The phosphorus and nitrogen nutrition of bambara groundnut (*Vigna subterranea* (L.) Verdc.) in Botswana soils

An exploratory study

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An exploratory study

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PROPOSITIONS

1. It is a paradox that an indigenous African crop, which produces an almost completely balanced food, is one of the most drought tolerant, easy to cultivate crops which makes little demand on the soil, should be relegated in its own countries without being accorded any research attention and, worse still, earns the "accolade" of poor man's crop.
   Modified after Doku, V.E. (1997). Problems and prospects for the improvement of bambara groundnut. Proceedings of the international bambara groundnut symposium, University of Nottingham U.K. 23-25 July 1996. University of Nottingham, U.K. pp.19-27.

2. The suitability of bambara groundnut as a low-input smallholders' crop, depends on a combination of a low P requirement, an effective N_2 fixing capacity, flexibility in the length of the growing period and shade tolerance.

3. The soil moisture content is in Botswana the most important factor determining soil P availability and P uptake by bambara groundnut.
   This thesis

4. Application of P fertilizer to bambara groundnut improves P uptake and growth only if rates exceed a certain level.
   This thesis

5. Reduced early plant growth due to P stress has severe negative consequences for pod filling. P application at a later stage cannot amend this situation.
   This thesis

6. Although Botswana soils are deficient in P, farmers growing rainfed bambara groundnut cannot be advised to use P fertilizers for this crop. Application of P in a crop rotation including bambara groundnut, however, might be a feasible option to improve the P nutrition of this crop.

7. The success of the bambara groundnut crop in the preceding year can be observed the following year.
   Linnemann, A.R. (1990). Cultivation of bambara groundnut (Vigna subterranea (L.) Verdc.) in Western Province Zambia. Tropical Crops Communication 16, Dept.Trop.Crop Sci., Wageningen Agricultural University, pp.33.

8. In further research on phosphorus fertilization of bambara groundnut, the role and contribution of mycorrhizas in P nutrition should get attention, especially because bambara groundnut is often grown in P-poor soils and its rooting is often poor.
Broek, H.A.M. van den (1998), MSc thesis, WAU.

9. The future of Botswana agriculture lies below the topsoil.

10. Our minds are like a parachute, and we crush when they do not open up.

Abstract

Plant species differ in their mineral nutrient requirement and nutrient use efficiency. Information on the phosphorus (P) and nitrogen (N) requirement of the leguminous crop bambara groundnut (*Vigna subterranea* (L.) Verdc.) is scanty and sometimes contradictory. This has led to a study on mineral nutrition of bambara groundnut with the following objectives: (i) to investigate the effects of applied P and N on growth and development of bambara groundnut in Botswana soils, and (ii) to investigate the P and N uptake, shoot concentrations at different growth and development stages of bambara groundnut and how uptake, internal concentration and growth are related. The experimental programme consisted of six pot experiments on P and N ferilization, a large field experiment with P and irrigation as treatments, and a farm survey to study the P status of soils and bambara groundnut plants grown in farmers' fields.

In low P soils, bambara groundnut responded to fertilizer P only when it becomes available to the seedling within two weeks after sowing. It was shown that soil moisture rather than P in the soil determined P availability to bambara groundnut. Analysis of the critical shoot P concentration showed that in traditional farms of Botswana bambara groundnut was always grown under suboptimal P levels. Therefore, in low P soils, P fertilization will be beneficial to bambara groundnut only when the soil moisture content during the first to weeks after sowing is near field capacity and the fertilizer is placed close to the seedling.

Both under P-limiting and P non-limiting conditions, bambara groundnut seemed to be able to meet its N requirement by N_2 fixation, probably supplemented with mineral N from the soil. Therefore, N fertilization is not necessary and can sometimes have negative effects on plant growth and lead to reduced seed yields.

Keywords: bambara groundnut (*Vigna subterranea*), phosphorus, nitrogen, soil moisture, Botswana.

Dedicated to the memory of my parents Gabofetane and Modirwa, and grandparents Thapiso and Seretsenye Letsididi.

Preface

This thesis is a spin-off from an European Union (EU) funded project on bambara groundnut in which my home institution, Botswana College of Agriculture (BCA), and Wageningen Agricultural University (WAU) collaborated with other universities in Europe and Africa to evaluate the potential for bambara groundnut as a food crop in semi-arid Africa. The work reported in this thesis addresses one of the project objectives "to recommend suitable management practices to stabilise the yields of bambara groundnut under rainfed conditions" and in particular the mineral nutrition of bambara groundnut. I hope the understanding of the phosphorus and nitrogen nutrition of bambara groundnut as found in this thesis, will complement the work done by other partners in the EU-programme on bambara groundnut to increase the yield of the crop. Although my research work addressed part of the objective of the EU-programme on bambara groundnut research, it was however funded separately by Botswana College of Agriculture and Wageningen Agricultural University.

During the struggle to get the research work done in Botswana, I got tremendous support from members of staff of BCA and the Department of Agricultural Research (DAR) of the Ministry of Agriculture which is highly appreciated. I want to recognise the contribution of Dr. J.S. Kiazolu (former Senior Lecturer in Soil Science, BCA) at the very inception of the research work which laid a solid foundation for the subsequent research programme. From DAR I want to recognise and express my gratitude to Dr. G.S. Maphanyane for her day-to-day guidance in conducting experiments and writing reports. Your commitment and the criticism and encouragement you gave helped this project to come to a happy ending. I thank my promotor Prof. Dr. Marius Wessel for his guidence in preparation of the research proposal and the thesis. You did not only enrich my stay at WAU academically, but also showed me part of the The Netherlands and its heritage. I thank my co-promotor Dr. Willem Keltjens for his patience and always finding time to read and discuss my manuscripts. It was gratifying to have someone like you as a supervisor. The assistence and friendship of Conny Almekinders, Martin Brink, Jaap Nelemans, Mary Omosa, René Rietra, Willeke van Tintelen, Chris van Uffelen, Liping Weng, collegues at both Departments of Agronomy and Soil Science & Plant Nutrition at WAU is appreciated.

Many people were involved in the execution of experiments and the farm survey reported in this thesis. First of all I thank my field assistant Agisanyang Ngwako and the casual labourers from the Content Farm in Sebele who were involved in the day-to-day activities of both the field and pot experiments. Without their cooperation I would not have completed the project in time. The irrigition design for the field experiment was the idea of Mr. Otsoseng Oagile and the late Petso Motswasele, and it is appreciated. I am gateful to Mrs. T. Mpuisang and Mrs. T.K.Y. Morake who assisted in determining the amount of irrigation water applied and matters regarding pest control, respectively. I want to thank Keikanelwe Ntone, Kgatleng District Agricultural staff and their farmers for assistance and cooperation in the farm survey.

There was the laboratory work to be done and I thank all those who provided technical assistance and cleaning of the glassware. I especially want to thank B. Ditshane, A. Fisher, Mr. Gopane, L. Letsine, B. Makoba, O. Mogobe, C. Moloi, S. Moroka, L. Mosarwe, B. Mosomong, R. Mothokodise and L. Patrick.

The data collected was statistically analysed with the assistance of J. Makori, Dr. R.M. Sakia, B. Sebolai, the late Neo Seitshiro and others, and I am grateful.

I am also a part-time livestock farmer, and always I request relatives to take responsibility during my absence. I thank my uncles E.P.S. and S.G.G. Letsididi and my sister Doris Ramolemana for their patience and accepting extra responsibilities to maintain my hobby. I also thank my in-laws, Lizzy and George Rakgoasi, for the support they gave my wife during my absence.

Finally, I want to express my appreciation to my family, Sue, Bojotlhe, Thato, Tshepo and Maipelo, for their patience, and especially the encouragement and support of my wife. All this was through the love of God. Thank you.

GR.

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Chapter 1

General introduction

1.1 Bambara groundnut

Importance

In the past decades a combination of high yielding cultivars, fertilization, irrigation or adequate rainfall gave a spectacular increase in food production in the humid tropics of Asia. This did not happen in Africa and especially in the semi-arid zones food production did hardly increase. Lack of water and income precluded the use of the so called Green Revolution Technology, and this means that the farmers have to rely on rainfed food crops which are adapted to the prevailing environment. One of the leguminous crops adapted to a wide range of climatic conditions, but especially semi-arid conditions is bambara groundnut (*Vigna subterranea* (L.) Verdc.).

Bambara groundnut is adapted to a wide range of soils and its popularity with small farmers in Africa is attributed to the ability to produce yields on poor soils. Like other legumes it can fix atmospheric nitrogen through symbiosis with rhizobia. As a leguminous crop, bambara groundnut is useful in crop rotations because it may improve the nitrogen status of the soil. Mukurumbira (1985) found that bambara groundnut has a higher residual nitrogen effect than groundnut, maize or fallow. The crop has also been reported to be drought tolerant and able to produce some yield where other crops such as groundnut (*Arachis hypogaea*) fail (Linnemann and Azam-Ali, 1993).

Bambara groundnut contributes to the livelihood of small farmers as a source of protein and income (Linnemann and Azam-Ali, 1993; Brink *et al.*, 1996; Mulila-Mitti and Kanenga, 1997; Sesay *et al.*, 1997). The crop is mainly grown for the seeds, but the vegetative parts may be used as fodder. An important advantage of bambara groundnut is that not only mature, but also immature seeds can be consumed by humans.

The major producers of bambara groundnut are Nigeria, Niger, Ghana and Ivory Coast, but the crop is also widely grown in eastern and southern Africa (Mazhani and Appa Rao, 1985; Linnemann and Azam-Ali, 1993). The annual world production is estimated to be around 330 000 MT, with about 50% produced in West Africa (Coudert, 1982). The importance of bambara groundnut in Botswana is discussed in section 1.3.

Chapter 1

Growth and development

Reproductive development in bambara groundnut is known to be influenced by temperature and photoperiod. In glasshouse studies Brink (1998) found that bambara groundnut selections from Botswana and Zimbabwe were mostly not sensitive to day length with regard to onset of flowering but all were strongly sensitive with regard to the onset of podding. The rate of progress from sowing to flowering was influenced by temperature only, while the rate of progress from sowing to podding was influenced by both photoperiod and temperature. It was also found that leaf formation continues for a longer period under long day length, resulting in a greater leaf area per plant. However, total dry weight was not influenced by day length but the percentage of dry matter accumulated in pod structures was influenced indirectly by the effect of photoperiod on podding. For bambara groundnut selections from Botswana ('DipC94' and 'GabC92'), it was found that under day lengths of 12.0 to 14.0 hours day^{-1} it takes about 45 days from sowing to flowering and about 31 days from flowering to podding when the average monthly temperatures vary between 26.8-32.5 °C and 13.2-19.3 °C during day and night, respectively. The onset of podding is the most important event in bambara groundnut development as it coincides with a major shift in assimilate partitioning, mainly directed towards pod growth. The photoperiod difference between locations in Botswana was found not to be large enough to merit using selections with different photoperiod sensitivities for different locations (Brink, 1998). The time from sowing to maturity of bambara groundnut plants in the field is reported to range from 90 to 170 days (Linnemann and Azam-Ali, 1993).

In glasshouse studies at Nottingham University, soil moisture deficit was found to decrease plant growth, but did not affect the time to flowering. The onset of podding was delayed in the stressed plants, and the dry matter/water use ratio varied from 1.8 to 3 g kg^{-1} for irrigated and low moisture treatments, respectively. Dry matter partitioning to roots was found to be greater than 40% during early growth and was consistently greater for the low moisture treatments. Harvest indices were extremely small under low moisture conditions with a mean of 0.03, compared to 0.47 under irrigation (Collinson *et al*, 1996; Anon., 1997).

At Wageningen Agricultural University in glasshouse studies, bambara groundnut plants grown in hydroponics with high P-supply continued vegetative growth longer than plants with low P-supply. Low P-supply plants invested more in their root system than plants with non-limiting P-supply, leading to shoot-root ratios of 2.6-3.0 in low-P plants, compared to ratios of 4.1 to 7.3 for high-P plants (Anon., 1997).

1.2 Research

1.2.1 General

According to Rachie and Silvestre (1977), the most important legume crops in Africa are cowpea (*Vigna unguiculata*), groundnut (*Arachis hypogea*) and bambara groundnut. Seed yields of bambara groundnut in Africa are on average 650-850 kg ha^{-1}. Compared to the other two legume crops (cowpea and groundnut), bambara groundnut has received very little research attention although it has a good potential as a hardy crop (Linnemann, 1994). However, recently bambara groundnut benefited from a research programme "Evaluating the potential for bambara groundnut as a food crop in semi-arid Africa" (Anon., 1997). The project, which was funded by the EU, was a collaboration between European (University of Nottingham-United Kingdom and Wageningen Agricultural University-The Netherlands) and African (University of Botswana-Botswana, University of Sierra Leone-Sierra Leone and Sokoine University of Agriculture-Tanzania) countries. Some of the project objectives were the following:

1. To identify suitable agro-ecological regions, seasons and agronomic practices for the cultivation of bambara groundnut genotypes in Botswana, Sierra Leone and Tanzania.
2. To predict yields of bambara groundnut genotypes in these zones and the sensitivity of yield to genetic and environmental factors.
3. To recommend suitable management practices to stabilize the yields of bambara groundnut in rainfed environments.
4. To establish general principles underlying the growth and development of bambara groundnut in rainfed environments.

Experimental evidence from the project on bambara groundnut indicated that bambara groundnut is capable of attaining significantly greater yields than those achieved by farmers. In controlled-environment glasshouse experiments, yields of more than 3.5 t ha^{-1} were achieved under non-limiting soil moisture. Under rainfed conditions, field crops achieved yields in excess of 3.0 t ha^{-1}. Because of the effect of day length on podding, sowing date was identified as having a crucial influence on final pod yield (Anon., 1997).

1.2.2 Fertilizer studies

Attempts have been made to increase bambara groundnut yield through application of nutrients and improvement of the nitrogen fixing capacity.

Phosphorus

Sandy soils in Africa are usually deficient in nutrients such as phosphorus, and these soils are predominantly used for bambara groundnut. Research conducted in Malawi, Nigeria, Swaziland, Zambia has failed to show any response of bambara groundnut to the application of phosphorus fertilizers at rates up to 147 kg P ha^{-1}, and sometimes yields were even depressed by P fertilization (Anon., 1975; Cumberland, 1978; Anon., 1979; Anon., 1980; Nnadi *et al.*, 1981; Musonda, 1988). However, Tanimu and Yayock (1990) reported in Nigeria in a field experiment with different combinations of phosphorus, potassium and nitrogen a significantly higher yield from 22 kg P ha^{-1} than at other phosphorus levels. Wassermann *et al.*, (1984) in South Africa reported an increase in total DM at a P rate of 30 kg P ha^{-1}, but seed yield was not increased.

In a hydroponic experiment at Wageningen Agricultural University, bambara groundnut has shown P-toxicity symptoms in a nutrient solution where other crops were grown without any problem (Kamstra, 1995). However, it should be noted that nutrient uptake in a nutrient solution may be different from that under soil conditions where the uptake is affected by more factors.

Nitrogen

The response to nitrogen application is generally poor. For example, in Nigeria a starter application rate of 20 kg N ha^{-1} did not increase yield (Nnadi *et al.*, 1976) or even decreased it, although the effect was not significant (Tanimu and Yayock, 1990). Increasing the level of nitrogen up to 140 kg N ha^{-1} did not significantly increase yield in Malawi and Zambia (Anon., 1971, 1973; Lungu and Mbewe, 1986; Musonda, 1988), and in some cases yields decreased (Anon., 1970). However, Dadson and Brooks (1989), in Togo-West Africa, reported a significant increase in total dry weight and seed yield from a treatment of 50 kg N ha^{-1}. Stanton *et al.*, (1966) (according to Linnemann and Azam-Ali, 1993) reported a yield increase from fertilizing with 8.5 kg N ha^{-1} (40 kg ha^{-1} sulphate of ammonia) three weeks after sowing. An increase in yield was also reported in Malawi when 38 kg N ha^{-1} (180 kg ha^{-1} sulphate of ammonia) was banded on the ridge one month after planting (Anon., 1962). Late application of nitrogen has been found to improve plant growth and yield, and reduced senescence in other leguminous crops such as cowpea (Tayo, 1981, 1986: Elowad and Hall, 1987) and soybean (Isfa, 1991).

A combination of nitrogen and phosphorus applied at sowing in Malawi, Nigeria and Zambia generally gave a marginal increase or could even depress yields (Anon., 1970, 1973; Musonda, 1988; Tanimu and Yayock, 1989, 1990).

Dinitrogen fixation

Bambara groundnut has been reported to nodulate with bacteria of the cowpea inoculation group (Somasegaran *et al.*, 1990), while Gueye and Bordeleau (1988) in Senegal found that both indigenous and introduced *Rhizobium* strains nodulated all 24 bambara groundnut genotypes tested. Experiments have also been conducted to evaluate the effect of *Rhizobium* inoculation on the quantities of nitrogen fixed by bambara groundnut. In both greenhouse and field experiments, inoculation with *Rhizobium* increased nodule number, nodule weight, N content of the leaves, stems and roots, and N accumulations surpassed those gained by the mineral N fertilizer treatment (Thompson and Dennis, 1977; Brooks *et al.*, 1988; Mafongoya, 1988; Gueye, 1992). Good nodulation through inoculation has been observed to increase the nitrogen fixing capacity of bambara groundnut and could provide up to 70% of the plant N (Gueye, 1992). In Ghana, nitrogen fixation by bambara groundnut was also reported to increase soil N by 106 kg ha^{-1} in an Eutric Nitosol (Dennis, 1977).

Application of nitrogen at a rate of 50 kg N ha^{-1} in Togo, West Africa was reported to suppress nodulation in bambara groundnut (Dadson and Brooks, 1989). Suppression of nodulation has also been reported in other legumes such as cowpea when N was applied at rates of more than 20 kg ha^{-1} (Graham and Scott, 1984). Thompson and Dennis (1977) in Ghana also observed a decrease in the number of nodules of bambara groundnut when Ca and Mg were added.

Potassium and other nutrients

An application of 25 kg K ha^{-1} increased yields in an experiment in Swaziland (Anon., 1979). Tanimu and Yayock (1990) in Nigeria also reported an improvement in seed yield from an application of 25 kg K ha^{-1}. However, Musonda (1988) did not get a response with rates up to 183 kg K ha^{-1}.

For an increase of yields, Messiaen (1975) recommended the use of a fertilizer containing phosphorus and potassium. Indeed some studies seem to indicate that potassium either combined with phosphorus or nitrogen would increase yield. Tanimu and Yayock (1989) obtained the highest yield from a combination of 25 kg K ha^{-1} plus 11 kg P ha^{-1}. Bambara groundnut responded favourably also to the application of 50 kg N ha^{-1} (229 kg ha^{-1} ammonium sulphate) plus 67 kg K ha^{-1} (113 kg ha^{-1} potassium chloride) (Musonda,1988). A combination of three nutrients (N, P and K) in Nigeria, Senegal and Zambia seemed to have no effect and sometimes depressed yields (Tardieu, 1958; Goli and Ng, 1987; Anon., 1989). In Congo, Ghana and South Africa, liming was reported to increase bambara groundnut shoot dry weights and yields (NILCO, 1960; Thompson and Dennis, 1977; Wassermann *et al.*, 1984).

1.3 Bambara groundnut in Botswana

Botswana lies in the centre of Southern Africa, between 18° and 27° south of equator, and 20° and 29° east of the Greenwich. The climate is semi-arid to arid, average rainfall varies from 650 - 700 mm in the extreme north, to 150 - 200 mm in the extreme southwest, with 400 - 500 mm in the eastern side of the country. Most rain falls in the summer, and generally starts in late October and continues till March/April. There is great variation in the amount of rainfall and distribution each year. Summer temperatures are around 23 to 28 °C with a range of about 10 °C above or below this average (Sims, 1981). Between October and April, day length changes from 12.7 hours in October to 13.7 hours in December and back to less than 12 hours in April (Harris and Azam-Ali, 1993). Between 60 and 70% of the country is covered by the Kalahari sands. Most of the crop farming activities are in the eastern side of the country where the soils are sandy loams, and loamy sands with small areas of heavier soils in depressions and valley bottoms. Natural fertility of these soils is low, being deficient in P, having low levels of mineral N and very little organic matter (Sims, 19981; Beynon, 1991).

In Botswana, bambara groundnut is usually grown for both home consumption and for sale and this dual purpose is the main reason for growing the crop. The main problem for bambara groundnut cultivation in Botswana is low rainfall. The crop is mainly grown by women who also carry out most of the work. The area under cultivation per farm is small, usually less than 0.5 ha. Intercropping with cereal crops occurs but most of the farmers grow it as a sole crop. The plant densities vary between 2 500 and 167 000 plants ha^{-1}. About half of the farmers plant the crop in rows, while the other half broadcast and plough to cover the seed with soil. With regard to crop management, most farmers plough their fields and weed once a season, while all farmers practice earthing-up (cover the stems and pods with soil). The use of external inputs such as fertilizers and pesticides is low. Yields obtained are low, usually less than 500 kg ha^{-1} (Brink *et al.*, 1996). Information is lacking on fertilizer response of bambara groundnut in Botswana soils. The map of Botswana is given in Appendix 1 and climatic data in Appendix 2.

1.4 Objectives of the study

Reasons to study the effects of P and N fertilizer application on growth of bambara groundnut were:

- that little systematic research has been carried out in this field and the results so far obtained are not in agreement with each other;
- that an important objective of the EU research programme was "to recommend suitable management practices to stabilize the yields of bambara groundnut in rainfed environments", which includes fertilizer use;
- that phosphorus is the most limiting nutrient in Botswana soils; and
- that furthermore soils are low in organic matter, thus also low in mineralizable N.

