 50 exposures were made at regular intervals throughout the growing season.

Results

The mean evaporation loss in cc per hour of the readings taken during each month are given in table 8, together with the losses expressed on the basis of the loss in the R stand being 100%.

TABLE 8

MONTHLY ' EVAPORATION ' DATA FROM SOIL POINTS

Month	Mean Monthly Evaporation in cc per hour				Relative evaporation with R as 100.			
	Stand				Stand			
	R	E	H	T	R	E	H	T
October	1.19	.67	.67	.69	100	56	56	58
November	.39	.28	.30	.38	100	72	77	98
December	.48	.32	.31	.34	100	67	65	71
January	.78	.49	.39	.54	100	63	50	69
February	.63	.38	.36	.41	100	66	57	65
March	.58	.39	.32	.39	100	67	55	67
April	.44	.27	.24	.30	100	61	55	68
May	.44	.28	.24	.28	100	64	55	64
Mean	.62	.39	.35	.42	100	63	57	68

Discussion

As only six runs were taken during each month, and as these were taken over different lengths of time, it is not intended that the results for one month should be compared with other months; although the expected overall pattern was obtained with high October readings, low November and December readings, a rise in readings during the dry summer months and a fall in readings with the onset of cooler weather in autumn.

Comparison of the reductions in the E, H and T stands relative to the R readings as 100 shows that there is a reasonably consistent ratio between the various stands over the growing season, with a tendency for the grass stands to have a relatively low loss in the warmest month (October), and a relatively high loss in more humid conditions (November-December). Although the T plot always had the highest relative evaporation of the grass stages, the differences between the three grass stages (with the exception of November) are small compared with the differences between the grass stages and the R stand. With the R reading taken as 100 there is generally a drop of over 30 to the T reading, with a difference of 12 between the grass stands. The E readings are slightly lower than the T readings, with the H stand having the lowest reading of all, again with the exception of November.

Relative exaporation losses at half an inch height can therefore be expressed by R $\gg$ T $>$ E $>$ H. The different relationships of the R and T readings as obtained by points and atmometers is a reflection of the habit of the two stands. The R, E and H stands have a similar falling off in leaf density with height between ½" and 8", but the short dense T stand (plate 8) has a marked change in leaf density between these two heights.

These results indicate that the evaporative stress on an emerging seedling would be the same in any grass stage of reasonable density, regardless of the species composition, but that the environment would be less 'arid' than in sparsely covered conditions such as those in the R stand. When the differences in protection and density between the various representative stands of any one stage are considered, it is suggested that differences in the evaporative power of the air at near ground level could only be effective in controlling succession in the very early stages of colonisation on any area. Even in these situations the differences in evaporative stress are only likely to be of importance under conditions of soil moisture stress.

Conclusions

Allowing for the limitations involved in the use of soil points as atmometers, it has been shown that the evaporation losses at the half inch level within the successional stages studied were in the following order of decreasing evaporation-

$$R > T > E > H$$

It is considered that these differences could only be a minor causal factor of succession in the very early stages of colonisation.

(c) Soil Temperature

Many studies have been made of soil temperatures under various agricultural treatments and under natural communities, and the effect of plants in reducing surface temperatures through shading by leaves or litter is well known. The higher surface soil moisture levels often encountered under closed communities further reduce soil temperature levels as compared with open communities. Richardson (1958), for example, found that the maximum surface temperature attained on the bare surface of pit heaps was 50°C, whereas under two grass communities the corresponding maxima were 26° and 20°C. Differing soil temperatures recorded under different communities can effect plant habitats by their effect on the mineralisation of nitrogen, the survival and germination of seeds (Daubenmire, 1959) and through the different temperature requirements of plant root systems for optimum growth, as demonstrated for *Eragrostis curvula* by Leigh (1960).

The only studies of soil temperatures under highveld communities have been by Israelstam (1953) and Story (1938). Israelstam found that the greatest differences in the mean monthly soil temperatures between a bare fallow soil and a soil under a ruderal community was 4.4°C, although the measurements were only taken over six months from June to November. When the soils were moist, differences were minimised or eliminated. Story showed that the soil temperatures were lower under a climax Themeda veld than in an area of 'old fallow' abandoned for 16 years.

Methods

Some time was spent initially in endeavouring to bring some available soil thermographs into operation, but owing to the erratic functioning of these instruments it was decided they were too unreliable for use. Instead laboratory thermometers with the bulb centre at one inch below ground level were used to measure maximum temperatures at approximately 1400 hours. Laboratory thermometers are still used by many workers for field soil temperature studies, examples being the papers of Hamilton and Bucholtz (1955) and MacHattie and McCormack (1961). Hamid and Shaw (1955) showed that soil temperature measurements made at one to six inches with laboratory thermometers had an average error of 1°F or less.

The thermometers were checked against each other before being placed out, and were checked again on final removal from the stands. Using alcohol thermometers the exposed dye gradually bleached in intense light, but the dye was redistributed by pulling the liquid thread down into the bulb by means of a salt/ice freezing mixture.

Five thermometers were placed in each of the R, E, H and T plots, the top of each thermometer leaning to the south so that neither the thermometers, nor the steel rods used to support them, could shade the ground near the recording bulb. Readings were also taken by approaching from the south so the vegetation above the bulb would not be disturbed in any way. Whenever temperatures were measured descriptive notes of soil moisture, cloud cover and air temperature were taken.

The readings of soil temperature were, on the average, taken on eleven days in each month, so emphasis is laid on comparison between plot readings, and to a much lesser extent in comparison between monthly readings for any one plot.

Results

The mean monthly temperatures from November to May are given in table 9, together with the number of days each month when recordings were taken. Thus the average of 30° for plot R in December is based on a total of 55 readings.

TABLE 9

MEAN MONTHLY MAXIMUM SOIL TEMPERATURES

Month	No. of Readings	Stand			
		R	E	H	T
November 1961	16	32	27	24	25
December "	11	30	26	22	25
January 1962	11	40	30	26	29
February "	10	35	27	25	26
March "	9	27	23	22	23
April "	8	21	18	18	18
May "	10	22	15	15	16
Mean for growing season		30	24	22	23

TABLE 10

GROUPING OF SOIL TEMPERATURES

Groups	No. of Readings	Mean readings for each stand			
		R	E	H	T
Readings with R temp < 30	20	25	23	20	22
" " " 30-35	15	33	27	24	26
" " " > 35	22	39	30	26	28

The data for November to March has been presented in a different form in table 10. The mean daily readings from the R plot have been split into three groups, namely readings less than $30^{\circ}C$, readings between 30° and $35^{\circ}C$ and readings above $35^{\circ}C$. The corresponding readings from the other plots have been grouped according to the readings of the R plot, and the mean temperature calculated within each group for the four stands.

Discussion

The results in table 9 clearly show that the R soil had a higher surface temperature throughout the growing season than the remaining soils, and show the influence of soil moisture to the extent that the dry months of January and February (see fig. 7) had the highest temperatures. From November to March the extreme monthly differences between the grass plots ranged from 1° to $4^{\circ}C$, whereas the differences between the R plot and the grass plot giving the highest temperature (the E plot) ranged from 4° to $10^{\circ}C$.

The variation was greatest in the R and E plots as a result of the differing types of cover present within each plot, and was least in the T plot as a consequence of the uniform cover on this plot, shown in plate 8. The variation in the Eragrostis plot, for example, was caused by one of the measuring sites being in the bare inter-tussock areas of E. curvula, where the temperature was closer to that recorded in the R soil.

The results given in table 10 indicate that under conditions of low R temperature that there was very little difference between the R temperatures and those under the grass stages, but with higher R temperatures the difference between the temperatures under the R plot and the grass plots becomes increasingly large. Reference to the notes made at each recording showed, as would be expected, that soil moisture was by far the most important factor in the recording of low temperatures over the summer months, and it would appear that while the surface soil was moist that differences recorded in maximum soil temperature between a bare and covered plot at one inch depth would only be of the order of 3°C.

These results, considered from the view point of seedling development, suggest that low soil moisture levels are likely to be the most important factor in causing seedling death in the R plot, rather than soil temperature; though an increasing temperature in a drying soil would increase the risk of seedling mortality, but would not be the cause of it. When soils were dry the lower temperatures under grass would be expected.

Laude et al (1952) studied the effect of high soil temperatures on seedling emergence of perennial grasses and found distinct differences between the temperature tolerance of different species, but the temperatures used were higher than would occur in wet or drying soils at Frankenwald, and even in dry soil would only be obtained on bare areas.

As the temperature regime of moist soil under the four stages is similar, it would appear unlikely that succession could be influenced by different stages of succession having a selective effect on seeds with different temperature requirements for germination, or on species with differing root temperature requirements for growth.

It would also appear to be doubtful whether higher soil temperatures would result in an increased rate of mineralisation in the surface layers of the R soil, as it is known (Harmson and van Schreven, 1955) that mineralisation virtually ceases in dry soil.

As there is no experimental evidence concerning the effect of dry heat on dormant seeds, with the exception of Eragrostis curvula (Leigh, 1960), it is impossible to say whether the higher R soil temperatures would influence succession by causing differential death of surface seeds.

Conclusions

Accepting the limitations imposed by nature of the data available it would appear valid to conclude as follows:-

(1) When the surface soils under the R, E, H and T stages were dry during summer the maximum R temperature was about 10°C higher than the maximum temperatures under the grass stages at the one inch depth.

(2) When surface soils were moist R soil temperatures were only about 3°C higher than temperatures under grass.

(3) The faster drying out of the R soil would lead to an increase in maximum soil temperatures before a corresponding increase took place under grass cover.

(4). As a result of (2) it is unlikely that temperature regimes of moist soil will vary enough between the various stages to differentially favour the germination of seeds with different germination requirements, or species with different root temperature requirements.

(5) The higher soil temperatures recorded in a dry or drying soil under bare ground could be a contributing cause of seedling death, but are not likely to be an initiating cause.

(6) When the variation between the temperature measurements within each plot is considered, and also the likely variation between examples of the one seral stage, together with the question of aspect, it appears that as long as a reasonably thick cover is present on any area that the soil temperatures under this cover would not vary greatly with species composition.

(7) No conclusions can be drawn as to whether the higher R soil temperatures would lead to a higher mineralisation rate, or to a greater death of dormant seeds, than occurs under grass stages.

(d) Soil Physical Properties

Analyses of the physical properties of soils from under different vegetation types, in particular from the R, E, H and T plots, were undertaken with the following aims.

a To characterise some soils, especially those of experiment T6B, as at the 1961/1962 season so that future workers would be able to follow changes in physical properties with changes in vegetation.

b To compare the results obtained with those of previous workers who have investigated soil properties in relation to succession.

c To enable a clearer interpretation of the soil moisture results presented in the next section. This, in particular, was the reason for the soil moisture/tension and bulk density measurements.

The soils used in analyses were each from a bulked sample composed of six subsamples.

For convenience the soil physical properties will be classified into two groups, depending on whether the property is a soil moisture/tension relationship or otherwise, the discussion for all properties being found in part (j) of this section.

(1) Soil Moisture/Tension Relationships

i Field capacity

Three small areas were cleared on both the R and T plots, and a low bank was formed around each area. The areas were well flooded with water, and were then covered with plastic and left for 48 hours. After this time three samples were taken from the 1 to 4 inch depth in each area for soil moisture determinations. The average results from the 9 subsamples were 9.3% for the R soil and 12.9% for the T soil with the respective standard errors ($\pm \frac{s}{\sqrt{n}}$ where $s^2 = \frac{1}{n-1}\Sigma(x-\bar{x})^2$) being $\pm$ 0.3% and $\pm$ 0.2%. In common with other data given in this section the results have been graphed in Figure 5 to give the soil moisture characteristics or pF curves for the R and T soils. The field capacity results have been graphed at pF 3.1, the value given by Daubenmire (1947). Piper (1950) gives pF 3.2, but a range of lower values are given by Marshall (1959).

Attempts to use the Bouyoucos technique of determining field capacity, as outlined by Wright (1934), were unsatisfactory. The method, where saturated soil is placed on a Buchner funnel and suction applied, gave very high values with great variation between replicates.

ii Tensions of 0 to 100 cm suction (pF 2)

These measurements were taken on a Haines' apparatus, which consists of a sintered glass plate connected to a burette by tubing. When the apparatus is filled with water it is possible to impose tensions of up to a convenient height of 100cm on the soil sample placed on the sintered glass plate. Duplicate determinations were carried out on the R and T topsoils and subsoils, the results being presented in figure 5, and in table A4 in the Appendix.

iii Filter paper equilibrium method

This method was suggested by Gardner (1937) and the method is further described by Leeper (1952). Although this technique is not used to the same extent as the pressure membrane method, good agreement between the two methods has been obtained by Muirhead (1962) and Warren (1962), especially at higher tension levels. Determinations were carried out on the R and T topsoils, and the results are graphed in figure 5, and are given in table A5 in the Appendix.

iv Vapour pressure measurements

Measurements of soil pF above wilting point are commonly made by this technique, where soil samples are held for several weeks in an atmosphere of known relative humidity, hence of known tension. The relative humidity control was obtained by using different concentrations of sulphuric acid (Wilson, 1921)

Fig 5

BETWEEN PAGE 46 AND PAGE 47 SEE 35MM FICHE in a vacuum dessicator. Measurements in triplicate were made at two pF levels for the R, E, H and T top soils and for the R and T subsoils, known as RS and TS, and are presented in table 11 and are incorporated in figure 5.

TABLE 11

pF RELATIONSHIPS - VAPOUR PRESSURE MEASUREMENTS

Percent Moisture Content in Each Soil

(a) pF 4.2

Replicate	Soil R	E	H	T	RS	TS
1	4.5	5.0	6.1	5.8	4.4	7.1
2	4.1	4.7	6.2	6.2	4.0	7.4
3	4.5	4.4	5.4	5.8	3.9	7.4
Mean	4.4	4.7	5.9	5.9	4.1	7.3

(b) pF 5.0

Replicate	Soil R	E	H	T	RS	TS
1	1.7	1.9	2.8	3.1	1.6	3.4
2	1.5	2.2	3.0	3.0	1.8	3.4
3	1.7	1.7	3.0	3.1	1.7	3.4
Mean	1.6	1.9	2.9	3.1	1.7	3.4

V Wilting point - the sunflower technique

The use of sunflowers as indicators of wilting point is common practice, the technique being described by Piper(1950). The determinations were made in duplicate on the R and T topsoils and subsoils, the values being presented in table 12. In view of the evidence given by Ursic (1961) the moisture contents are graphed in figure 5 at suctions of 22-27 atmospheres (pF 4.4) rather than pF 4.2.

TABLE 12

pF RELATIONSHIPS

Wilting Point as determined by Sunflower

Replicate	Soil R	T	RS	TS
1	2.9	5.6	3.8	4.1
2	3.0	5.5	3.7	5.3
Mean	3.0	5.6	3.8	4.7

vi Air dry moisture content

Air dry moisture contents for the R, E, H and T topsoils and for the R and T subsoils were determined on duplicate samples, and the results are presented in table 13.

TABLE 13

pF RELATIONSHIPS - AIR DRY MOISTURE CONTENT

Percent moisture content in each soil

Replicate	Soil R	E	H	T	RS	TS
1	e.7	0.6	0.7	0.6	0.5	0.8
2	0.3	0.6	0.7	0.8	0.6	0.8
Mean	0.5	0.6	0.7	0.7	0.6	0 8

(2) Other Soil Physical Properties

i Sticky point

Determinations of sticky point were made in triplicate on the R, E, H and T topsoils and in quadruplicate on the R and T subsoils, following the suggestions given by Piper (1950) for obtaining reproduceable measurements of this index in light textured soils. The results are given in table 14.

TABLE 14

STICKY POINT VALUES

Percent moisture content in each soil

Replicate	Soil R	E	H	T	RS	TS
1	13.1	14.3	16.5	19.0	15.7	18.2
2	14.0	14.1	15.5	18.7	15.3	16.1
3	13.2	13.6	15.0	18.9	14.2	21.1
4	-	-	-	-	15.1	16.5
Mean	13.4	14.0	15.7	18.9	15.1	18.0

ii Water stable aggregates

The percentage of water stable aggregates was determined for the 10 blocks of experiment T6B and for the T soil and also for additional soils representing fallow soils (F), seral Eragrostis (E2), Hyparrhenia (H2) and purple veld (T2). The area of soil E2 is described in chapter VI (b) and the areas of soils H2 and T2 in chapter VI (a). The F soil was from a paddock under crop in the 1961/1962 season, but the sampling was made before the crop was sown and was after a winter fallow.

The wet sieving method used has been described in detail by Gillard (1960). The determinations were done in duplicate and are presented in table 15 and in graphical form in figure 6.

TABLE 15

PERCENTAGE WATER STABLE AGGREGATES

Soil	Replicate 1	2	Mean	Soil	Replicate 1	2	Mean
1960(R)	44	37	41	1952	61	66	64
1959	41	43	42	1951(H)	69	71	70
1958	31	40	36	T	83	73	78
1957(E)	50	41	46	F	28	27	28
1956	54	54	54	E2	80	74	77
1955	64	68	66	H2	82	83	83
1954	61	59	60	T2	84	82	83
1953	69	67	68				

iii Mechanical analyses

Mechanical analyses of the soils described in part ii above, and also of the R and T subsoils were carried out by African Explosives and Chemical Industries using the hydrometer technique, and the results are given in table 16.

TABLE 16

MECHANICAL ANALYSIS DATA

Percentage composition of various fractions

Soil	Sand			Silt			Clay		
	Rep.1	Rep.2	Mean	Rep.1	Rep.2	Mean	Rep.1	Rep.2	Mean
1960(R)	76	80	78	18	16	17	6	4	5
1959	78	82	80	16	12	14	6	6	6
1958	78	80	79	14	14	14	8	6	7
1957(E)	78	80	79	14	12	13	6	8	8
1956	74	72	73	16	18	17	10	10	10
1955	76	74	75	14	18	16	10	8	9
1954	80	76	78	12	14	13	8	10	9
1953	72	74	73	18	16	17	10	10	10
1952	70	70	70	22	18	20	8	12	10
1951(H)	72	74	73	18	16	17	10	10	10
T	78	78	78	16	14	15	6	8	7
F	76	80	78	18	12	15	6	8	7
E2	80	84	82	18	12	15	2	4	3
H2	78	76	76	14	17	16	3	[illegible]	8
T2	78	76	76	16	17	17	6	7	7
RS	72	74	73	19	17	18	9	9	9
TS	64	68	66	19	17	18	17	15	16

iv Keen - Raczkowski measurements

Keen - Raczkowski tins of approximately 28cc were used in the manner described by Wright (1934). Determinations were made in triplicate on the R, E, H and T soils of apparent density, moisture retaining capacity, percentage porosity, specific gravity and percentage volume expansion, and the results are summarised in table 17.

The differences between the values of volume expansion, specific gravity and percentage porosity are not considered to be significant.

TABLE 17

SOIL PHYSICAL PROPERTIES AS MEASURED BY THE KEEN - RACZKOWSKI TECHNIQUE

Soil	Apparent Density	Moisture Capacity	Percent Porosity	Specific Gravity	Percent Vol. Expansion
R	1.43 g/cc	29.5%	42.3%	2.48 g/cc	0.6%
E	1.50	28.2	44.0	2.56	1.4
H	1.36	34.7	46.3	2.47	1.9
T	1.26	38.5	46.6	2.38	1.3

v Bulk Density

Preliminary estimates of bulk density were taken by using a core sampler of 620 cc capacity. Determinations were made on the R, E, H and T topsoils with four replicates per stand, and with six replicates on the R and T subsoils. The topsoil was sampled on two occasions to see if there was any variation in bulk density with soil moisture, one sampling being taken after rain with the soil moisture above field capacity, the other sampling being in the range of pF 4.2 to pF 3.7. The bulk densities and mean soil moisture contents of the two samplings are given in table 18.

TABLE 18

BULK DENSITY DETERMINATIONS (gm/cc)

(a) Topsoils

	Soils							
	R		E		H		T	
Date	11/61	2/62	11/61	2/62	11/61	2/62	11/61	2/62
Replicate								
1	1.68	1.72	1.55	1.32	1.43	1.14	1.37	1.35
2	1.41	1.52	1.51	1.49	1.49	1.24	1.44	1.32
3	1.59	1.66	1.55	1.27	1.48	1.34	1.26	1.16
4	1.64	1.63	1.53	1.55	1.32	1.55	1.48	1.42
Mean	1.58	1.63	1.54	1.41	1.43	1.32	1.39	1.31
Moisture %	10.1	4.5	11.4	6.3	15.1	9.1	15.2	8.7

(b) Subsoils

Soil	Replicates 1	2	3	4	5	6	Mean	Soil Moist. %
RS	1.63	1.40	1.60	1.58	1.45	.135	1.50	6.9
TS	1.27	1.57	1.42	1.48	1.42	1.44	1.43	6.6

As a number of 100 cc sampling tubes became available it was decided to make further topsoil density determinations of the R, E, H and T soils and of the F, E2, H2 and T2 soils. 10 tubes were used in each soil, and the mean bulk densities, standard errors for bulk density and mean soil moisture values at sampling are given in table 19

TABLE 19

BULK DENSITY DETERMINATIONS (gm/cc)

10 samples from each soil

Property	Soil							
	R	E	H	T	F	E2	H2	T2
Bulk Density	1.55	1.48	1.42	1.33	1.48	1.40	1.40	1.35
Standard Error	±.02	±.03	±.01	±.03	±.03	±.04	±.03	±.02
Moisture %	12.0	14.1	15.4	16.5	13.4	12.7	15.3	14.8

vi Specific gravity

The specific gravity of the R, E, H and T topsoils and the R and T subsoils was determined by the method described by Wright (1934), a vacuum pump being used for the withdrawal of air from the soil/water suspension. Initially duplicate measurements were made, but where these varied to any extent, a third measurement was taken, all three results being included in the calculation of the mean, the results being tabulated in table 20.

TABLE 20

SPECIFIC GRAVITY DETERMINATIONS
Results in gm /cc

Replicate	Soil					
	R	E	H	T	RS	TS
1	2.56	2.57	2.57	2.48	2.46	2.58
2	2.54	2.56	2.56	2.58	2.61	2.56
3	-	-	-	2.54	2.61	-
Mean	2.55	2.57	2.57	2.53	2.56	2.57

vii Soil porosity

Using the data given in sections v and vi it is possible to calculate the percentage porosity for undisturbed soil cores by the usual formula (Baver, 1956).

$$\text{Percentage pore space} = \left(1 - \frac{\text{apparent specific gravity}}{\text{real specific gravity}}\right) \times 100$$

The bulk density figures used are those given in tables 18b and 19 and the specific gravity of the F, E2, H2, and T2 soils has been taken as 2.55. The porosity results are then as follows:-

	Soils									
	R	E	H	T	F	E2	H2	T2	RS	TS
%Porosity	39	42	45	57	42	45	45	47	41	44

viii Percolation rate

Measurements of soil percolation rate were carried out on the R, E, H and T stands by the method used by Rose-Innes (1939) and other workers at Frankenwald, e.g., Jansen (1959a) and Gillard (1962b). Steel cylinders of 5.5 cm diameter were hammered into the ground with the minimum possible disturbance and 100 cc of water, that is a head of 4.2 cm, were added and the length of time required for the water to soak away recorded. Although this method does not yield the same information as a properly conducted infiltration trial, it has an advantage that in being such a simple technique it is possible to carry out a large number of replications. An almost identical technique is described by Daubenmire (1959).

On the 25th January 1962 twenty measurements were made in each stand and the mean times required for infiltration of 100 cc in each block, together with the longest and shortest times, and the soil moisture at the four inch depth as measured on the previous day, are given in table 21. A similar run, with only five cylinders in each stand was made on soil moistened to above field capacity on the 29th and 30th November 1961, and the results are also given in table 21 in the form described above.

Further rain fell after the soil moisture measurements in part (b) were taken and before the percolation tests were commenced and a few points fell during the trial. The trial had to be ended at 30 hours when one of the five tubes in each grass stand still had traces of free water.

TABLE 21

SOIL PERCOLATION DATA

(a) Dry soil, 20 cylinders in each stand. Times in minutes.

Soil	Soil moisture	Mean time	Shortest time	Longest time
R	5.1%	12.6	4.0	35.0
E	7.3	4.1	1.0	14.0
H	10.9	7.2	1.0	30.0
T	9.9	16.4	3.5	36.5

(b) Wet soil, 5 cylinders in each stand. Times in hours.

Soil	Soil moisture	Mean time	Shortest time	Longest time
R	7.0%	0.6	0.2	1.1
E	11.6	12	0.2	30
H	14.9	9	1.0	30
T	14.7	12	1.1	30

(3) Soil Physical Properties--Discussion

When a soil that has been cropped for some time is abandoned, it would be expected from consideration of the voluminous literature on the effect of pasture leys on soil physical properties that there would be a gradual 'improvement' in these properties. The reasons for expecting these improvements in soils left under grass will not be discussed, but for a full coverage of this subject reference can be made to Baver (1956), in particular to his discussion on the effect of roots on soil aggregation.

The term 'improvement' covers such trends as an increased stability to wetting, lowered bulk density, increased porosity, higher moisture retaining capacity and a higher field capacity, probably associated with a higher wilting point, but nevertheless with an overall increase in available water, and an increase in sticky point. Smaller changes in mechanical analyses results would be expected, but a soil that has been cropped for several years is likely to have a lower colloid content than nearby virgin or grassland soil.

Studies by Billings (1938) on the physical properties of soils under various seral stages through to a pine stand showed an increase in water holding capacity and in the moisture equivalent, and a decrease in bulk density. Rose-Innes (1939) working with the seral soils of the highveld found an increase in colloid content and moisture retaining capacity and a decrease in permeability as succession advanced. However in most cases there was little difference between the grassland soils, but rather between these soils and the presumed 'climax' scrub. Coetzee (1945) examined soils from under Eragrostis, Hyparrhenia and Trachypogon, and found that there was virtually no difference in clay or colloid content, but that the Trachypogon soil had a considerably higher moisture retaining capacity. In Themeda veld Story (1938) found a decrease in permeability from ploughed land through seral vegetation to Themeda veld, and found a higher wilting point and slightly higher water retaining capacity in Themeda soil than in seral soil.

In considering the results obtained in this study the different cropping histories of the soils, as outlined in chapter II, should be considered. It would be expected, for example, that the ' improvements' from the R and E soils through to the H soil would be quite marked. In addition as the R soil is further up the slope it would be expected that this soil would be lighter textured through its profile than the T soil which is lower down the catena. Thus the recorded increases in water stable aggregates, sticky point and porosity, and the decrease in bulk density are all to be expected. There is almost no change in the specific gravity of the soils, which is to be expected from the dominating sand fraction in all samples. The specific gravities are of the expected order as although a value of 2.60 - 2.65 is the average

S.G. for the mineral portion of soils, soil values are slightly lower as a result of the presence of organic matter.

The porosity values are typical of lighter soils, as sandy soils usually have a lower porosity than clays (Baver, 1956), but in view of the pore-size distribution of these sandy soils it is virtually impossible for lack of aeration to be a limiting factor for growth under normal field conditions.

The soils are not likely to restrict root growth by mechanical impedance, with the possible exception of the R soil which has a porosity of 39% compared with the limiting value of 40% suggested by Hidding and van den Berg (1961).

Analyses of the F, E2, H2, and T2 soils showed the same pattern as the T6B soils, with the F soil having the weakest aggregate stability of any of the soils tested and a high bulk density.

There is a change in the percolation rate of the various stands from E > H > R > T under dry conditions, where the order is of decreasing percolation rate, to R > H > E = T for wet conditions. The change in the position of the R soil cannot be explained satisfactorily, but it may be due to the sealing action or the pore-size distribution of the surface crust on the R soil. Lower percolation rates would be expected in wet soil under grass cover as a result of roots blocking soil pores. Sedgley and Barley (1958) found that grass roots in a sandy loam reduced capillary flow, at 30 cm tension, from .026 cm per hour to .005 cm per hour. These results were found to be due to lateral root growth rather than to main adventitious root growth (Barley and Sedgley, 1961). Although the R plot had a faster rate of percolation than the grassland plots in wet soil, visual inspection showed that this plot could have the greatest run-off. This was a result of the large proportion of bare ground on the R plot as compared with the thick litter and mulch on the other plots (chapter II) where water was retained and given opportunity to percolate.

The results of the soil moisture/tension properties of these soils show the expected results in that there is a general tendency for soil moisture levels at any given tension to increase with a longer period of plant revegetation. Thus the T soil has a higher field capacity and wilting point than the R soil, but there is an overall increase in the range of available water.

Baver (1956) claims that "soil structure is the key to soil fertility", because of the importance of the air and water relationships of the soil in determining a soil's fertility. However in these soils that have been investigated it does not appear that the physical relationships would limit soil fertility. None of the differences between the soils appear to be significant enough to favour any particular group of species.

Conclusions

The soils of experiment T6B showed a general 'improvement' in soil physical conditions with a longer period of rest from cultivation and an advance in succession, and analyses from other areas showed a similar trend. It is considered that this improvement in soil physical properties would not be a causal factor in succession, and that it is related to the history of soil cultivation and revegetation rather than to succession of definite species.

(c) Soil Moisture

No overseas studies of soil moisture in relation to secondary succession have been encountered, and the only sampling carried out on the highveld was done by Rose-Innes (1939) and Story (1938). Rose-Innes sampled under various seral stages on one occasion, while Story studied seasonal variations under Themeda veld and seral vegetation. Both workers encountered higher soil moisture levels under higher seral or climax stages, but if the small differences recorded by Story are considered in relation to the wilting points of the soils, there was no significant difference between the available soil moisture regimes. If the soils studied by Rose-Innes showed the same rise in wilting point percentages as the soils studied in section (d), then although there was an increase in soil moisture percentages as succession advanced, there would be little or no increase in available water.

