The Phosphorus Content of the Grasses of Bechuanaland in the Course of their Development.

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In general little is known concerning the metabolism of mineral substances in plants. Seasonal changes in the ash content particularly have only been studied on broad lines and without many conclusive results. For some time it was accepted that a migration of phosphates, nitrogenous substances and potassium took place in autumn from the dying leaves of trees to the axis and reserve-organs of the plant (Swart 1914, Czapek 1921, p. 447). However, doubts as to the truth of this hypothesis arose when Dulk (cited after Czapek 1921, p. 447) found in autumn leaves of Fagus as much phosphorus as in spring. Investigations on other perennials were scarcely done except for Laserpitium (Swart 1914, p. 67) and Hops (Hall 1919).

It is not astonishing that nothing definite is known concerning the influence of rain on ash-content. In Europe, where rain is rarely a limiting factor, the problem is probably less acute than in South Africa, where rain is of paramount importance as a limiting factor, and a study of its influence therefore of great interest.

From results obtained in the investigation of Lamsiekte ("Cause and Prevention of Lamziekte," Theiler, Green and Du Toit, 1921; and the "Influence of Phosphorus on the Live Stock Industry" Theiler, Green and Du Toit, 1924), it has been seen that the distribution of the phosphorus in the grass plant is of great importance. Analyses done on collective samples of mixed dry and green material taken at fairly long intervals gave the first indications, but the details were still obscure. A further investigation was therefore begun, in which at short intervals the leaves, stalks, spikes and roots of each species were analysed separately. The state of the different organs, especially of the leaves and roots, at the time of sampling, was carefully noted. The rainfall was registered and the soil moisture determined every week, as previously described. (Henrici 1926, p. 623).

The other meteorological factors which proved necessary for the interpretation of the results were taken from the data kept at the Armoedsvlakte laboratory near Vryburg, where the work was carried on from winter 1924 to winter 1925.

More than 2,000 analyses were done in the course of the investigation, the majority on the following species of grasses at Armoedsvlakte:—

Anthephora pubescens, Nees.
Digitaria eriantha, Steud.
Eragrostis superba, Peyr.
Eragrostis Lehmanniana, Nees.
Aristida uniplumis, Licht.

Aristida congesta, R. and S.
Sporobolus fimbriatus, Nees.
Cymbopogon plurinodis, Stapf.
Themeda triandra, Hack.
Fingerhuthia africana, Lehm.
Chrysopogon serrulatus.
Pogonarthria falcata, Rendle.
and the annual *Tragus racemosus*, All.

Observations on the veld showed that grass on a pure sand farm remained fresh considerably longer than the grasses of Armoedsvlakte, in spite of a similar rainfall, and analyses were made at regular intervals of about six weeks on four grasses of Biesjesvlakte, a sand veld farm, situated about 18 km. west of Armoedsvlakte, towards the Kalahari. The grasses investigated were *Anthephora pubescens*, Nees, *Sporobolus fimbriatus*, Nees, *Aristida uniplumis*, Licht., and *Cymbopogon marginalis*, Stapf. Contrary to the Armoedsvlakte veld, that of Biesjesvlakte was poor in species, but rich in individuals. Aristida was the dominant grass, with a large amount of *Cymbopogon marginalis*.

As is the case over the greater part of Bechuanaland, both farms are characterised by a phosphorus deficiency in the soil. A few of the neighbouring farms have a higher rainfall and better soil than Armoedsvlakte. The farm Dry Harts, south of Vryburg, owned by Colonel Rodger, is such a farm. Every year a portion of the ground is flooded by a spruit, bringing down a soil much richer in phosphorus and causing a natural manuring. The remainder of the farm lies over stony kopjes, where the soil is similar to the rest of Bechuanaland, but the rainfall is generally higher. Samples of characteristic grasses were taken from both areas at intervals of about six weeks. If possible, samples of the same species were taken from both the vlei and the kopje, but several were limited to one area.

The following grasses were investigated:—

Themeda triandra, Forsk., from flood area and kopje.
Digitaria eriantha, Steud, from flood area and kopje.
Aristida congesta, R. and S., from flood area and kopje.
Eragrostis superba, Peyr., from flood area and kopje.
Eragrostis Lehmanniana, Nees, from flood area and kopje.
Cymbopogon plurinodis, Stapf., from flood area and kopje.
Aristida uniplumis, Licht, from the kopje.
Anthephora pubescens, Nees, from the kopje.
Chrysopogon serrulatus, from the kopje.
Pogonarthria falcata, Rendle, from the kopje.
Panicum coloratum, Linn, from the flood area.
Setaria nigrirostis, Dur. and Schinz, from the flood area.
Chloris virgata, Schwartz, from the flood area.
Cynodon Dactylon, Pers., from the flood area.

Method.

On account of the large number of analyses which had to be done and the extremely small amounts of grass available under certain meteorological conditions, a method which required little material and which could be adapted to conditions in a laboratory removed from a town, and without water pressure and gas, was necessary. The volumetric method for the determination of phosphorus (precipitation with ammonium molybdate in presence of nitric acid, solution of precipitate in Pemberton caustic potash and titration with nitric acid) was useless, as no efficient suction pump was available at Armoedsvlakte. The colorimetric method of Deniges as used by Atkins (1924) for determination of water-soluble P_2O_5 in soil was adapted for determination of P_2O_5 in plant ash. Analyses on the grass were done by both methods in the chemical laboratory of Onderstepoort, and as can be seen from the following table the results were comparable:—

Material.	Per cent. P_2O_5. Volumetric Method.	Per cent. P_2O_5. Colorimetric Method.
Eragrostis abyssinica from Ermelo	0.235	0.230
Themeda from Armoedsvlakte	0.217	0.219
Mixed grass from Armoedsvlakte	0.158	0.159
Eragrostis abyssinica fed at Onderstepoort ...	0.222	0.221

The following reagents are required for the colorimetric method adapted to plant work:—

A 10 per cent. aqueous solution of calcium acetate.

A 10 per cent. aqueous solution of ammonium molybdate.

A 0.2 per cent. solution of phenolphthalein in 50 per cent. alcohol.

Dilute ammonia, 1 volume liq. amm. fortis to 3 volumes water, s.g. 0.96.

A solution of microcosmic salt containing 2.94 grs. per litre. This solution is diluted to 1/100 and preserved with toluol. For actual use as the standard 10 c.c. of this solution are diluted to 100, which is then equivalent to 1 mgr. P_2O_5 per litre or 0.1 mgr. P_2O_5 per 100 c.c.

Reagent A is a solution of ammonium molybdate in sulphuric acid. 100 c.c. of a 10 per cent. ammonium molybdate solution are added to 300 c.c. of a solution of 50 per cent. sulphuric acid. Before mixing the whole of the two solutions, a trial has first to be done to see if no blue colour is developed. Several bottles, even of Merck's sulphuric acid, had to be discarded because the acid showed a faint blue green colour when added to the molybdate. As soon as a low concentration of phosphorus is tested, this colour may interfere.

Reagent B is a stannous chloride solution, which must be freshly made up daily, 0.1 gr. of pure tin and a drop of 4 per cent. copper sulphate solution are warmed with 2 c.c. of concentrated hydrochloric acid until dissolved and the solution diluted to 10 c.c.

Nitric acid.
Dilute hydrochloric acid.
Strong hydrochloric acid.
 In a modification described below.
Sulphuric acid.
Sodium sulphate.
Copper.