In view of these facts, a study was undertaken to increase the understanding of the P and N nutrition of bambara groundnut and if possible to make fertilizer recommendations for growers in Botswana. The hypotheses of the study were that:

(1) phosphorus is limiting growth and development of bambara groundnut in Botswana soils;

(2) soil moisture content may limit the P uptake and the N_2 fixation process or both;

(3) bambara groundnut has a high P efficiency (uptake and internal use);

(4) limiting P supply affects N supply to bambara groundnut through suboptimal N_2 fixation;

(5) there may be need for additional N in certain development stages when:

(i) the N_2 fixation process is not yet active (early growth);

(ii) when this process slows down (pod filling stage); and

(iii) when P supply is no longer a growth limiting factor.

The main factors underlying these hypotheses and their interrelationships studied are schematically shown in Figure 1.1.

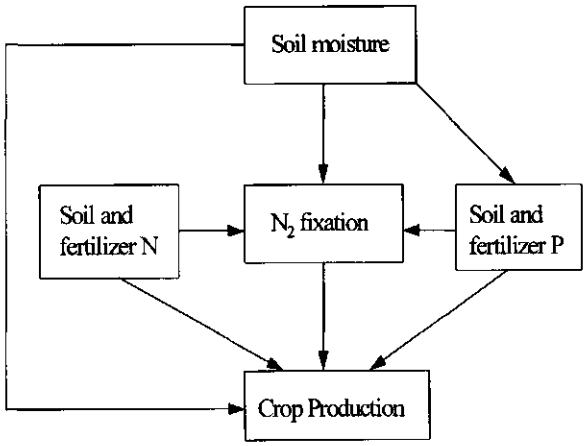

Figure 1.1. Diagram showing the possible direct and indirect effects of phosphorus (P) and nitrogen (N) fertilization, N_2 fixation and soil moisture on crop production.

1.5 Outline of the thesis

Following the Introduction, Chapter 2 describes the response of bambara groundnut to P fertilizer in a pot and a field experiment under different soil moisture regimes. In both experiments the same soil with a low P content was used. The finding that the responses of bambara groundnut to P fertilization in the pot and field experiment differed led to three hypotheses; (i) that lack of response in the field may be an indication of low P requirement, (ii) that bambara groundnut has a high P efficiency (uptake and internal use), and (iii) that the positive response in the pot experiment in which P was thoroughly mixed with the soil is an indication that extra P might be only effective if applied and available at the very early stage of plant development. In Chapter 3.1, the P requirement and P efficiency of bambara groundnut are compared to those of maize and pigeon pea. The timing of P application on bambara groundnut is discussed in Chapter 3.2. The findings that in the previous experiments addition of fertilizer P did not affect the P concentrations in the shoots was a reason to investigate the critical P concentrations of bambara groundnut. These were established in a sand culture experiment reported in Chapter 4.1. The critical P concentrations were subsequently used to assess the P nutrition of bambara groundnut plants in farmers' fields (Chapter 4.2). The critical P concentrations indicated that in the preceding experiments bambara groundnut plants, also those receiving additional P, had been growing under P limiting conditions. This prompted the research reported in Chapters 5 and 6 to find out if nitrogen would become the next limiting factor once the P supply and uptake is adequate. Finally in Chapter 7 the main findings of the study are discussed in relation to the hypotheses, the results from research on other tropical legumes and the bambara groundnut growing practice in Botswana.

Chapter 2

Response of bambara groundnut (*Vigna subterranea* (L.) Verdc.) to phosphorus fertilization

2.1 Introduction

As reported in Chapter 1 bambara groundnut generally shows a poor response to P fertilization even when grown in P-poor soils. Furthermore no information is available on the response of bambara groundnut to P fertilization in Botswana, where low soil P availability is one of the limiting factors in crop production (Beynon, 1991). Therefore, a series of studies was undertaken to investigate the growth- and development response of bambara groundnut to applied P in a representative low available-P soil. As a first orientation, a short-duration pot experiment was conducted to investigate the effect of P fertilization on the early growth of bambara groundnut (from sowing to flowering). Subsequently the response to P was studied in a field experiment with and without irrigation.

2.2 A preliminary pot experiment

This was a short term preliminary pot experiment conducted in a soil collected from a site intended for a P fertilization field experiment to determine whether on low P soils bambara groundnut responds to P fertilization. Furthermore, some attention was paid to possible differences in response among cultivars and the capacity of the N_2 fixation system under natural soil conditions. Two bambara groundnut selections were grown in a P-poor soil fertilized with P at seven rates, with or without inoculation of the seed with a well known *Rhizobium* strain.

2.2.1 Materials and methods

The experiment was conducted on the grounds of the forestry nursery of the Botswana College of Agriculture, Sebele (24°33′ S; 25°54′ E; 994 m) for a period of 51 days and it ran from 13 th December 1994 to 2 nd February 1995. Maximum and minimum temperatures varied between 33.1-34.7 °C and 19.2-19.5 °C, respectively. A loamy sand (Ferric Luvisol; Joshua, 1991) collected from a 40 year old bush fallow field was used. The soil was sieved to remove stones and analysed to determine the main chemical characteristics which are given in Table 2.1. The determination of pH was in $CaCl_2$ (0.02 *M*) using a 1:5 soil/solution ratio; P by Bray no.2 extractant; exchangeable basic cations and CEC by ammonium acetate, and organic carbon by the Walkley and Black (1934) method.

The treatments were seven P fertilizer levels (0, 80, 160, 240, 320, 400, 480 mg P per pot; on weight basis of 2 000 000 kg soil ha^{-1} corresponding to 0, 10, 20, 30, 40, 50, and 60 kg P ha^{-1}), two inoculum levels (with and without), and two bambara groundnut selections ('Diphiri Cream' and 'Zimbabwe Red'). 'Diphiri Cream' is a local selection (cultivar) collected from a farmer in the Southern part of Botswana near Kanye, while 'Zimbabwe Red' is a selection from Zimbabwe. The experiment was arranged in a completely randomized design with treatments replicated three times. Single superphosphate was crushed and thoroughly mixed with the soil. No mineral nutrients other than P were added. The bean inoculant bacteria *-Rhizobium leguminosarum* biovar *phaseolin-* (5×10^8 cells g^{-1}) was applied at the rate of 500 g per 50 kg seed, with sugar solution used as sticker. White plastic bags with a top diameter of 25 cm and a depth of 24 cm holding 16 kg of soil were used. Three seeds were sown per bag and thinned to one seedling 17 days after sowing (DAS). The soil moisture content was maintained at about field capacity, and the plants were exposed to natural light intensity, temperature and day length.

The number of leaves of individual plants was taken weekly starting from 28 DAS. The experiment was terminated at flowering stage, 51 DAS. At harvest, the plants were separated into shoots (leaves, petioles and stems), roots and nodules. Fresh weight of nodules was taken, and other plant parts were oven-dried at 70°C for 24 hours and weighed. The shoots were then separated into leaf blades, petioles and stems. The dried leaf blades were ground in a plant grinder with a two mm sieve and subsequently analysed for N and P. Samples of 1.25 g dry material were digested in a 20 ml sulphuric acid-selenium mixture at 330 ^{0}C for 2 hours using a Tector 2020 Digester. After cooling, four ml of hydrogen peroxide was added to the digest and the digestion was continued for two hours at 330 ^{0}C. The digest was made up to 200 ml with distilled water, and the above mentioned elements were then determined. Nitrogen was determined from a sample of 25 ml using a BUCHI 323 distillation unit and titrated with 0.0055 M H_2SO_4. Phosphorus was determined with a UV Spectrophotometer. The data were subjected to ANOVA using SAS (1985) statistical programme and differences between means were tested for significance with the least significant difference ($LSD_{0.05}$).

Table 2.1. The main chemical characteristics of the soil used in the preliminary pot experiment.

pH-$CaCl_2$	P-Bray (mg P kg^{-1})	Organic carbon (wt.%)	Exchangeable cations (cmol (+) kg^{-1})				CEC (cmol (+) kg^{-1})
			Ca	Mg	K	Na	
4.8	8.4	0.4	1.30	0.93	0.60	0.04	4.69

2.2.2 Results

Number of leaves

The number of leaves per plant significantly increased with an increase in phosphorus rate (Fig. 2.1a). The highest number of leaves per plant was observed at the highest P rate. The two selections differed significantly at 35, 42 and 49 DAS with higher number of leaves for 'Diphiri Cream' than 'Zimbabwe Red'. There was no significant effect of adding bean inoculant.

Dry matter production

Phosphorus fertilization significantly increased shoot dry matter (DM) of the two bambara groundnut selections at 51 DAS with no significant difference between them (Fig. 2.1b). The shoot DM of both selections increased linearly ($r^2 = 0.90$) with increasing P rate. At a P rate of 480 mg P pot^{-1} shoot DM was increased with about 50% relative to the unfertilized treatment. Phosphorus fertilization had no significant effect on root DM and nodule fresh weight. There was also no significant effect of adding bean inoculant on shoot and root DM, neither on nodule fresh weight.

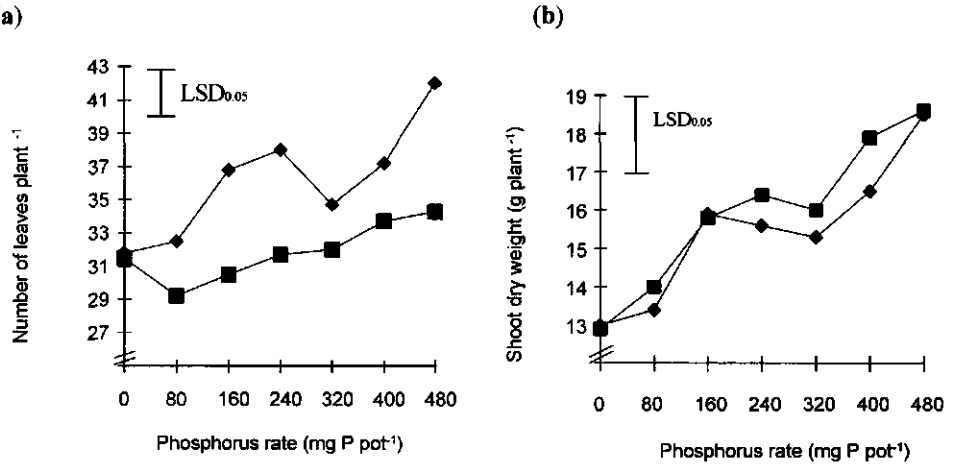

Figure 2.1. Effect of phosphorus fertilization on number of leaves (a) for 'Diphiri Cream' (◆) and 'Zimbabwe Red' (■) at 49 days after sowing and on shoot dry weight (b) at 51 days after sowing.

Chapter 2

Mineral composition of leaf blades

Application of P fertilizer or inoculum had no significant effect on N and P concentrations of leaf blades at 51 DAS (Table 2.2). Also the selections were not significantly different in N and P concentrations. However, total shoot P and N contents were significantly increased with increase in P rate (Fig. 2.2a-b). The shoot P and N contents of the two selections were not significantly different. At the highest P rate, the shoot P content of 'Diphiri Cream' was doubled, relative to the unfertilized treatment (Fig. 2.2a). The increase in shoot N content at the highest P rate was 30% relative to the unfertilized treatment (Fig. 2.2b).

Table 2.2. Effect of phosphorus fertilization on mineral nutrient concentrations of 'Diphiri Cream' and 'Zimbabwe Red' leaf blades at 51 days after sowing averaged over plus and minus inoculation.

P rate (mg pot^{-1})	Nitrogen (%)		Phosphorus (%)	
	'Dip. Cream'	'Zim. Red'	'Dip. Cream'	'Zim. Red'
0	2.87	3.00	0.14	0.21
80	3.11	2.57	0.17	0.14
160	2.70	3.11	0.19	0.17
240	2.68	2.72	0.16	0.16
320	2.87	2.85	0.17	0.17
400	2.91	2.80	0.21	0.19
480	2.66	2.80	0.19	0.20
Mean	2.83	2.85	0.18	0.18
S.E. (56 D.F.)	0.102		0.017	
C.V. (%)	12.5		32.8	

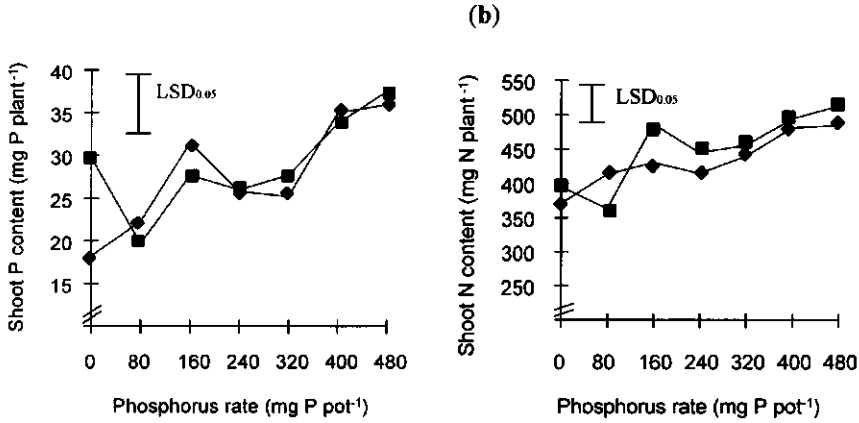

Figure 2.2. Effect of phosphorus fertilization on shoot P content (a) and shoot N content (b) of 'Diphiri Cream' (◆) and 'Zimbabwe Red' (■) at 51 days after sowing.

2.3 A field experiment.

The increase in shoot DM of bambara groundnut after P fertilization as observed in the preliminary pot experiment was linear with increasing P rates up to the highest rate of 480 mg P pot^{-1}, corresponding to 60 kg P ha^{1} . To avoid limited P supply in the field experiment the maximum P rate was increased to 80 kg P ha^{-1}. As the selections showed the same response to P fertilization, only the selection 'Diphiri Cream' was used. As the results of the preliminary study showed that the indigenous *Rhizobia* were sufficiently effective in nodulating bambara groundnut no additional *Rhizobium* was used. With the low rainfall and its poor distribution in Botswana, low soil moisture availability might be a growth limiting factor, directly due to an absolute water shortage, or indirectly by lowering P availability in the soil. Therefore, in this field experiment different P rates were combined with two soil moisture regimes, rainfed and irrigated.

2.3.1 Materials and methods

The experiment was conducted from 18 th December 1995 to 22 nd April 1996 at Botswana College of Agriculture using a soil similar to that used in the preliminary pot experiment (Table 2.1) with a P level of 6.2 mg P kg^{-1} (P-Bray) in the top 0-20 cm. Maximum and minimum temperatures varied between 26.2-30.2 °C and 11.5-18.6 °C, respectively. Day length varied

from about 13.7 hours in December to 11.3 hours in April. The treatments, two soil moisture levels (rainfed and irrigated) and five P fertilizer levels (0, 10, 20, 40 and 80 kg P ha^{-1}) were arranged in a split-plot design and replicated four times. The moisture levels were the main plots and the P rates subplots. There was a 10 m wide space between the main plots in each block and between the blocks to avoid mist-spray between the treatments during overhead irrigation. The subplots were 6 m x 6 m with a path of one metre in between. Single superphosphate was broadcast and worked into the soil with a digging fork. No mineral nutrients other than P were applied. 'Diphiri Cream' seed, dressed with captan at a rate of 12 g/10 kg seed, was sown in rows at a distance of ten cm and a depth of five centimetres. The distance between the rows was 40 cm. Plants were thinned at 23 DAS to a distance of 50 cm giving a plant density of about 54 000 plants ha^{-1}. Earthing up (covering the stems and pods with soil) was done with a hoe at the onset of podding (64 DAS).

Sprinklers with a radius of 20 m were used for irrigation. The quantity of water applied was estimated by placing several cans in the plot at the beginning of the irrigation, and measuring the collected water with a measuring cylinder at the end. Tensiometers were used for monitoring the soil moisture potential. Irrigation was applied when the soil moisture potential was pF 2.6, as recommended for loamy sands (Stegman *et al.*, 1983). The total amount of water received by each plot throughout the growing period was 414 mm for irrigated and 360 mm for rainfed plots. The distribution of rainfall and the time and quantity of irrigation is given in Appendix 3.

At each harvest, a sample of six plants was taken from one spot in each plot during vegetative growth (28 DAS), 50% flowering (49 DAS, when 50% of the plants in a plot had at least one open flower), 50% podding (78 DAS, when half of the 12 plants marked for monitoring pod development had at least one pod 0.5 cm long), and mid-podding (99 DAS, three weeks after 50% podding). At sampling, the number of leaves per plant was counted and the plants were separated into shoots, roots, nodules and pods when applicable. Fresh nodule weight was taken and all other plant parts were oven-dried at 70°C for at least 24 hours and weighed. The final harvest of 12 plants per plot was taken from the centre of the plot when the leaves turned yellow (126 DAS). From this sample, the weight of the aerial parts, pod number, pod yield, and total seed yield were recorded. Ground leaf blades from all the sampling periods were analysed for N and P concentrations as described for the preliminary pot experiment. Statistical analysis of data was done as described before.

2.3.2 Results

Effect of phosphorus fertilization

There was no significant effect of phosphorus fertilization nor a phosphorus-moisture interaction on growth of bambara groundnut except for a short lived increase in root DM and nodule fresh

Table 2.3. Effect of phosphorus fertilization and soil moisture levels on phosphorus and nitrogen concentrations (%) of 'Diphiri Cream' leaf blades at different growth stages in a field experiment at Sebele, Botswana.

P rate (kg ha^{-1})	28 DAS[1]		49 DAS		78 DAS		99 DAS	
	Rain	Irrig.[2]	Rain	Irrig.	Rain	Irrig.	Rain	Irrig.
			Phosphorus concentration					
0	0.18	0.24	0.22	0.23	0.13	0.12	0.12	0.11
10	0.18	0.23	0.21	0.20	0.17	0.15	0.13	0.12
20	0.21	0.20	0.20	0.20	0.14	0.14	0.11	0.12
40	0.20	0.22	0.20	0.22	0.16	0.13	0.11	0.13
80	0.21	0.22	0.21	0.19	0.15	0.16	0.11	0.11
Mean	0.19b	0.22a	0.21a	0.21a	0.15a	0.14a	0.12a	0.12a
S.E. (24 D.F.)	0.019		0.014		0.072		0.010	
C.V.(%)	17.9		13.1		14.6		16.9	
			Nitrogen concentration					
0	3.30	3.58	3.79	3.76	2.55	2.80	2.45	2.36
10	3.35	3.53	3.76	3.71	2.69	2.76	2.63	2.43
20	3.52	3.42	3.83	3.71	2.64	2.68	2.32	2.51
40	3.51	3.61	3.84	3.55	2.63	2.67	2.16	2.68
80	3.52	3.25	3.89	3.79	2.97	2.64	2.22	2.31
Mean	3.44a	3.48a	3.82a	3.70a	2.70a	2.71a	2.35a	2.46a
S.E. (24 D.F.)	0.14		0.10		0.19		0.14	
C.V.(%)	8.3		5.1		13.7		11.3	

[1] DAS = days after sowing.

[2] Rain and Irrig. means rainfed and irrigated treatments, respectively.

Within a growth stage, different letters indicate significant differences.

weight at the 50% flowering stage. The yield (number of pods per plant, pod dry weight and seed weight) and leaf blade P and N concentrations (Table 2.3) were also not significantly affected by P fertilization. The leaf blade P and N concentrations in the field at 49 DAS were on average 0.20% and 3.75%, respectively and similar to those of the preliminary pot experiment at 51 DAS (Table 2.2). Phosphorus fertilization had no effect on shoot P content (Table 2.4).

Effects of irrigation

Irrigation significantly increased all plant parameters measured except root DM. The high shoot DM for irrigated- compared to rainfed plants resulted in a significantly higher number of pods and total seed weight per plant after irrigation (Table 2.5). On a hectare basis the mean final seed yields for rainfed and irrigated plots were 2.8 t and 4.2 t ha^{-1} , respectively. Irrigation had no significant effect on leaf blade P and N concentrations (Table 2.3), but a positive effect on the P uptake expressed by the shoot P contents (Table 2.4). Irrigation significantly increased shoot P content at 28 and 99 DAS. The shoot P contents increased with plant age up to 78 DAS and decreased at 99 DAS (mid-podding). This reflects a re-allocation of shoot P to the pods. Based on literature (Linnemann, 1986; Linnemann and Azam-Ali, 1993) the P quantities in the pods of rainfed and irrigated treatments are of the order of 130 mg P and 146 mg P $plant^{-1}$, respectively.

2.4 Discussion

In a pot experiment with a small soil volume a linear response to added P was found when this was thoroughly mixed with the soil just before sowing, while in a field experiment on the same soil no response to P was found. An obvious explanation for this phenomenon is that in the pots the root densities were that high that the low quantity of available P became depleted and that this resulted in a response to an external P source. In the field, plants can exploit a larger volume of soil and thus have access to more soil P. This effect of soil volume per plant on P availability is reflected in a lower total above ground dry matter production of plants grown in pots with unfertilized soil (13.0 g shoot DM $plant^{-1}$ at 51 DAS) than that of comparable plants grown in the field (16.0 g shoot DM $plant^{-1}$ at 49 DAS) at the same growth stage.

Another explanation for the difference in response to P between the pot and field experiment might be the mode of P application. In the pot experiment P was mixed with soil before sowing, giving plants access to added P already at an early age. In the field P was applied to the soil surface and superficially worked into the soil, giving a situation in which added P might stay out of the reach of plant roots during the early or the entire growing period. This idea leads to the hypothesis (studied in Chapter 3.2) that the response of bambara groundnut to added P depends on the growing stage in which it becomes available to the plant.

Table 2.4. Effect of phosphorus fertilization and soil moisture levels on shoot phosphorus content (mg plant^{-1}) of 'Diphiri Cream' plants at different growth stages (DAS = days after sowing).

P rate (kg ha^{-1})	28 DAS[1]		49 DAS		78 DAS		99 DAS	
	Rain	Irrig.[2]	Rain	Irrig.	Rain	Irrig.	Rain	Irrig.
0	2.3	4.7	35.4	37.8	89.6	87.4	76.1	88.1
10	2.1	3.8	38.7	43.3	109.9	116.9	85.3	98.0
20	3.4	3.2	35.8	34.0	111.0	110.3	78.1	91.7
40	2.8	3.2	42.5	34.5	108.8	104.3	76.5	92.8
80	3.9	4.1	41.2	44.0	116.9	137.8	82.2	91.3
Mean	2.9b	3.8a	38.7a	38.7a	107.0a	111.3a	79.6b	92.4a
S.E. (24 D.F.)	0.23		2.35		5.17		3.69	
C.V.(%)	31.2		27.1		13.4		19.2	

[1] DAS = days after sowing.

