Photothermal regulation of phenological development and growth in bambara groundnut (*Vigna subterranea* (L.) Verdc.)

Promotoren: dr. ir. M. Wessel,
hoogleraar in de tropische plantenteelt

dr. ir. R. Rabbinge,
hoogleraar in de theoretische produktie ecologie

Co-promotor: dr. ir. E. Westphal,
universitair hoofddocent in de tropische plantenteelt

Photothermal regulation of phenological development and growth in bambara groundnut (*Vigna subterranea* (L.) Verdc.)

Anita R. Linnemann

Proefschrift
ter verkrijging van de graad van doctor
in de landbouw- en milieuwetenschappen
op gezag van de rector magnificus,
dr. C.M. Karssen,
in het openbaar te verdedigen
op vrijdag 16 december 1994
des namiddags te vier uur in de aula
van de Landbouwuniversiteit te Wageningen

CIP-DATA KONINKLIJKE BIBLIOTHEEK, DEN HAAG

Linnemann, Anita R.

Photothermal regulation of phenological development and growth in bambara groundnut (*Vigna subterranea* (L.) Verdc.) / Anita R. Linnemann. - [S.l.: s.n.]
Thesis Wageningen. - With ref. - With summary in Dutch.
ISBN 90-5485-335-2
Subject headings: bambara groundnut / phenology / photoperiods.

Cover design: Ernst van Cleef

STELLINGEN

1. Dagneutraliteit voor begin van bloei en vruchtzetting is een ongewenste eigenschap in bambara aardnoot genotypen in regenafhankelijke teeltsystemen in semi-aride gebieden.
Dit proefschrift.

2. Gezien de grote invloed van daglengte op aspekten van groei en ontwikkeling in bambara aardnoot dient karakterisering van genotypen onder gestandaardiseerde omstandigheden plaats te vinden om mondiale uitwisseling van gegevens zinvol te doen zijn.
Dit proefschrift.

3. De verschuiving in aandacht binnen het teeltkundige onderzoek van plant en gewas naar hogere hiërarchische niveaus mag niet leiden tot verwaarlozing van deze lagere niveaus.

   Fresco, L.O. (1992). Zo niet nu, wanneer dan ? Inaugurele rede. Landbouwuniversiteit Wageningen. p. 17.

4. Bij experimenten naar de daglengtegevoeligheid van een gewas met onbepaalde bloeiwijzen dienen in de loop van de tijd meerdere oogsten te worden uitgevoerd als behandelingen worden vergeleken op basis van opbrengst.
Dit proefschrift.

5. Daglengte-onderzoek dat de gewasontwikkeling niet verder volgt dan de bloei geeft bij bambara aardnoot onvoldoende inzicht om het gedrag onder uiteenlopende daglengte-omstandigheden te kunnen voorspellen.

   Summerfield, R.J.; E.H. Roberts, R.H. Ellis and R.J. Lawn (1991).Towards the reliable prediction of time to flowering in six annual crops. I. The development of simple models for fluctuating field environments. *Experimental Agriculture* 27: 11-31.

6. Kleine hoeveelheden toxische stoffen kunnen het onderzoekprogramma van een AIO vergiftigen.
Dit proefschrift.

7. Het landbouwkundig onderzoek (van statistiek tot agronomie) gaat uit van homogeniteit en uniformiteit van gewassen en groeiomstandigheden en is derhalve te weinig ontwikkeld om adequate oplossingen aan te dragen voor de landbouw die zijn oogstzekerheid voornamelijk te danken heeft aan het benutten van diversiteit en omgevingsheterogeniteit.

8. Een toename van de welvaart in ontwikkelingslanden leidt uiteindelijk tot een afname van het areaal peulvruchten.

9. Een liefhebberij die met passie wordt uitgevoerd heet hobby indien de algemene mening is dat het om een positieve aktiviteit gaat, en verslaving als men de bezigheid laakbaar vindt.

10. Menige (landbouwkundige) traditie is ontstaan omdat men van generatie op generatie niet de moeite heeft genomen iets nieuws te bedenken.

11. Bij de huidige werkdruk aan de Landbouwuniversiteit dient bij medewerkers van 50 jaar en ouder het in de Andes traditionele kauwen van cocabladeren te worden bevorderd.

12. Het stemt tot nadenken dat vooral wonderdokters en hoogleraren de wettelijk onbeschermde titel van professor voeren.

13. Zolang er onzekerheid blijft bestaan over onze zorg voor het leefmilieu, verdient het aanbeveling bij de keuze van straatnamen de voorkeur te geven aan Bomenweg boven Bomenlaan.

Stadsplattegrond Wageningen. Behorend bij de gemeentegids 1994.

Anita R. Linnemann
Photothermal regulation of phenological development and growth
in bambara groundnut (*Vigna subterranea* (L.) Verdc.)
Wageningen, 16 december 1994

aan mijn ouders

'Knowledge is the only instrument of production that is not subject to diminishing returns.'

J.M. Clark, 1927. Journal of Political Economy, October.

Abstract

The photothermal regulation of phenological development and growth in bambara groundnut (*Vigna subterranea*) was studied to elucidate the crop's potential and limitations in current or future cropping systems. Eight accessions from the germplasm collection of the International Institute of Tropical Agriculture (IITA) were used for a preliminary assessment of sensitivity to photoperiod. In some accessions, photoperiods of 14 h or longer delayed or inhibited the onset of two developmental stages, flowering and podding, in comparison with photoperiods of 11 h or less. Within an accession, podding was always affected more than flowering. Microscopic studies in the laboratory enabled the cause of the delay or absence of the onset of podding under long photoperiods (14 h or more) to be identified as a check in the growth of fertilized ovaries. The minimal inductive period for the onset of podding was determined for two accessions differing in sensitivity to photoperiod. In the comparatively photoperiod-sensitive accession, the time of pod induction in relation to pod position on the plant was studied too. Three accessions were used to test whether the rate of progress towards flowering and the rate of progress towards podding could be described as functions of mean diurnal temperature and/or photoperiod. Finally, earlier indications that photoperiod influences growth as well as development were verified. The results of the experiments demonstrate the flexibility in the development of bambara groundnut, particularly in relation to changes in photoperiod. This flexibility largely explains why the crop can produce itself under marginal conditions in rain-fed areas.

additional keywords: photoperiod, temperature, morphogenesis

Voorwoord

Het voorwoord bij een proefschrift vertoont overeenkomsten met de aftiteling van een boeiend televisieprogramma. Dan blijkt immers pas duidelijk hoeveel mensen aan het projekt hebben meegewerkt. Dit proefschrift zou niet tot stand zijn gekomen zonder de medewerking die ik op allerlei terreinen van velen mocht ondervinden.

Allereerst gaat mijn dank uit naar Egbert Westphal, mijn dagelijkse begeleider in de afgelopen periode. Hij is degene die de bambara aardnoot in Kameroen heeft "ontdekt", en die het vakgroepsonderzoek aan dit gewas heeft geïnitieerd. Een betrouwbaarder steun en toeverlaat had ik mij niet kunnen wensen. Ik heb veel geleerd tijdens onze wekelijkse besprekingen, niet alleen ten aanzien van het onderzoek maar ook van zijn brede belangstelling voor de zaken daarnaast, zoals literatuur en kunst.

Mijn beide promotoren, Marius Wessel en Rudy Rabbinge, wil ik bedanken voor de belangrijke rol die zij met name bij de verslaglegging hebben gespeeld. Marius vanaf het begin van het project, en Rudy voornamelijk tijdens de eindfase. Niet alleen kon er altijd tijd worden gevonden voor het becommentariëren van mijn teksten, zelfs kregen jullie er tot mijn schrik niet genoeg van want de vraag om meer tekst werd herhaaldelijk gesteld.

Veel collega's van de Vakgroep Tropische Plantenteelt (nu sectie binnen de vakgroep Agronomie) ben ik dank verschuldigd. Jan Bink voor alle achtergrondsinformatie over daglengte-gevoeligheid van gewassen en het overdragen van zijn ervaring met het experimentele onderzoek op de vakgroep; John Mohede voor zijn coördinerende rol; Jan Wienk voor de toegang tot de financiële middelen, en vooral ook voor zijn hulp bij het creëren van de faciliteiten voor mijn enige daglengte x temperatuur proef; Eppie Zandvoort voor haar adviezen bij het microtoomwerk; Joke Belde, Ildikó van de Linde, Linda Termeulen-Putman, de heer Roos, Jochem Schneemann en Mariëlle Schreuder voor het uitvoeren van deelonderzoek en het verrichten van waarnemingen in de proeven; Roel Boekelman voor zijn tekenwerk; Marita van den Bergh voor haar bijdrage aan de bambara bibliografie; Hermine Bouwknegt-Doosje, Ellen Rustenhoven, Géke Visser en Hanneke Westra voor het verzorgen van de administratie rond het projekt; Jaak van Zee voor zijn nimmer verflauwende toezicht op de technische installaties.

Eén groep collega's wil ik apart noemen. Gezamenlijk hebben zij zorg gedragen voor het meest wezenlijke onderdeel van het onderzoek, namelijk de verzorging van de planten. Een taak die veel aandacht en tijd vroeg, ook in de weekenden ! Tevens

hebben zij me geholpen bij het verrichten van oogstwaarnemingen. Hartelijk dank: de heer Boltjes, Marinus Hoefakker, Frits Menkman, Casper Pillen (pas sinds kort bij Agronomie, maar al wel vertrouwd met bambara aardnoot), Harry Scholten, Taede Stoker, Gerrit Timmer en Evert Verschuur.

In totaal hebben 42 studenten geparticipeerd in het onderzoek aan de bambara aardnoot. Het was stimulerend om met jullie samen te werken. Gaandeweg vonden we antwoorden op onderzoeksvragen, en bovendien stuitten we dikwijls op weer nieuwe vragen. Bij deze wil ik jullie graag allen bedanken: Niels Anten, Sandra Bot, Marius Boven, Anneke Brandts, Lénette van den Brink, Willemine Brinkman, Sam Chin-A-Tam, Henno Couprie, Wendy Dannenburg, Hans Dijkstra, Ronny Dobbelsteijn, Marleen van der Dussen, Ton Elie, Jeanet Emmens, Ciska van Ewijk, Stefan Fokkink, Einar Folmer, Daniël van der Gaag, Sandra Gilissen, Marcel Groen, Gilbert Heim, Elleke van den Hengel, Robert Jan Hijmans, Ireen de Jonge, Annemarie Koopmans, Yanti Kusumanto, Yvonne Leenaars, Martin van Maaren, Toos van Oers, Bart Ooms, Jan Portegijs, Lars van Raay, Wirender Rambocus, Lisanne Reinders, Bart Schuiling, Meena Sewtahal, Charlotte Stenfert Kroese, Juliette Stout, Erik Tielkes, Johan Wijk, Coco van der Wolk en Corné van Zwieten.

Bij de start van het onderzoeksproject met de bambara aardnoot beschikte de vakgroep slechts over enkele herkomsten. In de loop der jaren is deze collectie uitgegroeid tot meer dan 180 herkomsten. Ik ben iedereen erkentelijk die hier zijn zaadje aan heeft bijgedragen: Chris Bosch, Gerard de Bruijn, Arnoud Budelman, Harry van den Burg, Jan Cornelis, Wendy Dannenburg, Toby van Hameren, Pieter Hekstra, Willem Hoogmoed, Heleen Koenraads, Margo Kooijman, Hal Mettrick, John Mohede, Dr. Ng (IITA), Jan-Arie Nugteren, Petra Penninkhoff, Jan van der Ploeg en Alet Versnel, Jos Sijm, Lammert Sipkens, Dr. Swanevelder, Ed Verheij en Prof. Wormer.

Dat het niet eenvoudig is om onderzoek te starten aan een "nieuw" gewas heb ik geweten, maar dat geldt met name ook voor Willem Keltjens van de Vakgroep Bodemkunde en Plantevoeding. Steeds als er niet eerder geziene verkleuringen of vlekken op de bladeren optraden, werd zijn advies ingewonnen. Ik ben hem dankbaar voor alle hulp die hij heeft gegeven. Ook denk ik met plezier terug aan de proeven naar de mangaan- en calciumhuishouding van de bambara aardnoot die later in samenwerking tussen onze vakgroepen zijn uitgevoerd.

Mijn dank gaat ook uit naar medewerkers van de Vakgroep Microbiologie, de heer Lie en de heer Houwers. In de aanvangsfase van het onderzoek hebben zij meegewerkt aan het bepalen van de geschikte *Rhizobium*-stam voor inoculatie van mijn proefplanten. Vervolgens kon ik voor iedere proef opnieuw bij hen terecht voor het benodigde inoculatie-materiaal.

De mooiste herinneringen aan de afgelopen jaren van onderzoek bewaar ik aan mijn studiereizen naar Nigeria en Zambia. Het welslagen van deze reizen heb ik te danken aan hen die ter plaatse alles tot in de puntjes hadden verzorgd: tolken, onderdak, vervoer..... zelfs de boer(inn)en waren al gevraagd om thuis te blijven voor een vraaggesprek. Balarabe, many thanks for all your efforts that made my study tour to Nigeria so valuable and unforgettable. Goof Bus, Moosho Imakando, Willem en Marleen Heemskerk, Wilma Slobbe en Harm de Vries, hartelijk dank voor al jullie inspanningen en voor de gastvrijheid die ik bij jullie heb genoten.

En als de proeven dan tot een goed einde zijn gebracht, begint het werk om de gegevens te analyseren en vast te leggen op papier. Onontbeerlijk was daarbij de inbreng van medewerkers van de Vakgroep Wiskunde, met name van Aad van Eijnsbergen, Martin van Montfoort en André Otten. De medewerkers van de foto- en tekenlokatie van de Dreijen ben ik erkentelijk voor het verzorgen van de illustraties bij mijn verhalen. Herman van Keulen wil ik bedanken voor zijn inspanningen voor mijn eerste en mijn laatste manuscript. Ik was blij met je constatering dat al die jaren van opleiding hun vruchten bleken te hebben afgeworpen.

Veel nuttige opmerkingen en aanwijzingen op mijn concept-artikelen heb ik gekregen van mijn lotgenoten in het promovendi-overleg. Bijzonder was de manier waarop in een vrolijke sfeer (sic) die genadeloos kritische groep elkaars' artikelen ontleedde en tegen het licht hield. Hank Bartelink, Lammert Bastiaans, Janette Bessembinder, Bert Bos, Tjeerd Bouma, Martin Brink, Anne Marie van Dam, Pascal Denoroy, Bjørn Dirks, Stella Efdé, Wouter Gerritsma, Hans Gijzen, Barbara Habekotté, Jeroen de Koning, Peter Kooman, Koen Kramer, Cor Langeveld, Robert van Loo, Harrie Lövenstein, Herman Peppelenbos, Teunis van Rheenen, Herman van Roermund, Bert Schnieders, Reinoud Seegers, Nico Stutterheim, Leo Vleeshouwers, Johan Warringa en Rommie van der Weide, dank voor jullie inspanningen.

I wish to thank Dr Sayed Azam-Ali (University of Nottingham), Prof. E.H. Roberts and Dr R.J. Summerfield (University of Reading), Dr Nazmul Haq (then at the University of Southampton), Dr Ray Fordham and Dr Ken Giller (Wye College, University of London) for the exchange of views on grain legume research during my visit to England in 1989, and later. I am also grateful to Dr Peter Craufurd and Dr R.H. Ellis for their contributions to the article on photoperiod x temperature effects on bambara groundnut.

Tenslotte heeft Joy Burrough-Boenisch het Engels van al mijn manuscripten gecorrigeerd. Ik ben haar dankbaar voor de manier waarop zij mijn teksten heeft verhelderd.

Rest mij nog het thuisfront. Elsku Eggert, ég er þer þakklát fyrir vinskap undan farin ár. Það hvernig þú á jákvæðan hátt studdir mig - við vinnu mína ennig þar fyrir utan - met ég mjög mikils.

Anita R. Linnemann

Contents

page

Account

Parts of this thesis have been included into the following publications:

Chapter 2 Linnemann, A.R. (1991). Preliminary observations on photoperiod regulation of phenological development in bambara groundnut (*Vigna subterranea* (L.) Verdc.). *Field Crops Research* 26: 295-304.

Chapter 3 Linnemann, A.R. (1993). Phenological development in bambara groundnut (*Vigna subterranea*) at constant exposure to photoperiods of 10 to 16 h. *Annals of Botany* 71: 445-452.

Chapter 4 Linnemann, A.R. (in press). Phenological development in bambara groundnut (*Vigna subterranea*) at alternate exposure to 12 and 14 h photoperiods. *Journal of Agricultural Science*.

Chapter 5 Linnemann, A.R. (submitted). Phenological development in bambara groundnut (*Vigna subterranea*) transferred from 14-h to 11-h photoperiods. *Journal of Agricultural Science*.

Chapter 6 Linnemann, A.R. and P.Q. Craufurd (in press). Effects of temperature and photoperiod on phenological development in three genotypes of bambara groundnut (*Vigna subterranea*). *Annals of Botany*.

Chapter 7 Linnemann, A.R.; M. Wessel and E. Westphal (accepted). Photoperiod regulation of development and growth in bambara groundnut (*Vigna subterranea*). *Field Crops Research*.

Chapter 1

General introduction

1.1 Leguminous secondary crops in sustainable agriculture

The big challenge for current agricultural research is the development of sustainable cropping systems for different agro-ecological environments throughout the world. Many disciplines are involved in the search for cropping systems for marginal areas that are more sustainable than those currently prevailing. Agronomists contribute to this research at various levels. At the regional level, agronomists evaluate the suitability of land for agriculture on the basis of physical and economic factors. At farm level, they assess the optimal combination of agricultural activities. As for arable farming, agronomists study the growth of crops in relation to environmental factors and also the effect of cropping on the natural resource base. At crop level, they study agronomic measures to attain optimal crop growth and production under the given conditions. Moreover, they take soil coverage into account, as well as biomass production, in view of the role which crop residues play in maintaining soil organic matter. At plant level, they specify the characteristics that enable the plant to make optimal use of light, nutrients, water and the length of the growing season.

One important characteristic of leguminous crops is their capacity to fix atmospheric nitrogen, which makes them less dependent on the mineral nitrogen of the soil than other crops. This quality makes them important in cropping systems, particularly on intensively used, infertile soils. Their actual contribution to long-term soil fertility depends on the amount of root and aboveground crop residues left in the field. Crop diversification, obtained by cultivating one or more secondary crops in addition to the main food crops, can stabilize cropping systems in various ways, such as by inhibiting the build-up of pests, reducing disease incidence and improving soil use. Also, it has been observed that many of the so-called 'neglected crops' are those eaten principally by the poor (Lipton, 1990). Legumes are important as a foodstuff in their diets because of their relatively high protein content, and the complementarity of these proteins with those of cereals when digested at the same time.

A crop must be thoroughly understood at plant level if it is to be optimally incorporated into existing or future cropping systems. The functioning of plants in their agro-ecological environment is partly determined by their phenology, i.e. development in relation to biophysical conditions and changes in season. Phenology

is a major factor in adapting plants to their ecological surroundings because it determines to what degree plants can adjust their life-cycle to annual variations in growth conditions. This thesis focuses on aspects of the phenology of a leguminous secondary food crop, bambara groundnut (*Vigna subterranea* (L.) Verdc., syn. *Voandzeia subterranea* (L.) Thouars). The selection of bambara groundnut is appropriate in view of its significant place in cropping systems and in the rural diet in semi-arid to sub-humid Africa.

1.2 Bambara groundnut

Bambara groundnut (Fig. 1.1) belongs to the Leguminosae, subfamily Papilionoideae. It is a food crop cultivated for its subterranean pods. This legume is an indeterminate, annual herb up to 30 cm in height. It has creeping, much-branched lateral stems just above ground level. Trifoliolate leaves are carried on erect petioles, produced at the nodes of the prostrate stems. Flowers normally occur in pairs on peduncles at the base of the petioles. After pollination and fertilization the peduncles lengthen, thus bringing the ovaries underground.

Bambara groundnut is mainly cultivated on small farms in Africa, most often by female farmers who use the crop for home consumption and only sell surpluses on the local market. World production of bambara groundnut was estimated at 330 000 t annually in 1982, with about half being produced in West Africa (Coudert, 1984). The crop is one of rural Africa's most popular grain legumes: among the grain legumes of the African lowland tropics, bambara groundnut ranked third in terms of annual production in the mid-seventies, after groundnut (*Arachis hypogaea* L.) and cowpea (*Vigna unguiculata* (L.) Walp.) (Rachie and Silvestre, 1977). Seed yields in Africa average 650-850 kg ha^{-1} (Stanton *et al.*, 1966), with large differences between countries. Though often said to be a low yielder, there is ample evidence that, with good seed and management, bambara groundnut can match the yields of even the most productive legumes. In Zimbabwe, for instance, a yield of 3870 kg ha^{-1} has been obtained (Johnson, 1968).

The cultivation of bambara groundnut is of particular importance in semi-arid areas. In such regions the crop has a distinct agro-ecological niche: adverse growing conditions, such as limited water supply and low soil fertility, depress yields to a lesser extent than for other legumes, as e.g. for groundnut (National Research Council, 1979). In addition, the crop has a reputation for resisting pests and diseases, though as yet there is no scientific evidence to support this contention.

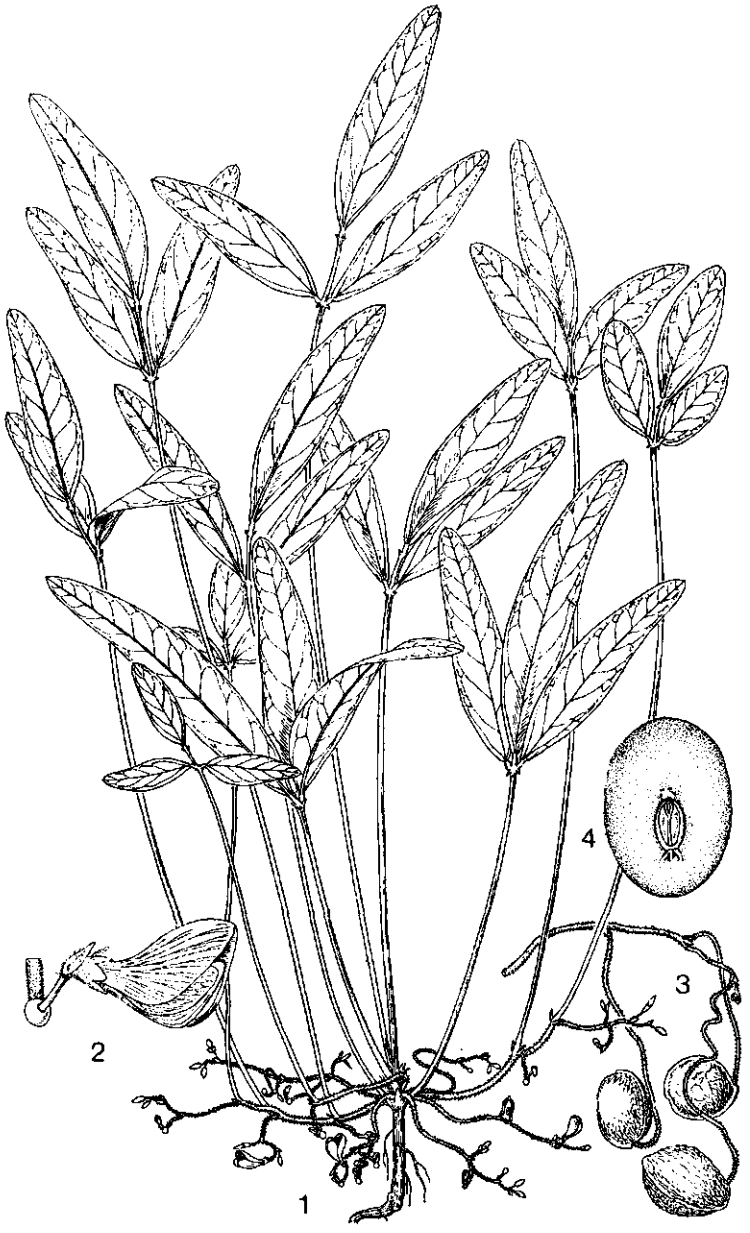

Figure 1.1. Bambara groundnut (*Vigna subterranea* (L.) Verdc.). - 1, habit of flowering plant; 2, flower; 3, fruits; 4, seed. From L.J.G. van der Maesen and S. Somaatmadja (Eds), (1989). Plant Resources of South-East Asia No. 1. Pulses. Pudoc, Wageningen. p. 75.

The demand for bambara groundnut in the West African market is larger than the quantities offered for sale, according to a report by the International Trade Centre UNCTAD/GATT (Coudert, 1984). Expanded production and trade should benefit both the supplying and the importing countries. On the export side, sales could increase the earnings of the rural sector. In the importing countries larger supplies of bambara groundnut could serve as an added source of high-protein food for the population.

The importance of bambara groundnut and the lack of knowledge of the crop are widely recognized (National Reseârch Council, 1979). For instance, the potential of the crop has not been established. The crop's morphogenesis has not been described, let alone been explained. Yet the research on this crop is very limited at the moment. Some work is being done at national research stations and universities in Africa. This research is mainly restricted to breeding activities focused on selection of better yielding lines within local materials, and some agronomic experiments such as fertilizer trials. The important role bambara groundnut may play in the food production (quantitatively and qualitatively) and the absence of clear insight in its potential and limitations required a concerted research effort. Therefore, in 1993 an EU-funded collaborative research project called 'Evaluating the potential for bambara groundnut as a food crop in semi-arid Africa' was started with the participation of universities in Botswana, Sierra Leone, Tanzania, the United Kingdom and the Netherlands. The present study was conducted prior to the EU-funded collaborative research programme.

1.3 Objective and approach of the study

The objective of this study was to assess the influence of photoperiod and temperature on development and growth of bambara groundnut. This information is required to determine the appropriate role for this crop within different agro-ecological zones. For this purpose, the following approach was used.

Literature review. An extensive literature search formed the beginning of the research project on bambara groundnut. The results of this study were published as an annotated bibliography (Linnemann, 1986, updated in 1992), and later also as a review article (Linnemann, 1987) and a chapter in a book on underutilized crops (Linnemann and Azam-Ali, 1993). At the outset of the project, information on the crop was also collected through correspondence with experts on the crop, who were listed by the National Research Council (1979).

Germplasm. Preliminary trials were started with germplasm from Mozambique to become acquainted with the crop. In the meantime, requests for seed samples were sent to colleagues working in semi-arid areas in Africa and to the International Institute of Tropical Agriculture which at the time held a bambara groundnut collection of about 1200 accessions (IITA, 1987). A number of these accessions were used for the experiments reported in this thesis. The term 'genotype' is used in this thesis as an alternative to 'accession', acknowledging that the genetic make-up may be heterogeneous and/or heterozygous. Voucher specimens have been deposited at the Herbarium Vadense, Wageningen.

Field studies. Field surveys were conducted as part of the research, in 1988 in Northern Nigeria, and in 1990 in Western Province, Zambia. The objectives were to clarify the present status of the crop: who grows the crop, what is its relevance within the farm system, where is it grown and how, what are the problems in cultivation and what are the prospects for the future. Data were collected by interviewing farmers and taking field records. Simultaneously, more bambara groundnut germplasm was collected. The results of the surveys have been presented in two communications of the Department of Tropical Crop Science (Linnemann, 1988; 1990).

Experimental programme. The experiments with bambara groundnut were mostly conducted in a greenhouse in which various photoperiod treatments could be installed at a set temperature regime, and in growth chambers and phytotrons under fully controlled environmental conditions. Plants grown in greenhouses displayed normal growth and development. However, cultivation in the growth chambers and phytotrons proved impossible. In the growth chambers a toxic substance (dibutyl-phthalate) killed the plants, while in the phytotrons plant growth was abnormal. Plants of certain accessions invariably suffered from stunted growth, curled leaves and/or tumescences, particularly on the underside of the leaves. This reduced the number of experiments with combined photoperiod and temperature effects to one large trial which was conducted in greenhouses of the Centre for Plant Breeding and Reproduction Research in Wageningen. In addition to the work in the greenhouses, anatomical studies on embryo development were carried out in the laboratory.

1.4 Outline of the thesis

This thesis addresses photothermal regulation of phenological development in bambara groundnut as follows. Preliminary observations on photoperiod sensitivity of the crop are described on the basis of three experiments (Chapter 2, Experiments 1, 2 and 3).

Chapter 3 presents a further quantification of photoregulation of development in a Nigerian genotype 'Ankpa 4' under constant photoperiod regimes of 10 to 16 h (Experiment 4). Particular emphasis was placed on the development of embryos in ovaries from plants under different photoperiods to further elucidate the absence of podding under photoperiods of 14 h or longer (Experiment 5).

Subsequently, two reciprocal transfer experiments were conducted, to ascertain in which developmental phase photoperiod sensitivity to podding occurs. Two genotypes were used (Chapter 4): one was photoperiod-insensitive to flowering and photoperiod-sensitive to podding (Experiment 6 with 'Tiga Nicuru' from Mali) and the other was photoperiod-sensitive to both flowering and podding (Experiment 7 with 'Ankpa 4' from Nigeria). The results are compared with the photoperiod sensitivity of other crops.

The effects of a 14-h photoperiod (which retards podding) during a period of variable length prior to an 11-h photoperiod (which induces podding) on flowering, yield and particularly the position of pods on plants of genotype 'Ankpa 4' were studied (Chapter 5, Experiment 8). The position of pods on the plants is discussed in relation to the synchronization of pod development.

The methodology describing the rate of progress towards flowering as functions of mean diurnal temperature and/or photoperiod (Roberts and Summerfield, 1987; Summerfield *et al.*, 1991) was tested by imposing factorial combinations of four photoperiods and three mean diurnal temperatures on plants of three Nigerian bambara groundnut genotypes, 'Yola', 'Ankpa 2' and 'Ankpa 4' (Chapter 6, Experiment 9). In addition, this methodology was evaluated as a means to describe the developmental rate for podding.

The last experiment was conducted to verify earlier indications that photoperiod not only influences development in bambara groundnut but also affects pod growth (Chapter 7, Experiment 10). Dry matter partitioning was therefore studied by sequentially harvesting bambara groundnut genotypes 'Tiga Nicuru' and 'Ankpa 4'.