The Method of Analysis.—The various organs of the plants were collected separately. The leaves were in most cases divided into young and old, and the dry matter determined by weighing out one gram of fresh leaves, drying it at 104° C. and weighing again. The roots were carefully washed and dried, and the stalks and spikes dried at 104° C. After drying, the material was either finely cut up with scissors or ground in an Alexander mill and accurately weighed out into Berlin crucibles, 4-6 cm. in diameter. 0.1 gms. of leaves, spikes and young stalks were taken and 0.2 gms. of roots and old stalks. 0.5 gms. of brown leaves and standing stalks was used. In modification of the method the ground grass was moistened with calcium acetate and ashed over a large alcohol burner. Treatment with calcium acetate prevents loss of P_2O_5 and gives a better ash when cool, $\frac{1}{2}$ c.c. of concentrated nitric acid was added and in the case of the leaves evaporated to dryness immediately. In analyses of roots and stalks it was advisable to allow the ash to stand with the nitric acid for at least six hours, preferably over night, as this appears to eliminate the loss by spitting. The crucibles were evaporated almost to dryness on a water bath and ashed again. With the exception of certain roots of Dry Harts flood area, which contained a considerable amount of iron, the ash was completely white. The ash was dissolved in 2 c.c. of concentrated hydrochloric acid and 3-5 c.c. water, or in 10 c.c. of 10 per cent. sulphuric acid, just bringing to the boil over a small flame, carefully avoiding spitting. The alcohol reservoir burner was turned very low and proved most satisfactory, the spirit lamps had a tendency to flare up, causing the operator to shake and spill the contents. The contents of the crucibles were stirred, filtered and the filter washed. In the case of using hydrochloric acid, the residue consisted of silica, in the case of sulphuric acid calcium sulphate was not dissolved. The latter procedure was used only in a limited number of analyses, towards the end of the investigation; it has the advantage of not introducing into the solution any other acid than contained in reagent A.

To the acid solution a few drops of phenolphthalein were added and sufficient dilute ammonia to produce a definite pink colour. Dilute HCl or H_2SO_4 was then added drop by drop until the pink colour had entirely disappeared. *It is essential that the excess acid is neutralised before the final determination.* After neutralisation the solution was transferred to a 100 c.c. measuring cylinder and made up to about 90 c.c. 2 c.c. of reagent A and 10 drops of reagent B were added, the solution made up to 100 c.c., shaken and allowed to stand for 3-5 minutes. If the temperature was high, the colour developed fully in 3 minutes, but in colder weather it was advisable to allow the solution to stand for 5 minutes. Care must be taken not to expose the solution to higher temperature, i.e. to let them stand over a heater or in the sun, as the reagent A develops a blue colour without any phosphate, which may interfere with the final readings.

Atkins prescribes five drops of stannous chloride solution; but with the concentration of P_2O_5 found in the investigated grasses, this amount appeared to be insufficient to develop full colour. Special attention was given to this point and it was found that full colour was developed

with 0.2 mgr. P_2O_5 in 100 c.c. solution by 5 drops stannous chloride;
with 0.3 mgr. P_2O_5 on 100 c.c. solution by 10 drops stannous chloride;
with 0.4 mgr. P_2O_5 in 100 c.c. solution by 15 drops stannous chloride.

It was further settled that 10 drops of stannous chloride added to 0.1 mgr. P_2O_5 in 100 c.c. solution gave the same colour as 5 drops, and 15 drops of stannous chloride added to 0.3 mgr. P_2O_5 in 100 c.c. solution the same as 10 drops. As it happened that the concentrations mostly worked with extended from 0.15-0.25 mgr. in 100 c.c. 10 drops of stannous chloride were added as a rule. Only in analyses of seeds or very young haulms where higher concentrations of P_2O_5 were expected, 15 drops were added.

A standard was prepared as described before, 2.94 gms, microcosmic salt per litre diluted 100 times, and then a further 10 times, thus containing 0.1 mgr. P_2O_5 per 100 c.c. when ready for use, and reagents A and B added. Five determinations could be made with one tube of standard solution. It is not advisable to keep a standard longer than 20 minutes as it fades appreciably after 30 minutes.

The solutions of the plant ash were compared with the standard in Duboscq's colorimeter. The blue colour faded on standing, the less concentrated the solution the more rapidly the fading took place, hence the reading had to be taken directly after the period allowed to develop full colour.

The effect of diluting very concentrated solutions to half strength to make the colorimetric comparison nearer, was tried, but the error caused by working with the very dark coloured solution was so small as to be negligible. The colorimeter could be read between 0.075-0.3 per cent. P_2O_5 if the standard was set at 3.00 cm. For higher concentrations, however, diluting was necessary, the diluting had better be carried out before reagents A and B are added. In any case to the final dilution 2 c.c. of reagent A had to be given to develop the colour quantitatively. Great care had to be taken with the addition of stannous chloride. An excess of this salt in hydrochloride acid causes in the diluted solution often a cloudiness and greenish tint of the developed colour. A more concentrated solution of stannous chloride in less acid would probably serve the purpose better, but as the dilution was scarcely used in this work, this point was not further investigated. In no case should a concentrated solution to which stannous chloride is already added be diluted, and 10 drops stannous chloride more added, but the amount of stannous chloride still to be added has to be calculated according to the table above. This means of course that a preliminary approximative determination has to be done.

All values are calculated in percentage of the dry matter.—From the reading on the Duboscq colorimeter the precentage of P_2O_5 was calculated as the relation of the standard to the solution times the concentration of the standard, giving the percentage of P_2O_5. A practical example may illustrate this.

The standard contained 0.1 mgr. P_2O_5 per 100 c.c. when ready for use. The solution of the plant ash was made up to the same volume and the standard reading set at 3.00 cm. of the colorimetric scale. The reading of the unknown was then 3:2.50. Hence $\frac{3\cdot00}{2\cdot50} \times 0.1$ mgr. is the amount of P_2O_5 in 100 c.c. solution, this is 0.12 mgr.

0.1 gr. of material being used, therefore, there is 0.12 mgr. P_2O_5 in 0.1 gr. = 0.120 per cent.

As can be seen from this example, to obtain the phosphorus in percentage it comes to dividing the two readings on the colorimeter and multiplying by 0.1. For practical purposes a table was worked out with all possible relations of standard and unknown, so that the percentage could be seen directly in the table.

It may be emphasised that the relation of sulphuric acid to ammonium molybdate in reagent A does not give the best possible colour with the phosphorus standard and the 10 drops stannous chloride. It is too acid; a relation of 1:1 or even 2:1 gives a darker blue colour. As the human eye is not very susceptible for light blue colours in the colorimeter, it would probably be worth while to try if the reaction with these relations of sulphuric acid to ammonium molybdate 1:1 or 1:2 are quantitative. If more ammonium molybdate than sulphuric acid is taken, the developed colour is too dark for colorimetric readings.

Instead of the dry ashing described in this method a wet combustion was also tried out and proved to be most satisfactory and time saving if enough burners are available. The reason why it is not applied in an outside laboratory was simply the lack of burners. The wet combusion is done as follows:—

The 0.1 gr. plant material is combusted with 2 c.c. concentrated sulphuric acid and 1.0 gm. sodium sulphate. This relation of sulphuric acid and sodium sulphate proved to give the quickest combustion under the flame conditions and did not let the acid boil off.

More acid or more sodium sulphate were both less favourable. They let the acid boil off so that after cooling the solution got solid in no time. The combustion was done in a Pyrex glass tube over a rather small flame. 0.1-0.2 gr, copper foil was added to accelerate the combustion. With the copper foil the combustion of 0.1 gr. substance took 15-24 minutes to give an absolutely clear solution, which after cooling was neutralised in a measuring cylinder with dilute ammonia. The slightly yellow colour of the undiluted solution vanished entirely on diluting. The copper served as well as indicator. so that no phenolphthalein had to be added. Controls without copper took about twice the time for full development of colour. A whole phosphorus analysis including the weighing of 0.1 gr. can be done by this method in 25-40 minutes, the idea is of course to do as many combustions together as possible. The combustions have, however, to be supervised the whole time, as spitting occurs frequently.

Instead of sodium sulphate, potassium persulphate or nitric acid was added to the sulphuric acid to accelerate combustion. Potassium persulphate did not accelerate much, and was less effective than sodium sulphate; moreover the solution was spitting continuously.

A few drops of nitric acid added to the sulphuric acid finished the combustion in a few minutes, but afterwards the colour was not fully developed; probably a secondary reaction took place, an oxidation of stannous chloride as an excess of stannous chloride developed a dark colour for a moment, but it vanished immediately.