[2] Rain and Irrig. means rainfed and irrigated treatments, respectively.

Within a growth stage, different letters indicate significant differences.

Table 2.5. Effect of soil moisture levels on shoot dry weight, number of pods and total seed weight of 'Diphiri Cream' at different growth stages in a field experiment at Sebele, Botswana.

Period (DAS)	Shoot dry weight (g plant^{-1})		Number of pods per plant		Total seed weight (g plant^{-1})	
	Rainfed	Irrigated	Rainfed	Irrigated	Rainfed	Irrigated
78	72.6b	80.7a	98.2b	133.0a	-	-
99	68.9b	80.0a	152.4b	178.0a	-	-
126	69.6b	80.2a	127.2b	173.1a	51.4b	77.2a

Within a parameter, different letters indicate significant differences.

Phosphorus fertilization had no effect on leaf blade P concentrations in both the preliminary pot experiment and the field experiment, but there was an increase in P uptake with increase in shoot DM. Shoot P concentrations in the field experiment for rainfed and irrigated treatments were maintained around the critical P level for bambara groundnut, being around 0.15% at 78 DAS as determined in Chapter 4. This points to a maximum dilution of the P taken up, and a maximum P use efficiency. The fact that the level of the leaf blade P concentration was maintained at the same level at all P rates in the pot experiment but also under irrigated field conditions with relatively high yields, indicates that P availability was always marginal or even deficient. Under all conditions, P availability was limiting plant growth. In the pot experiment this is shown by the linear response of the shoot DM to P fertilization (Fig. 2.1b). In the field, applied P was not utilized and bambara groundnut seemed to cover its requirement with the P already present in the soil, also when growth and P uptake were relatively high with irrigation. At a soil level of 6.2 mg P kg^{-1} soil (P-Bray) seed yields of even 4.2 tons ha^{-1} were achieved, but still at leaf P concentrations at around the critical level and without any response to P fertilization. Obviously, under rainfed conditions only a small fraction of the P present in the soil is available. This fraction seems not to be increased by P fertilization. Consequently, plants keep suffering from P deficiency also after fertilization. Contrary to P fertilization, irrigation greatly improved growth and increased P uptake, especially in the early stage of development (28 days after sowing) and during podding (99 days after sowing). Evidently, part of the P pool present in the soil becomes available under improved soil moisture conditions, probably due to improved P diffusion to the root. Apparently, soil moisture seems to be the factor regulating P availability rather than the soil P content, at least under the prevailing non-irrigated field conditions. Eliminating the most limiting factor, that is suboptimal soil moisture, improves plant P nutrition, but, based on the shoot P concentrations, being still critical.

Although under the prevailing field conditions, soil moisture is assumed to be the factor regulating P availability and thus growth, water deficiency is not the first growth limiting factor. Under rainfed conditions, soil moisture indirectly affects growth by limiting P supply, leading to shoot P concentrations around or below the critical level. With water shortage as first growth limiting factor, plant growth will be inhibited by water stress, generally resulting in an accumulation of nutrients, inclusive P. This was not observed in the field trial.

Nitrogen nutrition in both the pot and the field experiment seemed to be adequate, irrespective of the rate of P supply, addition of bean *Rhizobium* or soil moisture content. Nitrogen concentrations in the leaf blades were high in all treatments, indicating that N nutrition was sufficient (Tables 2.2 and 2.3). *Rhizobium* activity in the soil used seems to be high enough to meet the plant requirement. Adding extra inoculum to the soil seems to be not necessary and therefore this treatment was omitted in subsequent experiments. Phosphorus fertilization and soil moisture level did not affect plant N nutrition. Whether N_2 fixation capacity will also be high enough under conditions where P is no longer limiting growth, and plant N requirement will be higher, is subject of a further study (Chapters 5 and 6).

An important conclusion from the field research is that the soil moisture content seems to be the important factor determining soil P availability and P uptake in these relatively P-poor soils. Therefore P fertilization alone does not stimulate P availability under dry soil conditions, but irrigation does, resulting in increased P uptake and higher DM. This increase in P availability after irrigation, though relatively high and resulting in significantly increased dry matter production and seed yield is not that high that it supplies the plant with sufficient P. The shoot P concentration still remains marginal. Another important finding is that surface application of P is not effective even under improved soil moisture conditions.

Finally, as the two selections used did not differ in dry matter production and showed the same dry matter response to added P, only one selection 'Diphiri Cream' was used in the subsequent experiments.

Chapter 3

Factors affecting the response of bambara groundnut (*Vigna subterranea* (L.) Verdc.) to phosphorus fertilization

3.1 A comparison of the P uptake patterns of bambara groundnut, maize and pigeon pea

3.1.1 Introduction

In the previous chapter, a positive response to P fertilization by bambara groundnut (*Vigna subterranea*) was found in a pot experiment but not in a field experiment. Lack of response by bambara groundnut to P fertilization in our field experiment, even with a seed yield of 4.2 t ha^{-1}, implied that there was enough available soil P after irrigation to meet the requirement and probably also to meet the requirement of even a high P demanding crop like a cereal. The poor response of bambara groundnut to P fertilization in the field could also mean that it has a low P requirement, possibly combined with a high P efficiency (efficiency involves P acquisition by the roots (uptake) and internal utilization by the plant). Efficiency in acquisition is frequently defined in terms of the total uptake per plant or specific uptake rate per unit root length and efficiency in internal utilization (internal use efficiency) as dry matter production per unit nutrient in the dry matter (Marschner, 1997). These questions have led to a pot experiment where the P requirement and P efficiency (uptake and internal use efficiencies of soil and fertilizer P) of bambara groundnut were compared to those of maize (*Zea mays*) and pigeon pea (*Cajanus cajan*). Maize is considered to have a high P requirement (Arnon, 1975), while pigeon pea has a high uptake efficiency by mobilizing soil P fractions normally not available to other crops (Ae *et al.*, 1990).

3.1.2 Materials and methods

The experiment was conducted on the grounds of the forestry nursery of Botswana College of Agriculture, Sebele using a low P loamy sand (Ferric Luvisol, Joshua, 1991). The chemical characteristics of the soil are given in Table 3.1. Analytical methods are given in Chapter 2.

The experiment ran for 78 days from the 4 th October to the 21 st December 1996. The plants were harvested when they switched from vegetative growth to pod filling stage. Maximum and minimum temperatures varied between 30.0-32.7 °C and 16.6-17.8 °C, respectively. It has been found that under the prevailing day length and temperature it takes for bambara groundnut about 45 days from sowing to flowering and another 31 days from flowering to podding, while after

Table 3.1. Selected chemical properties of the soil used.

pH-$CaCl_2$	P-Bray (mg kg^{-1})	Organic carbon (wt%)	Exchangeable cations (cmol (+) kg^{-1})				CEC (cmol (+)kg^{-1})
			Ca	Mg	K	Na	
4.6	6.2	0.4	1.3	0.93	0.60	0.04	4.69

podding vegetative growth stops (Brink, 1997; Chapter 2). The treatments were three crops, maize - *Zea mays* (L). var. Kalahari Early Pearl), bambara groundnut (*Vigna subterranea* (L.) selection 'Diphiri Cream'- Sebele progeny), pigeon pea (*Cajanus cajan* (L.) var. ICPL 87105-Sebele progeny) and five levels of phosphorus (0, 70, 140, 280 and 560 mg P pot^{-1}; on weight basis of 2 000 000 kg soil ha^{-1} corresponding to 0, 10, 20, 40 and 80 kg P ha^{-1}). The experiment was arranged in a completely randomized design with treatments replicated four times. White plastic bags (diameter 25 cm x 24 cm deep) holding 14 kg of soil were used for growing the crops. Single superphosphate was crushed and thoroughly mixed with the soil before planting. Three seeds were sown per bag and thinned to one seedling 12 days after sowing (DAS). To bambara groundnut and pigeon pea no minerals other than P were applied. To the non-N_2 fixing maize plants, in addition to P, urea at a rate of 350 mg N pot^{-1} per application (based on a weight basis of soil per hectare corresponding to 50 kg N ha^{-1}), was dissolved in 250 ml of water and applied at 28, 42, and 56 DAS. The plants were sprayed with Kombat (active ingredient: Cypermethrin / pyrethroid 200 g L^{-1}) at a rate of 5 ml per 20 litres of water to control grasshoppers. The soil moisture content was maintained at field capacity and the plants were exposed to natural daylight, temperature and day length.

Data recorded at final harvest (78 DAS) were dry weight of plant components (shoot, roots, nodules and pods) and number of nodules, where applicable. At harvest, maize had just started silking. The plant parts (shoot and roots) were oven-dried at 70°C for 24 hours, while pods were air dried for two weeks. The ground dry shoot material was analysed for P as described in Chapter 2. Statistical analysis of data was as described in Chapter 2.

3.1.3 Results

Dry matter production

The effects of P fertilization on shoot dry matter production are given in Table 3.2. Relative to the zero P treatment, maize had a significant dry matter increase of about 50% at all P rates, while for bambara groundnut only P rates of 280 mg P pot^{-1} or more gave a significant response of 30-60%. In pigeon pea P fertilization tended to give a small increase in dry matter production,

but this effect was not significant. Table 3.2 further shows the large differences in total dry matter production between the species. The differences between the P responses of maize and bambara groundnut are further illustrated in Figure 3.1a where the relative dry matter yields (as a percentage of the maximum yield) are given.

Phosphorus fertilization significantly increased root dry matter weight of maize only. The root-shoot ratios clearly show that under the experimental conditions bambara groundnut developed a relatively small root system (Fig.3.1b). Bambara groundnut has in all treatments a root-shoot ratio of about 0.2, while for maize and pigeon pea values between 0.4 and 0.5 were found.

Shoot phosphorus status

The effects of P fertilization on P nutrition of the experimental plants are given in Table 3.3 and Fig. 3.2. Shoot P concentrations are hardly affected by P application except when the highest rates are used (Fig. 3.2). The maize shoot P concentrations are very low while the bambara groundnut shoot P values are two to two and half times higher but still low. Pigeon pea had the highest shoot P concentrations.

Table 3.2. Effect of phosphorus fertilization on shoot dry matter of maize, bambara groundnut and pigeon pea at 78 days after sowing.

Phosphorus rate (mg P pot^{-1})	Shoot dry matter (g $plant^{-1}$)		
	Maize	Bambara groundnut	Pigeon pea
0	70.8	22.1	7.0
70	104.6	26.5	9.1
140	106.2	27.3	8.8
280	108.7	35.2	9.8
560	104.9	29.0	6.4
Mean	99.0	28.1	8.3
C.V. (%)	10.3	15.3	23.4
S.E. (15 D.F.)	5.08	2.13	0.97
$LSD_{0.05}$ (Phosphorus)	15.3	6.4	n.s.

n.s. = not significant

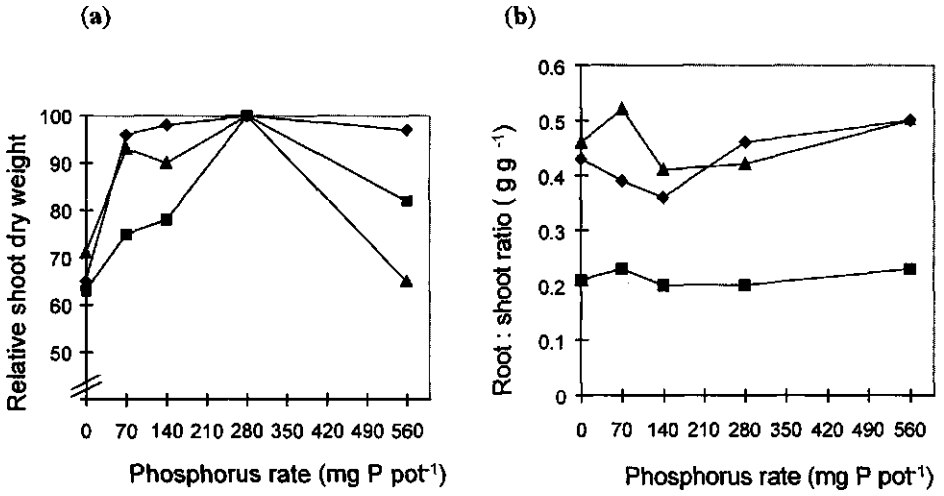

Figure 3.1. Effect of phosphorus fertilization on relative shoot dry weight (a) and root-shoot ratios (b), of maize (◆), bambara groundnut (■) and pigeon pea (▲) at 78 days after sowing (highest shoot DM yield = 100).

In maize there was a steady increase of shoot P content with increasing P rates (Table 3.3). This effect is already present at the lowest P rate of 70 mg P pot^{-1} and is associated with a dry matter increase of about 50% (Table 3.2). In bambara groundnut this positive effect of P fertilization on shoot P content and shoot dry matter shows up at a four times higher P rate. From Tables 3.2 and 3.3 it can also be seen that maize growth heavily depends on additional fertilizer P, that bambara groundnut also needs fertilizer P for maximum shoot development, but that pigeon pea hardly relies on additional fertilizer P.

3.1.4 Discussion

Under the prevailing growth conditions response to P fertilization differed very much among the three species, reflected in both P utilization and growth response. While maize and pigeon pea already reached 90% of their maximum shoot dry matter production at the lowest P rate (70 mg P pot^{-1}), bambara groundnut required a four times higher P rate to realize a similar relative dry matter production.

Table 3.3. Effect of phosphorus fertilization on shoot P content of maize, bambara groundnut and pigeon pea at 78 days after sowing.

Phosphorus rate (mg P pot^{-1})	Shoot phosphorus content (mg P plant^{-1})*		
	Maize	Bambara groundnut	Pigeon pea
0	28.0	27.0	11.2
70	49.0 (21.0)	28.5 (1.5)	14.0 (2.8)
140	53.1 (25.1)	31.7 (4.7)	14.8 (3.6)
280	62.3 (34.3)	46.4 (19.4)	17.6 (6.4)
560	99.0 (71.0)	51.7 (24.7)	18.3 (7.1)
Mean	58.3	37.0	15.2
C.V. (%)	12.3	18.5	17.7
S.E. (15 D.F.)	3.59	3.42	1.3
$LSD_{0.05}$ - (Phosphorus)	10.8	10.3	4.0

* Figures between the brackets represent the amount of P originating from the P fertilizer.

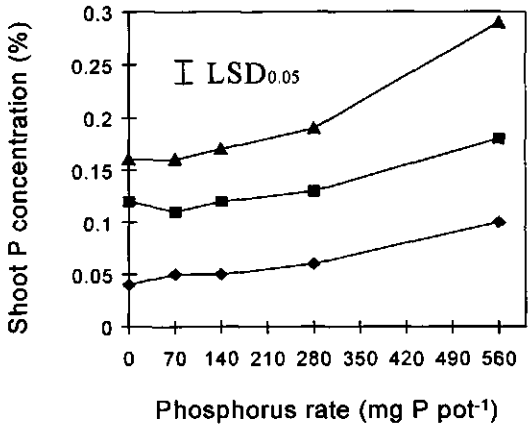

Figure 3.2. Effect of phosphorus fertilization on shoot P concentration of maize (◆), bambara groundnut (■) and pigeon pea (▲) at 78 days after sowing.

When analysing plant growth in relation to P nutrition, two major components have to be considered, that is (i) plant P requirement and (ii) plant P utilization. Plant P requirement, the minimum amount of P to be taken up to achieve maximum dry matter production, was much lower with the two leguminous species than with maize. With bambara groundnut and pigeon pea, maximum shoot DM yields of 35.2 and 9.8 g plant^{-1} were accompanied by shoot P concentrations of 0.13% and 0.18%, respectively. This results in P requirements of 46.4 and 17.6 mg P plant^{-1}, at least if determined for a growth period of 78 days and restricted to shoots only. With maize, the experimental data have to be handled with caution. While with pigeon pea and bambara groundnut shoot P concentrations of 0.13 and 0.18% correspond well with their minimum P concentrations (Reuter and Robinson, 1986; Chapter 4), internal P concentrations in maize plants were far below the minimum P concentration, indicated by Reuter and Robinson (1986) to vary between 0.10-0.15%. In our experiment, only at the highest P rate maize approached a shoot P concentration of 0.10% with a shoot dry matter yield of 104.9 g plant^{-1}. Based on these data, corresponding P requirement for maize would be 99.0 mg P plant^{-1}, but a level of 148.5 mg P plant^{-1} (based on 0.15% P in shoot) would probably be more realistic. Shoot P concentrations in maize far below the minimum concentration, as measured for all P rates except the highest one, illustrate that at all lower P rates maize was severely suffering from P deficiency. Extremely low internal shoot P concentration ($\leq$0.05% P) measured at 78 DAS can only be the result of a strong dilution of internal P, due to prolonged biomass production (photosynthesis) at stagnating P uptake. In this experiment maize grown for 78 days at different P rates seemed to have produced equal amounts of biomass (except at zero P), resulting in increased internal P dilution and thus increasing P deficiency with decreasing P rate.

Though P requirement of maize was at least two and five times as high as that of bambara groundnut and pigeon pea, respectively, these data have to be handled with care if transferred to practice. Only part of the growth cycle was completed (78 DAS), calculations are based only on above-ground parts and, if extrapolated from plant to crop level the plant density in the field has to be incorporated. On the other hand, if differences in minimum P concentrations among species can be assumed to be small, P requirements will directly be related to total dry matter production per ha. Rough estimates from practice give total DM (excluding grain) data of 7.0, 4.5 and 3.7 t ha^{-1} for maize (Sigunga, 1997), bambara groundnut (Collinson *et al.*, 1996; Chapter 2) and pigeon pea (Ae *et al.*, 1990), respectively. This agrees with the high P requirement of maize relative to the two legumes as found in this experiment.

Phosphorus utilization, the second component involved in plant P nutrition, is regulated by both P uptake efficiency, and internal P use efficiency. Uptake efficiency is frequently defined as total uptake per plant or as uptake per unit root length (Marschner, 1997). In this work total P in shoots at 78 DAS was assumed to represent total P taken up per plant, while final root/shoot dry weight ratios of the species were used as a parameter characterizing the relative root density of a species. Maize showed to be very efficient in P uptake. Contrary to bambara groundnut and pigeon pea, P uptake by maize almost linearly increased with increasing P fertilization rate (Table 3.3). A relative high root density, reflected by a high root/shoot ratio, combined with a high P requirement and a small rooted soil volume (pot

experiment) led to this linear response with maize. Phosphorus uptake with pigeon pea was low with almost no response to P fertilization, though root/shoot ratio was as high as that of maize. Evidently P requirement seems to act as a sink that indirectly controls P uptake of pigeon pea. Phosphorus uptake pattern of bambara groundnut was quite different from that of maize and pigeon pea. Up to 280 mg P pot^{-1} not much increase in P uptake was observed, while from this level on P uptake reached more or less a maximum at a level just in between maize and pigeon pea. Probably because of a low root/shoot ratio (low root density) bambara groundnut seems not to be able to benefit from fertilizer P, at least if doses applied are below a certain critical level. Only at P rates equal or greater than 280 mg P pot^{-1}, soil P availability seems to be high enough to supply poorly rooted bambara groundnut plants with adequate amounts of P. Increase in P uptake was accompanied by improved growth, indicating P uptake at lower P rates was inadequate.

Due to high P uptake and high P requirement the major fraction of P absorbed by maize originated from fertilizer P (up to 71%), making fertilization with phosphorus necessary for maize grown under the prevailing conditions. Just contrary, bambara groundnut and pigeon pea seemed to be able to cover up to 80% and 94% of their P by P originating form soil, probably due to their low P requirement. Therefore, fertilization of pigeon pea with P seems to be beneficial only at low rates. Whether this is partly related to additional plant specific P mobilizing strategies such as (i) root exudation of organic acids, or (ii) mycorrhiza symbiosis, is possible (Ae *et al.*, 1990), but has not been subject of study in this experiment. Fertilization of bambara groundnut with P seems to improve uptake and growth only if rates exceed a certain level. This level will probably depend on soil type, soil moisture status (Chapter 2) and plant density.

The internal P use efficiency, characterised by the amount of biomass produced per unit P absorbed (Janssen, 1998) differed very much between the three species. Maize showed the highest internal use efficiency (Table 3.4). On average maize produced 1.89 g DM per mg P taken up, while values for bambara groundnut and pigeon pea were only 0.79 and 0.56 g per mg, respectively. Because of severe P deficiency, extremely high P use efficiencies of maize at low P rates have to be considered as artefacts. Under those conditions the plants would probably not have completed their growth cycle, inclusive seed production. More realistic values of internal P use efficiencies will probably be those from treatments used to calculate P requirements. Then the values of 1.06, 0.76 and 0.56 g DM per mg P taken up were obtained for maize, bambara groundnut and pigeon pea, respectively. These data illustrate that maize is still the most efficient species, while the two legumes behave more or less similar.

Finally, the results of this experiment clearly illustrate that the lack of response of field-grown bambara groundnut to P fertilization (Chapter 2) cannot be attributed to exceptionally high P use efficiency of this crop. If compared with maize, a species well known to require high P fertilizer applications (Arnon, 1975), P uptake and internal use efficiency of bambara groundnut and pigeon pea were much lower. The potential of bambara groundnut to realize

high relative yields on P poor soils without fertilization as in our field trial has to be attributed to its low P requirement. However, as shown in Chapter 2, under Botswana field conditions relatively high P uptake and relative high seed yields (4.2 t ha^{-1}) could be achieved with bambara groundnut by improving the soil moisture level by irrigation, without P fertilization.

Table 3.4. Effect of phosphorus fertilization on internal P use efficiency of maize, bambara groundnut and pigeon pea at 78 DAS.