In view of the importance of soil moisture in competition in grasslands a study of the soil moisture regimes under the R, E, H and T stands was carried out in 1961/1962.

Methods

The soil moisture studies were made by using the gypsum block resistance units of the type described by Jansen (1959 b). At the time the blocks were installed it was intended to use the calibration curves given by Jansen, but as the season progressed and soil moisture/tension relationships were obtained, it became obvious that new curves would have to be drawn up as the soil moisture values read off Jansen's curve under dry conditions were far too low. The technique used to derive the new calibration curves is described in part five of the Appendix. Calibration curves were drawn up for the R, E, H and T topsoils and for the R and T subsoils.

The Frankenwald soil is well suited to the use of gypsum blocks as it has a low clay content (section (d) of this chapter), and a negligible salt content (chapter IV).

Five blocks were installed at each of four depths (4", 10", 18", and 30") in each stand, these depths being midpoints over sampling ranges of 7", 7", 10" and 12", to a total depth of 36".

The blocks were selected for uniformity of resistance when saturated, and each block was installed at the bottom of a hole made by a narrow auger.

Temperature measurements for adjustment of the topsoil readings were made by specially installed thermometers (distinct from those installations described in section (c)), but measurements for the subsoil were from a thermograph. The resistance readings could then be corrected when required by use of the nomogram given by Aitchison et at (1951). A reading of 2,000 ohms at 20°C, for example, is equivalent to readings of 1,500 ohms at 10°C and 2,300 ohms at 30°C. If corrections for temperature were not made the maximum resultant error would be about one-tenth of the soil moisture percentage, but in most conditions the error would be equal to or less than one-twentieth of the soil moisture percentage.

Resistance measurements were made at approximately weekly intervals throughout the growing season, with two extra sets of measurements in winter 1962.

Results

The results are presented as soil moisture percentages by weight in table A6 in the Appendix, as 'readily available water' by volume in table A7 in the Appendix and for the R and T soils as 'mean soil moisture tension' (Taylor, 1952b) in table A8 in the Appendix. The results have also been presented in graphical form, the soil moisture percentages by weight being graphed in figure 7, the moisture percentages at pF 4.2 being indicated at the left hand side of the graphs. The 'readily available water' for the four stands and the mean soil moisture tensions for the R and T stands have been plotted in figure 8, where the tension values are graphed in thousands of centimetres of tension. The figure of 15,000 centimetres (or 14.7 bars) can for convenience be considered as 15 atmospheres (one atmosphere equalling 1,034 cm), or 'wilting point'.

The conversion of soil moisture percentage by weight to 'readily available water', or water held at tensions lower than pF 4.2 (as determined by vapour pressure measurements - section (d) of this chapter) involves converting moisture percentages by weight into moisture percentages by volume, using the bulk density data in section (d) and then calculating the water volume held in each sampling zone. The volume of water held at tensions higher than pF 4.2 is calculated in the same manner, and extra water held above this volume can be termed 'readily available water', and this term can be considered as a depth, i.e. so many inches of available water. This manner of expressing soil moisture has been used by many workers in irrigation as it is convenient when used with the normal practice of adding so many inches or centimetres of water, but has also been used by workers in dryland agriculture (e.g., Slatyer, 1955). The value of pF 4.2 is not considered to be a definite limit of available water, but is rather used as a convenient measure of the limit of readily available water; the concept of wilting point being fully discussed by Slatyer (1957).

When the readily available water in a soil has dropped below zero, the graphs in figure 8 could be kept at zero, but they have been carried on so that the extent of the negative value is an indication of the severity of moisture stress.

The pF curves for the R and T soils have been given (figure 5) and these have been used to derive the 'mean soil moisture tension' as defined by Taylor (1952b), which can be considered as the 'integrated soil moisture tension' (Taylor, 1952a, 1952b). The mean soil moisture tension for each sampling between the 29th November and the 29th April for the two stands has been derived by 'integrating' the tension present at the various depths on each occasion, and final mean moisture tensions for the whole growing season, that is integrated for both depth and time has been given in table A8.

BETWEEN PAGE 60 and 61, SEE 35MM FICHE

Calculations were made of evapotranspiration, assuming that rain falls of less than 0.2 cm were ineffective, unless falling before or after a day with a fall of over 0.2 cm, and also assuming a 25% loss of moisture through run-off (mainly in the R plot) or interception (mainly in the grass plots). The estimate for interception was based on the studies of Clark (1940). Evapotranspiration values usually averaged from 0.20 to 0.30 cm per day when moisture was freely available, to 0.15 to 0.20 cm per day when soil moisture was limiting and fell to [illegible] cm per day in autumn. However detailed analysis of evapotranspiration is not warranted with the experimental data available.

Discussion

The soil moisture percentages by weight show that the following relations usually hold for the four depths investigated.

At 4 inches H > T > E > R (H having the highest soil moisture)

8 " H = T > E > R

18 and 30" H = T > E = R

As a general rule there is less variation from week to week as the depth of sampling increases, that is the surface soil is subject to the most violent fluctuations in moisture content. This situation is observed in almost all soil moisture studies (e.g. Harrold and Dreibelbis, 1958). The soil moisture percentages in the surface soil are occasionally higher than the field capacity values given in section (d). There are two possible reasons for this.

1 The field capacity measurements were made after 48 hours free drainage, yet some of the soil moisture measurements were made only 24 hours or less after rain. The moisture content of the bulk density samples, determined gravimetrically not long after rain (table 19), was above 15% for the T and H stands whereas

the field capacity was 12,9% for the T stand.

2 Gypsum blocks are not as sensitive in measuring soil moisture contents at or above field capacity as they are in the range of field capacity to wilting point (Baver, 1956).

Although the graphs of soil moisture percentages indicate clear and consistent differences between the four stands, the graphs of readily available water (figure 8) show that from March to August 1962 the amount of readily available water was much the same for the four stands, and that the R, L and T stands were similar in this regard from November 1961 to March 1962.

The graphs of the R and T mean soil moisture tensions (figure 8) again show a similar relationship, but as they illustrate a different aspect of the soil moisture relationships compared with the corresponding readily available water graphs, it should not be expected to see an exactly parallel relationship between the two sets of graphs. Although the mean soil moisture tensions of the R and T stands were reasonably close throughout the growing season, different depths contributed to a differing extent in the two stands.

Table A6 shows that the R topsoil at 4" exceeded a pF of 4.2 on more occasions than the T topsoil, but that at 18" and 30" the R soil never fell below pF 4.2 whereas the T subsoil exceeded tensions of pF 4.2 at these depths. This emphasises the need for considering moisture percentages in relation to tension, as this table also shows that in all cases except one the soil moisture percentages were higher at 30" in the T subsoil than in the R subsoil, and in all cases except three at the 18" depth.

The relative contributions of topsoils and subsoils in the R and T stands to the readily available water in the two profiles are again brought out in table A7. The fact that the tension in the R subsoil never rose above pF 4.2 does not mean that water was never limiting in this stand, as Doss et al (1962) concluded that under their conditions if the surface soil layers were dry, the supply of water from the deeper soil layers was insufficient to maintain normal transpiration requirements. Reference to tables A6 and A7 show that these comparisons between the R and T soils also apply between the R and E soils, and to a lesser extent the R and H soils.

The high total and available moisture levels under the H stand over the first half of the growing season deserve further consideration, and in this connection it is noted that the readings in the H stand on the 16th January may be somewhat low, and that the true level of available water could be at point A marked on figure 8. There is no doubt however that the H soil was at a lower moisture tension than soils of other stages over the December - March period, as indicated by the superior growth of ruderals in this stand (chapter II). The assumed lower amount of transpiring leaf surface in this stand would have resulted in less demand on soil moisture supplies, and yet there would have been a greater retention of moisture in the H profile than in the R profile, where the amount of transpiring leaf surface is also assumed to be less than in the E and T stands. As the development of plants in the H stand was not checked so much during the dry January - March as was the case in the other stands, they may have 'caught up' with the growth in the other stands resulting in the similar levels of readily available water recorded in all four stands from March to August.

The lower moisture losses from the less vigorous H stand as contrasted with the other more vigorous plots are also in accord with the finding of Liacos (1962). Liacos found that soil moisture losses were higher from a lightly grazed grassland than from either sluggish ungrazed or heavily grazed vegetation.

The lower rate of moisture loss from Hyparrhenia over the summer period could also be linked with the findings of Mitchell and Closs (1958). These authors showed that under high radiation levels moisture losses from tall grass stands were lower than from short grass stands, although under low radiation more water could be lost from the tall grass stands. This change was a result of the heat transfer pattern at the soil surface and within the vegetation.

During January to March notes were taken of the reaction of species to dry conditions, and the purple veld species appeared to be the most severely affected, as would be expected from the available water data (table A7 and figure 8). The annual ruderals in the R, E and H stands were held back by the dry conditions, but to a lesser extent in the H stand. The young Hyparrhenia plants in the R block were more effected than those in the H block, while Paspalum commersonii and Cyperus esculentes, especially the latter, were badly set back. However the overall impression was that under these exceptionally dry conditions (part seven of the Appendix), all species in each area of vegetation reacted similarly to water stress.

Conclusions

In an exceptionally dry year there appeared to be only slight differences in the tolerance of most individual species, as assessed by visual observation, to dry conditions.

Soil moisture measurements in the R, E, H and T stands showed that the H stand had higher levels of readily available water during the first half of the growing season than the other three stands, but all stands had similar available moisture levels over the second half of the growing season and in the winter months. The R topsoil dried out faster and held less water than the topsoils under grass, but the R subsoil was at a lower moisture tension than the subsoils under grass, the H subsoil having the lowest tension of the grass subsoils and the T subsoil the highest.

(f) Summary of chapter III

The main difficulty in studying the physical environment of air and soil in relation to secondary succession is that there is so much variation between the different stands of any one successional stage. And as most old fields are usually in a mixture of two stages, there is no such thing as a 'typical' stand of each stage. This comment, to a lesser extent, even applies to purple veld. The position is further complicated as it is still not certain in which stage several species should be placed (see chapter IX).

The only approaches, therefore, are to study one stand of each stage and to objectively as possible extend the results to cover the stage as a whole, or, preferably, to study several representatives of the one sta[illegible]

The studies of light int[illegible]nd evaporative power of the air at two levels within the [illegible]cted A, E, H and T stands have shown that at the near ground level there was little difference between the three grass stands in these two factors, and that differences were more dependent on plant density than on species composition. This was not the case at higher levels of four and eight inches where the H stand, and to a lesser extent the E stand, were more protected than the T stand as a result of the different life form of the species involved. There were only small differences between the wet and dry surface soil temperatures of the grass stages, and these differences were largely dependent upon plant density, and not on species composition.

The R stand has, as expected, been shown to be more 'arid' in its aerial environment than the grass stages, but the fact that it is so does not mean that the difference is of necessity a causal factor in succession.

The difference between the near ground level environment of the R stand and the grass stands is due to the mulch or litter layer of the latter (see table 1) as well as to differences in species life form. The importance of mulch in altering the the micro-environment of the soil surface has been pointed out by Willard (1952), Moore (1943) and Weaver and Rowland (1952). These authors state that mulch generally results in a higher and less variable moisture content - even though interception would lower the effectiveness of light falls (Clark, 1940), less surface crusting, lower maximum temperatures and lower light intensity levels; conditions which would generally favour seedling establishment.

However mulch in grassland can either be present between actively growing plants which would exploit any additional water held as a result of the mulch, or can be between unhealthy and inactive grasses, such as enclosed and protected grassland, which would not utilise this water to the same extent. Hence mulch would aid seedling establishment more in the second instance than in the first.

It is also reasonably certain that soil physical properties are not a direct causal factor of succession, but the importance of soil moisture is still uncertain. Further soil moisture investigations could well solve some of the problems associated with secondary succession, such as the failure of seedlings to establish in vigorous grassland (Leigh, 1960), but such investigations would have to be more detailed than those carried out in the 1961/1962 season, with more stands being studied with greater replications in each stand. The fluctuations of soil moisture in the 1-2" depth definitely merit investigation, and all measurements, especially those of low moisture content, would have to be related to moisture tension.

Therefore if further investigations of the aerial and physical edaphic factors in succession are contemplated, it is suggested that they be concentrated on light and soil moisture. It is considered that further studies of soil temperature and the evaporative power of the air (hence of humidity, wind and air temperature) are not warranted.

Consideration of the range of readings around the mean values of the environmental properties investigated (i.e. figures 2 and 3), and of the variation in these values with different heights within the stands, and of the variation between different stands of the one successional stage suggests that the aim laid out by Anon (1959), that of simulating different micro-environments by artificial measures, would be extraordinarily difficult or even impossible.

CHAPTER IV

SOIL FERTILITY IN RELATION TO SECONDARY SUCCESSION

Recent studies at Frankenwald on succession have concentrated on the role of soil fertility, with particular reference to available nitrogen. In this review only the soil chemical aspects of soil fertility will be considered, as soil physical properties have been discussed in the previous chapter.

Working on the highveld succession, Stiven (1957) showed that after three weeks incubation nitrate nitrogen production from five soils investigated was 5.11 ppm - fallow (equivalent to the R soil), 2.31 ppm - Cynodon, 1.68 ppm - Eragrostis and 0.35 ppm - Hyparrhenia with no nitrate production from a Trachypogon soil. Soil perfusion studies confirmed that mineralisation was rapid in the fallow soil, progressively lower in the seral grassland soils and very low in the Trachypogon soil. Pots of representative soil were placed out in the open, and the concentration of nitrate in the drainage water was determined over approximately five months, these results being reproduced in figure 9. It should be noted that the order of nitrate loss in the five soils was completely reversed over this period. Stiven attributed the initially low nitrate levels under purple veld to the production of an anti-biotic by Trachypogon spicatus, and showed that extracts of Trachypogon roots and soil inhibited bacterial growth at irregular intervals throughout the year. Two comments can be made on this suggestion.

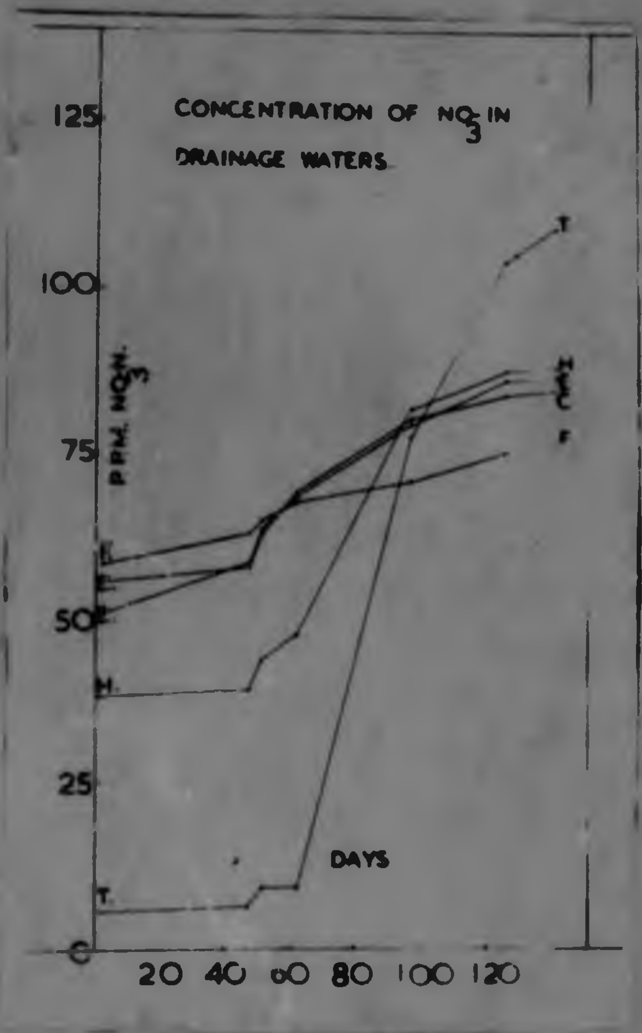


Figure 9. The change in concentration of nitrate nitrogen in drainage water from pots containing soil from fallow, Cynodon, Eragrostis, Hyparrhenia and Trachypogon stages. Results are from Stiven (1957).

Firstly, all literature agrees that low nitrate levels under permanent grassland are the usual condition. Richardson (1938) showed that the free nitrate level under old grassland was very low and was constant throughout the year, and these facts were further emphasised by Harmsen and van Schreven (1955). Simpson (1962) recorded varying nitrate levels under a cool season grassland, but the reasonings given to explain these fluctuations would support the suggestion that the variations beneath a summer rainfall grassland during the growing season would be very low. Even the assumed short term grasslands of Eragrostis, Cynodon and Hyparrhenia investigated by Stiven had progressively reduced nitrate nitrogen levels as the age of the grassland increased.

Some authors have suggested that this lowered mineralisation is caused by excretions from living roots, but these claims have been rejected by most workers (Harmsen and van Schreven, 1955), as the reduction in available nitrogen can be satisfactorily explained on the basis of the content and carbon/nitrogen ratios of the decomposed and undecomposed organic matter in the soil. Barrow (1957), for example, has explained the stimulation of grassland from renovation by reasoning along these lines.

Secondly, it is suggested that there is insufficient evidence for the claimed inhibitory effect of Trachypogon on mineralisation. Apart from one test of fallow soil all investigations of Stiven were either on Trachypogon roots or soil.

Tests carried out on a wide range of plant species at the Michigan Agricultural Experiment Station have shown that almost half the species tested contained one or more constituents that inhibited bacterial growth. It is recognised that the various reports from this station (e.g. Lucas et al, 1955) indicate that grasses generally have not the same level of anti-biotic activity as other plant groups. Even so, it is suggested that before attributing the low mineralisation rate in purple veld to anti-bacterial substances extracted by ether from Trachypogon, a range of species and soils from seral stages and purple veld should have been tested. Even if Trachypogon was shown to be the only species to have anti-bacterial properties, further tests would be needed to show that this activity was responsible for the initially low mineralisation rate of soil removed from purple veld.

The decline in mineralisation rate under the seral grassland soils has already been referred to, and it is assumed that this decline with increasing age of grassland would take place independently of any species change. Even after only one or two years of grass ley without legumes there is usually a decline in available nitrogen, and Theron and Haylett (1953) referred to nitrogen starvation in the second and subsequent years of a grass ley.

The build up of total nitrogen under grassland is assumed to be of the pattern shown in figure 10, taken from Russell (1956), though equilibrium may be attained faster under the warmer conditions of the highveld.

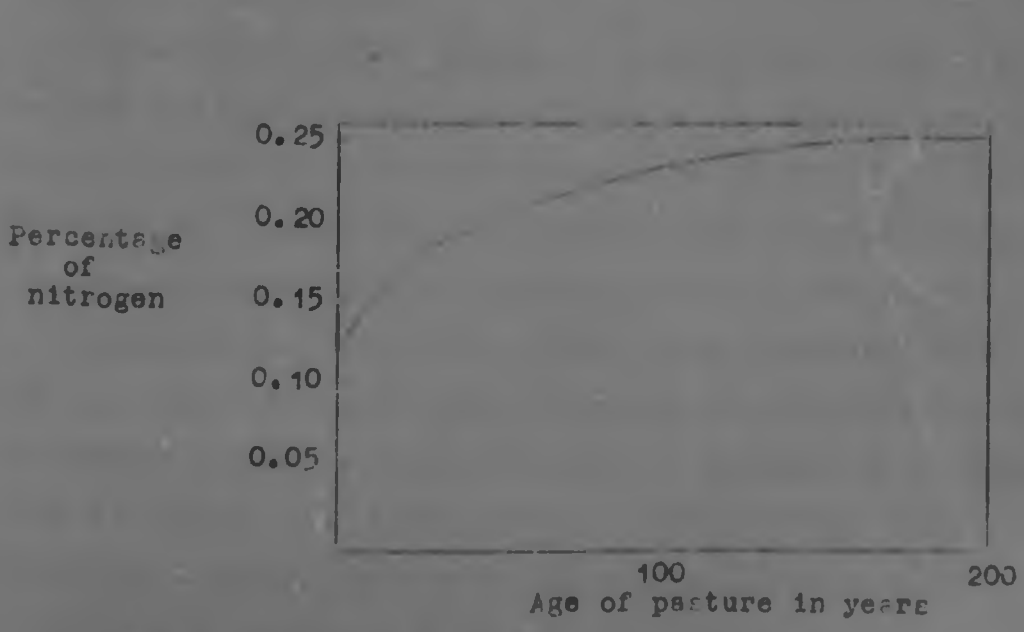


Fig. 10. Build up of nitrogen under grassland (from Russell, 1956)

Harmsen and van Schreven have also referred to the rapid build up of root residues and organic matter in the early stages of a grass ley. Komurov (1961) found that the build up of root material and humus was more rapid under perennial grasses than under the usual early stages of succession. It would therefore be expected that when soils which had been under grass for different lengths of time were removed to pots, that it would take the longest time for soil that had been under permanent grassland to reach a state where nitrogen made available by mineralisation was free to be leached out. However when free nitrogen was produced in this soil higher levels could be expected as more substrate would be available. This would explain the reversal of the mineralisation rates shown in figure 9.

Fallow soils recently abandoned from cropping would be expected to have low available nitrogen levels, but Harmsen and van Schreven have noted that even after many years of cropping that soils can still mineralise appreciable quantities of nitrogen if sufficient humus remains. As the surface of such areas on the highveld is often bare after the removal of the last crop, it is quite likely that the available nitrogen status of those soils in springtime is appreciably higher than it is in grassland soils.

It would therefore appear valid to suggest , with reservations for unpredictable conditions in the first two or so years, that actual fertility in terms of immediately available nitrogen will decline with succession, but potential fertility in terms ofpotentially available nitrogen will increase.

Thus the left hand side of the graph reproduced from Stiven (figure 9) represents the actual fertility at the time of sampling, and the right hand side is approaching the potential fertility. The terms used are those of Roux (1953), but it should be noted that there is no clear division between these two states of fertility. The terms refer to the extreme ends of a gradual fertility change.

Rice et al (1960) have indicated that the general pattern on abandoned fields in Oklahoma is for a build up in phosphorus and total nitrogen to take place with time, and suggestions have been made that the deep rooting forbs of the ruderal stage may be important in bringing back nutrients from the deeper layers of the soil. It is perhaps a doubtful point whether the highveld ruderals would have a greater rooting range than the maize grown during cropping.

Nye and Greenland (1960) have examined in detail the soil fertility aspect of succession in the tropical areas of Africa, but conditions under the plant communities considered bear little relationship to the highveld grasslands.

Stiven (1957) recorded a decrease in exchangeable calcium and an increase in exchangeable magnesium as succession advanced, but little work on nutrient levels in relation to highveld succession has been done apart from that on available nitrogen.

Studies have been made by Roux (1954), Jong and Roux (1955), Lecatsas (1961) and Roux and Warren (personal communication) on the seedling growth of purple veld and seral species in relation to nitrogen concentration of culture solutions. These workers have shown that Eragrostis curvula, Hyparrhenia hirta and Trachypogon spicatus seedlings have a decreasing optimum nitrate requirement for growth, but there is a discrepancy between Lecatsas and Roux in regard to the actual optimum level of nitrate nitrogen for growth of Trachypogon spicatus. Preliminary data given by Jong and Roux indicated that ruderal dicotyledons have a low nitrogen tolerance, equivalent to that of Trachypogon. Yet these species grow in soils with the highest free nitrogen levels (Stiven, 1957).

Results of field experimentation on the effect of soil fertility on succession have been described by Davidson (1961).

Davidson showed that although high nitrogen treatments changed the rate of accession there was little alteration in the course of succession. High nitrogen levels reduced the proportion of dicotyledons in the first year of succession and slowed down the rate of invasion of Hyparrhenia hirta into the primary grass stage. This experiment was, however, laid out on old fallows grassland with only one year of cropping, and it will be suggested later on (chapter IX) that a limited period of cropping could have an effect on the following succession.

Furthermore the results given by Davidson (1962 - table 8) show that the actual yield of Hyparrhenia in a high nitrogen treatment was the same as in an unfertilized control, even though it formed a lower percentage composition of the herbage in the nitrogen treatment.

Leigh (1960) has shown that even under the very high nitrogen treatment of 189 lb of nitrogen per acre that Hyparrhenia was still invading swards of Eragrostis laid out on a well cultivated old fallow soil which previously supported a Hyparrhenia dominant pasture. Under a treatment of 47 lb of nitrogen per acre Hyparrhenia gained very markedly over Eragrostis in a two year period. Although the population of dicotyledonous weeds was low in both treatments, the production from these species was greatest in the high nitrogen treatment (Leigh, 1960, table 122, excluding figures for Phytolacca and Solanum). The Fallows Fertility Experiment described by Davidson was mown twice a year, and this may have favoured the supression of dicotyledons under high nitrogen treatments. Assuming that the vigour of both the dicotyledons and the grasses was increased by nitrogen, mowing would probably favour the grasses owing to the different growth habit of the two groups. Again assuming that the vigour of both Eragrostis and Hyparrhenia were increased by nitrogen, the mowing would probably favour Eragrostis more than Hyparrhenia.

It should also be noted that purple veld species can grow satisfactorily on newly ploughed land. In the denuded quadrats laid out by Stiven (1957) discussed in chapter VI the freshly ploughed area was colonised by purple veld species, and Davidson (1961) mentioned that Trachypogon grew in cultivated soil in nursery plots. Rose-Innes (1939) stated that the growth of Trachypogon was better on freshly ploughed soil than in undisturbed veld. This was noted by the present author (chapter VI). These observations emphasise the hazard of making assumptions from laboratory experiments, such as the statement "Under such conditions (i.e., freshly ploughed virgin veld) Trachypogon apparently cannot grow at all." - Roux (1954). Davidson also points out that Eragrostis and Cynodon are known to grow on the poorest agricultural soils.

Summarising the laboratory and field experiments reviewed it is suggested that as the highveld secondary succession advances that actual fertility decreases, but potential fertility increases. Conditions of available nitrogen have in some cases influenced the rate of succession, but the overall pattern of succession has not been altered by changes in soil fertility far greater than those likely to be encountered in the usual cropped land which is not fertilized after abandonment.

(a) Soil Chemical Analyses.

The topsoils from the ten blocks of experiment T6B, the T, F, E2, H2 and T2 topsoils and the R and T subsoils were analysed for available phosphorus, potassium, calcium and nitrogen, and for organic carbon, percentage total nitrogen, pH and free sodium. Each topsoil sample was composed of six subsamples taken from 0-3 inches before the opening rains, and the subsoils were taken from bulk samples.

All the analyses, apart from those of available nitrogen and one set of pH measurements, were done by African Explosives and Chemical Industries, using standard laboratory techniques. The analyses done by this body were all in duplicate.

Available nitrogen was determined by leaching soil with 0.5M K_2SO_4 brought to pH 1 by sulphuric acid, and then distilling off all inorganic nitrogen as ammonia by the addition of Devarda's alloy. The ammonia was collected in boric acid and standard HCl was titrated into this solution. The rather indefinite endpoint obtained in this titration, using Tashiro's indicator, was the limiting factor in this technique. The soils for the available nitrogen analyses, specially sampled with six subsamples, were dried at 55°C immediately after sampling (see Piper, 1950), and then stored in an air tight container over calcium chloride. Even so comparisons can only be made between the soils sampled on this one occasion, and values can not be compared with results from other samplings.

Results

The full results of the analyses are given in table A9 in the Appendix, while results for the R, E, H and T soils are summarised in table 22.

TABLE 22

ANALYSES OF THE R, E, H AND T SOILS

Property	SOILS R	E	H	T
Available P_2O_5 ppm	20	26	9	8
Avail. potash % K_2O	0.008	0.010	0.010	0.009
Avail. calcium % CaO	0.018	0.017	0.023	0.018
Organic carbon %	0.7	0.9	1.1	1.2
Total nitrogen %	0.053	0.059	0.076	0.083
Carbon/Nitrogen ratio	13	15	14	14
Available nitrogen ppm	29	12	11	10
pH (A.E.&C.I.)	5.2	5.5	5.5	5.5
pH (author)	5.0	5.5	5.3	5.4
Sodium % Na_2O	-	-	-	-

Discussion

(1) Available phosphorus

As phosphate had been added at each cropping of the T6B plots there was an expected overall decline in available phosphorus from the 1959 to the 1951 plot, with the more recent 1960 (R) plot being equivalent to the 1956 plot. The F soil, being currently fertilized and cropped, was very high in available phosphorus.

(2) Available potassium

There was little variation between all soils in this property.

(3) Available calcium

There was considerable variation between soils and between duplicate analyses of this property, but there were no consistent trends. The F soil had the highest value, probably as a result of current fertilization.

(4) Available nitrogen

There was an overall fall in available nitrogen in the T6B soils with an increasing period of revegetation, but the results were rather erratic.

(5) Total nitrogen

There was an overall increase in total nitrogen with an increasing period of revegetation of the T6B soils, the increase being depicted graphically in figure 6. The irregularities in the graph are associated with variation between duplicate determinations (table A9), except for the fall from the 1960 to the 1959 plot, which is probably associated with past treatment (chapter II).

(6) Organic carbon

There was an increase in organic carbon in the T6B soils from the R to the T soils, the increase being depicted graphically in figure 6. The RS carbon content was low, as would be expected, but the TS level was surprisingly high.

(7) Carbon/nitrogen ratio

Topsoil values fell between 12:1 and 16:1, 14:1 being the common figure. Buchman and Brady (1960) quote the usual range as being from 8:1 to 15:1. The variation in the ratio bore no relationship to succession or length of time since the last cultivation.