In the final chapter (Chapter 8), the results of the research project are put into context. Agronomic implications of photosensitivity of crop development for the place of bambara groundnut within the cropping system, for breeding and selection and for the spread of genotypes in Africa are discussed. Topics meriting further research are indicated.

Chapter 2

Preliminary observations on photoperiod regulation of phenological development in bambara groundnut (*Vigna subterranea*)

Abstract. The effects of photoperiod on the development of bambara groundnut (*Vigna subterranea* (L.) Verdc.), a leguminous food crop cultivated mainly in Africa, were studied. In eight selections from the International Institute of Tropical Agriculture, two groups were distinguished: (a) day-neutral for flowering, with fruit-set delayed by long photoperiods (14 h); and (b) day-neutral for flowering, with fruit-set inhibited by long photoperiods. Two more categories, (c) delayed flowering and no fruit-set under long photoperiods, and (d) no flowering at long photoperiods, were found in later research, not reported here, on other selections. The delay or absence of fruit-set in long photoperiods is caused by the growth of fertilized ovaries being checked. Photoperiod affects plant phenology; plants grown in a 14-h photoperiod continue leaf production much longer than plants grown in 10-h or 12-h photoperiods, and therefore after 101-103 days their leaf areas may be three times larger.

2.1 Introduction

Bambara groundnut (*Vigna subterranea* (L.) Verdc., syn. *Voandzeia subterranea* (L.) Thouars), a pulse, is cultivated by smallholders over much of semi-arid Africa. Estimated world production is 330 000 t annually, about half of it in West Africa (Coudert, 1984) where, in terms of production, the crop ranks third among the pulses after groundnut (*Arachis hypogaea* L.) and cowpea (*Vigna unguiculata* (L.) Walp.) (Sellschop, 1962). Immature seeds are cooked and used as an early source of food during the rainy season, whereas fully ripe seeds are cooked or pounded into flour. Valuable traits of bambara groundnut include symbiotic fixation of nitrogen (Brooks *et al.*, 1988; Dadson *et al.*, 1988) and a high protein content of the seeds (ca. 18%). Moreover, the crop is reported not to be greatly affected by pests and diseases, and to yield better than certain other crops (groundnut, for example) under less favourable growing conditions, such as low soil fertility and limited water supply (National Research Council, 1979).

A study done by the International Trade Centre UNCTAD/GATT in 1982 (Coudert, 1984) concluded that the demand for bambara groundnut in West Africa exceeds the present supply. Increased production would give farmers an additional source of

income and improve the quality of the local diet, which often consists mainly of cereals. Seed yields are low and variable, averaging 650-850 kg ha^{-1} (Stanton *et al.*, 1966). There is little basic information on the ecophysiological requirements of the crop, thus making it difficult to define breeding strategies and recommend improved cultural practices for higher and more consistent yields.

Photosensitivity in crops is an adaptation to conditions that cause the length of the growing season to fluctuate. In cowpea, for example, a crop which is grown under similar ecological conditions as bambara groundnut, the photosensitive cultivars always flower and set fruit when the rains end, thus giving a secure yield in their own location (Wien and Summerfield, 1980). This paper describes photoregulation of development in bambara groundnut under day-length regimes of 10 to 14 h. These photoperiods, which are generally used to characterize day-length responses in tropical short-day plants, cover the variation during the growing season in the cultivation areas north and south of the equator.

2.2 Materials and methods

Three experiments were conducted in a greenhouse at Wageningen Agricultural University. The first studied the response of eight selections to different photoperiods, the second investigated the development of ovaries under different photoperiods, and the third focused on how vegetative development is influenced by day-length.

Plants in pots on trolleys were exposed to an 8-h period of natural daylight, extended with low-intensity, fluorescent (Philips TLD 36-W tubes) and incandescent light (Philips 40-W bulbs) of 10 μmol m^{-2} s^{-1} PAR at plant height to achieve the desired photoperiod. Average relative humidity was 60%, or less on sunny days.

Experiment 1. Eight selections of *V. subterranea* from the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria, were exposed to two day-length treatments, short days of 11 h and long days of 14 h. There were eight plants from each selection in each day-length. These were randomized over eight trolleys (four per day-length), each of which accommodated 16 pots. Plants were grown in 20-l pots filled with coarse sand, and with the lower 3 cm suspended in a nutrient solution in the trolleys. Day and night temperatures averaged 26 °C and 23 °C, respectively. Data recorded were number of days to first open flower and, at harvest, leaf area and percentage of plants with fruits. Harvesting took place 105-108 days after sowing.

Pollen fertility was investigated by staining with lactophenol acid fuchsin (Sass, 1964) and an *in-vitro* germination test carried out with Van Tieghem's (1869) hanging-drop technique in a medium with boric acid 10 mg l^{-1} and 30% sucrose (Stanley and Linskens, 1974). Ovaries of plants from both photoperiod treatments were embedded in Technovit 7100, a cold-curing resin on a hydroxyethyl methacrylate basis, supplied by Kulzer & Co. GmbH, Wehrheim, Germany. The embedded tissue was sliced with a microtome and studied under the microscope.

Experiment 2. A selection with a compact, erect habit from Mali was used. It is a bunch type according to Doku's (1969) classification, because of its high ratio of petiole length to internode length. Plants were either grown continuously under a regime of long days (14 h) or for six weeks under a regime of long days before being transferred to a regime of short days (12 h). Under both regimes, six-week-old plants, which had flower buds, open flowers and approximately 40 undeveloped ovaries each, were treated to obtain four groups: (1) plants with a maximum of five open flowers and from which all flower buds had been removed; (2) plants with a maximum of five flower buds and from which open flowers had been removed; (3) plants from which all open flowers and flower buds had been removed; and (4) intact plants. Any new flowers subsequently produced by plants of Groups 1, 2 and 3 were removed as they appeared. Two trolleys were required per day-length treatment, to accommodate the plants. The four treatments were replicated four times per trolley, resulting in 16 pots per trolley and eight replicates.

Plants were grown in 5-l pots filled with a steam-sterilized soil mixture. Average day and night temperatures were 26 °C and 22 °C, respectively. At harvest, 102-105 days after sowing, the numbers of full-grown fruits were determined.

Experiment 3. Two selections with a similar growth habit were used, one from Mali (see Experiment 2) and one from The Gambia. The plants were grown under a regime of long days (14 h), or under a regime of short days (12 h or 10 h), or under a combination of long and short days obtained by switching them from long days (14 h) to short days (10 h or 12 h) after 21, 42 or 63 days. Each day-length treatment occupied a single trolley accommodating 15 pots of each selection.

The plants were grown in 5-l pots filled with a steam-sterilized soil mixture. The average day and night temperatures were 25 °C and 20 °C, respectively. At harvest, 101-103 days after sowing, leaf area and seed weight per plant were determined.

2.3 Results and discussion

Photoperiod did not affect the number of days to first open flower in any of the eight selections in Experiment 1. Variation among selections in days to first open flower was small, the earliest flowering being at 40 days after sowing and the latest four days afterward. With a photoperiod of 14 h, fruit-set was delayed or even absent, whereas all plants set fruit in the short-day treatment of 11 h (Table 2.1). Evidently, bambara groundnut requires short days for fruit-set. The day-length of 14 h was short enough to induce flowering, but did not result in fruit-set for all selections.

Table 2.1. Country of origin, days to first flower, leaf area per plant at harvest and percentage of plants with fruits for eight selections of bambara groundnut at day-lengths of 11 and 14 h (Experiment 1).

Selection	Country of origin	Mean no. of days to first flower	Mean leaf area (cm^2)		Mean % of plants with fruits	
			11 h	14 h	11 h	14 h
TVsu 9	unknown	40	385	1293	100	100
TVsu 216	Ghana	44	598	2730	100	0
TVsu 409	Cameroon	40	255	2086	100	88
TVsu 463	Cameroon	43	393	1905	100	50
TVsu 465	Cameroon	41	324	1631	100	63
TVsu 777	Zambia	41	374	1400	100	25
TVsu 931	Zambia	42	606	1409	100	0
TVsu 1034	Zimbabwe	41	550	1663	100	25

A response indicating specific day-length requirements for successive stages of development has been observed in other crops too. Steele *et al.* (1985), for example, report that in photosensitive cowpea cultivars there is a range of short-day requirements for inflorescence initiation, and that some cultivars require even shorter days before initiated inflorescences expand and flower. Okra (*Abelmoschus* spp.) is a non-leguminous short-day plant, some cultivars of which require specific day-lengths for successive development stages. The cultivar recommended in the Ivory Coast, 'Perkins Long Pod' Ivorien, has a critical photoperiod of between 13.5 and 14 h for flower initiation, and of between 13 and 13.25 h for anthesis and fruit-set. Even at

photoperiods longer than 12-12.5 h, both anthesis and fruit-set are negatively affected (Siemonsma, 1982).

Two groups of selections were distinguished on the basis of their response to photoperiod in Experiment 1: (a) day-neutral for flowering with a quantitative response to short days for fruit-set, i.e., number of days to flowering was independent of day-length, and fruit-set was delayed by long photoperiods; and (b) day-neutral for flowering, with an obligate response to short days for fruit-set, i.e., number of days to flowering was independent of day-length and there was no fruit-set under long photoperiods.

In a trial with ten selections obtained from Nigerian markets (Linnemann, unpublished observations), one was found to have delayed flowering under conditions of long photoperiods (> 14 h). Observations on 16 other selections from IITA grown under 8-h or 24-h photoperiods confirm these findings (Nishitani *et al.*, 1988). Moreover, some of these IITA selections did not flower at all under long photoperiods. Thus, an additional two groups of selections can be distinguished: (c) one with a quantitative response to short days for flowering in combination with an obligate response to short days for fruit-set, i.e., delayed flowering and no fruit-set under long photoperiods; and (d) one with an obligate response to short days for flowering, i.e., no flowering at long photoperiods. None of the selections obtained from Nigerian markets or from IITA had a day-neutral response for both flowering and fruit-set.

The results of Experiment 1 also showed strong influence of day-length on vegetative development; plants grown under a 14-h photoperiod produced 2.3 to 8.2 times more leaf area than those growing under an 11-h photoperiod (Table 2.1), because they had more leaves. The plants under the longer day-length probably used their assimilates mainly to produce new leaves. However, under a photoperiod of 11 h, the sink presented by the growing fruits prevented further vegetative development after the onset of flowering.

Plants grown under a 14-h photoperiod, but with no fruit-set, were found to have large numbers of undeveloped ovaries, which remained on the plant after flowering. To ascertain why the growth of the ovaries was inhibited, intact flowers, pollen and ovaries were examined under the microscope. Germination of pollen was tested, and ovaries of plants grown under the 11-h and 14-h photoperiods were embedded in resin, sliced with a microtome, and compared. No differences were found for flowers, pollen or ovaries collected two or three days after anthesis at the different day-lengths. Thus, no explanation was found for the inhibition of fruit-set under long photoperiods.

Transferring plants from long days (14 h) to short days (12 h) in Experiment 2 showed that ovaries produced under the 14-h photoperiod could develop into full-grown fruits under short-day conditions (Table 2.2). This confirms the viability of pollen and ovaries, and demonstrates successful fertilization under long-day conditions. Evidently, long days inhibit fertilized ovaries from developing into full-grown fruits.

Table 2.2. Number of full-grown fruits plant^{-1} on plants grown continuously under long days (LL) or for 6 weeks under long days before being transferred to short days (LS), for various treatments (Experiment 2).

Treatment	Mean number of full-grown fruits plant^{-1}	
	LL	LS
Plants with max. 5 open flowers. Flower buds and new flowers removed.	2.0 a[1]	10.8 b
Plants with max. 5 flower buds. Open flowers, also new ones, removed.	2.1 a	10.0 b
Plants with only ovaries already present. All open flowers, flower buds and new flowers removed.	1.0 a	10.1 b
Intact plants	2.3 a	9.5 b

[1] Means with same letter do not differ significantly ($P = 0.01$)

The observed influence of photoperiod on leaf-area development in Experiment 1 was investigated further in relation to yield in Experiment 3. Two selections, day-neutral for flowering and with fruit-set delayed by long days, were grown under various photoperiods. Figure 2.1 shows mean leaf area and seed weight per plant at harvest. Planting density in the trial, measured as distance between plants, is comparable to a spacing of 20 x 30 cm in the field, resulting in 166 500 plants ha^{-1}, a realistic density for selections with a compact growth habit (Linnemann, 1987; 1988). Based on that density, the best yields in this trial, viz. 866 and 1032 kg ha^{-1} for the selections from The Gambia and Mali, respectively, are slightly higher than the average of 650-850 kg ha^{-1} achieved under field conditions (Linnemann, 1987).

Plants grown under the 14-h photoperiod produced longer internodes than those grown under 10 h or 12 h. This phenomenon was also observed under conditions of natural daylight only, and for other selections also (Fig. 2.2). Consequently, either classifications of bambara groundnut selections (Doku, 1969; Begemann, 1988) should be based on characteristics that are not influenced by photoperiod, or the environmental conditions under which measurements of certain morphological traits were carried out should be described in detail.

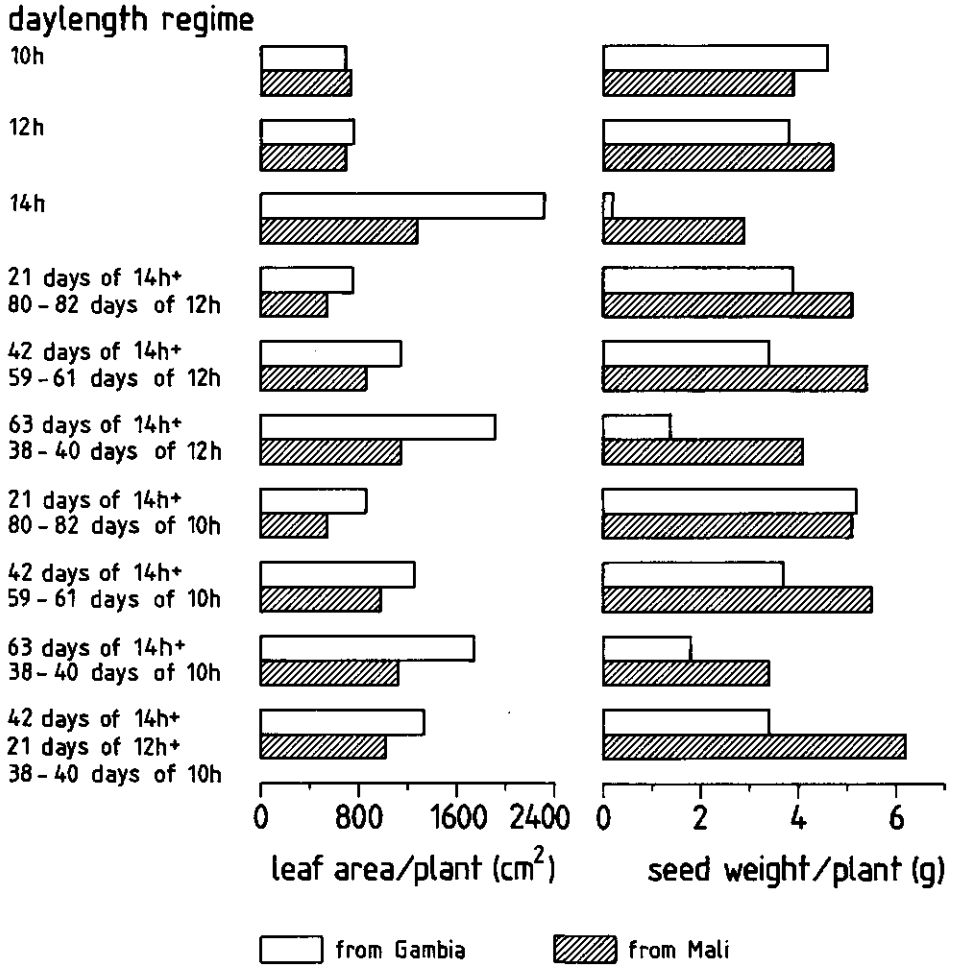

Figure 2.1. Mean leaf area and seed weight per plant for two selections of bambara groundnut, from The Gambia and from Mali, when grown under different day-length conditions (Experiment 3).

Plants grown continuously under photoperiods of 10 h or 12 h showed similar leaf-area development (Fig. 2.1). Continuous exposure to a 14-h photoperiod regime, however, resulted in a considerably greater leaf area. Plants transferred from long days (14 h) to short days (10 h or 12 h) had larger leaf areas the longer they were grown under the long photoperiod.

Seed yields of the selection from The Gambia showed exactly the opposite trend. Continuous exposure to photoperiod regimes of 10 h, 12 h or 14 h resulted in decreasing yields. Yields from plants transferred from long days (14 h) to short days (10 h or 12 h) decreased as the length of the period under long days increased. The treatment in which plants were transferred from long to short days in steps (42 days @ 14 h + 21 days @ 12 h + 38-40 days @ 10 h) was intermediate in leaf-area development and seed weight per plant.

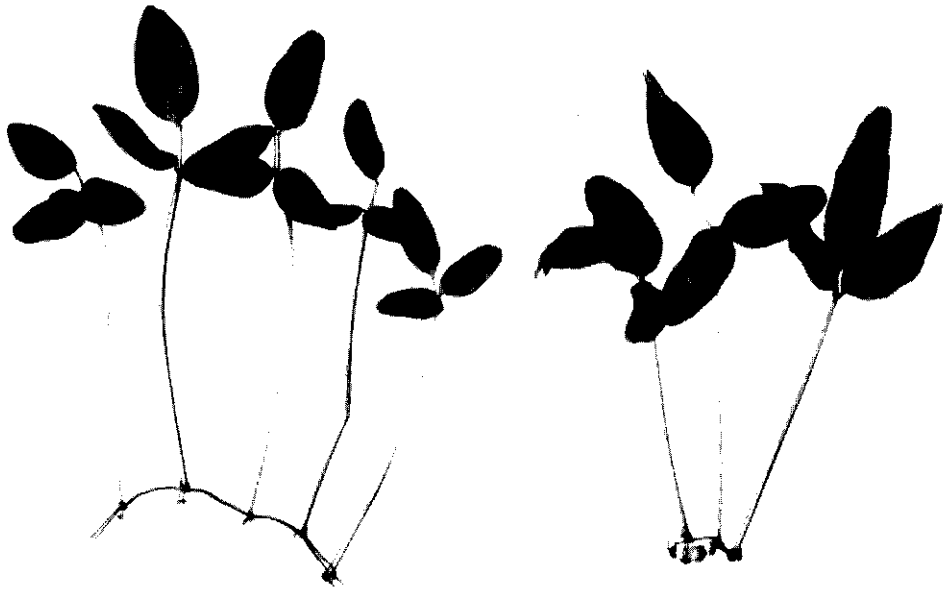

Figure 2.2. Branches of a bambara groundnut selection from Indonesia grown under a photoperiod of 14 h (left) or 12 h (right).

For the selection from Mali, continuous exposure to the 12-h photoperiod regime resulted in higher yields than when grown continuously under the 10-h or 14-h photoperiod regimes. The 14-h photoperiod gave the lowest yield. When plants were transferred from long (14 h) to short days (10 h or 12 h), those which had had a period of 42 days at 14 h gave higher yields than those that had had 21 or 63 days at 14 h. However, the highest yield for this selection was obtained following the stepwise transfer from long to short days: 42 days @ 14 h, followed by 21 days @ 12 h and 38-40 days @ 10 h.

The results from Experiment 3 show that there is a direct relation between vegetative development and day-length. Cultivating plants for longer periods under a 14-h photoperiod resulted in larger leaf areas. The relation between leaf-area development and yield, and the causal relation between photoperiod and leaf-area development for selections differing in growth duration and sensitivity to photoperiod, require further investigation. Further research is also needed to determine the influence of temperature on photoregulation and the consequences of photosensitivity for crop performance in the field. Quantitative information on the effects of photoperiod and temperature on vegetative development of the crop can be used in crop-growth models to predict yields and define production constraints.

Chapter 3

Phenological development in bambara groundnut (*Vigna subterranea*) at constant exposure to photoperiods of 10 to 16 h

Abstract. The flowering and fruit-set of a bambara groundnut selection from Ankpa, Nigeria, were studied in greenhouses at constant exposure to photoperiods of 10, 12, 12.5, 13, 14 and 16 h. The development of embryos was determined in ovaries from plants under photoperiods of 11.5 h and ≥ 14 h. The beginning of flowering, recorded as the number of days from sowing to the first open flower, was delayed by lengthening the photoperiod. It started 7 d later under 16 h than under 10 h. This difference increased during the production of the next nine open flowers. Lengthening the photoperiod also caused a delay in the beginning of fruit development. Under 13 h it was delayed by more than 40 d compared with fruit development under 10 h. Some plants under 14 and 16 h even failed to produce pods. After the beginning of fruit development dry matter partitioning to pods was substantially less under 14 and 16 h photoperiods than under photoperiods of 13 h or less; this was reflected in a strong reduction of pod growth rates. Under an 11.5 h photoperiod two groups of ovaries could be distinguished. In both, embryo development was identical up to 17 d after anthesis, but then the embryos in the first group continued to develop until they were full-grown at about 41 d after anthesis, whereas the growth of the embryos in the second group stopped. Embryo development under a photoperiod of ≥ 14 h was similar to that in the ovaries with discontinued embryo growth under the 11.5 h photoperiod. Healthy-looking embryos were found in ovaries up to 32 d after anthesis under a photoperiod ≥ 14 h. From then onwards embryos started to shrivel and degenerate. Finally, the ovaries aborted.

3.1 Introduction

World production of bambara groundnut [*Vigna subterranea* (L.) Verdc., syn. *Voandzeia subterranea* (L.) Thouars], a pulse with subterranean fruit-set, is estimated at 330 000 t annually. About half of this quantity is from West Africa (Coudert, 1984). In terms of production, bambara groundnut ranks third among the grain legume crops of the African lowland tropics after groundnut (*Arachis hypogaea* L.) and cowpea [*Vigna unguiculata* (L.) Walp.] (Rachie and Silvestre, 1977). The crop is cultivated by smallholders over much of semi-arid Africa where it has its own agro-ecological niche; under less favourable growing conditions, such as limited water supply and low

soil fertility, it yields better than other legumes, for example, groundnut (National Research Council, 1979).

Although bambara groundnut has produced seed yields of nearly 4 t ha^{-1} in Zimbabwe (Johnson, 1968), average yields are low and variable, ranging from 650 to 850 kg ha^{-1} (Stanton *et al.*, 1966). These low yields result partly from the marginal areas used for the cultivation of the crop, and are partly attributable to the results of breeding and agricultural research being limited. Basic information on the ecophysiological characteristics of the crop is scarce. This hampers breeding and the development of improved cultural practices for higher and more consistent yields. Crop phenology, i.e. crop development in relation to climate and changes in season, is a major factor in adapting plants to their ecological environment because it determines to what degree plants can adjust their life-cycle to annual variations in growth conditions.

Phenology is mainly regulated by temperature and/or photoperiod in most crops. These environmental factors modulate time to flowering by (Wallace, 1985): (1) the rate of node and therefore leaf development; (2) any change in node to flower; and (3) any vernalization requirement. Predictive, linear models of photothermal response for time to flowering are currently being developed for crops which have been thoroughly researched, such as cowpea and soya bean [*Glycine max* (L.) Merr.] (Roberts *et al.*, 1988; Aiming, 1990; Summerfield *et al.*, 1991).

Preliminary observations on photoperiodic regulation of phenological development in bambara groundnut indicated marked differences in response to photoperiod among genotypes (Linnemann, 1991). In certain genotypes photoperiods of 14 h or longer do delay or inhibit the beginning of two developmental stages, flowering and fruit-set, in comparison with photoperiods of 11 h or less. Within a genotype, the effect on fruit-set is always stronger than on flowering. Plants that flowered but failed to produce fruits under photoperiods of 14 h or longer had many undeveloped ovaries. Microscopic studies showed that pollen, intact flowers and ovaries collected 2 or 3 d after anthesis from plants subjected to photoperiods of 14 h or longer, did not differ from those collected from plants subjected to photoperiods of 11 h or less. Moreover, ovaries produced under a 14 h photoperiod developed into full-grown fruits under a 12 h photoperiod regime. The delay or absence of fruit-set under photoperiods of 14 h or longer was therefore attributed to the growth of fertilized ovaries being checked.

To be able to improve bambara groundnut genetically and agronomically, the photoperiodic regulation of its phenological development must be understood, so that the possibilities of interactions between genotype, sowing date/latitude and plant density can be exploited optimally. This paper presents a further quantification of

photoregulation of development in bambara groundnut under day-length regimes of 10 to 16 h (expt 4) with particular emphasis on the development of embryos in ovaries from plants growing under different photoperiods (expt 5).

3.2 Materials and methods

Two experiments were conducted in greenhouses at Wageningen Agricultural University (51°58' N), The Netherlands. In the first, flowering and fruit-set were studied in relation to number of leaves, and dry matter production and distribution at constant photoperiods between 10 and 16 h. In the second, the development of embryos in ovaries from plants under photoperiods of 11.5 h and $\geq$ 14 h was investigated. A genotype from Ankpa (7°22' N), Nigeria, was used. The racemes of this genotype consist of two yellow flowers, each with a single pistil, on a short axillary peduncle. At the base of the pistil is a superior, unilocular ovary with two, apparently anatropous ovules (Fig. 3.1). The plants were grown in 5-l pots filled with a mixture of sand and humous potting compost (1:1 v/v). Day and night temperatures averaged 26 and 22 °C, respectively. Average daily relative humidity was 60%, or less on sunny days.

Figure 3.1. Longitudinal section of a bambara groundnut ovary on the day of anthesis. pl, Pistil; oy, ovary; oe, ovule. Bar = 183 μm.

Experiment 4. Plants were grown under the natural photoperiod from sowing on 2 Apr. 1990 (13 h 35 min) up to 18 Apr. 1990 (14 h 41 min). The natural photoperiod is defined as the interval between sunrise and sunset plus the time when the position of the centre of the sun is 3 ° below the horizon. From 19 Apr. 1990 onwards, plants were exposed to one of the following six day-length treatments: 10, 12, 12.5, 13, 14 and 16 h. During these treatments the plants received an 8 h period of natural daylight, which was extended in sheds with low-intensity, fluorescent (Philips TLD 36 W tubes) and incandescent light (Philips 40 W bulbs) of 10 μmol m^{-2} s^{-1} PAR at plant height to achieve the desired photoperiod. Thus, the differences in total PAR between treatments were negligible. Each day-length treatment was applied to two trolleys carrying 30 pots each containing one plant. The trolleys were arranged in a randomized complete block design with two replicates.

The dates of the first, fifth and tenth open flower were recorded for all plants. Ten plants per trolley, chosen at random at the beginning of the day-length treatments, were used for fortnightly counts of the number of unfolded leaves and for analysis at the final harvest. The final harvest took place when the leaves started to drop, i.e. at 129, 142, 156, 156, 163 and 163 d after sowing for the plants under 10, 12, 12.5, 13, 14 and 16 h, respectively.

Samples of four plants at a time from the remaining 20 pots per trolley were taken at regular intervals from 12 d after plants had produced five flowers onwards, to monitor fruit development. Data recorded were number of leaves, and weight of leaf blades and other aerial parts after drying for at least 24 h at 105 °C, and, if applicable, number and dry weight of seeds.

Experiment 5. The natural photoperiod was used as the longer photoperiod treatment, because there was insufficient space in the greenhouses with facilities to control the day-length. Plants were therefore either grown for the whole period under the natural photoperiod, or for the first 4 weeks under the natural photoperiod followed by a regime of 11.5 h. The natural photoperiod varied from 15 h 32 min at sowing (at the beginning of May 1990) to 17 h 33 min on the longest day in June to 14 h 24 min at the last harvest at the end of August 1990. Flowers were marked on the day they opened. Groups of plants were harvested at intervals of 2 or 3 d from 8 weeks after the beginning of flowering onwards. At harvest the number of days after anthesis was determined for marked flowers and ovaries, after which the material was stored in a solution of 90 ml alcohol (70%), 5 ml acetic acid and 5 ml formalin (40 %) (FAA). Subsequently, flowers and ovaries were embedded in Technovit 7100 (Kulzer & Co. GmbH, Wehrheim, Germany), a cold-curing resin on a hydroxyethyl methacrylate

basis. The embedded tissue was sliced with a microtome and embryo development was studied under the microscope.

3.3 Results

Flowering and fruit-set. Lengthening the photoperiod delayed flowering (expt 4, Table 3.1). Under a photoperiod of 10 h plants required less than 43 d from sowing to produce their first open flower, against nearly 50 d under 16 h. The increase in the delay of flowering was largest when the photoperiod was increased from 12 to 13 h, namely 2.4 d. The delay was more pronounced for the fifth and tenth open flowers than for the first open flower. Apparently, longer photoperiods not only delayed the appearance of the first open flower, they also continued to influence the production of subsequent flowers.

In expt 4 two variables were used to determine the beginning of fruit development: (1) the number of days from sowing to the presence of the first pod (length > 0.5 cm) in a sample of four plants; and (2) the number of days from sowing until all four plants of a sample had at least one pod.

Table 3.1. Days from sowing to first, fifth and tenth flower for a selection of bambara groundnut from Ankpa, Nigeria at six day-lengths (expt 4).

	Day-length (h)					
Flower	10	12	12.5	13	14	16
1st	42.8	44.6 a*	45.7 ab	47.0 b	47.0 b	49.7
5th	45.8	48.4 a	54.3 b	57.5 b	58.9 b	66.5
10th	47.1	52.6 a	61.2 b	65.1 bc	68.6 c	77.5

* Means with same letter in the same row do not differ significantly ($P = 0.05$). Data on plants under photoperiods of 10 and 16 h were excluded from the statistical analysis because their coefficients of variance were, respectively, smaller and larger.

In all treatments, samples were found with at least one pod per four plants (Table 3.2). The number of days until the first pod was found varied inconsistently under photoperiods from 12.5 to 16 h, probably as a result of sample size and sampling frequency. Moreover, genetic variability caused a certain amount of variation. In fact, the variation within the plant population with respect to fruit-set became larger as photoperiod increased.

Table 3.2. Days from sowing to first and last plant with at least one pod (length > 0.5 cm) in a sample of four plants of bambara groundnut at six day-lengths (expt 4).