Phosphorus rate (mg P pot^{-1})	Phosphorus utilization efficiency (DM / unit P taken up; g mg^{-1})		
	Maize	Bambara groundnut	Pigeon pea
0	2.53	0.82	0.63
70	2.13	0.93	0.65
140	2.00	0.86	0.59
280	1.74	0.76	0.56
560	1.06	0.56	0.35
Mean	1.89	0.79	0.56

The questions that still remain are (i) whether such yields without P fertilization can be achieved only on virgin soils and if so, (ii) what rates of P fertilization will be necessary to maintain adequate yields in permanent cultivation systems or to increase yields. In pot experiments however, soil P availability seems to be insufficient to cover the relatively low P requirement of bambara groundnut plants, due to the limited soil volume exploitable per plant.

3.2 Growth and development of bambara groundnut as affected by time of phosphorus application

3.2.1 Introduction

Availability of phosphorus at early stages of plant growth has been found to have a great effect on growth and yield (Jones and Warren, 1954; Smid and Bates, 1971; Arnon, 1975). Phosphorus

sources and methods of application have also been found to differ in their effect on early plant growth (Reisenauer, 1963; Krigel, 1967; Smid and Bates, 1971; Scott and Blair, 1988).

Bambara groundnut has been reported to thrive and produce some yield under adverse conditions such as limited water supply and low soil fertility (National Academy of Sciences, 1979; Collinson *et al.*, 1996). It has been found that bambara groundnut has a relatively low P requirement with most of the dry matter produced by making use of soil P (Chapter 3.1). The low P requirement partly explains why bambara groundnut did not respond to P fertilization under field conditions but responded in a pot experiment where soil volume seemed to limit the amount of P available per plant (Chapter 2).

A positive response to P fertilization by bambara groundnut in the pot experiment, where the fertilizer was ground and thoroughly mixed with the soil, implied also a "starter P effect", e.g. the need for additional P at the very early stage of plant/root development (Chapter 2).

This led to the hypothesis that additional P might only be needed at the very early stage of plant/root development. The assumption was based on the idea that in the pot experiment the roots of young bambara groundnut plants "meet" the fertilizer P directly after germination, while in the field, where the non-ground fertilizer was broadcast and ploughed under with a digging fork, this happens only at a later stage. This might be particularly relevant for bambara groundnut because of its poor root system (Chapter 3.1). The P response in the pot experiment might thus be a "starter effect". To check this hypothesis, a pot experiment was conducted in which different times of P application were compared.

3.2.2 Materials and methods

The experiment was conducted on the grounds of the forestry nursery of Botswana College of Agriculture with the same soil as used in Chapter 3.1 for a period of 78 days from the 25 th October 1996 to 11 th January 1997. Maximum and minimum temperatures varied between 30.0-32.7 °C and 16.6-18.7 °C, respectively. The treatments included a control (no P fertilization) and three times of P fertilizer application (sowing, two and four weeks after sowing (WAS)). Phosphorus was applied at a rate of 420 mg P pot^{-1}, on weight basis of 2 000 000 kg soil ha^{-1} corresponding to 60 kg P ha^{-1}. White plastic bags holding 14 kg of soil were used for growing the plants. Three seeds of bambara groundnut selection 'Diphiri Cream' (Sebele progeny) were sown and thinned to one plant per pot 14 DAS. The treatments were arranged in a completely randomized design with five replicates. For treatment application at sowing, single superphosphate (SS) was crushed and thoroughly mixed with the soil. For the times of application at two and four WAS, the crushed SS was dissolved in 250 ml of water and applied to the soil. No minerals other than P were applied. The soil moisture content was maintained at field capacity and the plants were exposed to natural light, temperature and day length. Data recorded at the final harvest (78 DAS) were dry weight of plant components (shoot, root, nodules and pods) and shoot P concentration. The ground dry shoot material was analysed for P as described in Chapter 2. Statistical analysis of data was as described in Chapter 2.

3.2.3 Results

Shoot dry matter production.

The increase in shoot DM, relative to control, was 70% for P application at both sowing and two WAS (Fig. 3.3). If applied four WAS, the increase was only 25%, being no longer significantly different from the zero P treatment. Contrary to shoots, dry weight of roots, nodule number and nodule dry weight were not significantly affected by P fertilization, irrespective of time of application (Table 3.5). The root:shoot ratios (on dry weight basis) did not differ significantly, but they tended to be higher for treatments control and P application at four weeks after sowing, compared to P application within two weeks from sowing.

Pod yield

Phosphorus fertilizer application significantly increased pod dry weight per plant, relative to the zero P treatment, if supplied within two WAS. If supplied during this period, pod dry weights were increased by a factor of six to seven (Fig. 3.4). If applied four WAS, however, pod yields were no longer significantly affected. With both shoot and pod DM weights, positive effects of P fertilization were clearly restricted to application during the first two weeks after sowing. Effects of P fertilization on pod yield were much stronger than on shoot dry weights.

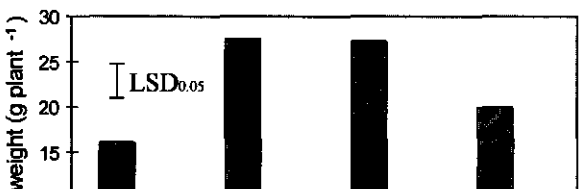

Figure 3.3. Effect of time of phosphorus fertilization on shoot dry weight of 'Diphiri Cream' plants at 78 days after sowing. (0P = control; S = P at sowing; 2 WAS = P at 2 weeks after sowing ; 4 WAS = P at 4 weeks after sowing.

Table 3.5. Effect of time of phosphorus application on shoot and root dry weights and root:shoot ratios of 'Diphiri Cream' plants at 78 days after sowing.

Treatments	Shoot dry weight (g plant^{-1})	Root dry weight (g plant^{-1})	Root : shoot ratios (dry weight)
Control	16.1	3.34	0.21
P at sowing	27.5	4.14	0.15
P at 2 WAS*	27.3	3.88	0.14
P at 4 WAS	20.1	3.70	0.20
C.V. (%)	15.1	19.3	27.8
S.E. (16 D.F.)	1.54	0.32	0.02
$LSD_{0.05}$	4.61	n.s.	n.s.

*WAS = weeks after sowing; n.s. = not significant.

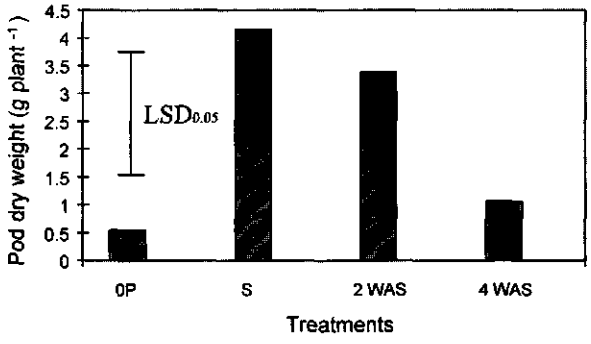

Figure 3.4. Effect of time of phosphorus fertilization on pod dry weight of 'Diphiri Cream' at 78 days after sowing. (0P = control; S = P at sowing; 2 WAS = P at 2 weeks after sowing; 4 WAS = P at 4 weeks after sowing.

Shoot phosphorus status

Phosphorus fertilization had no significant effect on P concentration of the shoot (Table 3.6). The shoot P concentrations were in the same range as in the previous experiment (Chapter 3.1), that is 0.11-0.13%. Shoot P contents, reflecting P uptake, were affected by P fertilization in a similar way as shoot dry weights (Table 3.5). Plants supplied with extra mineral P during the initial stage (sowing to two WAS) took up much more P (50-70%) than unfertilized plants or plants receiving mineral P at four WAS.

Table 3.6. Effect of time of phosphorus application on shoot P concentration and shoot P content of 'Diphiri Cream' at 78 days after sowing.

Treatments	Shoot P concentration (%)	Shoot P content (mg P plant^{-1})
Control	0.12	19.6
P at sowing	0.12	34.7
P at 2 WAS*	0.13	34.7
P at 4 WAS	0.11	23.2
C.V. (%)	17.5	27.2
S.E. (16 D.F.)	0.01	3.41
$LSD_{0.05}$	n.s	10.2

*WAS = weeks after sowing; n.s = not significant

3.2.4 Discussion

The observed response of shoot dry matter production of potted bambara groundnut plants to P given at sowing (ground P fertilizer thoroughly mixed with the soil at or before planting) is in line with the results obtained in two previous pot experiments, where it was due to a combination of low P content of the soil and limited soil volume (Chapters 2 and 3.1). The data show that the response only occurs when P is applied (and well distributed in soil) at a very early stage of seedling development, in this experiment within two WAS. Phosphorus application beyond this

stage apparently does not improve shoot growth. This means that the critical time for P application with positive effect on plant growth is within two weeks after sowing.

The fact that P application does not affect root development suggest that bambara groundnut seedlings do not extra invest in this organs, irrespective of P supply. Despite the fact that plants receiving P at four WAS have a "normal" root system, no extra P is taken up during later stages. This may be due to the absence of an appropriate sink. It may mean that shoot growth (sink) of bambara groundnut is determined at early stages of growth, with P stress leading to a relatively small sink that can not be altered by a too late increase in soil P availability.

Phosphorus application had no effect on pod number but a very strong effect on pod weight. For control and P application at four WAS treatments the average pod dry weight plant^{-1} were 0.5 and 1.0 g, respectively, while 4.0 g for P application at sowing. This indicates that under P stress the aerial parts did not supply sufficient assimilates for pod filling. Reduced early growth apparently has great consequences for pod filling. This shows the importance of a "starter P" on production of bambara groundnut and that a poor start can not be made good by a later P application.

Finally, the findings of this experiment that there is a critical time for P application may partly explain the lack of response to applied P in our field experiment (Chapter 2). In this field trial, the fertilizer was broadcast and worked into the soil with a digging fork. This is different from the pot experiments where the fertilizer is thoroughly mixed with the soil, and the seedlings can make use of it directly after germination. Under field conditions, probably the seedlings meet the fertilizer only after some time and missed the critical time for P in bambara groundnut. This can mean that under field conditions if the soil P status is low, broadcasting the fertilizer is not the best way to increase P availability at early growth stages of bambara groundnut. Fertilizer placement in the rooting zone before planting may overcome this problem.

Chapter 4

Phosphorus levels in shoots of bambara groundnut (*Vigna subterranea* (L) Verdc.)

4.1 Critical shoot phosphorus concentration of bambara groundnut. A sand culture approach

4.1.1 Introduction

Preceding fertilizer experiments with bambara groundnut gave positive responses to P application in pot experiments and no response in a field experiment (Chapters 2 and 3). Differences in rootable soil volume and in method of P application may well account for the differences in response. In all experiments reported on so far the P concentrations of leaf blades and shoots were not affected by P treatments, even when shoot dry matter was increased. This might mean that in all these experiments bambara groundnut plants maintained a shoot P concentration around the critical level by diluting the extra P taken up into the extra biomass.

To check this idea a sand culture experiment with different P treatments was conducted to establish the critical P levels for bambara groundnut. In accordance with Epstein (1972) a critical level was defined as the nutrient concentration of the tissue associated with 5 or 10% reduction in maximum growth due to deficiency of that nutrient.

4.1.2 Materials and methods

The experiment was conducted in a greenhouse at Botswana College of Agriculture, Sebele for a period of 78 days (podding) from 20 th August to 5 th November 1997. The average monthly temperatures ranged from 27.5 to 32.8 °C during the day and 15.0 to 20.5 °C at night.

Washed coarse river sand was used for growing the plants. The main chemical characteristics of the sand were: pH 7.4; P Bray 3.8 mg P kg^{-1}; organic carbon 0.02 (wt.%); CEC 1.00 (cmol (+) kg^{-1}); exchangeable cations (cmol (+) kg^{-1}): Ca 1.35, Mg 0.30, K 0.04 and Na 0.04. The determinations of the chemical characteristics of the sand are as described in Chapter 2. The treatments, 12 P levels, were 0.207, 0.414, 0.828, 1.656, 3.312, 6.625, 13.25, 26.5, 53.0, 79.5, 106 and 159 mg P $plant^{-1}$ for the whole growing period. Phosphorus (NaH_2PO_4 dissolved in water) was added to the plants at 12 different rates according to the relative addition rate technique (RAR; Ingestad, 1986). With this technique P was added during the entire growth

period in accordance with the plants actual growth rate, the latter varying from maximum to severely limited. Patterns of maximum growth rate and corresponding P uptake versus time were obtained by constructing a standard curve based on growth and shoot P concentrations of a previous greenhouse pot experiment (Chapter 5). Phosphorus was weekly added to the pots at different rates, increasing with time according to the growth rate of the plants, varying from low to high on the bases of intended growth and corresponding P requirement.

The experiment was arranged in a completely randomized design with treatments replicated four times. Three seeds of 'Diphiri Cream' were sown in white pots (five litre) containing eight kg of sand and thinned to one seedling 13 days after sowing (DAS). A minus P nutrient solution was prepared with deionized water and applied weekly starting from sowing. The nutrient solution used was of the following composition (mmol L^{-1}): 3.75 NH_4NO_3; 1.25 K_2SO_4; 1.00 $MgSO_4$; and trace elements (umol L^{-1}) 82 Fe (Fe-EDTA); 46 B (H_3BO_3); 9 Mn ($MnSO_4.H_2O$); 0.3 Cu ($CuSO_4.5H_2O$); 0.8 Zn ($ZnSO_4.7H_2O$) and 0.01 Mo (MoO_3). The nutrient solution was applied according to the RAR technique (Ingestad, 1986) based on the N requirement of bambara groundnut determined from a standard growth curve and shoot N concentrations from a previous experiment (as for P above). Contrary to P, all the pots received the same amount of nutrient solution which increased with time according to the growth rate of the plants. The smaller quantities of nutrient solution at early stages of growth were added once a week while the large quantities at later growth stages were distributed throughout the week. The pH of the nutrient solution was maintained between 5.7 and 6.0. Water stress was prevented by applying deionized water daily to each pot in addition to the nutrient solution. At advanced plant growth the saucers under the pots were filled up with deionized water or nutrient solution.

At final harvest (78 DAS), leaf number was recorded and plants separated into shoots, roots, nodules and pods. The leaf blades were separated from the petioles to determine the total leaf area per plant. The leaf area per plant was determined by stacking 20 fully matured leaves and cutting through them with a one centimetre diameter cork borer. The weight of the 20 leaf blade discs and total weight of the leaf blades per plant were taken. A factor relating weight of the leaf blade discs to their area was determined and used to calculate the total leaf area per plant (leaf area per plant = total leaf weight per plant x (area of the 20 leaf blade discs (15.71 cm^2) divided by weight of the discs)). The plant parts were oven-dried at 70°C for 24 hours and weight taken. The shoots were ground and analysed for P as described in Chapter 2. Data analysis was the same as in previous chapters. The critical P concentration was determined from the relation between shoot dry matter production and shoot P concentration and defined as the concentration giving 90% of its maximum shoot dry matter (DM).

4.1.3 Results

Plant growth and dry matter production

From Figure 4.1a-c it can be seen that P rates of 26.5 to 159 mg P plant^{-1} significantly increased number of leaves, leaf area and shoot DM per plant, relative to the lowest P rate. Beyond a supply of 106 mg P plant^{-1} further increases were no longer significant. Between P rates 0.207 and 26.5 mg P plant^{-1}, the plants were stunted and showed chlorotic blotches and brownish spots on older leaves, and as growth progressed, the chlorotic areas on leaf edges became necrotic. The P deficiency symptoms were only on older leaves, while later maturing leaves had no symptoms.

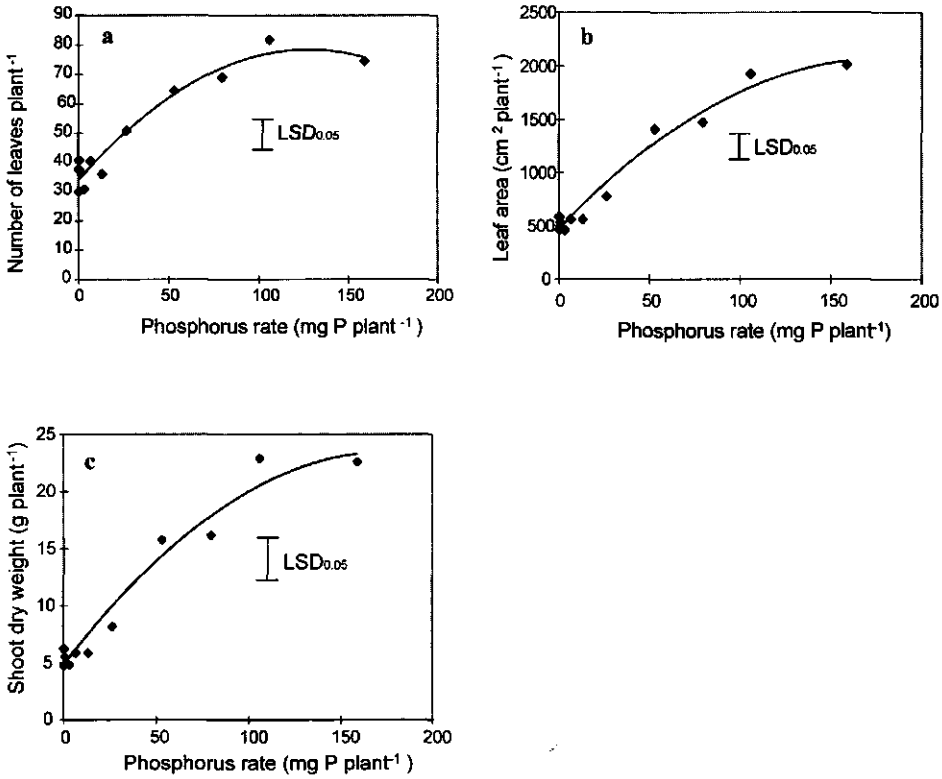

Figure 4.1. Effect of level of phosphorus application on the number of leaves (a), total leaf area (b), and shoot dry weight (c) of 'Diphiri Cream' plants at 78 days after sowing.

Traces of P deficiency were also noticed on plants given 53.0 mg P plant^{-1}, but none at P rates of 79.5 to 159 mg P plant^{-1}. The P effect observed on shoot growth was similar for root and nodule growth and pod development; the number of days to flowering and podding was not affected by P rate.

Shoot phosphorus concentration

Shoot P concentration significantly increased with increased level of P fertilization and varied between 0.07 and 0.20%. The increases in P concentration were significant at P additions higher than 53 mg P plant^{-1} (Fig. 4.2). In agreement with the observed visual P deficiency symptoms at P rates between 0.207 and 26.5 mg P plant^{-1}, shoot P concentrations within this range were low and varied between 0.07 and 0.09%.

Nutrient calibration curves relating shoot P concentrations to shoot DM, number of leaves and leaf area per plant are shown in Figures 4.3a-c. The critical shoot P concentrations associated with a 10% reduction in maximum shoot DM, number of leaves plant^{-1} and leaf area plant^{1}, determined visually from the graphs in Figures 4.3a-c, were essentially the same for the three parameters being 0.15%, 0.15% and 0.16%, respectively. The critical nutrient range for the three parameters was from 0.15 to 0.20%.

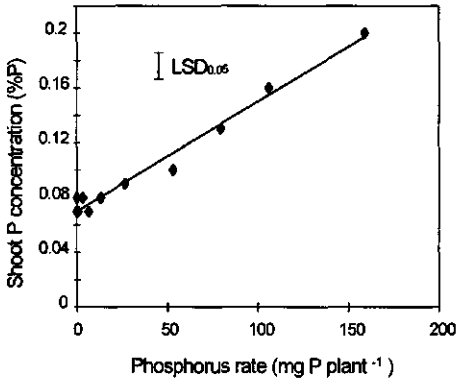

Figure 4.2. Effect of the level of phosphorus application on shoot phosphorus concentration of 'Diphiri Cream' plants at 78 days after sowing.

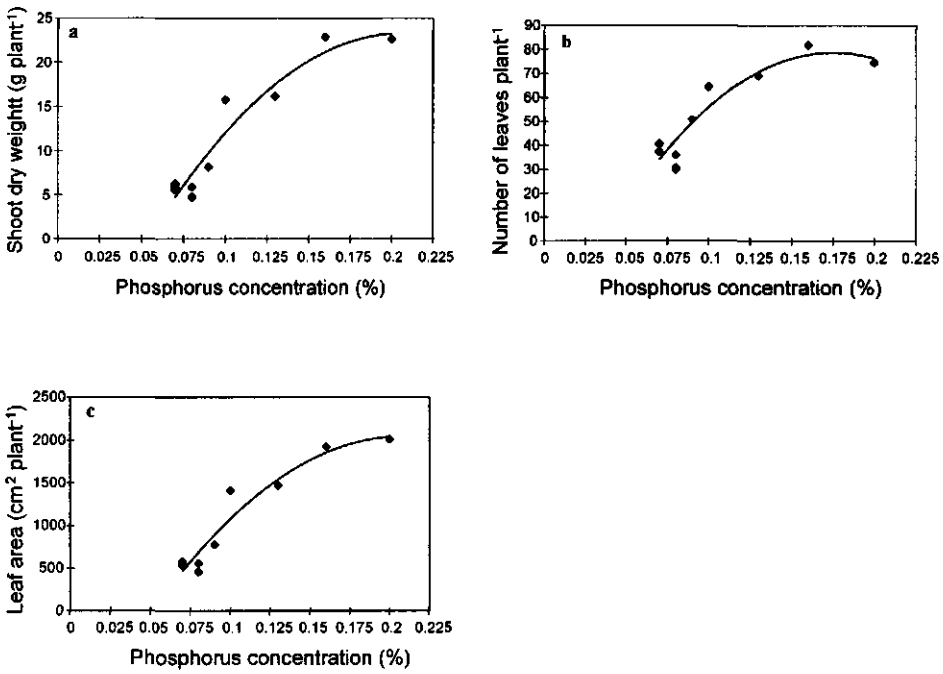

Figure 4.3. Relationship between shoot P concentration and shoot dry weight (a), number of leaves (b), and leaf area (c) of 'Diphiri Cream' plants at 78 days after sowing.