(8) pH

Within experiment T6B there was a slight increase from the 1960 plot to the 1955 plot, with an even smaller fall to the 1951 plot, the changes being illustrated in figure 6. The only interesting difference was the value of 6.2 recorded in the F soil which had been fertilized with urea.

(9) Free sodium

Sodium, expressed as percentage Na_2O, could not be detected in any soil.

Conclusions

1 With an increasing period of revegetation in the T6B plots there was a rise in organic carbon and total nitrogen, but a fall in available nitrogen.

2 There were no significant changes in available calcium, available potassium or pH.

3 Cropped lands fertilized with phosphates showed a fall in available phosphorus as succession took place.

4 The results, together with those of sections (b) to (d) are further discussed in section (e) of this chapter.

(b) Soil Fertility Pot Trial

Pot trials have been used by workers in a wide range of ecological and soil fertility studies (e.g. Moore, 1961; Evans 1960). Of special interest is the standard trial used for soil fertility work in California described by Wagle and Vlamis (1961), where lettuce is the test species.

Methods

The following trial was set up to evaluate the relative fertility of the R, E, H and T soils, with particular reference to nitrogen. As discussed in the preceeding review nitrogen had been suggested as an important factor in controlling the rate, even if not the course, of succession.

Earthenware pots were filled with two kilogrammes of air dry soil, and four pots of each soil type were left untreated, while four were treated with nitrogen at a rate equivalent to four hundredweight of ammonium sulphate per acre. Altogether 32 pots were used, eight from each of the four soil types. The nitrogen was applied as a solution to the surface of the pots and at the same time each pot was sown with 20 lettuce seeds. The surfaces of the pots were then covered with 50 cc of washed river sand, and the pots were placed out in a glass-house and periodically their positions were interchanged.

The germinating lettuce were thinned out to five per pot, and an occasional transplanting from extra sowings carried out as required. The plants were cut at soil level after 10 weeks and were weighed before and after drying at 50°C. During the first six weeks a check was kept of the number of lettuce and dicotyledonous and monocotyledonous 'weed' seedlings emerging.

Checks taken with mercury thermometers showed that the normal daily soil temperatures at the one inch depth were 20-25°C at 0900 hours, 30°C at 1300 hours and 25°C at 1700 hours.

Results

The seedling emergence data, given in table 23, shows that the T soil had the lowest viable seed content of the four soils. There was no significant effect of nitrogen on the emergence of monocotyledons, but nitrogen caused a 50% reduction in the emergence of lettuce seedlings, and a 75% reduction in the emergence of dicotyledons. The greater reductions with dicotyledons would be expected from the results of Jong and Roux (1955). The reduction of germination which occurs when fertilizer is placed in contact with seed is ell known (as in abstracts in Anon, 1962)

TABLE 23

SEEDLING COUNTS: EACH FIGURE A MEAN OF FOUR POTS

Soil	Lettuce		Monocots		Dicots	
	Untreat.	Nitro.	Untreat.	Nitro.	Untreat.	Nitro.
R	15	4	17	15	17	5
E	7	4	17	18	16	4
H	10	6	25	24	18	7
T	15	8	9	6	7	1
Mean	12	6	17	16	15	4

('t' tests showed that differences between treated and untreated pots of each soil were all insignificant for monocot seedlings, were significant for the four soils to < 0.01 for dicot sedlings, and in the case of lettuce seedlings were significant to < 0.05 for all but the E soil.)

The treatment yields in grammes are given in table A10 in the Appendix, but the results are summarised in table 24, where the oven dry yield of each treatment is expressed as relative fertility in terms of the untreated R soil as 100.

TABLE 24

RELATIVE FERTILITY OF THE R, E, H AND T SOILS - LETTUCE TRIAL

(R untreated as 100)

	Soil			
	R	E	H	T
Untreated	100	72	43	26
With nitrogen	21	21	41	27

Discussion

Table 24 shows there was a fairly consistent falling off in fertility from the R to the T soil, and there was also a corresponding falling off in leaf colour from a healthy green in the R soil to a pale yellow green for the T soil. The growth of lettuce in the treated soil was very poor - the plants only started to come away before harvesting.

Analysis of variance showed the differences between the oven dry weight production from the four untreated soils were significant at the 0.05 level, whereas differences between the the nitrogen treated soils were not significant.

It was asumed that the low production of the treated soils was due to the nitrogen being applied as a solution to the soil surface in the immediate vicinity of the germinating seeds and extending root systems.

The conclusions from this experiment are incorporated in section (e).

(c) Further Pot Trial

Methods

In order to clarify the results obtained in the lettuce trial and to verify the hypothesis used to explain the poorer growth in soils treated with nitrogen, further investigations were carried out on the pots used in the previous experiment.

The pots were re-sown to maize, but owing to uneven establishment the first two sowings had to be abandoned. An even establishment of three seedlings per pot was obtained with the third sowing, and the plants were harvested at six weeks and weighed before and after oven drying at 50°C.

Results

The harvest results are given in table 25, again with the R untreated soil as 100, and the actual weights are given in table A10 in the Appendix. It was also found that the dried stems ranged from 28 to 31% of the total dry plant weight for the untreated soils and from 22 to 26% for the treated soils.

TABLE 25

RELATIVE FERTILITY OF THE R, E, H AND T SOILS - MAIZE TRIAL

(R untreated as 100)

	Soil			
	R	E	H	T
Untreated	100	75	80	67
With nitrogen	110	117	111	113

Discussion

The results show that there is little difference in fertility between the nitrogen treated soils, and that in the untreated soils there is still the same trend as in the lettuce trial, though differences between the soils were smaller and no longer significant. This would be expected as the mineralization of soil organic matter that had taken place since the soils were placed out would have favoured the build up of available nitrogen in the grassland soils. Also more nitrogen would have been removed from the R and E soils by the lettuce experiment, though the amount would be small, the total loss from the ruderal pots being about 0.22 gm of nitrogen (assuming 20% protein of 16% nitrogen). It is also unlikely that maize would give the same results as lettuce even under identical conditions.

In the nitrogen treated soils deficiency symptoms of potassium appeared and this could have limited yield. The addition of nitrogen was also found to increase the proportion of leaves to stem of the maize plants.

The conclusions from this experiment are incorporated in section (c).

(d) Seedling Growth Trial

In a further study to evaluate the role of soil fertility in succession, representative seedlings from each of the R, E, H and T stands were grown in soils from these stages.

Methods

16 small earthenware pots were filled with 500 gm of air dry soil from each of the R, E, H and T stages, giving a total of 64 pots for the trial. Four pots of each soil type were planted with germinated seeds of *Tagetes minuta*, four with *Eragrostis curvula*, four with *Hyparrhenia hirta* and four with *Trachypogon spicatus*. It is recognised that these available pots used for this trial were rather small, but it is considered that they were of adequate size for a study of seedling growth.

As the seed samples of Hyparrhenia and Trachypogon had a very low germination level, transplanted germinated seeds were used for the four species, three seedlings being planted out in each pot in the form of an equilateral triangle. Seed from several sources of Hyparrhenia had to be used, and one source proved to be of a lower and 'stumpier' strain.

The pots were placed out for several weeks prior to transplanting the seedlings, and were watered lightly to germinate seeds present in the surface soil, as otherwise excessive weed germination would have made operation of the trial very difficult. The watering doubtlessly led to some mineralisation and release of nitrogen, but there would have been a much greater upset in soil fertility if sterilisation had been used to kill seeds. A count was kept of the germinating seedlings removed, and the results of these counts are presented and discussed in chapter VI(c). After six weeks from transplanting seedling heights were measured and then fresh and oven dry (50°C) weights.

Results

The oven dry weights are presented in table 26, the values being referred to the growth of Tagetes in the R soil as 100.

The actual fresh weight, dry weight, percentage dry matter and height data are given in table All in the Appendix.

TABLE 26

SOIL FERTILITY AND SEEDLING GROWTH

(T. minuta in the R soil as 100, based on O.D. weights)

Soil	Species				'Mean'
	T. minuta	E. curvula	H. hirta	T. spicatus	
R	100	109	84	44	84
E	56	101	85	43	71
H	53	30	71	23	44
T	38	43	30	20	33
'Mean'	62	71	68	33	58

Analysis of variance of the actual oven dry weights showed that differences between the plant species were significant at the 0.05 level, differences between soils just failing to attain this level.

Discussion

Tagetes and Trachypogon showed a consistent decline in bulk production from the R soil to the T soil, as shown in the lettuce trial. The only change in this order for the Hyparrhenia seedlings was between the R and E soils, and this was due to a larger number of the shorter, stumpier and slower growing strain being used in the R soil pots. The presence of this strain was responsible for the somewhat erratic height data for Hyparrhenia. There was also a decline in the production of Eragrostis from the R to the T soil, with the exception of a very low production in the H soil. Two of the four pots of Eragrostis in this soil gave very poor growth, and no explanation can be offered for this. The poor growth in this species/soil combination was responsible for the differences between the soils failing to attain the 0.05 level of significance.

In comparing the growth of the four species it is most noticeable that Trachypogon was slower growing in all soils.

The seedling development of this species is rapid during the actual period of emergence, but subsequently is very slow.

Eragrostis seedlings gave the highest yield in three of the four soils, and could well have given the highest yield in the H soil but for the experimental error discussed above.

This does not necessarily mean that Eragrostis would outyield Tagetes in their first year of growth, although the poor growth of Tagetes in these soils has already been mentioned (Chapter II). The higher yield of Tagetes in the R soil as against the H soil is the opposite of the growth recorded in the field. This further suggests that under field conditions soil moisture was not as limiting in the H soil as it was in the R soil.

The conclusions from this experiment are incorporated in section (c).

(c) Summary of Chapter IV
Soil fertility and secondary succession

Wherever trends of soil fertility in relation to succession are mentioned in this summary, it is with the understanding that the period of time since cropping is the important factor, rather than changes in species composition over that time. The relative importance of these two different concepts can only be determined by examination of a large number of old fields of differing composition and a known history.

The results of chemical analyses of the successional soils indicated that, of the major nutrients, available nitrogen and available phosphorus decreased as succession advanced, though the latter trend at least was dependent upon the fertilizer applied while the land was cropped; on the other hand total nitrogen and organic carbon increased with succession. No trends were observed with exchangeable calcium and potassium.

Thus, as suggested in the earlier review, these results indicate that actual fertility fell as succession advanced, but potential fertility, in terms of potential mineralisation, increased.

The results of the pot trials, described in sections (b) and (c) confirmed these suggestions, with fertility expressed as lettuce yields falling as succession advanced, but with a second trial, using maize, showing the expected smaller differences between soils. The maize trial also suggested that available nitrogen was the limiting deficiency of the actual fertility of the grassland soils.

Seedlings of four species, Tagetes minuta, Eragrostis curvula, Hyparrhenia hirta and Trachypogon spicatus were grown in R, E, H and T soil, and there was again a general decline in growth for all species as the soil came from a more advanced stage. Jong and Roux (1955) showed that these species had markedly different tolerances of nitrogen, yet they gave the same reaction to these soils of varying fertility. Eragrostis gave the highest bulk production of the four species tested in three of the four soils, and Trachypogon had the lowest yield in each soil type.

Conclusions

The results presented above and the review of literature suggest that for succession on the highveld sandy soils:-

(1) As succession advances actual fertility will usually decline, but potential fertility will increase.

(2) Under unfertilized conditions the normal range of soil fertility will not markedly influence succession and even under fertilized conditions the rate, rather than the course of succession, will be influenced.

CHAPTER V

THE PRODUCTION OF GERMINATION INHIBITORS

The presence of an anti-bacterial substance in Trachypogon spicatus was demonstrated by Slinger (1953), and Roux (1953) inhibited seed germination with leachates from Trachypogon plants grown in sand with nutrient solution. Stiven (1957) found that ether extracts of Trachypogon roots and soils clearly inhibited bacterial growth at irregular intervals throughout a year of testing and that some extracts also inhibited seed germination. On one occasion an extract from the 'F' soil (equivalent to the R soil) was found to possess no anti-bacterial properties, but apart from this test extracts were only prepared from Trachypogon roots and soil. The lower number of germinating seedlings from purple veld soil was also advanced as additional evidence for the production of germination inhibitors by Trachypogon.

There is still a great divergence of views about the importance of possible germination or growth inhibitors produced by higher plants, these substances being termed 'kolines' by Grummer and Beyer (1960). This divergence is well illustrated by a comparison of the recent reviews of Woods (1960) and Garb (1961). Woods adopts a cautious outlook and states that although many claims have been made about the role of germination and growth inhibitors, there are few substantiated cases of their ecological effectiveness that can be cited. Garb is much less restrained and states "differential plant growth inhibitors appear to play a substantial role in many botanical relationships." Much of his evidence is indirect, particularly when such occurences as monospecific stands, growth patterns around trees and reduction of crop yield by weeds are produced as 'proof' of the effectiveness of inhibitors.

Bonner (1950) had previously stated that "the alleged existence of plant toxic substances would seem to be somewhat better supported than it has been in the past." Bonner further commented that complete evidence to show that toxic substances were effective under normal or field conditions was available only in respect to <u>Artemesia absinthium</u> and <u>Encelia farinosa</u>.

The methods that have usually been employed in the laboratory to test for inhibitors involve soaking chopped up dried or living plant tissue, and seeing if the resultant extract effects seedling grown in culture solutions. As evidence has been produced by Cannon et al (1962) to show that extracts produced from macerated plant material are not comparable with extracts from intact material, it appears to be preferable to use the latter. If the interest is in germination inhibitors the extracts are generally used to moisten filter paper on which test seeds are germinated (Evenari, 1949). Leachates from plants grown in pots have also been used to test whether these plants excrete germination inhibitors. However as Grummer and Beyer (1960) have pointed out, there is very little evidence to show how effective these reactions obtained in the laboratory are under field conditions, and they further comment that many of the interactions between plants that can be demonstrated in petri dishes disappear when the experiments are carried out in soil. Cannon et al (1962) and Harper (1961) have also emphasised the need for great care in the interpretation of laboratory experiments on inhibitors.

The studies of Lawrence and Kilcher (1962) show that many common plantsproduce germination inhibitors under laboratory conditions. These authors extracted one part of dried plant material with 10 parts of water and used the extract to germinate seeds placed on sand. Out of eleven plant species tested six had a pronounced effect, including *Agropyron repens* (discussed further below), lucerne (*Medicago sativa*), dandelion (*Taraxacum officinale*) and *Sorghum almum*. An extract effective against seeds of one species was generally effective against seeds of all species. The authors stated that this was only a screening technique and was in no way proof of the ecological effectiveness of inhibitors.

Two of the species subject to detailed laboratory and field studies in connection with germination and growth inhibitors will be briefly discussed. Chopped roots and rhizomes of *Agropyron repens* when incubated with soil produce substances toxic to seedlings, and it was suspected that this species was ecologically favoured by these inhibitors. However further tests by Welbank (1961) showed that similarly prepared extracts from Italian Ryegrass (*Lolium multiflorum*) and lucerne (*Medicago sativa*) had a similar retarding effect on the growth of radicles of rape seedlings, although they did not have the same effect on hypocotyl growth. Welbank stated "Evidently the production of toxic substances by decay is far from being a specific property of Agropyron rhizomes and roots...". Welbank (1960) also germinated test seeds on top of Agropyron roots removed from culture solutions and found that germination was not inhibited, and so cast further doubt on the importance of germination or growth inhibitors as factors in the competitive power of *Agropyron repens*.

The closely investigated case of *Encelia farinosa*, mentioned by Bonner (1950) as being one of the two well documented cases of inhibition, illustrates the caution that is required when investigating inhibitors. Field studies on the shrubs of the Mojave desert had shown that no shrub dependent herbs grew under *Encelia farinosa* although they grew under *Franseria dumosa*. This lead to the suggestion that Encelia produced germination or growth inhibitors, and Gray and Bonner

(1948a) found that extracts from Encelia leaves killed tomato seedlings grown in water culture. They also (1948b) identified the substance responsible, synthesised it, and found that the synthesised compound had the same effect as the original extract on tomato seedlings. However, Muller (1953) showed that leaves of _Franseria dumosa_ extracted in the same way were equally toxic to tomato seedlings, and Muller and Muller and Muller (1956) showed that this was the case for anotherspecies of bush which had herbs growing underneath.

These examples of Agropyron and Encelia clearly show that the presence of an inhibitor 'in vitro' does not mean that this substance is automatically effective 'in vivo', and also emphasise the need for testing a series of plants, as well as the plant suspected of producing the inhibitors. Grummer (1961) has summarised the available data for these and three other species which have been intensively studied, and results in all cases do not allow a definite statement that inhibitor production from these species plays a dominant role in their relationships with surrounding plants.

However recent work by Martin and Rademacher (1960) and Grummer and Beyer (1960) has shown that in laboratory conditions interactions between species can be obtained where competition for light, water and nutrients has been avoided, and where the experimental techniques used have avoided many of the usual pitfalls.

There is also considerable disagreement about the mode of action of many of the 'inhibitors' demonstrated in the laboratory. Evenari (1949) states that osmotic pressure and pH do not explain most of the inhibitions recorded, but detailed investigations by Duym et al (1947) on the inhibiting action of an extract from seedballs of _Beta vulgaris_ showed that the osmotic effect of inorganic components was mainly responsible for the inhibition produced, and any action of specific inhibitory substances was only slight and secondary. Miller (1962) showed that extracts of cattle dung, poultry manure and lucerne/grass hay reduced germination and growth, and concluded that salt content of extracts was the main inhibiting factor.

This review illustrates the need for great care in making claims for the ecological effectiveness of germination or growth inhibitors. It also appears that any project on inhibition is best handled by having an initial screening stage in which the species concerned and its associated species are periodically tested for production of inhibitors. If the species being studied does show distinctive inhibitory properties, then a detailed study is required to determine the effectiveness of these properties under field conditions.

(a) Regular Sampling Trials

Methods

The following screening technique was used over the 1961/1962 growing season to see if extracts from *Trachypogon spicatus* had a different effect upon seed germination than extracts of other associated species.

The activity of the extracts prepared was tested by determining their effect on the amount and rate of germination of *Eragrostis curvula* seed. *Eragrostis curvula* was selected because it was a common seral perennial grass and as its germination had been 'inhibited' in purple veld soil in the pot trial of Stiven (1957), mentioned further in chapter VI(c). Also all the testing could be carried out using one sufficiently large 1958 seed sample of high viability.

Extracts were obtained from unmacerated roots of *Eragrostis curvula*, *Hyparrhenia hirta* and *Trachypogon spicatus*, and from the surface (0-2") soil near the butts of these species, and also from soil in the R stand, at intervals of four to five weeks. Six plants of each species were removed and their roots were cut off and bulked. Soil samples from each of these sites, and from six sites in the R stand, were bulked into one sample of each type. The sampling of grasses was done near the E, H, and T plots, but was not done in the plots owing to the environmental studies being carried out.

Soil extracts were prepared by soaking one part of soil in five parts of deionized water, the soil weight being on an oven dry basis as calculated from the soil moisture content determined on a seperate sample. For the first two of the routine tests root extracts were prepared by soaking one part of fresh roots in twenty of water, but tests three to eight had in addition a seperate and more concentrated extract of one part roots to five of water. In addition to these routine determinations some extra extrac[illegible] were prepared from purple veld perennial dicots, purple veld [illegible]ves and mulch, roots of purple veld species other than T[illegible]gon, and from corms of <u>Cyperus esculentus</u>.

The extracts were allowed to soak with a very occasional stirring for 24 hours, after which they were filtered through a Whatman's number one paper. This paper allowed some colloidal material to pass through, but this was intentional in case any germination inhibitors present were attached or attracted colloidal particles. If the germination tests were not commenced on the day the extract was prepared, the solutions were stored at 5°C. pH measurements were made of all extracts using a glass electrode.

Each extract was added to four petri dishes each with 50 seeds of Eragrostis on filter paper placed on a thin layer of washed river sand. The control dishes were treated with deionized water. The amount of solution used to wet the sand to near saturation was in the ratio of 1 part of water to 1.7 parts of sand by volume. The dishes were placed out in room conditions of 20 - 25°C, conditions for the last test being slightly below 20°C.

Initially germination counts were made at 48 or 36 hours after the trial commenced to check on any early differences in the germination rates in the various extracts, followed by one intermediate and one final count. However as the advantages of the 'Average Time of Germination' formula became apparent in other investigations, it was decided to make daily counts so this value could be calculated and both the average time of germination and the final germination percentage be used to test for germination inhibitors.

The 'average time of germination' is calculated from the following formula;

$$\text{Average Time} = \frac{\sum gt}{\sum g}$$

't' is the time in days since the beginning of the test, and 'g' is the number of seeds germinating on that one day.

Special Ether Extracts

In view of the inhibitory action on germination of the Trachypogon root extracts prepared by Stiven (1957), extractions were made of the roots and soils used in test eight by a method as close as possible to that of Stiven. Soil and fresh finely ground roots were extracted by soaking them in ether for 24 hours, filtering off the extract, and then taking up water soluble substances in distilled water after allowing the ether to evaporate. The solution was tested in exactly the same manner as described in the above paragraphs.

Results

The final germination percentages for all the samplings are given in table 27, the average times of germination for samples 6, 7, and 8 in table 28 and the pH values of the extracts in table 29.

The soils were sampled in moisture conditions varying from 0.6 to 6.5% for the R soil, 2.0 to 10.2% for the E soil, 2.0 to 12.6% for the H soil and 2.3 to 12.4% for the T soil.

Differences significant at the 5% level were shown between the germination percentages from solutions in sample 1, sample 3 and in sample 7, and between the average time of germination of the ether extracts of sample 8.

The 48 or 36 hour counts made on samples 1 to 5 were usually within 5% of the final germination percentage, and there is no point in presenting these values.

TABLE 27

THE EFFECT OF ROOT AND SOIL EXTRACTS ON THE GERMINATION PERCENTAGES OF SEED OF ERAGROSTIS CURVULA

Date collected	Sample No. 1 4/9	2 4/10 1961	3 8/11	4 8/12	5 16/1	6 15/2 1962	7 21/3	8 2/5	(ether) 8 2/5
Extract									
Control	86	89	89	88	89	86	90	87	88
R soil	91	92	90	84	84	82	93	87	90
E soil	83	86	89	86	87	93	90	85	92
H soil	84	87	88	86	86	83	88	88	90
T soil	89	89	83	90	88	92	85	87	92
Egu roots 1:20	92	87	89	87	91	89	89	90	88*
Hyph roots 1:20	88	92	89	81	86	86	87	90	87*
Tras roots 1:20	89	88	0	84	88	85	86	88	88*
Egu roots 1:5	-	-	91	90	87	90	84	90	-
Hyph roots 1:5	-	-	90	87	90	84	85	90	-
Tras roots 1:5	-	-	88	85	89	88	89	91	-
Special tests	-	-	-	A88	-	B90 C93	D90	-	-

(A - roots of purple veld dicots, B - green leaves of purple veld grasses, C - corms of _Cyperus esculentos_, D - purple veld mulch)

* The concentration of the ether root extracts was not 1:20, but was equal to the concentrations used by Stiven (1957).

TABLE 28

THE EFFECT OF ROOT AND SOIL EXTRACTS ON THE AVERAGE TIME OF GERMINATION OF SEED OF ERAGROSTIS CURVULA

Average time in days

	Sample no.			
	6	7	8	8(other)
Date collected	15/2	21/3	2/5	2/5/1962
Extract				
Control	2.2	2.0	3.4	3.3
R soil	2.3	2.1	3.5	3.5
E soil	2.2	2.0	3.5	3.5
H soil	2.2	2.0	3.4	3.6
T soil	2.2	2.0	3.5	3.7
Egu roots 1:20	2.1	2.0	3.3	3.4
Hyph roots 1:20	2.2	2.0	3.2	3.4
Tras roots 1:20	2.0	2.0	3.3	3.8
Egu Roots 1:5	2.0	2.1	3.5	-
Hyph roots 1:5	2.1	2.1	3.5	-
Tras roots 1:5	2.1	2.1	3.5	-
D - mulch	-	1.9	-	-
B - veld leaf	2.1	-	-	-
C - corms	2.1	-	-	-

TABLE 29

pH VALUES OF ROOT AND SOIL EXTRACTS

	Sample No.								
	1	2	3	4	5	6	7	8	(other) 8
Date collected	4/9	4/10	8/11 1961	8/12	16/1	15/2 1962	21/3	2/5	2/5
Extract									
Control	8.0	5.5	5.5	6.5	6.5	7.3	N.D.	N.D.	N.D.
R soil	5.5	6.5	6.4	6.8	5.8	7.6	6.3	6.5	6.6
E soil	7.5	7.0	6.0	6.8	6.2	7.5	6.4	6.3	6.1
H soil	7.0	5.5	5.4	6.5	7.0	7.1	6.7	6.6	6.5
T soil	7.0	6.5	7.4	7.1	5.4	7.5	7.0	6.6	6.2
Egu roots 1:20	5.5	7.0	6.9	6.5	5.0	7.6	7.9	7.2	5.8
Hyph roots 1:20	5.5	6.5	6.7	5.6	5.1	7.0	8.3	6.8	3.6
Tras roots 1:20	5.5	6.5	2.2	5.7	4.6	7.1	7.8	6.8	6.7
Egu roots 1:5	-	-	N.D.	6.8	5.5	6.8	8.1	7.7	-
Hyph roots 1:5	-	-	7.6	6.1	5.0	7.3	8.5	7.0	-
Tras roots 1:5	-	-	N.D.	5.6	5.6	6.6	5.0	7.1	-

(N.D. = not determined)

Discussion

The results given above show that there was no worthwhile inhibiting or stimulating effect of any of the extracts on the germination of Eragrostis seed, with the single exception of the Trachypogon spicatus 1:20 root extract of the 8/11/1961. Extra testing and checking of this result were carried out and are detailed in part six of the Appendix, and it is concluded that the inhibiting properties of this extract were in no way a general property of purple veld roots or soil at this time; as illustrated by the failure of the 1:5 Trachypogon root extract to effect germination.

Extracts of purple veld leaves and mulch, and extracts of purple veld grasses other than Trachypogon, the testing of the latter extracts being described in part six of the Appendix, also failed to inhibit the germination of Eragrostis as did the specially prepared ether extracts.

Although four statistically significant differences in germination percentage and average time of germination were obtained these are not considered to be of biological significance, especially when the variation in the results given above are compared with those of workers using a similar technique who did obtain biologically significant results, (e.g. Lawrence and Kilcher, 1962). With the exception of sample 3 the statistical significant differences resulted from where one extract slightly favoured germination compared with the control, whereas another extract reduced germination. Only in one of these three cases of statistical significance was the retarding extract from Trachypogon spicatus.

The pH of the deionized water used varied considerably, but the pH values of all the extracts fell between 5.5 and 8.5 with the exception of the Trachypogon 1:20 root extract of the 8/11/1962 which was 2.2.

Thus use of a screening technique failed to demonstrate the presence of a germination inhibitor in root or soil extracts from representative stages of the high veld secondary succession, and it is therefore suggested that inhibition would not be important in field conditions.

The fact that Trachypogon spicatus is usually only the second or third most important species out of the 10 or so major species in purple veld is a further stumbling block to the acceptance of the inhibition theory. The existence of a monospecific stand is used as evidence for the production of inhibitors (Garb, 1961), yet purple veld is far from being monospecific. It would appear to be necessary to assume that although the inhibitor from Trachypogon is active against seral grasses, it is inactive, or less active, against the other purple veld grasses.

A further problem is provided by the growth of ruderals in purple veld that has been ungrazed or unmown for several years. It would be necessary to assume that the production of the inhibitor ceases under these conditions.

Finally it can be noted that in the lettuce fertility trial described in chapter IV the germination of lettuce seeds was greatest in the T soil, even though the T soil had the lowest germination of buried seeds (table 23).

Conclusions

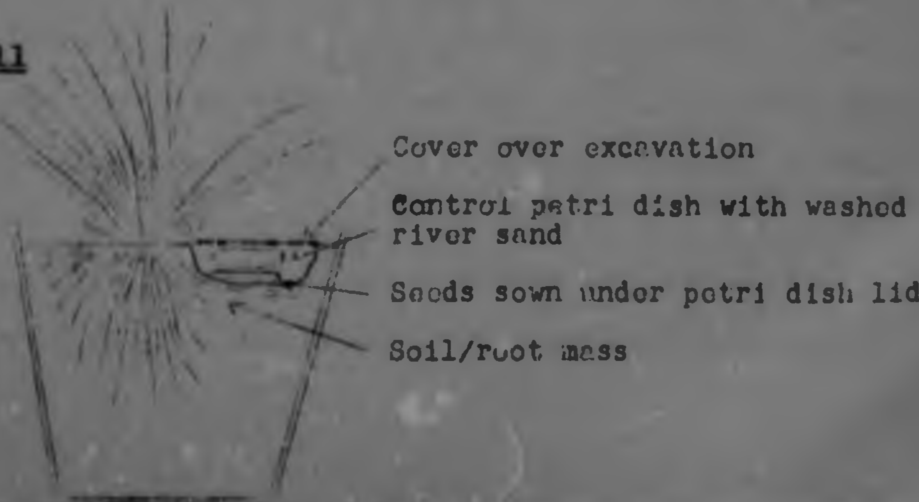
A screening test carried out showed that root and soil extracts from seral and purple veld communities had no effect on the germination of Eragrostis curvula seed. It is therefore suggested that it is unlikely that inhibitors play any appreciable part in determining the course of succession in the field.