	Day-length (h)					
	10	12	12.5	13	14	16
One fruiting plant in sample	70	91	108	101	119	105
All plants in sample fruiting	80	105	115	122	-*	-*

* No samples with four fruiting plants were found under photoperiods of 14 and 16 h.

Under a photoperiod of 10 h the first sample of four fruiting plants was found 80 d from sowing. More than 40 d later such a sample was found under 13 h. Under 14 and 16 h no samples of four fruiting plants were found. Photoperiod apparently has a much stronger effect on the beginning of fruit-set than on the beginning of flowering.

Leaf appearance, dry matter production and distribution. The rate of leaf appearance was similar for all six day-length regimes up to 52 d after sowing when all treatments had started to flower (expt 4, Fig. 3.2). From then on, the leaf appearance rate decreased under the 10 h photoperiod, whereas the five other treatments continued to produce about one leaf d^{-1}. This rate of leaf appearance was maintained until 129 d after sowing under the 16 h photoperiod; plants under the photoperiods of 12, 12.5, 13 and 14 h had reduced leaf appearance rates from 80-100 d after sowing. The leaf appearance rates after the beginning of flowering reflected differences in vegetative *vs.* generative growth between treatments. The different leaf appearance rates led to

large differences in the number of leaves per plant. At 129 d after sowing the average number of leaves per plant under 10 h was about 40, against about 120 under 16 h.

At harvest, there were no differences in the number of pods and seed weight per plant under photoperiods shorter than 14 h (expt 4, Table 3.3). However, under the photoperiods of 14 and 16 h these yield attributes were lower. Although differences were not significant, plants grown under the 10 h photoperiod tended to have the lowest weight of leaf blades and total dry matter (excluding roots), the highest average seed weight and harvest index, and the longest period between the beginning of fruit-set and harvest.

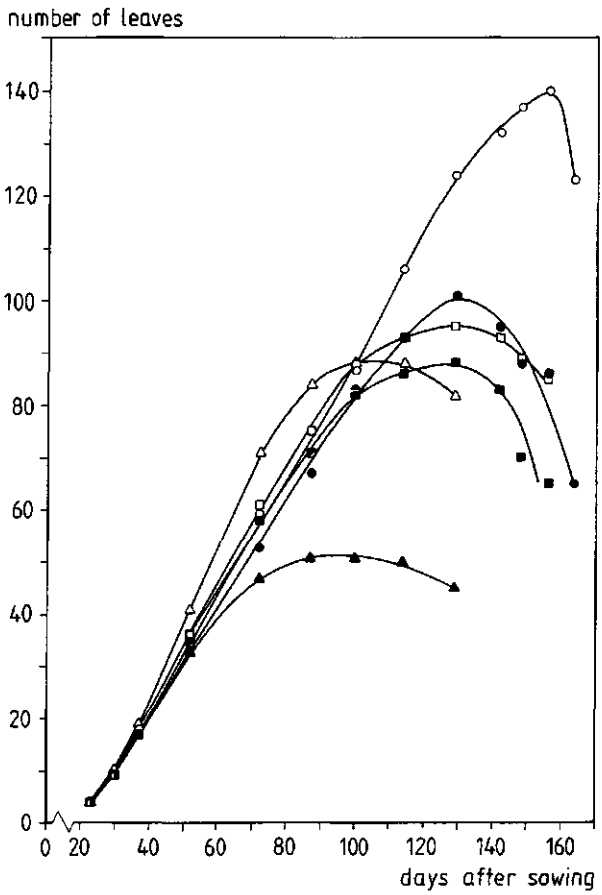

Figure 3.2. Number of leaves per plant from 23 d after sowing until harvest under photoperiods of 10 h (▲), 12 h (△), 12.5 h (■), 13 h (□), 14 h (●) and 16 h (○) for a selection of bambara groundnut from Ankpa, Nigeria.

Table 3.3. Harvest data on bambara groundnut at six day-lengths (expt 4).

	Day-length (h)					
	10	12	12.5	13	14	16
No. of pods per plant	7.3 a[§]	10.4 a	9.9 a	9.1 a	3.6 b	3.0 b
Seed weight (g per plant)	4.3 a	5.0 a	4.4 a	4.1 a	1.6 b	1.4 b
Shelling percentage	66	69	67	69	62	49
Average seed weight (g)	0.58	0.48	0.44	0.45	0.44	0.47
Weight of leaf blades (g per plant)	6.7	9.5	8.6	9.3	9.1	11.8
Weight of other aerial parts (g per plant)	7.3	10.9	10.6	10.8	8.7	11.3
Total dry matter (excluding roots, g per plant)	18.3	25.4	23.6	24.2	19.4	24.5
Harvest index	0.23	0.20	0.19	0.17	0.08	0.06
Days from fruit-set to harvest:						
- at 1st criterion[*]	59	51	49	56	45	59
- at 2nd criterion[o]	49	37	42	35	-	-
Pod growth rate (g per plant d^{-1})[#]	0.11	0.14	0.13	0.11	0.06	0.05

[*] Days from fruit-set to harvest is calculated as the harvesting date minus the date when the first plant of a sample of four had at least one pod (length > 0.5 cm).

[o] Days from fruit-set to harvest is calculated as the harvesting date minus the date when all plants of a sample of four had at least one pod (length > 0.5 cm).

[#] Defined as daily increase in pod weight [(seed weight per plant x 100)/shelling percentage] for the period between the harvesting date and the date when the first plant of a sample of four had at least one pod (length > 0.5 cm).

[§] Means with same letter in the same row do not differ significantly ($P = 0.05$).

Ovary development. The cause for the delay in or absence of fruit development under photoperiods of 14 and 16 h, as observed in expt 4, was further investigated in expt 5 by comparing reproductive growth under photoperiods of 11.5 and $\geq$ 14 h. On the day of anthesis germinating pollen was present on the stigma of flowers, irrespective of day-length (expt 5, Fig. 3.3). Ovaries from plants under conditions of $\geq$ 14 h hardly increased in size after anthesis. Their average length was 0.96 $\pm$ 0.08 mm and their width 0.35 $\pm$ 0.04 mm on the day after anthesis. Under the 11.5 h photoperiod some ovaries started to grow at about 7 d after anthesis, while others did not develop. Consequently, ovaries of the same age differed in size. These differences became more pronounced with progress in growth period. Therefore, ovaries collected $\geq$ 7 d after anthesis from plants under the 11.5 h photoperiod were divided into two groups: ovaries showing signs of growth and ovaries which did not develop.

Embryo development. The anatomical studies of ovaries under the 11.5 h photoperiod showed that fertilization took place on the day of anthesis (expt 5, Fig. 3.4 A). One day later a small embryo was visible (Fig. 3.4 B) which slowly developed during the following days into a spherical embryo (Fig. 3.4 C). From about 24 d after anthesis, a period of linear increase in embryo size began (Fig. 3.4 D), which lasted for about

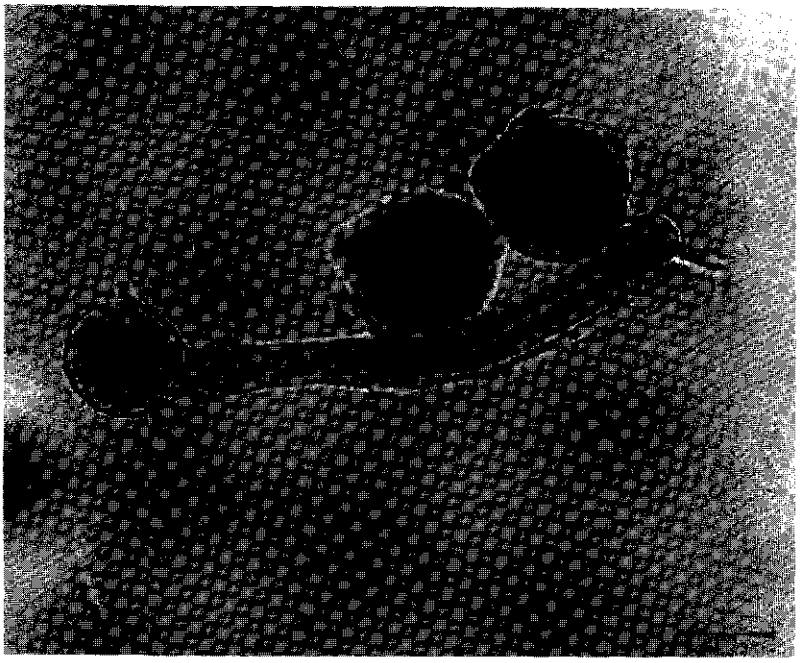

Figure 3.3. Germinating pollen of bambara groundnut. pt, Pollen tube. Bar = 18 μm.

1 week. This was followed by a decrease in growth. At approximately 41 d after anthesis the embryo reached its final size (Fig. 3.5); on average it was 2.75 mm long and 1.18 mm wide (Fig. 3.4 E).

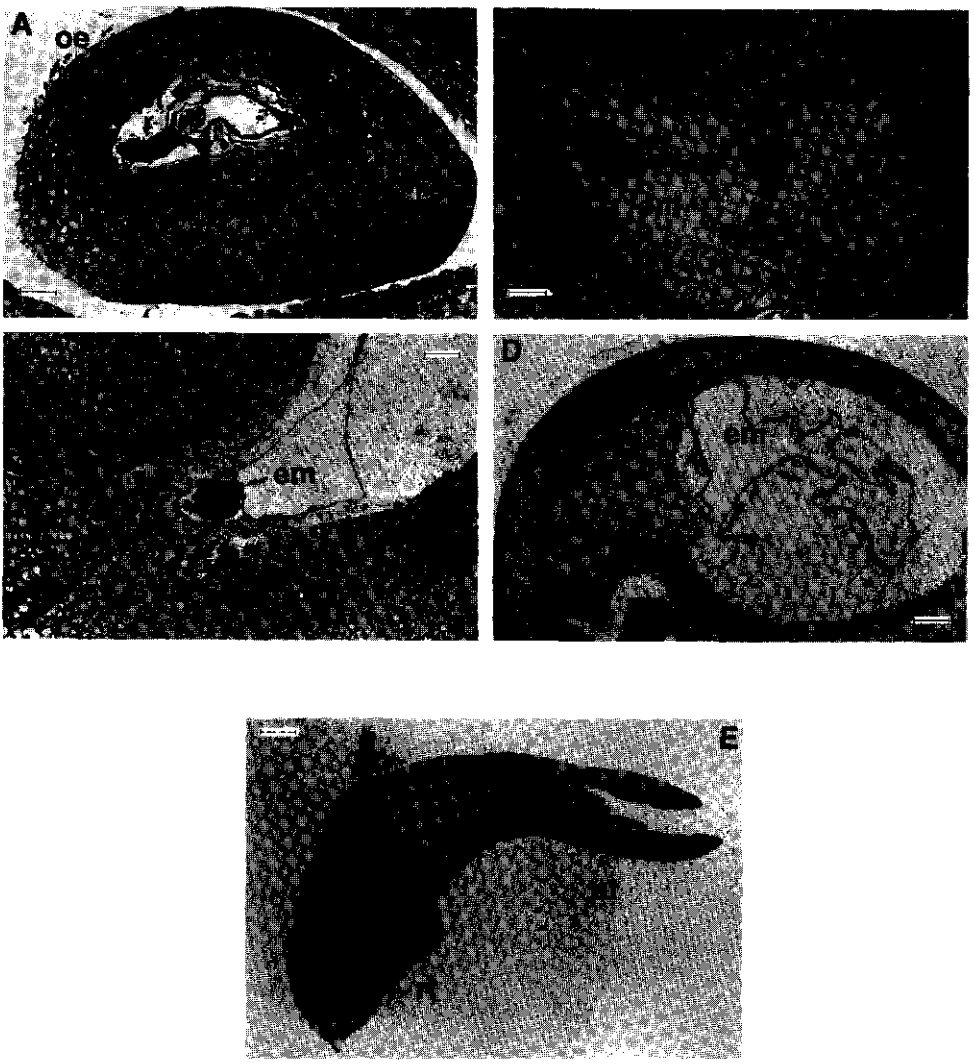

Figure 3.4. Embryo development of bambara groundnut under an 11.5 h photoperiod on the day of anthesis (A), and 1 d (B), 7d (C), 29 d (D), and 59 d (E) after anthesis. oe, Ovule; cpt, contents of pollen tube; em, embryo; pt, plumelet; rt, rootlet. A, Bar = 18 μm; B, bar = 13.5 μm; C, bar = 18 μm; D, bar = 183 μm; E, bar = 277 μm.

Analysis of ovaries which did not develop from 7 d after anthesis under a photoperiod regime of 11.5 h, revealed that embryos had stopped their growth at 17 d after anthesis at a diameter of 29 $\pm$ 18 μm. Embryos of up to 49 d after anthesis had the same average size as embryos at 17 d after anthesis.

The growth of embryos under a photoperiod of $\geq$ 14 h (Fig. 3.5) was similar to that under the 11.5 h photoperiod up to 17 d after anthesis (Figs 3.6 A, B). Thereafter the growth of embryos stopped, just as in the group of ovaries which did not develop under the 11.5 h photoperiod. Healthy-looking embryos (Fig. 3.6 C) were found in ovaries up to 32 d after anthesis. From then on embryos started to shrivel. This coincided with degeneration of the ovules (Fig. 3.7) and ended with abortion of the ovary.

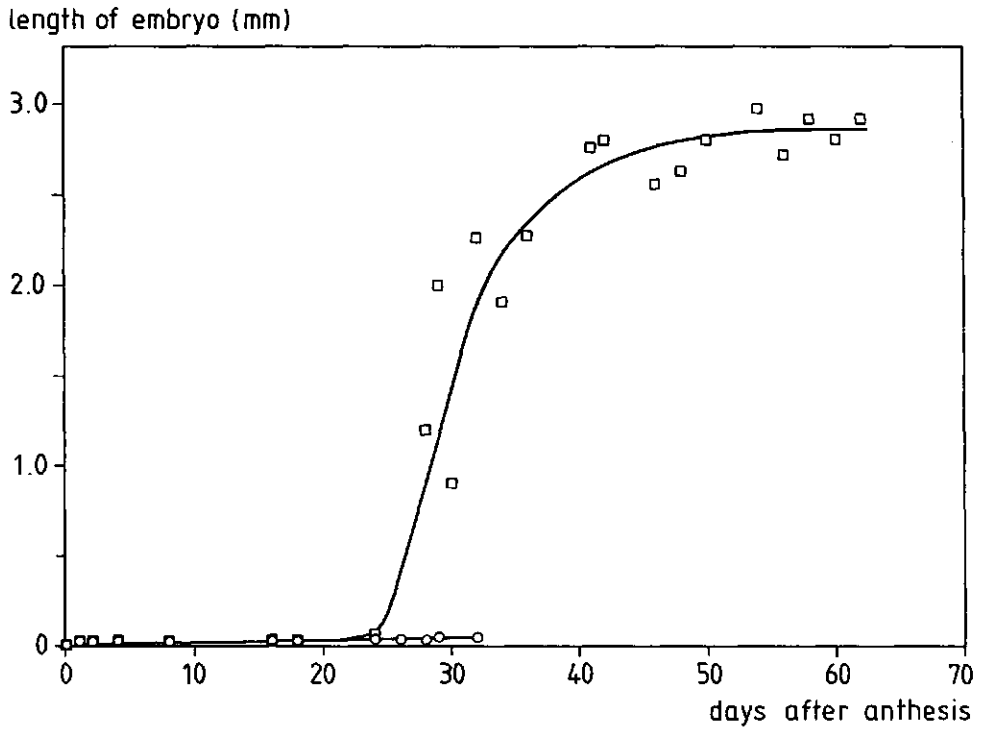

Figure 3.5. Embryo development of bambara groundnut under an 11.5 h photoperiod (□), and a photoperiod of $\geq$ 14 h (○).

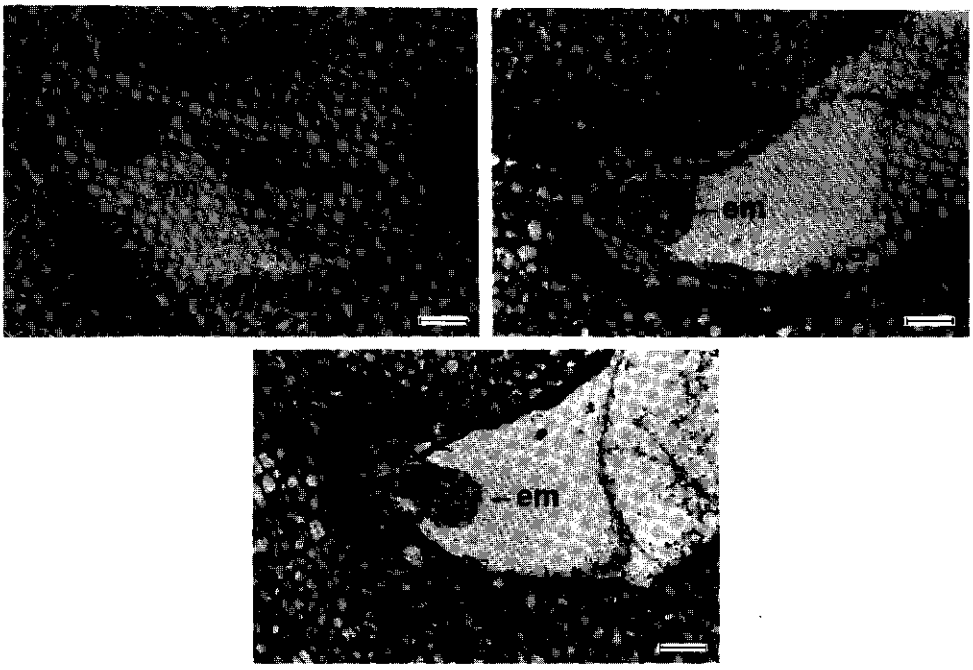

Figure 3.6. Embryo development of bambara groundnut under a photoperiod of ≥ 14 h at A, 3 d; B, 17 d; and C, 27 d after anthesis. em, Embryo. Bars = 13.5 μm

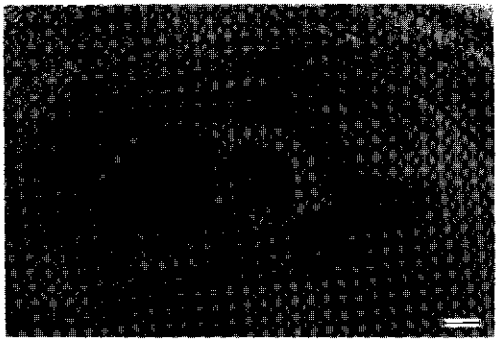

Figure 3.7. Ovary of bambara groundnut with two shrivelled ovules at 34 d after anthesis under a photoperiod of ≥ 14 h. oy, Ovary; oe, ovule. Bar = 183 μm

3.4 Discussion

Photoperiod regulation of flowering and fruit-set. The development of bambara groundnut was strongly influenced by differences in photoperiod between 10 and 16 h. The beginning of flowering, recorded as the number of days from sowing to the first open flower, was delayed by lengthening the photoperiod. This delay became more pronounced during the production of subsequent flowers; differences among treatments in the number of days to the fifth and the tenth open flower increased steadily. Lengthening the photoperiod also caused a delay in the beginning of fruit development. This effect was stronger than the photoperiod regulation of flowering. It even resulted in plants that failed to produce fruits at 14 and 16 h. Photoperiod is apparently a strong regulating factor in the adaptation of genotypes to the ecophysiological environment at their latitude of origin. This implies that high-yielding genotypes do not necessary yield well when taken to another latitude, where the yearly course of the photoperiod is different.

Consequently, the effect of photoperiod on the beginning of flowering in bambara groundnut is comparable to that in other short-day plants. Therefore it should be possible to develop predictive, linear models for the photothermal response of the beginning of flowering in bambara groundnut that are similar to the models for other grain legumes (for example Summerfield *et al.*, 1991). However, for a complete characterization of bambara groundnut, it appears necessary to include the photothermal response of fruit-set in the predictive models. But this would reduce the value of these models as tools for fast screening in plant breeding programmes. Models for other crops do not include the photothermal response of fruit-set, indicating that this response is considered to be of secondary importance for these crops. This is reflected in the limited number of studies on the effect of photoperiod and temperature on aspects of crop growth and development other than flowering. The few existing recent studies, however, present results that are comparable to those for bambara groundnut. Flohr, Williams and Lenz (1990), for instance, report that groundnut cv. NC Ac 17090 flowered irrespective of photoperiod, but that day-lengths of more than 15 h increased the time required for peg and pod initiation, and the time for each fruit to mature. This was accompanied by a reduction in the partitioning of assimilates to the pods and/or the duration of rapid pod growth. Reduction of the partitioning of dry matter into seeds was also found in soya bean (determinate genotype 'Ransom') after the dark period was interrupted to simulate a relatively long photoperiod (Cure *et al.*, 1982).

Dry matter partitioning. The use of assimilates for vegetative *vs.* generative growth was reflected by the length of the period during which the leaf appearance rate was

maintained at about one leaf d^{-1}. This period ended 52 d after sowing for plants under the 10 h photoperiod and at 129 d for plants under the 16 h photoperiod. Even after the beginning of fruit-set, photoperiod influenced the partitioning of assimilates over vegetative and generative plant parts in bambara groundnut. Partitioning of assimilates favoured leaf and stem production under 14 and 16 h photoperiods, whereas under photoperiods of 13 h or less the assimilates were primarily used for pod and seed growth. This resulted in pod growth rates being substantially lower under 14 and 16 h photoperiods than under the other photoperiods. The average pod growth rate under a photoperiod of 13 h, for example, was 0.11 g per plant d^{-1}, and it was 0.06 g per plant d^{-1} under 14 h (Table 3.3). The physiological factors (relative sink strengths and/or hormonal balances) that underlie the observed patterns in dry matter distribution require further study.

The influence of photoperiod on dry matter partitioning was also reflected in the harvest index (HI). HI declined steadily from 0.23 at 10 h to 0.06 at 16 h (Table 3.3). This result confirms the observation by Lawn (1989) that when a photosensitive genotype of a certain species is grown at shorter photoperiods than the photoperiod at the latitude of its normal adaptation, the trend is towards a shorter vegetative growth period combined with a larger HI in situations in which other climatic factors remain favourable. Yet the plants under 10 h with the highest HI did not produce the highest yields, as their total dry matter production at harvest was lower than that of other treatments. The highest yield, though not statistically significant, was obtained under 12 h, where plants took longer to mature than those under a photoperiod of 10 h.

Embryo development. Plants under a photoperiod of $\geq$ 14 h produced ovaries with healthy-looking, undeveloped embryos whose growth stagnated when they were a maximum of 29 $\pm$ 18 μm long. The combination of this observation with the earlier finding that ovaries produced under a 14 h photoperiod can develop into mature fruits under photoperiods of 12 h or less (Linnemann, 1991), implies that fertilization took place irrespective of day-length, resulting in ovaries whose further development depended on, firstly, an inductive photoperiod and, secondly, a sufficient supply of assimilates. As long as those conditions were not met, the ovaries remained on the plant without further growth. The period during which ovaries maintained the potential to develop into full-grown fruits, could last for 32 d after anthesis. Thereafter the embryos started to shrivel and degenerate. Finally, the ovaries aborted. Under a photoperiod regime of 11.5 h some ovaries developed into mature fruits, and most ovaries contained embryos of similar size to those under conditions of $\geq$ 14 h. These, too, started to degenerate when conditions remained unfavourable for further growth. Further growth may have been restricted by an insufficient supply of

assimilates and/or by the active, regulating control system, which involves growth substances, their levels, ratios and gradients.

The experiments show the plasticity of phenological development in bambara groundnut. Flowering and fruit-set were both delayed by lengthening the photoperiod, the effects being cumulative.

Chapter 4

Phenological development in bambara groundnut (*Vigna subterranea*) at alternate exposure to 12 and 14 h photoperiods

Summary. The development phase in which photoperiod sensitivity for podding occurs was determined for two bambara groundnut genotypes grown in 1987 and 1990 in glasshouse experiments in the Netherlands, namely genotypes 'Tiga Nicuru' from Mali (day-neutral for flowering and photoperiod-sensitive for podding) and 'Ankpa 4' from Nigeria (photoperiod-sensitive for both flowering and podding). Eighteen photoperiod treatments were given to each genotype. Two treatments consisted of a constant 12 or 14 h photoperiod and started 21 days after sowing for 'Tiga Nicuru' and 18 days after sowing for 'Ankpa 4'. Eight treatments were introduced by transferring plants with at least 20 flower buds (33-day-old plants of 'Tiga Nicuru' and 35-day-old plants of 'Ankpa 4') from a 12 to a 14 h photoperiod or *vice versa*. In 'Tiga Nicuru' transference was for 4, 8, 12 days or until harvest, and in 'Ankpa 4' it was for 8, 12, 16 days or until harvest. Another eight similar treatments were given to plants transferred after having had at least 20 open flowers (48-day-old plants of 'Tiga Nicuru' and 62-day-old plants of 'Ankpa 4'). Transferring plants of 'Tiga Nicuru' to the 12 h photoperiod for at least 8 days induced podding. Plants were susceptible to podding induction for nearly 4 weeks: podding was induced in plants which had been in the natural photoperiod ($\geq$ 15.5 h) for 21 days, followed by 12 days in the 12 h photoperiod and subsequently in the 14 h photoperiod until harvest, and it could still be induced in 48-day-old plants that had had $>$20 open flowers. However, transference to the 12 h photoperiod for 16 days did not induce podding in 'Ankpa 4'. Transferring plants from the 12 to the 14 h photoperiod or *vice versa* caused differences in the number of flowers and pods/plant, petiole length and leaf area. The influence of photoperiod was most obvious on the number of pods/plant. Leaf area and number of pods/plant seem suitable parameters for modelling crop growth under different photoperiods. Leaf area development correlated with the number of developing pods/plant, but was also more directly influenced by the prevailing photoperiod.

4.1 Introduction

Bambara groundnut (*Vigna subterranea* (L.) Verdc., syn. *Voandzeia subterranea* (L.) Thouars) is an indeterminate pulse with subterranean fruit-set. The plant may grow up

to 30 cm tall and has prostrate, much-branched, leafy lateral stems just above ground level. Differences in the length of internodes result in bunched, intermediate and spreading types. Cultivated forms usually have a bunched or intermediate growth habit. In terms of production, bambara groundnut ranks third among the grain legume crops of the African lowland tropics after groundnut (*Arachis hypogaea* L.) and cowpea (*Vigna unguiculata* (L.) Walp.) (Rachie & Silvestre 1977).

Observations on photoperiodic regulation of phenological development in bambara groundnut have indicated differences in response to photoperiod between genotypes (Linnemann 1991). In certain genotypes, photoperiods of 14 h or longer retard or even inhibit the onset of two developmental stages, flowering and podding, by comparison with photoperiods of 12 h or less. In a photoperiod-sensitive genotype from Ankpa in Nigeria, for example, development under photoperiods of 14 h or longer was retarded much more than under photoperiods of 13 h or less (Linnemann 1993), and the onset of flowering, progress of flowering, onset of podding and progress in pod growth were all retarded. Podding was affected more than flowering: some plants flowered but failed to produce pods under photoperiods of 14 and 16 h. These plants had many undeveloped ovaries, some of which developed into full-grown fruits after transference to a 12 h photoperiod (Linnemann 1991). Microscopic studies showed that under an 11 h 30 min photoperiod two groups of ovaries could be distinguished (Linnemann 1993). In both, embryo development was identical up to 17 days after flowering, but then the embryos in the first group continued to develop until they were full-grown, whereas the embryos in the second group stopped growing. Under a photoperiod > 14 h, embryo development was similar to the group 2 embryos under the 11 h 30 min photoperiod. The delay or absence of podding under photoperiods of 14 h or longer was therefore attributed to the growth of ovaries being checked.

This paper presents an assessment of the developmental phase in which photoperiod sensitivity for pod production in bambara groundnut occurs, and quantifies the number of short days of 12 h needed to induce podding in plants otherwise grown under photoperiods of 14 h. In addition, the effect of transferring plants from a 12 to a 14 h photoperiod or *vice versa* on number of flowers, petiole length and leaf area is described, to determine similarities to the influence of photoperiod on the number of pods for future models of crop growth. Two genotypes were used, one from Mali (Expt 6) and one from Nigeria (Expt 7). They represented the range in photoperiodic response within the germplasm collection of the Department of Agronomy, Wageningen Agricultural University, which at the time held > 130 randomly collected accessions.

4.2 Materials and methods

Two experiments were conducted in glasshouses at Wageningen Agricultural University (51°58' N), the Netherlands. Plants were grown individually in 5 litre pots filled with a mixture of sand and humus-rich potting compost (1:1 v/v). Plants in pots on trolleys were exposed to an 8 h period of natural daylight, extended in sheds by low-intensity, fluorescent (from Philips TLD 36 W tubes) and incandescent light (from Philips 40 W bulbs) of 10 μmol/m^2/s photosynthetically active radiation (PAR, 400-700 nm) at plant height, to achieve the desired photoperiod. Thus, the differences in total PAR between treatments were negligible. Average temperatures were between 26-30 °C during the day and 22-25 °C at night.

Experiment 6. The genotype 'Tiga Nicuru' from Kuna (20 km NW of Macina; 14°13' N) in Mali was used. It had been used in earlier experiments (Linnemann 1991). It flowers irrespective of photoperiod but has retarded podding under photoperiods of 14 h or longer. Plants were the first generation of material collected in 1985. They were grown under the natural photoperiod from sowing on 1 May 1987 (15 h 32 min) up to 21 May 1987 (16 h 42 min). In this study the natural photoperiod was defined as the period between sunrise and sunset, plus the period of twilight during which the position of the centre of the sun is between 0 and 3 ° below the horizon. On 22 May (21 days after sowing (DAS)), when the average number of unfolded leaves per plant was seven, uniform plants were selected and allocated to 18 photoperiod treatments. Two treatments were subjected to a constant photoperiod of 12 or 14 h throughout the experiment. Eight treatments were imposed by transferring plants with at least 20 flower buds (33 DAS) from the 12 to the 14 h photoperiod or *vice versa* for 4, 8 or 12 days, or until harvest. Another eight treatments were effected by applying the same procedure to plants which had had at least 20 open flowers (48 DAS). Each treatment consisted of one pot. One replication of the 18 treatments occupied two trolleys: one trolley for the 12 h photoperiod and another for the 14 h photoperiod. There were four replications in a completely randomized block design.