Remarks on the Plant Material.—As has been described in a previous paper ("Wilting and Osmotic Phenomena of Grasses and other Plants under Arid Conditions") the *grass leaves* at Armoedsvlakte are often wilted, folded or rolled. Their condition, when gathered for analysis, was carefully noted and the old and young leaves were, where possible, analysed separately. Certain grasses, e.g. *Pogonorthria aristida*, had so few leaves that a separation was impracticable and old and young were analysed together. With a few exceptions, which are specially marked in the tables, the young leaves were always either folded or rolled, although quite fresh. They had not passed the unfolding stage (Goebel, 1924, p. 130).

Old leaves fold only when in a state of at least incipient drying and frequently return so to their youthful position.

The Roots.—The roots of the Armoedsvlakte grasses have a peculiar morphological development. A complete investigation has not yet been done, but the present work offered an excellent opportunity for the accumulation of preliminary data.

Two types of roots can be distinguished. The first is an ordinary root with a corky epidermis and generally plentiful soft branch roots, but no root hairs. The second type is characterised by a special cortex tissue, which sometimes lies very loosely round the central cylinder and can easily be peeled off. At other times it is more firmly connected with the vascular tissues and is thicker, but can be removed in one piece without much difficulty. This tissue commences about 3-6 cms. behind the growing point. During the rainy season it is very thick, and especially towards the crown of the root, covered with root hairs. These root hairs are apparently not of the ordinary type, but are long lasting, as Whitaker (1921) describes, for basipilose roots. The only difference between Whitaker's description and the roots of Armoedsvlakte grasses is that at Armoedsvlakte the superficial tissue is much thicker and is removable. In most of the grasses this tissue shrinks as the soil dries, the root hairs temporarily disappear and the cortex tissue may be developed only as a smooth skin. At this time rootlets often appear towards the growing point, but when the removable tissue is well developed branching is scarcer, and limited to the apex of the root. Root hairs and abundant secondary roots rarely appear at the same time; one is always reduced. No rootlets at all are developed on young roots of this type.

For some time it was believed that this type of root was limited to certain species of grasses, while the corky root was characteristic of others. This apparently is not the case. *Eragrostis superba* and *Pogonarthria falcata* certainly have the thick tissue all the year round and it is never reduced to an ordinary skin, but the type is not limited to these two species, but is widely distributed under certain meteorological conditions. In nearly all the investigated species it appeared in the rainy season, but disappeared at the commencement of a drought. The tissue peels off and the root probably forms a corky layer. This removable cortex tissue, where it occurs only temporarily, is not nearly as highly developed as in the case of *Eragrostis superba* and often exists only as a removable skin. Except in *Eragrostis superba* the roots on one plant are of both types always having a few corky roots. *Digitaria* has seldom, and then even poorly developed roots with absorptive tissue. The removable cortex tissue is called "absorptive," as from its spongy nature there is no doubt that it acts as a water reservoir, holding the water for some time.

In conclusion it may be said that under certain meteorological and edaphic conditions the investigated grasses develop a spongy cortex tissue, which in only a few species remains unchanged. Quite probably the conditions of the formation of the cortex tissue in *Eragrotis superba* and *Pogonarthria* are less restricted than in the other grasses.

There is no doubt that the amount of rain is not the only controlling factor in the formation of the absorbing tissue. It was found, for example, that *Anthephora pubescens*, from the sand veld of Biesjesvlakte showed the spongy cortex at a time when the same plant at Armoedsvlakte developed only corky roots. The rainfall of both places was the same, but the sandy Biesjesvlakte soil retained the water better than that of Armoedsvlakte. Four weeks later, after soaking rains *Anthephora* had also developed the absorbing tissue at Armoedsvlakte.

As has already been pointed out, these root types have not been anatomically investigated, and it is at present not clear whether the two types are interchangeable on one and the same root. Roots which were actually dying down never had the absorbing tissue, but old ones often had. The peeling off of this tissue does not cause the death of the root. It is possible that a greater proportion of the new roots is developed during the rainy season with absorbing tissue on account of the abundant water, but it is improbable that during the drought young roots of the other types are formed, the water being insufficient to allow growth. More probably the one root type changes to the other. As the soil dries the root hairs on the absorbing tissue die down so that the tissue becomes smooth. It shrinks more and more and is finally loosened from the central cylinder, while at the same time a corky layer is probably produced between the bundle and the tissue. When the cortex tissue falls off entirely, the corky root is ready. The corky root is always much thinner than the one with absorbing tissue. If this hypothesis is correct, new roots with absorbing tissue will be formed after every rain. It would also explain why the corky type of root does not show basipilose root hairs, as the tissue producing them has been lost. A definite conclusion can only be arrived at after direct experiments with roots. Grass roots appear to be very plastic, as under certain conditions in pot cultures roots are developed which show neither the absorbing tissue nor the corky layer, but have root hairs on two sides, but not all round the root.

In consideration of the fact that the spongy tissue is undoubtedly for water storage, it is peculiar that most of the roots lose this tissue during a drought, when it would appear to be most essential. Those grasses which retain it permanently are certainly less susceptible to drought before the spring rains.

In consideration of these facts the condition of the root has always been carefully observed.

Relation between the Phosphorus Content of the Aerial and Subterranean parts of the Plant.—The phosphorus content of the grass leaves is undoubtedly of enormous importance in the feeding value of the grass. If the phosphorus is expressed simply in percentage, one important factor, the amount of available grass, is entirely neglected. If it is found that young grass contains two to three times as much phosphorus as old grass, it cannot be concluded that in spring the cattle get two to three times as much phosphorus as they do later in the year. In spring the amount of green grass is so small that the cattle get not more but rather less phosphorus than later, when the phosphorus content of the leaves is much less, but the amount of grass has considerably increased.

In the present investigation it was not possible to obtain any data as to the exact amount of green grass of each species at all times of the year. Probably a record of the time required to collect a definite amount would give a fair estimate. It might be suggested that in a later investigation weekly determinations be made of the phosphorus content of the grass in three one square meter plots, regardless of species, separated into green and brown leaves, or living and dead parts, as in the spring the cattle take only the green leaves. The results would probably be interesting to the farmer.

In order to obtain an approximate idea of the relations between the green leaves, brown leaves, haulms and roots, a whole plant of each species was taken every few weeks, carefully cleaned and the amount of each organ determined. The samples were all taken from a spare camp, which was not grazed. The weekly determination of the phosphorus in the organ was then calculated for the whole plant and the relation between the organs determined. Analyses of dead organs were not made weekly, as even over long periods the phosphorus content appeared to be constant except immediately after dying down. These values were also of importance in considering the migration of the phosphorus from one organ to another.

On grazed veld the relation between the organs is naturally disturbed, but this too lies beyond the scope of this investigation.

The method of comparing single tufts has its drawbacks. In spite of all care being taken it is not possible to obtain identical plants, and individual fluctuations cannot be avoided. This applies to all samples taken from the veld.

Soil Analyses.—Soil samples were taken from Biesjesvlakte and the vlei and kopje area of Dry Harts. The chemical and mechanical analyses were kindly undertaken by the Division of Chemistry in Pretoria. The soil of Armoedsvlakte has been analysed on a previous occasion and the data of that paper taken (Theiler, Green, du Toit, 1924, p. 39).

Soil, Armoedsvlakte, Vryburg.

	Dolomitic Areas. Per cent.	Leached Areas. Per cent.
Chemical Analysis—		
Moisture	6.88	0.77
Loss on Ignition	27.47	2.58
Insoluble Matter (HCl)	31.07	90.18
Iron Oxide and Alumina	1.56	6.1
Lime	12.07	0.16
Magnesia	21.34	0.12
Total Potash	0.11	0.42
Total Phosphoric Acid	0.12	0.03
Available Potash	0.016	0.011
Available Phosphoric Acid	0.001	0.0005
Nitrogen	0.24	0.08
CO_2 expressed as $CaCO_3$	45. 0	0.12
Mechanical Analysis—		
Fine Gravel	0.12	4.82
Sand	5.3	30.66

	Dolomitic Areas. Per cent.	Leached Areas. Per cent.
Fine Sand	19.19	48.82
Silt	10.83	1.95
Fine Silt	8.52	1.91
Very Fine Silt	6.00	1.61
Clay	7.47	7.15
Reaction to Litmus	Alkaline	Alkaline

Soil of Verona (Dry Harts, Vryburg District).