(b) Pot Tests

A different technique of testing living roots for the production of germination inhibitors was developed by Welbank (1960). Plants were grown in culture solutions and roots of these plants were then removed from the solution and were placed around the base of petri dishes. The seeds of the test species were then germinated on filter paper placed over the roots.

A similar technique was used to study *Trachypogon spicatus* but the plants were grown in soil. In December 1961 three tussocks of Trachypogon growing at Frankenwald were taken back to the University and were transplanted into purple veld soil in three 12" earthenware pots. The plants were then left for five months, when a section of the surface soil was removed so as to expose as many roots as possible among the soil mass. 100 seeds of *Eragrostis curvula*, of the same seed sample as used in the testing already described, were then sown onto the soil and roots in a circle of 3" diameter, and the soil was moistened and covered by a petri dish lid. A second petri dish containing 100 Eragrostis seeds on moist river sand was placed on top of the lower dish, and the excavation and petri dishes were covered over. Both surfaces were kept moist throughout the experiment. Only one excavation was made in each pot, a diagrammatic representation of each pot being given in fig. 11.

Fig. 11



To avoid the risk of rain getting under the cover, the pots were moved under an unheated glasshouse, but owing to the location of the glasshouse there was little direct sunlight on the pots, and with the low May temperatures the rate of germination of the Eragrostis seed was considerably slower than the rates recorded in the previous section. Daily germination counts were made for the duration of the experiment.

Results

The germination percentage and average time of germination for each pot is given in table 30.

TABLE 30

THE EFFECT OF T. SPICATUS ROOTS ON THE GERMINATION OF E. CURVULA SEED

	Seed in contact with roots		Controls on river sand	
	% germination	Av. time (days)	% germination	Av. time (days)
Replicate 1	82	9.3	75	12.1
" 2	80	10.5	72	12.7
" 3	71	9.7	75	10.5
Mean	78	9.8	74	11.8

Discussion

These results indicate that living Trachypogon roots and their surrounding soil had no inhibiting effect on either the amount or rate of germination of Eragrostis seed under these experimental conditions. There was in fact a slightly higher and faster germination of seed sown in direct contact with the soil/root mass, but such small differences could easily be due to differences between the soil and sand temperatures and moisture tensions.

As the conditions of this experiment approximated field conditions to a much closer extent than most investigations of germination inhibitors, these results support the suggestion already put forward that *Trachypogon spicatus* does not inhibit the germination of Eragrostis seed under such conditions.

Conclusions

Seed of *Eragrostis curvula* sown on a soil/root mass of *Trachypogon spicatus* germinated at a slightly faster rate than did seed on washed river sand. This adds further weight to the suggestion that *Trachypogon spicatus* does not excrete germination inhibitors.

CHAPTER VI

STUDIES OF SUCCESSION AND SOIL SEED CONTENT ON FIELD LANDS

(a) Denuded quadrats

Denuded quadrats involve removing the vegetation from an area and studying the following recolonisation. Two studies of this type carried out in Oklahoma prairie are of particular interest.

Rice and Penfound (1954) have described how an area of prairie, thoroughly ploughed on one occasion, returned to a near climax state by the end of the second season, though this was to some extent due to the presence of perennating parts of the climax grasses. There was an increase in the bulk production of grasses which was attributed to an increase in available nitrogen.

Penfound and Rice (1957) compared the changes in plant composition which took place over five years on an area that was ploughed every year, as compared with an adjoining untouched area. At the end of the first year the climax species were still present on the ploughed area, but secondary species, originally present in very low numbers, now dominated. At the end of the third season climax species were very infrequent and secondary species had given way to ruderal species, which were absent from the original vegetation and were present to a minor degree at the end of the first year. After five years no climax grasses remained, secondary species were of still lower importance, and ruderals were dominant. These changes would appear to be largely due to two parallel chains of events. Firstly there would be a reduction in the available seed and perennating part population of the climax species with each ploughing, and at the same time a rapid build up of seeds of the ruderal species would take place under the once a year ploughing treatment. The secondary species would be intermediate in both trends.

In an unpublished report Gilliland (1939) described the results obtained from six denuded quadrats laid out in purple veld. Two of these quadrats repopulated with mixed annual and perennial species, but for the remaining four it was recorded that they "are remarkable for the absence of any ephemeral population of annuals". The second season charts for these four quadrats referred to were examined and the seedling densities were 7, 15, 54 and 7 seedlings per square metre. Most of these seedlings were grasses, 49 of those in the quadrat with 54 being Heteropogon contortus. These counts can be compared with the densities of 123, 545, 952 and 12 seedlings per square metre for the R, E, H and T stands in August 1961 (chapter II). The word "remarkable" in the quoted comment refers to the fact that the result was unexpected, but does not mean that it contradicted earlier results.

Stiven (1957) laid out denuded quadrats in purple veld with three treatments of denudation, namely, ploughing-discing-harrowing, digging out with forks and scraping of vegetation. The re-appearance of seedlings was slow, but the following were the mean seedling counts after three months for each treatment in an area of 100 sq. yard.

	Monocotyledons	Dicotyledons
Ploughed & harrowed	107	4
Dug up	278	16
Scraped	360	33

The ploughed plots had the least regrowth, possibly as a result of greater burial of seeds, and the lowest proportion of dicotyledons. Not only were the seedling counts very low, being one to four per square yard, but there were very few dicotyledons and most of the grasses were of the purple veld type, notably Brachiaria serrata. Seedling establishment and the proportion of dicotyledons to monocotyledons, are unlikely to be effected by the usual soil fertility ranges.

Stiven assumed that this result bore no relation to the seed content of the soil, and attributed it to the fact "that the subclimax community makes the edaphic habitat unsuitable for the establishment of any other communities in the succession." i.e., the soilwas effected by germination inhibitors.

van Rensburg (unpublished report) has summarised the data obtained from blocks M and U1 laid out in 1934-1935 and 1937 respectively. Block M was laid out on seral grassland with very scattered purple veld species and U1 was laid out on old fallow cultivated for at least one season. Various cultivation and fertilizer treatments were used and untreated control plots were left in both blocks.

Comparison of the results shows that all treatments of block U1 (the pre-cultivated area) had a far greater cover of ruderals in the first year of revegetation than the treatments of block M in their first year. Taking all the ruderal species as listed by Rose-Innes (1939), with the exception of Cyperus esculentes, the ruderal species formed about 2% of the total composition on all treatments of the M block in the first year of revegetation, and from 19% of total composition on the control U1 blocks in their first year to 75% on the ploughed blocks. Thus very low numbers of ruderals were present after one years ploughing of mixed seral grassland (block M) as well as for the case of purple veld (Stiven, 1957)

The cover of Eragrostis/Cynodon on the other hand was greater in block M than in block U1 in the first year of succession, with the exception of a kraal manure treatment in block U1 which had a very heavy growth of Cynodon, greater than that recorded on the fertilizer treatments. This result suggests that additional Cynodon may have germinated from seed in the manure.

Blocks M and N have been used to support the contention that purple veld could replace seral grasses, but although there was an increase in cover of the purple veld species between 1934-35 and 1941 (van Rensburg, unpublished) the percentage increase was the same as that of the other grass stages. However the main point is that 'high' purple veld species (i.e. Trachypogon) appeared in the first season of succession, and it is suggested that the one years cultivation on the old grassland was insufficient to destroy all the seed reserves or perennating parts of these purple veld grasses.

Story (1938) gave photographic evidence to show that an area of completely bare ground can be colonised by Themeda triandra in less than one year, under conditions where seral grasses were absent.

(i) 1961/1962 investigations.

Methods

Two 10 x 10 yard denuded quadrats were marked out in an area of purple veld, and two in an adjacent area of Hyparrhenia hirta about 30 yards away. The Hypharrhenia quadrats were close to a maize field with many ruderals, the nearest quadrat being about 15 yards from the field. Each quadrat was botanically analyzed with 200 point quadrats prior to ploughing.

The soil was too dry to plough before the opening rains, and was only ploughed on the 13th December 1961. On the 19th December the quadrats were thoroughly hoed and levelled out as shown in plate 14. Throughout the rest of the summer occasional chipping had to be made of the regrowth from scattered old tussocks.

Results

The results of point quadrat analyses of the original cover, expressed as percentage basal cover, are given in table 31. These illustrate the gross differences between the plots. A few rare plants of Eragrostis curvula were noted in the purple veld quadrats, and Cynodon dactylon was scattered throughout the Hyparrhenia quadrats. No ruderal dicotyledons were noted among the tussocks at any time during the growing season.

When the regrowth from the old tussocks was being chipped after the initial levelling, it was noted that the most regrowth came from purple veld dicotyledons and Cynodon.

Visual observation throughout the growing season showed that there was virtually no recolonisation of the area in autumn 1962, and the only ruderals present on the quadrats were as follows:-

Hyparrhenia quadrat No. 1.	Nil
" " " 2.	1 Erodium sp., 1 Datura sp., 1 Tagetes minuta
Purple veld quadrat No. 1.	1 Datura sp.
" " " " 2.	5 Erodium sp. (?)

As there was little competition between plants for soil moisture, they were well developed, the one Tagetes plant being bigger than any growing in experiment T6B.

Visual observation at the end of the 1962/1963 season showed that ruderals were from very rare to scattered in the four quadrats. E. curvula was the dominant grass on all the plots, and E. racemosa was common. C. dactylon was common in the Hyparrhenia quadrats, but was scattered to rare in the purple veld quadrats. Trachypogon spicatus was very scattered in the purple veld quadrats, as were tussocks of other purple veld species, but was absent in the Hyparrhenia quadrats, where H. hirta was scattered.

TABLE 31

PERCENTAGE BASAL COVER OF DENUDED QUADRATS

Species	Purple veld quadrats No. 1	Purple veld quadrats No. 2	Hyparrnenia quadrats No. 1	Hyparrnenia quadrats No. 2
Trachypogon spicatus	7.0	4.0	-	-
Tristachya hispida	3.0	8.0	-	-
Elyonurus argenteus	2.5	0.5	-	-
Digitaria trichlaenoides	3.0	-	-	-
Diplachne biflora	4.0	-	-	-
Heteropgon contortus	0.5	-	1.5	-
Misc. purple veld sp.	2.0	2.0	1.5	-
Hyparrhenia hirta	-	-	7.5	9.5
Eragrostis curvula	-	-	-	3.5
Eragrostis racemosa	-	2.0	3.5	1.0
Misc. seral sp.	-	0.5	-	3.0
Total cover	22.0	17.0	14.0	17.0

It was suggested in Chapter II that a number of Hyparrhenia plants must have established in the 1951 or once cropped block in the first year or so of abandonment. The results presented in this section confirm that Hyparrhenia can re-establish on a denuded area, even though there was no period of cropping in this instance.

Conclusions

Denudation of areas under Hyparrhenia hirta and purple veld resulted in very little invasion of ruderals. Colonisation during the first complete season after denudation was mainly by primary grass stage species, originally present in low numbers. Purple veld species regenerated only in purple veld quadrats and H. hirta in Hyparrhenia quadrats.

(ii) Additional Experiment on Denuded Quadrats - 1962/1961

To further determine the importance of the original flora in determining succession on denuded ground it was proposed to clear areas in each of the ruderal, primary grass, secondary grass and purple veld stages, and to sow a different portion of each area with representative seed of the four stages. The actual investigations were carried out by Cain and Tomson (unpublished report) and the final clipping of quadrats was done by Gillard (personal communications).

Areas were ploughed in each of the four stages in early March 1962 and establishment counts of naturally regenerating seedlings were made in mid-April. Seed of the four stages was collected but as a result of the poor germination from H. hirta and T. spicatus disseminules only small amounts of seed were available for sowing in September 1963.

Each cleared area was divided into five plots, one plot being left unsown and the other four plots being sown with B. pilosa and T. minuta, E. curvula and C. dactylon, H. hirta, and purple veld seed (largely T. spicatus) respectively. Each plot of 16 square yards was sown with the same number of seeds, equivalent to E. curvula at one pound per acre.

Results.

The results of the establishment counts, as percent presence in 100 quarter metre quadrats, are given in table 32.

TABLE 32

DENUDED QUADRATS - 1962/1963 - ESTABLISHMENT COUNTS

Percent presence of selected species in 100 ¼ metre quadrats

Species	Stand			
	Ruderal	P. Grass	S. Grass	P. Veld
Tagetes minuta	42	3	1	-
Bidens pilosa	7	-	1	2
Verbena sp.	1	-	-	-
Misc. Dicots	43	12	2	-
Cyperus esculentes	73	12	-	-
Cynodon dactylon	20	11	-	-
P. Veld grasses	-	-	-	2
Misc. monocots	-	1	-	-

Clip quadrats were taken in March 1963 and the results of weighing air dry herbage are given in table 33. The clippings from each plot were sorted into the four seral stages. Among the ruderals production from monocotyledons generally outweighed that from dicotyledons.

TABLE 33

DENUDED QUADRATS - 1962/1963

Clipped quadrat results - values in lbs/morgen

(RS = ruderal stage, PGS = primary grass stage, SGS = secondary grass stage, PV = purple veld)

Sown to:	Ruderal Plots Clipping weights RS	PGS	SGS	PV	Primary Grass Stage Plots Clipping weights RS	PGS	SGS	PV
Ruderals	1780	20	-	-	1840	10	-	-
Erag/Cynodon	700	P	-	-	490	40	-	-
Hyparrhenia	740	110	-	-	950	60	P	-
Trachypogon	690	P	-	P	740	300	-	P
Unsown	1100	[illegible]	-	-	710	[illegible]	-	-

Sown to:	Secondary GrassStage Plots Clipping weights RS	PGS	SGS	PV	Purple Veld Plots Clipping weighhs RS	PGS	PGS	PV
Ruderals	150	50	-	-	340	P	-	P
Erag/Cynodon	270	60	-	P	80	140	-	P
Hyparrhenia	330	P	-	-	80	10	140	10
Trachypogon	150	P	P	P	70	P	-	80
Unsown	130	80	P	-	170	P	60	P

(P indicates present, but below 10 lb/ morgen)

Discussion

The results of the germination counts show a marked fall off in the number of regenerating dicotyledonous seedlings from the ruderal to the primary grass plots, with very low numbers in the secondary grass and purple veld plots. Grasses, apart from C. dactylon, were virtually absent, and the only purple veld grass seedlings were in the purple veld plots.

The results of the clipping studies are rather inconclusive, which is only to be expected with the low numbers of seeds sown and with the small plots used.

There was a fall off in the production of ruderals from the ruderal to the purple veld plots. The production of primary grass species was highest in the primary grass stage plots, and the production of purple veld species was highest in the purple veld plots. With one exception purple veld species did not appear except in plots where they were naturally present or were sown. On the other hand it is difficult to explain the fact that the ruderal species had the highest production of any of the stages in the purple veld plots. This result is quite at variance with the low ruderal content of the denuded quadrats referred to in section (i). However as mentioned previously most of the ruderals in this experiment were monocotyledons.

Assuming that sufficient numbers of viable Hyparrhenia and Trachypogon seed can be collected it is suggested that a repetition of this experiment would be profitable, using larger plots and areas of ground with known history and botanical composition and with at least two areas denuded in each seral stage. To sample the larger plots more reliably frequency counts may be preferable to clipped quadrats.

Conclusions

A factorial experiment is described where areas of different seral stages were cultivated and sown to seed of these stages. The results indicated that there is a different seed content in soil beneath the different stands, but the original components of the vegetation in the older seral stages did not dominate the regenerating vegetation to the expected extent.

Recommendations have been made about the repetition of this experiment.

(b) Field Botanical Analyses

1. Old Cultivation Areas

Three different areas of abandoned cultivation land were botanically analysed by determining species frequency from 40 throws of a quarter-metre quadrat. The areas were selected after examination of old aerial photographs, Frankenwald photos of three different ages being available, and after consultation with the previous farm foreman who had been on the farm for over 50 years. All three sites had been cultivated, cropped and abandoned 20 to 30 years ago and had not been cultivated since, though it is assumed that they have been lightly grazed.

Results

The results of the frequency determinations are given in table 34, and reference can be made to table A1 in the Appendix for the significance limits likely to be obtained with the use of 40 quadrats. Brief descriptive notes on the areas are given below.

Area 1. Originally used for squatter cultivation this area has been abandoned for over 30 years. The area was dominated by *Stoebe vulgaris* and *Eragrostis sp.*, mainly *E. gummiflua*, with *Hyparrhenia hirta* along the old cultivation banks. *Cynodon dactylon* was very rare, and *Tristachya hispida* was not seen at all.

Area 2. There was a lot of bare ground on this area, *Eragrostis sp.* again being dominant with scattered *H. hirta* along low banks and depressions. *C. dactylon* was present as scattered small and stunted shoots. *Trachypogon spicatus* was very rare and no *T. hispida*, *Panicum natalense*, *Elyonurus argenteus* or *Brachiaria serrata* were seen.

Area 3. *S. vulgaris* and *H. hirta* were the dominant species, but Stoebe bushes were smaller than in area 1, and *Eragrostis sp.* were less frequent. Again no *T. hispida*, *E. argenteus* or *P. natalense* were seen. The area had young pine trees growing on it from seed blown from a nearby roadside planting.

It was unfortunate that experiments M and N could not be studied as these blocks had been left for over 20 years since abandonment, but it was decided that as virtually no pegs were left on the area that too much risk would be involved in trying to relocate the experimental plots.

TABLE 34

BOTANICAL ANALYSIS OF OLD CULTIVATION AREAS

Percentage Frequency as determined from 40 quadrats

Stage	Species	Area 1	Area 2	Area 3
Bare Ground	% bare ground (estimated)	10	60	40
Primary Grass Stage	Eragrostis curvula	(73)	90	43
	Eragrostis gummiflua	(-)	13	68
	Eragrostis racemosa	23	65	65
	Eragrostis plana	8	25	10
	Eragrostis sp.	5	-	5
	Perotis indica	-	5	5
	Pogonarthria squarrosa	3	20	3
	Paspalum commersonii	-	3	5
	Aristida congesta	3	18	5
	Cynodon dactylon	3	38	5
	Andropogon eucomus	3	-	-
	Trichoneura grandiglumis	3	-	5
	Monocymbium ceresiiforme	13	-	-
Secondary Grass Stage	Hyparrhenia hirta	10	5	38
	Schizachyrium semiberbe	5	-	-
Purple Veld	Andropogon amplectans	5	-	-
	Themeda triandra	-	3	-
	Brachiaria serrata	5	-	-
	Panicum natalense	3	-	-
	Elyonurus argenteus	8	-	3
	Trachypogon spicatus	5	5	3
	Misc. purple veld grasses	-	5	-
Ruderal dicots	Conyza ambigua	5	-	-
	Bidens schimperi	-	3	-
	Gnaphalium luteo-album	-	3	-
Perennial dicots	Stoebe vulgaris	28	8	30
	Indigofera sp.	3	-	-
	Senecio sp.	10	-	-
	Misc. dicots	10	28	13

Discussion

These results cast considerable doubt upon the concept of purple veld replacing seral stages. Previous evidence for this assumed replacement has been very meagre. The last worker concerned was Crook (1950) who held to the idea of purple veld replacing the seral stages, but was far from decided about the question, commenting that "the Hyparrhenia hirta dominated stage may, however, persist practically unchanged for a very long time, especially when the area is an old fallow".

Regretably there are few areas of old cultivation land with a known history, but high purple veld species show no signs of regaining their former dominance on areas from which they were removed by cultivation until 25 years ago. It is suggested that they will never regain this dominance, a view agreed to by Dr.A. D. Hall (personal communication).

These results also demonstrate that a thick, and persistent Hyparrhenia stage is not an inevitable feature of secondary succession before the proposed final invasion of purple veld. Most of the seral areas observed on Frankenwald and the bankenveld had a mixed vegetation from the various seral stages, sometimes as a mixture of species and sometimes as a mosaic of stages. A similar observation was made by van Rensburg (1942).

Conclusions

Analyses of old abandoned cultivation lands have emphasised that these areas are usually in a mixed state and that succession is not a fixed step by step process. There has been no appreciable invasion by purple veld in land abandoned for 25 to 30 years, and the question is raised as to whether this final invasion does actually take place.

ii An Abandoned Road

Running through Frankenwald is an old dirt road abandoned about 1930 and not disturbed since. In one area the road passes through seral grassland, and 400 yards on through purple veld. In both areas frequency determinations were made with 20 throws of a quarter-metre quadrat on the community established on the old road and on the adjacent community on both sides of the road.

Results and Discussion

The results, given in table 35, show very clearly that the composition of the road vegetation is a refledtion of the composition of the adjacent communities. In view of evidence brought forward in the preceeding subsection it could be assumed that the roadside communities have not changed appreciably since 1930, in which case the differences in the road vegetation in the two areas would be most likely due to the different seed being available for colonisation.

TABLE 35

ANALYSIS OF VEGETATION ON AN OLD ABANDONED ROAD AND THE ADJACENT PASTURE IN TWO AREAS

Percentage frequency as determined from 20 quadrats

(a) Road passing through purple veld

Spedies	Road vegetation	Adjacent vegetation
Primary Grass Stage		
Aristida congesta	4	-
Cynodon dactylon	-	4
Eragrostis curvula	4	-
Eragrostis gummiflua	8	-
Eragrostis racemosa	28	16
Monocymbium ceresiiforme	20	-
Secondary Grass Stage		
Hyparrhenia hirta	4	-
Cymbopogon excavatus	-	4
Purple Veld		
Andropogon sp.	-	4
Heteropogon contortus	44	16
Harpechloa falx	-	16
Panicum natalense	4	-
Brachiaria serrata	12	28
Digitaria tricholaenoides	-	4
Elyonurus argenteus	64	96
Tristachya hispida	8	40
Trachypogon spicatus	100	100
Stoebe vulgaris	12	-

Table 35 (continued)

(b) Road passing through Eragrostis/Hyparrhenia		
Species	Road Vegetation	Adjacent vegetation
Hyparrhenia hirta	28	26
Eragrostis plana	48)	8)
Eragrostis curvula	28) 84	56) 68
Eragrostis gummiflua	8)	4)
Sporobolus pyramidalis	4	-
Cynodon dactylon	20	12
Setaria pallide-fusca	8	-
Tagetes minuta	4	8

iii Purple Veld Ploughed Once

An area of purple veld was accidentally ploughed in 1958 and had not been ploughed since. Species frequency on the ploughed portion and also on the surrounding purple veld was determined from 40 throws of a quarter metre quadrat. Basal cover was determined from 600 point quadrats on each area.

Results and Discussion

TABLE 36

THE EFFECT OF A SINGLE PLOUGHING ON PURPLE VELD

BOTANICAL ANALYSES

Species	Percent Frequency		Percent Basal cover	
	Ploughed	Purple Veld	Ploughed	Purple Veld
Purple veld sp.				
Trachypogon spicatus	10	70	0.8	2.2
Tristachya hispida	8	70	-	3.2
Elyonurus argenteus	10	70	0.3	4.8
Themeda triandra	8	22	-	1.7
Brachiaria serrata	15	43	0.4	1.7
Other P.V. sp.	13	20	1.0	3.4
			2.5	17.0
Seral grasses				
Hyparrhenia hirta	48	18	1.2	-
Eragrostis racemosa	33	78	0.2	3.7
Eragrostis curvula	63	22	4.8	-
Eragrostis plana	40	18	2.3	1.3
Cynodon dactylon	65	5	3.0	-
Other seral grasses	30	3	0.2	0.3
			11.7	5.3
Seral dicots	8	-	-	-
Bare ground/Litter			85.8	77.7

The result of the botanical analyses given in table 36, especially the frequency figures, show that the unploughed area had a small but significant population of seral grasses. The proportion of these grasses was greatly increased by the single ploughing while the basal cover of the purple veld grasses was reduced to 15% of that in the unploughed purple veld. It is suspected that many of the Trachypogon and allied species present on the ploughed veld were old tussocks that had not been killed out by the ploughing. These tussocks were more vigorous than those in the undisturbed veld.

These trends are similar to those recorded by Penfound and Rice (1957) in the first year of their five year ploughing sequence discussed in section (a) of this chapter, namely that after ploughing there was a great increase in the number of seral grasses and a corresponding reduction in the importance of the 'climax' grasses, with a slight invasion of ruderal species.

The case of Eragrostis racemosa deserves special mention. Originally it was intended to classify this species in with purple veld, as was done by Davidson (1961), but subsequently it was found that this species had many properties of a seral grass and it was placed in the primary grass stage, as done by Rose-Innes (1939).

The reproductive capacity, seed weight and seed viability data of this species support the suggestion that it is a seral species, as does its reaction to over-grazing (Gillard, 1962b). The evidence brought forward in the previous subsection shows that it is strongly associated with seral species (table 34), although it is also associated with purple veld (table 35).

In this case a single ploughing resulted in a reduction in the frequency of E. racemosa, and as most of the plants on the ploughed area were seedlings and not plants that survived ploughing, there was a greater reduction in basal cover. Considering the overall properties of this species, it was expected that it would have at least maintained itself in the ploughed area to the extent it was present in the original pasture.

Soil from the ploughed area, as soil E2, was used for certain studies described in chapters III and VI, as a second example of primary grass stage soil. Table 36 shows that E. curvula, E. plana and C. dactylon comprised 71% of the total basal cover of this area. The E2 soil was different from the E soil in that there had never been a ruderal stand on the E2. If such a stand had been present in 1959/1960 traces of it would have been clearly visible in 1961.

Conclusions

One year's ploughing in an area of purple veld with a small proportion of seral species was sufficient to greatly reduce the number of purple veld grasses and to increase the number of seral grasses.

(c) Buried Viable Seeds

Most studies of buried viable seeds have dealt with the relationship of weed seed populations to various cultivation practices, examples being the papers of Budd et al (1954), Roberts (1958) and Warington (1958).

Champness and Morris (1948) studied the population of buried viable seeds in relation to pasture and soil types, and noted that many unimportant pasture components had great numbers of buried viable seeds, whilst some of the dominant species had low seed levels. Guyot (1960) found that fields abandoned for many years still had dormant seeds of cultural adventives present, and that the buried viable seed content of adventive species was a reflection of past as well as present vegetation.

Oosting and Humphreys (1940) followed buried viable seed changes in relation to secondary succession and found that for herbaceous stands the number of germinations from any one age class or stage may be usually correlated with dominance in vegetation. This relationship was only a general one, and there were some examples of species where the buried viable seed pattern had little or no relation to changes in vegetation. However most of the grasses dominant in the later stages had very few or no seeds in soil of the earliest stages, whilst most of the important species of the vegetation and soil seed content of the early stages had few or no seeds in soil from the later stages.

Many of the studies of buried viable seeds have been carried out on soil as sampled in the field, but some investigators (Budd et al, 1954; Warington, 1958) have reduced the soil volume by washing.

For detailed studies it is generally recommended that the soil be kept moist for two years or growing seasons, but almost all workers agree that most germinations occur in the first 'year', Budd et al recording 75% of all germinations in the first year. In many cases the 'year' may be an effective period of less than six months.

The depth of sampling also varies between investigators. Chippendale and Milton (1932) noted that viable seeds were found at 10 - 14" in one soil, but only at 3" in another, and they found that this was due to the activities of earthworms. They suggested that where deep ploughing was not practised seeds would not be washed down by rain to any appreciable extent and would be in the shallower layers of the soil unless earthworms were active. Roberts (1958) sampled to six inches in regularly cultivated soil and Guyot (1960) sampled to four inches on old cultivation soils.

The number of samples taken varies greatly with the worker and the size of samples, and the need for replication has been emphasised by Champness (1949).

Methods

Samples of the R, E, H, T, F, E2, H2 and T2 soils were collected on the 4th October 1961. Twenty-four samples of 0-3" were collected in each soil, and the samples were bulked and thoroughly mixed. Each bulked sample was then divided into two lots, and from each lot four earthenware plates were filled with 500 gm of air dry soil per plate.

The plates were placed in a greenhouse and were kept moist and covered with a glass frame to reduce the risk of seed contamination. Lot A plates were placed out on the 10th October and Lot B plates on the 23rd October. Plates containing sterile sand were among the soil plates to check on possible seed contamination. With space at a premium the plates were very tightly packed and it is likely that isolated cases of splashing of seed may have taken place. This could never have resulted in a mass transfer of seed, but could only result in an appearance of a species in a soil where it would not be expected. As the glasshouse was heated during winter to a minimum of 20°C, conditions favourable to germination (chapter VII) prevailed for over 9 months.

Seedling counts were taken on the 13/11/1961, 20/12/1961, 8/2/1962, 11/4/1962 and 25/7/1962. Seedlings of important grasses were grown in pots to assist identification and specimens of seedlings appearing were 'grouped' and then grown to be identified. However the grouping of the many different seedlings emerging proved to be very difficult, especially for grasses, and in the results only the positive identifications have been kept seperate and the remaining classes have been lumped into one group. If any further work of this type is to be done, it is suggested that the first season be devoted to classification and identification of seedlings before commencing further experiments.

Results

The total number of seedlings of each species or group germinating from both lots, (i.e. 4,000 gm soil) are given in table 37, the results for each individual lot in table A12 in the Appendix and the percentages of seedlings removed at each sampling date in table 38.