4.1.4 Discussion

The critical shoot P concentration and range for bambara groundnut determined visually from the graphs were 0.15% and 0.15-0.20%, respectively. Stunted growth seemed to be the major symptom of P deficiency of Bambara groundnut and was observed in plants with shoot P concentrations less than 0.10%. This demonstrates the important role of P in growth and development of bambara groundnut.

The critical level of a nutrient means that at that level that element is still slightly limiting growth (Smith, 1962). A shoot P concentration of about 0.15 % seemed to be critical for bambara groundnut and therefore an indication that plants that produce biomass with that P level in their shoots are at least marginally supplied with P. In our field experiment, at 78 DAS, shoot P

concentrations were around the critical P level, being 0.15 and 0.14% for rainfed and irrigated treatments, respectively (Chapter 2). The plants in our pot experiments were also suffering from P deficiency with shoot P concentrations of 0.11-0.13% (Chapters 3.1 and 3.2). Probably in our field experiment, where there was no response to P fertilization, P supply was still limited and broadcasting of the fertilizer did not bring it close enough to the roots of the seedlings at the critical time (Chapter 3.2).

The critical shoot P level of bambara groundnut determined in this experiment has, however, demonstrated that the P status of Bambara groundnut plants in all our previous experiments (pot and field) was marginal. As shown in Chapter 2, this seems to be due not only to a low soil P status, but to a combination of low soil P and low soil moisture content, probably strengthened by a relatively poor root development of bambara groundnut (Chapter 3.1).

4.2 Shoot phosphorus levels in bambara groundnut plants in farmers' fields in Botswana

4.2.1 Introduction

Shoot P concentrations in the field experiment (Chapter 2), in which bambara groundnut did not respond to applied P, were around the critical P level as determined in the sand culture experiment (Chapter 4.1). This might mean that the content of available P in the soil was probably not high enough to meet the P requirement of the crop.

As an inadequate P supply was encountered on a soil cleared from a well developed bush fallow vegetation (Chapter 2), it may be expected that a more outspoken P shortage can occur on unfertilized permanently (frequently) cropped farmers' field. To check this assumption, a survey was conducted to assess the P nutritional status of the crop using the critical concentrations established in the sand culture experiment as a reference.

4.2.2 Materials and methods

For this study, ten farmers growing cream coloured bambara groundnut were randomly selected from the Kgatleng District in Eastern Botswana, within a radius of 60 km from Botswana College of Agriculture, Sebele (24°33′ S; 25°54′ E, 994 m). The farmers were selected by extension workers on the basis of their interest and many years of experience with the crop. The farmers were requested to grow the crop as usual and keep records of planting date and yield of pods at harvest. Where the farmer did not keep a record of the planting date, it was estimated with information given by the farmer. The farmers were visited at least once a month to monitor the

farming operations and to collect information on the cropping activities. The nearest weather station to the farms was at Sebele and the rainfall data from this station is used to generally describe the climatic conditions in the survey area (Fig. 4.4).

Planting in the farms was done between 8 th November and 20 th December 1996 and the area under bambara groundnut per farm varied between 0.08 and 2.17 ha. The main criterion determining the date of planting was the availability of rains. The area under bambara groundnut was determined with a measuring tape. Three farmers (30%) had broadcast the seed and ploughed to cover it with soil, while the rest planted in rows with either a tractor or an animal drawn planter after ploughing. None of the farmers applied fertilizer during the survey period, but one farmer (No. 2; Table 4.1) applied P fertilizer in the previous season while another (No. 9) about eight years ago. In all the farms, the crop was a pure stand planted on the flat land without ridges.

Plant and soil samples from each farm were taken around 78 days after sowing (DAS), which was 50% podding stage (Ramolemana *et al.*, 1997). The sampling period was estimated from the planting date as provided by the farmers. A sample of six plants 10 m apart was taken from the middle of the area under bambara groundnut starting five metres from the edge. The soil sample collected per farm was a composite of 24 subsamples taken with an auger (20 mm diameter and 30 cm long) to a depth of 20 cm. At each of the spots where the six plants were sampled, four soil subsamples were taken. Three soil subsamples were taken at a radius of 50 cm around each plant selected for sampling, with the fourth on the spot where the plant was grown.

The plant shoots were oven-dried at 70°C for 24 hours and dry weight taken. The six plants were then ground in a plant grinder with a 2 mm sieve to make one composite sample, subsequently analyzed for N, P and K, as described in Chapter 2. The soil samples were air dried for two weeks and later analysed for mineral nutrients as described in Chapter 2.

Pod production estimates from the area under bambara groundnut in each farm, as obtained from the farmers, were converted to yields per hectare. Data on plant densities of bambara groundnut in the farms involved in the study were not collected. Correlations of parameters measured from both plant and soil samples were determined using the SAS (1985) statistical programme.

4.2.3 Results

Soil phosphorus status

The soil P levels (P-Bray) of the ten farms ranged from 2.8 to 9.1 mg P kg^{-1} with the highest at farm No. 2, the farm where P fertilizer was applied the previous season (Table 4.1). On average, P-Bray of the fields was 4.4 mg P kg^{-1} soil. The difference between other soil characteristics were small (Table 4.1). The pH levels of the soils were rather low, on average 4.6.

Table 4.1. Some chemical characteristics of soils from 10 different bambara groundnut farms.

Farm	pH	P-Bray (mg kg^{-1})	Org. carbon (wt. %)	CEC (cmol (+) kg^{-1})	Exchangeable cations (cmol (+) kg^{-1})			
					Ca	Mg	K	Na
1. Masule	5.06	3.33	0.17	3.96	1.49	0.74	0.33	0.04
2. Lekorwe	4.22	9.08	0.22	280	0.52	0.32	0.33	0.04
3. Mosekiemang	4.62	2.77	0.19	2.08	0.87	0.32	0.16	0.04
4. Motswasele	4.43	2.97	0.13	2.08	0.42	0.28	0.20	0.04
5. Thamage	4.50	2.88	0.16	2.04	0.92	0.24	0.20	0.04
6. Gare	4.67	3.33	0.25	2.12	0.70	0.26	0.16	0.04
7. Masupu	4.91	4.10	0.26	2.44	1.01	0.42	0.29	0.04
8. Ntlhwasane	3.95	3.78	0.26	1.60	0.11	0.15	0.12	0.04
9. Tlhase	4.11	7.18	0.19	1.96	0.60	0.28	0.20	0.04
10. Maotsela	5.50	4.27	0.13	2.68	1.20	0.51	0.29	0.04
Average	4.6	4.4	0.20	2.40	0.78	0.35	0.23	0.04

Shoot nutrient status

The shoot P concentrations ranged from 0.10 to 0.16% with the highest level again on farm No. 2, the farm where P fertilizer was applied the previous season (Table 4.2). Total P in the plants (represented by the shoot P content in mg P $plant^{-1}$) shows variations with a factor of 4. The variation in shoot P content was however due to variation in shoot DM (Table 4.2). Variations in shoot N and K concentrations were observed, but the lowest levels measured being respectively 2.14 and 1.56% are adequate, as compared to means of 2.70 and 1.13% at the same growth stage from a previous field experiment (Chapter 2).

Estimated pod yields varied between 635 and 875 kg ha^{-1} (Table 4.2). This variation was much less than the observed variation in shoot DM $plant^{-1}$.

Table 4.2. Mineral nutrient status of plant samples collected at 78 days after sowing and pod yield estimates at final harvest from 10 different bambara groundnut farms.

Farm	Shoot DM (g plant^{-1})	Shoot P (%)	Shoot N (%)	Shoot K (%)	Total P (mg plant^{-1})[2]	Yield (kg ha^{-1})
1. Masule	76.3	0.12	2.35	1.88	92	875
2. Lekorwe	23.8	0.16	2.60	2.26	38	778
3. Mosekiemang	54.8	0.15	2.33	2.25	82	806
4. Motswasele	54.6	0.11	2.14	2.19	60	759
5. Thamage[1]	19.1	0.12	2.30	2.11	23	n.a.
6. Gare	28.9	0.11	2.35	1.64	32	635
7. Masupu	47.5	0.13	2.60	1.96	62	875
8. Ntlhwasane	29.4	0.11	2.62	1.78	32	673
9. Tlhase	36.7	0.10	2.38	1.56	37	740
10. Maotsela	25.2	0.13	2.09	1.85	33	700
Average	39.6	0.12	2.38	1.95	49	760

[1]The crop was later destroyed by porcupines and ground squirrels.

[2] Shoot P content

No correlations were found between soil P levels on the one hand and shoot DM and shoot P concentration on the other hand. Correlations between shoot P content and shoot DM, shoot DM and pod yield, soil organic matter content and shoot N concentration were significant.

4.2.4 Discussion

The average soil P content of 4.4 mg P kg^{-1} found in the ten bambara groundnut farms in Botswana is generally considered to be low, compared to a minimum of P-Bray of 10 mg P kg^{-1} required for sorghum (Beynon, 1991). Shoot P concentrations were also low (Table 4.2). Only in two fields shoot P concentrations reached the level of 0.15 and 0.16% which corresponds with the critical shoot P level for bambara groundnut. In all other fields, plants showed shoot P

concentrations between 0.10 and 0.13% which correspond with moderate to severe P deficiency. This means that in all those fields P supply was suboptimal.

The shoot P content of rainfed plants from our field experiment (Chapter 2) was 109 mg P plant^{-1}, being about twice as high as the average of plants grown on the traditional farms investigated in this study (Table 4.2). Plant growth and shoot P content of only one farm (No.1) was similar to that of our rainfed treatment with a shoot dry weight of 76.3 g plant^{-1}. Probably during the field experiment (1995/96) the rainfall distribution was better than in the 1996/97 growing season, when the survey was carried out (Fig.4.4). Differences can not be explained on the basis of differences in total rainfall between the years 1995/96 and 1996/97, being respectively 633 and 676 mm.

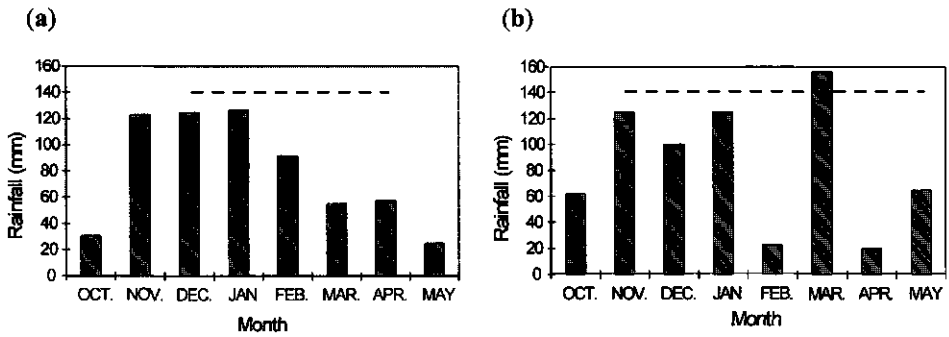

Figure 4.4. Rainfall distribution during the 1995/96 (a) and 1996/97 (b) planting seasons as recorded at Sebele Botswana Meteorology Station. (---- bambara groundnut growth period).

Since the shoot P content was directly related to the shoot dry matter weight (growth), the latter probably acting as a sink for P uptake, differences in shoot P content between our field experiment and most of the farm-grown plants may also be due to differences in cultivation technique. Plant density, weed control and crop protection in our experimental plots were probably better than in farmers' fields.

Finally, whether the low seed yields as presented in Table 4.2 are a direct result of a too low P content of the soil is questionable. Probably without irrigation P availability was very low leading to low P uptake and P deficiencies. A direct water stress can also be involved. Besides P deficiency, also a low plant density contributes to the low yields in farmers fields. Therefore, yield increases can only be achieved by irrigation in combination with increased plant density, and subsequently followed by P fertilization.

Chapter 5

Response of bambara groundnut (*Vigna subterranea* (L.) Verdc.) to mineral nitrogen fertilizer application if grown under non-limiting phosphorus conditions

5.1 Introduction

Nitrogen fixation by legumes depends on different soil conditions such as the availability of mineral nutrients like nitrogen (Allos and Bartholomew, 1955; Hartfield *et al.*, 1974; Graham and Scott, 1984) and phosphorus (Aguilar and Van Diest, 1981; Israel, 1987). In our previous studies with bambara groundnut grown in P-poor soils, however, phosphorus fertilization did not affect nodulation nor shoot N concentration (Chapters 2 and 3). Shoot N concentrations were not affected even when shoot DM was increased by improved soil moisture conditions or by P application to the soil. Evidently under the prevailing conditions total N supply, consisting of N_2 fixed by the plants plus mineral nitrogen from mineralization was sufficient to meet the plants N requirement also at higher dry matter (DM) production. However, in all previous experiments, carried out both in the field and in pots, bambara groundnut plants were growing under marginal P conditions with shoot P concentrations around or below the critical level, irrespective of the treatment (P fertilization, irrigation) or DM production. This raises the question whether the plant N supply will still be adequate if bambara groundnut plants are grown under conditions where P will be no longer marginal or deficient. Under such conditions, higher DM production will not only increase the plant N requirement, but also the N_2 fixation might behave differently. If P in the plant is directly involved in the N_2 fixation process (Israel, 1987), a lack of response of N_2 fixation to P fertilization can be expected as long as the plant P status is not affected by P fertilization and remains at the deficient level. Such conditions prevailed in all previous experiments.

Therefore, the main objectives of this experiment are to find out (i) whether with bambara groundnut the capacity of the N_2 fixation process, possibly supplemented with some native soil mineral N, is high enough to meet the plant N requirement also under non-limiting P conditions, and (ii) whether at internal P concentrations exceeding the critical level, the amount of fixed N_2 increases with increasing internal P status. This might indicate the P-dependency of the N_2 fixation process.

To answer the above questions, a pot experiment was carried out with bambara groundnut plants grown in a P-poor soil fertilized at sowing with or without mineral N in combination with different rates of P, the latter up to levels leading to luxurious internal P levels.

5.2 Materials and methods

The experiment was conducted from the 2 nd July to 7 th November 1996 in a greenhouse at Botswana College of Agriculture with the same soil as described in Chapter 3.1. The average monthly temperatures varied between 30-34°C during the day and 18-21°C at night.

The treatments composed of two nitrogen levels (0 and 350 mg N pot^{-1}; on weight basis of 2 000 000 kg soil ha^{-1} corresponding to 100 kg N ha^{-1}) and five phosphorus levels (0, 105, 210, 315 and 420 mg P pot^{-1} corresponding to 0, 30, 60, 90 and 120 kg P ha^{-1}). White five-litre pots (25 cm diameter x 25 cm height) holding seven kg of soil were used for growing the plants. Smaller pots than in previous experiments were used to have a high root density and increased contact of the plant roots with applied P. This was done to increase P uptake by the plants. The treatments were arranged in a completely randomized design with three replicates. Single superphosphate was crushed and thoroughly mixed with the soil. Urea was dissolved in 250 ml of water and applied evenly over the soil immediately after sowing. No mineral nutrients other than P and N were applied. Three seeds of 'Diphiri Cream' were sown per pot and thinned to one seedling 19 days after sowing (DAS). The experiment was started while it was still winter when light intensity was low and day length was sometimes less than 12 hours. To achieve optimal growth Philips light bulbs (75 W) were used for increasing light intensity and day length for the period between sowing and 115 DAS. The bulbs were automatically switched on and off at 6:00 and at 18:00 hours, respectively. The soil moisture content was maintained at field capacity. From flowering onwards, water was poured into saucers to avoid damaging flowers. The plants were sprayed with Benlate (a.i.Benomyl) and Garden Ripcord (a.i.Cypermethrin) to control mildew disease and aphids, respectively. Earthing up (covering of pods with soil) was done 70 DAS.

Samples were taken at the vegetative growth stage (35 DAS), 50% podding (76 DAS, when half of the plants had at least one pod which was 0.5 cm long), and at the final harvest when leaves turned yellow. The final harvest of plants that received additional mineral nitrogen was at 115 DAS while those without N fertilization at 128 DAS. Data recorded were shoot, root and nodule dry weights, number and dry weight of pods and seed yield per plant. Root and nodule weights were taken only at 76 DAS. The plant parts (shoot, root and nodules) were oven-dried at 70°C for 24 hours, while pods were sun dried for two weeks. The dry shoots were ground in a plant grinder with a 2 mm sieve, and analysed for N and P as described in Chapter 2. Statistical analysis of the data was as described in Chapter 2.

5.3 Results

Dry matter production

Shoot dry matter (DM) after P fertilization (without additional N) was at all sampling dates twice as high as the control (-P; -N treatment) (Table 5.1). An increase in P rate beyond 105 mg P pot^{-1}

did not further increase shoot DM at all sampling periods. At early podding (76 DAS), N fertilization significantly increased shoot DM of P fertilized plants by 15-32%, relative to -N. There were no significant differences in shoot DM at 35 DAS and final harvest between -N and +N plants neither with or without P fertilization. The plants given extra mineral N matured early (115 DAS), compared to -N plants (128 DAS).

Table 5.1. Effect of phosphorus and nitrogen application on shoot dry weight of 'Diphiri Cream' plants at different growth stages (days after sowing; DAS).

Phosphorus (mg P pot^{-1})	Shoot dry weight (g plant^{-1})					
	35 DAS		76 DAS		115/128 DAS*	
	-N	+N	-N	+N	-N	+N
0	1.18	1.44	9.23	9.82	12.46	12.83
105	1.99	1.95	20.20	23.23	22.18	24.87
210	1.97	1.98	21.34	25.63	24.94	24.76
315	1.97	2.16	19.9	26.34	23.32	24.74
420	2.27	2.29	21.30	26.91	24.24	26.31
Mean	1.88	1.96	18.41	22.39	21.43	22.70
C.V. (%)	13.1		12.0		11.7	
S.E. (20 D.F.)	0.10		1.0		1.05	
$LSD_{0.05}$	0.30		2.95		3.10	

* +N plants harvested at 115, while -N at 128 DAS.

Relative to the control, increases in dry weight after P fertilization (-N) were low for roots (about 25%), but the nodule dry weight was increased two and half times after P fertilization (Table 5.2). Effects of P fertilization on root growth were significant with maximum root dry weight at 105 mg P pot^{-1} and then decreasing with further increase in P rate. With the exception of the zero P treatment, nodule dry weights at different P rates were not significantly different. Nitrogen application had no significant effect on root and nodule dry weights.

Table 5.2. Effect of phosphorus and nitrogen application on roots and nodule dry weight of 'Diphiri Cream' plants at 76 days after sowing.

Phosphorus (mg P pot^{-1})	Dry weights (g plant^{-1})			
	Roots		Nodules	
	-N	+N	-N	+N
0	5.20	4.38	0.69	0.48
105	7.81	7.85	1.77	1.42
210	6.58	7.11	1.79	1.68
315	5.89	5.73	1.56	1.50
420	5.66	7.14	1.83	1.56
Mean	6.23	6.44	1.53	1.33
C.V. (%)	15.4		19.8	
S.E. (20 D.F.)	0.40		0.12	
$LSD_{0.05}$	1.17		0.34	

Pod and seed yield

Number of pods and pod dry weight after P fertilization (-N) were on average increased three and four times, relative to control, respectively (Table 5.3). Phosphorus fertilization beyond a rate of 105 mg P pot^{-1} did not further increase the number of pods and pod dry weight. Seed yield after P fertilization (-N) was on average increased four and half times, relative to control, with no difference between P rates. Nitrogen application had no significant effect on number of pods, pod dry weight and seed yield (Table 5.3).

Table 5.3. Effect of phosphorus and nitrogen application on number of pods, pod and seed dry weight of 'Diphiri Cream' at final harvest (115 and 128 DAS)*.

Phosphorus (mg P pot^{-1})	Number of pods plant^{-1}		Pod wt. (g plant^{-1})		Seed wt. (g plant^{-1})	
	-N	+N	-N	+N	-N	+N
0	31.7	24.7	11.9	6.0	8.8	4.5
105	91.0	74.7	48.4	44.3	40.1	36.9
210	92.7	81.0	45.0	46.0	37.8	38.4
315	89.0	105.0	50.2	49.6	42.0	41.6
420	90.0	71.3	45.9	38.6	38.7	32.5
Mean	79.0	71.3	40.3	36.9	33.5	30.8
C.V. (%)	24.1		21.0		22.7	
S.E. (20 D.F.)	7.39		3.3 0		2.97	
$LSD_{0.05}$	21.8		9.74		8.77	

* +N plants harvested at 115, while -N at 128 DAS

Shoot nutrient status

Phosphorus

The increases in shoot P concentration due to P fertilization (-N) were very significant at all three harvests (Table 5.4). The effects of the various P rates were significantly different from control at all sampling periods, with the highest rate giving the highest shoot P concentration. The -N plants at the highest P rate developed necrosis on leaf edges which started at flowering and continued until early podding stage, which was suspected to be due to exceptionally high shoot P concentrations. The high shoot P concentrations for this treatment at 35 and 76 DAS confirm this. For the corresponding +N plants, shoot P concentrations were equally high or lower and plants did not show leaf necrosis (Table 5.4). There was a strong decrease in shoot P concentration between 76 DAS and final harvest. Shoot P content followed a similar trend as the shoot P concentration, with the highest shoot P concentration giving the highest shoot P content. Phosphorus fertilization at a level ≥105 mg P pot^{-1}

increased the shoot P concentrations beyond the critical shoot P range (0.15-0.20%) for bambara groundnut as determined from a sand culture at 78 DAS (Chapter 4).