Harvest was 82-90 DAS, when some plants started to wilt, possibly because of *Rhizoctonia solani* infection. Data recorded were the day of the first open flower, number of pods, average length of the 20 longest petioles and leaf area/plant (as measured by a LiCor area meter, Model 3100). In addition, the total number of flowers was determined by daily counts of open flowers for six treatments (the constant photoperiods of 12 and 14 h, plus the four treatments which were transferred for a period of 8 days, namely the treatments transferred from 12 to 14 h or *vice versa* after having produced at least 20 flower buds and after having had at least 20

open flowers). At harvest, the total number of flowers was estimated for all treatments by counting the number of pedunculi per plant and multiplying by two (every pedunculus bears two flowers).

Experiment 7. In this experiment, a genotype bought in a market in Ankpa (7°22' N), Nigeria, was used. This genotype, 'Ankpa 4', had been used in a previous experiment (Linnemann 1993). It is photoperiod-sensitive for both flowering and podding. Plants were the first generation of material collected in 1988. They were grown individually in pots under the natural photoperiod, from sowing on 16 August 1990 (15 h 15 min) up to 2 September 1990 (14 h 8 min). On 3 September, plants were selected and allocated to 18 treatments. The periods spent in the new photoperiod were longer than in Expt 6: 8, 12, or 16 days, or until harvest for both developmental stages. The transfer day for plants that had produced at least 20 flower buds (henceforth called bud stage) was 35 DAS, and for plants that had produced at least 20 open flowers (henceforth called open flower stage) was 62 DAS (by which time plants that had been under the 12 h photoperiod since the start of the treatments had produced at least 20 open flowers). Each treatment consisted of one pot. Two replications of the 18 treatments occupied two trolleys: one trolley for the 12 h photoperiod and the other for the 14 h photoperiod. Because of the heterogeneity of the material, there were ten replications in a completely randomized block design. Harvest was 122-125 DAS. Data recorded were the day of the first open flower and the number of pods/plant. In addition, the leaf area/plant was determined for two randomly-selected replications (using a LiCor area meter, Model 3100). Open flowers were not counted because of lack of time.

4.3 Results

Time of flowering. All plants of genotype 'Tiga Nicuru' started flowering between 39 and 45 DAS. On average, flowering started 41 DAS. There were no differences between treatments ($P = 0.05$). In the treatments in which open flowers were counted daily, it was noted that plants subjected to the 14 h photoperiod or transferred for 8 days from the 14 to the 12 h photoperiod (both developmental stages) were still flowering at the time of harvest (i.e. 82-90 DAS). In contrast, plants grown under the 12 h photoperiod or transferred for 8 days from the 12 to the 14 h photoperiod (both developmental stages) stopped producing flowers between 63 and 72 DAS. Under the constant 12 h photoperiod, genotype 'Ankpa 4' started flowering 42 DAS but under the constant 14 h photoperiod flowering did not start until 48 DAS.

Number of flowers. On average, 'Tiga Nicuru' had 94 flowers/plant under the 12 h photoperiod (Table 4.1). Transference from the 12 to the 14 h photoperiod only increased the number of flowers significantly ($P = 0.05$) if plants were transferred in the bud stage and were not returned to the 12 h photoperiod. The number of flowers thus obtained was 232 per plant, or nearly 2.5 times the number of flowers of plants under the constant 12 h photoperiod.

Table 4.1. Number of flowers and average length of the 20 longest petioles/plant in bambara groundnut genotype 'Tiga Nicuru' as affected by transference from a 12 to a 14 h photoperiod.

Photoperiod treatment	Number of flowers	Petiole length (mm)
12 h throughout	94	99
from 12 to 14 h at		
≥ 20 flower buds per plant		
for 4 days	122	96
for 8 days	123	105
for 12 days	121	104
until harvest	232	109
from 12 to 14 h at		
≥ 20 open flowers per plant		
for 4 days	104	94
for 8 days	89	97
for 12 days	99	103
until harvest	91	93
S.E. (24 D.F.)	16.0	4.8

The average number of flowers per 'Tiga Nicuru' plant under the 14 h photoperiod was 272 (Table 4.2). The fewest flowers (151 per plant) were obtained from plants transferred in the bud stage to the 12 h photoperiod and not returned.

Number of pods. On average, 'Tiga Nicuru' produced 28.0 pods/plant under the 12 h photoperiod, but only 3.3 under the 14 h photoperiod (Fig. 4.1). Podding was not affected by transferring plants from the 12 to the 14 h photoperiod ($P = 0.05$), not even when the plants were transferred until harvest. Plants transferred for 4 days from the 14 to the 12 h photoperiod had similar pod numbers to plants grown under

Table 4.2. Number of flowers and average length of the 20 longest petioles/plant in bambara groundnut genotype 'Tiga Nicuru' as affected by transference from a 14 to a 12 h photoperiod.

Photoperiod treatment	Number of flowers	Petiole length (mm)
14 h throughout	272	141
from 14 to 12 h at		
≥ 20 flower buds per plant		
for 4 days	258	132
for 8 days	245	120
for 12 days	168	119
until harvest	151	120
from 14 to 12 h at		
≥ 20 open flowers per plant		
for 4 days	321	122
for 8 days	249	129
for 12 days	208	128
until harvest	187	127
S.E. (24 D.F.)	72.6	4.4

the constant 14 h photoperiod. Plants transferred from the 14 to the 12 h photoperiod for 8 days (both developmental stages) produced more pods/plant than plants kept under the constant 14 h photoperiod ($P = 0.05$).

In 'Ankpa 4', the average numbers of pods/plant under the 12 and 14 h photoperiods were respectively 6.2 and 1.8 (Fig. 4.1). Unlike the results for 'Tiga Nicuru', podding in 'Ankpa 4' was reduced by transferring plants from the 12 to the 14 h photoperiod (both developmental stages) and keeping them there until harvest ($P = 0.05$). Moreover, the sooner the plants were transferred, the greater the decrease in the number of pods: the number of pods/plant was 0.6 in plants transferred from the bud stage but was 3.4 in plants transferred from the open flower stage onwards. Transferring plants from the 14 to the 12 h photoperiod increased the number of pods/plant, but only when plants were not returned to the 14 h photoperiod ($P = 0.05$). Again there was a difference between the two stages in which plants were transferred; on average there were 5.4 pods/plant transferred at the bud stage and 7.8 pods/plant transferred from the open flower stage onwards.

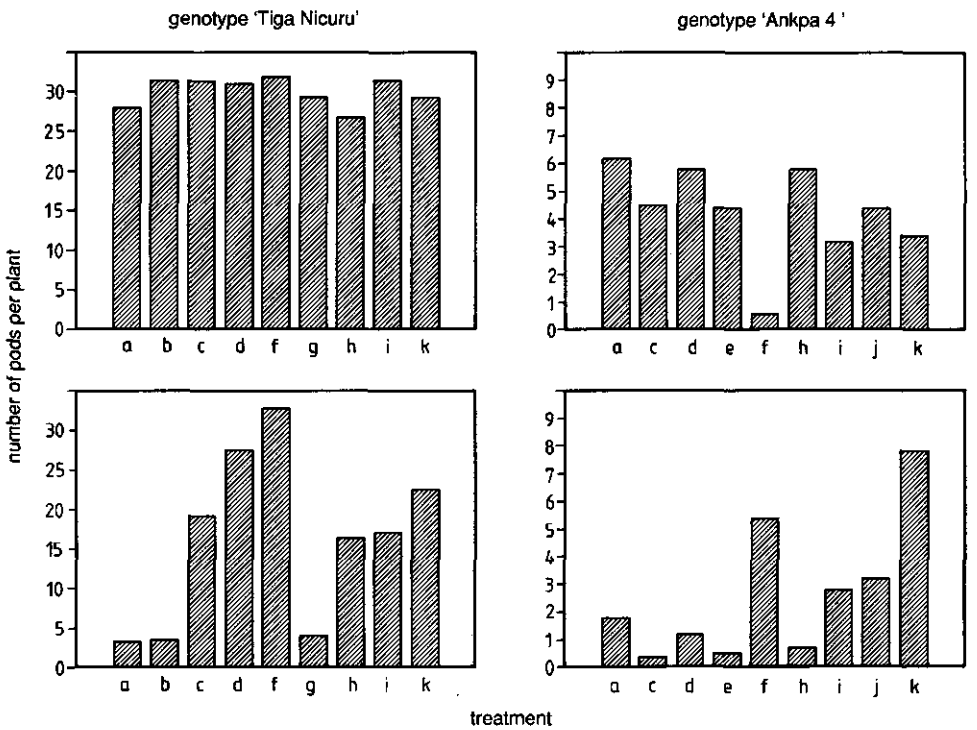

Figure 4.1. Number of pods/plant in two bambara groundnut genotypes ('Tiga Nicuru' and 'Ankpa 4') as affected by transference from a 12 to a 14 h photoperiod (A and B) or *vice versa* (C and D). Plants with ≥ 20 flower buds were transferred for (a) 0 days, (b) 4 days (only genotype 'Tiga Nicuru'), (c) 8 days, (d) 12 days, (e) 16 days (only genotype 'Ankpa 4'), or (f) until harvest, and plants which had produced ≥ 20 open flowers were transferred for (g) 4 days (only genotype 'Tiga Nicuru'), (h) 8 days, (i) 12 days, (j) 16 days (only genotype 'Ankpa 4'), or (k) until harvest. The S.E. for 'Tiga Nicuru' (24 D.F.) was 6.70 for transference from 12 to 14 h, and 6.29 *vice versa*. The S.E. for 'Ankpa 4' (72 D.F.) was 1.06 for transference from 12 to 14 h, and 0.93 *vice versa*.

Petiole length. The average lengths of the 20 longest petioles per plant for genotype 'Tiga Nicuru' were 99 mm under the 12 h photoperiod and 141 mm under the 14 h photoperiod (Tables 4.1 and 4.2). Transferring plants from the 12 to the 14 h photoperiod increased the petiole length in only one treatment ($P = 0.05$): the petioles of plants transferred to the 14 h photoperiod in the bud stage and left there until harvest were on average 10 mm longer than the petioles of plants in the constant 12 h photoperiod (Table 4.1). Transferring plants from the 14 to the 12 h photoperiod always resulted in shorter petioles, except for plants that were transferred in the bud stage for a period of 4 days ($P = 0.05$, Table 4.2).

Leaf area. Leaf area/plant under the constant 12 h photoperiod was 515 cm^2 in 'Tiga Nicuru' and 2185 cm^2 in 'Ankpa 4' (Table 4.3). Plants of 'Tiga Nicuru' transferred

Table 4.3. Leaf area/plant in bambara groundnut (genotypes 'Tiga Nicuru' and 'Ankpa 4') as affected by transference from a 12 to a 14 h photoperiod.

Photoperiod treatment	Leaf area (cm^2)	
	'Tiga Nicuru'	'Ankpa 4'
12 h throughout	515	2185
from 12 to 14 h at		
≥ 20 flower buds per plant		
for 4 days	552	
for 8 days	679	1787
for 12 days	704	2119
for 16 days		2254
until harvest	939	2739
from 12 to 14 h at		
≥ 20 open flowers per plant		
for 4 days	479	
for 8 days	492	2159
for 12 days	575	2186
for 16 days		1786
until harvest	536	2133
S.E. (24 D.F.)	65.5	
S.E. (8 D.F.)		423.6

to the 14 h photoperiod in the bud stage for 8 days or longer, ended up with a greater leaf area than plants under the constant 12 h photoperiod ($P = 0.05$). The largest increase was obtained in plants left in the 14 h photoperiod until harvest: their leaf area was > 1.8 times the leaf area under the 12 h photoperiod.

On the other hand, leaf area was decreased by transferring plants in the bud stage from the 14 to the 12 h photoperiod for 12 days or longer, or by transferring plants in the open flower stage to the 12 h photoperiod until harvest ($P = 0.05$, Table 4.4). In 'Ankpa 4' transference from the 12 to the 14 h photoperiod did not alter the leaf area per plant compared with a treatment of 12 h throughout, nor did transference from the 14 to the 12 h photoperiod result in differences with the constant 14 h photoperiod ($P = 0.05$, Tables 4.3 and 4.4).

Table 4.4. Leaf area/plant in bambara groundnut (genotypes 'Tiga Nicuru' and 'Ankpa 4') as affected by transference from a 14 to a 12 h photoperiod.

Photoperiod treatment	Leaf area (cm^2)	
	'Tiga Nicuru'	'Ankpa 4'
14 h throughout	1380	1832
from 14 to 12 h at		
≥ 20 flower buds per plant		
for 4 days	1181	
for 8 days	1209	2095
for 12 days	712	2072
for 16 days		2353
until harvest	677	1969
from 14 to 12 h at		
≥ 20 open flowers per plant		
for 4 days	1142	
for 8 days	1242	1978
for 12 days	1067	2646
for 16 days		2430
until harvest	930	2135
S.E. (24 D.F.)	169.8	
S.E. (8 D.F.)		357.9

4.4 Discussion

Number of flowers and pods. The results of these experiments confirm that onset of flowering is photoperiod-insensitive in genotype 'Tiga Nicuru' from Mali (Linnemann 1991), and photoperiod-sensitive in 'Ankpa 4' from Nigeria (Linnemann 1993). Changing the photoperiod did not affect the number of flowers/plant when compared with the constant photoperiods, except for one treatment. The number of pods/plant in 'Tiga Nicuru' tended to be inversely correlated with the number of flowers/plant. However, there were considerable differences in the ratio between the number of pods/plant and the number of flowers/plant: under the 12 h photoperiod 'Tiga Nicuru' gave 28 pods from 94 flowers (*c*. 3 : 1), whereas after a single transfer of plants in the bud stage from the 12 to the 14 h photoperiod a similar number of pods (32) was produced from 232 flowers (*c*. 7 : 1). The maximum number of pods produced under the circumstances of this experiment was *c*. 30 for 'Tiga Nicuru', and did not increase with the number of flowers.

The difference in the number of pods/plant between 'Tiga Nicuru' and 'Ankpa 4' is large. This is partly caused by a genotypic difference in pod size and number; 'Tiga Nicuru' typically produces many small pods, whereas 'Ankpa 4' gives relatively few large pods. In addition, it seems that the number of pods/plant is decreased by subjecting plants of the more photoperiod-sensitive genotype, 'Ankpa 4', to an inductive 12 h photoperiod from an early stage in their development onwards. Postponing the transfer from non-inductive to inductive photoperiods might result in higher pod numbers in 'Ankpa 4' than found in this experiment, as, for instance, was found in a previous experiment in which the highest yields were obtained by subjecting plants to 42 days at 14 h, followed by 21 days at 12 h and 38-40 days at 10 h (Linnemann 1991).

Induction of podding. In 'Tiga Nicuru' the 4 day transfer from the 14 to the 12 h photoperiod was the only one not to induce podding, but in 'Ankpa 4' podding was not even induced by the 16 day period under 12 h. In 'Tiga Nicuru', a transfer for 8 days to the 12 h photoperiod (both developmental stages) increased the number of pods/plant compared with plants under the 14 h photoperiod. Longer transfers increased pod numbers. Podding therefore appears to be induced once a genotype-specific number of days at 12 h has been exceeded, and from that point onwards the number of pods/plant increases concomitantly with an increase in the duration of the period under the 12 h photoperiod. This increase probably stops when the maximum number of pods/plant (apparently *c*. 30 for 'Tiga Nicuru' in this experiment) is reached.

'Tiga Nicuru' is susceptible to induction of podding for nearly 4 weeks: podding was induced in plants kept for 21 days in the natural photoperiod ($\geq$ 15.5 h), then 12 days in the 12 h photoperiod and subsequently in the 14 h photoperiod until harvest, and it could still be induced in 48-day-old plants that had produced more than twenty open flowers.

Genotypic differences in photoregulation of podding. Photoperiod influenced podding in both genotypes but more so in 'Ankpa 4' than in 'Tiga Nicuru'. Firstly, 'Tiga Nicuru' responded faster than 'Ankpa 4' to the inductive influence of the 12 h photoperiod; 8 days of 12 h were sufficient to induce podding in this genotype, whereas 16 days of 12 h were insufficient to obtain podding in 'Ankpa 4'. Secondly, the developmental stage which was most sensitive to photoperiod differed between the genotypes. In 'Tiga Nicuru' transference from 14 to 12 h in the bud stage tended to give higher numbers of pods/plant than transference in the open flower stage. The opposite was seen in 'Ankpa 4'. Thirdly, induction of podding in 'Tiga Nicuru' was irreversible; it could not be stopped by transferring plants from the 12 to the 14 h photoperiod. Even plants transferred from the 12 to the 14 h photoperiod in the bud stage produced the same number of pods as the plants that received the 12 h photoperiod throughout, whereas the plants transferred in the bud stage actually only received 12 days of 12 h (between the day on which the plants were allocated to the treatments (21 DAS) and the day of the transfer to the 14 h photoperiod (33 DAS)). In 'Ankpa 4', however, podding was reduced by transferring plants to the 14 h photoperiod. This reduction even occurred in two treatments that were transferred in the open flower stage, i.e. after plants had already received 62 minus 18 (i.e. 44 days) of 12 h.

Petiole length. The data on petiole lengths in this experiment demonstrate the influence of photoperiod on this plant characteristic; under the influence of the 14 h photoperiod the length of petioles increased. Petiole length differed more between treatments than the number of flowers/plant. However, the differences in petiole lengths seem too imprecise to describe differences in photoperiod for crop growth modelling.

Otherwise, the influence of photoperiod on petiole length, as on the length of internodes (Linnemann 1991), implies that petiole length is also unsuitable for genotype characterization (IBPGR/IITA/GTZ 1987) unless the photoperiodic circumstances are standardized.

Leaf area. In 'Ankpa 4', the data on leaf area measured at harvest showed no statistically significant differences between plants that had been transferred and those

that had not. This is attributable to the limited number of observations (plants from only two replications were measured) and the large scatter of data (probably caused by the heterogeneity of the seed).

Leaf area data on 'Tiga Nicuru' showed a fairly strong negative correlation with the number of pods in plants transferred from the 14 to the 12 h photoperiod ($r = 0.84$); the largest leaf areas/plant were in the treatments with the fewest pods. However, there was no such correlation in plants transferred from the 12 to the 14 h photoperiod where the leaf area of plants increased by > 80% compared with the plants under the 12 h photoperiod, but there were no differences in the number of pods/plant. This implies that leaf area development is not only related to the number of developing pods on a plant, but is also more directly dependent on the prevailing photoperiod. The latter relation was demonstrated earlier by a reduction of pod growth rates under photoperiods of 14 h or longer compared with photoperiods of 13 h or less (Linnemann 1993).

Partitioning of assimilates. Studies on common bean (*Phaseolus vulgaris* L.) with additional data on groundnut and other crops (Wallace *et al.* 1993) have demonstrated that photoperiod gene(s) often control the partitioning of photosynthate toward reproductive growth or toward continued vegetative growth. The effects of photoperiod on the onset of podding in bambara groundnut, on leaf area development, and on the relation between these two can be explained by the underlying photoperiod-controlled partitioning of assimilates. Under 14 h photoperiods, assimilates were predominantly used for vegetative development, which resulted in extensive leaf areas/plant. After podding had been induced by the 12 h photoperiod, assimilates were also used for pod and seed growth. The amount of assimilates available for pod growth depends on the total amount of assimilates produced (partly determined by actual leaf area), as well as on the photoperiod-controlled partitioning of these assimilates.

Comparison with other crops. The phenomenon of photoperiod-induced fruiting does not appear to be prominent in crops that are photoperiod-sensitive to flowering other than bambara groundnut, but this requires further study. Photoperiod-sensitive crops other than bambara groundnut go through a basic vegetative phase as they develop towards flowering. This phase comprises two subphases: a pre-inductive (or juvenile) and a photoperiod-sensitive phase. The presence of a pre-inductive phase is an adaptive advantage of genotypes, as it delays sexual reproduction until the plant has attained a certain size (Wareing 1987). In cereals, the pre-inductive phase for flowering can be as short as 2 or 3 DAS for early genotypes (i.e. when plants have about three leaves), or > 40 days in late genotypes (Squire 1990). Most tropical

grain legumes have no pre-inductive phase for flowering (Summerfield & Wien 1980). Most common cultivars of soya bean, for example, lack such a phase (Major & Kiniry 1991). However, in the photoperiod-sensitive accession G2120, the pre-inductive phase lasted from emergence until the first trifoliolate leaf was fully unfolded (Shanmugasundaram & Lee 1981), whereas four cultivars investigated by Collinson *et al.* (1993) had a pre-inductive phase which varied from 11 to 33 days. This pre-inductive phase prevented USA-adapted cultivars from flowering prematurely in short tropical daylengths.

No pre-inductive phase for podding in bambara groundnut was found in the experiments reported in this paper possibly because the transfers were started too late. Yet in 'Ankpa 4' the differences (not statistically significant) in pod numbers between transference in the bud and open flower stage suggest that this genotype has juvenility in the bud stage. If juvenility exists in 'Tiga Nicuru', it must be present in the first 21 DAS (before plants have seven unfolded leaves).

Implications for the spread of genotypes. The genotypic differences found in the photoregulation of podding have implications for cultivating genotypes outside the latitudes of their origin. When genotype 'Tiga Nicuru', with its day-neutral flowering and photoperiod-induced podding, is grown at latitudes of $< c.\ 14°$, podding will be induced early and quickly, resulting at best in reduced yields and at worst in crop failure because of pod rot during the end of the rains. On the other hand, when genotype 'Ankpa 4', with its photoperiod-sensitive flowering and podding, is cultivated at latitudes $> c.\ 7°$, flowering and podding will be retarded by photoperiod, thereby increasing the likelihood that plants will die from drought before they have matured. This photoregulation of podding imposes restrictions on the dissemination of photosensitive germplasm of bambara groundnut.

Chapter 5

Phenological development in bambara groundnut (*Vigna subterranea*) transferred from 14-h to 11-h photoperiods

Summary. Aspects of photoregulation of phenological development in bambara groundnut were studied in a greenhouse experiment in the Netherlands. The influence of a 14-h photoperiod (which retards podding) during a period of variable length prior to an 11-h photoperiod (which induces podding) on flowering, yield and on the position of pods on the plants was determined. The third generation of three plants of genotype 'Ankpa 4' from Nigeria was used as the split factor in a split plot set-up with three replicates. The main plots were four daylength treatments: a period of 21, 28, 41 or 54 days under the 14-h photoperiod before transference to the 11-h photoperiod. Plants transferred after 28 or more days, started flowering sooner the earlier they were transferred. Plants transferred after 21 and 28 days began flowering simultaneously, thus indicating juvenility. At harvest, 135 days after sowing, the total seed dry weight per plant was higher for plants transferred after 41 and 54 days than for plants transferred after 21 days. Plants transferred after 28 days gave an intermediate value. Most (79-91%) pods were produced on branches that developed on nodes 1 - 4 of the main axis. There were no differences in the fractional distribution of the pods along the main axis in plants transferred after 28 or more days. Pods of plants transferred after 21 and 28 days were more evenly distributed over the nodes of the first two primary branches than pods of plants transferred after 41 and 54 days. Plants of the latter treatments produced their pods more towards the tips of the branches and concentrated on two neighbouring nodes (nodes 5 and 6 for plants transferred after 41 days and nodes 6 and 7 for plants transferred after 54 days). Delaying the induction of podding in this experiment therefore resulted in higher seed yields per plant and a more synchronized development -and hence maturity- of pods.

5.1 Introduction

Bambara groundnut (*Vigna subterranea* (L.) Verdc., syn. *Voandzeia subterranea* (L.) Thouars) has been grown for many centuries in the tropical regions of Africa south of the Sahara (Linnemann & Azam-Ali 1993). This leguminous crop is cultivated for its subterranean seeds. These are consumed fresh when semi-ripe, as a pulse when dry and mature, or ground into flour. Bambara groundnut is an indeterminate, annual

herb up to 30 cm in height. It has prostrate, much-branched lateral stems just above ground level. The trifoliolate leaves are carried on erect, grooved petioles, produced at the nodes of the creeping stems. Flowers are normally carried in pairs on peduncles at the base of the petioles. After pollination and fertilization the peduncles lengthen, thus bringing the ovaries underground.

Simultaneous maturity of all the fruits on one plant is a desirable trait in food production systems where harvesting is a single event. Fruits that mature long before the harvest date, are more likely to be attacked by pests and diseases, and/or to germinate prematurely. Large yield losses may be the result. In bambara groundnut for example, yield loss resulting from pod rotting in the humid environment of Ibadan was found to be 1.5% rotten pods at 115 days after sowing and 37.3% 35 days later (Goli & Ng 1988). Because of the indeterminate habit of bambara groundnut, pods develop and mature over a long period. The first pods normally develop from early flowers close to the main axis of the plant. During the growing season the branches develop and flowers and pods continue to be produced. However, small-scale bambara groundnut farmers often solve the problem of uneven maturity by harvesting the pods as they mature (Kay 1979).

Bambara groundnut genotypes differ in their response to photoperiod (Linnemann 1991). This has implications for breeding locally-adapted varieties. In a photoperiod-sensitive genotype from Ankpa in Nigeria, for example, the onset of flowering, progress of flowering, onset of podding and progress in pod growth in plants under photoperiods of 14 h or longer were all retarded compared with plants under photoperiods of 13 h or less (Linnemann 1993). Podding was affected more than flowering: some plants flowered but failed to produce pods under photoperiods of 14 and 16 h. These plants had many undeveloped ovaries, some of which developed into full-grown pods after transference to a 12-h photoperiod regime. Hence the delay or absence of podding under photoperiods of 14 h or longer was attributed to the growth of fertilized ovaries being checked. Transference from a 14-h to a 12-h photoperiod for 16 days or less was insufficient to induce podding in this genotype from Ankpa (Linnemann, submitted). Pods were only produced by plants which were not returned from the 12-h to the 14-h photoperiod.

This paper presents a further quantification of photoregulation of development in bambara groundnut. In an experiment the influence of a 14-h photoperiod during a period of variable length was determined on yield and on the position of pods which developed after transference to an 11-h photoperiod. The aim of the trial was to establish the conditions that would induce pods to develop on nodes close to one

another, thus resulting in more even development and maturity than when pods develop on nodes scattered over the branches.

5.2 Materials and methods

The experiment was conducted in a greenhouse at Wageningen Agricultural University (51°58' N), The Netherlands. A genotype collected in a market in Ankpa (7°22' N), Nigeria, was used. This genotype, 'Ankpa 4', had been used in previous experiments (Linnemann 1993, submitted). It is photoperiod-sensitive for both flowering and podding. Plants were the third generation of three parent plants randomly selected from the material collected in 1988. This planting material was used instead of the original seed lot to create a greater genetic homogeneity within treatments, to enable the differences between treatments to be expressed more clearly.

The trial was conducted as a split plot experiment with three replicates. The main plot set-up was a randomized complete block design with 12 units. The main plot treatments were four daylength treatments: a period of 21, 28, 41 or 54 days under a 14-h photoperiod before transference to an 11-h photoperiod. A main plot consisted of a trolley carrying 30 pots, each containing one plant. Each main plot was split into three for the different progenies. Plants were grown in 5-l pots filled with a mixture of sand and humus-rich potting compost (1:1 v/v). Seed was sown on 2 April 1991. Eight days later plants had emerged. Plants received an 8-h period of natural daylight, which was extended in sheds by low-intensity, fluorescent (Philips TLD 36 W tubes) and incandescent light (Philips 40 W bulbs) of 10 μmol m^{-2} s^{-1} photosynthetically active radiation (PAR, 400-700 nm) at plant height to achieve the desired photoperiod. Thus, the differences in total PAR between treatments were negligible. Average temperatures were between 26-30 °C during the day and 22-25 °C at night. Average daily relative humidity was 60%, or less on sunny days.

The date of the first open flower and the number of leaves per plant on the day of the onset of flowering were recorded for all plants. Five plants per progeny per trolley, randomly chosen at the beginning of the daylength treatments, were used for analysis at the final harvest, 135 days after sowing. To monitor plant habit and pod development, random samples of three plants (one of each progeny) were taken from the remaining fifteen pots per trolley at fortnightly intervals from the time that 50% of the plants of a treatment had started flowering. Thus, the intermediate harvests were: 52, 66, 80, 94 and 108 days after sowing for plants transferred after 21 and 28 days; 66, 80, 94, 108 and 121 days after sowing for plants transferred after 41 days; and 80, 94, 108 and 121 days after sowing for plants transferred after 54 days. At the

intermediate and final harvests, plants were drawn schematically, using different symbols for different nodes (Fig. 5.1). A letter at every branch indicated its order: p (primary, i.e. growing on the main axis), s (secondary, i.e. growing on a primary branch) or t (tertiary, i.e. growing on a secondary branch). In addition, the number of leaves per plant was recorded, as well as total aboveground dry matter (excluding roots) after drying for at least 24 h at 105 °C, and, if applicable, number and dry weight of pods and seeds.

The schematic drawings were used to derive the following quantitative data on certain plant characteristics: the number of primary, secondary and tertiairy branches; the position of the first open flower on the first two, equally old primary branches on nodes 1 and 2 of the main axis (only for the intermediate harvests taken 80, 94 and 108 days after sowing, when all treatments were sampled); the distribution of the pods over the length of the main axis; and the position of the pods on the branches. Data were analysed with SPSS-PC.

5.3 Results

Onset of flowering. Plants transferred after 21 or 28 days from the 14-h to the 11-h photoperiod, were the first to flower (Table 5.1): on average, 49.7 and 51.5 days after sowing, respectively. Plants transferred after 41 days flowered about ten days later. Plants transferred after 54 days needed ten days more for the onset of flowering. Progenies differed in the onset of flowering (Table 5.2). There was a 5-day difference between the average date of the onset of flowering for the earliest and the latest progenies. No interaction was found between main plot treatments and progenies for the onset of flowering, nor for any of the other effects studied.

The number of days between the day of transference from the 14-h to the 11-h photoperiod and the onset of flowering was inversely related to the duration of the 14-h photoperiod (Table 5.1). The largest difference between two consecutive treatments (5.2 days) was for plants transferred after 21 days compared with plants transferred after 28 days. Differences between progenies were as for the onset of flowering (Table 5.2).