TABLE 37

TOTAL SEEDLING NUMBERS PER 4,000 GM OF SOIL

(a) Monocots	Soil							
	R	E	H	T	F	E2	H2	T2
Cyperus esculentes	72	59	8	12	5	-	7	2
Fimbristylis sp.	93	62	55	-	1	4	22	2
Eleusine indica	13	52	-	1	24	-	-	-
Eragrostis curvula	2	12	4	-	-	5	1	-
Cynodon dactylon	3	5	17	6	14	11	10	-
Hyparrhenia hirta	-	-	9	-	-	1	28	2
Trachypogon spicatus	-	-	-	3	-	-	-	4
Other sp.	28	26	51	37	-	43	30	52
Total Monocots	211	216	144	59	44	64	98	72

(b) Dicots	R	E	H	T	F	E2	H2	T2
Acanthospermum xanthoides	59	-	-	-	-	-	-	-
Corrigiola littoralis	10	20	17	-	3	-	-	-
Tagetes minuta	75	4	1	-	9	-	1	-
Gnaphalium luteo-album	9	2	32	4	4	-	1	1
Conyza ambigua	9	2	6	-	16	2	3	1
Portulaca cleracea	-	1	-	-	9	-	1	-
Oldenlandia sp.	17	2	6	-	1	18	2	-
Other dicots	66	9	44	3	3	11	12	3
Total Dicots	245	40	106	7	45	31	20	5
Total all sp.	456	256	250	66	89	95	118	77
Ratio dicots/monocots	1.2	0.2	0.7	0.1	1.0	0.5	0.2	0.1

TABLE 38

PERCENTAGES OF SEEDLINGS IN EACH LOT REMOVED AT EACH COUNT

	Date of count				
	13/11/1961	20/12/1961	8/2/1962	11/4/1962	25/7/1962
Lot A	14	77	5	2	2
Lot B	26	63	6	4	1

Discussion

The overall buried viable seed levels are perhaps slightly lower than the usual values recorded, and this would be expected from the one year germination period. The H soil, for example, can be taken as 55 million buried viable seeds per acre. Brenchley and Warrington (1930) recorded a level of 150 million seeds per acre, and the results of most workers are usually around 50 to 100 million seeds per acre.

The results given in table 38 show that most germinations occured within the first few weeks of placing out, when, unfortunately, identification was more difficult than later on.

The T soil had a much lower seed content than the R, E and H soils; and the T and T2, and to a lesser extent the E2 and H2 soils, had a few seeds of ruderals. Ruderal plants were very sparse in the E2 soil, as shown in section (b) of this chapter, and in section (a) a complete absence of ruderals in the H2 andT2 areas was noted. One unusual feature of the results is thelow content of buried viable dicotyledonous seeds in the E soil, and no adequate explanation can be offered for this.

Reference was made in the preceeding review to the fact that many workers have found that some species with high seed numbers are unimportant pasture components, and this was the case for <u>Fimbristylis sp.</u>, <u>Corrigiola littoralis</u> and <u>Oldenlandia sp</u>. <u>Eleusine indica</u> plants were very rare in the R and E stages, yet there were many seeds of this species present. Plate 16 shows the usual size of an isolated clump of *Fimbristylis sp.* in the R stand.

There is, however, an overall close relationship between the soil seed content and past or present vegetation. Hyparrhenia and Trachypogon seeds, both with very characteristic seedlings, were confined to soils in which they had been growing and seeding. *Portulaca oleracea* was present as plants in the F stand and as seeds in the F soil, but was absent in the R stand and soil. Again *Acanthospermum xanthoides* common in the R stand and soil, was absent from the F stand and soil. One interesting exception is the low count of *Gnaphalium luteo-album* in the E soil, where a viable seed content at least equal to the H soil was expected, which would also have brought the dicotyledon/monocotyledon ratio for this soil to the expected level.

In view of the fact that the T, H2 and T2 stands were all 50 yards or closer to stands of vegetation rich in ruderal species, the low levels of ruderal seeds recorded indicate that seed dissemination may not be as widespread or efficient as previously accepted, although it must still be recognised that there are a small number of ruderal seeds in these grassland communities where ruderal plants are absent.

Conclusions

These results clearly demonstrate that different stands of vegetation have different quantities and types of buried viable seeds even though the stands can be adjacent to each other. The soil seed content of minor pasture components is in many cases not a true reflection of their abundance as plants, but the soil seed content of important pasture species is usually related to their past or present growth in the soil concerned. Grassland soils free from ruderals have a very low buried viable seed population of these species, even though they may be close to cultivation fields where ruderals are growing.

Other Evidence of Seed Populations in Seral Soils

i From previous work

Stiven (1957) gave seedling counts from the pot/leaching trial where various soils were taken within a "few yards" of each other, and were therefore claimed to have a similar seed population. The total counts from seven pots of each soil type are given in table 39, together with individual counts of five selected species.

TABLE 39

SEEDLINGS REMOVED FROM VARIOUS SOIL TYPES - Stiven (1957)

Species	Soil				
	Fallow	Cynodon	Erag.	Hyparr.	Trachy.
Tagetes minuta	11	1	14	2	1
Elcusine indica	23	6	47	-	-
Cynodon dactylon	-	15	17	-	-
Eragrostis sp.	21	9	24	12	-
H. hirta	-	-	-	[illegible]	-
Total all species	108	77	115	46	25

Stiven argued that as all the seed population must have been the same that germination inhibitors were responsible for the low count in the Trachypogon soil, hence, for example, the absence of <u>Eragrostis sp</u>. must have been caused by the inhibitor. Even apart from the low Trachypogon soil count it is still necessary to explain the low and yet characteristic Hyparrhenia soil seed population. In view of the results given in the section above, and of the results of the germination inhibitor investigations (chapter V) it is suggested that the different seedling counts shown in Table 39 are a reflection of different soil seed populations.

ii Evidence from 1961/1962 investigations

In the seedling growth trial described in chapter IV pots of R, E, H and T soil were watered to germinate most of the viable seeds present. The watering was done to destroy viable seeds rather than to establish them, so many more seeds may have germinated, but not emerged. Hence only the gross differences in the total count of emerging seedlings, and in counts of individual species, given in table 40, are of importance. Again as only six samples of soil were bulked for each stand the replication is insufficient for detailed analysis of buried viable seeds.

TABLE 40

SEEDLING COUNTS FROM 8,000 GM. OF SOIL

Species	Soil			
	R	E	H	T
Cyperus esculentes	27	35	10	-
Fimbristylis sp.	33	19	19	-
Eleusine indica	29	48	9	-
Misc. monocots	20	54	37	3
Total monocots	109	156	75	3
Total dicots	42	52	26	4
Total all sp.	157	208	101	7

While the differences between R, E, and H stages given in table 40 cannot be considered to be real differences, the very low seedling numbers of the T soil are again further evidence of a low seed population of this stage, or else of a very potent germination inhibitor which was not present in soil sampled at the same time (chapter V).

The differences recorded in soil seed content in the lettuce fertility trial (section (b), chapter IV) were not so extreme, but the total count for the T soil seedlings was still only 40% of the count for the other three stages.

Conclusions

Indirect evidence from three trials further suggests that buried seed populations under different vegetation types are also different, especially in the case of purple veld soil.

(d) Rooting habits in relation to secondary succession

A review of previous work

Studies on the rooting habit of representative species of the highveld succession have been carried out, with increasing amount of detail, by Murray (1934), Rose-Innes (1939) and Coetzee (1945). The studies have been confined to the study of root bisects, and have not dealt with the weight of roots produced in the various pastures.

A brief summary of the data accumulated is presented for each of the seral stages.

(1) Ruderal Stage

Rose-Innes concluded that the root systems of the plants examined were all of one type, having extensive superficial lateral systems combined with a deep taproot system. Coetzee recorded similar characteristics for Erigeron canadensis.

(2) Primary Grass Stage

Rose-Innes found a greater range of root systems than in the ruderal stage, but on the whole the systems tended to be shallow rooted. However all three workers found that Cynodon dactylon had many roots in the deeper soil levels, as well as an extensive root system in the surface soil. Coetzee excavated Eragrostis chloromelas and concluded that this species could absorb water from 36". So although some primary species such as Aristida congesta and Eragrostis racemosa may be shallow rooted, C. dactylon and E. curvula (though only sub-species chloromelas was investigated) have effective rooting systems over a range of approximately three feet. Burton et al (1954) found that 30 to 35% of C.dactylon roots were below 24", and concluded that this was partially responsible for the drought resistant nature of this species, as a drought susceptable grass under similar conditions had only 6% of roots below this depth.

(2) Secondary Grass Stage

Hyparrhenia hirta was found by both Rose-Innes and Murray to have well developed lateral roots as well as an extensive deeper rooting system.

(3) Purple Veld Stage

Coetzee found that the only species that could absorb water from the extreme surface were *Heteropogon contortus* and *Monocymbium ceresiiforme*, while *Trachypogon spicatus*, *Brachiaria serrata* and *Alloteropsis semialata* were the only deep rooted species. The remaining species were reasonably shallow rooted, especially *Tristachya hispida*. Rose-Innes on the other hand found that all members of this stage investigated had deeper root systems, *Brachiaria serrata* being an exception. The same comment for Brachiaria was made by Murray.

There is certainly a cons[illegible] difference between the findings of Rose-Innes and Coe[illegible] regards the rooting system of purple veld, but this may be due to different sites being investigated, as Coetzee has stressed the importance of soil type in determining root penetration.

From his findings Rose-Innes concluded that as secondary succession advanced towards the grassland climax, the horizontal superficial type of root system gradually gave way to a more deeply penetrating vertical type. However in view of the findings of Coetzee this 'trend' is very much open to doubt, and it would appear from all the investigations that all grass stages have a reasonable absorbing system in both the shallow and deeper layers.

The generalisations made by Rose-Innes as to the effectiveness of rooting systems are at times rather sweeping, as indicated in the following quotation - "It can be seen that the root systems of the ruderals immediately prevent the invasion of deeper rooted plants by their superficiality. All supplies of water percolating down through the soil after rain are likely to be absorbed before they can reach deeply situated roots." The last statement has shown to be false in in the soil moisture studies in chapter III where it is seen that the R subsoil remained at a lower moisture tension than the T subsoil throughout the growing season.

In the case of seedling establishment by invasion it may be assumed from evidence in chapter I that the main significance of the established root system lies in its competing power for soil moisture rather than for soil nutrients. Therefore determinations of soil moisture, which take into account evaporation from the surface, would give more information about the susceptibility of a stand to invasion by seedling establishment than deductions from root bisects.

The soil moisture studies reported in chapter III showed that the surface of the R soil was usually at a higher tension than the surface of the T soil, whereas the reverse held for subsoils. This would support the suggestion that exploitation of the subsoils by roots of ruderals is not as great as in the case of purple veld and other grasses. Doss et al (1962) also found that soil moisture extractions were a good indication of effective rooting depth.

Conclusions

Previous studies of rooting habit in relation to succession have been reviewed, and conflicting results noted in the case of purple veld. It is suggested there may be little difference between the rooting habits of the seral and purple veld grasses, but that ruderals may have less extensive subsoil systems.

The need for caution in the interpretation of root bisects has been emphasised.

CHAPTER VII

PROPERTIES OF SEEDS AND SEEDLINGS

(a) Growth under different light intensities

Studies of the effect of reduced light intensity on Themeda veld were carried out by Story (1938) who placed hessian screens giving different light intensities over seral and climax veld. In the seral veld *Aristida congesta* was killed out under 33% of full sunlight, but *Eragrostis curvula* and *Cynodon dactylon* persisted. Cynodon persisted to some extent under 15% of full sunlight, but was killed out under 9%. In climax veld most of the grasses persisted under 33% full sunlight, although in some cases the form of growth was altered. Cohen (1940) found that mature plants of *Stoebe vulgaris* remained alive in a severely stunted condition at 10% of full sunlight. No other experiments relating light intensity and succession, or light intensity and the growth of mature highveld species have been located.

Lecatsas (1961) investigated the reaction of *Stoebe vulgaris* seedlings to different light intensities and found that optimum growth was obtained at one-eighth normal sunlight. A similar method was used to study the reaction of representative seral and climax species to varying light intensities.

Seedlings grown under a range of decreasing light intensities would be expected to show increasing etiolation, increasing moisture content of tissues and an increasing shoot/root ratio (Daubenmire, 1959). The possible reasons for the earlier decline in root production as against top production have been discussed by Blackman and Wilson (1954).

Methods

Thin plastic containers of 2" diameter and holding approximately 450 gm of soil or sand were placed out in large metal trays of 4' x 4' x 3". The trays were filled with half an inch of water which kept the soil in the cups moist by soaking through holes plugged with paper in the bottom of the cups. Five germinated seeds of the one species were planted out in each container, four of the seedlings being at the corners of a 'square', with the fifth in the centre of the 'square'. Two containers with each species were placed out under light intensities of 100, 40, 20 and 3% full sunlight. Screens of hessian were used to obtain the reduced light intensities, screening being recommended by Daubenmire (1959) as being closer to natural conditions than can be obtained by using artificial light.

The initial experiment was carried out with the following species, Tagetes minuta, Bidens schimperi, Eragrostis curvula, Hyparrhenia hirta, Elyonurus argenteus and Trachypogon spicatus. The seedlings were transplanted out into river sand and a diluted nutrient solution (Meyer and Anderson, 1946 - complete solution) was applied to the water in which the pots were standing. The trays were placed out on the Botany Department roof in late January and were left for 4 weeks. The seedlings were then removed and root and shoot weights and shoot heights were determined for all species.

Following the poor results of the first trial a second trial was commenced in mid March lasting for five weeks. In this trial a sandy loam soil was substituted for the river sand and no nutrient solution was added. The reaction of most of the test species to varying fertility levels had been previously determined (chapter IV) and found to be similar.

Results

The results of both runs were extremely disappointing. The first run was complicated by the fact that just after commencement a few ofthe emerging seedlings in the control containers were removed by birds. To overcome this coarse wire netting was placed over the containers. Seedling growth was still very poor, and it was thought that despite the use of a layer of gravel around the seedlings and on top of the sand, evaporation may have resulted in an excessively high concentration of nutrient ions around the seedling roots. To avoid this possibility a sandy loam without added nutrients was used in the containers for the second run, but seedling growth was slightly poorer than in the first run. A further complication in both runs was that heavy storm rains caused damage to seedlings, even under a covering of hessian.

Since the pots were standing in water the low tension levels of about 10 cm may have been responsible for the poorer growth in the sandy loam as compared with the sand used initially, and perhaps even for the poor growth in the sand.

The Trachypogon seedlings failed to take in both runs, as did Eragrostis seedlings in the second run.

To assist in the clarification of results both runs have been considered as duplicates, even though carried out under different conditions; and the mean value of the dry weight and fresh weight of tops and the dry weight of roots (relative to full sunlight growth for each species as 100), the percentage dry matter (dry weight/wet weight x 100), the ratio of dry tops to dry roots and the seedling heights are given in table 41. In view of the erratic results values for each of the above properties for each run are given in table A13 in the Appendix.

Converting the actual yields to values relative to full sunlight as 100 has drawbacks, but it enables better comparison of the two runs, and makes the graphical representation of the results given in figure 12 much easier. To enable easier comparisons the figure is in the form of graphs rather than histograms. The actual height and dry weight figures were of the same order as those given for Stoebe vulgaris by Lecatsas (1961). The results for Stoebe have been incorporated in graphs a and e in figure 12. Plate 16 shows the top growth obtained from representative containers of Tagetes minuta in Run B.

TABLE 41

SEEDLING GROWTH UNDER DIFFERENT LIGHT INTENSITIES

(Height and weight values under full sunlight for each species as 100)

	Height					Fresh weight (tops)				
% Light	Bid	Tag	Egu	Hyph	Ela	Bid	Tag	Egu	Hyph	Ela
100	100	100	100	100	100	100	100	100	100	100
40	100	180	90	140	90	64	107	54	110	96
20	230	400	200	290	180	102	230	81	177	100
3	190	220	60	70	90	28	30	8	23	50

	Dry weight (tops)					Dry weight (roots)				
% Light	Bid	Tag	Egu	Hyph	Ela	Bid	Tag	Egu	Hyph	Ela
100	100	100	100	100	100	100	100	100	100	100
40	51	88	59	72	96	48	61	42	52	87
20	72	114	71	96	89	42	40	23	[illegible]	46
3	8	9	6	8	25	2	12	-	4	-

	% Dry matter					Dry tops/dry roots				
% Light	Bid	Tag	Egu	Hyph	Ela	Bid	Tag	Egu	Hyph	Ela
100	23	22	27	31	31	.70	.52	.35	.31	.37
40	20	15	30	25	31	.77	.86	.50	.28	.41
20	14	12	23	17	25	1.17	1.49	1.09	.87	.72
3	6	6	20	11	12	3.13	2.66	-	1.00	-

(Bid = Bidens schimperi, Tag = Tagetes minuta, Egu = Eragrostis curvula, Hyph = Hyparrhenia hirta, Ela = Elyonurus argenteus)

Discussion

The pattern of height variation was the same for all species, with little or no elongation at 40% full sunlight but with much greater elongation at 20% sunlight. The pattern of change at lower intensities than this was dependent on the period of growth. The seedlings under 3% sunlight extended the fastest initially, but then remained static or fell back

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light intensities in the characteristics measured.

(3) From consideration of the field light intensity and soil moisture data given in chapter III and from points (1) and (2) above it is suggested that the majority of sites in all stands could be invaded by seedlings of all the species tested. It is appreciated however that seedling reaction to a screened light intensity of 20% full sunlight would not be identical to the reaction to an average field light condition of 20%.

(4) Even though shaded areas may have slightly lower moisture tensions than bare areas, the shade induced reduction of the seedling root system may result in greater moisture stress to the seedling, despite the lower moisture tensions; as pointed out by Daubenmire (1959) and Milthorpe (1961). Milthorpe has also suggested that the shade induced reduction of root growth could lead to a reduction in nutrient uptake in competition with other plants.

(5) It is suggested that any future studies of this type be carried out under clear glass, with the soil moisture content in each pot being controlled by weighing.

Conclusions

The techniques used to investigate seedling growth under different light intensities were unsatisfactory and possible improvements have been suggested.

However the results obtained indicate that the representative species from the different seral stages will give a similar reaction to varying light intensity; and that differential responses to varying light conditions are not likely to be a causal factor in enabling different species to invade seral stages.

(b) Temperature Requirements for Germination

A study of seed germination requirements in relation to temperature has in many instances enabled a clearer understanding of the vegetation types concerned. An example is the work carried out by Went and Westergaad (1949), where the type of desert plant germinating after rains was shown to be dependent upon the temperature regime.

Barenbrug (1935) writing on the highveld grasses commented that "a list of temperatures, where each species would give the optimum results in the shortest possible time, should be compiled", but no work of this type has been carried out.

Methods

Studies on the germination requirement of a species are usually commenced with tests at a range of constant temperatures, as in the studies by Burbidge (1945). With the number of species involved in these investigations it was decided to carry out tests at 10, 20, 30, 40 and 50°C, and also at room temperature with a minimum of 20°C and a maximum of 35°C. This maximum was over a brief period when the petri dishes were directly exposed to sunlight. The constant temperature tests were carried out in ovens for 40° and 50°C, in a germination cabinet for 20° and 30°C and in a refrigerator for 10°C. All the chambers were completely dark except for when they were opened to check for germinations.

Four petri dishes, each containing 50 disseminules or seeds, were used for most tests, two dishes being used for the 10°C tests for all species and for other instances marked by an * in table 42(b). The seeds were germinated on a filter paper placed on top of washed river sand, and the sand was kept moist, but not saturated, throughout. Daily counts of germinating seeds were made for the first week, but after that counts were omitted on some days. Owing to the low viability of the purple veld grasses the only species that could be tested from this stage was Elyonurus argenteus.

Disseminules were used for tests on H. hirta, Aristida congesta and Elyonurus argenteus, but actual seeds were used for the remaining grass species.

Results

The mean germination percentages and average times of germination are given in table 42.

TABLE 42

GERMINATION CHARACTERISTICS OF SELECTED SPECIES

(a) Average time of germination (in days)

Species	Temperature °C 10	20	30	40	50	20-35
Tagetes minuta	14.2	2.7	1.6	0.0	0.0	2.7
Bidens schimperi	10.2	1.2	1.3	0.0	0.0	1.5
Conyza amibgua	16.6	3.4	4.3	0.0	0.0	3.8
Oenothera biennis	30.0	3.7	4.4	0.0	0.0	4.0
Rhyncelytrum repens	0.0	3.2	1.9	3.1	0.0	3.1
Eragrostis curvula	26.3	2.5	1.7	1.5	0.0	2.2
E. chloromelas	24.9	4.1	2.2	2.3	0.0	3.1
E. robusta	30.5	3.9	2.7	2.7	0.0	3.2
Aristida congesta	-	3.4	1.7	1.9	0.0	3.6
E. racemosa	0.0	4.1	2.8	-	0.0	2.8
Hyparrhenia hirta	0.0	4.0	3.1	2.1	0.0	6.9
Eragrostis capensis	0.0	4.3	5.7	3.6	0.0	2.9
Elyonurus argenteus	0.0	18.3	6.2	10.8	0.0	5.3

(b) Germination percentage

Species	Temperature °C 10	20	30	40	50	20-35
Tagetes minuta	79	76	79	0	0	85
Bidens schimperi	99	92	90	0	0	87
Conyza ambigua	57	63	12	0	0	71
Oenothera biennis	19	71	42	0	0	83
Rhyncelytrum repens	0	81	66	29	0	86
Eragrostis curvula	19	94	93	82	0	86
E. chloromelas	29	71	74	68	0	71
E. robusta	8	68	62	35	0	65
Aristida congesta	-	46 *	37	39 *	0 *	35
E. racemosa	0	48	4	-	0	82
Hyparrhenia hirta	0	10	8	6	0	6
Eragrostis capensis	0	23	58	25	0	96
Elyonurus argenteus	0	11 *	10	1 *	0 *	5

Discussion

The only species which gave a greater and faster germination under conditions of variable temperature and light, as compared with constant temperature, were Eragrostis racemosa and E. capensis.

The optimum results for the dicotyledonous species, as measured by the amount and rate of germination, would be obtained at or just above 20°C, whereas the optimum results for the grasses would generally be at about 30°. All four dicotyledonous species failed to germinate at 40°, whereas all grasses germinated at this temperature, in some cases germinating faster than at 30°, though with a reduced germination percentage. A faster germination with a lower germination percentage at higher temperatures is a frequent occurrence, and, for example, has been noted by Burbidge (1945) and Hassis (1928). At 10° the germination of the dicotyledons was generally faster and greater than the germination of the grasses.

In correlating the results of laboratory experiments such as these with field observations the average time of germination is just as important a character from the ecological point of view as the germination percentage, although both values are required to give a balanced picture. The germination percentage, for example, was the same for the three annual dicotyledons at 20° and 10°, but the average time of germination was five to ten times longer at 10°.

The results for the ruderal and primary grass stage species suggest that at a constant temperature of 20° and a variable temperature of 20°-35° there is little difference between species as regards the rate of germination, though Bidens schimperi was slightly faster in these tests. The two slowest species to germinate were Hyparrhenia hirta and Elyonurus argenteus.

Germination tests of a wider range of species, usually with at least two seed samples of each species, were carried out in conditions equivalent to the variable temperature conditions described above, and these results are given in the next chapter. The data given here suggests that this temperature range is the most suitable for the comparison of the germination capacity of different species.

As the rainfall regime of the highveld is of a reasonably reliable summer distribution there are no important winter growing species and so great differences in the germination requirements of seeds would not be expected. Such differences would occur in areas of erratic rainfall, or in areas of both summer and winter rainfall.

The mean summer temperature for the moist soils of the highveld, as distinct from the maximum values given in table 9 of chapter III, would almost certainly be below the optimum temperature for even the dicotyledons, and would be well below the optimum temperature for the grasses.

In chapter III it was also shown that there was comparatively little difference between the various seral stages in the temperature of moist soils at one inch depth, though such differences would increase as the surface was approached. This would result in moist ruderal or fallow soil being slightly warmer than grassland soils, and so conditions in bare soil, if sufficiently different to favour the germination of any group of species, would favour grasses rather than dicotyledons. This would contrast with the cooler conditions in the moist grassland soils which would favour dicotyledons relative to grasses. Both these deduced trends go against the normal course of succession, indicating that a differing temperature requirement for germination between various seral species is not a causal factor of succession.

Conclusions

Selected species from different seral stages were germinated under six temperature regimes and the germination percentage and average time of germination were determined. Only Eragrostis capensis and Eragrostis racemosa gave increased germination with fluctuating temperatures and light, as against a constant temperature level.

As a general rule the ruderal dicotyledons gave a greater and more rapid germination than seral grasses at low temperatures (10°C), but the reverse held at 40°C. The optimum temperatures for germination of the two groups would be at about 20°C and 30°C respectively.

From consideration of the soil temperature data presented in chapter III it appears certain that that differing temperature requirements for germination between various seral species would not be a causal factor of succession.

(bi) Germination of Hyparrhenia hirta Disseminules

No samples of Hyparrhenia seed from Frankenwald were on hand at the start of the 1961/1962 season, and a number of disseminule samples collected in various parts of South Africa by officers of the Department of Agriculture had to be used for studies such as those reported in chapter IV (d).

Germination tests of the samples, which were mostly of 1961 origin, were carried out in the usual manner described earlier, using 200 fertile florets foreach test. The results of the tests are given in table 43, listing the germination percentage only.

TABLE 43

PERCENTAGE GERMINATION OF HYPARRHENIA HIRTA SEED SAMPLES

Sample Number	% Germination	Sample Number	% Germination
153	6.5	146	10.0
158	2.0	144	5.0
145	4.5	148	11.0
147	4.5	152	8.0
		Bulked other samples	2.0

Discussion and Conclusions

These results suggest that Hyparrhenia hirta has a consistently low germination capacity.

(bii) Viability of Stored Seed

A number of old seed samples collected in 1954/1955 were tested to see if they had retained viability under laboratory conditions. Unfortunately no records had been left as to their initial viability, but testing showed that a few samples were still viable. The 1955 samples of Aristida congesta and Eragrostis robusta were those used in the temperature/time tests described earlier.

This proved that seed samples of some highveld species could retain their viability under laboratory conditions for a period of six years.

(c) Germination Requirements of Cynodon dactylon

In view of the important role of Cynodon dactylon in succession, it was decided to carry out germination experiments on a sample of Cynodon seed harvested in 1960-1961 with approximately 98% of disseminules containing seeds. Previous tests by Weinbrenn (quoted in Hall, 1948) had shown a marked increase in germination from 0-3% to 85-96% when seeds were germinated in direct sunlight, but it was left undecided as to whether light had any effect additional to that of alternating temperature. This question had not been resolved by Israelstam (1953).

Methods

Experiment 1

Using petri dishes in the manner described in section (b), four dishes each with 100 seeds of Cynodon were left to germinate under six conditions as follows:-

A Seeds were placed in a room and were exposed to indirect sunlight of intensities of up to 200 foot candles, but never in direct sunlight (±10,000 f.c.); hence the temperature range was 15-25°C.

B Seeds were placed in an incubator at 30°C ± 1°C.

C Seeds were placed on an open bench in a greenhouse, and were exposed to direct sunlight from about 0800 to 1430 hours; hence with a temperature range of 15-35°C.

D Seeds were placed out as for C, but the seeds were tested by the alcohol flotation method described by Israelstam, and the seed had not floated in 95% alcohol, i.e., was sound or 'viable'.

E. As for D, but seeds had floated in alcohol i.e., were unsound or 'not viable'.

F The untreated seeds were in petri dishes near the dishes of C, D and E but were placed in a tarnished 10" copper oven. By taking temperatures in moist sand in petri dishes inside and outside theoven, and by using minimum thermometers to record night temperatures it had been established that the sand temperatures inside and outside the oven were virtually the same at any given time, the greatest difference being about 2°C, yet seeds inside the oven were excluded from light.

This experiment would further test the claim that constant temperatures or normal laboratory temperatures would retard germination, would check on the alcohol flotation method as a test of sound seeds, and would determine whether alternating temperatures were effective without light. The experiment was laid out on the 6/12/1961 and was left for 6 weeks.

Experiment 2

After the conclusion of experiment 1 a second trial was laid out on the 27th February 1962 and was also continued for 6 weeks, using only 2 dishes of 100 seeds for each treatment. Treatments A, B, C, and F were repeated, but the following new treatments were included.

G Seeds were placed out on a laboratory bench two feet away from those in treatment A, but unlike A the direct rays of the sun fell on the dishes for two to three hours every afternoon; hence the maximum temperature in the dishes was 35°C.

H Seeds that were sound when tested in alcohol were placed in the light proof copper oven along with those of treatment F.

I Seeds that were unsound when tested in alcohol were placed out in the oven with those of treatments F and H.

Results

The results of experiments 1 and 2 are given in table 44, being expressed as percentage germination and as average time of germination in days.

TABLE 44

CYNODON DACTYLON GERMINATION EXPERIMENTS

Treatment	EXPERIMENT 1 % germ.	Av. Time	EXPERIMENT 2 % germ.	Av. Time
A Lab. conditions	2	30 days	6	51 days
B 30°C ± 1°C	1	40	4	27
C Greenhouse, light	1	19	71	19
D As C, sound seed	14	18	-	-
E As C, unsound seed	3	19	-	-
F Greenhouse, no light	45	11	97	16
G Lab. with sunlight	-	-	90	17
H As F, sound seed	-	-	94	16
I As F, unsound seed	-	--	56	14

Discussion

From experiment 1 it was concluded that Cynodon seed germinated more rapidly and readily under conditions of fluctuating temperatures without light. Fluctuating temperature with light gave almost negligible germination as did constant temperature germination treatments. The soaking of seed in 95% alcohol appeared to have a stimulating effect on germination, with the result that even unsound seed gave a better germination than the untreated seed in the same position. Experiment 2 was designed to clarify some of the problems raised from experiment 1, but when this experiment was laid out three factors had changed compared with the first experiment, namely the age of seed, the intensity of light and radiation received was lower, and the length of exposure to direct sun in the glasshouse was reduced by about an hour.