Chemical Analysis—	Flood Area.	Kopje Area.
	Per cent. of Air-dried Fine Earth.	
Analysis of HCl Extract.		
Insoluble Ignited Residue	69.94	85.67
Soluble Silica	0.11	0.18
Fe_2O_3 and Al_2O_3	15.95	8.25
MnO	trace	trace
CaO	0.83	0.18
MgO	1.22	0.58
K_2O	0.69	0.53
P_2O_5	0.09	0.07
Analysis of the Citric Acid Extract.		
Soluble Silica	0.23	0.047
Fe_2O_3 and Al_2O_3	0.38	0.123
CaO	0.24	0.038
MgO	0.10	0.043
K_2O	0.019	0.014
P_2O_5	0.007	0.003
Nitrogen	0.13	0.105
Mechanical Analysis—		
Gravel, 1 mm	1.4	42.0
Fine Earth, 1 mm.	98.6	58.0
Moisture	4.35	0.94
Loss on Ignition	6.65	4.05
Solubility in n/5 HCl	6.57	1.58
Carbonates	0.195	0.005
Reaction to Litmus	Alkaline	Acid
Coarse Sand	9.5	18.1
Fine Sand	22.3	59.2
Silt	7.1	3.8
Fine Silt	9.3	2.5
Very Fine Silt	11.0	3.2
Clay 0.002 mm.	23.2	7.1

Soil of Biesjesvlakte.

Chemical Analysis—	Per cent. of Air-dried Fine Earth.
Analysis of HCl Extract.	
Insoluble Ignited Residue	93.44
Soluble Silica	0.09
Fe_2O_3 and Al_2O_3	4.02
MnO	trace
Mg.O.	0.11
Ca.O	0.10
K_2O	0.20
P_2O_5	0.02

Analysis of the Citric Acid Extract.	Per cent. of Air-dried Fine Earth.
Soluble Silica	0.041
Fe_2O_3 and Al_2O_3	0.060
CaO	0.030
MgO	0.014
K_2O	0.012
P_2O_5	0.0005
Nitrogen	0.042

Mechanical Analysis—

Gravel 1 mm.	10.0
Fine Earth	90.0
Moisture	0.49
Loss on Ignition	1.50
Solubility in n/5 HCl	0.77
Carbonates	0.005
Reaction to Litmus	Acid
Coarse Sand	34.2
Fine Sand	55.4
Silt	1.1
Fine Silt	0.9
Very Fine Silt	2.5
Clay 0.0012 mm.	3.2

For the present moment only the figures of the phosphorus will be discussed. For available phosphorus the leached area of Armoedsvlakte where most of the grass samples were taken, and of Biesjesvlakte, are similarly poor. Then follows the dolomitic area of Armoedsvlakte. The kopje area of Verona (Dry Harts) has three times as much available phosphorus as the dolomitic area of Armoedsvlakte. The highest percentage of available phosphorus is found in the flooded area of Verona (Dry Harts).

Attention may be drawn to the fact that the distribution of the total phosphorus is quite different. The lowest percentage is found in Biesjesvlakte, the leached soil in Armoedsvlakte follows. The kopje area of Dry Hart has more than twice as much as the latter, but the flood area has but little more than the kopje area. The highest percentage is found in the dolomite area of Armoedsvlakte.

Results.

The results on Armoedsvlakte grasses will be discussed first, followed by those of Biesjesvlakte and Dry Harts. A table has been drawn up for each plant showing the percentage of phosphorus in the different organs throughout the year, and charts have been drawn for roots and leaves. It was found impossible to do the same for stalks and spikes as the phosphorus content could not be expressed as a function of the season. Haulms appeared so irregularly, even after the rains, that it proved impossible collecting at intervals of 8-15 days to have each successive sample older than the last.

Before discussing individual tables and charts some theoretical questions must be considered regarding the distribution of phosphorus in the plant and eventual losses. Deductions from these must be borne in mind in the interpretation of the tables.

In general we can expect a loss of phosphorus during flowering as a large amount goes off in the pollen, and a further decrease when the plant sheds its seeds.

In a phosphorus deficient soil it is possible for a leaf which contains a large proportion of phosphorus when young to have a small amount when older because there is insufficient phosphorus in the soil to keep up with the rapidly elongating organs. This would appear in the percentage value but not in the actual phosphorus content of the aerial parts. Phosphorus may also be drawn from the old leaves by the formation of stalks and spikes, or even by a new formation of young leaves.

As long as the haulms and leaves do not lose all their phosphorus in the autumnal dying down, the plant must lose a certain amount of phosphorus. The strong winds in Bechuanaland often break off the haulms and leaves which still contain phosphorus capable of migration. This is no loss of phosphorus to the soil as the parts decay on it, but is is a sensible loss to the plant. Through grazing a loss of phosphorus occurs, but this factor cannot be considered here.

So far only the loss of phosphorus from the aerial parts has been considered. If the idea of phosphorus loss is extended to the root, a decrease may be expected as soon as sprouting begins, and a low value be looked for at the time of most intensive growth. It might be possible for secondary factors to annul this effect, as for instance, a heavy rain bearing a large amount of phosphorus to the root from soil which is far removed from the plant, so that a decrease in the phosphorus of the root would be scarcely noticeable. A better development of the root would enable it to reach more soil and consequently more phosphorus, so that no decrease would occur.

Phosphorus might be lost by a dying down of portions of the root, as by the peeling off of the absorbing tissue, and this loss would not be easy to trace. It is peculiar to note that two very different factors, the time of most active growth and drought, influence the phosphorus content in the same direction.

Of the factors which tend to increase the phosphorus in the individual organs, the rainfall is the most important as it brings the phosphorus within the reach of the root. An accumulation of phosphorus in the root may also occur by a migration from the dying organs. This dislocation may take place in the drought periods of summer or in autumn, when the leaves are slowly being killed by frost.

From these theoretical discussions, it will be seen that the change in the percentage of phosphorus in the parts of the plant is not a simple problem, and as the above-mentioned processes may take place at short intervals, or even simultaneously, it will be difficult to explain every result in the analyses.

The tables and charts of the Armoedsvlakte grasses may now be discussed. (Tables 1-13, Charts 1-13.)

The percentage of phosphorus in the green leaves varies from about 0.125 per cent. to 0.400 per cent. This is a rather wide range, and it is obvious that different species can take up very varying amounts of phosphorus from the same soil. The values obtained for *Chrysopogon serrulatus* (Table 6) in November and December may be compared with those of other grasses. It is peculiar that this relatively high phosphorus content lasts only for about two months, when the value sinks again to the average of the other grasses.

Sporobolus fimbriatus then takes the leading part for a short time and a study of the tables shows that nearly every grass has a few weeks of exceptionally high values, but the times of these periods do not correspond. The excess over the other grasses may, of course, not be as great as with those two aforementioned plants, but it exists nevertheless. From this it appears that not only are the different species capable of taking up different amounts of phosphorus from the same soil, but the individual species may take up very varying amounts in the course of the season. The expression " regulate " is purposely avoided. If a true regulation took place the plant would react independently at any time unless hindered by water deficiency, and under favourable conditions would take up sufficient phosphorus to fulfil all its functions, which is certainly not the case with Bechuanaland grasses. Probably a real regulation is hindered by the deficiency of water, but this is not the only limiting factor.

The phosphorus content of one species fluctuates greatly in the course of the year. There is no continual decrease although there is a decided tendency to lower values towards autumn. The fluctuations depend partly on the meteorological factors, but all species are not influenced to the same degree, and the same factor has not the same influence at all times of the year.