Number of leaves. The number of leaves per plant at the onset of flowering was similar for plants transferred after 21 and 28 days (Table 5.1). On average, these plants had 25 leaves each. Plants transferred after 41 days had 35 leaves at the onset of flowering, whereas plants transferred after 54 days had 41 leaves. One of the

progenies had on average four leaves more at the onset of flowering than the other two progenies (Table 5.2).

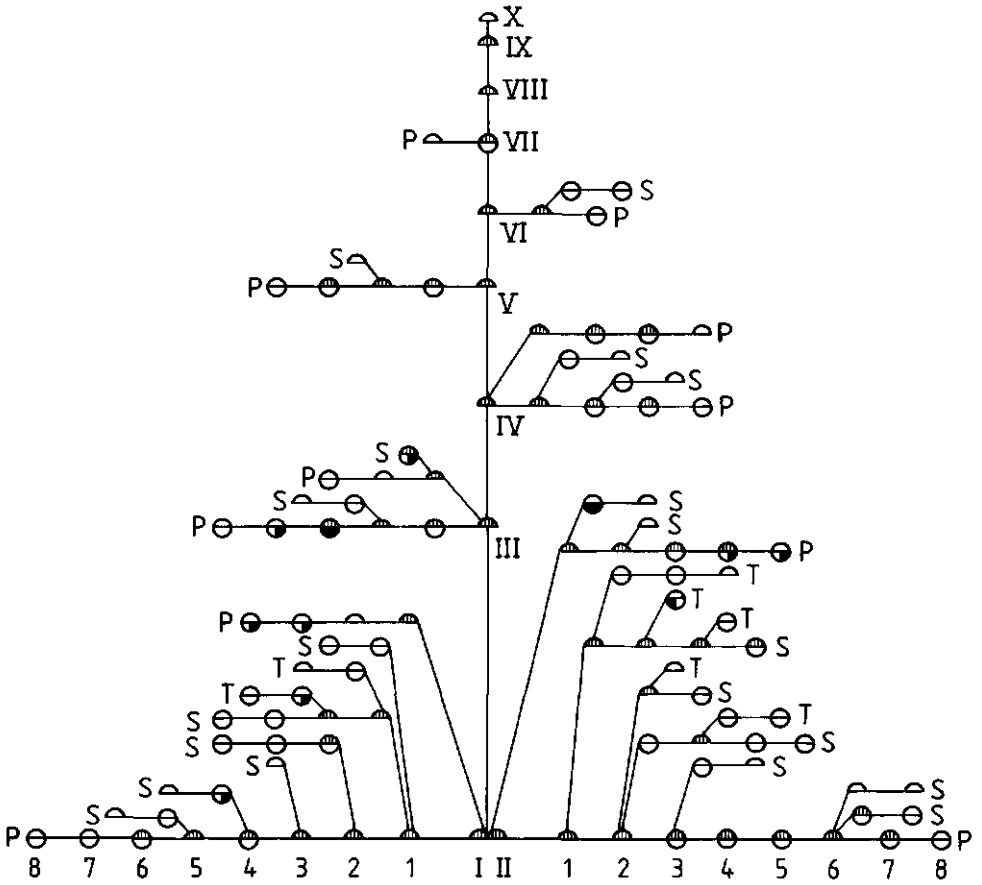

Figure 5.1. Example of a schematic drawing of the habit of a bambara groundnut plant (in this case of a plant transferred after 41 days from a 14-h to an 11-h photoperiod). Roman numerals indicate node number on main axis, Arabic numerals indicate node number on the first two primary branches and letters indicate branch order: primary (p), secondary (s) or tertiary (t). Symbols are used for a node without (⌓) or with a leaf (⌓), with ovaries and without (⊖) or with a leaf (⊖), and without a leaf with one (⊖) or two full-grown pods (⊖), and with a leaf and one (⊖) or two (⊖) full-grown pods.

The rate of leaf development was similar for all treatments before the onset of flowering. The following linear relation, based on counts of leaf numbers on 23, 37 and 51 days after sowing, describes the rate of leaf development during this period: -14.2 + 0.78 t (r^2 = 0.96), in which t is the period from sowing in days. In other words, 'Ankpa 4' produced three leaves every four days during the first 51 days after sowing.

Table 5.1. Growth characteristics of bambara groundnut, genotype 'Ankpa 4' from Nigeria (averages per plant of three progenies) for treatments that received 21, 28, 41 or 54 days under a 14-h photoperiod before transference to an 11-h photoperiod.

	days under a 14-h photoperiod				
	21	28	41	54	S.E. (6 d.f.)
onset of flowering (days after sowing)	49.7 a	51.5 a	61.9 b	71.3 c	1.32
period between transference and onset of flowering (days)	28.7 a	23.5 b	20.9 b	17.3 c	1.32
no. of leaves at the onset of flowering	23.7 a	25.6 a	35.2 b	40.8 c	1.39
no. of leaves at harvest	44.2 a	44.8 a	45.7 a	53.1 a	3.63
no. of pods	4.1 a	4.7 a	6.7 a	7.2 a	1.60
total seed dry weight (g)	1.00 a	1.36 ab	2.50 b	2.70 b	0.580
average seed dry weight (g)	0.24 a	0.29 ab	0.37 bc	0.38 c	0.036
total dry matter, excl. roots (g)	9.5 a	10.3 a	11.5 a	13.0 a	1.55
harvest index	0.10 a	0.13 ab	0.22 c	0.21 bc	0.036
no. of primary branches	13.7 b	14.5 a	12.8 c	12.4 c	0.27
no. of secondary branches	18.0 a	19.1 a	16.8 a	18.5 a	2.73
no. of tertiary branches	2.5 a	2.3 a	2.2 a	2.5 a	0.72

Means within a row with the same letter do not differ significantly (P = 0.05).

At the final harvest, similar numbers of leaves per plant were found for all treatments (Table 5.1). On average, a plant had 47 leaves. Therefore the plants which spent 21 or 28 days in the 14-h photoperiod produced more leaves per plant in the period between the onset of flowering and harvest than the plants which spent 41 or 54 days in the 14-h photoperiod. The number of days used for the production of one leaf in the period between flowering and harvest were: 4.2, 4.3, 7.0 and 5.2 days for plants which were transferred after 21, 28, 41 and 54 days, respectively. One of the progenies had fewer leaves than the two other progenies (Table 5.2).

Table 5.2. Growth characteristics of three bambara groundnut progenies from genotype 'Ankpa 4', Nigeria (averages per plant of four daylength treatments).

	progeny			
	1	2	3	S.E. (16 d.f.)
onset of flowering (days after sowing)	55.8 a	59.0 b	60.9 c	0.58
period between transference and onset of flowering (days)	19.8 a	23.0 b	24.9 c	0.58
no. of leaves at the onset of flowering	30.2 a	29.6 a	34.2 b	0.88
no. of leaves at harvest	48.0 b	44.6 a	48.4 b	1.26
no. of pods	5.2 a	6.0 a	5.8 a	0.48
total seed dry weight (g)	1.80 a	2.05 a	1.83 a	0.313
average seed dry weight (g)	0.33 a	0.33 a	0.31 a	0.040
total dry matter, excl. roots (g)	11.0 a	10.8 a	11.4 a	0.41
harvest index	0.15 a	0.18 a	0.16 a	0.015
no. of primary branches	14.0 a	12.4 b	13.8 a	0.34
no. of secondary branches	16.3 a	18.7 b	19.2 b	1.02
no. of tertiary branches	1.4 a	3.2 b	2.5 ab	0.53

Means within a row with the same letter do not differ significantly ($P = 0.05$).

Yield characteristics. The total seed dry weight per plant was higher for plants transferred after 41 and 54 days than for plants transferred after 21 days (Table 5.1). Plants transferred after 28 days gave an intermediate value. No statistically significant differences were found between treatments for the number of pods per plant, but the trend was for number of pods to increase concomitantly with the number of days under the 14-h photoperiod. The average seed dry weight was again higher for plants transferred after 41 and 54 days than for plants transferred after 21 days. The average seed dry weight for plants transferred after 28 days was intermediate. No differences were found between progenies for total seed dry weight and number of pods per plant, nor for the average seed dry weight (Table 5.2).

Dry matter production and harvest index. Differences between treatments in total aboveground dry matter per plant were not statistically significant (Table 5.1). However, the total aboveground dry matter per plant tended to increase with the period that plants were under the 14-h photoperiod before transference to the 11-h photoperiod (Table 5.1). The harvest index (seed dry weight/total dry matter) of plants transferred after 41 and 54 days was more than twice the value obtained for plants transferred after 21 days (Table 5.1). An intermediate value was found for plants transferred after 28 days. Progenies did not differ in total aboveground dry matter nor in the harvest index (Table 5.2).

Number of primary, secondary and tertiary branches. The number of primary branches per plant differed between treatments (Table 5.1). The highest number was found for plants transferred after 28 days. The lowest values were for plants transferred after 41 and 54 days. Plants transferred after 21 days had an intermediate number of primary branches per plant. No differences between treatments were found for the number of secondary and tertiary branches per plant. On average, plants had about 18 secondary and 2.5 tertiary branches each.

Progenies differed in the number of primary, secondary and tertiary branches per plant. Progeny three had relatively high numbers in all three classes of branches. Progeny one combined a high number of primary branches with low numbers of secondary and tertiary branches, whereas progeny two had the opposite: a low number of primary branches with high numbers of secondary and tertiary branches.

Position of the first flowers. Seedlings have two leaves: one on the first and one on the second node of the main axis. These nodes are so close that their order cannot be determined macroscopically. Soon after germination the first two primary branches develop simultaneously in the axils of the two leaves on the main axis. The position of the first open flower on each of these two, equally old primary branches was

determined at the three intermediate harvests when plants of all treatments were sampled (i.e. 80, 94 and 108 days after sowing). The position of the first flower was expressed as the node number on which the flower developed, counting from the main axis. There were no differences between plants transferred after 21 or 28 days (Table 5.3): on average, the first flowers developed on node 2.9 from the main axis in plants transferred after 21 days and on node 3.3 in plants transferred after 28 days. Plants transferred later, produced their first open flower on a higher node number, i.e. further from the main axis: transferring plants after 41 and 54 days caused differences of 1.0 and 2.4 nodes, respectively, in the position of the first flower, compared with plants transferred after 28 days. There were no differences between progenies in the position of the first open flower.

Once flowering had started, plants produced a pedunculus with two flowers at every node that subsequently developed. Thus, all plants produced many ovaries.

Table 5.3. Average node number on which the first open flower developed on the first two branches on the main axis of bambara groundnut plants (averages of three progenies) that received 21, 28, 41 and 54 days under a 14-h photoperiod before transference to an 11-h photoperiod.

	days under a 14-h photoperiod				
	21	28	41	54	S.E. (6 d.f.)
average node number	2.9 a	3.3 a	4.3 b	5.7 c	0.30

Means within a row with the same letter do not differ significantly ($P = 0.05$).

Distribution of pods along the main axis. Most (79-91%) pods were produced on branches that developed on nodes 1 - 4 of the main axis (Table 5.4). The fractional distribution of pods along the main axis (expressed as the total number of pods produced on the branches of a node on the main axis divided by the total number of pods per plant) indicated no differences for plants transferred after 28 or more days. Only plants that were transferred after 21 days had a somewhat different pod distribution: they had a higher fraction of pods on nodes 1 and 2 than plants

transferred after 28 days, whereas the fraction on node 3 was less than that of all other treatments. In general, the fraction of pods decreased as the node number on the main axis increased, except in plants that were transferred after 21 days.

Differences between progenies were found in two instances: the fraction of pods of progeny 1 on node 3 (0.12) was smaller than that of progenies 2 and 3 (0.20 and 0.21, respectively), and the fraction of pods of progeny 2 on node 5 (0.03) was smaller than that of progenies 1 and 3 (0.14 and 0.11, respectively).

Table 5.4. Distribution of pods along the main axis (expressed as the total number of pods produced on the branches of a node on the main axis divided by the total number of pods per plant) for bambara groundnut plants (averages of three progenies) that received 21, 28, 41 or 54 days under a 14-h photoperiod before transference to an 11-h photoperiod.

	days under a 14-h photoperiod				
node number on main axis	21	28	41	54	S.E. (6 d.f.)
1 and 2[1)]	0.63 a	0.50 b	0.61 ab	0.55 ab	0.050
3	0.08 a	0.22 b	0.18 b	0.22 b	0.034
4	0.08 a	0.14 a	0.12 a	0.13 a	0.039
5	0.14 a	0.09 a	0.07 a	0.06 a	0.048
6	0.05 a	0.03 a	0.02 a	0.03 a	0.024
7 and up	0.02 a	0.02 a	0.01 a	0.01 a	0.010

Means within a row with the same letter do not differ significantly ($P = 0.05$).

1) No distinction between branches from nodes 1 and 2 was possible, because they developed simultaneously.

Position of pods on the branches. Branches that developed on nodes 1 and 2 of the main axis could be divided into five groups: (1) the first two primary branches of similar age, (2) their secondary branches, (3) 1-4 primary branches that formed later,

(4) their secondary branches and (5) a few tertiary branches. All treatments and progenies had a similar fraction of pods in each of these five groups of branches: on average, 0.16 of the pods that developed on the branches of nodes 1 and 2 on the main axis occurred on the first two primary branches, 0.41 on their secondary branches, 0.22 on the later-formed primary branches, 0.14 on their secondary branches and 0.07 on tertiary branches.

The distribution of the pods on the first two primary branches was calculated as the number of pods on a node divided by the total number of pods on these two primary branches (Fig. 5.2). Treatment effects were found for the fraction of pods on nodes 4 and 7. Plants transferred after 21 and 28 days had a larger fraction of pods on nodes 4 than plants transferred after 41 and 54 days. A greater fraction of pods on nodes 7 was found in plants transferred after 21 and 54 days than in plants transferred after 41 days. Plants transferred after 28 days had an intermediate value.

Differences appeared in the way that the pods were distributed over the first two primary branches. The pod distribution pattern for plants transferred after 21 days showed two peaks: the first on node 4 and the second on nodes 6 and 7 (Fig. 5.2 A). Plants transferred after 28 days had a fairly even pod distribution with similar fractions on nodes 4 up to 8 (Fig. 5.2 B). The pod distribution patterns of plants transferred after 41 and 54 days peaked sharply: on nodes 5 and 6 for plants transferred after 41 days and on nodes 6 and 7 for plants transferred after 54 days (Figs 5.2 C, D).

The comparisons of positions of pods on other primary branches and on the secondary branches gave no unambiguous pod distribution patterns.

5.4 Discussion

Induction of flowering. Plants transferred after 28 or more days from the 14-h to the 11-h photoperiod flowered sooner the earlier they were transferred. There was no difference, however, in the onset of flowering between plants that had received 21 or 28 days under 14-h photoperiod before transference: plants of the progenies used seem to have a juvenile phase during which flowering cannot be induced by an 11-h photoperiod. According to Summerfield and Wien (1980), most tropical grain legumes have no pre-inductive (juvenile) phase for flowering. The bambara groundnut progenies in this experiment would therefore be exceptions, like, for example, the four soya bean cultivars investigated by Collinson *et al.* (1993), which had a juvenile phase which varied from 11 to 33 days.

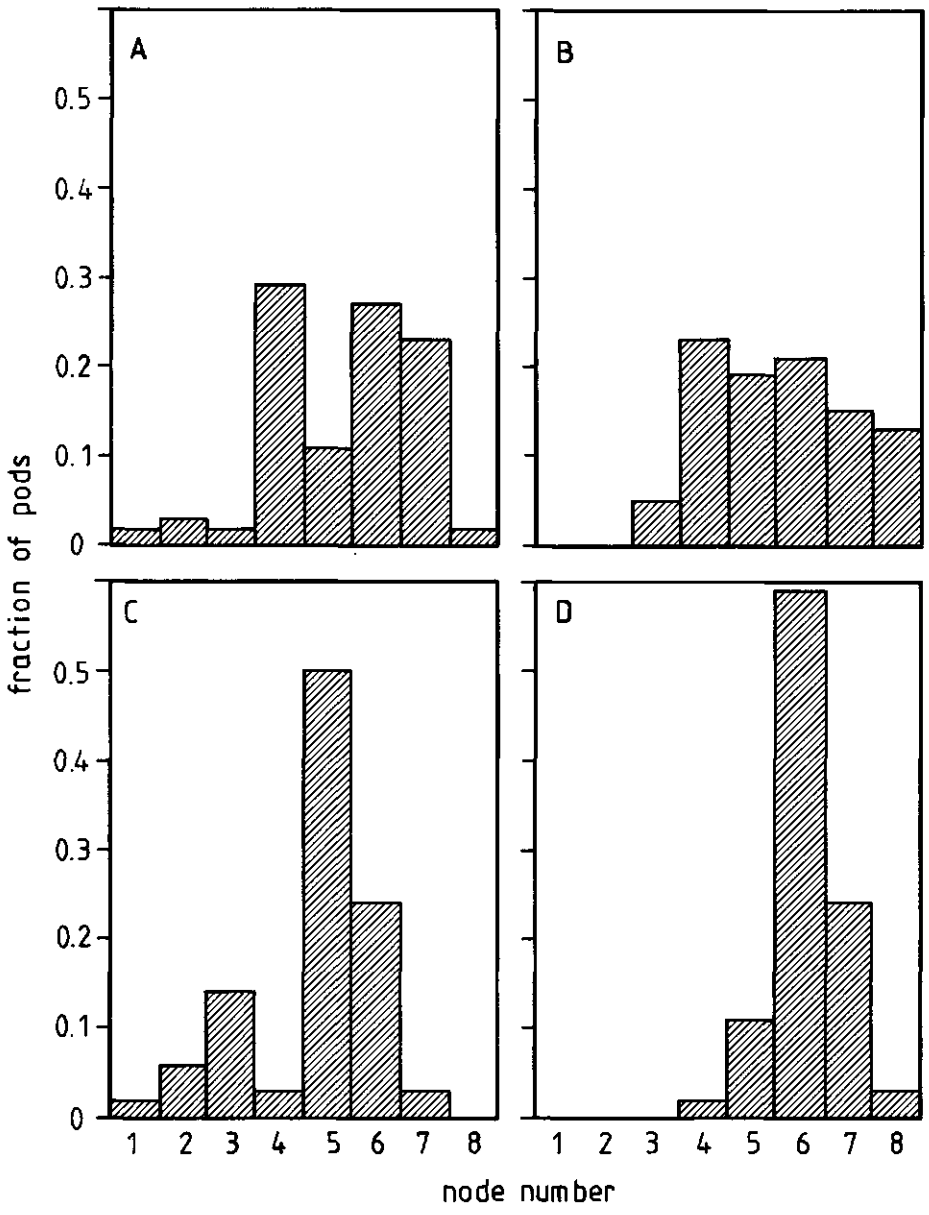

Figure 5.2. Fractional distribution of the pods over the nodes of the first two primary branches that developed on nodes 1 and 2 of the main axis for plants that were transferred from a 14-h to an 11-h photoperiod after 21 (A), 28 (B), 41 (C) and 54 days (D).

The length of the sojourn in the 14-h photoperiod affected the onset of flowering (Table 5.1). This small inductive effect of the 14-h photoperiod accumulates over time, thus shortening the period necessary under the 11-h photoperiod to induce flowering. This corroborates Roberts and Summerfield (1987) who state that, in short-day plants, any photoperiod longer than the base photoperiod can have some inductive effect, at least up to the ceiling photoperiod.

Vegetative features. Plants transferred after 21 or 28 days had 25 leaves at the onset of flowering. The number of leaves at the onset of flowering increased when plants remained for a longer period under 14-h photoperiod before transference to the 11-h photoperiod. As the leaf area per plant increased with the number of leaves, plants with a later onset of flowering had a larger leaf area. These plants therefore had a greater capacity to produce assimilates which could be used for reproductive and continued vegetative growth. This hypothesis is supported by the fact that the total aboveground dry matter per plant tended to increase concomitantly with the length of the period that plants were in the 14-h photoperiod before transference.

Yield characteristics. Number of pods per plant tended to increase with the number of days under the 14-h photoperiod. A similar increase was found for the total seed dry weight per plant and the average seed dry weight. In combination with the findings on treatment-induced differences in leaf numbers at flowering and total aboveground dry matter, these results lead to the conclusion that early induction causes plants to use assimilates for early reproductive growth, at the expense of continued vegetative growth and of total seed yields per plant. An early start of reproductive growth is therefore only a sound strategy in areas where the duration of the growing season is limited, e.g. by water shortage.

Position of flowers and pods. There was no difference in the position of the first open flower on the first two primary branches for plants transferred after 21 and 28 days. This position, at about node number 3, is apparently the minimal distance between the main axis and the first node to flower. The position of the first open flower shifted towards the tips of the branches when plants spent more time under the 14-h photoperiod before transference to the 11-h photoperiod. Roughly, this shift was one node per additional fortnight under the 14-h photoperiod. This shift is in accordance with Wallace (1985) who states that one of the ways temperature and/or photoperiod can modulate time to flowering is by causing a different node to flower.

No differences in the fractional distribution of pods along the main axis were found in plants transferred after 28 or more days (Table 5.4). Differences in the total

number of pods per plant between these treatments were therefore evenly distributed over the branches that developed on the different nodes of the main axis.

The pods on the primary branches were located nearer the tips of the branches in plants that were transferred late, i.e. after 41 or 54 days (Fig. 5.2). Moreover, the pods produced by these plants were more concentrated on a small number of nodes on the primary branches than pods of plants transferred after 21 and 28 days. Pods therefore develop and mature more evenly if plants are transferred late to the inductive 11-h photoperiod, than if plants are transferred early.

Materials and methodology. In a future experiment to investigate the position of pods it would be preferable to use an accession that produces more pods per plant. However, when selecting this accession it must be taken into account that number of pods per plant is probably correlated with sensitivity to photoperiod: personal observations indicate that the more photoperiod-sensitive genotypes tend to have fewer large pods, whereas photoperiod-insensitive genotypes have many small pods.

The results obtained with the three progenies in this experiment are probably not representative for genotype 'Ankpa 4' as a whole. For instance, the three progenies flowered later than genotype 'Ankpa 4' did in previous experiments (Linnemann 1993, submitted). However, the fact that the results from the three progenies are not typical of genotype 'Ankpa 4', does not invalidate the conclusion from this experiment that early induction of photoperiod-sensitive bambara groundnut accessions leads to lower total seed yields per plant and more uneven maturity than late induction.

Chapter 6

Effects of temperature and photoperiod on phenological development in three genotypes of bambara groundnut (*Vigna subterranea*)

Abstract. Factorial combinations of four photoperiods (10, 11.33, 12.66 and 16 hd^{-1}) and three mean diurnal temperatures (20.2, 24.1 and 28.1 °C) were imposed on nodulated plants of three Nigerian bambara groundnut genotypes (*Vigna subterranea* (L.) Verdc., syn. *Voandzeia subterranea* (L.) Thouars) grown in glasshouses in The Netherlands. The photothermal response of the onset of flowering and the onset of podding were determined. The time from sowing to first flower (f) was determined by noting the day on which the first open flower appeared. The time taken to pod (p) was estimated from linear regressions of pod dry weight against time from sowing. Developmental rates were derived from the reciprocals of f and p. In two genotypes, 'Ankpa 2' and 'Yola', flowering occurred irrespective of photoperiod and $1/f$ was controlled by temperature only, occurring sooner at 28.1 than at 20.2 °C. The third genotype, 'Ankpa 4', was sensitive to temperature and photoperiod and f was increased by cooler temperatures and photoperiods $>$ 12.66 hd^{-1} at 20.2 °C and $>$ 11.33 hd^{-1} at 24.1 and 28.1 °C. In contrast, p was affected by temperature and photoperiod in all three genotypes. In bambara groundnut photoperiod-sensitivity therefore increases between the onset of flowering and the onset of podding. The most photoperiod-sensitive genotype with respect to p was 'Ankpa 4', followed by 'Yola' and 'Ankpa 2'. There was also variation in temperature-sensitivity between the genotypes investigated. Evaluation of bambara groundnut genotypes for adaptation to different photothermal environments will therefore require screening for flowering and podding responses.

6.1 Introduction

Bambara groundnut (*Vigna subterranea* (L.) Verdc., syn. *Voandzeia subterranea* (L.) Thouars), a pulse with subterranean fruit-set, is cultivated by smallholders over much of semi-arid Africa (Linnemann and Azam-Ali, 1993). Under less favourable growing conditions, such as limited water supply and infertile soil, it yields better than other legumes, for example, groundnut (*Arachis hypogaea* L.) (National Research Council, 1979). Average yields are low, ranging from 650 to 850 kg ha^{-1} (Stanton *et al.*, 1966). Efforts are therefore being made to raise yields by breeding and improved cultural practices.

The recognition of the influence of temperature and photoperiod on crop development has led to the demand for inexpensive and rapid screening methods to establish the response of newly collected or developed plant materials over a wide range of environmental conditions. The ensuing research on grain legumes has focused on a methodology to predict the time taken to flower. Analyses of experimental observations have shown the advantages of using the developmental rate for flowering ($1/f$, defined as the reciprocal of the number of days until the first flower opens) instead of the actual time to flowering (f) (Roberts and Summerfield, 1987; Summerfield *et al.*, 1993). Summerfield *et al.* (1991) have shown that the response of $1/f$ to temperature and photoperiod can be quantified in a wide range of tropical and temperate species by a model incorporating three response planes: a thermal, photothermal and a plane of maximum delay (Fig. 6.1).

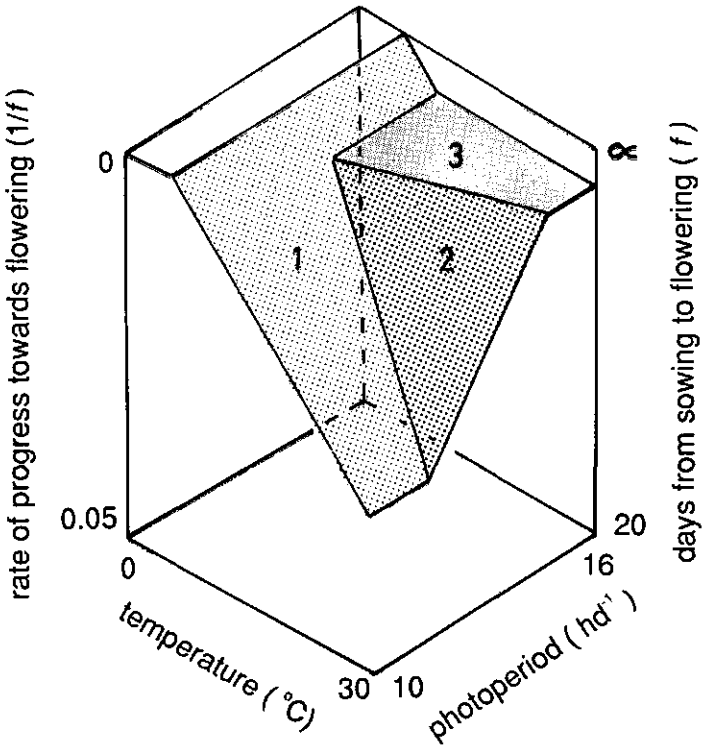

Figure 6.1. A hypothetical example of the general photothermal model describing the effects of temperature and photoperiod on days from sowing to flowering (f) and $1/f$ in a short-day plant. 1, thermal plane; 2, photothermal plane; 3, plane of maximum delay.

In genotypes that are insensitive to photoperiod, and in photoperiod-sensitive genotypes growing in photoperiods below the critical photoperiod (P_c, that photoperiod above which flowering is delayed in short-day plants (SDP)), when mean temperature (T, °C) is between the base (T_b) and optimum (T_o) temperature, then $1/f$ is given by:

$$1/f = a + bT \quad [1]$$

where a and b are genotype-specific constants. This is the thermal plane.

In photoperiod-sensitive genotypes when photoperiod is above P_c (for SDP), then $1/f$ is affected by temperature and photoperiod and is given by:

$$1/f = a' + b'T + c'P \quad [2]$$

where P is mean photoperiod (hd^{-1}) and a', b' and c' are genotype specific constants. This is the photothermal plane. In some genotypes of cowpea (*Vigna unguiculata* (L.) Walp.) (e.g. TVu 1188: Hadley *et al.*, 1983) there is no thermal response within the photothermal plane and a special form of equation 2 applies:

$$1/f = a' + c'P \quad [3]$$

The intersection of the thermal and photothermal plane is the P_c, which usually varies with temperature and is given by:

$$P_c = [(a-a') + (b-b')T] / c' \quad [4]$$

where a, a', b, b' and c' are genotype-specific constants from equations 1 and 2.

The upper boundary of the photothermal plane is the ceiling photoperiod (P_{ce}), above which in SDP neither temperature nor photoperiod affect $1/f$ and therefore:

$$1/f = d' \quad [5]$$

where d' is a genotype-specific constant. This is the plane of maximum delay.

Preliminary observations on the photoperiodic regulation of phenological development in bambara groundnut, revealed marked differences in response to photoperiod (Linnemann, 1991). In a photoperiod-sensitive genotype from Ankpa, Nigeria, for instance, development under photoperiods of 14 hd^{-1} or longer was delayed compared to that under photoperiods of 13 hd^{-1} or less (Linnemann, 1993). The onset of flowering, progress of flowering, the onset of podding and progress in pod growth were all retarded, but the effect on podding was greater than on flowering: some plants failed to produce pods under photoperiods of 14 and 16 hd^{-1}, even though they had flowered profusely and had produced large numbers of fertilized ovaries.

In the work reported in this paper three genotypes of bambara groundnut from Nigeria were grown in factorial combinations of four photoperiods and three

temperature regimes. Photothermal effects on days from sowing to flowering and podding were investigated using the model outlined above.

6.2 Materials and methods

Environmental conditions. Factorial combinations of four photoperiods (10, 11.33, 12.66 and 16 hd^{-1}) and three mean diurnal temperatures of 20.2, 24.1 and 28.1 °C (provided by day/night temperature regimes of 22/18, 26/22 and 30/26 °C) were imposed on nodulated plants of three bambara groundnut genotypes at the Centre for Plant Breeding and Reproduction Research in Wageningen, The Netherlands (51°58' N). However, technical malfunction during the experiment caused the loss of one treatment combination (20.2 °C, 11.33 hd^{-1}). Photoperiods and temperature regimes included the most common conditions experienced by bambara groundnut in its cultivation areas (Linnemann, 1987).