The results from experiment 2 clearly show the stimulating effect of limited amounts of direct sunlight, treatment G compared with treatment A, and again suggest that an excessive amount of sunlight, treatment C, reduces the amount and rate of germination. However the best germination was again recorded in the light proof oven, showing that alternating temperatures are the key to increased germination rather than light sensitivity.

Treatments F, H and I again indicate that testing of seed with 95% alcohol may eliminate the unsound from the sound seeds, but will include some sound seeds with the unsound.

Conclusions

(i) Constant or slightly variable temperatures, with or without low light intensity, were unfavourable conditions for the germination of *Cynodon dactylon* seed.

(ii) Fluctuating temperatures with or without direct sunlight greatly increased the amount and rate of germination of *C. dactylon* seed, but there is evidence that daylong exposure to sunlight in summer decreased germination.

(iii) The seeds found to be unsound by the alcohol flotation method had a considerable proportion of viable seeds, and in experiment 1 there was evidence that this treatment stimulated germination.

(iv) For a complete understanding of the germination of *C. dactylon* controlled laboratory conditions will be necessary.

CHAPTER VIII

SEED CHARACTERISTICS AND AVAILABILITY

(a) Seed and Disseminule Characteristics

The relationship between seed properties and succession was discussed in detail by Salisbury (1942) who found that species occupying open or disturbed habitats generally produced a great number of light seeds, while those of a closed or woodland habitat produced fewer and larger seeds. These trends were related to the fact that seedlings of the first group of species usually had to establish or pioneer an area where there was only competition between seedlings, whereas seedlings ofthe second group had to compete against established plants, often trees or shrubs. The small seed size of the first group was not directly due to most of these species being annuals, but rather that open or disturbed habitats selected for annual plants or plants with a high reproductive capacity.

Work by Rose-Innes (1939) brought out the following points regard [illegible] seed characteristics and the highveld secondary successio[illegible]

1 As succession [illegible]ances there is a greater amount of parasitism by insects.

2 As succession advances there is an overall increase in the weight of disseminules.

3 As succession advances there is less fertile seed set.

4 As succession advances seed is usually slower to germinate.

Barenbrug (1935) had previously commented for Urelytrum squarrosum and Trachypogon spicatus that "all the seed collected by me was infested by larva, I have not been able to obtain a single viable embryo". Dickenson (1939) also found that the germination percentage of Purple veld species wasvery while those under 20% were still growing vigorously.

There was a drop in fresh weight and dry weight production at 40% sunlight, though 20% sunlight yielded more than the control. No satisfactory explanation can be offered for this drop, especially in the case of dry weight production, though it may be connected with the definite reduction in stem thickening which took place at the 40% level without any corresponding change in elongation, or possibly to variation in seedling reaction to low moisture tension. Lecatsas (1961) recorded a similar trend with Stoebe vulgaris, where growth at 38% full sunlight was 49% of the control, whereas growth at 12.5% sunlight was 320% of the control. This could indicate that there is a definite physiological reason for the fall in production at about 40% full sunlight, but this appears rather unlikely. The results of Lecatsas also appear to be subject to considerable experimental error, although not so much as in the experiment described (see values for S. vulgaris in figure 12).

Root production showed a decline with decreasing light intensity, and the ratio of shoot to root production increased slightly at 40% sunlight and markedly at 20% sunlight. In some cases the dried root weights at 7% sunlight were so small that they could not be measured. The percentage dry matter of all species fell as light intensity decreased, though it was always higher in the grasses. These trends in root/shoot ratio and dry matter content were expected, as indicated in the preceeding review.

Even allowing for the great experimental errors the following points are worthy of note:-

(1) Seedlings of species from all stages gave better top growth over a four to five week period under 20% sunlight than in full sunlight.

(2) All the species showed the same reactions to varying

low. Bunting (1938) stated that seeds of seral Aristida sp. germinated in a shorter time than seeds of climax members of this species, and also produced more seed than the climax members. Blake (1935) also found that climax prairie constituents in the U.S.A. gave lower germination percentages than seral species.

As the reproductive capacity of representative species of the highveld succession was being determined (described in section (b) of this chapter) it was necessary to further investigate points 3 and 4 brought out by Rose-Innes. No studies were made of point 1, but further investigations were carried out on point 2, as Rose-Innes had measured the average disseminule weight, regardless of whether the disseminules held seed or otherwise. This work was extended in 1961/1962 to find the average seed weight and the average weight of a fertile disseminule. The seed weight gives an indication of the energy reserves available to the seed, and the disseminule weight is related to the ease of dissemination. As the contribution of the seed weight to the disseminule weight varies, both characteristics should be known.

Methods

100 seeds or disseminules from different samples of the various species were dissected to find the percentage sound seed of the samples. The sound seeds were removed and examined to ensure they had not been chipped and all the seeds of each species were bulked. In addition the 100 empty disseminules of each sample were weighed, and the average empty disseminule weight determined. As the number of seeds available for seed weight determinations varied, each sample was halved, and the average seed weight was determined separately for each half.

Germination tests were carried out on 100 seeds or disseminules of each sample within a few weeks after collection in 1961/1962. The tests were done at room temperature of 15-25°C with peak periods of 35°C when the petri dishes were exposed to full sunlight for about two hours. The disseminules were placed on filter paper on top of moist washed river sand in petri dishes. Where the seeds are usually enclosed in disseminules, the tests were of disseminules, the cases where tests were done on actual seeds being indicated by * in table 45.

The percentage of sound seed in disseminules of Eragrostis curvula was determined by soaking the florets containing near mature seed in a solution of sodium hypochlorite, after the manner described by Wright and Streetman (1959). The sound seed can then be seen through the bleached glumes. However this was not done until February 1962, and the figure of 24% 'fertility' would probably be lower than that for the culms which shed seed in November-December 1961.

Results

The findings for the grasses have been listed in table 45a, where the individual seed weight, empty disseminule weight and full disseminule weight are given for each species, together with the mean percentage sound seed and the mean germination percentage and average time of germination. The numbers of different seed samples of each species used to derive the mean values are also listed.

No seed weight data is given for Tristachya hispida, for out of the hundreds of disseminules examined only one sound seed was found. Most of the disseminules had never contained seed, and virtually all the remainder were parasitised by larvae.

As a result of practical difficulties only the total disseminule weights are given for the dicotyledons listed in table 45b, and not the weights of the separate components.

The weight given would be very close or the same as that of full disseminules, as a result of the high sound seed percentages.

TABLE 45

SEED CHARACTERISTICS OF SOME HIGHVELD SPECIES

(a) Monocotyledons

Species	No. of samples	Indiv seed wt(mg)	Indiv diss. wt(mg)	Full diss. wt(mg)	sound seed %	% germ	Av. time germ. (days)
Purple veld							
Uralytrum squarrosum	3	5.62	9.50	15.12	4	0	-
Themeda triandra	1	2.00	N.D.	N.D.	23	0	-
Trachypogon spicatus	6	1.82	3.51	5.33	4	3	34
Heteropogon contortus	2	1.67	4.82	6.49	29	12	12
Andropogon amplectans	3	1.39	2.44	3.83	15	1	41
Elyonurus argenteus	2	0.91	1.69	1.60	9	3	5
Panicum natalense	4	0.49	0.18	0.67	5	0	33
Tristachya hispida	5	N.D.	N.D.	N.D.	0	0	-
Secondary							
Hyparrhenia hirta	3	0.55	1.06	1.61	10	1	12
Cymbopogon excavatus	2	0.61	0.65	1.26	23	5	40
Eragrostis capensis	2	0.30	N.A.	0.30	N.D.	96	3 *
Primary							
Paspalum pauciciliatum	2	1.42	0.74	2.16	29	7	51 *
Eleusine indica	2	0.79	N.A.	0.79	N.D.	17	11 *
Aristida congesta	4	0.32	0.40	0.72	78	3	30
Rhyncelytrum repens	1	0.27	N.D.	N.D.	N.D.	86	3
Cynodon dactylon	2	0.28	0.08	0.36	12	13	N.D.
Eragrostis curvula	2	0.19	N.A.	0.19	24	71	3 *
Trichoneura grandiglumis	1	0.19	0.08	0.27	74	38	17
Andropogon eucomus	3	0.14	0.20	0.34	55	34	35
Perotis indica	2	0.12	0.08	0.20	51	11	35

(continued on page 147)

Table 45 (continued)

Species	No. of samples	Indiv seed wt(mg)	Indiv. diss. wt(mg)	Full diss. wt(mg).	Sound seed %	% germ.	Av. time germ. (days)
Primary (cont)							
Pogonarthria squarrosa	1	0.08	0.04	0.12	N.D.	47	4
Monocymbium ceresiiforme	3	N.D.	0.70	N.D.	1	0	-
Eragrostis gummiflua	2	0.03	N.D.	N.D.	N.D.	99	6 x
Eragrostis racemosa	2	0.0[illegible]	N.A.	0.05	N.D.	82	3 x

(N.D. = Not determined, N.A. = Not applicable)

(b) Dicotyledons

Species	No. of samples	Total diss. wt. (mg)	% sound seed	% germ.	Av. time germ. (days)
Conyza ambigua	2	0.03	67	55	14
Gnapthalium luteo-album	2	0.01	N.D.	70	11
Senecio sp.	2	0.04	81	44	23
Bidens schimperi	2	N.D.	92	52	24
Tagetes minuta	2	0.82	81	82	8
Acanthospermum xanthoides	1	20.10	N.D.	66	120
Ursinia nana	1	1.45	98	0	-
Oenothera biennis	3	0.70	N.A.	83	4

(N.D. = Not determined, N.A. = Not applicable)

Discussion and Conclusions

The results in table 45 clearly show the trends observed by Rose-Innes. The 'average' seed weight of the purple veld grasses is approximately six times that of the primary grass stage species, and the 'average' sound disseminule weight is about ten times that of the primary species. On the other hand the primary grasses averaged about four times the percentage sound seed of the purple veld grasses. Furthermore most of the sound seed among the purple veld grasses was found in the 'low' species, such as Heteropogon contortus, Andropogon amplectans and Themeda triandra, rather than the 'high' purple veld grasses such as Trachypogon spicatus, Tristachya hispida and Urelytrum squarrosum. Cain and Tomson (1962-unpublished Frankenwald report) found that the average percentage of sound seed in 13 samples of Trachypogon and 6 samples of Hyparrhenia hirta was 5% and 12% respectively, these values being similar to those given in table 45.

The seeds of the early seral species usually gave a higher and more rapid germination than seed from the later seral stages, though there were several exceptions to this trend, notably Aristida congesta and Perotis indica. The rapid germination of the 1955 sample of Aristida used in the temperature requirement examinations (chapter VII) suggests that this species may germinate better in the second or subsequent years after collecting.

Although the trends mentioned above are reasonably clear, there are so many exceptions that they, in themselves, could never be the sole causal factor of succession. However these results will be referred to in the following sections of this chapter, and also in chapter IX.

(b) Average Seed Output from Individual Plants

The 'average seed output', as defined by Salisbury (1942), is obtained by counting the seed output of a number of individual plants of each species until a graph plotting the progressive average against the number of plants counted shows little variation.

If the germination percentage of the seed sample is known, the average seed output can be multiplied by this factor to give the 'reproductive capacity'. Salisbury noted that "competition as a factor effecting the reproductive capacity appears to be no less important, sometimes perhaps more so, than climatic or edaphic conditions", and that it was therefore essential to obtain data of this type from plants growing under natural conditions.

Salisbury also pointed out that the modal value of any property such as capsules per plant is usually less than the average value, as there are commonly a few individuals with many capsules and many individuals with few capsules. Greig-Smith (1947) showed how this could be allowed for in studies of seed production, but in the investigations described the procedure involved would havebeen far too time consuming for field use.

By comparing the reproductive capacity of various species of the one genus, Salisbury was able to show that the possession of a high reproductive capacity is a positive asset to a species in its spread, and not just a device to ensure survival alone. Stevens (1932) showed that weed species, which are almost always effectively and widely spread, usually produce large quantities of viable seed.

The only determinations of the reproductive capacity of highveld species were by Poultney (1952) who found that *Trachypogon spicatus* had a reproductive capacity of 59 viable seeds per plant, compared with a range of 604 to 10,000 for 17 subspecies of *Eragrostis curvula*.

Methods

From January to April 1961 measurements were made on the seeding capacity of a range of seral and purple veld species. The procedure used was similar to that of Salisbury, but had to be changed to some extent as this work was mainly on grasses, whereas Salisbury's measurements were almost all on dicotyledons.

With grasses the average number of seed heads (seed-bearing culms) per plant was determined, followed by the average number of fertile florets per seed head. This latter figure can be arrived at in one step in the case of species with one fertile floret per spiklet, e.g., *Trachypogon spicatus*.

If there is more than one fertile floret per spikelet, the average number of spikelets per seed head and the average number of fertile florets per spikelet must both be known. In the following tables fertile florets are referred to as 'seed', indicating potential seed.

From the above values the average number of fertile florets per plant can be determined, and this has been termed the 'potential seed output'. This figure can be multiplied by the fertility percentages given in section (a) to give the average seed output, and also by germination percentages to give the reproductive capacity.

Almost all the plants examined in this study were from an area around experiment T6B, and there were only isolated cases where specimens from other areas of Frankenwald were used. Counts were only taken from grass tussocks, and not from grasses in their first year of establishment. Counts were not taken on areas that received-abnormal moisture supplies, as seed head production was usually heavier and more prolonged on those areas (plates 17 and 18).

Generally about 50-90 plants or seed heads were examined to determine the average for each characteristic, these numbers, for the greater part, being at least equal to the numbers examined by Salisbury; but even so it can be appreciated that counting the seeds per seed head of a species such as *Gnapthalium luteo-album* is rather time consuming, and the following comment of Salisbury "often however the data are limited by either the time factor or the number of specimens available" holds for this work.

For two of the species concerned, *Eragrostis gummiflua* and *Pogonarthria squarrosa*, heads were taken and the seed

TABLE 46a

AVERAGE SEED OUTPUT AND REPRODUCTIVE CAPACITY DATA - MONOCOTS

Character

Species	Seed heads per plant (a)	Spikelets per seed head (b)	'Seed' per spikelet (c)	Potential seed output (a x b x c)	Sound seed per seed head	Average seed output (potential output x % sound seed)	Reproductive capacity (from viability %s)
Eragrostis curvula	10.9	503	4.6	25,200		6,050	4,300
Eragrostis gummiflua	8.2	ND	ND	ND	374	3,060	3,030
Aristida congesta	15.6	91.[illegible]	[illegible].0	1,420		1,110	43
Pogonarthria squarrosa	11.5	ND	[illegible]	ND	1,270	14,600	6,860
Andropogon eucomus	8.0	5.7	[illegible].6	1,850		1,020	629
Eragrostis racemosa	13.9	21.1	12.1	3,550		ND	ND
Hyparrhenia hirta	14.4	135	1.0	1,940		194	19
Cymbopogon excavatus	6.0	25[illegible]	1.0	1,520		350	76
Eragrostis capensis	8.7	11.9	13.6	1,410		ND	ND
Andropogon amplectans	8.0	68.7	1.0	550		83	6
Monocymbium ceresiiforme	12.5	4.0	7.1	355		4	0
Themeda triandra	6.6	11.1	1.0	73		17	0
Panicum natalense	3.6	285	1.0	1,030		52	0
Urelytrum squarrosum	8.2	20.4	1.0	167		7	0
Trachypogon spicatus	4.1	30.3	1.0	124		5	4
Tristachya hispida	9.0	2.7	1.0	24		.1	0

(ND = Not determined)

was hand threshed out, and by using seed weight values the weight of seeds per head was converted to number of seeds per head. As some seed may have fallen from the heads, this method would tend to underestimate the seed production. For these two species this technique proved to be much faster than the usual approach.

TABLE 46b

AVERAGE SEED OUTPUT AND REPRODUCTIVE CAPACITY DATA

DICOTS

Character	Bidens schimperi	Tagetes minuta	Conyza ambigua	Gnapthalium luteo-album	Oenothera biennis
Seeding stems per plant	NA	NA	1.4	1.5	3.3
Seed heads per stem	5.9	68	482	188	8.5
Sound seeds per seed head	28.2	4.5	109	87.9	163
Sound seed per plant) Average seed output)	166	306	73,500	24,800	4,560
% viability (section a)	52	82	55	70	83
Reproductive capacity	86	251	40,400	17,400	3,790

(NA = Not applicable, whole plant treated as one stem)

Results

The data obtained for the selected monocotyledonous and dicotyledonous species, using theterms previously defined, are summarised in table 46a and 46b respectively, and the detailed results are given in tables A14, A15 and A16. It is difficult to express the results for different species under compact table headings, but *Andropogon eucomus* is the only misfit in that the headings for this species in the first three columns of table 46a should be 'seed bearing culms per plant' (average 8.0), 'seed heads per culm' (average 5.7) and 'spikelets perseed head' (average 40.6). These changes also apply to the tables of detailed results of this species.

In the detailed analyses of results the number of items counted, the maximum, minimum and mean values, and the standard error of each count ($\pm$ s/n) are given. The standard error is usually of the order of 10% of the mean in tables A14, A15 and A16. The figures given in these tables are given to three places for all determinations.

Figure 13 shows therange of values commonly encountered in the number of seed heads per plant and the number of seeds per seed head, frequency histograms being given for three species foreach of the above properties. The histograms show, particularly in the case of 'seed heads per plant' that the modal value is less than the average value. The distribution of seeds per seed head is closer to the normal distribution curve. The only species where there were regular occurences of mature plants or tussocks without seed heads were _Trachypogon spicatus_ and _Elyonurus argenteus_.

The average seed output data for selected species from the various stages can be summarised as follows (excluding _E. racemosa_, _E. capensis_ and _M. cerosiifera_) -

Stage.	No. of species.	Average seed output
Ruderal	5	20,700
Primary grass	5	5,170
Secondary grass	2	272
Purple veld	6	27

Average seed output figures are given in preference to reproductive capacity figures as the former do not discriminate against species such as _Aristida congesta_, _Urelytrum squarrosum_ and _Themeda triandra_ which appear to have a delayed germination.

If the seral species which were the most frequent in experiment T6B (see chapter II) are taken, the seed production data is as follows:-

BETWEEN PAGE 153 and 154 SEE 35mm FICHE

Species/Stage	Potential Seed Output	Average Seed Output	Reproductive Capacity
Mean of C. ambigua and G. luteo-album	-	49,200	28,900
E. curvula	25,200	6,050	4,300
H. hirta	1,940	194	19
6 purple veld species	332	27	2

Discussion and Conclusions

The ruderal species which gave the lowest seed output were B. schimperi and T. minuta, which, as mentioned in chapter II, seem to be more aggressive as weeds of cropland rather than in a true ruderal community. Among the grasses the potential seed output, sound seed output and reproductive capacity almost always decreased as species come from a later seral stage.

It is recognised that this data is only for a restricted number of species, and is from limited sampling through a single season. Even so it is considered to adequately demonstrate that a falling off in seed production takes place as succession advances. The significance of these results will be further considered in following discussions.

(c) Average Seed Output From Stands: Time of Seeding

Although it was felt that the first step in arriving at quantitative data on seed output should be that of a thorough examination of the average seed output of individual species, it was acknowledged that further studies were required on the seed output of stands of vegetation. Stands of weeds have been shown by Harper (1960) and Harper and Gajic (1961) to have a self regulating seed output that is to a considerable extent independent of density, and Harper (personal communication) stressed the importance of determining output of seeds from stands. However Salisbury (1942) held that the average output per plant as measured in the field was a more satisfactory measure. These different views appear to be related to the type of study on which each worker was engaged.

Methods

Preliminary determinations of seed production from stands were carried out in 1961/1962 over a 2,000 sq. yard area of purple veld and a 225 sq. yard area of seral Eragrostis-Hyparrhenia. The seed head production in the purple veld was determined by counting the number of seed heads of each species in 50 quarter-metre quadrats thrown on six occasions throughout the growing season. The seral area was sampled on two occasions throughout the growing season. Both these areas were botanically analysed with 600 point quadrats enabling seed head production to be expressed in terms of the basal cover of each species. By using the figures given in the previous section for the number of sound or viable seeds per head (seed-bearing culm) it is possible to estimate the actual and viable seed production of the two stages. The number of seeds per seed-head is affected by habitat to far less an extent than the number of seed heads per plant (Salisbury, 1942).

Results

The results of the purple veld investigations given in table 47A list the percentage ground cover of each species, the estimated number of seed heads produced and the potential and actual seed production for an area of 100 square metres. The equivalent results for the seral area are given in table 47B. For some purple veld grasses the number of potential seeds per seed head had not been determined, and in these cases, marked by an x in table 47A, an allowance was made to enable the estimation of thepotential seed production of the

TABLE 47

(A) SEED PRODUCTION OF PURPLE VELD

Species	% basal cover	Maximum no. culms	Potential seed prod.	Actual seed prod.
Tristachya hispida	9.0	3,600	9,750	100
Eragrostis racemosa	-	240	61,300	NA
Elyonurus argenteus	3.8	240	4,800	432
Trachypogon spicatus	4.3	200	6,060	242
Andropogon amplectans	0.8	144	9,900	1,480
Brachiaria serrata	0.2	128 *	12,800	NA
Cymbopogon excavatus	0.2	120	30,500	7,020
Eragrostis capensis	0.2	64	10,400	NA
Diplachne biflora	-	56 *	11,200	NA
Urelytrum squarrosum	-	48	978	39
Eragrostis curvula	-	24	5,560	1,330
Digitaria trichlaenoides	3.8	16 *	3,200	NA
Panicum natalense	-	16	4,560	228
Heteropogon contortus	-	16 *	1,600	464
Setaria sp.	-	8 *	800	NA
Hyparrhenia hirta	-	8	1,080	108
Themeda triandra	-	8	90	21

(B) SEED PRODUCTION OF SERAL GRASSLAND

Species	% basal cover	Maximum no. culms	Potential seed prod.	Actual seed prod.
Eragrostis curvula	5.2	3,680	8,530,000	2,050,000
Hyparrhenia hirta	4.2	3,360	454,000	45,400

These production figures have been calculated for an area of 100 square metres in both grassland types.

NA = Not available

purple veld area. The results of the seperate samplings of seed heads per quadrat on the two areas are given in table A17 in the Appendix. The maximum production of seed heads was estimated from graphs of the actual counts, and graphs for four species, expressed as seed head production per unit area of basal cover are given in figure 14, and clearly illustrate the early seeding of Tristachya hispida and Elyonurus argenteus compared with Trachypogon spicatus. The results in table A17 also emphasise thevirtual absence of flowering in Digitaria tricholaenoides.

Observations throughout the growing season showed that the primary stage grasses, such as Paspalum commersonii, Eragrostis curvula, Perotis indica and Aristida congesta flowered early in the season, but could carry on flowering throughout depending upon the soil moisture conditions, while Tristachya, Brachiaria serrata and Elyonurus do not resume flowering once their brief flowering period is ended. The times of flowering for the grasses are in agreement with those given by Glover (1937).

Discussion and Conclusions

If thepotential seed production figures from the purple veld area are considered in relation to basal cover, it can be calculated that 38% of potential seed was produced by purple veld species comprising 98% of basal cover, 24% of potential seed was produced by secondary species which comprised 2% of basal cover, and the remaining 38% of potential seed was produced by primary species which were not recorded in 600 point quadrats. Unfortunately the results for the actual seed production are not complete, but qualitative examinations carried out on those species which are marked as 'NA' in table 47A suggest that a similar pattern of actual seed production in relation to succession would be obtained.

BETWEEN PAGE 157 and 158 SEE 35mm

(In the calculations given above E. racemosa is considered to be primary stage and E. capensis secondary stage.)

These results also indicate that the buried viable seed content of soil beneath the purple veld area would only have a limited relationship to vegetation growing on the area. Ploughing and removal of the present purple veld plants would be expected to produce a pasture with a greatly increased proportion of secondary and primary species - as has been demonstrated for another area (chapter VI).

The differences between the seed production from the two grassland types are also striking. The production of potential seed from Eragrostis and Hyparrhenia, which were the two most important grasses on the seral area, was about 50 times that of the potential seed production of all the grasses on the purple veld area. With only two samplings of seed heads in the seral stage, the true difference may be even greater.

Calculations based on the plant density of individual species in the R, E and H plots (table 2, chapter II) and on the reproductive capacity of individual plants of the same species, (table 46, this chapter), give an estimate of the seed output of the three stands. One such calculation shows that a population of Conyza ambigua in an area of 100 square metres, with the same plant density as the R plot, would have an actual seed output of approximately 78,000,000 seeds. A figure such as this, when contrasted with the results in table 47, suggest that a stand of ruderal species would have a greater seed output than a stand of primary species.

Even allowing for the experimental error involved, the results presented in this section show a clear trend towards a reduction in seed output as succession advances. The seed output from a stand of purple veld species has been shown to be particularly low. The results from this section will be referred to later in this thesis.

Time of seeding of ruderals

Following on the observations on the time of seeding of grasses, notes were taken throughout the growing season on the time of flowering of the main ruderal species, as Glover (1937) does not list flowering times for most of these. The observations, expressed as early, mid, late and very late flowering are summarised in table 48.

TABLE 48

FLOWERING DATA FOR IMPORTANT RUDERAL SPECIES - 1961/1962

Species	Sept/Oct	Nov/Dec	Month Jan	Feb	Mar	Apr	May
Oenothera biennis	EF	MF	MF/LF	LF	LF	VLF	-
Ursinia nana	EF	MF	MF/LF	LF	LF	VLF	-
Acanthospermum xanthoides	-	EF	MF	LF	VLF	-	-
Gnapthalium luteo-album	-	-	EF	MF	MF/LF	VLF	-
Conyza ambigua	-	-	EF	MF	MF/LF	VLF	-
Senecio sp.	-	-	EF	MF	MF/LF	VLF	-
Bidens schimperi	-	-	--	VEF	MF	LF	-
Tagetes minuta	-	-	-	-	EF	MF	VLF

Oenothera and Ursinia flower throughout the growing season depending on the soil moisture level, whereas the annual composites do not run to head until December or January. Oenothera can even flower before the opening rains, as shown in a photograph by Leigh (1958).

Keever (1950) has shown that time of seeding may be critical in determining secondary succession in the first two years, depending upon the cultivation treatment given to the final cropping. It would be possible, for example, that one particular pattern of cultivation would favour the late flowering Tagetes. Further knowledge is required about the phasic development of the highveld ruderals before any statements could be made to this effect, but it would appear unlikely that the time of seeding of ruderals would be as important as in the case given by Keever. Piemcisc (1951) has also shown how the different periods of phasic development and flowering time of ruderals may determine the early succession among these annual species.

(d) Seed Dissemination

Seed dispersal and the role of the various disseminating agents have been discussed in many books and papers, such as Weaver and Clements (1938), and Rose-Innes (1939) has given photographs and detailed descriptions of the mode of dissemination of many of the highveld species.

The dispersal mechanisms of the important highveld ruderal dicotyledons can be classified into two groups, as follows:-

Dispersal by wind	Dispersal by animals
Conyza ambigua	Acanthospermum xanthoides
Senecio sp.	Bidens sp.
Gnapthalium luteo-album	Tagetes minuta

The only important grasses which appear to have well developed and effective mechanisms for dispersal are Aristida congesta and Heteropogon contortus, dispersed by adhesion to animals, and Andropogon eucomus dispersed by wind. Story (1938) refered to the dispersal of Aristida congesta seeds on the legs and muzzles of cattle, but noted that Themeda triandra was not dispersed in this manner. Although many of the grass disseminules have awns of some description, observation indicates that these are of limited effectiveness. If this is so, any widespread dissemination of these grasses must be by wind or passage through the digestive tradt (Harlan, 1956).

The only work located on wind dissemination of grasses was that by Bunyon (1936) who studied wind dispersal of seeds in dust storms and concluded that wind distribution of grass seed is largely limited to movement for short distances along the surface of the soil, the distance depending on the amount of obstruction present.

Rice et al (1960) found that fruits of little bluestem grass (Andropogon scoparius) were dispersed to a very limited extent but that seeds of the annual Aristida oligantha were carried for long distances. These facts were used to explain the early invasion of the latter species and the very slow invasion of the former.

There is a little more knowledge about seed dispersion through the digestive tract of animals, although much of the work has been done on the spread of shrub seed, the study of Timmons (1942) on the spread of prickly pear by rabbits being an example. Harmon and Keim (1934) found that calves pass a higher percentage of viable seed than do other domestic animals, the percentages being calves 9.6, hogs 8.8, horses 8.7, sheep 6.4 and chickens 0.2.

Burton and Andrews (1948) found that most seeds of grasses and legumes that passed through cows were recovered on the second and third day after feeding, but some were still being passed on the tenth day. In most cases the smaller seeds passed through more quickly and suffered less damage than the larger seeds. Passage reduced the viability of most seeds but increased that of Cynodon dactylon. Weinbronn (in Hall, 1948) also found that germination of Cynodon dactylon was stimulated by passage through the digestive tracts. Lehrer and Tisdale (1956) and Krefting and Roe (1949) also found that although viability was usually reduced by passage through the digestive tract, there was almost always some seed that remained viable.

Green (1961) suggested that the role of wind in seed dispersal has been overemphasised and Levina (1956) found that in the Russian steppes species with dispersal by elastic mechanisms were the most important group. Harper (1960) states that, although it is often considered that outbreaks of weed infestation may arise by wind dissemination from a neighbouring field or from uncultivated margins, there is increasing evidence to show that this is a rare occurence and that long distance transport of seed in appreciable numbers is most unusual. A similar observation was made by Poole and Cairns (1940) in their study of Senecio jacobaea.