Table 5.4. Effect of phosphorus and nitrogen application on shoot phosphorus concentration of 'Diphiri Cream' plants at different growth stages (days after sowing, DAS)

Phosphorus (mg P pot^{-1})	Shoot P concentration (%)					
	35 DAS		76 DAS[1]		115/128 DAS[2]	
	-N	+N	-N	+N	-N	+N
0	0.09	0.12	0.11	0.12	0.07	0.08
105	0.21	0.19	0.20	0.17	0.06	0.06
210	0.28	0.27	0.21	0.20	0.09	0.08
315	0.35	0.31	0.27	0.20	0.10	0.10
420	0.39	0.40	0.32	0.25	0.13	0.14
Mean	0.26	0.26	0.22	0.19	0.09	0.09
C.V. (%)	11.8		11.7		15.9	
S.E. (20 D.F.)	0.013		0.010		0.006	
$LSD_{0.05}$	0.12		0.03		0.02	

[1] N application significant only at 76 DAS.

[2] +N plants harvested at 115, while -N at 128 DAS.

Nitrogen

Phosphorus fertilization (-N) significantly increased shoot N concentration at 76 DAS, relative to control (Table 5.5). An increase in P rate beyond 105 mg P pot^{-1} did not further increase shoot N concentrations. At final harvest, P fertilization had no significant effect on shoot N concentrations.

At 76 DAS, N fertilizer depressed the shoot N concentrations especially when P fertilizer was applied (Table 5.5). Also at the final harvest, N fertilization in the presence of P decreased

shoot N concentration, with the highest P rate giving the lowest N concentration. The lower shoot N concentrations at 76 DAS and final harvest in +N plants corresponds with the yellowing of leaves as observed between flowering and early podding stages, which intensified at the pod filling stage and led to early maturity.

Table 5.5. Effect of phosphorus and nitrogen application on shoot nitrogen concentration of 'Diphiri Cream' plants at different growth stages (days after sowing-DAS)

Phosphorus (mg P pot^{-1})	Shoot N concentration (%)					
	35 DAS		76 DAS[1]		115/128 DAS[2]	
	-N	+N	-N	+N	-N	+N
0	3.11	3.16	2.18	1.60	1.72	1.97
105	2.92	3.38	2.89	2.03	1.51	1.52
210	3.12	3.06	2.47	1.87	1.67	1.40
315	2.81	3.03	2.77	1.77	1.58	1.43
420	2.84	3.08	2.72	1.85	1.78	1.37
Mean	2.96	3.20	2.61	1.83	1.65	1.54
C.V. (%)	11.1		11.6		8.3	
S.E. (20 D.F.)	0.14		0.10		0.05	
$LSD_{0.05}$	n.s.		0.31		0.23	

[1] N application significant at 76 DAS and final harvest.

[2] +N plants harvested at 115, while -N at 128 DAS. n.s. = not significant.

The increases in shoot N content after P fertilization followed a similar trend as shoot N concentrations. Average increases in shoot N contents after P fertilization (-N) were 30, 360 and 172 mg N plant^{-1}, relative to control, at 35, 76 DAS and final harvest, respectively (Table 5.6). At 35 and 76 DAS, a further increase in P rate higher than 105 mg P pot^{-1} did not change the shoot N content. At final harvest, there was a slight increase in shoot N content with increase in P rate. Contrary to shoot DM, N fertilization significantly decreased the shoot N content at 76 DAS by 18%, relative to -N (Table 5.6). This decrease in shoot N content is in agreement with the decrease in shoot N concentration at 76 DAS for +N plants (Table 5.5).

At final harvest, N fertilization had no significant effect on shoot N content. However, it has to be considered that N in the pods has not been included in the shoot N contents as presented in Table 5.6. This can quantitatively be very important at the final harvest.

Table 5.6. Effect of phosphorus and nitrogen application on shoot nitrogen content of 'Diphiri Cream' plants at different growth stages (days after sowing; DAS).

Phosphorus (mg P pot^{-1})	Shoot N content (mg N plant^{-1})					
	35 DAS		76 DAS[1]		115/128 DAS[2]	
	-N	+N	-N	+N	-N	+N
0	31.0	45.5	201.2	155.9	213.3	252.8
105	59.1	65.8	584.5	472.5	337.7	379.7
210	61.7	60.5	537.9	482.4	414.9	343.5
315	55.2	71.0	551.0	467.5	367.8	354.3
420	64.1	71.4	577.6	498.4	431.3	362.3
Mean	55.5	62.9	490.4	415.4	353.0	338.5
C.V. (%)	20.0		19.3		13.8	
S.E. (20 D.F.)	4.8		35.7		19.4	
$LSD_{0.05}$	14.3		105.3		57.3	

[1] N application significant.

[2] +N plants harvested at 115, while -N at 128 DAS.

5.4 Discussion

The positive response of shoot, root and nodule dry weights and shoot P and N concentrations to P fertilization, as found in this study, agrees with the critical P level for bambara groundnut (Chapters 4). In previous experiments shoot DM and seed yields were increased by P application only under pot conditions with shoot P concentrations remaining around or below the critical P level. The shoot P concentrations in this study reached levels above the critical P range for bambara groundnut (Chapter 4), which means that the plants were no longer

suffering from P deficiency. Consequently, growth was significantly increased by P fertilization.

In this study, improved P availability increased nodule dry weights and shoot N concentrations (Table 5.2 and 5.5). This might point to a positive effect of improved P nutrition on N_2 fixation. Plants fertilized with P but not with N showed optimum growth and seed yield at shoot P and N concentrations at early podding stage of 0.20% and 2.89%, respectively (Tables 5.1, 5.2, 5.3, 5.5). However, shoot N concentrations in our previous field experiment (Chapter 2) were similar, being 2.70% at 78 DAS both with and without irrigation. This means that plants in that field experiment were also adequately supplied with N, though shoot P concentrations were around or below the critical level (0.15%P). Evidently phosphorus seemed not to have limited N nutrition in that field experiment. On the other hand, shoot N concentrations in previous pot experiments (Chapter 3) were much lower and varied between 1.68 and 2.03%, with shoot P concentrations always varying around or below the critical level. This might point to a reduced N_2 fixation at suboptimal P supply. Evidently, results of the various experiments are not in agreement with each other with respect to the possible role of P nutrition in the plant N_2 fixation capacity and further research on this subject is needed.

Application of N at sowing under non-limiting P conditions did not affect shoot, root and nodule dry weights nor N nutrition of bambara groundnut. This means that under the prevailing conditions, bambara groundnut plants were able to meet their N requirements through N_2 fixation, in addition to mineral N from the soil. In fact mineral N fertilizer had a negative effect which led to early maturity and low number of pods and low seed yields (Table 5.3). Plants given mineral fertilizer N at sowing seemed to do better at the initial phase of growth and were during that period probably well supplied with N originating from the soil N, from N fertilizer and to a limited extent from N_2 fixation. This is shown by the higher shoot DM with this treatment at 76 DAS (Table 5.1). However, later on mineral N in the soil seemed to be exhausted and plants apparently did not have the potential to switch on the very short term to N_2 fixation. This led to growth stagnation of +N plants. That this process has already been started at 76 DAS is shown by the lower shoot N concentrations and lower shoot N content of +N plants at that time (Tables 5.5 and 5.6). Plants fed with extra mineral N fertilizer changed from a luxurious N to poor N supply with a corresponding early maturity. With N_2 fixing plants (-N plants) N supply steadily goes on, with a continuous growth and retarded maturity. Though nodule dry weights of plants with and without extra mineral N fertilizer were similar at 76 DAS, the low shoot N concentration and low shoot N content of the former indicate that N_2 fixation capacity was reduced after N fertilization. Further, N fertilization seemed to have a negative effect on pod set (Table 5.3). The low number of pods and low pod yield for the +N treatment in the absence of P could be responsible for the high shoot N concentration at final harvest (Table 5.5). The high shoot N concentration for this treatment may be an indication that the poor pod set limited the reallocation of internal N from the shoot to the pods. Therefore, mineral N fertilization to bambara groundnut seemed not to be necessary, also not under non-limiting P conditions.

About the contribution of soil mineral N to the N nutrition, more detailed work has been carried out (Chapter 6). However, based on the low organic matter content of the soil used (Chapter 2), N delivered to the plant via mineralization can be expected to be low. Consequently, N in plants without N fertilization will mostly originate from N_2 fixed by the plant.

Finally, in bambara groundnut grown under non-limiting P conditions, nitrogen fixation possibly supplemented with some native soil mineral N seemed to be sufficient to meet the N requirements for optimal growth. Under the experimental conditions, application of mineral N fertilizer to bambara groundnut plants at sowing did not improve the plant N nutrition nor growth. It only resulted in early maturing of plants.

Chapter 6

Response of bambara groundnut (*Vigna subterranea* (L.) Verdc.) to mineral nitrogen fertilizer. Effect of time of application

6.1 Introduction

In the previous pot experiment (Chapter 5) it was found that under non-limiting phosphorus conditions growth of bambara groundnut did not respond to mineral N fertilizer if applied at sowing time. In the literature, however, there is evidence that during certain developmental stages bambara groundnut is likely to experience a shortage of N. One of those stages is the onset of podding, when a major shift in assimilate partitioning takes place from vegetative parts to pods (Brink, 1998; Chapter 2). This is likely to have implications for the supply of nodules with assimilates and this may limit nodule development and its N_2 fixing capacity. It has been reported for other leguminous crops that N_2 fixation can not always meet the plant N requirement for optimal yield, and that with low soil N levels the yield potential can be limited (Harper, 1974; Bhangoo and Albritton, 1976; Ingestad, 1980). Flowering might be another stage during which N supply is important. Both in cowpea and soybean N application at flowering has been reported to retard leaf senescence leading to an extended vegetative growth period and increased seed yield (Elowad and Hall, 1987; Isfa, 1991).

These considerations prompted the idea to investigate the effect of N fertilization on bambara groundnut if applied at the following development stages: at sowing (as in the previous experiment), at early vegetative growth, at (50%) flowering and (50%) podding. To separate the contributions of soil mineral N and N_2 fixation to the N nutrition of bambara groundnut plants, treatments with sterilized and unsterilized soil were incorporated in the experiment. For the sterilized soil treatment it was assumed that the plants would be completely dependent on soil mineral N for growth. Therefore, this study was conducted to determine the potential of bambara groundnut to utilize mineral N fertilizer applied at different growth stages, and to assess the contribution of soil mineral N to N nutrition of bambara groundnut plants.

6.2 Materials and methods

A pot experiment was conducted from 26 th November 1996 to 3 rd April 1997 on the grounds of the forestry nursery of Botswana College of Agriculture, with a similar soil as used in Chapter 3.1. Maximum and minimum temperatures varied between 26.5-32.4 °C and 16.3-18.7 °C, respectively.

There were six treatments as indicated in Table 6.1. The treatments were arranged in a completely randomized design with five replicates. For the vegetative stage, N fertilization was at 28 days after sowing (DAS); 50% flowering stage was defined as when 50% of the plants had at least one open flower and this was at 45 DAS; 50% podding stage was when half of the plants had at least one pod with a length of about 0.5 cm, and this was at 69 DAS. For the sterilized soil treatment, the soil was sterilized by wetting and heating at 80 °C for two and half hours using a Camplex- Electric Soil Sterilizer, Cat. No. HD5112. White ten-liter pots (diameter 35 cm x 35 cm depth) holding 14 kg of soil were used for growing the plants. Crushed single superphosphate applied at a rate of 420 mg P pot^{-1} (on weight basis of 2000000 kg soil ha^{-1} corresponding to 60 kg P ha^{-1}) was thoroughly mixed with the soil. Urea at a rate of 525 mg N pot^{-1} (corresponding to 75 kg N ha^{-1}) was dissolved in 250 ml water and evenly applied over the soil at different growth stages. No mineral nutrients other than P and N were applied. Three seeds of 'Diphiri Cream' were sown per pot and thinned to one seedling at 17 DAS. The soil moisture content was maintained at field capacity. After flowering, water was poured into saucers to avoid damaging the flowers.

Samples were taken at different stages of growth as described in Table 6.1. The final harvest included all the treatments and took place 128 DAS when the leaves were yellow. Data recorded were dry weight of plant components (shoot, roots, nodules and pods where applicable), number of nodules and pods. Shoots, roots and nodules were oven-dried at 70 °C for 24 hours, while pods were air dried for two weeks. The shoots were ground in a plant grinder with a two mm sieve, and analysed for N as described in Chapter 2. Statistical analysis of data was carried out as described in Chapter 2.

Table 6.1. Description of the different treatments and times of plant sampling. S1 = vegetative stage; S2 = 50% flowering stage; S3 = 50% podding stage; S4 = final harvest.

Treatment	Sampling time[1]
T1 (no N fertilization; control)	S1; S2; S3; S4
T2 (no N fertilization; soil sterilization)	S1; S2 ; S3; S4
T3 (N fertilization at sowing)	S1; S2; S3; S4
T4 (N fertilization at vegetative stage; 28 DAS)	S2; S3; S4
T5 (N fertilization at 50% flowering; 45 DAS)	S3; S4
T6 (N fertilization at 50% podding; 69 DAS)	S4

[1] With treatment T2 sampling S2 and S3 were delayed with two weeks compared to other treatments.

6.3 Results

Dry matter production

Compared to the control treatment (T1), nitrogen fertilization did not significantly affect shoot dry matter (DM), irrespective of time of application (Table 6.2). However, N application at sowing (T3) tended to give the highest and N application at 50% flowering (T5) the lowest shoot dry weight at the final harvest. In general the plants given extra mineral N at 50% flowering (T5) matured earlier than plants with other treatments. Though sterilization (T2) increased shoot DM by 89% at the 50% flowering stage, at all other stages sterilization had no significant effect on shoot DM (Table 6.2). On the other hand, sterilization significantly affected flower initiation. The 50% flowering and also the 50% podding stages were delayed with about two weeks by sterilization. This might explain the high shoot DM at 50% flowering with the sterilization treatment.

Nodulation

Soil sterilization significantly reduced nodule formation (number and biomass), but did not inhibit it completely (Table 6.3). In all treatments nodule number and nodule dry weight per plant increased with time, but in sterilized soil the increase was much less. At 50% flowering, nodule number and nodule dry weight after sterilization were two and a half times lower than that of the control. At 50% podding there was still a clear negative effect on nodulation. Plants grown in sterilized soil had on average 170 nodules and the control plants 400 nodules. Data on nodulation at final harvest are missing because most nodules were decomposed at that time. Effects of N fertilization on nodulation differed with plant age. At 50% flowering stage, nodulation was not significantly affected by N fertilization. However, mineral N fertilizer tended to reduce nodulation at the 50 % podding stage, but only if applied late during the growing season.

Pod and seed yields

At final harvest, plants fertilized with N at sowing (T3) gave a significantly lower number of pods per plant (Fig. 6.1a), while soil sterilization did not affect pod number. Total pod dry weight per plant (shell plus seed) at final harvest gave a similar pattern as pod number (Fig. 6.1b). Again plants fertilized with N at sowing yielded the lowest pod DM, but due to a great variability in pod and seed dry weights, differences between treatments were not statistically significant ($P \leq 0.05$).

Table 6.2. Effect of a single dose of nitrogen applied at different growth stages and soil sterilization on shoot dry weight of 'Diphiri Cream' plants at vegetative (28 DAS), 50% flowering (45 DAS), 50% podding (69 DAS) and final harvest (128 DAS).

Treatment	Shoot dry weight (g plant^{-1})			
	Vegetative stage	50% flowering	50% podding	Final harvest
Control (T1)	1.03	6.56	18.3	22.9
Sterilized soil (T2)	0.79	12.3[1]	15.5[1]	27.0
N at sowing (T3)	1.32	7.01	20.1	34.1
N at vegetative stage (T4)	-	7.70	20.4	28.8
N at 50% flowering (T5)	-	-	21.1	18.4
N at 50% podding (T6)	-	-	-	23.6
C.V. (%)	25.4	33.0	21.4	30.8
S.E.	0.12	1.24	1.83	3.56
$LSD_{0.05}$	0.38	3.73	n.s.	n.s.
n	15	20	25	30

[1] There was a 2 weeks delay in harvesting these treatments at 50% flowering and 50% podding.
n.s.: not significant; *n*: number of observations.

Shoot N status

Effects of time of N application on shoot N concentration are presented in Table 6.4. At the 50% flowering stage, N fertilization gave a significantly higher shoot N concentration if applied at the vegetative stage (T4). At the final harvest, shoot N concentrations were increased by N fertilization if applied at sowing (T3). Soil sterilization (T2) significantly affected shoot N concentration only at the 50% flowering stage. At this stage, shoot N concentration of plants grown in the sterilized soil was 60% of the control. Furthermore, with all treatments shoot N concentrations decreased with plant age from levels around 3-3.5% at the vegetative growth stage down to 1-1.5% at the final harvest.

Table 6.3. Effect of a single dose of nitrogen applied at different growth stages and soil sterilization on number of nodules and nodule dry weight of 'Diphiri Cream' at vegetative (28 DAS), 50% flowering (45 DAS) and 50% podding (69 DAS) stages.

Treatment	Vegetative stage	50% flowering	50% podding
	Number of nodules per plant		
Control (T1)	34	142	397
Sterilized soil (T2)	3	56[1]	172[1]
N at sowing (T3)	29	170	562
N at vegetative stage (T4)	-	149	479
N at 50% flowering (T5)	-	-	262
C.V. (%)	63.2	54.7	31.1
S.E.	6.26	31.6	52.1
$LSD_{0.05}$	19	n.s.	154
	Nodule dry weight (mg plant^{-1})		
Control (T1)	144	600	1970
Sterilized soil (T2)	1	240[1]	770[1]
N at sowing (T3)	8	600	1870
N at vegetative stage (T4)	-	280	1550
N at 50% flowering (T5)	-	-	1110
C.V. (%)	292	51.4	29.2
S.E.	0.07	0.10	0.19
$LSD_{(0.05)}$	n.s.	300	560
n	15	20	25

n.s.: not significant; *n*: number of observations.

[1]There was a 2 weeks delay in harvesting these treatments at 50% flowering and 50% podding.

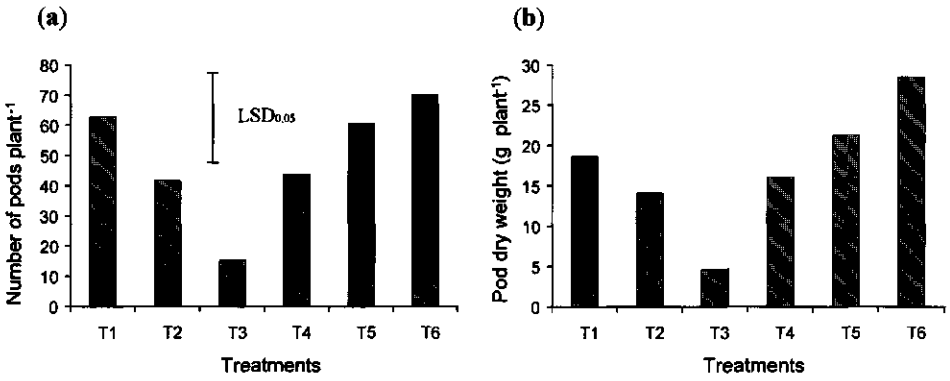

Figure 6.1. Effect of nitrogen fertilization at different growth stages and soil sterilization on number of pods (a) and pod dry weight (b) of 'Diphiri Cream' at final harvest. (Treatments: T1=control; T2=sterilized soil; T3= N fertilization at sowing; T4=N fertilization at vegetative; T5=N fertilization at 50% flowering; T6=N fertilization at 50% podding).

Soil sterilization did not affect the shoot N content of bambara groundnut plants. However, it has to be considered that plants grown in sterilized soil developed more slowly and reached the 50% flowering and 50% podding stage about 2 weeks later than plants with the other treatments (Table 6.5). Consequently, harvest of the T2 treated plants was also delayed with two weeks. Nitrogen fertilization significantly affected shoot N contents. At the vegetative stage, shoot N content was increased if plants were fertilized with N as sowing (T3). Though at later harvests effects of N fertilization on shoot N content were mostly not significant, N fertilization tended to increase shoot N content irrespective of time of application. The N contents at the final harvest given in Table 6.5 represent shoot N contents and do not include N in the pods. This quantity can be very important at the final harvest.

Table 6.4. Effect of a single dose of nitrogen applied at different growth stages and soil sterilization on shoot nitrogen concentration of 'Diphiri Cream' plants at vegetative (28 DAS), 50% flowering (45 DAS), 50% podding (69 DAS) and final harvest (128 DAS).

Treatment	Shoot N concentration (%)			
	Vegetative stage	50% flowering	50% podding	Final harvest
Control (T1)	2.77	1.98	1.64	1.10
Sterilized soil (T2)	3.05	1.20[1]	1.35[1]	1.00
N at sowing (T3)	3.23	2.03	1.91	1.37
N at vegetative stage (T4)	-	2.55	1.62	1.04
N at 50% flowering (T5)	-	-	1.88	0.88
N at 50% podding (T6)	-	-	-	1.08
C.V. (%)	23.0	12.2	18.7	15.5
S.E.	0.31	0.11	0.14	0.08
$LSD_{0.05}$	n.s	0.32	n.s.	0.22
n	15	20	25	30

n.s.: not significant; *n*: number of observations.

[1] There was a 2 weeks delay in harvesting these treatments at 50% flowering and 50% podding.

6.4 Discussion

Results of this work clearly illustrate the redundancy of a supplementary fertilization of bambara groundnut with mineral nitrogen, at least under the prevailing conditions. Nitrogen application at flowering did not extend the vegetative growth period and not increase seed yield, as hypothesized in the Introduction of this chapter. Nitrogen applied at sowing even reduced pod formation and seed yield. A lack of response to N fertilization, as observed, is an indication that this leguminous crop can meet its N requirement by N_2 fixation plus mineral N present in the soil.

Table 6.5. Effect of a single dose of nitrogen applied at different growth stages and soil sterilization on shoot nitrogen content of 'Diphiri Cream' plants at vegetative (28 DAS), 50% flowering (45 DAS), 50% podding (69 DAS) and final harvest (128 DAS).