Temperature regimes were assigned to three glasshouses; thus, each temperature regime occurred only once. Within each glasshouse the daylength treatments were divided over four compartments of 3.2 x 1.5 m each, accommodating 24 randomized pots of each genotype. All plants received an 8 h period of natural daylight. The total global daily radiation during this 8 h period of natural daylight averaged 1244, 1353, 1176 and 697 J cm^{-2} during June (second half only), July, August and September, respectively. Seventy-six percent of outside radiation was transmitted through the glasshouse structure. Low-intensity, fluorescent (Philips TLD 36 Watt tubes) and incandescent light (Philips 40 Watt bulbs) of 10 μmol m^{-2} s^{-1} photosynthetically active radiation (PAR, 400-700 nm) at plant height were used to achieve the desired photoperiod (Summerfield and Roberts, 1987), after separating and covering the treatments with lightproof tent-cloth (a double layer of LS100 from Ludvig Svensson Ltd Company). Thus, the differences in total PAR between treatments were negligible. Relative humidity was maintained at 60%.

Plant material and culture. The three genotypes were collected in Nigeria. Their testa colours and eye patterns are given according to the Munsell Color Charts for Plant Tissues (1972) and the bambara groundnut descriptor list (IBPGR/IITA/GTZ, 1987), respectively. A cream-coloured genotype (colour 2.5 Y 8/4) was from Yola market (9°14' N), and will be referred to as 'Yola'. Ninety percent of the seeds of this genotype had no pattern. The other 10% had a dark grey eye (colour 10 R 6/2) forming an almost triangular shape (eye pattern no. 4). The other genotypes, 'Ankpa 2' and 'Ankpa 4', were from a market in Ankpa (7°22' N). 'Ankpa 2' consisted for 93% of cream-coloured seeds (colour 2.5 Y 8/4) with a dark red, butterfly-shaped eye

(colour 5 R 3/4 and eye pattern no. 6), and contiguous dots of the same dark red colour. This seed lot also had about 7% of uniform, very dark purple (darker than colour 10 R 3/2) and brown seeds (colour 10 R 4/8). 'Ankpa 4' consisted of about 60% uniform, light brownish seeds (colours 7.5 YR 7/6 and 10 R 7/4) and about 40% uniform, dark brown seeds (colours 2.5 YR 4/6, 2.5 YR 4/8 and 10 R 3/6).

At 7°, near Yola, the monthly mean daylength (including civil twilight) varies from 12.52 hd^{-1} in June to 11.73 hd^{-1} in December, and at 9°, near Ankpa, from 12.64 hd^{-1} in June to 11.62 hd^{-1} in December (Kowal and Knabe, 1972). The most photoperiod-sensitive genotype in this experiment, 'Ankpa 4', has delayed flowering and erratic podding under photoperiods of 14 hd^{-1} or longer (Linnemann, 1993).

Seeds of uniform size were selected. The average seed weight for 'Yola', 'Ankpa 2' and 'Ankpa 4' was 800, 600 and 900 mg, respectively. Seeds were surface sterilized, sown on 15 June 1990 in trays of sand, and germinated at 28 °C. Three days later the seeds were planted in 5-l pots filled with a mixture of sand and humus-rich potting compost (1:1 v/v), at the rate of one seed per pot. They were then also inoculated with *Rhizobium* spp. strain CB 756 from the Department of Microbiology, Wageningen Agricultural University.

Data collection. The dates of the first open flower were recorded for all plants. Nine plants from each genotype x temperature x photoperiod combination were chosen at random for the final harvest on 24-26 September 1990. The remaining 15 plants per factorial combination were used for three intermediate harvests to monitor pod development. The sampling dates differed for every genotype x temperature combination; the first intermediate harvest was at about two weeks after the genotype had started to flower at that particular temperature. The second sample was harvested one week later, and the third after another two weeks for all treatments except for 'Ankpa 4' at 20.2 °C (all photoperiods); the interval between the second and the third intermediate harvest of these treatments was only one week. Dry weight of developing pods (length between 0.5 and 1.0 cm) and full-grown pods (length $\geq$ 1.0 cm) was recorded per plant at the intermediate and final harvests.

Data analysis. Average pod dry weight per plant was regressed against time for the data from the intermediate and final harvests of each treatment combination to determine the onset of podding. In some cases the relation between pod dry weight and time was not linear and therefore three instead of four points were used to determine the regression line. This was applied to factorial combinations that showed no increase in pod dry weight after the third intermediate harvest (last point ignored) and to the combinations with no pod yield during the first and second intermediate

harvests (first point ignored). With the exception of 'Ankpa 2' at 20.2 °C in the 10 hd^{-1} photoperiod regime (r^2 = 0.72), the r^2 from these linear regressions with three or four points was $\geq$ 0.90. In four exceptional cases the onset of podding could not be determined from linear regressions because pod growth rates were negligible, and the date was estimated as the date of an intermediate or the final harvest.

Subsequently, the relations between developmental rate for flowering ($1/f$) and podding ($1/p$) and mean temperature and photoperiod from sowing to flowering or podding were evaluated using equations 1 to 5. The thermal model (equation 1) was applied first. Then an iterative procedure was used to test the significance ($P \leq 0.05$) of photoperiod (equation 2) and a series of increasingly complex models thereafter based on a reduction in the residual sums of squares of the deviations of model estimates from observations (see Summerfield *et al.*, 1993). In those photothermal environments where there was no podding ('Yola' and 'Ankpa 4' in 16 hd^{-1} at 20.2, 24.1 and 28.1 °C, and 'Ankpa 4' in 12.66 hd^{-1} at 28.1 °C) an arbitrary figure of 365 days was used to enable the model to be fitted. These data do not affect the estimates of the parameters for the thermal and photothermal plane, since they all lie in the plane of maximum delay.

6.3 Results

Days to first open flower. Photoperiod had no effect on times from sowing to the appearance of the first open flower (f) in 'Ankpa 2' and 'Yola' (Table 6.1) and $1/f$ was therefore determined solely by temperature (Table 6.2). Thermal time (Θ) for f (i.e., $1/b$) and T_b (i.e., $-a/b$) were similar in 'Ankpa 2' and 'Yola', with mean values of 800 °Cd and 3.1 °C, respectively.

Days from sowing until the appearance of the first open flower was affected by both temperature and photoperiod in 'Ankpa 4' (Table 6.1). Photoperiods longer than 11.33 hd^{-1} delayed flowering at 24.1 and 28.1°C while photoperiods longer than 12.66 hd^{-1} were required to delay flowering at 20.2°C (Table 6.1). Thus P_c varied with temperature. The earliest and latest flowering times were 38 days after sowing (DAS) in 10 hd^{-1} at 28.1°C and 64 DAS in 16 hd^{-1} at 28.1 °C, respectively (Table 6.1). These responses were best described by a two plane model, with a thermal and photoperiod-sensitive plane (i.e., the temperature effect in the photothermal plane was not significant) (Table 6.2). The T_b in 'Ankpa 4' was 1.4 °C, less than for 'Yola' and 'Ankpa 2', and Θ for flowering when $P < P_c$ was 1111 °Cd. The critical photoperiod, which is where the thermal and photothermal planes meet (Fig. 6.1), varied from 14.9 hd^{-1} at 20 °C to 8.7 hd^{-1} at 29 °C (Table 6.3), inferring that

photoperiod became more limiting at warmer temperatures. There was no indication that a photoperiod of 16 hd^{-1} was above the ceiling photoperiod.

Onset of podding. In contrast to *f*, all three genotypes were sensitive to photoperiod with respect to the onset of podding (Fig. 6.2).

'Ankpa 2', the first genotype to start flowering, also produced the first pods. The onset of podding varied from 46.5 DAS in 11.33 hd^{-1} at 28.1 °C to 73.5 DAS in 16 hd^{-1} at 20.2 °C. Podding occurred sooner at 28.1 °C than 20.2 °C and sooner in short (10 and 11.33 hd^{-1}) than long ($\geq$ 12.66 hd^{-1}) photoperiods. The onset of podding in 'Ankpa 2' was therefore affected by temperature and photoperiod and could be described by a photothermal plane (Table 6.2). The onset of podding was thus hastened by warmer temperatures (*b* was positive) and delayed by photoperiod (*c'* was negative), both effects being small but significant ($P < 0.001$).

Table 6.1. Number of days from sowing to the appearance of the first open flower (± standard deviation) for three genotypes of bambara groundnut from Nigeria grown in four photoperiods and three mean diurnal temperature regimes.

Genotype	Photoperiod (hd^{-1})	Mean diurnal temperature (°C)		
		20.2	24.1	28.1
'Ankpa 2'	10	44.7±1.7	36.4±1.8	32.4±2.5
	11.33	---	35.7±1.2	31.4±2.3
	12.66	45.0±2.4	36.6±1.4	30.6±0.9
	16	48.8±2.4	36.5±1.0	30.9±1.0
'Yola'	10	50.7±6.5	38.6±1.8	34.4±1.8
	11.33	---	37.7±1.9	33.5±1.3
	12.66	48.3±3.7	39.5±2.5	34.4±2.0
	16	53.0±2.5	41.5±3.9	34.4±2.7
'Ankpa 4'	10	51.0±2.8	42.8±2.1	38.3±2.0
	11.33	---	43.3±3.0	39.1±2.6
	12.66	50.7±1.7	48.3±5.7	51.5±13.0
	16	56.3±2.9	56.0±14.6	64.4±21.4

--- Missing value due to technical failure

Table 6.2. Fitted relations between developmental rate to first flower and the onset of podding and mean temperature (T) and mean photoperiod (P) in three genotypes of bambara groundnut grown in factorial combinations of four photoperiods (10, 11.33, 12.66 and 16 hd^{-1}) and three temperatures (20, 24 and 28 °C).

Genotype	Equation fitted	n	Parameters			T_b (°C)	r^{2*} (%)
			a or a' (SE)	b or b' (SE)	c' (SE)		
First open flower							
'Ankpa 2'	$a + bT$	11	-0.0039 (0.0019)	0.0013 (0.0001)	-	3.0	96.4
'Yola'	$a + bT$	11	-0.0038 (0.0022)	0.0012 (0.0001)	-	3.2	94.5
'Ankpa 4'	$a + bT$	4	-0.0013 (0.0080)	0.0009 (0.0004)	-	1.4	82.6
	$a' + c'P$	7	0.0487 (0.0084)	_	-0.0017 (0.0003)		
Onset of podding							
'Ankpa 2'	$a' + b'T + c'P$	11	0.0161 (0.0023)	0.0005 (0.0001)	-0.0008 (0.0001)	-	91.2
'Yola'	$a + bT$	4	-0.0020 (0.0052)	0.0007 (0.0002)	-	2.9	97.4
	$a' + c'P$	7#	0.0665 (0.0055)	_	-0.0038 (0.0001)		
'Ankpa 4'	$a + bT$	4	-0.0007 (0.0021)	0.0006 (0.0001)	-	1.2	98.7
	$a' + c'P$	7#	0.1960 (0.0670)	_	-0.0108 (0.0034)		

* r^2 is for the overall model when one or two planes are fitted

\# where no podding occurred podding was assumed to start at 365 d

Table 6.3. Values of the critical photoperiod (hd^{-1}) where thermal and photoperiod-sensitive planes were identified in 'Yola' and 'Ankpa 4' at temperatures of 20, 23, 26 and 29 °C.

		Temperature (°C)			
Genotype	Character	20	23	26	29
'Ankpa 4'	$1/f$	14.9	12.8	10.8	8.7
'Yola'	$1/p$	12.6	12.0	11.4	10.7
'Ankpa 4'	$1/p$	13.2	12.5	11.8	11.1

The onset of podding was also significantly delayed by photoperiod in both 'Yola' and 'Ankpa 4', and no pods were formed at any temperature in 16 hd^{-1} photoperiods (Fig. 6.2). In both genotypes the onset of podding was hastened in short photoperiods (10 and 11.33 hd^{-1}) by warmer temperatures. In contrast, at a longer photoperiod (12.66 hd^{-1}) onset of podding was delayed by warmer temperatures (Fig. 6.2). The photothermal response of $1/p$ of both 'Yola' and 'Ankpa 4' was described by a two plane model, comprising thermal and photoperiod-sensitive planes, and therefore similar to the model used to describe flowering in 'Ankpa 4' (Table 6.2). The T_b values for f and p were similar, 3.2 and 2.9 °C in 'Yola' and 1.4 and 1.2 °C in 'Ankpa 4', respectively. 'Ankpa 4' was the most photoperiod-sensitive genotype (c' = -0.0108) followed by 'Yola' (c' = -0.0038) and 'Ankpa 2' (c' = -0.0008).

The delay in podding at higher temperatures in longer photoperiods evident in Fig. 6.2 can be attributed to P_c varying with temperature (Table 6.3). For example, in 'Ankpa 4' at 20 °C, P_c = 13.2 hd^{-1} and therefore $1/p$ in 12.66 hd^{-1} and 10 hd^{-1} is determined by temperature only and p is similar in these two photoperiod regimes. However, as temperature increases P_c decreases, such that at 26 °C P_c = 11.8 hd^{-1} and therefore photoperiods of 12.66 hd^{-1} or greater delay $1/p$.

No podding occurred at 16 hd^{-1} in any temperature: these photoperiods may have been longer than P_{ce}. More intermediate photoperiods between 12.66 hd^{-1} and 16 hd^{-1} are required to determine P_{ce}.

The relation between observed and predicted f and p is shown for the three genotypes in Fig. 6.3, and confirms that these simple linear rate models describe the responses of bambara groundnut to temperature and photoperiod well.

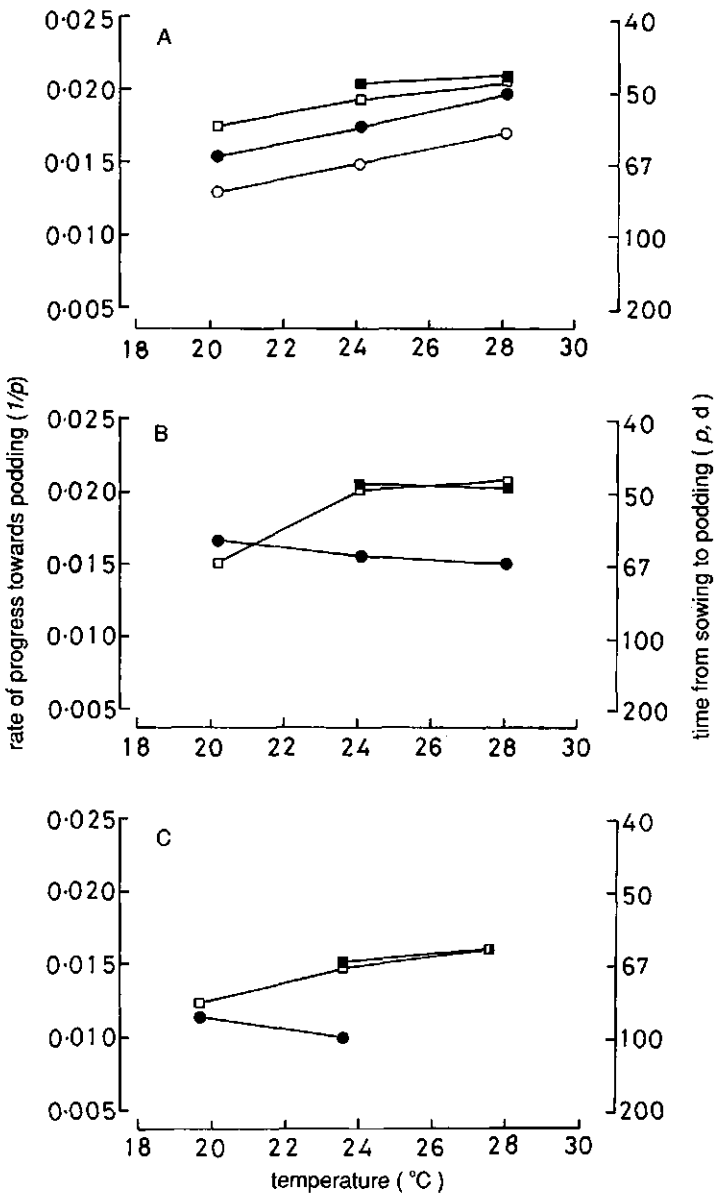

Figure 6.2. Rate of progress towards podding ($1/p$) in bambara groundnut genotypes 'Ankpa 2' (A), 'Yola' (B) and 'Ankpa 4' (C) as affected by temperature under photoperiods of 10 (□), 11.33 (■), 12.66 (●) and 16 hd^{-1} (○).

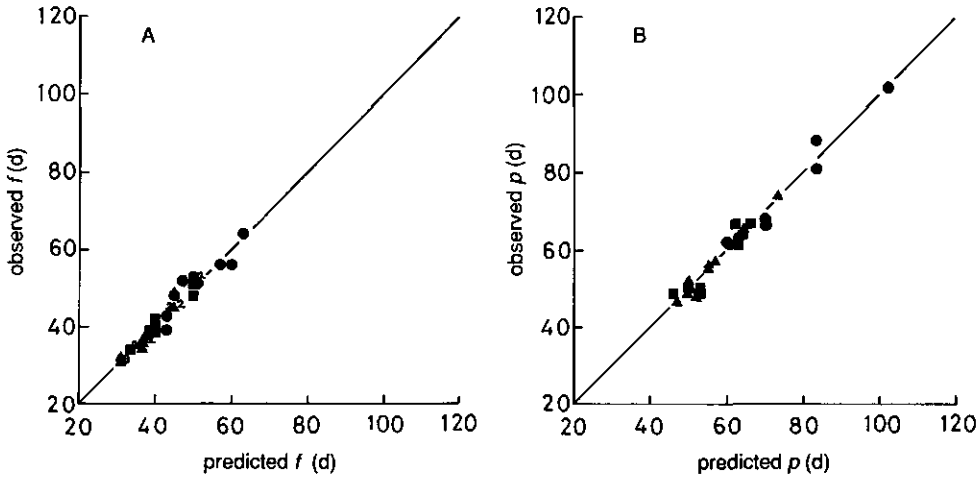

Figure 6.3. Relation between observed and predicted times to first flowering (A) and to podding (B) in 'Ankpa 2' (▲), 'Yola' (■) and 'Ankpa 4' (●) using the equations and parameter values given in Table 6.2. Diagonal line shows perfect agreement between observed and predicted values.

6.4 Discussion

Research methodology. The onset of flowering could be determined quickly and accurately in a large number of plants by recording the day of the first open flower. The standard deviation of the average number of days from sowing to the first open flower was less than $\pm$ 4 days for all but five treatments (Table 6.1). The standard deviation was particularly large for 'Ankpa 4' under 12.66 hd^{-1} at 28.1 °C and under 16 hd^{-1} at 24.1 and 28.1 °C. Genetic differences within the population apparently manifest themselves under conditions that retard flowering.

It was more difficult to assess the onset of podding, because the pods develop underground. As the pods develop in a different layer of soil than the roots, it should be possible to remove the soil regularly to monitor pod development. Although this method would yield accurate data it was rejected in our study, because the effects of soil disturbance on pod development are unknown. The sampling method we used has other disadvantages: (1) it requires large numbers of plants for destructive harvesting, (2) it is labour-intensive, and (3) data on pod growth have to be used to deduce the onset of podding.

It is also apparent that in the most photoperiod-sensitive genotypes, 'Yola' and 'Ankpa 4', a photoperiod of 16 hd^{-1} was too inhibitory to pod production. An additional intermediate photoperiod of 14 hd^{-1} would be more appropriate for determining the effects of photoperiod and temperature on podding.

Photothermal response of flowering and podding. The results of this experiment demonstrate that bambara groundnut genotypes which are insensitive to photoperiod with respect to flowering, 'Ankpa 2' and 'Yola', are not necessarily insensitive to photoperiod for all phases of their development, and that there are significant effects of photoperiod on the period between flowering and podding. Harris and Azam-Ali (1993) have reported a similar response from a Zimbabwean bambara groundnut grown at twenty weekly sowings in Botswana. It always flowered approximately 48 DAS but the number of days to first podding varied from 52 to 98 DAS, depending on photoperiod, which varied from 12.6 to 13.7 hd^{-1}. Flower, peg and pod production in groundnuts are also affected by photoperiod (Flohr *et al.*, 1990). However, in cowpea no such differential effects of photoperiod on the onset of flowering and pod maturity have been found (Hadley *et al.*, 1983).

The estimated T_b values in the three bambara groundnut genotypes reported here, between 1.9 and 3.2 °C, are also much lower than in cowpea, where values of 8 to 10 °C have been reported (Hadley *et al.*, 1983). The estimation of T_b in the present study entailed considerable extrapolation (the lowest temperature used was 20 °C) and should be regarded with caution.

This paper shows that the influence of temperature and photoperiod on flowering and podding can be evaluated using the three-plane model of Roberts and Summerfield (1987) and Summerfield *et al.* (1991). These models successfully identified and described differences in thermal- and photoperiod-sensitivity for flowering and podding. However, more effective, and ideally non-destructive, methods to determine the onset of podding are required before large-scale screening of podding can be carried out.

In summary, photoperiod-sensitivity in bambara groundnut increases between the appearance of the first open flower and the onset of podding, irrespective of whether genotypes were insensitive or sensitive to photoperiod with respect to flowering. Furthermore, there was variation in temperature- and photoperiod-sensitivity between the genotypes investigated.

Chapter 7

Photoperiod regulation of development and growth in bambara groundnut (*Vigna subterranea*)

Abstract. The influence of constant photoperiods of 10, 12, 14 and 16 h on development and growth in two bambara groundnut genotypes (*Vigna subterranea* (L.) Verdc., syn. *Voandzeia subterranea* (L.) Thouars) was studied in a greenhouse experiment in the Netherlands. Data on dry matter accumulation were collected by sequential harvesting. Photoperiod influenced the onset of flowering in one genotype ('Ankpa 4') and the onset of podding in both ('Tiga Nicuru' and 'Ankpa 4'). Under 14 and 16-h photoperiods plants of 'Ankpa 4' produced no pods. Photoperiod did not influence total aboveground dry matter production per plant in 'Ankpa 4' and had only a slight effect on 'Tiga Nicuru'. Photoperiod indirectly affected dry matter partitioning via its influence on development: in both genotypes assimilate distribution changed after the photoperiod-induced onset of podding. In addition, a direct influence of photoperiod on partitioning was observed. Firstly, just after the onset of flowering (40 DAS), 'Tiga Nicuru' plants under 10 and 12-h photoperiods had accumulated more dry matter as leaf blades and less as stem material than plants under 14 and 16-h photoperiods. Secondly, for plants of 'Ankpa 4' the increase in pod dry weight per plant under the 10-h photoperiod was nearly double the increase under the 12-h photoperiod. This difference was associated with a smaller number of developing pods under the 12-h photoperiod. Photoperiod apparently strongly affects the number of developing sinks and, as a consequence, the total sink-strength of the plant, irrespective of the numerous ovaries present on plants of all treatments (including plants of 'Ankpa 4' under 14 and 16-h photoperiods).

7.1 Introduction

Bambara groundnut (*Vigna subterranea* (L.) Verdc., syn. *Voandzeia subterranea* (L.) Thouars) is a leguminous food crop which is cultivated for its subterranean pods (Linnemann and Azam-Ali, 1993). Among the grain legumes of the African lowland tropics, bambara groundnut ranks third in terms of annual production, after groundnut (*Arachis hypogaea* L.) and cowpea (*Vigna unguiculata* (L.) Walp.) (Rachie and Silvestre, 1977). Cultivation of bambara groundnut is of particular importance in semi-arid areas, where the crop has a distinct agro-ecological niche: adverse growing conditions, such as limited water availability and low soil fertility, depress yields to

a less extent than in other legumes, for instance, groundnut (National Research Council, 1979). This stability of production (at a low absolute level) explains the popularity of the crop in subsistence farming: growers prefer the certainty of a comparatively low yield of bambara groundnuts to the chance of a high yield of e.g. groundnuts in a favourable year.

There are bambara groundnut breeding programmes and research into improved cultural practices to increase and stabilize yields in West (e.g. Goli and Ng, 1988; Tanimu and Yayock, 1990) and Southern Africa (e.g. Msekera Regional Research Station, 1989; Swanevelder, 1991). However, the impact of these efforts has been restricted by the limited knowledge on the crop's ecophysiological requirements. For instance, it is essential to understand crop phenology, i.e. crop development in relation to biophysical conditions and changes in season, for the goal-oriented selection of well-adapted genotypes and the identification of optimal planting times.

The phenological development of bambara groundnut has been studied since 1986 at Wageningen Agricultural University. Genotypes with varying degrees of photoperiod sensitivity have been identified (Linnemann, 1991); the least sensitive genotype, 'Tiga Nicuru', was photoperiod-insensitive for the onset of flowering, with a quantitative short-day response for the onset of podding, and the most sensitive genotype, 'Ankpa 4', was photoperiod-sensitive for the onset of flowering and of podding. Moreover, under photoperiods of 14 h or longer progress in flowering and in pod growth in 'Ankpa 4' was retarded compared with photoperiods of 13 h or less (Linnemann, 1993). The delay or absence of the onset of podding in bambara groundnut genotypes could be traced to a check in the growth of fertilized ovaries.

All previous experiments focused on the influence of photoperiod (once in combination with temperature) on the phenological development of bambara groundnut (Linnemann, 1991; 1993; in press; submitted; Linnemann and Craufurd, in press). Differences in crop development, however, are inextricably related to dry matter accumulation and distribution. This paper describes an experiment in which the influence of photoperiod on dry matter partitioning of bambara groundnut genotypes 'Tiga Nicuru' and 'Ankpa 4' was studied by sequential harvesting.

7.2 Materials and methods

The experiment was conducted in a greenhouse at Wageningen Agricultural University (51°58' N), the Netherlands, with two genotypes: 'Tiga Nicuru' from Kuna (20 km NW of Macina; 14°13'N) in Mali and 'Ankpa 4' from Ankpa (7°22'N)

in Nigeria. Seeds of 'Tiga Nicuru' were the fourth generation of material collected in Mali in 1985. Seeds of 'Ankpa 4' were the first generation of the original seed lot that was collected in 1988.

The trial was conducted as a split plot experiment with three replicates. Main plot treatments were four daylengths: a constant photoperiod of 10, 12, 14 or 16 h. Each main plot was split into two for the different genotypes, which were allocated at random. The experimental set-up was a randomized complete block design with 12 main plots. A main plot consisted of a trolley carrying 34 pots, each containing one plant, i.e. 17 pots per sub plot.

Plants were grown in 5-l pots filled with a mixture of sand and humus-rich potting compost (1:1 v/v). Seed was sown on 21 May 1992. Plants received an 8-h period of natural daylight, which was extended in sheds by low-intensity, fluorescent (from Philips TLD 36 Watt tubes, colour number 83) and incandescent light (from Philips 40 Watt bulbs) of 10 μmol m^{-2} s^{-1} photosynthetically active radiation (PAR, 400-700 nm) at plant height to achieve the desired photoperiod. Thus, the differences in total PAR among treatments were negligible. Average temperatures were between 26-30 °C during the day and 22-25 °C at night. Average daily relative humidity was 60%, or less on sunny days.

The date of the first open flower was recorded for all plants. Five plants per genotype per trolley, randomly chosen at the beginning of the daylength treatments, were used for analysis at the final harvest, 124 days after sowing (DAS). To monitor plant growth and development, random samples of three plants per genotype were taken per trolley on 40, 61, 82 and 103 DAS. At the intermediate and final harvests, leaf area per plant was determined (using a LiCor area meter Model 3100), as well as dry weights of leaf blades, stem material (petioles and branches) and developing and full-grown pods ($\geq$ 0.5 cm) after drying for at least 24 h at 105 °C. Root weight per plant could not be determined; the roots of bambara groundnut are so thin and fragile that it is extremely difficult to rinse them without losing parts of them.

Onset of podding was determined as in Linnemann and Craufurd (submitted), by plotting average pod dry weight per plant (y-axis) against time (x-axis) for the data from certain intermediate and final harvests. The intersection with the x-axis determined by linear regression is defined as the onset of podding. Data from 82, 103 and 124 DAS were used to assess the onset of podding in all genotype x photoperiod combinations that produced pods. Data from 61 DAS were included in the regression only for plants of 'Tiga Nicuru' under 10 and 12-h photoperiods.

Analysis of variance was with the procedure ANOVA of SAS (Statistical Analysis System). Analysis of the influence of photoperiod in the split plot set-up revealed a statistically significant interaction between daylength (main factor) and genotype (split factor) for the plant characteristics studied. Since we were mainly interested in the effect of daylength, analysis was conducted per genotype and these data are presented. Mean separation was by Student's t-test.

7.3 Results

Onset of flowering and podding. On average the onset of flowering started 35 DAS in 'Tiga Nicuru', irrespective of photoperiod treatment (Table 7.1). About ten days later plants of 'Ankpa 4' under 10 and 12-h photoperiods opened their first flower. Longer photoperiods delayed flowering in 'Ankpa 4': plants under a 16-h photoperiod needed 40 days more for the onset of flowering than plants under 10 or 12-h photoperiods.

Table 7.1. Number of days from sowing to the first open flower and to the onset of podding for two genotypes of bambara groundnut at constant photoperiods of 10, 12, 14 and 16 h.

	photoperiod (h)				
	10	12	14	16	LSD (0.05)
genotype 'Tiga Nicuru'					
- flowering	36.1	35.6	34.6	34.9	N.S.
- podding	56.0	58.5	81.7	81.0	7.18
genotype 'Ankpa 4'					
- flowering	45.1	46.0	73.9	86.6	6.72
- podding	74.9	81.1	---	---	3.53

N.S.: not significant ($P = 0.05$).
---: no onset of podding

Under both a 10-h and a 12-h photoperiod, plants of 'Tiga Nicuru' started podding about 20 days after the onset of flowering (Table 7.1). Increasing the photoperiod

from 12 to 14 h delayed the onset of podding by 23 days. The increase from 14 to 16 h gave no further delay. About 46 days after the onset of flowering all plants were producing pods. In 'Ankpa 4', only two treatments produced pods during the trial period. Under a 10-h photoperiod plants started podding about 30 days after the onset of flowering, and under a 12-h photoperiod about 35 days after the onset of flowering.