These authors showed that 60% of the Senecio seeds were deposited at the base of plants, and that almost all the remainder were held within the seed heads. Although the seeds were equipped with a pappus, and the average seed weight was 0.3mg, only 0.5% of seeds became windborne outside the seed producing area, and most of these were deposited within five yards.

Clements and Shelford (1939) comment that migration in natural communities is much more restricted than is commonly supposed, and that dissemination is of chief significance in the colonisation of primary and secondary bare areas and in supplying newcomers for the stages in the ensuing succession.

Methods of studying seed dispersal by clinging to or by passage through animals are fairly straight forward, but studies of wind dispersal present greater difficulties. The only techniques would seem to be by the use of seed traps, such as the wire trap used by Boe (1955) in his study of the dispersal of Larix occidentalis and the 'wood-wool' traps of Poole and Cairns (1940), the use of similar equipment to spore traps where spores are trapped by air passing through a filter (Gregory et al, 1961) and the use of glass smeared with vaseline as used by Sreeramulu and Ramalingam (1961) in their study of Lycopodium and allied spores. It can be noted that although there are 9.4×10^7 Lycopodium spores per gram, these workers found that there was an appreciable fall out of spores in the immediate vicinity of the liberating source.

(1) Seed dispersal of ruderals in experiment T6B

During the dry weather in the summer of 1962 it was noticed while washing the atmometer cups that wind dispersed composite seed was adhering to the moist porous surface. Counts on the 21st February were made of seed and floral parts, but on the three counts made subsequently only seeds were counted, the seeds being either *Gnapthalium luteo-album* or *Conyza ambigua*, though some of the 'Conyza' seed on the cups in the H stand may have been of *Senecio sp*.

Results

The total number of these seeds that collected on the four cups at each station is given in table 49, the grand total excluding the first count on the twenty-first February.

TABLE 49.

SEEDS ADHERING TO LIVINGSTONE ATMOMETERS

Date	21/2	28/2/62			6/3/62			21/3/62			Grand
Stand	'seeds'	Coa	Gnl	Total	Coa	Gnl	Total	Coa	Gnl	Total	total
K	5	1	1	2	4	2	6	20	3	23	31
E	35	6	45	51	1	100	101	18	79	97	249
H	49	9	52	61	35	70	105	117	202	319	485
T	0	0	0	0	0	0	0	0	0	0	0
Out.	1	0	0	0	2	0	2	2	1	3	5

(Coa = *Conyza ambigua*. Gnl = *Gnapthalium luteo-album*)

Discussion

The seed collected on each cup was consistently dependent upon the concentration of seed heads in the immediate vicinity of the atmometer, and, with only four cups in each stand, the figures given should not be regarded as a complete picture of the seed production in each stand.

When it is considered that the T stand was about 50 yards from the H plot, and that the 'outside' atmometers were much closer to the T6B plots, one cup being only 15 feet from the 1956 plot, these results strongly suggest that dispersal of Conyza and Gnapthalium seeds is not as widespread as may be expected, and that the number of seeds deposited per unit area falls away very sharply as the distance from the seeding plant increases. The few seeds which were deposited on the 'outside' atmometers could also have been blown from ruderals along the edge of experiment T6B South.

If the movement of light ruderal seed is less than anticipated, it follows that wind dissemination of grass seed, especially of late seral and purple veld grasses, would be very limited. This would especially apply in dense grassland where seed cannot blow along the soil surfaces. Species such as Conyza and Gnapthalium are light and are specially adapted for wind dissemination (discussion and photographs given by Rose-Innes, 1939) whereas grass disseminules of the later stages are usually about 100 times heavier (section (a), this chapter) with no adaptations for wind dispersal.

Conclusions

The numbers of wind blown seeds of *Conyza ambigua* and *Gnapthalium luteo-album* that adhered to Livingstone atmometers showed that the number of wind dispersed seed deposited per unit area fell away sharply with increasing distance from the parent plants. Comparison of seed weights and disseminule structure suggests that wind dissemination of grass seed would be much less than for the two ruderal species mentioned.

(2) Dissemination by cattle dung

Samples of cattle dung were taken in February 19 2 from the O.G. (overgrazed) unit and the V.A. (veld arable) unit at Frankenwald. The samples were collected in a very fresh condition to avoid the entry of dung beetles, and were then placed out to air dry. Air drying prior to keeping the samples moist for seed germination made the following handling and sub-sampling considerably easier, and probably reduced the risk of high nitrogen levels hampering seed germination.

On the 14th March 600 gm of each sample of air dry dung was placed out in four earthenware plates, each plate containing 150 gm. The samples were kept moist until the end of July in a heated glasshouse, giving a germination period of over four months. Seedling counts without the removal of seedlings were made in late March and April, and seedlings were removed in May, June and July.

Results

Table 50 gives the progressive emergence counts at each sampling date of monocotyledonous and dicotyledonous seedlings for the four replicates of both samples of dung.

TABLE 50

PROGRESSIVE COUNT OF SEEDLING ESTABLISHMENT FROM CATTLE DUNG

(a) Overgrazed unit

Sample	Dates									
	27/3/62		10/4/62		29/5/62		28/6/62		25/7/62	
	Mon.	Dic.	Mon.	Dic.	Mon.	Dic.	Mon.	Dic.	Mon.	Dic.
A	11	1	57	8	145	9	172	10	193	11
B	22	8	89	13	184	19	187	19	190	19
C	50	7	185	16	252	26	253	28	[illegible]	28
D	55	9	105	17	229	24	233	[illegible]	[illegible]	26
Total	138	25	436	54	810	78	845	83	887	84

(b) Vold Arable Unit

Sample	Dates									
	27/3/62		10/4/62		29/5/62		28/6/62		25/7/62	
	Mon.	Dic.	Mon.	Dic.	Mon.	Dic.	Mon.	Dic.	Mon.	Dic.
A	11	2	33	5	78	7	81	8	82	8
B	15	3	32	7	43	7	49	14	49	14
C	12	-	59	6	61	3	62	9	62	9
D	16	-	24	1	51	1	56	7	57	7
Total	54	5	148	19	233	18	148	38	250	38

(Mon. = monocotyledons, Dic. = dicotyledons)

All but 11 of the 1137 monocotyledons removed were seedlings of Cynodon dactylon, and Amaranthus sp. was the most frequent dicotyledon.

Assuming that the average steer defecates 5.8 lb of air dry dung each day (Gillard, 1962a) the total figures at the last count in table 50 can be multiplied by 4.4 to give an estimate of the number of viable seeds dispersed per beast per day, or assuming 12 defecations per day (Gillard, 1962a) the totals can be multiplied by 0.37 to give an estimate of the number of seeds in each dung pat. Thus at the time of sampling each beast on the O.G. unit was dispersing about 4,000 viable seeds each day, approximately 90% of these seeds being Cynodon dactylon. Plate 19 illustrates the vigorous seedling growth of Cynodon in the samples of dung.

Discussion

It must of course be recognised that this sampling was made on only one occasion throughout the growing season, and that the total number of viable seeds in the dung, and the relative composition of the different species could vary widely over the growing season, but nevertheless the following points can be made.

1 The results indicate that cattle droppings could be a very important factor in determining the amount of seed present on any area.

2 The species which has the greatest proportion of viable seeds in dung need not be the most important constituent of the grazed pasture.

Cynodon dactylon, for example, comprised 8.5% of the total basal cover of the O.G. unit in 1960, and 1.9% of the V.A. unit (Gillard, 1962b), but 91% and 85% of the viable seeds in dung from cattle grazing on these units were of this species. Hence selective dissemination of seeds by dung could influence seed availability, and hence succession on any area. The results obtained in this study, for example, can be linked with the comment of van Rensburg (1942) that under heavy grazing, fallows have been known to revert to Cynodon dactylon within one year.

3 As the review of literature indicated that smaller seeds were better suited to passage through the digestive tract of animals, and as it is shown in section (a) of this chapter that seeds of the seral grasses are generally lighter than seeds of purple veld grasses, it is suggested that cattle droppings would favour the spread of the former group.

Conclusions

Samples of cattle dung taken on one day of the 1961-1962 growing season were shown to contain large numbers of viable seeds, 90% being seeds of Cynodon dactylon. It is suggested that dissemination of seeds by cattle dung could favour the spread of seeds of the seral grasses, and by influencing seed availability, could, in some cases, influence the course of secondary succession.

(e) Summary of Chapter VIII

From the results of the studies reported in the previous sections of this chapter, together with the results of earlier workers on succession on the highveld and other areas, the following general principles can be stated.

As the highveld succession advances there is:-

(1) A greater amount of seed parasitism by insects.

(2) An overall increase in seed weight.

(3) An overall increase in disseminule weight.

(4) A slowing down of the rate of germination.

(5) A reduction in the amount of potential and fertile seed set.

(6) A decrease in the efficiency of the spread of disseminules.

That is, as succession advances, seeds produced are fewer, slower to germinate, more likely to be parasitised and less likely to be spread. In other words seed availability decreases markedly as succession advances. The significance of this will be discussed in the next chapter, but as expressed by Weaver and Clements (1938), who used 'mobility' in the sense of 'availability', "the relation of mobility to succession is obvious". Leith (1960) has also referred to succession as "essentially a problem of plant migration".

CHAPTER IX

GENERAL CONCLUSIONS

(a) Discussion

In recent studies of the casual factors of highveld secondary succession the importance of aerial and edaphic factors has been emphasised. Davidson (1961) stated "Secondary succession repeats itself with remarkable similarity wherever it is initiated in any one region, and the continuing causes are undoubtedly the aerial and edaphic factors of the environment". It is noticeable however, that in recent years many of the conclusions of earlier workers of the 1938-1940 period have been overlooked, and there have been virtually no references to overseas studies on secondary succession.

Of the earlier workers Dickenson (1939) stated that "the study of seeds and their problems.....I feel has more potentialities than any other branch in the study of secondary succession". Rose-Innes (1939) stated "the factors of mobility and viability of seed are extremely important and influence the course of succession to a very marked extent.", and also "The final conclusions I have to make upon this work (i.e. secondary succession) are that the mobility, viability and availability of disseminules are the most important factors in operation, that root habitats have an important effect upon succession once the disseminules are deposited, and lastly, that habitat factors of the soil are of comparatively little importance in influencing either the course or velocity of secondary succession as studied in this area."

Story (1938) concluded that re-invasion of *Themeda triandra* into seral vegetation was very slow because "Themeda seeds are not transported by cattle, and are far too heavy for wind dispersion. For this reason, seedlings are not found far from the parent plant, but remain clustered around as shown in photo 13. This is without doubt the main reason that Themeda is so slow to take in areas of fallow land". Story also stated that Themeda established much better in bare areas than amidst seral vegetation and "it thus appears that Themeda is one of the advanced grasses not because of, but in spite of its reaction to shading....". It was further noted that by artificial seeding almost any species, including Elyonurus argenteus and Trachypogon spicatus could be made to act as a pioneer. Artificial seeding of Themeda seeds in seed heads appears to be the best way of re-establishing this species on old cultivation lands (Farmer's Weekly, personal communication).

The findings of these earlier workers have not been over-thrown, and apart from some revised ideas about rooting systems (chapter VI), and for the recent studies showing that available nitrogen can influence the velocity of succession, need no modification.

It appears that the recent line of work may have developed because succession has been regarded as too much of a fixed and rigid sequence, whereas van Rensburg (1942) commented "succession cannot be regarded as a process where one forever and always definite phase will give way to the next at a certain stage, and the development does not always take place along definite lines or during fixed periods of time. We must rather picture the different stages of succession as an uneven or mosaic structure." This viewpoint has been emphasised in studies of old abandoned cultivation lands (chapter VI).

If the highveld secondary succession is defined as being the revegetation of destroyed areas of 'sub-climax' grassland, and such a definition is implicit in Davidson (1961) - page 2, surely more attention should be paid to the revegetation of once destroyed but uncropped areas where Davidson's statement that "secondary succession repeats itself with remarkable similarity wherever it is initiated in any one region" does not hold. Evidence brought forward in chapter VI from past and present highveld studies and from overseas work show that under these conditions the 'normal' succession does not usually take place. It was shown, for example, that the ruderal stage was often negligible or non-existant.

It has been mentioned how Story (1938) found that Themeda could reestablish better on bare areas than in seral vegetation. Because species B follows species A, it does not follow that B requires the environment of A to establish. As Keever (1950) has said, "the second invador may finally attain dominance in spite of, and not because of, the changes in environment brought about by the first dominant". This view can be compared with that in the Frankenwald Experiment guide (Anon, 1959) where it is stated "it is hoped to prove eventually the hypothesis that succession is due to biotic reactions, i.e., that each community produces an environment which is unsuitable for itself and suitable for the next stage of succession".

Oosting (1956) discussed the regular sequence of changes that are characteristic of secondary succession and continued- "Surely, one might assume that here reaction is most effective and that each of these distinct communities prepares the way for the next as it inhibits its own continuation. Actually it has been shown that neither reaction nor edaphic change need be involved." He further recognised that "Other perennials may have few seeds or low rates of dissemination, further to delay their appearance.", and concluded "Although, obviously, the species of later stages are competitively successful they do not necessarily require the earlier stages to prepare or modify the environment for them." Piemeisel

(1951) stated "The community first on the ground is there because of its rapid migration and development and the second, because of its greater capacity to hold the ground once it gets there".

Some overseas workers have shown how the pattern and rate of succession can vary with circumstances. Savage and Runyon (1937), for example, found that cropped fields cultivated lightly for a year or two and then abandoned reverted to the original cover much more rapidly than those tilled for longer periods, as a result of survival of vegetative parts and persistence of seeds. These authors also found that abandoned areas enclosed with virgin pastures recovered much more quickly than similar areas enclosed without virgin pastures, and this was attributed to the spread of seed by livestock. There were only a few instances of an orderly succession of grasses from the edge of the fields, and it was concluded that wind dissemination was of comparatively little importance.

Studies of edaphic factors in relation to highveld succession have been carried out by Rose-Innes (1939), Stiven (1957), Leigh (1958) and the present author (chapters III and IV). Available nitrogen has been shown to be the edaphic factor most likely to be a causal factor in succession, yet as Davidson (1961) has stated, although it can alter the rate of succession, the course is not changed. Furthermore Leigh (1960) has shown that _Hyparrhenia hirta_ can invade _Eragrostis curvula_ under conditions of very high nitrogen, and Eragrostis and _Cynodon dactylon_ have been known to grow on the poorest of agricultural soils (Davidson, 1961). Considering all the work that has been carried out it would appear most unlikely that edaphic factors are the important causal factors of succession.

Studies on aerial environment in relation to succession have been carried out by Story (1938) in the Themeda veld and by Israelstam (1953) and the present author (chapter III) at Frankenwald. As discussed in chapter III it is very difficult to know what is a 'typical' community of each stage that studies can be centered on. There is quite a variation between the ungrazed representatives of each stage, but if grazed and mown stands are considered the variation is very wide.

Considerable caution is required in interpreting results of investigations of aerial factors. Davidson (1961) for example, has stated that "Under normal conditions the ruderals provide cover which reduces the soil temperature and evaporation from the surface soil, and thereby enables the establishment of Cynodon seedlings (Israelstam, 1953)." The first half of this quotation can be accepted, but the second is somewhat misleading. Israelstam showed that Cynodon in artificial containers gave higher germination under ruderal than under fallow conditions, but there was still some germination under the fallow environment. Even assuming that these results apply completely to conditions in the soil, it would have to be shown that Conyza ambigua, for example, did not give the same result. Reference has already been made to the fact that a Cynodon sward has been obtained in one year by heavy grazing, a condition which would allow germinating Cynodon seedlings very little protection from ruderals.

From consideration of all the available data it is suggested that aerial factors are generally not causal of secondary succession, though shading and light relationships may be critical in determining the success of some species such as Hyparrhenia hirta (see chapter III).

Extensive testing has failed to show any trace of germination inhibitors produced by Trachypogon spicatus, but this does not prove that such substances are absent in field conditions. However in view of the evidence brought forward for their claimed activity, it is suggested that inhibitors can be forgotten until further positive evidence is produced for their action.

A preliminary study of the germination requirements of seeds and of the reaction of seedlings to varying light intensities (chapter VII) indicated that these relationships would not be a causal factor of succession, whereas studies of seed availability (chapter VIII) produced substantial evidence that this could be causal of succession, particularly in the early stages.

An attempt has been made to summarise our knowledge on the course of succession in figure 15. The species at the left of each row of representative species from each stage are those which grow best under conditions of high fertility and fairly heavy grazing. Those species at the right of each row are favoured by low fertility and no grazing. This figure is only a general picture and it must not be taken to mean that any species cannot grow on an area until this area has been colonised by species of the earlier seral stages. The purple veld species are not in any particular order, and there are many species not listed in this figure.

With this previous discussion in mind an attempt will be made to explain some aspects of succession on the highveld.

Following the usual pattern it is reasonable to expect that continued cropping on cultivation land will favour the build up of 'weed' or ruderal seed. Perennial grasses will be destroyed by cropping, and any of their seedlings establishing will be destroyed before they can seed to an appreciable extent, and so their seed supply will decrease. However some weed plants would almost certainly escape cultivation, or would germinate after cultivation, and so set seed. Furthermore many weeds, especially composites, have the ability to mature seeds even when infloresences are cut off in the

THE GENERAL PATTERN OF SECONDARY SUCCESSION ON HIGHVELD SANDY SOILS

ruderal stage	largely monocots few dicots → varying to largely dicots few monocots →	
primary grass stage	Cynodon dactylon Eragrostis curvula Eragrostis racemosa Eragrostis gummiflua Aristida congesta Pogonarthria squarrosa Eragrostis plana Sporobolus pyramidalis with ruderal dicots	heavy grazing ⇅ moderate grazing → →
'low' purple veld/ secondary grass stage	Eragrostis racemosa Heteropogon contortus Themeda triandra Andropogon amplectans Cymbopogon excavatus Hyparrhenia hirta with ruderal dicots	heavy grazing ← — ? → — ? →
'high' purple veld	Trachypogon spicatus Tristachya hispida Elyonurus argunteus Digitaria tricholaenoides Urelytrum squarrosum with ruderal dicots	

Abandonment after cropping for several years

Figure 15

flowering stage (Gill, 1938). So weeds, which are in a sense adapted to the crop (Bunting, 1960) will at least maintain their seed reserves, and most likely increase them. Therefore when cropping land is abandoned a dominant ruderal and annual population can be expected.

Weeds are usually well equipped for dissemination, and so a species success may be linked with an effective dispersal mechanism as was found by Piemeisel (1938) to be the case with Russian-thistle. (Salsola pestifer). The important highveld weeds can be disseminated by animals or wind, and produce large numbers of viable seed (chapter VIII).

Once the land is abandoned ruderal growth will continue, but some seed of perennials will enter the community, and some may survive the cropping. The resultant seedlings will be small in the first year, but will usually dominate over annuals in following years (see chapter I). The two most important of these grasses in the Frankenwald area are Eragrostis curvula and Cynodon dactylon. Eragrostis sets large quantities of light and viable seed (chapter VIII), and Cynodon also sets light seed and is well equipped for invasion with its rhizomatoous habit, as shown in the greater cover of this species on the 1960 T6B plot as against the 1959 plot (chapter II).

Grazing on the highveld speeds up the invasion of these grasses, and this is attributed to the edible nature of the herbaceous ruderals (as shown in plate 21), the superior growth of grasses under high nitrogen conditions brought about by dung and urine, the effect of trampling on the erect ruderal herbs and to the likelihood of dung patches disseminating grass seed (chapter VIII).

The effect of mowing on succession at this point has not been experimentally assesed, but it would be expected to favour the grasses and handicap the herbaceous ruderals, perhaps to a lesser extent than grazing. Heavy grazing, or mowing with nitrogenous fertilizer application, will maintain Eragrostis and Cynodon, but under negligible or no grazing these grasses will loose their vigour (Chapter II).

Under conditions other than those of heavy grazing and high fertility these primary grasses will be invaded, though the difficulty of invasion has been demonstrated by Leigh (1960). Although some of the invading species would be favoured by their height once they established, e.g. Hyparrhenia hirta and Cymbopogon excavatus. Low available nitrogen may be the cause of the common occurence of species such as Stoebe vulgaris and Eragrostis gummiflua on old lands (chapter VI). It is however emphasised that Hyparrhenia can invade bare or ruderal areas, as in the 1960 T6B plot (chapter II), depending on seed availability.

The evidence given in chapter VI also indicates that the 'high' or 'characteristic' purple veld species, Trachypogon spicatus, Tristachya hispida, Elyonurus argenteus, Digitaria tricholaenoides and Urelytrum squarrosum will not become dominant on areas from where they have been eliminated by cropping. Purple veld grasses, especially the 'high' species, usually produce very few viable seeds and these are ill equipped for dissemination (chapter VIII). Some of the purple veld species may re-invade, but in many cases it is undecided where some of these species should be classified, as shown by the different classification used by Rose-Innes (1939), Crook (1950), Davidson (1961) and the present author.

Species which are particularly hard to classify are Themeda triandra, Cymbopogon excavatus and Heteropogon contortus (all described as secondary by Crook, and as 'sub-climax' by Davidson), Monocymbium ceresiiforme and Diplachne biflora (discussed by Rose-Innes) and Eragrostis racemosa (see chapter VI). Eragrostis racemosa and Heteropogon contortus are the first and second most important species in the 'purple veld' type grass land of the V.A. unit, yet in the analysis of the purple veld seed area (chapter VIII) these species were not recorded with 600 point quadrats. The fact that there is still disagreement about the classification of these important species even after 20 or more years of investigations is a good indication that sucession is not a fixed and regular sequence.

(b) Summary

Although previous workers such as Davidson (1961) have emphasised that the highveld succession is a dynamic process which can move in various directions at varying speeds, it has been assumed that succession was largely due to the changing micro-environment of the various seral stages in relation to species requirements. Also it has been assumed that each successional stage can only develop, or else develops more readily, after the stage preceeding it.

As a result of the work outlined in this thesis it is concluded that many factors, such as the history of the disturbed area, micro-environment, seed availability, soil fertility, palatability and reaction to trampling are causal of some of the various movements of the highveld succession.

Emphasis has been laid on the importance of seed and rhizome availability as causal factors of succession, and the limited succession on disturbed but uncropped grassland has been explained on this basis of seed availability.

It has also been concluded that species of any stage can invade a seral area regardless of whether the area has been or is colonised by species from earlier seral stages. It has been noted that there are usually species from at least three of the successional stages growing in any seral area and that succession is not a rigid stage by stage process.

On cropped areas it is suggested that the seed supply of ruderals will build up during cropping while the seed reserves of other species decrease, leading to the dominance of ruderals on abandonment. However the ruderal community will include or will soon include scattered perennial grasses, notably those of the primary grass stage, and although initially inconspicuous these grasses will usually become dominant in about the third year of abandonment. It has been shown that the primary stage grass species as a whole produce far more viable seed than the secondary and purple veld stage grasses, and there is evidence to suggest that seed dissemination of the primary stage species would be more effective. The later and slower invasion of the secondary grass stage species could be largely a result of their lower reproductive capacity and a dispersal that is less efficient. There is also restricted evidence indicating that seedlings of the primary grasses may develop more rapidly than seedlings of the secondary grasses.

Finally it has been suggested that a re-invasion of the 'high' purple veld grasses may not take place on areas from where these species have been eliminated.

CHAPTER X

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APPENDIX - PART ONE

MISCELLANEOUS TABLES AND TABLES OF DETAILED RESULTS

TABLE A1

LIKELY ERRORS IN FREQUENCY DETERMINATIONS

95% confidence limits for the binomial distribution and limits obtained by the use of 't', giving values for 20 and 50 observations.

Taken from Greig-Smith (1947).

% frequency observed	20 observations Binomial		't'		50 observations Binomial		't'	
0	0	17	-	-	0	7	-	-
10	1	31	0	24	3	22	0	19
20	6	44	1	39	10	34	6	31
30	12	54	8	51	18	44	17	43
40	19	64	17	63	27	55	20	54
50	27	73	27	73	36	64	36	64
60	36	81	37	83	45	73	46	74
70	46	88	49	92	56	[illegible]	57	83
80	56	94	61	99	66	90	69	84
90	69	99	76	100	78	97	81	100
100	83	100	-	-	93	100	-	-

TABLE A2

FREQUENCY DATA FOR LIGHT INTENSITY HISTOGRAMS

DATA USED TO CONSTRUCT FIGURES 2 AND 3.

Percentage of observations in each light intensity grouping.

(a) At the half inch level

Light intensity group	Stand R	Stand E	Stand H	Stand T
0.0 - 9.9	1	25	33	35
10.0 - 19.9	5	31	33	27
20.0 - 29.9	8	16	14	15
30.0 - 39.9	8	9	7	6
40.0 - 49.9	11	7	6	6
50.0 - 59.9	8	3	2	4
60.0 - 69.9	9	5	4	3
70.0 - 79.9	12	1	1	1
80.0 - 89.9	13	2	-	2
90.0 - 100.0	25	1	-	1
	100	100	100	100

(b) At the four inch level

Light intensity group	Stand R	Stand E	Stand H	Stand T
0.0 - 9.9	-	1	-	-
10.0 - 19.9	-	12	15	4
20.0 - 29.9	2	8	18	9
30.0 - 39.9	3	18	25	8
40.0 - 49.9	4	17	13	9
50.0 - 59.9	9	10	8	11
60.0 - 69.9	18	12	7	15
70.0 - 79.9	18	10	9	13
80.0 - 89.9	18	6	1	13
90.0 - 100.0	28	6	4	18
	100	100	100	100

TABLE A3

DETAILED MONTHLY EVAPORATION RECORDS FROM LIVINGSTONE ATMOMETERS IN CC PER DAY.