Treatment	Shoot N content (mg N plant^{-1})			
	Vegetative stage	50% flowering	50% podding	Final harvest[2]
Control (T1)	28	130	298	250
Sterilized soil (T2)	26	148[1]	214[1]	278
N at sowing (T3)	42	142	382	468
N at vegetative stage (T4)	-	194	326	310
N at 50% flowering (T5)	-	-	396	160
N at 50% podding (T6)	-	-	-	256
C.V. (%)	29.6	23.2	22.8	39.9
S.E.	4.2	15.9	32.9	51.2
$LSD_{0.05}$	13.1	n.s.	97	149
n	15	20	25	30

n.s.: not significant; *n*: number of observations.

[1] There was a 2 weeks delay in harvesting these treatments at 50% flowering and 50% podding.

[2] The amount does not include N in the seed.

Nitrogen fertilization

The absence of a positive response of bambara groundnut to N fertilization corresponds with shoot N concentrations as measured (Table 6.4). At all four sampling times, shoot N concentrations of control plants are almost similar to those of N-fertilized plants. Moreover, measured shoot N concentrations in control plants of 2.77% N at vegetative and 1.64% N at the 50% podding stage are an indication of adequate N supply (Reuter and Robinson, 1986; Chapter 5). Evidently, relatively high nodulation rates of control plants (Table 6.3) seem to be

accompanied by a *Rhizobia* activity high enough to supply plants with sufficient nitrogen. The contribution of soil mineral N will be discussed later.

As hypothesized (Introduction) and observed with other leguminous crops (Elowad and Hall, 1987; Isfa, 1991) late application of mineral N might extend the photosynthetic active period and improve pod and seed yield of bambara groundnut. However, results of this experiment clearly demonstrate that a supplemental application of mineral N at 50% flowering stage did not increase pod and seed yield with bambara groundnut. Just contrary, after N application at 50% flowering stage shoot development was completely stopped (Table 6.2), and the final pod and seed yields were similar to those which did not receive extra N.

When extra N was applied at sowing, pod and seed yields were even reduced. When applied at that time plants took up more N (Tables 6.4 and 6.5), and showed a higher final shoot DM production. However, the higher final shoot dry matter production was completely realized during the podding stage (Table 6.2). Evidently, extra N taken up prolonged the period of shoot biomass production by maintaining a re-allocation of nitrogen and carbohydrates to the shoot at the expense of pod and seed production (Fig. 6.1). Lower final pod and seed after N fertilization at sowing are in agreement with findings of a previous experiment (Chapter 5). However, while in both experiments N fertilization at sowing resulted in lower pod and seed yields, yield reductions in the two experiments were effected differently. While in the previous experiment early maturing was the main reason for reduced yield, in the present experiment it was just extended vegetative growth after N application at sowing that led to reduced pod and seed yield. There is no real experimental evidence to explain differences in response to N fertilization at sowing between the two experiments. Only amounts of N and P fertilizer applied were different in the two experiments.

Nodulation and soil sterilization

During the period of vegetative growth, nitrogen nutrition after soil sterilization was adequate despite a severe reduction in root nodulation. Evidently mineral N present in soil, originating from mineralization, was sufficient to meet the plants N requirement during the initial phase of growth. Also at 50% flowering, when nodulation was still poor, plants seemed to contain enough N to maintain a shoot dry matter production equal to that of control plants. However, if compared with the control, average shoot N concentration at that moment was lowered by soil sterilization to a level too low for a normal generative development, expressed by a delay of flowering with about two weeks. Evidently, at the flowering stage soil mineral N was no longer sufficient. However, in this experiment soil sterilization was not completely successful and from the beginning on some nodulation was observed in sterilized soil (Table 6.3). At 50% flowering stage, nodulation seemed to be too low to supply the bambara groundnut plants with enough N to maintain adequate internal N concentrations. Some time later, however, nitrogen nutrition of plants grown in sterilized was no longer different from controls. After a temporary lack of N_2

fixation, *Rhizobium* activity seems to have been recovered and to have become active enough to supply the plants with enough N, even at low nodulation. This implies an extraordinary high N_2 fixation capacity of nodules present in sterilized soil, or excess nodulation in controls.

From this experiment it was not possible to quantify the contribution of soil mineral N to N nutrition of bambara groundnut because the soil sterilization method as used seemed to be not 100% effective. Results at least indicate that during the vegetative phase soil mineral N clearly contributed to the nitrogen nutrition of bambara groundnut, but soon afterwards it became of minor importance, probably due to depletion.

Finally, fertilization of bambara groundnut with nitrogen seemed to be not beneficial, irrespective of time of application. If N fertilization affected pod and seed yield, effects were negative.

Soil mineral N seems to contribute to the N nutrition of bambara groundnut, but only during the vegetative phase. A further quantification of this contribution has to be done, with special emphasis to the soil organic matter content of the soils used.

Chapter 7

General discussion

In this chapter, the results of a study on mineral nutrition of bambara groundnut are discussed in relation to the general objectives as presented in Figure 1.1 (Chapter 1). Factors such as soil P content, soil moisture content, time and rate of P fertilization, and root development are discussed in relation to P nutrition of bambara groundnut and its possible role on other plant processes such as nitrogen fixation. The N_2 fixation process per se is not investigated, but the effects of mineral fertilizer P on nodulation (number of nodules and nodule dry weight) and shoot N accumulation are considered as representing the role of P in nitrogen fixation. Also discussed is the need for extra mineral N and its effects on nitrogen fixation. The chapter is concluded with the implications of the results for bambara groundnut farmers in Botswana.

Phosphorus nutrition

Like other crops, bambara groundnut requires P for growth and development. Under low P conditions, shoot P concentrations are kept at or below the critical shoot P level and dry matter production is limited. The observed response of shoot dry matter production of potted bambara groundnut to P fertilization in this study was due to a combination of low P content of the soil and limited soil volume (Chapter 2). Although bambara groundnut did not respond to P fertilization in the field at a soil P content of 6.2 mg P kg^{-1} (P-Bray) there was an increase in P uptake with increase in soil moisture availability irrespective of P fertilization. Under improved soil moisture conditions, soil P availability was increased but it was not sufficient for optimal growth as shown by a shoot P concentration which was around the critical level. This means that also after irrigation soil P availability limited plant growth and seed yield. Therefore, seed yields of more than 4.2 t ha^{-1} in Botswana soils can be expected only if the soil moisture content is adequate and soil P is increased.

One of the explanations for the lack of response to P fertilization by bambara groundnut in our field experiment with a soil apparently low in P, was that it has a low P requirement (Chapter 3.1). About 80% of the P requirement of bambara groundnut could be met by P originating from the soil. However, the internal P use efficiency was low. Probably the low P requirement may explain why bambara groundnut has been reported to grow well in low fertility soils (National Research Council, 1979, Wassermann *et al.*, 1984). In potted bambara groundnut plants the positive response only occurs when P is applied (and well mixed with the soil) at a very early stage of seedling development (Chapter 3.2). Phosphorus application beyond two weeks after sowing did not improve shoot growth and seed yield. The importance of adequate levels of available P in soils during the seedling stage has been reported also for maize (Arnon, 1975) and tomato (Jones and Warren, 1954). The fact that there is a critical time for P in bambara groundnut

can also partly explain the lack of response to P fertilization in our field experiment (Chapter 2) where fertilizer P was broadcast and worked into the soil with a digging fork. This apparently did not bring it close enough to the seedling at the critical time. Furthermore, bambara groundnut was shown to have a relatively small root system, two times lower than that of maize and pigeon pea (Chapter 3.1). A root-shoot ratio of 0.2 as found in this study is comparable to that reported for bambara groundnut by Collinson *et al.*, (1996). The poor root system of bambara groundnut may also have limited the P availability to the seedling at the critical time and have contributed to the poor P response under field conditions. A poor root system and a critical time for P application in bambara groundnut means that for positive results, fertilizer P should be placed as close as possible to the seed at sowing.

The critical shoot P level (0.15% P) as determined in a sand culture experiment (Chapter 4) showed that bambara groundnut plants in our experiments were grown under P limiting conditions irrespective of the treatment, P fertilization and irrigation (Chapter 2 and 3). A seed yield of 4.2 t ha^{-1} from our field experiment with a shoot P concentration around the critical level is an indication of the potential of bambara groundnut to produce well under P limiting conditions if the soil moisture content is sufficient. This is also in line with literature that it can produce considerable yields in low fertility soils (National Research Council, 1979; Wassermann *et al.*, 1984). Bambara groundnut farmers in Botswana do not apply fertilizer or manure to the crop (Brink *et al.*, 1996), and the shoot P concentrations of bambara groundnut plants in the farmers' fields as found in this study were around or below the critical P level (Chapter 4). Farmers attribute low yields to poor rainfall (Brink *et al*,. 1996) and in this study it has been shown that soil moisture content is important for P uptake. Probably the P status of bambara groundnut plants from farmers field was low because of a combination of low soil P content and low soil moisture content. The results show that the shoot P concentration, in addition to the soil analysis, can be a useful guide for monitoring the P status and P requirement of bambara groundnut.

In other leguminous crops P fertilization increased shoot N concentrations which is thought to have resulted from improved N_2 fixation (Kang and Nangju, 1983; Israel, 1987; Othman *et al.*, 1991). This effect was not found in our experiments when shoot P concentrations were around or below the critical P level. It might mean that, thanks to an efficient and possibly low P demanding N_2 fixing mechanism, bambara groundnut plants on P-poor soils in Botswana are not suffering from N deficiency. This view is supported by the high shoot N concentrations found in farmers' fields (Chapter 4).

In our experiments P nutrition did not affect the development of bambara groundnut plants, e.g. the time it takes from sowing to flowering, podding and seed maturity. As long as internal P concentrations were around or below the critical level addition of P resulted in increased shoot dry matter but did not affect the number of pods. This improved pod filling and increased seed weight. With P shortage yield is thus not sink-limited but mainly source-limited. Lack of soil moisture has been reported to decrease pod numbers (Ameyaw and Doku, 1983; Collinson *et al.*, 1996; Chapter 2). When this occurs in P-poor soils it has in two ways a negative effect on seed

yield, a direct one on pod numbers and an indirect one on pod filling through reduced availability of soil P.

Nitrogen nutrition

In this study bambara groundnut did not respond to nitrogen fertilization (Chapters 5 and 6), making it obviously different from other leguminous crops that respond positively to N fertilization (Allos and Bartholomew, 1955; Hartfield *et al*, 1974; Minchin *et al.*, 1981; Elowad and Hall, 1987; Isfa, 1991). Nitrogen fertilizer applied to bambara groundnut at sowing even reduced pod formation and seed yield. Application of mineral N fertilizer at rates more than 20 kg N ha^{-1} has been reported to suppress nodulation in cowpea and other leguminous crops (Richardson et al., 1957; Allos and Bartholomew, 1955; Graham and Scott, 1984). Contrary, nodulation (number of nodules and nodule dry weight) in bambara groundnut continues even at mineral N fertilizer rates of up to the equivalent of 100 kg N ha^{-1}. However, application of N at flowering (49 DAS) seemed to be the only time when N fertilization of bambara groundnut had negative effects on nodulation (number of nodules and nodule dry weight) (chapter 6). This seems to suggest that the flowering stage is a critical time for nodulation which is in line with the observation of Dakora *et al.*, (1992) that the negative effect of applied N fertilizer on nodulation and N_2 fixation of bambara groundnut was severe between 43 and 56 DAS. This shows that application of mineral N can have negative effects on N nutrition of bambara groundnut.

Our experimental results indicate that the N_2 fixing mechanism of bambara groundnut plays an important role in meeting the N requirement of the crop. The results in chapter 6 showed that poor nodulation, e.g. in the treatment with sterilized soil, resulted in delay in flowering and podding and this underlines the importance of having effective *Rhizobia* in the soil. Fortunately bambara groundnut seems to nodulate freely with indigenous rhizobia in Botswana soils as found in our study (Chapter 2). Gueye and Bordeleau (1988) in Senegal also found that both indigenous and introduced *Rhizobium* strains nodulated all 24 bambara groundnut genotypes tested. The ability to nodulate with the indigenous *Rhizobia* and the capacity to meet N requirement from N_2 fixation and soil N indeed makes bambara groundnut an important crop for resource poor farmers.

Implications of the study

Water is a scarce resource in Botswana and under the prevailing conditions it appears to be the most important factor in the production of bambara groundnut. Soil moisture shortage restricts P availability to bambara groundnut plants and decreases pod production. Under Botswana conditions, with its short growing season, it is important to sow bambara groundnut as soon as the early rains are steady. By doing this, plants can benefit directly after planting from increased P availability which is a prerequisite for realizing at least part of its potential yield. To avoid moisture stress at a later stage, wide spacing of bambara groundnut plants is a good strategy

which many farmers seem to adopt. It is however clear that for reliable high yields, first of all adequate soil moisture is needed followed by optimal plant densities and timely application of P fertilizer. In our field experiment, irrigated fields with a plant population of 54 000 plants ha^{-1} produced a yield of about 4.2 tonnes seed ha^{-1}. Assuming that not only the pods but the entire plants are harvested, then the total amount of P removed from the field is of the order of 25 kg ha^{-1}. Due to the fact that the experimental plants were grown on a soil cleared from a well developed fallow vegetation this quantity of P could be taken up from the soil. However when bambara groundnut is grown on more or less permanently cropped soil additional P will be needed of the same order of magnitude as given above. Tentatively it can be concluded that Botswana farmers growing rainfed bambara groundnut cannot be advised to use P fertilizers. If however they can irrigate their crop and plant at high density, P fertilization at a rate of about 30 kg P ha^{-1} can be recommended whereby P fertilizers should be placed in the soil close to the seeds. Determining shoot P concentrations at the early podding stage might be a suitable diagnostic means to monitor the P nutrition of the crop and to refine this rather general P fertilizer recommendation.

As to nitrogen, our experimental results suggest that bambara groundnut can meet its requirements by N_2 fixation and supplementary N uptake from the soil, implying that N fertilization is not needed.

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Summary

Bambara groundnut (*Vigna subterranea* (L.) Verdec.) is a legume crop grown especially by small farmers mainly in semi-arid parts of Africa both in mixed cultivation and pure stands. It is considered as a hardy crop because of its drought tolerance, resistance to pests and diseases and ability to yield on chemically poor soils. The crop produces edible seeds which can be eaten unripe or stored as dried pulse for later consumption. In Botswana it is grown under semi-arid conditions by small farmers as a minor crop. Attempts have been made to increase the bambara groundnut yield through application of nutrients and improvement of the nitrogen-fixing capacity. This research has not been undertaken systematically and especially the responses to P and N fertilizers did not show a clear pattern. Given the low available P levels and the limited N supply in Botswana soils, a research programme was undertaken to investigate the P and N nutrition of bambara groundnut. The main objectives of the study were:(i) to investigate the effects of applied P and N on growth and development of bambara groundnut in Botswana soils, and (ii) to investigate the P and N uptake, shoot concentrations at different growth and development stages of bambara groundnut and (iii) how uptake, internal concentration and growth are related. The experimental programme consisted of five pot experiments and a large field experiment with P and irrigation as treatments in which bambara groundnut was grown on a representative low P soil. In addition a sand culture experiment was conducted to establish the critical P concentration in bambara groundnut shoots. The critical P levels were subsequently used to determine the P status of bambara groundnut plants in farmers' fields.

In Chapter 2 the question was whether bambara groundnut will respond to P fertilization in a P-poor soil in the absence and presence of added *Rhizobium* inoculum, whether bambara groundnut selections are different with respect to P nutrition, and whether soil moisture level under field conditions limits P uptake. In a preliminary pot experiment, which was terminated at flowering (51 days after sowing; DAS), the response of bambara groundnut shoot dry matter (DM) to P fertilization (fertilizer ground and thoroughly mixed with the soil) was positive and linear. There was no effect of P fertilization on nodulation both in the absence and presence of added inoculum. Leaf blade P and N concentrations were not affected by P fertilization. The two selections showed basically the same response to P fertilization. The indigenous rhizobia seemed to be sufficiently effective in nodulating bambara groundnut. In the field, P fertilization (fertilizer broadcast after ploughing and worked into the soil with a digging fork) had no effect on bambara groundnut plants, while irrigation increased all plant growth parameters except root DM. Total seed yield was 2.8 t and 4.2 t ha^{-1} for rainfed and irrigated treatments, respectively. Leaf blade P and N concentrations were not affected neither by P fertilization nor by soil moisture content. However, irrigation increased the uptake of P. Evidently, part of the P pool present in the soil becomes available under improved soil moisture conditions, probably due to improved P diffusion to the roots. The lack of response to applied P in the field experiment with a low P soil might imply that when root growth is not restricted by soil volume as is the case in pot experiments, available soil P was enough to meet the P requirements of bambara groundnut.

This could mean that compared to other crops like cereals bambara groundnut has a low P requirement possibly combined with a high P efficiency.

This hypothesis was tested in a pot experiment (reported in Chapter 3.1) in which the P uptake and the internal P use efficiency of bambara groundnut were compared to those of maize and pigeon pea. Maize is a crop with a high P requirement and pigeon pea has the capacity to use soil P normally not available to other crops. The response of shoot dry matter to added P was highest for maize, intermediate for bambara groundnut and lowest for pigeon pea. Compared to the other two crops bambara groundnut had a very low root-shoot ratio. The P uptake of maize was two and five times higher than that of bambara groundnut and pigeon pea, respectively. Contrary to maize, most of the P requirement of the other two crops could be met with P originating from soil. Maize had the highest internal P use efficiency, on average producing 1.89 g DM per mg P taken up, against values of 0.79 for bambara groundnut and 0.56 for pigeon pea. Therefore, lack of response by bambara groundnut to P fertilization in the field cannot be attributed to an exceptionally high P efficiency, but probably to its low P requirement.

Another reason for the difference in response of bambara groundnut to applied P as found in pot- and field experiment could be the mode of fertilizer application. In the pot experiment, P fertilizer was thoroughly mixed with the soil before planting while in the field experiment P was broadcast and worked into the top-soil with a digging fork. This means that in pots the P fertilizer is directly after germination available to the plant and in the field at a later stage or not at all during the growing period. This idea led to a pot experiment described in Chapter 3.2, in which different timing of P application was studied. The effects of application at sowing, two weeks and four weeks after sowing were studied. It was found that large significant DM responses are only found when P is applied within two weeks after sowing and that this early application is also needed for a high seed yield. This indicates that under field conditions broadcasting of fertilizer at sowing is not an effective way to supply bambara groundnut plants in time (e.g. directly after germination) with additional P.

In the field and pot experiments (Chapters 2 and 3), P fertilization had no effect on the shoot P concentration of bambara groundnut plants irrespective of the treatment (P rate, time of P application and irrigation). This led to the question whether internal shoot P concentrations found in bambara groundnut plants in previous experiments were adequate or not. To answer this question, the critical shoot P concentration of bambara groundnut was determined in a sand culture experiment using 12 P rates varying between 0.21 and 159 mg P $plant^{-1}$ for the whole experimental period. The critical P value, determined graphically and associated with 10% reduction in maximum shoot dry weight, was about 0.15% with a critical range of 0.15 to 0.20%. The critical P value showed that bambara groundnut plants in our previous experiments (pots and field) were growing under suboptimal P levels. Subsequently a farm survey was conducted on ten farms to assess the soil P status of bambara groundnut fields in Botswana under farmers' conditions, and to compare the P nutritional status of those field-grown plants with the critical shoot P concentration determined from our sand culture experiment (Chapter 4.2). Soil and plant samples from each of the ten farms selected for the survey were collected at about 78 DAS and analysed for P. The soil P levels from 80% of the farms were below five milligrams P kg^{-1} (P-

Bray). On two farms, shoot P concentrations were at the critical level and on the other farms below the critical level.

In all previous experiments, bambara groundnut plants were growing under marginal P conditions with shoot P concentrations around or below the critical level, irrespective of the P fertilization and irrigation treatments, while the N nutrition was adequate. This raises the question whether the plant N supply will still be adequate if bambara groundnut plants are grown under conditions where P will be no longer marginal or deficient. Under such conditions, higher DM production will not only increase the plant N requirement, but also the N_2 fixation might behave differently. To answer these questions, a pot experiment described in Chapter 5 was conducted to find out whether (i) the capacity of the N_2 fixation process, possibly supplemented with some native soil mineral N is high enough to meet the plant N requirement also under non-limiting P conditions, and (ii) at internal P concentrations exceeding the critical level, the amount of fixed N increases with increasing internal P. In the experiment, bambara groundnut plants were fertilized with different rates of P with or without additional mineral N. Phosphorus fertilization increased shoot, root, and nodule dry weights, seed yield, shoot P and shoot N concentrations and shoot P and shoot N contents at all sampling periods. Nitrogen fertilization on the other hand had no effect on the parameters measured but influenced the time to plant maturity. Under non-limiting P conditions bambara groundnut seems to be able to meet its N requirement from N_2 fixation and soil mineral N. The results indicate that no mineral fertilizer N should be supplied at sowing, but this does not rule out the possibility that at a later stage additional N may be needed. One of those might be the onset of podding, when a major shift in assimilate partitioning from vegetative growth to pod filling takes place. To investigate this, the effect of N fertilization at different development stages of bambara groundnut: at sowing (as in the previous experiment), at the early vegetative growth, at (50%) flowering and (50%) podding, was investigated in a pot experiment (Chapter 6). To separate the contributions of soil mineral N and N_2 fixation to the N nutrition of bambara groundnut plants, treatments with sterilized and unsterilized soil (control) were incorporated in the experiment. Nitrogen fertilization did not affect shoot dry weight and seed yield. Only N fertilization at 50% flowering decreased nodule number and nodule dry weight, shoot N concentration and shoot N content. This can mean that the flowering stage is critical for nodule formation in bambara groundnut. Sterilization of soil decreased nodule number and nodule dry weight. Shoot N concentration of plants grown in sterilized soil was decreased only at the 50% flowering stage, and poor N nutrition at early stages of growth delayed the flowering and podding stages by two weeks. Shoot N concentration of the sterilized soil treatment recovered despite the low nodule number and nodule dry weight, implying a high N_2 fixation efficiency of nodules present. It was not possible to quantify the contribution of the soil mineral N to the N nutrition of bambara groundnut because nodules were present in the sterilized soil treatment throughout the experimental period. Nitrogen fertilization, irrespective of time of application or growth stage was not beneficial to plant growth and reproduction.