Total aboveground dry matter per plant. For plants of 'Tiga Nicuru', no influence of the photoperiod treatments was found on total aboveground dry matter per plant 61, 82 and 103 DAS (Table 7.2). At the first intermediate harvest (40 DAS) plants under the 14-h photoperiod were slightly heavier than those under 10 and 12 h. At the final harvest (124 DAS) plants under 10 and 12-h photoperiods had accumulated slightly less dry matter than those under the 16-h photoperiod.

In 'Ankpa 4', total aboveground dry matter per plant during the trial period did not differ among treatments.

Table 7.2. Total aboveground dry matter per plant (g) at 40, 61, 82, 103 and 124 days after sowing (DAS) for two genotypes of bambara groundnut at constant photoperiods of 10, 12, 14 and 16 h.

	photoperiod (h)				
	10	12	14	16	LSD (0.05)
genotype 'Tiga Nicuru'					
- 40 DAS	2.7	2.7	3.2	3.0	0.40
- 61 DAS	6.5	6.6	8.1	7.5	N.S.
- 82 DAS	14.4	14.7	14.8	14.8	N.S.
- 103 DAS	16.0	18.0	20.0	19.7	N.S.
- 124 DAS	16.2	16.7	23.6	25.8	7.03
genotype 'Ankpa 4'					
- 40 DAS	3.8	4.1	4.2	4.6	N.S.
- 61 DAS	10.4	12.2	13.2	11.4	N.S.
- 82 DAS	21.2	20.4	20.2	22.7	N.S.
- 103 DAS	26.8	28.9	28.7	29.1	N.S.
- 124 DAS	31.8	32.4	31.1	33.3	N.S.

N.S.: not significant ($P = 0.05$).

Partitioning of dry matter. Plants of 'Tiga Nicuru' under the four photoperiod treatments could be divided into two groups on the basis of the aboveground dry matter partitioning (Fig. 7.1). The first group consisted of the plants under the 10 and 12-h photoperiods, and the second of the plants under 14 and 16 h. The latter group had a higher dry weight of leaf blades per plant during the later part of the growing period (from 82 DAS onwards), a higher dry weight of stem material (petioles and branches) per plant throughout the experiment, and a lower dry weight of pods during the intermediate harvests 82 and 103 DAS. At final harvest (124 DAS) the dry weight of pods per plant did not vary among treatments.

In 'Ankpa 4', differences among treatments in dry matter distribution occurred for the first time at 82 DAS: plants under 10 h differed from the others because part of the dry matter was found in the pods. At the following harvest (103 DAS) these plants had a lower dry weight of leaf blades and of stem material per plant than those under the other treatments. They also had the highest dry weight of pods per plant. Plants under the other three treatments had the same amounts of dry matter in leaf blades and stem material, but plants under 12 h had a dry weight of pods of 2.6 g per plant, whereas podding was still absent under 14 and 16 h. At final harvest, plants under 10 h had the lowest dry weights of leaf blades and stem material in combination with the highest dry weight of pods per plant. Plants under 14 and 16 h had the highest dry weights of leaf blades and stem material but no pods. Plants under 12 h occupied intermediate positions.

Number of pods per plant. Plants of 'Tiga Nicuru' only once showed a differential number of pods per plant during the trial: 82 DAS plants under 10 and 12-h photoperiods had more pods per plant than those under 14 and 16 h (Table 7.3). In 'Ankpa 4', plants under the 10-h photoperiod had consistently more pods per plant than plants under the 12-h photoperiod from 82 DAS onwards (Table 7.3).

Dry matter partitioning in relation to development. About five days after the onset of flowering in 'Tiga Nicuru' (40 DAS), the percentage of total aboveground dry matter in the leaf blades was higher for plants under 10 and 12 h photoperiods (69.4 - 70.7%) than for plants under 14 and 16 h photoperiods (65.2 - 66.4%, LSD(0.05): 2.02%) (Fig. 7.2).

Dry matter accumulated between 61 and 82 DAS was mainly (70.8 - 68.0%, LSD(0.05): 10.39%) used for pod growth in plants under 10 and 12-h photoperiods, in which podding started on 56 and 59 DAS, respectively (Fig. 7.2). In plants under 14 and 16-h photoperiods, it was used for vegetative growth: 91.9 - 94.9% was found as weight increases of leaf and stem material.

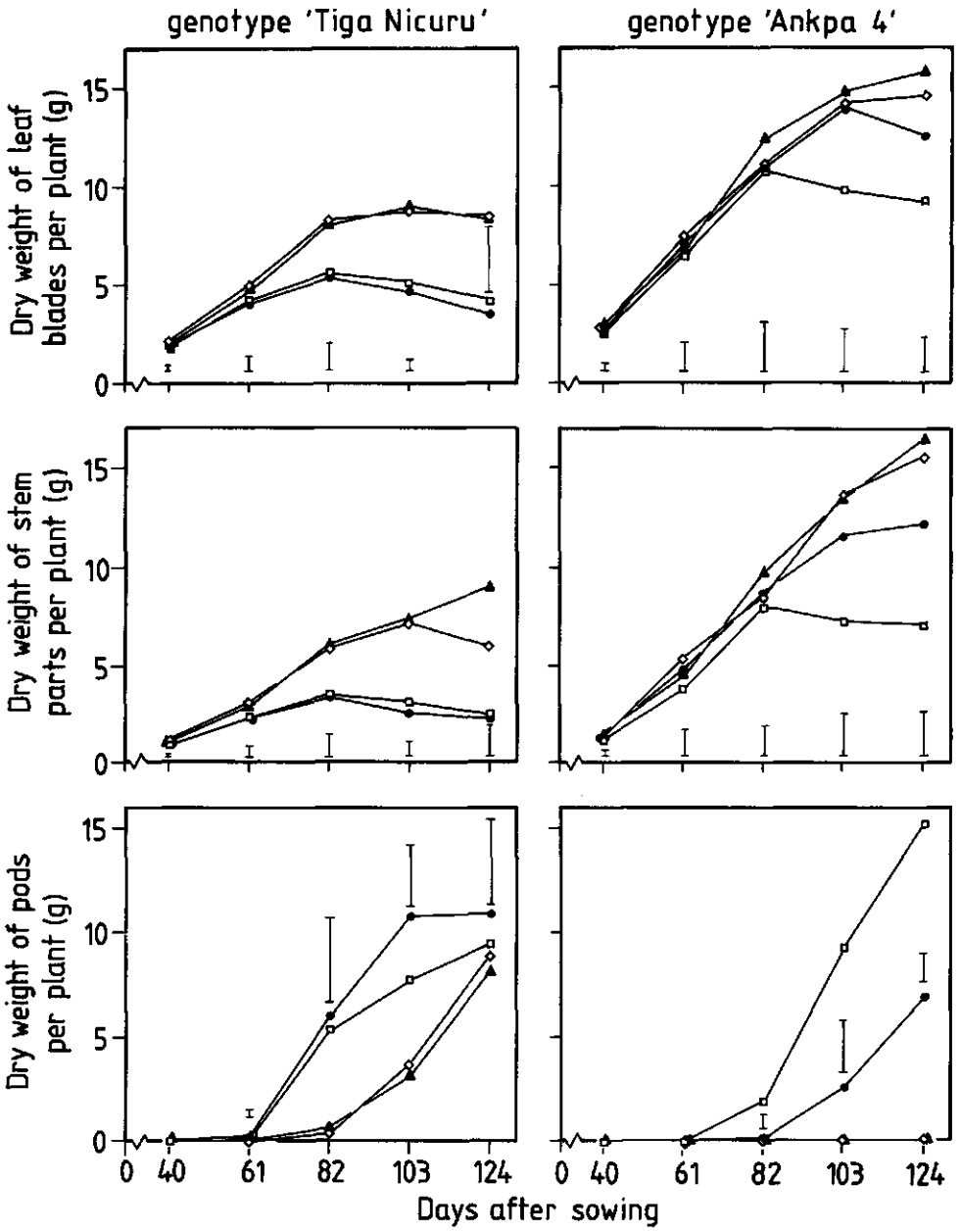

Figure 7.1. Dry weights of leaf blades, stem material (petioles and branches) and pods (g plant^{-1}) 40, 61, 82, 103 and 124 days after sowing (DAS) for bambara groundnut genotypes 'Tiga Nicuru' and 'Ankpa 4' at constant photoperiods of 10 (□), 12 (●), 14 (◇) and 16 h (▲). Vertical bars represent LSD at P = 0.05.

In 'Ankpa 4', dry matter that accumulated up to 61 DAS was distributed similarly over leaf blades and stem material for all photoperiod treatments (Fig. 7.2). Dry matter produced between 61 - 82 DAS was partly (18.1%, LSD(0.05): 7.25%) used for pod growth in plants under the 10-h photoperiod, while plants under the other photoperiod treatments only grew vegetatively. The increase in total aboveground dry matter between 82 and 103 DAS was completely (100%) allocated to pod growth in plants under the 10-h photoperiod, and partly (36.2%, LSD(0.05): 28.87%) in plants under the 12-h photoperiod. No pod growth occurred under the 14 and 16-h photoperiods.

Table 7.3. Number of developing and full-grown pods ($\geq$ 0.5 cm) per plant at 61, 82, 103 and 124 days after sowing (DAS) for two genotypes of bambara groundnut at constant photoperiods of 10, 12, 14 and 16 h.

	photoperiod (h)				
	10	12	14	16	LSD (0.05)
genotype 'Tiga Nicuru'					
- 61 DAS	4.2	5.9	0.0	0.0	N.S.
- 82 DAS	18.5	21.0	3.2	5.1	9.71
- 103 DAS	22.6	19.9	23.4	19.2	N.S.
- 124 DAS	15.7	18.7	27.1	22.9	N.S.
genotype 'Ankpa 4'					
- 61 DAS	0.0	0.0	0.0	0.0	N.S.
- 82 DAS	9.8	0.9	0.0	0.0	2.43
- 103 DAS	22.4	8.7	0.0	0.0	1.72
- 124 DAS	21.9	16.7	0.0	0.0	4.11

N.S.: not significant ($P = 0.05$).

Specific leaf weight and leaf area per plant. For plants of genotype 'Tiga Nicuru', specific leaf weight varied among photoperiod treatments: up to 103 DAS, plants under the 10 and 12-h photoperiods had heavier specific leaf weights than plants under the 14 and 16-h photoperiods (Table 7.4). No treatment effect was found at final harvest. The differences in specific leaf weight were associated with differences in leaf area per plant: throughout the trial period plants under 10 and 12 h had a smaller leaf area per plant than plants under 14 and 16 h ($P = 0.05$, data not presented).

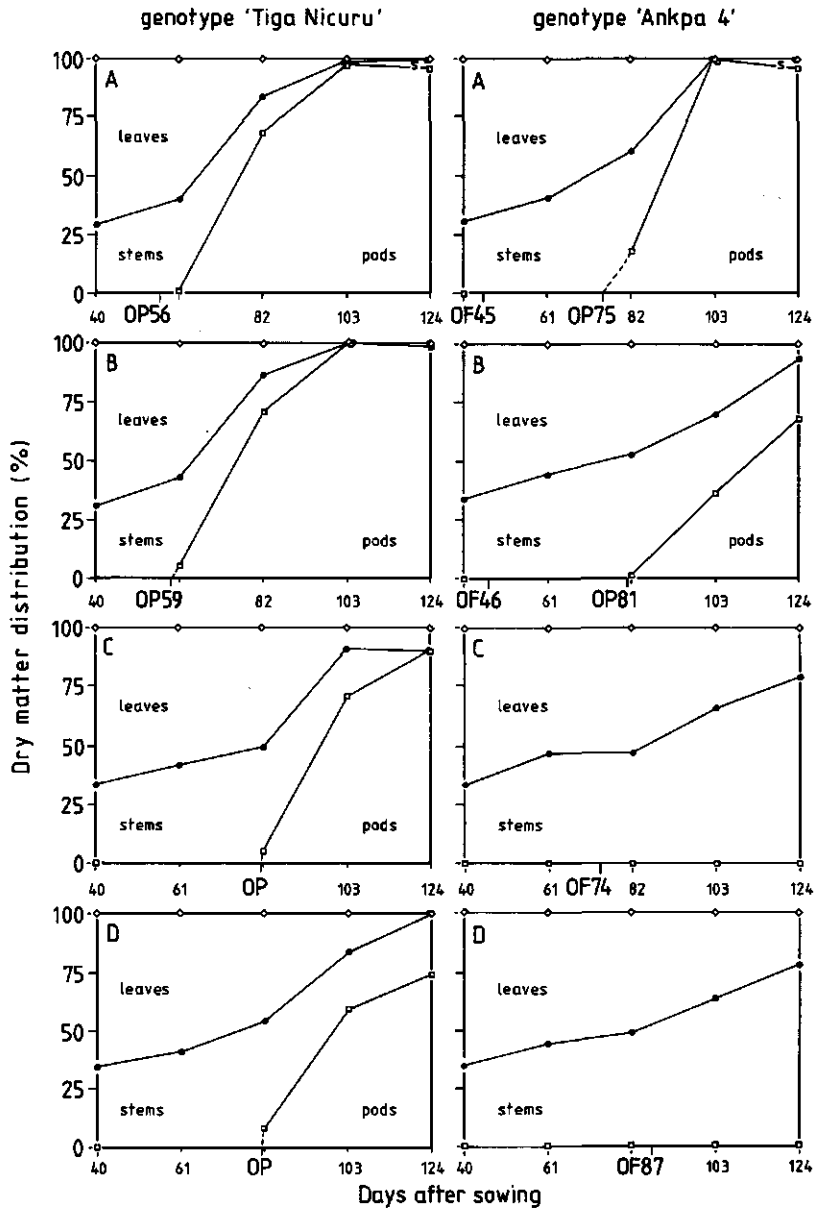

Figure 7.2. Partitioning (in terms of percentage) of the increase in total aboveground dry matter since the previous harvest over pods, stems and leaf blades for bambara groundnut genotypes 'Tiga Nicuru' and 'Ankpa 4' at constant photoperiods of 10 (A), 12 (B), 14 (C) and 16 h (D). OF = onset of flowering, OP = onset of podding.

For 'Ankpa 4', an effect of photoperiod on specific leaf weight was only found at the intermediate harvest at 103 DAS, when plants under 10 and 12 h had a heavier specific leaf weight than plants under 14 and 16 h (Table 7.4). Differences among treatments in leaf area per plant occurred for the first time 82 DAS: from then onwards, plants under 10 h had a smaller leaf area per plant than in the other treatments ($P = 0.05$, data not presented). From 103 DAS onwards, leaf area per plant for plants under 12 h was smaller than that of plants under 14 and 16 h.

Table 7.4. Specific leaf weight (mg cm^{-2}) at 40, 61, 82, 103 and 124 days after sowing (DAS) for two genotypes of bambara groundnut at constant photoperiods of 10, 12, 14 and 16 h.

	photoperiod (h)				
	10	12	14	16	LSD (0.05)
genotype 'Tiga Nicuru'					
- 40 DAS	4.2	4.1	3.9	3.6	0.18
- 61 DAS	3.7	3.7	3.0	2.9	0.32
- 82 DAS	3.8	3.9	3.3	3.0	0.39
- 103 DAS	3.9	3.9	3.3	3.3	0.25
- 124 DAS	4.3	4.3	4.2	3.6	N.S.
genotype 'Ankpa 4'					
- 40 DAS	3.8	3.7	3.7	3.6	N.S.
- 61 DAS	3.0	2.9	3.0	2.8	N.S.
- 82 DAS	3.7	3.2	3.1	3.2	N.S.
- 103 DAS	4.0	3.8	3.3	3.4	0.35
- 124 DAS	4.0	4.0	3.7	3.6	N.S.

N.S.: not significant ($P = 0.05$).

Rate of pod growth. For 'Tiga Nicuru', no effect of photoperiod was found on the rate of pod growth (Table 7.5), which averaged 0.18 g $plant^{-1}$ d^{-1} for the four treatments. In 'Ankpa 4', photoperiod influenced the rate of pod growth: the growth rate for plants under 10 h was nearly double the rate under 12 h (Table 7.5).

Table 7.5. Rate of pod growth (expressed as the daily increase in total pod dry weight per plant since the onset of podding in g plant^{-1} d^{-1}) for two genotypes of bambara groundnut at constant photoperiods of 10, 12, 14 and 16 h.

	photoperiod (h)				
genotype	10	12	14	16	LSD (0.05)
'Tiga Nicuru'	0.14	0.17	0.21	0.19	N.S.
'Ankpa 4'	0.31	0.16	0.00	0.00	0.047

N.S.: not significant (P = 0.05).

7.4 Discussion

Photoperiod induction of phenological development. Photoperiod influenced onset of podding only (genotype 'Tiga Nicuru'), or onset of both flowering and podding (genotype 'Ankpa 4'). In the literature, much attention has been paid to the influence of photoperiod (often in combination with temperature) on the onset of flowering in leguminous food crops (e.g. Summerfield *et al.*, 1991; 1993; Ellis *et al.*, 1994 a, b). The influence of these environmental factors on other aspects of crop development has been studied less frequently. Yet, photoregulation of stages of crop development other than flowering appears not to be restricted to bambara groundnut. In an experiment with eight soya bean genotypes (*Glycine max* (L.) Merrill), for example, the rate of development during the reproductive phase was generally negatively associated with the mean photoperiod (Mayers *et al.*, 1991). In groundnut, short-day treatments stimulated not only the numbers of flowers and pegs, but also the number of pods (Bagnall and King, 1991a, b). The findings on bambara groundnut in this paper, too, demonstrate the need to study crop development through until maturity to obtain the understanding of the phenology of the crop that is essential for the dissemination of genotypes and the selection of optimal cultural practices, such as the correct planting time.

Partitioning of dry matter in relation to photoperiod. Photoperiod indirectly influenced dry matter partitioning in bambara groundnut through its effect on development: in both genotypes the distribution of newly produced assimilates changed drastically after the photoperiod-induced onset of podding. In addition, there appeared to be a more direct influence of photoperiod on dry matter partitioning, as

was apparent in the distribution of dry matter over leaf blades and stem parts in plants of 'Tiga Nicuru' of identical development stage (plants under 10 and 12-h photoperiods versus plants under 14 and 16-h photoperiods, 40 DAS, Fig. 7.2). This is in accordance with Wallace *et al.* (1993) who conclude that photoperiod gene control over partitioning precedes (and causes) photoperiod gene control over days to flowering and maturity. Moreover, after the onset of podding, differences were found in the rates of pod growth for plants of 'Ankpa 4': pod growth under a 10-h photoperiod was nearly twice as fast as under a 12-h photoperiod (Table 7.5). This observation is supported by the difference in the slope of pod growth for plants under 10 and 12-h photoperiods in Figure 7.2. The difference in the rate of pod growth between plants of 'Ankpa 4' under 10 and 12-h photoperiods (Table 7.5) was positively associated with a difference in the number of developing pods (Table 7.3). It therefore seems that a lower rate of pod growth is caused by a lower number of simultaneously developing pods, rather than by the speed of individual pod growth.

The influence of photoperiod was also apparent on the leaf area per plant and specific leaf weight. Since the effect on leaf area per plant preceded the effect on specific leaf weight in 'Ankpa 4', it seems that leaf area growth is checked more strongly by photoperiod than leaf weight accumulation.

Photoperiod has been shown to influence dry matter partitioning in other leguminous food crops too. Morandi *et al.* (1988), for example, found that in soya bean more assimilates were partitioned to the seeds in short days, while in short days with interrupted nights the proportion partitioned to shoots was increased. Similar results were found for groundnut (Witzenberger, 1987; Witzenberger *et al.*, 1988): yields under long photoperiods were lower than under short photoperiods, as a smaller part of the assimilates was used for pod growth.

From our experiment no conclusions can be drawn about the mechanism that causes the differences in dry matter partitioning to pods in 'Ankpa 4' under the various photoperiod treatments. As for source-sink relations, it must be pointed out that under the longer photoperiods in this experiment (14 and 16 h), the source (leaf area) was at least as large as under the shorter photoperiods (10 and 12 h). Moreover, plants under 14 and 16-h photoperiods had an extensive potential sink which consisted of a very large number of fertilized, yet undeveloped, ovaries (Linnemann, 1993). The slower pod growth rates under increasing photoperiods therefore cannot be attributed to a shortage in the supply of assimilates. However, no assimilates were diverted to the ovaries. Apparently, photoperiod strongly affects the sink strength of the ovaries.

Harvest date in relation to yield. The results from the sequential harvests in this experiment show that the outcome of the study depends on the harvest date. The normal length of the growing period in the area where 'Tiga Nicuru' is cultivated, is about 3.5 months, which roughly corresponds with the harvest at 103 DAS. On that date, only the plants under the 12-h photoperiod had obtained the maximum dry weight of pods per plant (Fig. 7.1). Pods of plants under the 10, 14 and 16-h photoperiods were still gaining weight. It therefore seems plausible that the absence of an effect of photoperiod on pod dry weight per plant in 'Tiga Nicuru' is spurious. If the experiment had been continued, e.g. until 150 DAS, plants under the 14 and 16-h photoperiods might have outyielded those under the other treatments. This suggestion is supported by the fact that at the last harvest a large amount of dry matter was still present in the leaves and stems of plants under 14 and 16 h, and that redistribution of reserves to the pods - deduced from decreases in the weight of leaf blade and stem material - had not started until 103 DAS (Fig. 7.1). In plants under 10 and 12 h, redistribution had already started at 82 DAS. Maturity seems to be delayed under increasing photoperiods.

'Ankpa 4' matures in about 5 - 5.5 months under field conditions in its area of cultivation. Harvest at 124 DAS was too early to obtain the maximum dry weights of pods per plant for the various treatments (Fig. 7.1). Although the statistical analysis does not allow a comparison of 'Tiga Nicuru' and 'Ankpa 4', it can be argued that 'Ankpa 4' is a higher-yielding genotype when the growing season is longer. After all, onset of flowering in 'Ankpa 4' is later than in 'Tiga Nicuru' and hence the leaf area per plant (source) is larger at the onset of the pod-filling stage. Pod dry weight dynamics (Fig. 7.1) support this observation.

Implications for the spread of genotypes. The highest yields are invariably obtained from genotypes that make optimal use of the length of the growing season. 'Tiga Nicuru' is therefore too early-maturing for a location such as Ankpa in Nigeria, and 'Ankpa 4' is too late-maturing for cultivation in Mali. The criterion for selection of an adapted genotype within the present bambara groundnut germplasm collection would therefore be a growth duration that matches the local conditions. This probably implies an indirect selection for photosensitivity, as during several years of experimentation with bambara groundnut genotypes (predominantly from West Africa), it was found that genotypes originating from 'higher' latitudes (10-15° N) often combined a relatively short cycle length with a fairly weak response to photoperiod, whereas genotypes from 'lower' latitudes (5-10° N) were late-maturing and relatively photosensitive.

Chapter 8

General discussion

8.1 Major conclusions of this thesis

Influence of photoperiod on development and growth. Bambara groundnut genotypes differ in the photoperiod-sensitivity of their phenological development (Table 8.1), and this sensitivity increases between the onset of flowering and the onset of podding. The explanation for this difference in sensitivity cannot be derived from the results of the research described in this thesis. However, adaptation to the length of the growing season by photoperiod-sensitivity to the onset of podding appears to be more advantageous than regulation solely by photoperiod-sensitivity of flowering. After all,

Table 8.1. Overview of the genotypes used in the experiments and their characteristics.

			response to photoperiod		response to temperature	
Genotype	origin	latitude	flowering	podding	flowering	podding
'Ankpa 2'	Nigeria	7°22' N	-	+	+	+
'Ankpa 4'	Nigeria	7°22' N	+ [1]	+ [1]	+ [2]	+ [2]
'Tiga Nicuru'	Mali	14°13' N	-	+		
TVsu 9	unknown		-	+		
TVsu 216	Ghana	4°5'-11°0' N	-	+		
TVsu 409	Cameroon	1°4'-13°0' N	-	+		
TVsu 463	Cameroon	1°4'-13°0' N	-	+		
TVsu 465	Cameroon	1°4'-13°0' N	-	+		
TVsu 777	Zambia	8°1'-18°1' S	-	+		
TVsu 931	Zambia	8°1'-18°1' S	-	+		
TVsu 1034	Zimbabwe	15°3'-22°2' S	-	+		
Unnamed	The Gambia	13°1'-13°4' N	-	+		
'Yola'	Nigeria	9°14' N	-	+ [1]	+	+ [2]

-: response absent, +: response present
[1] photoperiod response only above the critical photoperiod
[2] temperature response only below the critical photoperiod

regulation via the onset of podding provides the plant with a longer period of flexible duration in its life cycle. Bambara groundnut therefore has a period of flexible duration at its disposal from sowing through to podding instead of having a flexible period from sowing to flowering and a fixed period from the onset of flowering to maturity as many legumes supposedly have as all the work on the prediction of flowering (see e.g. Summerfield *et al.*, 1991) suggests. Moreover, the period during which podding induction is assumed to occur in bambara groundnut coincides with one of the two periods per year in which the largest changes occur in the photoperiod (Fig. 8.1). This gives the plant a better opportunity to tune its development to the changes in season. The period of rapid changes in photoperiod lasts from about mid-August to mid-October in the growing areas in the northern hemisphere which are predominantly from 5 to 15 °N. In the southern hemisphere the main cultivation areas are further from the equator, and therefore considerable changes in photoperiod occur sooner after the longest day (21 December) than in the northern hemisphere, namely from about mid-January onwards.

The least sensitive genotypes, e.g. 'Tiga Nicuru', were photoperiod-insensitive to the onset of flowering with a quantitative short-day response to the onset of podding (Table 8.1). The most sensitive genotype, 'Ankpa 4', showed a quantitative short-day response to both the onset of flowering and podding. Moreover, progress in flowering and in pod growth was slower under photoperiods $\geq$ 14 h than in photoperiods $\leq$ 13 h. Only a limited number of genotypes were investigated in this research, so it is possible that the range in photoperiod-sensitivity among bambara groundnut genotypes is larger than reported here.

The least photoperiod-sensitive genotype required fewer short (12 h) days for the induction of podding than the most sensitive one: transference from a 14-h to a 12-h photoperiod for eight days induced podding in plants of 'Tiga Nicuru', but a transference for 16 days was insufficient to induce podding in 'Ankpa 4'. In 'Tiga Nicuru' podding could be induced by transferring 21-day-old plants which had not yet begun to flower to the 12-h photoperiod. This result suggests that genotypes with a weak response to photoperiod (i.e., onset of podding slightly delayed by unfavourable photoperiods) require a shorter inductive period to produce pods than those with a strong response to photoperiod (i.e., unfavourable photoperiods cause large delays in the onset of podding).

In 'Ankpa 4', the position of the first open flower on the primary branches was further away from the main axis when plants were kept under non-inductive photoperiods of 14-h for more than four weeks. Plants transferred from a 14-h to an 11-h photoperiod after 28, 41 and 54 days produced their first open flower on node

number 3.3, 4.3 and 5.7, respectively. Seed yields per plant were reduced by an early induction of podding: the total seed dry weight per plant was higher in plants transferred after 41 and 54 days from the 14-h to an 11-h photoperiod than in plants transferred after 21 days. From this result it is inferred that early induction caused plants to use assimilates for early reproductive growth, at the expense of continued vegetative growth. This limited the plants' source capacity, and consequently, their yielding ability. Plants which started to pod early, used the longer period they had between the onset of podding and harvest to continue to produce pods, but in comparatively small numbers. Late induction gave higher yields but also a more synchronized development - and hence maturity - of pods.

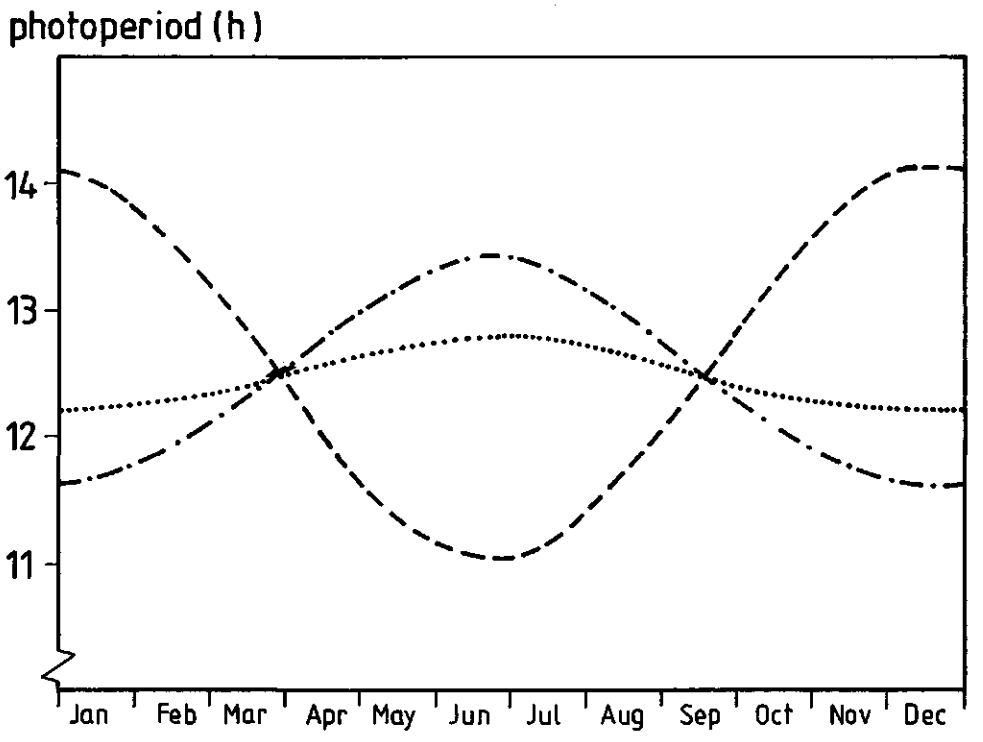

Figure 8.1. Annual course of the photoperiod (defined as the interval between sunrise and sunset plus the time when the position of the centre of the sun is 3° below the horizon) at 5° N (----), 15° N (—-—) and 25° S (– – –). Based on R.J. List (1958). Smithsonian Meteorological Tables. Sixth revised edition. Smithsonian Institution, Washington. pp. 506-507, 513.