Stand	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
	Month							
R 1	45	23	21	.24	21	23	21	18
2	48	22	21	23	21	1	16	20
3	-	25	23	22	22	20	17	15
4	-	-	-	26	25	25	20	17
R Mean	47	23	22	24	22	22	19	18
E 1	39	17	15	18	16	16	12	12
2	32	20	15	15	15	15	14	13
3	-	17	16	15	14	16	13	15
4	-	-	-	18	16	17	14	14
E Mean	36	18	15	17	15	16	13	14
H 1	30	16	17	18	13	16	14	13
2	29	18	17	16	14	16	15	15
3	-	17	16	18	15	18	13	14
4	-	-	-	17	15	15	15	14
H Mean	30	17	17	17	14	16	14	14
T 1	44	26	20	22	22	24	24	18
2	47	26	21	21	24	25	22	23
3	-	25	22	25	23	25	20	21
4	-	-	-	22	21	23	23	18
T Mean	46	26	21	23	23	24	22	20
Cleared 1	-	-	27	30	26	23	22	20
2	-	-	24	24	25	25	21	18
3	-	-	-	27	27	27	21	18
4	-	-	-	29	27	27	21	19
C Mean	-	-	26	28	26	26	21	19

TABLE A4

pF RELATIONSHIPS - AT TENSIONS OF 0 - 100 CM WATER (Haines' apparatus)

Tension	pF	Soil R	T	RS	TB
0	-	23.2%	32.6%	22.0%	26.1%
1.0	-	22.9	-	21.6	25.1
2.5	0.4	22.4	31.6	21.3	24.4
5.0	0.7	21.9	30.7	20.7	23.9
7.5	0.9	21.7	30.3	20.3	23.6
10.0	1.0	21.3	29.9	19.8	23.2
20.0	1.3	20.6	28.6	18.6	21.8
30.0	1.47	20.0	27.2	17.9	20.8
40.0	1.60	19.2	25.8	17.3	20.4
50.0	1.69	18.3	25.2	16.8	19.9
60.0	1.77	17.6	24.3	16.1	19.2
70.0	1.85	16.9	23.4	15.7	18.7
80.0	1.90	16.2	22.7	15.1	17.9
90.0	1.95	15.5	21.9	14.4	17.2
100.0	2.00	14.7	20.9	13.7	17.1

Results are means of duplicate determinations

TABLE A5

pF RELATIONSHIPS - FILTER PAPER EQUILIBRIUM DETERMINATIONS

(tabulating soil pF and the corresponding soil moisture %)

Soil							
R		T		RS		TS	
pF	%	pF	%	pF	%	pF	%
5.6	0.9	5.5	1.7	5.35	0.7	5.4	2.3
5.2	2.1	5.2	2.4	4.8	2.4	5.0	3.9
4.9	2.7	5.0	3.7	4.1	4.0	4.3	5.4
4.6	3.1	4.7	4.3	3.8	5.7	3.85	7.1
4.5	3.4	4.5	5.2	3.5	8.9	3.7	8.5
4.3	4.0	4.4	5.6	3.4	10.0	3.7	10.6
4.2	4.8	4.1	6.5	3.25	9.6	3.5	10.8
4.0	5.4	4.0	7.1	3.0	10.9	3.4	12.4
3.8	5.6	3.9	8.4	2.8	10.4	3.2	12.9
3.8	7.0	3.7	9.4	2.4	13.3	3.0	14.3
3.7	7.9	3.7	10.2			2.7	16.2
3.4	8.9	3.6	11.4				
3.6	9.2	3.6	12.6				
3.3	10.8	3.5	13.1				
3.1	10.6	3.3	13.7				
2.9	11.9	3.25	14.2				
2.8	12.2	2.95	15.0				
2.6	13.3	2.9	16.1				
2.5	13.8	2.85	16.5				
2.3	14.0	2.8	17.1				
		2.55	18.1				

TABLE A6

SOIL MOISTURE IN THE R E H AND T STANDS, 1961/1962. (as percent by weight)

Depth	4"				10"				18"				30"			
Stand	R	E	H	T	R	E	H	T	R	E	H	T	R	E	H	T
Date																
13/10/1961	-	4.5	-	-	-	5.4	-	-	-	8.2	-	-	-	10.8	-	-
26/10	-	4.3	4.6	4.1	-	4.9	7.8	5.2	-	6.4	11.0	7.2	-	7.7	13.0	13.0
8/11	-	7.9	11.4	11.2	-	7.8	11.2	10.2	-	8.3	10.4	10.2	-	8.3	10.6	11.1
21/11	5.6	8.0	14.4	11.3	7.6	9.3	13.6	12.4	11.0	9.2	13.4	10.6	9.7	8.6	13.6	10.8
29/11	7.0	11.6	14.9	14.7	7.9	10.2	14.9	14.3	11.0	8.5	13.8	11.3	11.3	8.8	15.6	10.8
7/12	5.8	9.7	14.5	12.7	7.3	9.5	13.7	13.4	10.7	10.3	13.8	13.4	12.8	9.8	15.7	13.3
14/12	5.1	10.1	14.5	13.0	7.5	10.2	11.3	13.5	11.0	10.8	14.1	13.8	13.5	11.3	15.7	13.7
19/12	6.2	11.5	16.0	14.8	7.2	10.2	14.2	13.8	8.9	10.5	13.5	13.9	14.0	11.1	15.1	14.2
28/12	6.2	10.6	14.5	13.8	7.4	9.7	13.7	13.2	9.4	10.2	12.9	13.4	11.5	10.8	14.3	13.1
16/ 1/1962	2.7	3.8	5.4	5.9	3.9	5.1	6.2	5.5	5.6	7.5	8.2	8.3	7.3	6.6	9.6	11.2
24/ 1/	5.1	7.3	10.9	9.9	4.6	4.8	6.1	5.7	5.4	6.6	10.4	6.6	6.1	6.1	10.5	9.4
31/ 1/	5.2	7.1	11.5	12.3	5.0	4.7	5.7	6.0	5.1	6.1	10.1	6.2	5.6	5.6	10.1	9.4
7/ 2/	5.8	8.5	12.9	10.6	6.4	5.9	9.3	6.9	6.4	5.6	10.4	6.1	5.5	5.4	10.7	8.8
15/ 2/	5.1	7.2	11.8	10.4	5.2	5.2	6.7	8.3	5.6	5.3	10.3	6.4	6.0	5.7	10.9	8.8
21/ 2/	4.8	6.8	9.5	9.6	5.4	6.2	7.8	8.2	7.2	5.6	9.2	6.8	6.0	5.1	8.9	8.8
28/ 2/	3.0	4.8	5.9	5.4	3.9	5.0	6.0	5.8	5.5	4.5	8.1	6.2	5.2	4.4	7.9	7.3
7/ 3/	1.9	3.7	3.7	3.4	3.2	4.3	4.4	3.4	4.6	5.2	6.5	5.6	5.0	5.0	7.1	6.2
13/ 3/	5.8	8.1	11.4	12.1	6.1	7.3	8.3	8.7	7.3	6.8	10.4	9.3	5.6	4.3	8.9	6.6
21/ 3/	4.3	6.4	8.9	8.1	5.4	7.2	8.0	8.3	7.3	6.1	9.1	8.3	5.5	5.2	8.7	7.5
28/ 3/	2.9	4.9	6.9	5.5	3.8	5.5	6.7	7.0	6.5	5.4	8.9	6.9	5.6	5.1	7.6	7.1
6/ 4/	5.8	8.6	11.3	10.6	6.7	9.2	11.1	10.0	9.4	9.1	10.2	11.3	8.4	8.2	10.5	9.9
12/ 4/	5.4	7.4	10.1	9.4	6.3	7.5	9.9	10.1	9.7	8.7	10.2	11.9	9.9	9.1	9.9	9.7
18/ 4/	4.6	7.1	10.7	8.3	6.3	8.8	10.2	10.1	10.6	9.9	11.9	12.8	9.0	10.7	11.9	10.6
27/ 4/	6.9	10.7	14.2	13.9	8.0	9.8	11.6	13.9	10.7	11.0	13.7	14.4	11.6	11.2	12.0	13.3
2/ 5/	5.9	8.9	[illegible]	11.9	7.2	9.6	10.1	12.9	10.9	11.2	12.6	14.0	11.3	11.5	12.6	13.9
10/ 5/	5.3	8.0	12.5	10.5	6.7	9.5	10.3	12.2	10.7	11.8	12.6	14.3	12.3	12.1	13.4	14.5
18/ 5/	4.6	7.4	12.2	9.6	6.3	9.1	9.7	11.8	10.4	11.0	11.9	13.8	11.5	10.5	13.5	13.6
23/ 5/	4.3	6.7	10.6	9.1	5.9	8.9	9.6	11.9	10.4	10.4	12.4	13.9	11.2	10.5	13.4	13.3
11/ 6/	3.7	6.0	8.6	8.1	5.3	6.8	8.5	10.7	9.4	10.0	11.2	12.4	10.5	10.0	12.4	13.1
14/ 8/	2.4	3.6	4.8	4.5	4.6	6.2	7.6	8.7	8.5	9.4	10.9	11.5	9.8	10.4	11.9	12.4
pF 4.2	4.4	4.7	5.9	5.9	4.4	4.7	5.9	5.9	4.1	5.0	6.5	7.3	4.1	5.0	6.5	7.3

Underlined values are at or below moisture content at pF 4.2

TABLE A7

'READILY AVAILABLE WATER' IN THE R, E, H AND T STANDS, 1961/1962

Centimetres of water in each sampling zone and profile

Date	R 4"	R 10"	R 18"	R 30"	R Total	E 4"	E 10"	E 18"	E 30"	E Total	H 4"	H 10"	H 18"	H 30"	H Total	T 4"	T 10"	T 18"	T 30"	T Total
13/10/1961	-	-	-	-	-	0.0	.2	1.2	2.6	4.0	-	-	-	-	-	-	-	-	-	-
26/10/	-	-	--	-	-	-0.1	.1	.5	1.2	1.7	-0.3	.5	1.7	2.9	4.8	-0.5	-0.2	0.0	2.5	1.8
8/11/	-	-	-	-	-	.9	.9	1.2	1.5	4.5	1.4	1.3	1.4	1.8	5.9	1.3	1.0	1.1	1.6	5.0
21/11/	.3	.9	2.6	2.5	6.3	.9	1.3	1.6	1.6	5.4	2.2	1.9	2.5	3.1	9.7	1.3	1.5	1.2	1.5	5.5
29/11/	.7	1.0	2.6	3.3	7.6	1.9	1.5	1.3	1.7	6.4	2.3	2.3	2.7	4.0	11.3	2.1	2.0	1.5	1.5	7.1
7/12/	.4	.8	2.5	3.9	7.6	1.3	1.3	2.0	2.1	6.7	2.2	2.0	2.7	4.1	11.0	1.6	1.8	2.3	2.6	8.3
14/12/	.2	.9	2.6	4.3	8.0	1.5	1.5	2.2	2.8	8.0	2.2	2.1	2.8	4.1	11.2	1.7	1.8	2.4	2.8	8.7
19/12/	.5	.8	1.8	4.5	7.6	1.8	1.5	2.1	2.7	8.1	2.6	2.1	2.6	3.8	11.1	2.1	1.9	2.4	3.0	9.4
28/12/	.5	.8	2.0	3.4	6.7	1.6	1.5	1.9	2.6	7.5	2.2	2.0	2.4	3.5	10.1	1.9	1.8	2.3	2.5	8.5
16/ 1/1962	-0.5	-0.1	.5	1.4	1.3	-0.2	.2	.9	.7	1.6	-0.1	.1	.6	1.3	1.9	0.0	-0.1	.4	1.7	2.0
24/ 1/	.2	.1	.5	.9	1.7	.7	.1	.6	.5	1.9	1.3	0.0	1.4	1.8	4.5	1.0	0.0	-0.2	.9	1.7
31/ 1/	.2	.2	.3	.7	1.4	.7	0.0	.4	.2	1.3	1.4	-0.1	1.3	1.6	3.2	1.5	0.0	-0.3	.9	2.1
7/ 2/	.4	.3	.8	.6	2.1	1.0	.4	.2	.1	1.7	1.8	.9	1.4	1.8	5.9	1.1	.2	-0.4	.6	1.5
15/ 2/	.2	.3	.5	.8	1.8	.7	.2	.1	.3	1.3	1.5	.2	1.4	1.9	5.0	1.1	.6	-0.3	.6	2.0
21/ 2/	.1	.3	1.1	.8	2.3	.6	.4	.2	0.0	1.[illegible]	.9	.5	1.0	1.0	3.4	.9	.5	-0.1	.6	1.9
28/ 2/	-0.4	-0.1	.5	.5	.5	.1	.1	-0.2	-0.3	-0.3	0.0	0.0	.6	.6	1.2	-0.1	0.0	-0.3	0.0	-0.4
7/ 3/	-0.7	-0.3	.2	.4	-0.4	-0.2	-0.1	.1	0.0	-0.2	-0.5	-0.3	0.0	.2	-0.6	-0.6	-0.6	-0.6	-0.5	-2.3
13/ 3/	.4	.5	1.2	.7	2.8	.9	.7	.7	-0.3	2.0	1.4	.6	1.4	1.0	4.4	1.5	.7	.8	-0.3	2.7
21/ 3/	0.0	0.3	1.2	.6	2.1	.5	.7	.4	.1	1.7	.7	.5	1.0	.9	3.1	.5	.6	.6	.1	1.8
28/ 3/	-0.4	-0.1	.9	.7	1.1	.1	.3	.1	0.0	.5	.2	.2	.9	.5	1.8	-0.1	.3	-0.1	-0.1	0.0
6/ 4/	.4	.7	2.0	1.9	5.0	1.1	1.2	1.5	1.5	5.3	1.4	1.3	1.4	1.8	5.9	1.1	1.0	1.5	1.1	4.7
12/ 4/	.3	.5	2.1	2.6	5.5	.8	.8	1.4	1.8	4.8	1.0	1.0	114	1.5	5.0	.8	1.0	1.7	1.0	4.5
18/ 4/	.1	.5	2.4	2.2	5.2	.7	1.1	1.6	2.5	5.9	1.2	1.1	2.0	2.4	6.7	.6	1.0	2.0	1.4	5.0
26/ 4/	.7	1.0	2.5	3.4	716	1.6	1.4	2.2	2.8	8.0	2.1	1.4	2.7	2.4	8.6	1.9	1.9	2.6	2.6	8.0
2/ 5/	.6	.8	2.6	3.3	7.3	1.1	1.3	2.3	2.9	7.6	1.7	1.1	2.2	2.7	7.7	1.4	1.7	2.5	2.9	8.5
10/ 5/	.3	.6	2.5	3.7	7.1	.9	1.3	2.5	3.2	7.9	1.7	1.1	2.2	3.0	8.0	1.1	1.5	2.6	3.1	8.3
18/ 5/	.1	.5	2.4	3.3	6.3	.7	1.2	2.2	2.5	6.6	1.6	1.0	2.0	3.1	7.7	.9	1.4	2.4	2.8	7.5
23/ 5/	0.0	.4	2.4	3.2	6.0	.6	1.1	2.0	2.5	6.2	1.2	.9	2.2	3.0	7.3	.8	1.4	2.4	2.6	7.2
11/ 6/	-0.2	.3	2.0	2.9	5.0	.4	.6	1.9	2.2	5.1	.7	.7	1.7	2.6	5.7	.5	1.1	1.9	2.5	6.0
14/ 8/	-0.5	.1	1.6	2.6	3.8	-0.2	.4	1.6	2.4	4.2	-0.3	.4	1.6	2.4	4.1	-0.3	.7	1.7	2.2	4.3

Any figure such as '.2' indicates that 0.2 centimetres of readily available water are present in that zone. Figures such as '-0.2' indicate deficiet of 0.2 centimetres of available water. Leaving the zeros off any figure above 0.0 helps comparison of the various readings in the table.

Preparation of these figures involved estimation of bulk densities and soil moistures at pF 4.2 for the E and H subsoil, but it is considered that this can be reasonably done in view of the known values for the R and T subsoils and all topsoils.

TABLE A8

MEAN SOIL MOISTURE TENSION FOR THE R AND T SOILS FROM

THE 29/11/61 TO 26/4/62

Date	Tension (cm) R profile	Tension (cm) T profile
29/11/61	1,940	2,220
7/12/	2,670	1.510
14/12	3,370	1,240
19/12	2,510	980
28/12	2,840	1,450
16/1/62	20,700	11,700
24/1	8,700	11,900
31/1	9,310	11,500
7/2	6,800	10,500
15/2	8,080	8,810
21/2	9,050	9,050
28/2	18,200	17,680
7/3	39,100	50,300
13/3	7,610	8,720
21/3	10,580	8,600
28/3	21,200	1[illegible],900
6/4	3,910	4,110
12/4	4,160	4,450
18/4	5,210	3,240
26/4	2,030	1,600
Mean profile tension for growing season	10,150	9,340

(The mean profile tension for the growing season is not the mean of the figures given above, but these have to be adjusted to allow for the differing time interval between observations)

TABLE A9

RESULTS OF SOIL CHEMICAL ANALYSES
(R = replicate, M = mean)

Soil		Available phosphate ppm P_2O_5 R1	R2	M	Available potash % K_2O R1	R2	M	Available calcium % CaO R1	R2	M	Organic carbon % R1	R2	M
1960	R	19	20	20	.007	.008	.008	.024	.012	.018	.6	.8	.7
1959		46	43	45	.007	.005	.006	.018	.012	.015	.7	.6	.7
1958		40	42	41	.007	.006	.007	.016	.012	.014	.7	.7	.7
1957	E	26	25	26	.010	.009	.010	.020	.014	.017	1.0	.8	.9
1956		22	21	22	.009	.007	.008	.020	.010	.015	1.1	.9	1.0
1955		12	11	12	.010	.012	.011	.018	.016	.017	1.1	1.0	1.1
1954		13	12	13	.010	.010	.010	.028	.016	.022	.9	.9	.9
1953		11	11	11	.010	.008	.009	.018	.018	.018	1.0	1.0	1.0
1952		13	14	14	.006	.008	.007	.012	.012	.012	1.1	1.0	1.1
1951	H	9	9	9	.008	.012	.010	.020	.026	.023	1.0	1.0	1.1
T		7	9	8	.010	.008	.009	.022	.014	.018	1.3	1.1	1.2
F		110	126	118	.012	.011	.012	.038	.038	.038	.8	.9	.9
E2		9	9	9	.007	.005	.006	.014	.012	.013	.9	1.0	1.0
H2		9	9	9	.006	.007	.007	.010	.008	.009	1.0	.9	1.0
T2		18	16	17	.009	.010	.010	.016	.016	.016	1.2	1.2	1.2
RS		6	7	7	.006	.006	.006	.012	.014	.013	.3	.3	.3
TS		7	8	8	.007	.008	.008	.008	.010	.009	.9	.7	.8

Soil Chemical Analyses (continued)

Soil		% Nitrogen Total R1	R2	M	C/N ratio	pH (AE&CI) R1	R2	M	pH (author) M	Available Nitrogen ppm
1960	R	.054	.053	.053	13	5.1	5.1	5.2	5.0	29
1959		.045	.044	.045	16	5.2	5.2	5.2	5.1	18
1958		.051	.050	.051	14	5.1	5.1	5.1	5.2	19
1957	E	.062	.056	.059	15	5.4	5.5	5.5	5.5	12
1956		.070	.066	.068	15	5.5	5.5	5.5	5.4	10
1955		.084	.069	.077	4	5.6	5.6	5.6	5.7	15
1954		.074	.072	.073	12	5.6	5.6	5.6	5.4	12
1953		.072	.074	.073	14	5.5	5.5	5.5	5.4	18
1952		.074	.085	.080	14	5.5	5.5	5.5	5.3	11
1951	H	.081	.075	.078	14	5.5	5.4	5.5	5.3	11
T		.086	.079	.083	14	5.5	5.5	5.5	5.4	10
F		.065	.071	.068	13	6.2	6.2	6.2	6.3	-
E2		.069	.064	.067	15	5.8	5.8	5.8	5.9	-
H2		.072	[illegible]	.071	14	5.5	5.5	5.5	5.6	-
T2		.086	.093	.090	13	5.3	5.5	5.4	5.5	-
RS		.034	.032	.033	9	5.8	6.0	5.9	-	-
TS		.060	[illegible]	.064	13	5.3	5.3	5.3	-	-

TABLE A10

RESULTS OF FERTILITY TRIALS

Total oven dry weight (in gm) for each treatment

Soil	(a) Lettuce trial Untreated	Nitrogen	(b) Maize trial Untreated	Nitrogen
R	6.88	1.44	5.36	5.92
E	4.96	1.44	4.00	6.28
H	2.96	2.84	4.28	5.96
T	1.80	1.84	3.60	6.08

TABLE A11

SEEDLING GROWTH IN RELATION TO SOIL TYPE

(a) Mean height of three seedlings in each treatment of four pots as measured before harvesting

Measured in cm to highest point as standing in pots

	Species				
	T. minuta	E. curvula	H. hirta	T. spicatus	Mean
Soil R	9.5	16.5 *	9.0	7.3	10.6
E	7.5	18.5	11.0	6.0	10.8
H	7.4	9.5	13.5	5.5	9.0
T	6.2	11.2	9.8	4.8	8.0
Mean	7.7	13.9	10.8	5.9	9.6

* Height lower in R soil than E soil due to bending of the topmost leaves, actual leaf growth longer in the R soil than E soil.

(b) Mean fresh weight in gm for each soil/species combination

	Species				
	T. minuta	E. curvula	H. hirta	T. spicatus	Mean
Soil R	.91	.78	.48	.24	.60
E	.52	.57	.52	.23	.46
H	.44	.20	.44	.12	.30
T	.32	.23	.16	.10	.20
Mean	.55	.45	.40	.17	.39

(c) Mean oven dry weight in gm for each soil/species combination

	Species				
	T. minuta	E. curvula	H. hirta	T. spicatus	Mean
Soil R	.133	.145	.111	.058	.112
E	.075	.134	.113	.057	.095
H	.071	.040	.095	.031	.059
T	.051	.057	.040	.026	.044
Mean	.083	.094	.090	.043	.078

(d) Percentage dry matter for each species/soil combination

	Species				
	T. minuta	E. curvula	H. hirta	T. spicatus	Mean
Soil R	14.6%	18.6%	23.2%	24.2%	20.2
E	14.4	23.5	21.7	24.8	21.1
H	16.1	20.0	21.6	25.8	20.9
T	15.9	24.8	25.0	26.0	22.9
Mean	15.3	21.7	22.9	25.2	21.3

TABLE A12

SEEDLING NUMBERS FOR TWO LOTS EACH OF 2,000 GM OF SOIL

Lot A given first, lot B second.

(a) Monocots

	Soil							
	R	E	H	T	F	E2	H2	T2
C. esculentes	39/33	30/29	3/5	5/7	3/2	-/-	-/7	1/1
Fimbristylis sp.	48/45	26/36	26/29	-/-	-/1	4/-	15/7	-/2
E. indica	2/11	30/22	-/-	1/-	5/19	-/-	-/-	-/-
E. curvula	-/2	7/5	2/2	-/-	-/-	-/5	-/1	-/-
C. dactylon	-/3	2/3	8/9	-/6	6/8	10/1	10/-	-/-
H. hirta	-/-	-/-	6/3	-/-	-/-	-/1	15/13	2/-
T. spicatus	-/-	-/-	-/-	3/-	-/-	-/-	-/-	-/8
Other sp.	10/18	15/11	23/28	11/26	-/-	19/24	25/5	32/30
Total	99/112	110/106	68/76	20/39	14/30	33/31	65/33	35/37

(b) Dicots

	R	E	H	T	F	E2	H2	T2
A. xanthoides	27/32	-/-	-/-	-/-	-/-	-/-	-/-	-/-
C. littoralis	6/4	13/7	9/8	-/-	1/2	-/-	-/-	-/-
T. minuta	9/66	-/4	-/1	-/-	3/6	-/-	1/-	-/-
G. luteo-album	2/7	2/-	12/20	-/4	2/2	-/-	-/1	
C. ambigua	1/8	2/-	5/1	-/-	5/11	1/2	1/2	-/1
P. oleracea	-/-	1/-	-/-	-/-	2/7	-/-	-/1	-/-
Oldenlandia sp.	3/14	1/1	6/-	-/-	-/1	2/16	1/1	-/-
Other dicots	30/36	8/1	31/13	-/3	2/1	10/1	5/7	3/-
Total	78/167	27/13	63/43	-/7	15/30	13/18	8/12	4/1

(Agreement between the two lots can be considered as satisfactory, the greatest discrepancy being in the numbers of T. minuta seedlings in the R soil.)

TABLE A13

SEEDLING GROWTH UNDER DIFFERENT LIGHT INTENSITIES

Height and weight values for full sunlight for each species as 100

'A' is the first run, 'B' the second, [illegible]

% Light	Bid A	Bid B	Tag A	Tag B	Hyph A	Hyph B	Ela A	Ela B	Egu A
Height									
100	100	100	100	100	100	100	100	100	100
40	120	80	240	110	160	110	80	100	90
20	290	160	440	360	300	280	200	150	200
3	220	160	270	170	70	-	90	-	60
Fresh Weight (tops)									
100	100	100	100	100	100	100	100	100	100
40	65	62	135	79	148	72	96	96	54
20	116	88	200	259	272	81	110	89	81
3	26	30	24	35	23	-	50	-	6
Dry Weight (tops)									
100	100	100	100	100	100	100	100	100	100
40	51	51	112	64	85	59	100	96	59
20	83	60	95	132	150	41	100	77	71
3	6	9	5	12	8	8	25	-	2
Dry Weight (roots)									
100	100	100	100	100	100	100	100	100	100
40	42	54	91	31	56	47	83	91	42
20	39	45	39	41	61	11	52	39	23
3	-	2	2	22	4	-	-	-	-
% Dry Weight (dry tops/fresh tops x 100)									
100	25	21	21	22	33	29	33	28	27
40	39	21	19	10	25	24	35	27	30
20	13	15	10	13	18	15	25	24	23
3	5	6	4	8	11	-	12	-	20
Dry tops/dry roots									
100	.77	.63	.65	.42	.42	.19	.35	.39	.35
40	.93	.60	.82	.89	.32	.24	.42	.40	.50
20	1.51	.84	1.60	1.38	1.03	.70	.67	.77	1.09
3	3.25	3.00	3.00	2.31	1.00	-	-	-	-

TABLE A14

REPRODUCTIVE CAPACITY DETERMINATIONS

Seeds per seed head (dicots) : Spikelets per seed head (monocots)

Species	No. heads examined	Mean value	Minimum value	Maximum value	Standard Error
Bidens schimperi	78	28.2	11	54	± 1.0
Tagetes minuta	51	4.5	2	7	[illegible].3
Conyza ambigua	57	109	9	295	9.6
Gnapthalium luteo-album	49	87.9	4	158	5.3
Oenothera biennis	50	163	17	266	9.9
Eragrostis curvula	56	503	66	2,073	56.6
Cynodon dactylon	86	120	51	250	4.4
Eragrostis ж gummiflua	47	374	40	1,540	49.8
Aristida congesta	59	91.2	18	220	5.8
Pogonarthria ж squarrosa	76	[illegible],270	100	16,200	45.5
Andropogon eucomus	8	5.7	1	22	0.4
Eragrostis racemosa	[illegible]	21.1	10	80	0.9
Hyparrhenia hirta	50	135	23	368	10.[illegible]
Cymbopogon excavatus	73	254	73	585	14.5
Eragrostis capensis	63	11.9	5	19	0.8
Andropogon amplectans	90	68.7	20	161	4.2
Monocymbium ceresiiforme	121	4.0	1	13	0.2
Themeda triandra	94	11.1	1	44	0.7
Panicum natalense	48	285	131	499	15.0
Urelytrum squarrosum	56	20.4	12	34	0.6
Trachypogon spicatus	84	30.3	13	60	0.5
Tristachya hispida	70	2.7	1	4	0.1

(19 Elyonurus argenteus seed heads averaged 20 'seeds' per seed head.

ж = Values are for seed per seed head.)

TABLE A15

REPRODUCTIVE CAPACITY DETERMINATIONS

SEED HEADS PER PLANT (MONOCOTS)

SEED HEADS PER SEEDING STEM (DICOTS)

SPECIES	No. specimens examined	Mean Value	Minimum value	Maximum value	Standard Error
Bidens schimperi	73	5.9	1	38	± 0.7
Tagetes minuta	41	68	4	318	3.9
Conyza ambigua	54	482	50	2192	45.2
Gnapthalium luteo-album	79	188	13	1297	22.4
Oenothera biennis	81	8.5	1	33	0.6
Eragrostis curvula	72	10.9	1	58	1.7
Eragrostis gummiflua	64	8.2	1	37	0.9
Aristida congesta	82	15.6	1	84	2.0
Pogonarthria squarrosa	93	11.5	1	58	1.2
Andropogon eucomus	81	8.0	1	30	0.7
Eragrostis racemosa	96	13.9	1	58	1.3
Hyparrhenia hirta	103	14.4	1	160	1.9
Cymbopogon excavatus	93	6.0	1	39	0.7
Eragrostis capensis	73	8.7	1	26	0.9
Andropogon amplectans	83	8.0	1	40	0.7
Monocymbium ceresiiforme	79	12.5	1	51	1.3
Themeda triandra	102	6.6	1	31	0.6
Panicum natalense	68	3.6	1	36	0.5
Urelytrum squarrosum	83	8.2	1	41	0.7
Trachypogon spicatus	114	4.1	0	21	0.4
Tristachya hispida	55	9.0	1	33	0.7

TABLE A16

REPRODUCTIVE CAPACITY DETERMINATIONS

SEEDING STEMS PER PLANT (DICOTS)

Species	No. plants examined	Mean value	Minimum value	Maximum value	Standard error
Conyza ambigua	84	1.4	1.0	7.0	± 0.1
Gnaphalium luteo-album	50	1.5	1.0	6.0	0.1
Oenothera biennis	89	3.3	0.0	16.0	0.6

'SEEDS' PER SPIKELET (MONOCOTS)

Species	No. spikelets examined	Mean value	Minimum value	Maximum value	Standard error
Eragrostis curvula	154	4.6	- 3	10	± 0.1
Andropogon eucomus	65	40.6	26	68	1.2
Eragrostis racemosa	75	12.1	6	32	0.5
Eragrostis capensis	71	13.6	6	21	0.4
Monocymbium ceresiiforme	92	7.1	5	12	0.2

TABLE A17

SEED HEAD PRODUCTION FROM TWO COMMUNITIES IN 1961/1962

(a) Purple veld Total seed head production from 50 quadrats each of 0.25 metres

Species	Dates of sampling 7/12	25/1	21/2	23/3	25/4	20/5	Estimated maximum
T. hispida	337	420	270	169	23	22	450
E. racemosa	26	19	24	29	13	11	30
E. argenteus	22	28	14	3	-	-	30
T. spicatus	-	-	1	23	21	11	25
A. amplectans	-	1	9	17	4	4	18
B. serrata	2	11	15	13	-	-	16
C. excavatus	-	-	3	5	14	4	15
E. capensis	1	2	8	2	-	-	8
D. biflora	-	5	7	5	4	8	7
U. squarrosum	-	-	-	6	-	3	6
E. curvula	2	1	-	3	2	3	3
D. tricholaenoides	2	1	-	-	-	-	2
P. natalense	-	2	2	-	2	2	2
H. contortus	-	-	-	2	-	-	2
Setaria sp.	1	-	-	-	-	-	1
H. hirta	-	1	1	1	-	-	1
T. triandra	-	-	-	1	1	-	1

(b) Eragrostis/Hyparrhenia veld Total seed head production 25 quadrats each of 0.25 metres

Species	Dates of sampling 21/2/62	1/3/62	Estimated maximum
E. curvula	229	130	230
H. hirta	202	205	210

Observations indicated that for each species the seed heads remained standing for long enough to ensure that the earliest heads did not fall over until seeding had virtually ended. Thus it is valid to estimate the maximum number of seed heads in the manner described.

APPENDIX - PART TWO

CALIBRATION OF A PHOTOMETER

A Weston photometer which had recently been refitted with a selenium receptor cell was made available in November 1961, but the instrument scale could only read to 250 foot candles (full sunlight being about 10,000 foot candles). The actual meter was enclosed in a portable wooden box of approximately 8" x 8" x 3", and the receptive cell was connected to the box by several feet of flex. The holder of the cell was only deep with a breadth of less than 2", so it could easily be inserted into vegetation with a minimum of disturbance.

It was known that if resistances of the order of 1,000-2,000 ohms were incorporated in series between the receptor cell and the meter, readings of full sunlight could be registered on the scale. The problem was to calibrate the scale readings, with resistances in circuit, against the true light intensity.

The only other photometer available for calibration purposes, but not for field use, recorded up to 600 foot candles. Attempts were therefore made to calibrate the first mentioned meter with resistances in circuit up to this level and then to continue the calibration curve by extrapolation, but this could not be done with any confidence. An opal glass screen was in position over the top of the cell during this and all other attempts at calibration.

A Weston photographic exposure meter was then used in an attempt to calibrate the photometer. This meter measured light intensity in candles per sq. foot, and multiplication of this reading by four gave a reading in foot candles (Sangamo Weston Pty. Ltd., personal communication). However because of the screen in front of the exposure meter cell light was only received from a limited field of view, compared with the wider receptive field of the photometer cell. Thus even though both instruments were pointed in the same direction,