Finally in Chapter 7 a general discussion of the main results on the responses of bambara groundnut to P and N fertilization in Botswana soils and the implications to bambara groundnut farmers is presented. It is concluded that P is important for growth and seed yield of bambara

groundnut, and the low P requirement may be responsible for its ability to thrive in chemically poor soils. But for a positive response to P fertilization to occur, the soil moisture content must be adequate and the fertilizer should be available to the seedling within two weeks after sowing. Bambara groundnut can meet its nitrogen requirement from N_2 fixation and soil mineral N, and there is no need for supplementary mineral N fertilizer. The shoot P concentrations at the early podding stage seem to be a suitable guide for monitoring the P status and P requirement of bambara groundnut.

Samenvatting

Bambara aardnoot (*Vigna subterranea* (L.) Verdec.) is een vlinderbloemig gewas dat veelal door kleine boeren in semi-aride gebieden van Afrika wordt geteeld, zowel in gemengde teelten als in monocultures. Tolerantie tegen droogte, resistentie tegen ziekten en plagen en het vermogen om bij lage chemische bodemvruchtbaarheid nog een oogst te geven maken het gewas geschikt voor teelt onder marginale omstandigheden. Het gewas produceert eetbare zaden die onrijp kunnen worden geconsumeerd, maar waarvan de peulen na drogen ook kunnen worden bewaard voor latere consumptie. In Botswana wordt het gewas veelal door kleine boeren geteeld als een bijgewas. Pogingen zijn ondernomen om de opbengst van de bambara aardnoot te verhogen door het gebruik van meststoffen en verbetering van het stikstofbindend vermogen van het gewas. Dit onderzoek is echter niet systematisch uitgevoerd en vooral de respons op een toediening van stikstof en fosfaat meststoffen gaf geen eenduidig beeld.

Met als uitgangspunten een lage fosfaat beschikbaarheid en een laag stikstof naleverend vermogen van bodems in Botswana is een onderzoek gestart met als doel de P en N voeding van de bambara aardnoot nader te bestuderen. De belangrijkste doelstelling van dit onderzoek was het bestuderen van: (i) de effecten van een bemesting met P en N op de groei, ontwikkeling en productie van de bambara aardnoot in Botswana, (ii) het verloop van de opname aan P en N en de gehalten aan de beide nutrienten in de spruit tijdens de teelt, en (iii) de samenhang tussen de opname en gehalten aan de beide nutrienten in de spruit enerzijds en de groei van de bambara aardnoot anderzijds.

Het onderzoek omvatte een vijftal potproeven evenals een uitgebreid veldexperiment met fosfaatbemesting en irrigatie als behandelingen, waarbij de teelt plaatsvond op een P-arme bodem representatief voor het merendeel van de bodems in Botswana. Bovendien werd een zand-culture experiment uitgevoerd om het kritisch P gehalte voor bambara aardnoot te bepalen. Dit kritische P gehalte werd vervolgens gebruikt om de P toestand van bambara aardnoot in velden van boeren vast te stellen.

De belangrijkste vragen in Hoofdstuk 2 zijn of de bambara aardnoot reageert op een P- bemesting bij een teelt op een P-arme grond en op een aanvullende enting van de bodem met een externe *Rhizobium* stam. Verder is nagegaan of verschillende bambara aardnoot cultivars verschillend reageren op P-bemesting en de P voeding van het gewas wordt beinvloed door de vochttoestand van de bodem. In een orienterende potproef die werd beëindigd bij het begin van de bloei (45 dagen na zaaien), bleek de droge stof (DS) van de spruit positief en lineair te reageren op P-bemesting (de P meststof was gemalen en intensief met de grond gemengd). Er werd geen effect

van P-bemesting gevonden op het aantal wortelknolletjes, ook niet na een enting met extern *Rhizobium*. Bemesting met P had geen effect op de gehalten aan P en N in de bladeren. De twee cultivars vertoonden eenzelfde respons op P-bemesting.

De reeds in de bodem aanwezige rhizobia activiteit bleek voldoende te zijn voor een adequate nodulatie van het bambara aardnoot gewas.

In het veld had een P-bemesting (breedwerpige toediening na ploegen van P meststof korrels die vervolgens met een vork werden ingewerkt) geen effect op de groei van de bambara aardnoot, terwijl irrigatie alle plant parameters, met uitzondering van de wortel DS, positief beinvloedde. De totale zaadopbrengsten in dit veldexperiment waren respectievelijk 4.2 en 2.8 ton/ha met en zonder irrigatie. De gehalten aan P en N in de bladeren werden niet beinvloed noch door P-bemesting, noch door irrigatie. Echter als gevolg van irrigatie was wel de totale P opname door het gewas verhoogd. Kennelijk komt bij een verbeterde vochttoestand van de bodem een deel van de P voorraad in de bodem beschikbaar voor de plant, waarschijnlijk als gevolg van een verhoogde diffusie van P naar de wortel. Het ontbreken van een respons op P-bemesting in het veldexperiment met een P arme bodem duidt wellicht op betere omstandigheden voor beworteling in het veld dan in potproeven. Als gevolg van een groter beworteld bodemvolume in het veld is de totale hoeveelheid beschikbare P voor het gewas onder de gegeven omstandigheden kennelijk voldoende en reageert het gewas dientengevolge niet op een P-bemesting.

Dit kan er op duiden dat in vergelijk met andere gewassen (bijvoorbeeld granen) de bambara aardnoot een lage P behoefte heeft, mogelijk in combinatie met een hoge P benutting.

Deze hypothese werd door middel van een potproef getoetst in Hoofdstuk 3.1 waarbij de P opname en interne P benutting van de bambara aardnoot werd vergeleken met die van mais en duivenboon. Mais is een gewas bekend om z'n hoge P behoefte, terwijl van duivenboon bekend is dat het gebruik kan maken van bepaalde P voorraden in de bodem die voor andere gewassen niet beschikbaar zijn. Mais vertoonde de grootste respons op P-bemesting, gevolgd door bambara aardnoot en duivenboon. In vergelijk met de twee andere soorten vertoonde de bambara aardnoot een zeer lage wortel-spruit verhouding (op DS basis). De P opname bij mais was twee, respectievelijk vijf maal zo hoog als die van de bambara aardnoot en duivenboon. In tegenstelling tot wat bij mais het geval was, bleek bij de twee andere gewassen de vooraad aan P in de bodem toereikend. Mais vertoonde de hoogste interne P benutting, met een gemiddelde DS productie van 1.89 g per mg opgenomen P. Deze waarden bedroegen voor de bambara aardnoot en duivenboon respectievelijk 0.79 en 0.56. Uit dit onderdeel kan geconcludeerd worden dat het ontbreken van een respons van de bambara aardnoot op P-bemesting in het veld niet toegeschreven kan worden aan een uitzonderlijk hoge P benutting, maar waarschijnlijk aan z'n lage P behoefte.

Een andere verklaring voor het verschil in respons op P-bemesting in de pot- en veldproeven kan berusten op een verschil in de wijze waarop de meststof werd toegediend. Terwijl de meststof in de potproeven was gemalen en homogeen werd verdeeld over het gehele potvolume voordat werd gezaaid, werd in de veldproef de meststof in korrelvorm breedwerpig toegediend en vervolgens met een vork ingewerkt. Dit heeft tot gevolg dat in potten het fosfaat meteen na kieming voor de plant beschikbaar is. In het veld zal het waarschijnlijk veel later voor de plant beschikbaar komen. Dit was aanleiding tot het opzetten van een potexperiment (Hoofdstuk 3.2)

waarin de P meststof op verschillende tijdstippen werd toegediend. Het effect van toediening bij zaaien, twee weken na zaaien en vier weken na zaaien werd bestudeerd. De resultaten gaven duidelijk aan dat P-bemesting slechts dan tot een significante toename in DS productie en tot een verhoogde zaadproductie leidt, wanneer de meststof binnen een periode van twee weken na zaaien wordt toegediend. Dit bevestigt de eerdere veronderstelling dat een breedwerpige toediening van P meststof in het veld geen effectieve manier is om de bambara aardnoot plant tijdig (direct na kieming) van voldoende P te voorzien.

In de veld- en potproeven (Hoofdstukken 2 en 3) bleek een P-bemesting geen effect te hebben op de P gehalten in de bladeren van de bambara aardnoot, ongeacht de aard van de behandeling (nivo van de P gift, tijd van P toediening en irrigatie). Dit gaf aanleiding tot de vraag of de P gehalten in de spruit van de bambara aardnoot, zoals gevonden in de voorafgaande experimenten, voldoende waren of niet. Om deze vraag te kunnen beantwoorden werd het kritisch P gehalte voor de spruit van de bambara aardnoot bepaald. Daartoe werd in een zand-culture experiment fosfaat op 12 nivo's aangeboden, varierend van 0.21 tot 159 mg P/plant voor de gehele experimentele duur. Het kritisch P gehalte, grafisch bepaald en corresponderend met een P gehalte in de spruit waarbij 90% van de maximale spruit DS productie wordt verkregen, bedroeg ongeveer 0.15% met een kritisch traject van 0.15-0.20%. Het kritisch P gehalte geeft aan dat bambara aardnoot planten in alle voorafgaande experimenten (pot- en veldproeven) onder suboptimale P voorziening groeiden.

Vervolgens (Hoofdstuk 4.2) werd een onderzoek uitgevoerd in de praktijk (op de boerderij). Bij een tiental boerderijen in Botswana werd de P toestand gemeten van gronden op percelen waarop onder 'praktijkomstandigheden' bambara aardnoot wordt geteeld. Ook het gewas op de percelen werd bemonsterd en na chemische analyse werden de P gehalten in het gewas vergeleken met het kritische P gehalte zoals gevonden in het zand-culture experiment (Hoofdstuk 4.1). De bodem- en gewasmonsters op elk van de tien boerderijen werden verzameld ongeveer 78 dagen na zaaien. De gehalten aan P in de bodem van 80% van de boerderijen waren lager dan 5 mg P/kg (P-Bray). Slechts op twee bedrijven werden P gehalten in de spruit gemeten gelijk aan het kritisch nivo, terwijl op alle andere bedrijven de P gehalten in het gewas lager waren dan het kritisch nivo.

In alle voorafgaande experimenten groeiden de bambara aardnoot planten bij marginale P voeding, gekarakteriseerd door P gehalten in de spruit op of onder het nivo van het kritisch gehalte, ongeacht bemesting met P of irrigatie. De N voeding van de planten in deze experimenten bleek steeds voldoende te zijn. Dit heeft geleid tot de vraag of the N voeding nog wel voldoende is als de groei van de bambara aardnoot niet langer meer geremd wordt door een suboptimale P voorziening. Onder dergelijke omstandigheden zal niet alleen als gevolg van een verhoogde droge stofproductie de behoefte aan N toenemen, maar gedraagt mogelijk ook het proces van de stikstofbinding zich anders. Om een antwoord te kunnen geven op deze vragen is een potproef uitgevoerd (Hoofdstuk 5) om na te gaan (i) of de capaciteit van het stikstofbindingsproces, mogelijk aangevuld met opname van minerale stikstof uit de bodem, toereikend is om de plant van voldoende N te voorzien ook onder omstandigheden waarbij de

P voeding niet langer meer groeilimiterend is, en (ii) of bij P gehalten van de spruit hoger dan het kritisch nivo de hoeveelheid N_2 die gebonden wordt, toeneemt met een verdere toename van het P gehalte in het blad. In dit experiment werden bambara aardnoot planten bij zaaien bemest met oplopende hoeveelheden P, al dan niet in combinatie met een gift aan minerale N. Een bemesting met P resulteerde niet alleen in een verhoogde DS productie van spruit, wortel en wortelknolletjes, maar ook in verhoogde zaad opbrengst en hogere opname en gehalten van P en N in de spuit. Een bemesting met minerale N had geen significant effect op de bovengenoemde plant parameters, maar beinvloedde (vervroegde) wel de veroudering van de planten. Ook onder condities waar P niet langer meer groeilimiterend is, schijnt de N_2 binding door rhizobium samen met minerale N in de bodem in de N behoefte van bambara aardnoot te kunnen voorzien. De resultaten maken duidelijk dat een N bemesting bij zaaien overbodig is, maar dit sluit niet uit dat een bemesting met N op een later tijdstip wel positieve gevolgen kan hebben voor de groei van de bambara aardnoot. Een dergelijk tijdstip zou kunnen zijn het begin van peulvorming, een moment waarop een grote verschuiving plaatsvindt in de assimilaten verdeling binnen de plant, n.l. van vegetatieve (spruit) naar generatieve delen (peulen). Om dit te onderzoeken is een potproef met de bambara aardnoot uitgevoerd waarbij minerale N werd toegediend: bij zaaien (zoals in het vorige experiment), vroeg tijdens de vegetatieve fase, bij 50% bloei en op het moment dat 50% van de planten peulen had (Hoofdstuk 6). Om de bijdragen van de N_2 binding en van minerale N uit de bodem aan de totale N voeding van de bambara aardnoot te kunnen ontkoppelen, waren behandelingen met gesteriliseerde en ongesteriliseerde potgrond (controle) in de proef opgenomen. Een bemesting met minerale N bleek noch de DS productie van de spruit, noch de zaad opbrengst te beinvloeden. Een N toediening op het moment van 50% bloei resulteerde in een afname van het aantal en het totale gewicht van de wortelknolletjes en verlaagde de N opname en het N gehalte in de bladeren. Dit kan er op duiden dat nodulatie bij de bambara aardnoot tijdens deze fase van de groei gevoelig is voor een verhoogd aanbod aan minerale N. Sterilisatie van de grond resulteerde in een afname van zowel het aantal als het totale gewicht van de wortelknolletjes. Het N gehalte in de spruit van planten geteeld in gesteriliseerde grond was lager op het moment van 50% bloei, waarbij tevens sprake was van een vertraagde bloei en peulvorming na sterilisatie, n.l. met ongeveer 2 weken. De aanvanklijk lagere N gehalten in de spruit van planten op gesteriliseerde grond herstelden zich later tijdens de groei ondanks de lage nodulatie. Dit duidt op een hoge efficientie van de aanwezige wortelknolletjes in de gesteriliseerde grond. Aangezien er na sterilisatie toch nog wortelknolletjes aanwezig bleken te zijn was het niet mogelijk om de bijdrage van minerale N uit de bodem in de totale N voeding van de bambara aardnoot te kwantificeren.

Duidelijk is evenwel dat een bemesting met stikstof voor de groei en zaadproductie van de bambara aardnoot geen meeropbrengst oplevert, ongeacht het moment van toedienen.

Tenslotte volgt in Hoofdstuk 7 een algemene discussie van de belangrijkste resultaten van dit onderzoek, met speciale aandacht voor de respons van de bambara aardnoot op een bemesting met P en N en de betekenis hiervan voor de telers van bambara aardnoot in Botswana. Het is duidelijk dat P belangrijk is voor de groei en zaadproductie van de bambara aardnoot. Uit een praktijkonderzoek bij boeren in Botswana bleek de fosfaat voeding van de bambara aardnoot in de meeste gevallen groeilimiterend te zijn. Dit kon worden aangetoond met behulp van het kritisch P gehalte voor bambara aardnoot verkregen uit de zand-culture proef. Dat bambara aardnoot in de praktijk bij een lage P-toestand van de bodem toch nog kan produceren is waarschijnlijk het gevolg van de relatief geringe P behoefte van het gewas.

Om de productie van het gewas te verhogen is een verbetering van de P voeding een voorwaarde. Echter onder de heersende klimaatsomstandigheden in Botswana belemmert vooral een vochttekort de aanvoer van voldoende P naar de wortel, ook wanneer door bemesting het P gehalte wordt verhoogd. Bemesting met P heeft dan ook pas zin nadat het vochtgehalte in de bodem is verbeterd, of door irrigatie of door een beperking van de teelt tot de seizoenen of streken met voldoende neeslag. Uit het onderzoek blijkt verder dat de bambara aardnoot slechts dan reageert op P indien de meststof binnen een periode van 2 weken na zaaien wordt toegediend. In de praktijk dient dan ook bij zaaien de meststof zo dicht mogelijk bij het zaad te worden aangebacht, zodat de plant(enwortel) meteen na kieming erover kan beschikken.

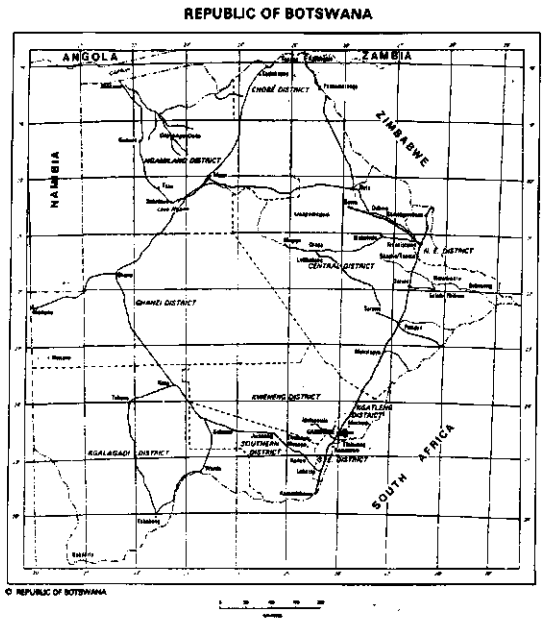
Een bemesting van de bambara aardnoot met minerale N leidt niet tot verhoogde groei en opbengst, ongeacht het moment waarop de meststof wordt toegediend. Kennelijk kan de plant via N_2 binding aangevuld met minerale N uit de bodem over voldoende N beschikken. Uit dit onderzoek blijkt dat een bemesting met N eerder leidt tot opbrengst derving dan tot opbrengst verhoging.

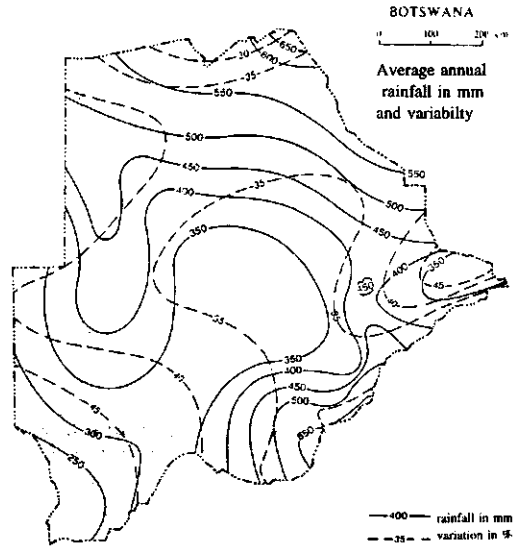
Curriculum vitae

Gaebewe Modirwa Ramolemana was born on 23 August 1956 in Serowe, Botswana. In 1982 he completed a B.Sc. in General Agriculture at the University of Botswana and Swaziland. In June 1982 he joined the Ministry of Agriculture in Botswana and worked as an Assistant Regional Agricultural Officer in the Department of Agricultural Extension Services until September 1983. From October 1983 to July 1986 he worked as a Research-Extension Liaison Officer in a joint project of Department- of Agricultural Research and Agricultural Extension Services in the Ministry of Agriculture. In August 1986 he went to USA to study for M.Sc. in agronomy and completed in June 1988. He continued with the position of Research-Extension Liaison Officer until March 1990. From April 1990 to September 1991 he worked as an Agronomist responsible for arable commercial farms (Pandamatenga Commercial Farms) under the Division of Crop Production of the Ministry of Agriculture. In October 1991, still in the Division of Crop Production, he was re-assigned as Senior Agricultural Officer Food Security. From October 1992 he joined Botswana College of Agriculture as a Lecturer in soils and soil fertility. In 1994 he got a Ph.D sand-witch fellowship from the Wageningen Agricultural University partly supported by Botswana College of Agriculture.

Appendix

Appendix 1. Maps of Botswana showing the location where the study was conducted (Gaborone) and the annual rainfall pattern.





Appendix 2. Long-term weather data Gaborone (24°40'S, 25°'E; altitude 100 m). R.H. = Relative Humidity; P.E.T. = Potential Evapotranspiration (Penmman).

Month	Av. Rainfall (mm) 1)	Max. Rainfall (mm) 1)	Min. Rainfall (mm) 1)	Av. max. temp (°C) 2)	Av. min. temp (°C) 2)	R.H. 08.00 (%) 3)	R.H. 14.00 (%) 3)	P.E.T. (mm) 4)
Jan	97	324	10	32.6	19.6	70	42	161
Feb	84	334	6	31.8	19.3	73	44	132
Mar	69	311	3	31.7	17.4	74	43	124
Apr	41	267	0	30.4	13.4	78	41	85
May	13	82	0	27.6	8.3	77	34	63
Jun	5	66	0	22.3	4.7	77	32	44
Jul	3	74	0	22.6	4.4	74	30	48
Aug	4	34	0	25.5	7.3	64	27	80
Sep	15	111	0	29.7	12.3	55	26	122
Oct	44	142	2	31.1	16.1	58	31	155
Nov	69	192	2	31.5	17.9	64	36	156
Dec	87	222	1	32.3	18.8	66	39	166
Annual	531	924	224	28.6	13.3	69	35	1336

1) 1925-1997
1) 1961-1996
3) 1963-1996
4) 1958-1975

Source: Anon., 1998

Appendix 3. The distribution of rainfall and the time and quantity of irrigation from sowing on the 18 th December 1995 until final harvest on the 22 nd April 1996 in a field experiment at Sebele Botswana.

Days from sowing	Rainfall (mm)	Irrigation (mm)	Total (mm)
0-10	24.0	-	24.0
11-20	0.5	9.0	9.5
21-30	48.0	9.0	57.0
31-40	116.5	-	116.5
41-50	14.5	-	14.5
51-60	27.8	-	27.8
61-70	-	12.0	12.0
71-80	69.0	-	69.0
81-90	-	12.0	12.0
91-100	-	12.0	12.0
101-110	42.0	-	42.0
111-120	-	-	-
121-130	18.0	-	18.0
Total	360.3	54.0	414.3