A meteorological factor can hardly be expected to influence directly the phosphorus content of the leaves, but it is, nevertheless, indirectly of some importance. A small amount of moisture in the atmosphere, for instance, increases the transpiration of the grasses (see *Henrici* 2, 1926), finally causing wilting. The question arises whether wilting has a direct influence on the percentage of phosphorus in the leaves, and if so in what direction. It is scarcely possible, from a study of the tables 1-13 to show any conclusions as to a uniform variation. Wilting does appear to influence the phosphorus content, but the influence is specific. One fact is noticeable in all species: *Wilting before the spring rains causes a decrease in the phosphorus in the leaves.* From the veld observations before the spring rains of 1924, an estimation could readily be made of the phosphorus content as compared to the last analysis. After the spring rains, however, *it was absolutely impossible to draw any conclusion* in this direction.

From Chart 51 (Soil Moisture) it can be seen that during July and the beginning of August the soil moisture was still relatively high, but during August and September it rapidly dropped to the percentage which at that time of the year caused wilting, thus bringing water into consideration as a limiting factor. At this time the plant was shooting, and owing to the water deficiency the leaves remained rather short. The phosphorus stored in the root and dry aerial parts during the winter travelled to the leaves with the water, and under the prevailing meteorological conditions a small rise in temperature caused wilting. It is peculiar that at this time the root was developed *after* the leaves, and the dry root, together with the dry soil acted so that the leaves lost water, not only by transpiration but by these channels as well. It is the condition which *Fitting* (1910) foresaw for his desert plants. With returning water some salts, among them probably phosphates, which have not been organically bound, but are still in the ionic form, may migrate. The amount which migrates in this way is not big, but is quite noticeable.

If wilting is observed after rain, it is usually due to excessive transpiration and not to loss of water towards the root. Before rain an increase of phosphates in the root might be expected to accompany wilting, if the root does not change in size and weight. By the method used in this investigation it is very difficult to show this, as a different plant is used for every determination and it is not visible in all the curves 1-12.

The importance of rains to plant life is so great and its influence on plant metabolism so different (see previous papers *Henrici* 1-2) that a uniform influence on the distribution of phosphorus is not to be expected. Rain causes the development of the root and the elongation of the present, and the shooting of new leaves. In the soil it dissolves and transports phosphorus from the surrounding areas to the vicinity of the grass roots. The root better developed and provided with root hairs or fine secondary roots, is better able to take up phosphorus. As more water goes to the aerial parts, more phosphorus can be carried there, but the percentage of phosphorus in the leaves does not necessarily increase, as it is possible that only new aerial parts are produced. The percentage of phosphorus will therefore depend on whether the velocity and transport of the phosphorus or the growth of the plant is the quicker.

As has already been pointed out, it cannot be decided from the behaviour of the leaves whether a drying out after the rains causes a decrease in phosphorus. The stalks, however, show this decrease clearly. They dry out slowly so that the bottom remains green when the top is quite dry, and the migration of the phosphorus towards the root is clearly shown by separate analyses of the green and dry portions of the same stalk. As haulms are produced at Armoedsvlakte several times during the year, this migration can easily be observed, especially in Autumn.

A plant in a phosphorus deficient soil will undoubtedly try to regain as much phosphorus as possible from the dying organs in order to have it available for new growth. When large numbers of leaves die during drought periods (January, 1925) phosphorus is withdrawn and the crop of young leaves after the next rain arise richer in phosphorus. The phosphorus is not translocated to the roots itself, consequently there is no increase of phosphorus in the roots during the drought period. It migrates probably partly so far as the root crown, the rest remaining in the dry leaves until the ensuing rain leaches it out and brings it to the roots which pass it to the aerial parts. From this it would appear as though the grass in Bechuanaland could regulate its phosphorus translocation very well but this is only true to a certain extent. It must be remembered that during the spring growth a general movement of water containing the nutrition salts, including phosphorus, takes place to the aerial parts of the plant, and that this water is not only used for the formation of new leaves, but flows through the brown leaves and haulms as well. The old stalks become green again (see previous papers, Henrici 1), and, which for the purpose of this discussion is more important, the phosphorus content of the dead organs increases (see tables 1-12, 14-26). From the economical point of view, it is absolutely incomprehensible that the grasses should waste the phosphorus in such a manner. In cases where the stalks become green again the phosphorus may be used in metabolism, but no reason can be seen for its going into the dead leaves, although it must be admitted that later it may be withdrawn.

The behaviour of the individual organs may now be considered.

Leaves.—From a study of the tables 1-12, it may be seen that for leaves values between 0.3 and 0.4 per cent. are rare, so that these values may be considered high for the grass of a poor Bechuanaland farm. Compared with the values obtained for other pasture grass the maximal values of Armoedsvlakte are low, but the present discussion is confined to Armoedsvlakte, and these values must be called high. *Themeda triandra* (table 1 and chart 1) attains the highest value of 0.39 per cent. on 10th September in young, but not the youngest leaves before the rains. On this date the roots generally were better developed, the new roots being provided with root hairs or secondary roots. From this time the maximal value decreases constantly, until at the end of November it reaches 0.3 per cent. After that it is generally much lower, only once in March attaining 0.3 per cent. The question arises whether the maximal values are attained at a definite period after the rain. Later on this is certainly not so, but here the next three maximal values occur 10-14 days after the rain at a time when the grass is very well developed. After November values higher than 0.27-0.3 (once in December and once in March) do not occur after even the heaviest rains, and the question arises whether the rain has any influence at all, or is just incapable of raising the phosphorus content to a certain height.

It is peculiar to note that the young leaves of *Themeda* often have a lower phosphorus content than older leaves analysed at the same time. This rarely occurs in other grasses. For a long time this peculiarity was observed at every second determination, so that one week the old, the next the young leaves had the higher phosphorus content and the third week corresponded to the first. The grass certainly does not obtain enough phosphorus from the root to provide the young leaves immediately with a larger amount of phosphorus. In the middle of December a minimal value of 0.15 per cent. for young leaves is found. The young leaves become old leaves in a few weeks especially when the existing old leaves dry out, so that young leaves with a low phosphorus content may become, in a few weeks, old leaves with a low phosphorus content. This would preclude that growth at any period of the year is very regular, which is certainly not the case, and another explanation must be sought.

It is difficult to say whether the supply of phosphorus to the young leaves is so small that an increase is visible only in the second week, or whether phosphorus migrates from the old to the young leaves. In the first case growth would precede the intake of phosphorus, which is certainly so, as the very young leaves of *Themeda* have less phosphorus than those about three weeks of age. At the third analysis the leaves have become old, and the process begins again.

To return to the question of rain, it appears that in December rain had no influence on the phosphorus content of the leaves, but the January drought undoubtedly lowered the values, and this is true for all species. During February and March the values rose owing to the heavy rains, but though the rain continued until the end of May, and the soil moisture was very high the phosphorus content decreased slowly. Only after the first frosts in May did a more rapid decrease take place, as the leaves began to dry out. A rapid migration of phosphorus towards the root takes place in the dying leaf, but phosphorus is never completely absent in the brown leaves and they are often broken off by the wind before half their phosphorus has been translocated. As has been pointed out, this phosphorus is lost to the plant but not to the soil.

The very late rains in the 1925 season caused a new shooting of leaves in May, and particularly in June. It is characteristic that these leaves did not develop under arid conditions, but in spite of this they were low in phosphorus and were likely to die down early. As the soil was moist at this time of the year the water deficiency cannot be held responsible for the small amount of phosphorus, although it is more difficult for the plant to draw water from a cold soil. Economically it may be said that this display of leaves in winter is a waste of material, both organic and inorganic, as at the first heavy frost the leaves die without to any great extent fulfilling their function.

Part of the phosphorus of the dying leaves is undoubtedly translocated to the roots, but not by any means all. In all the tables the maximal values for the roots are found in May and June, as soon as the leaves begin to decrease more rapidly. This phosphorus is a reserve supply from which the grass can draw to provide for its leaves in spring, and if leaves are produced in the middle of winter this reserve is used before its right time. The leaves die very quickly and translocate only a portion of their phosphorus back to the root. Whether the little assimilation that can be done with these leaves is worth their production and consequent loss of phosphorus is open to doubt.

Although it has been found that late rains have not the same influence on the phosphorus content that the spring rains have, investigations have still to be made as to whether the condition of the leaves after the rain, wilted, folded or fresh, is of any importance. As has been explained in a previous paper (Henrici 1) the condition of the leaves depends on soil moisture, evaporation and air temperature. As a result all the minimal values of 0.14-0.16 per cent. of phosphorus in the old leaves fall either in the time of summer drought (January, 1925) or in Autumn There is no direct relation between the position of the leaves and the phosphorus content in *Themeda*. Open leaves with small and large amounts of phosphorus are found at short intervals and folded leaves with all possible values of phosphorus content. This is not surprising as drooping and folding are the work of a moment, and the phosphorus content the resultant of the whole life history of the leaf and very different from the relation between the condition of the leaf and assimilation, which is also the work of a moment.

Although it has been shown that a single fall of rain or wilting has no effect on the phosphorus content, it must be emphasised that long continued rain or drought certainly does influence the percentage of phosphorus. The low values in January and the high values in November and February and March illustrate this.

Digitaria eriantha. (Table 2, chart 2.) The distribution of the maximal values of phosphorus in *Digitaria* differs greatly from that of *Themeda*, but they may, nevertheless, easily be explained by external or internal factors. They are found:—

(1) In very young leaves.
(2) As soon as the roots are better developed (19/9/24).
(3) After heavy rains in November and December.
(4) After heavy rains in February and March.

Minimal values, however, are found only in the drought period of January and the beginning of February and towards winter.

To explain these facts it is necessary to bear in mind that during the whole course of its development *Digitaria* depends far more on the rainfall than does *Themeda*. *Digitaria* and *Anthephora* are never well developed *before the rains*, as is the case with *Themeda* and *Eragrostis superba*. The dry leaves and haulms of *Digitaria* break off much sooner than those of *Themeda*, and the dead leaves collect between those still remaining on the plant. They are immediately leached on the soil and the phosphorus becomes available for the root more quickly than in the case of *Themeda* where the dry leaves remain on the plant and never totally lose their phosphorus. Part of the leached material is blown away and therefore lost to the plant, but a large proportion is left for immediate use, and the root has from the first more phosphorus in its neighbourhood. The very young leaf may therefore be rich in phosphorus, but on elongation the phosphorus decreases slightly. It is important to note that in *Digitaria* the growth does not precede the intake of phosphorus. With very few exceptions the young leaves contain considerably more phosphorus than the old, and during the rainy season in summer the young grass leaves contain two-thirds the amount of a European grass.

It is peculiar that in spite of the big influence of the rain on the phosphorus content of *Digitaria*, there is apparently no relation between the condition of the leaves, and the phosphorus content. Only before the spring rains is the wilted grass obviously poorer than the fresh grass. The explanation given for *Themeda* holds good in this case, and it is especially noticeable that the amount of dry matter has no influence on the percentage of phosphorus.

The influence of the development of the root on the phosphorus content of the leaves can easily be explained. The better developed the root, the better can it absorb the phosphorus from the soil particles, especially since (as a result of the leaching of the old leaves) there is more phosphorus in the immediate surroundings of the grass.

Digitaria is one of the grasses which for several weeks has a considerably higher phosphorus content than other grasses in the same soil. This is the case in the rainy season, when apparently the rain washes sufficient phosphorus to the root to bring about an increase in phosphorus in all the organs. The question arises as to why the other grasses are not affected in the same way, and the only possible explanation is that *Digitaria* is either capable of absorbing more phosphorus or has a better conducting power than other grasses. It has been found in previous investigations (Henrici 1926, 1 and 2) that the conducting mechanism of Armoedsvlakte grasses acts very slowly, but attention has not been paid to the possibility of *Digitaria* having a better system. However, except in extreme conditions, *Digitaria* and a few others can regulate the transpiration, and this suggests a better water and consequently salt supply to the leaves.

Eragrostis superba (table and chart 3) in its behaviour closely resembles *Digitaria*. The maximal values are again found in very young leaves at times of good root development and during the rainy seasons. Although long rainy periods undoubtedly have a favourable influence on the phosphorus content, a single even heavy shower has just the reverse effect, here again probably because growth is more rapid than the intake of phosphorus. *Eragrostis* is therefore peculiar in showing a lower phosphorus value after scattered spring rains than before, and no relation between the condition of the plant and the phosphorus content can be considered. In spite of this young leaves seldom have a lower value than old ones, as so often happens with *Themeda*.

The minimal values which are on an average slightly higher than those of the other two grasses, are at the same time from the end of December to the February rains and again in autumn.

The table and chart (4) of *Cymbopogon plurinodis* show nothing new in principle. There is no maximum at the time of better root development but at the first rain the roots become very rich in phosphorus, which appears in the subsequent determinations on leaves. The other maximal values are similar to those of the other grasses. It is peculiar that even the leaves produced late in autumn are exceedingly rich in phosphorus, although only for a short time before the phosphorus migrates back to the root.

Pogonarthria falcata (table and chart 5) is a grass of which the values are usually totally different from those of other grasses. It was the only grass which from the first had well-developed root hairs, and contrary to all the other grasses, they persisted all through the drought periods. In spite of this, *Pogonarthria* has no long periods characterised by a higher phosphorus content than that of the other grasses. The grass always had so few leaves that except in two cases it was impossible to divide them into old and young leaves. Once in December the young leaves reached 0.3 per cent., and it is remarkable that the other maximal values were found only after the 30th of March and in July, after the appearance of new leaves. It is not easy to explain this behaviour. *Pogonarthria* really appears to be a winter plant, at least as far as the leaves are concerned, as after May, 1925, they were much better developed than at any time in summer. During an ordinary winter in Bechuanaland the grass dies of the drought, but the winter of 1925 was extraordinarily moist and in spite of long continued heavy frosts two-thirds of the grasses had some green leaves, old or young, during the whole winter. Death is therefore more the effect of drought than of cold, as in Europe.

Table and chart 6 of *Chrysopogon serrulatus* are another good example of a grass having for a considerable length of time higher values than the others in the same veld. (November values.) The second period of maximal values, which at times exceed those even of *Digitaria*, lies between February and the end of April, although the high values are usually restricted to young leaves. *Chrysopogon* is also peculiar in having relatively high minimal values.

As the opposite of *Chrysopogon* is *Fingerhuthia africana* (table and chart 7) which has on an average a low phosphorus content. During the rainy season a few values over 0.3 per cent. are found. Neither plants with very young leaves nor those with well developed roots have high values.

Sporobolus fimbriatus (chart and table 8) behaves entirely differently. For some time before the rainy season it has exceedingly high values, and it is peculiar that they decrease during the first rainy period, again as a result of rapid growth and slow intake of phosphorus. After the second rainy period, from March to the beginning of May, high values are again found. The minimal values, 0.16-0.17 in January and the beginning of February, are on an average higher than those of the other grasses.

Aristida congesta (chart and table 9) seldom reaches 0.3 per cent., but it must be considered that it was never possible to separate old and young leaves. The first rain of Spring undoubtedly increases the phosphorus content of the leaves considerably, but not for long, and later rains have for a short time a favourable influence. The green leaves of *Aristida congesta* and *Aristida uniplumis* have the absolute minimum of 0.11 per cent. of phosphorus in January. The other minimal values are by no means low. It can scarcely be considered an accident that the lowest phosphorus value and the highest dry matter (77 per cent.) fall together. Although a direct relation between the condition of the leaves and the phosphorus content at any time has not been observed, there is no doubt that permanent wilting (see Henrici 1926, 1) which leads to a high dry matter, causes a translocation of phosphorus to the root, and the effect is the same as in the autumnal remigration. In the course of the year the percentage of dry matter at which such a remigration takes place changes, and it cannot be expected that the lowest phosphorus content is always found with the highest dry matter.

Aristida uniplumis (table and chart 10) is a grass which loses the major portion of its green leaves early in the year. The haulms, which remain green for a long time, and become green again at the bottom at the end of winter, take over a part of the photosynthetic function. The leaves are on the whole characterised by a low phosphorus content, the minimal value being even lower that that of *Aristida congesta*. Only once in November is a percentage of 0.32 per cent. reached, and the autumnal decrease of phosphorus begins very early. The second rainy period increases the phosphorus content somewhat, but only for a short time and not to such high values. Considering that the initial value was so low the percentage increase however, is rather great.

Anthephora pubescens (chart and table 11) is another plant with temporarily high values, as several times even in old leaves the percentage is over 0.3 per cent. Even before the rains wilting has no influence on the phosphorus content and only heavy and long continued rains produces really high values. The high values lie in different times compared with other grasses. They are from the middle of November to the end of December and from the middle of February to the beginning of May. Low percentages of dry matter generally correspond to high percentages of phosphorus.

Table and chart 12 of *Eragrostis Lehmanniana* again show maximal values in the rainy season and minimal values in January. Values obtained in the second rainy period are higher than those of the first and *Eragrostis Lehmanniana* had green leaves which contained even more phosphorus than the old leaves in May, all through the winter. There is often an interrelation between high dry matter and low phosphorus content.

The annual, *Tragus racemosus* (table and chart 13) has a special place amongst the investigated grasses, and was taken as an example of a weed. It only came up after the rains and was investigated until it died down. The whole curve is characterised by the lack of low and the abundance of high values, as it reaches the highest value found in Armoedsvlakte grasses of 0.45 per cent. *Tragus* is probably the best example of the fact that the intake of phosphorus on a given soil and in a given climate is specific. From the agricultural point of view this is a pure loss of phosphorus as the cattle did not eat this grass. The condition of the leaves has no influence on the phosphorus content.

Résumé of the leaf results.—In general it is found that the leaves of the perennial grasses with the exception of *Pogonarthria falcata*, have the highest amounts of phosphorus in the rainy seasons, and the lowest during drought and in autumn. In very few cases does a single shower cause an increase of phosphorus on account of the discrepancy between the growth and the intake of phosphorus. Temporary wilting accompanied by a decrease in phosphorus occurs frequently before the rains, but never after. High percentages of dry matter and low phosphorus are, however, sometimes interrelated, when the leaves tend to permanent wilting.

High values may appear in some of the grasses at other times, either in the very young leaves or when the root is specially well developed.

Roots.

The phosphorus content of the root is usually lower than that of the leaves, but exceptions are sometimes found in early spring or late autumn. This is remarkable considering the fact that the phosphorus must reach the leaves from the root. *A priori* it might be expected that the phosphorus would go from a place of high to one of low concentration. This can, of course, only be explained that in the leaves the phosphorus is already in an insoluble organic compound and no more in ionic form. As a rule the phosphorus content of the root has smaller fluctuations than that of the leaves, especially at a time when there are no extreme conditions. From the tables and charts 1-12 there is undoubtedly a maximum of phosphorus during the winter months, but in winter 1925 this maximum was disturbed by the continuous shooting of young leaves. In consequence the maximum is not at the same time for all grasses, but its first appearance is usually in May. The winter maximum is the result of the remigration of the phosphorus from the leaves and haulms. If no big intake from the soil occurs, sprouting is accompanied by a decrease in the phosphorus. It is difficult to estimate the extent of the intake from the soil under veld conditions, but it is probably rather small before the rains and most of the increase is due to translocated phosphorus.

An increase of phosphorus may occur towards winter or when the aerial parts die down on account of the drought. Consequently a kind of autumnal migration occurs in January (see especially tables 11 and 7), but the phenomenon is not as frequent as might be expected from the continuous dying down of haulms and leaves (see page 1090).

There is no doubt that a portion at least of the phosphorus is withdrawn from the dying plant material, but where it goes is not altogether known. It seems probable that it does not migrate back as far as the root, but only to the root crown, where it is stored for the use of the young leaves. Unfortunately the root neck was not analysed separately (although in future work it shall be done), so that, except for a few cases in which there is an accumulation of phosphorus at the bottom of the stem there is no analytical data to bear out this idea.

Discussion of the same factors as were considered for the leaves, reveals the following facts. In two-thirds of the investigated grasses the first rain, at the end of September, increases the phosphorus content, and this is therefore the time at which more phosphorus is taken up by the root. For a short time *Sporobolus fimbriatus, Chrysopogon serrulatus* and *Cymbopogon plurinodis* even show a big accumulation. It must not be concluded, however, that the first rain has no effect on the phosphorus content of *Digitaria, Eragrostis Lehmanniana, Fingerhuthia* and *Aristida congesta*. Probably the phosphorus absorbed was immediately further translocated. In the case of *Digitaria* it has been pointed out that growth does not proceed faster than the intake of phosphorus, as often occurs in other grasses. In principle the same occurs after most of the subsequent rains, but with a few exceptions in February no further accumulation of phosphorus in the roots takes place. The phosphorus is in every case conducted directly to the place where it is needed, the leaves or haulms. During the February rains a minimum of phosphorus occurs in the root, because the growth is so rapid that the drain on the phosphorus is enormous. During the spring rains growth consists largely of elongation of the leaves, in which little phosphorus is used, but in February many new leaves and haulms are formed, and the production of aerial parts requires a large amount of phosphorus.

It is astonishing to note that in addition to these phosphorus minima, scattered maxima occur in the second rainy season (tables 9, 6, 5, 4). The first are of the three grasses already mentioned with regard to the spring rains, and later of *Aristida congesta*. In some other cases there is an apparent maximal value (table 11), where the values at the end of January are very low, and rise again to the average value. Physiologically these maxima must be explained in a similar manner to those at the time of the spring rains. It is noteworthy that these three perennials are all grasses which for a certain portion of the year have very high percentages of phosphorus in the leaves.

From these deductions it is apparent that high root values result from two very different processes, the autumnal translocation of phosphorus from the aerial parts, which may occur at a time of drought, and the renewed intake from the soil when new phosphorus is available after rain. The two processes undoubtedly occur simultaneously on a small scale throughout the whole year, but are most pronounced at the time of maximal values. It is therefore difficult to show that a decrease of phosphorus in the leaves is accompanied by an increase in the root (see table 11).

While it has been proved that high phosphorus values in the root can be the result of two entirely different processes, it must also be pointed out that one factor, rain, may have two different effects, either an accumulation or a decrease, according to the relation between the growth and the phosphorus intake.

Some further points must yet be considered:—

(1) Whether the condition of the root has an influence on the intake and amount of phosphorus. As soon as the root is better developed there is a greater intake, but as the factors which cause good root development also stimulate the growth of the aerial parts, an accumulation of phosphorus rarely occurs. *Before* the rains, when there is root development without rapid growth of the aerial parts, it might be expected, and was indeed found in seven of the nine grasses which were under observation between the 10th and the 25th of September. *Pogonarthia* and *Digitaria* showed no accumulation,

but the former had good roots from the first, and the latter developed them only after the rains *Aristida congesta*, *Fingerhuthia* and *Anthephora* were brought under observation only in September and no conclusions could be drawn.

(2) Whether the different root types are capable of absorbing different amounts of phosphorus. This question also is difficult to answer, as the migration of the phosphorus again interferes. It cannot be too strongly emphasised that a low phosphorus content in the root is more likely to be the result of rapid translocation and consumption in the aerial parts than of a small intake. It is striking that *Eragrostis superba* (table 3), the grass with the thick absorptive tissue par excellence has the smallest root values, that *Fingerhuthia* (table 7) has very small values at the time of the development of the absorptive tissue, and that *Themeda* (table 1) and *Digitaria* (table 2) which have scarcely any absorptive tissue, never have such low values. The grasses which temporarily have high phosphorus values in the aerial parts (*Chrysopogon*, *Cymbopogon*. *Digitaria* and *Sporobolus*, tables 6, 4, 2, 8) have feebly developed, if any, absorptive tissue, and it might be supposed that the intake of these roots is better. Under these circumstances, however, there can be no inter-relation between the two facts.

As has been stated in the general introduction, not only excessive growth may cause a minimum in the phosphorus content of the roots, but also, in extreme cases, the dying down of roots or root parts under the arid conditions of January (*Digitaria*, table 2; *Pogonarthria*, table 5; *Sporobolus*, table 8; *Aristida uniplumis*, table 10; *Eragrostis superba*, table 3), but this phenomenon is not at all general. It may be conclusively stated, however, that drought, like rain, may have two effects, an increase caused by translocation of phosphorus from the aerial parts to the root, or an apparent decrease on killing the roots or root parts (which is the most extreme case. See paper on " Suction Force ").

It must still be considered whether the phosphorus content of the roots of the different grasses is about the same, or whether there are individual differences as in the leaves. There are differences on several points. The lowest values found vary from 0.036 per cent. to 0.068 per cent. and the highest from 0.120 per cent. to 0.260 per cent. Low maxima and low minima do not occur in the same species. *Fingerhuthia* (table 7) with the lowest maximum has a minimal value of 0.054 per cent.; *Cymbopogon* (table 4) with the highest maximum has a minimum of 0.062 per cent., but on the other hand *Aristida uniplumis* (table 10) has the lowest minimum with a maximum of more than 0.200 per cent., about the same as *Chrysopogon* (6) with the highest minimum. The position of the maximum and minimum does not define the general order of the phosphorus percentages in the root. *Anthephora*, *Aristida uniplumis*, *Sporobolus fimbriatus*, *Cymbopogon plurinodis* and *Themeda* (charts 11, 10 8. 4, 1) have temporarily high root values, not only in winter as in most of the other grasses, and their average root value is higher. *Pogonarthria* (chart 5) on the contrary, has a low average phosphorus content. *Sporobolus* (chart 8), *Chrysopogon* (6) and *Cymbopogon* (4) have their high root values at or before the time of high leaf values, especially in November.

Haulms.

From the tables 1-13 it is apparent that young (often not very young) haulms have a relatively high phosphorus content, and that the spike contains more than the axis or the stalk. The phosphorus content may increase until the spikes flower, but during and particularly after flowering, there is a decrease. There is therefore no storage of phosphorus in the young dough seeds. Only in exceptional cases when real hard apparently ripe seeds were observed later, was there an increase of phosphorus for the final formation of the seed. Such hard seeds were found abundantly in *Aristida congesta* (9) and *Tragus racemosus* (13) and a few in *Eragrostis superba* (3), *Eragrostis Lehmanniana* (12) and *Sporobolus fimbriatus* (8). With the regular and frequent veld observations it is not probable that such seeds were overlooked, and yet only unripe dough seeds, empty husks or husks with shrivelled seeds were found. It must be accepted that for some reason the formation of seeds capable of germination is impossible, and the seed shrivels. This fact was well brought out in *Eragrostis superba*, which produced haulms for the third time towards winter, and whose seeds were in the dough state at the first frost, after which they were observed to be shrivelled. In summer this factor is naturally excluded, but the end result is the same. An explanation is suggested by comparison with the weed *Tragus racemosus* (13). Here enormous amounts of phosphorus are transported to the ripening seeds, the phosphorus value going up to three times as much as that of other grasses. It really appears as though, in the other grasses, the lack of phosphorus is the reason for the inferior seeds. Although this explanation is not the only possible one, it is to a certain degree probable. It is also possible that there is some other reason for the seed not developing fully, and the fact that there is no increase in phosphorus simply a secondary consideration. Experiments on manured plots in the climate of Vryburg would furnish some information, but up to the present this has not been done.

It is peculiar that the perennial grasses attempt to produce haulms several times in the course of a season. In 1924-25 there were usually two appearances, as the first, shooting in October and November, died down during the February drought, and contained scarcely any hard seeds. The second haulms, produced after the February and March rains were mostly killed by the frosts in May. However, from these haulms a few ripe seeds were obtained, but it is doubtful whether they were capable of germination. *Aristida congesta* and *Tragus* are exceptions to this rule. No exact date on which new haulms were observed can be given, as they were especially in spring, very scattered, and haulms gathered in subsequent weeks were rarely of progressive ages.

As has been pointed out in the general introduction, a loss of phosphorus from the haulms may be expected on two occasions, once on flowering and again when the seeds are falling. The loss of phosphorus by the pollen does not appear to be considerable, but in most of the grasses it is distinctly noticeable. The loss of phosphorus on seeding can only be conclusively proved in those grasses which produce seeds capable of germination, particularly *Tragus racemosus* (13) and *Aristida congesta* (9) and in some exceptional cases of *Sporobolus* (8) and the two species of *Eragrostis* (3, 12). Some of the investigated grasses (*Anthephora*, *Eragrostis superba*, *Chrysopogon, Fingerhuthia* and *Aristida congesta*) lose their spikelets together with the ripe or shrivelled seeds, whereas others (*Cymbopogon, Themeda, Aristida uniplumis, Pogonarthria falcata*) keep the empty spikelets on the stalk throughout the whole winter. *Digitaria* and *Sporobolus* first lose their seeds, and some time after the empty spikelets fall. It is scarcely necessary to mention that in the first case the loss of phosphorus to the plant is greater than in the second, as the husks contain a fair proportion of phosphorus. This phenomenon is especially noticeable in late autumn.

It is certain that as soon as the seeds, whether ripe or shrivelled, disappear from the spikelets a translocation of phosphorus from the haulm and, if still present, from the spike, to the root takes place (see especially tables 12, 11, 10, summer spikes). During this translocation the stalk may become richer in phosphorus than the spike (table 10). Towards winter this translocation becomes more marked and as the haulms dry out the phosphorus migrates back towards the root, and in the internodes of the stalk, towards the root increasing amounts of phosphorus are found. The lowest internode remains green and turgescent when the rest of the haulm has completely dried out.

Towards spring, when the old haulms of some of the grasses become green again, there is an increase of phosphorus (*Pogonarthria* 5, *Sporobolus* 8, *Eragrostis Lehmanniana* 12). This lasts only for a short time and disappears when the new leaves appear (*Aristida uniplumis* 10).

In some cases new haulms are produced as late as May (*Sporobolus*, table 8. *Aristida congesta*, 9). Compared with the haulms of summer, they have all a low phosphorus content with the exception of *Aristida congesta*, which even towards winter produces haulms rich in phosphorus.

A comparison of the percentage of phosphorus in the haulms with that of leaves investigated at the same time, shows that only occasionally the spikes have the higher value. The exceptions are found in the very young haulms and *Tragus racemosus* and *Aristida congesta*, the two grasses which produced a large number of seeds capable of germination. Results obtained from other grasses differ so much from those of European experience (*Russel*, 1921, p. 67; *Johnson*, 1908, p. 171, in which older literature is discussed; *Hall*, 1919, p. 63) that they must be discussed more fully. In plant physiological text-books this migration of the phosphorus and other substances is not sufficiently emphasised, and more references are found in agricultural literature.

Unfortunately the original classical literature of *Arendt* (1859) and *Hornberger* and *E. v. Raumer* (1882) is not at my disposal, and the discussion must be confined to tables reprinted in *Swart* (1914), *Johnson* (1908) and *Czapek* (1921, II). From these data it is obvious that the ripening seed of any cereal is provided with phosphorus, so that when ripe it contains more than twenty times as much phosphorus as the leaves (Johnson, 1908, pp. 171 and 238). It is possible that in European meadow grass the relation is not so extreme, but unfortunately no data are available. There seems to be no doubt, however, that there is a relation between poverty in phosphorus and the production of seeds capable of germination. Tables 14-26, which will be discussed in the next paragraph, show still more clearly the difference between a plant producing seed capable of germination and one producing inviable seeds or seeds which do not mature.