Dry matter partitioning was indirectly affected by photoperiod through its influence on phenological development; the assimilate distribution changed after the photoperiod-dependent onset of podding. In addition, a direct influence of photoperiod on partitioning was found. For example, just after the onset of flowering, 'Tiga Nicuru' plants under 10- and 12-h photoperiods had accumulated more dry matter as leaf blades and less as stem material than plants under 14- and 16-h photoperiods. This seems a sound strategy, bearing in mind that short photoperiods (10 and 12 h) are related to relatively short periods of growth and long photoperiods (14 and 16 h) are related to long periods of growth. When the growing season is short, plants have to come into production quickly and therefore do not need further branching for continued vegetative growth. Ideally, the larger amount of dry matter in the leaf blades in plants under 10 and 12-h should have been associated with a proportionally larger leaf area. However, this was not the case: throughout the trial period, plants under 10 and 12 h had a smaller leaf area per plant (and higher specific leaf weights) than those under 14 and 16 h. Since the effect on leaf area per plant preceded the effect on specific leaf weight in 'Ankpa 4', it was concluded that leaf area growth is controlled more strongly by photoperiod than leaf weight accumulation.

Another direct influence of photoperiod on partitioning was visible as differences in the increase of pod dry weights per plant in 'Ankpa 4': the increase in pod dry weight per plant under the 10-h photoperiod was nearly double the increase under the 12-h photoperiod. Again, the expected duration of growth is shorter in plants under 10 h than in plants under 12 h. Their growth patterns varied accordingly: plants under 12 h continued to use a larger amount of assimilates for further vegetative growth than plants under 10 h, which used their assimilates mainly for reproductive growth.

The delay in or absence of the onset of podding in bambara groundnut genotypes could be traced to a check in the growth of fertilized ovaries, the plants' sinks. Photoperiod affected the number of developing sinks, and as a consequence, the total sink strength of the plant, irrespective of the number of ovaries present. Increases in total pod dry weight per plant were positively related to the number of developing pods. Plants invariably had large numbers of fertilized ovaries - often ten times more than the number of full-grown pods. The probable explanation for the production of such large numbers of ovaries is that it provides the plant with yet another possible flexible response to the highly variable conditions in its cultivation area.

Influence of temperature and photoperiod. The influence of temperature and photoperiod on flowering and podding in bambara groundnut can be evaluated successfully using the three-plane model for flowering proposed by Roberts and Summerfield (1987) and Summerfield *et al.* (1991). A thermal-sensitive plane

describes the developmental rate for flowering ($1/f$, i.e., the reciprocal of the number of days to first open flower) in 'Ankpa 2' and 'Yola'. In 'Ankpa 4', $1/f$ is best described by a two-plane model, with a thermal plane and a photoperiod-sensitive plane (i.e., the temperature effect in the photothermal plane was not significant). The critical photoperiod, which is where the thermal and the photothermal planes meet, became shorter at increasing temperatures.

The photothermal response of the developmental rate towards the onset of podding ($1/p$, i.e., the reciprocal of the number of days to the first pod) in 'Ankpa 2' is described by a single, photothermal plane. In this genotype, onset of podding was hastened by higher temperatures and delayed by increasing photoperiods. Onset of podding in 'Yola' and 'Ankpa 4' is described by a two-plane model, comprising thermal and photoperiod-sensitive planes (again no significant temperature effect in the photothermal plane). In both genotypes, the critical photoperiod became shorter at increasing temperatures.

8.2 Agronomic implications of the research findings

Crop husbandry. The photoperiod-sensitivity of podding in bambara groundnut secures timely maturation of genotypes in their latitude of origin. When a crop is sown during the first weeks after the onset of the rains, farmers may expect a secure harvest, assuming that no serious pest and disease problems occur. The adaptation conferred on the genotypes by their photoperiod-sensitivity prevents the crop reaching maturity before the end of the rainy season and, consequently, prevents yield losses due to pod rotting. Moreover, plants will generally not die from lack of water before they have produced pods, because their growth cycle is adjusted to the water availability at the end of the growing season.

Yield increases can be expected when the sowing date is advanced as close as possible to the onset of the rains, because this gives a longer period between sowing and the onset of podding, thus permitting more vegetative growth (and hence more capacity to produce assimilates) before the period of pod production.

The photoperiod-sensitivity of development and the heterogeneity of farmers' seed lots necessitate a certain strategy in maintaining seed for next season's crop. The practice of some farmers to harvest and consume the early maturing plants (Linnemann, 1990) constitutes a constant selection pressure for a delay in maturation. This depresses yields when the water availability at the end of the rainy season is less than in average years, since plants will not be able to make full use of their vegetative capacity. Seeds

for next season's crop should therefore be collected from all the healthy plants in a randomly selected part of the field.

Breeding and selection. An important consequence of the photoperiod-sensitivity of development for the characterization of bambara groundnut genotypes is that the plant's appearance and production largely depend on the growing conditions. This implies that genetic material from different locations should be evaluated under standardized environmental conditions.

Photoperiod-sensitivity is an essential trait of bambara groundnut under rain-fed conditions. This feature should therefore be maintained in developing new varieties.

Dissemination of genotypes over agro-ecological zones. During the years of experimentation with bambara groundnut genotypes (predominantly from West Africa, Table 8.1), it was found that genotypes originating from 'higher' latitudes (10 - 15° N) often combined a relatively short crop duration with a fairly weak response to photoperiod, whereas genotypes from 'lower' latitudes (5 - 10° N) matured late and their development was relatively photosensitive. The relevance of growth duration and photosensitivity of phenological development for the dissemination of these bambara groundnut genotypes can be illustrated with some hypothetical situations (ignoring temperature effects): 1) cultivation of genotype 'Tiga Nicuru' at 5° N (close to the latitude of origin of 'Ankpa 4'), 2) of genotype 'Ankpa 4' at 15° N (close to the latitude of origin of 'Tiga Nicuru'), and 3) cultivation of both genotypes at 25° S, close to the latitude of a bambara groundnut growing area in southern Africa (Arnold and Musil, 1983).

In situation 1, genotype 'Tiga Nicuru' experiences a shorter photoperiod than at its latitude of origin during most of the growing season (July-Sept., Fig. 8.1). Onset of flowering will not be affected, but onset of podding will be slightly earlier than at 15° N. The growth duration of 'Tiga Nicuru', which is already shorter than that of 'Ankpa 4', therefore decreases even more. The largest drawback for the cultivation of 'Tiga Nicuru' at 5° N is not the photoperiodic circumstances, but the fact that the crop matures before the end of the rainy season, and thus probably yields little because of pod rot, which is a serious problem under humid conditions (Goli and Ng, 1988).

In situation 2, genotype 'Ankpa 4' is grown under a photoperiod which is longer than at its latitude of origin during the first part of the growing season (July-Sept., Fig. 8.1). Onset of flowering may therefore be delayed. Onset of podding may be delayed as well, but only slightly, since the differences in photoperiod between 5 and 15° N

are small from the end of August until the end of October. Thus, the growth duration of 'Ankpa 4' at 15° N is expected to be longer than at its latitude of origin. Again, the photoperiodic circumstances will not be the greatest obstacle to the successful cultivation of this genotype at 15° N; the relatively long growth duration (already about 20-24 weeks at its latitude of origin) makes it impossible for the crop to mature on the water that is available after the rainy season ends. For comparison, the length of the growing season at Mopti (about 150 km north-east of the site where the 'Tiga Nicuru' seeds were collected) is computed at 14-16 weeks, assuming a soil water-holding capacity of 100-270 mm (Sivakumar *et al.*, 1984).

In situation 3, the photoperiod during the first three months of the growing season (Nov.-Jan., Fig. 8.1) is about 14 h. 'Tiga Nicuru' will have a delayed onset of podding, and will mature late. 'Ankpa 4' will have a strongly delayed onset of flowering, and the onset of podding will be delayed until the photoperiod becomes inductive again, possibly sometime in February or March, about 4 - 5 months after sowing. By that time there is insufficient rain to support the crop until maturity. Thus, with increasing distance from the equator the photosensitivity of phenological development gains in importance for the dissemination of genotypes.

8.3 Topics meriting further research

Methodological aspects. The research described in this thesis was mainly conducted on genotypes collected in farmers' fields and local markets. These genotypes were genetically heterogeneous and rather low-yielding, which had consequences for the set-up, execution and even the results of the experiments. The heterogeneity made it necessary to use a considerable number of plants for data collection at intermediate and final harvests. This reduced the number of genotypes that could be included in one trial. Heterogeneity also caused differences in the observations on the day of the first open flower in 'Ankpa 4' (compare Table 3.1 with Table 7.1). The plant populations of the various experiments apparently differed, even though representative subsamples were taken from the original batch of seed. These differences were most probably caused by the fact that only the first seeds that germinated were actually planted, and that after emergence only plants of similar appearance were allocated to the treatments. This does not weaken the conclusions on photoperiodicity in general. Yet it implies that the observations on 'Ankpa 4' may not always be representative of the entire batch of seed. Furthermore, the low production levels of the genotypes made it more difficult to obtain statistically significant differences between treatments, than if a high-yielding genotype had been used. Therefore in future fundamental research on bambara groundnut's response to environmental conditions it would

probably be advisable to select and multiply plants with extreme responses within a batch of seed. Batches of seeds only need to be used in their original composition when assessing how often and to what extent individual responses manifest themselves in practice.

Before large-scale screening for flowering and podding can be carried out, it is essential to find more efficient, and preferably non-destructive, methods to determine the onset of podding. Moreover, screening and experimentation would be facilitated if fully controlled environmental conditions could be used for year-round observations. So far, this has not been possible because of the effects of light source on crop morphology. Therefore, an artificial source of light that enables plants cultivated under it to resemble those grown in the field should be found.

Responses to photoperiod. This research focused on the influence of photoperiod on the onset of flowering and podding. The evidence that photoperiod-sensitivity increased between the onset of flowering and the onset of podding raises questions about the effect of photoperiod on later stages of development. Research into the effect of photoperiod on e.g. the end of flowering and the onset of maturity (defined, for instance, by leaf discolouration or leaf shedding) therefore seems justified.

Moreover, the range in photoperiod-sensitivity among bambara groundnut genotypes might be wider than reported in this thesis. The genotypes tested, for instance, all produced pods under photoperiods of maximal 16 h if allowed to grow for a sufficiently long period. Further research is needed to reveal whether there are any accessions that have a qualitative short-day response to the onset of podding, or which are photoperiod-insensitive to both the onset of flowering and the onset of podding.

Civil twilight. In this study, the natural photoperiod was defined as the interval between sunrise and sunset plus the time when the position of the centre of the sun is 3° below the horizon. This means that half of the period of daily twilight was included in the length of the natural photoperiod. There is no evidence, however, to confirm that this is the correct calculation of the length of the photoperiod that is relevant for the photoperiodic responses in bambara groundnut. For soya bean (*Glycine max* (L.) Merr.), common bean (*Phaseolus vulgaris* L.) and chickpea (*Cicer arietinum* L.) the inclusion of civil twilight in the photoperiodic daylengths seems justified, but in lentil (*Lens culinaris* Medik.) this gives an overestimation (Summerfield and Roberts, 1987).

The difference between the addition of civil twilight (i.e., the time when the position of the centre of the sun is 6° below the horizon) to the photoperiod or otherwise is

especially relevant further away from the equator: at 25° S, for example, daily duration of civil twilight is about 0.8 h. There might be differences in bambara groundnut's sensitivity to civil twilight at dawn and at dusk, as has been observed in onion (Tarakanov, pers. comm.). Furthermore, it is unknown whether genotypes differ in sensitivity to civil twilight.

Rate of change in photoperiod. In soya bean, for example, the rate of change in photoperiod has been found to affect the period from emergence to flowering (Constable and Rose, 1988). There is no information on the influence of a change in photoperiod and in the rate of change of photoperiod on development in bambara groundnut. This information could be important for extrapolating the results from experiments with constant photoperiods, such as most of those described in this thesis, to crop behaviour under natural growing conditions.

Responses to temperature. Information on the temperature response of growth and development in bambara groundnut is scarce. The base temperatures (T_b) reported in this thesis for the developmental rates for flowering and podding are about 3° C or lower. These values were obtained after considerable extrapolation (the lowest temperature used was 20 °C), and therefore warrant further investigation. Moreover, the T_b values for other developmental processes are of interest for a better understanding of crop behaviour, such as for the rate of germination and for leaf development. In addition, the optimal temperatures (T_{opt}) for the above-mentioned developmental rates should be assessed, as well as the differences in T_b and T_{opt} among genotypes.

Heterogeneity in seed saved by farmers. Seed batches from farmers and local markets are heterogeneous. This heterogeneity is expressed in the field in various ways, such as by the presence of plants differing in growth duration and morphology. The positive side of this heterogeneity is that it enables a flexible response to differences in growing conditions between years, as pointed out earlier. The negative side is that the attainable yield levels are decreased. After all, the highest yields may be expected from plants that make optimal use of light, nutrients and water, but some plants of this heterogeneous batch of seed will be too early and others too late to do so. And therefore, the more homogeneous the batch of seed, the higher its attainable yield. However, to attain this yield level, growth conditions (in particular water availability) must be controlled. At present, there is no such control: bambara groundnut growers depend on the prevailing weather conditions. Therefore, the minimal degree of heterogeneity should be assessed in relation to the possible fluctuations in the amount and duration of the rains between years for different locations.

The final conclusion that can be drawn from the research described in this thesis is that the demonstrated flexibility in the development of bambara groundnut genotypes in relation to changes (in particular to changes in photoperiod) is an essential property given the way the crop is grown at present. This flexibility largely explains why the crop produces under marginal conditions in rain-fed areas.

Summary

Introduction and objective (Chapter 1). Bambara groundnut (*Vigna subterranea* (L.) Verdc.) is an important secondary legume in cropping systems and in the rural diet in sub-Saharan Africa. It is cultivated for its subterranean pods, mainly on small farms, and most often by female farmers who grow the crop for home consumption and only sell surpluses on the local market. So far, little is known about the ecophysiological requirements of this crop.

The objective of the research described in this thesis was to assess the influence of photoperiod and temperature on phenological development and growth of bambara groundnut. This knowledge is essential to determine the appropriate place for this crop in cropping systems and agro-ecological zones. The research, which involved fieldwork in Nigeria and Zambia and literature and experimental research in The Netherlands, was conducted from 1986 to 1992.

Preliminary observations (Chapter 2). Eight accessions from the International Institute of Tropical Agriculture (IITA), Nigeria, were exposed to 11-h or 14-h photoperiods. All accessions were dayneutral for the onset of flowering. Differences were found for the onset of podding: the 14-h photoperiod delayed the onset of podding in six accessions, and inhibited it in the other two. The delay or absence of podding under the 14-h photoperiod resulted from the growth of fertilized ovaries being checked. Ovaries produced under the 14-h photoperiod developed into full-grown pods after transference to a 12-h photoperiod. Photoperiod also affected leaf production: under a 14-h photoperiod the leaf area per plant of a selection from The Gambia was three times larger than the leaf area per plant under a 10-h or 12-h photoperiod after a growth period of about 100 days.

Embryo development (Chapter 3). Embryo development was studied in 'Ankpa 4', a genotype from Nigeria. Photoperiod influenced the development of this genotype earlier than that of the genotypes in the previous experiments: under constant photoperiods from 10 to 16 h the onset of flowering, progress of flowering, the onset of podding and progress of pod growth were all delayed by lengthening the photoperiod.

Two groups of ovaries were distinguished under an 11.5-h photoperiod. In both, embryo development was identical up to 17 days after anthesis, but then the embryos in the first group continued to develop until they were full-grown at about 41 days after anthesis, whereas the growth of the embryos in the second group stopped.

Embryo development under a photoperiod of ≥ 14 h was similar to that in the ovaries with discontinued embryo growth under the 11.5-h photoperiod. Healthy-looking embryos were found up to 32 days after anthesis under the photoperiod of ≥ 14 h. Thereafter embryos began to shrivel and degenerate. Finally, the ovaries aborted.

Minimal inductive period for the onset of podding (Chapter 4). In a reciprocal transfer experiment the minimal inductive period for the onset of podding was determined, as well as the developmental phase in which photoperiod sensitivity to podding occurs. Two genotypes were tested: 'Tiga Nicuru' (dayneutral for flowering and photoperiod-sensitive to podding) and 'Ankpa 4' (photoperiod-sensitive to flowering and podding).

Transferring plants of 'Tiga Nicuru' from a 14-h to a 12-h photoperiod for 8 days induced podding, but podding was absent after a 4-day transfer. However, transference to the 12-h photoperiod for 16 days did not induce podding in 'Ankpa 4'.

Plants of 'Tiga Nicuru' were susceptible to podding induction for nearly 4 weeks. Podding was induced in plants which had been in the natural photoperiod (≥ 15.5 h) for the first three weeks (i.e., before flowering), followed by 12 days in the 12-h photoperiod and subsequently in the 14-h photoperiod until harvest. Podding could still be induced in 48-day-old plants that had had more than 20 open flowers.

In both genotypes transferring plants from the 12-h to the 14-h photoperiod or *vice versa* caused differences in the number of flowers and pods per plant, petiole length and leaf area. The influence of photoperiod was most obvious on the number of pods per plant. Leaf area and number of pods per plant seem suitable parameters for modelling pod growth under different photoperiods. Leaf area development was related to the number of pods per plant, but was also directly influenced by the prevailing photoperiod.

Time of pod induction in relation to pod position on the plant (Chapter 5). Plants of genotype 'Ankpa 4' were subjected to a period of 21, 28, 41 or 54 days under a 14-h photoperiod before transference to an 11-h photoperiod to determine the relation between the time of pod induction and pod position on the plant. Onset of flowering and seed yield per plant were determined too.

Plants transferred after 28 or more days, started flowering sooner the earlier they were transferred. Plants transferred after 21 or 28 days began flowering simultaneously, thus indicating juvenility. At harvest, 135 days after sowing, the total seed dry weight per plant was higher for plants transferred after 41 or 54 days than

for plants transferred after 21 days. Plants transferred after 28 days gave an intermediate value.

Most (79-91%) pods were produced on branches that developed on nodes 1 - 4 of the main axis. There were no differences in the fractional distribution of the pods along the main axis in plants transferred after 28 or more days. Pods of plants transferred after 21 or 28 days were more evenly distributed over the nodes of the first two primary branches than pods of plants transferred after 41 or 54 days. Plants of the latter treatments produced their pods more towards the tips of the branches and concentrated in two adjacent nodes (nodes 5 and 6 for plants transferred after 41 days; nodes 6 and 7 for plants transferred after 54 days). Delaying the induction of podding in this experiment therefore resulted in higher seed yields per plant and a more synchronized development -and hence maturity- of pods.

Photothermal regulation of development (Chapter 6). For three genotypes, the photothermal response of the onset of flowering (f) and the onset of podding (p) were determined in a factorial experiment with four photoperiods and three mean diurnal temperatures. The onset of flowering was determined by noting the day on which the first flower opened. The onset of podding was estimated from linear regressions of pod dry weight against time from sowing. Developmental rates were derived from the reciprocals of f and p. In two genotypes, 'Ankpa 2' and 'Yola', flowering occurred irrespective of photoperiod and $1/f$ was controlled by temperature only, occurring sooner at 28.1 °C than at 20.2 °C. The third genotype, 'Ankpa 4', was sensitive to temperature and photoperiod and f was delayed by cooler temperatures, photoperiods $>$ 12.66 h at 20.2 °C and photoperiods $>$ 11.33 h at 24.1 and 28.1 °C. In contrast, p was affected by temperature and photoperiod in all three genotypes.

Apparently, photoperiod-sensitivity increased between the onset of flowering and the onset of podding. The most photoperiod-sensitive genotype with respect to p was 'Ankpa 4', followed by 'Yola' and 'Ankpa 2'. There was also variation in temperature-sensitivity between the genotypes investigated.

Photoregulation of development and growth (Chapter 7). Genotypes 'Tiga Nicuru' and 'Ankpa 4' were grown under constant photoperiods of 10, 12, 14 and 16 h to study dry matter accumulation. Photoperiod influenced the onset of flowering in genotype 'Ankpa 4' only and the onset of podding in both. Under 14- and 16-h photoperiods plants of 'Ankpa 4' produced no pods. Photoperiod did not influence total aboveground dry matter production per plant in 'Ankpa 4' and had only a slight effect on 'Tiga Nicuru'.

Photoperiod indirectly affected dry matter partitioning via its influence on development: in both genotypes, assimilate distribution changed after the photoperiod-induced onset of podding. In addition, a direct influence of photoperiod on partitioning was observed. Firstly, just after the onset of flowering (40 days after sowing), 'Tiga Nicuru' plants under 10- or 12-h photoperiods had accumulated more dry matter as leaf blades and less as stem material than plants under 14- or 16-h photoperiods. Secondly, for plants of 'Ankpa 4' the increase in pod dry weight per plant under the 10-h photoperiod was nearly double the increase under the 12-h photoperiod. This difference was associated with a smaller number of developing pods under the 12-h photoperiod. Photoperiod apparently strongly affected the number of developing sinks and, as a consequence, the total sink strength of the plant. This was irrespective of the numerous ovaries present on plants of all treatments, including plants of 'Ankpa 4' under 14- and 16-h photoperiods.

Agronomic implications and research needs (Chapter 8). Bambara groundnut's observed photoperiod-sensitivity to the onset of podding has advantages over the adaptation to the length of the growing season by photoperiod-sensitivity to flowering only that is observed in other crops. Genotypes with a weak response to photoperiod (i.e., unfavourable photoperiods slightly delay the onset of podding) required a shorter inductive period to produce pods than genotypes with a strong response to photoperiod (i.e., unfavourable photoperiods severely delay the onset of podding). Early induction of podding decreased seed yields as it caused plants to use assimilates for early reproductive growth, at the expense of continued vegetative growth. Early induction also gave a less synchronized development - and hence maturation - of pods than late induction. Photoperiod also affected dry matter partitioning. Under short photoperiods (10 and 12 h) less dry matter was found as stem material than under longer photoperiods (14 and 16 h). Plants under short photoperiods come into production quickly and therefore do not need further branching for continued vegetative growth.

Photoperiod-sensitivity of podding secures the timely maturation of genotypes in their latitude of origin. Sowing as soon as possible after the onset of the rains enables the crop to exploit the length of the growing season optimally. The highest yields can therefore be expected under these conditions. Seeds for next season's crop should be collected from plants which represent the diversity in the whole field, to maintain the heterogeneity which confers the flexible response of the genotype to differences in environmental conditions.

Photoperiod-sensitivity implies that to characterize genotypes the growing conditions must be standardized, to obtain comparable results at different locations. Photoperiod-

sensitivity should be maintained when selecting and breeding new varieties. A hypothetical example is used to illustrate the consequences of photoperiod-sensitivity for the dissemination of genotypes.

It is recommended to use genetic material which is more homogeneous than that used for the experiments reported in this thesis for further experimental research on the basic factors that determine growth and development. Furthermore, an efficient, and preferably non-destructive methodology should be developed to determine the onset of podding. Cultivation of bambara groundnut under fully controlled environmental conditions would be improved considerably by developing a light source that would result in plants being morphologically similar to those in the field.

Research topics requiring further investigation include the question of whether photoperiod affects growth stages later than the onset of podding. In addition, the range in photoperiod-sensitivity among bambara groundnut genotypes might be wider than reported in this thesis. Further, it is unknown whether civil twilight contributes to the length of the photoperiod that plants experience, or what is the influence of a change (or rate of change) in photoperiod. Knowledge of temperature responses is scarce; therefore the base and optimum temperatures for developmental processes should be assessed. Finally, the desirable degree of heterogeneity of farmers' seed lots should be determined in relation to the possible fluctuations between years in the amount and duration of the rains. This heterogeneity and the flexibility in plant development in relation to changes in photoperiod largely explain why the crop can produce under marginal conditions in rain-fed areas.

Inleiding en doelstelling (Hoofdstuk 1). Bambara aardnoot (*Vigna subterranea* (L.) Verdc.) is een belangrijke secundaire peulvrucht in teeltsystemen in Afrika ten zuiden van de Sahara en speelt een voorname rol in de voedselvoorziening op het platteland. Het gewas wordt voor zijn ondergrondse peulen verbouwd, voornamelijk op kleine bedrijven, en meestal door boerinnen, die het gewas telen voor eigen gebruik en slechts de meerproduktie verkopen op de markt. Tot op heden is er weinig bekend over de ecofysiologische vereisten van dit gewas.

De doelstelling van het onderzoek dat wordt beschreven in dit proefschrift was het vaststellen van de invloed van daglengte en temperatuur op de fenologische ontwikkeling en groei van bambara aardnoot. Deze kennis is essentieel voor het bepalen van de meest geschikte plaats voor dit gewas in teeltsystemen en agro-ecologische zones. Het onderzoek, dat bestond uit veldwerk in Nigeria en Zambia en literatuur en experimenteel onderzoek in Nederland, vond plaats van 1986 tot 1992.

Oriënterende waarnemingen (Hoofdstuk 2). Acht herkomsten van het International Institute of Tropical Agriculture (IITA), Nigeria, werden blootgesteld aan fotoperioden van 11 of 14 uur. Alle herkomsten waren dagneutraal voor het begin van de bloei. Bij het begin van de peulvorming traden verschillen op: de fotoperiode van 14 uur vertraagde het begin van de peulvorming in zes herkomsten, en verhinderde deze in de overige twee. De vertraging of afwezigheid van de peulvorming bij een fotoperiode van 14 uur was het gevolg van een geremde uitgroei van bevruchte vruchtbeginsels. Na overplaatsing naar een fotoperiode van 12 uur ontwikkelden deze zich tot volgroeide peulen. De fotoperiode beïnvloedde tevens de bladproduktie; na een groeiduur van ongeveer 100 dagen was de bladoppervlakte per plant van een herkomst uit Gambia, bij een fotoperiode van 14 uur, drie maal zo groot als die bij een fotoperiode van 10 of 12 uur.

Embryo-ontwikkeling (Hoofdstuk 3). De embryo-ontwikkeling werd bestudeerd in 'Ankpa 4', een herkomst uit Nigeria. De fotoperiode beïnvloedde de ontwikkeling van deze herkomst eerder dan die van de herkomsten in voorafgaande experimenten. Bij constante fotoperioden, gelegen tussen 10 en 16 uur, werden zowel het begin van de bloei, de voortgang van de bloei, het begin van de peulvorming als de voortgang van de peulgroei vertraagd bij het langer worden van de fotoperiode.

Bij een fotoperiode van 11,5 uur werden twee groepen vruchtbeginsels onderscheiden. In beide vond een overeenkomstige embryo-ontwikkeling plaats tot en met 17 dagen

na bloei. Vanaf dat moment echter ontwikkelden de embryo's van de eerste groep zich verder totdat ze op ongeveer 41 dagen na bloei waren volgroeid, terwijl de groei van de embryo's van de tweede groep stagneerde. Eenzelfde stagnatie werd aangetroffen in de ontwikkeling van embryo's bij een fotoperiode $\geq$ 14 h. Hier werden embryo's met een gezond uiterlijk tot en met 32 dagen na bloei aangetroffen. Vanaf dat moment echter begonnen de embryo's te verschrompelen en te degeneren. Uiteindelijk aborteerden de vruchtbeginsels.

De minimum inductie periode voor het begin van de peulvorming (Hoofdstuk 4). De minimum inductie periode voor het begin van de peulvorming en het ontwikkelingsstadium waarin daglengte-gevoeligheid voor peulvorming optreedt werden bepaald in een wederkerig overzet experiment. Twee herkomsten werden getoetst: 'Tiga Nicuru' (dagneutraal voor bloei en fotoperiode-gevoelig voor peulvorming) en 'Ankpa 4' (fotoperiode-gevoelig voor bloei en peulvorming).

Door overzetten van planten van 'Tiga Nicuru' van een fotoperiode van 14 naar 12 uur werd na 8 dagen peulvorming geïnduceerd, terwijl er nog geen peulvorming optrad na 4 dagen. Echter, in 'Ankpa 4' induceerde overzetting naar een fotoperiode van 12 uur gedurende 16 dagen geen peulvorming.

Planten van 'Tiga Nicuru' waren gedurende bijna 4 weken gevoelig voor het induceren van peulvorming. Peulvorming trad op in planten die de eerste drie weken (dat is nog voor bloei) in de natuurlijk fotoperiode ($\geq$ 15,5 uur) waren opgegroeid, vervolgens 12 dagen in een fotoperiode van 12 uur en tenslotte tot de oogst in een fotoperiode van 14 uur hadden gestaan. Peulvorming kon nog steeds worden geïnduceerd in planten die 48 dagen oud waren en al meer dan 20 open bloemen hadden geproduceerd.

Het overzetten van planten van een fotoperiode van 12 naar 14 uur of *vice versa* resulteerde in beide herkomsten in verschillen in het aantal bloemen en peulen per plant, de bladsteellengte en de bladoppervlakte. De invloed van de fotoperiode was het meest uitgesproken op het aantal peulen per plant. Bladoppervlakte en aantal peulen per plant lijken geschikte parameters voor het modelleren van de peulgroei bij verschillende fotoperioden. De ontwikkeling van de bladoppervlakte was gerelateerd aan het aantal peulen per plant, maar werd daarnaast ook direkt beïnvloed door de heersende fotoperiode.

De samenhang tussen het tijdstip van peulinductie en de plaats van de peulen aan de plant (Hoofdstuk 5). Planten van herkomst 'Ankpa 4' werden gedurende 21, 28, 41 of 54 dagen bij een fotoperiode van 14 uur opgekweekt en daarna overgezet naar een

fotoperiode van 11 uur om de samenhang tussen het tijdstip van peulinductie en de plaats van de peulen aan de plant te bepalen. Tevens werden het begin van de bloei en de zaad opbrengst per plant geregistreerd.

Planten die na 28 of meer dagen werden overgezet, bloeiden eerder naarmate overzetting eerder plaatsvond. Planten die na 21 of 28 dagen waren overgezet, begonnen tegelijkertijd te bloeien, hetgeen wijst op juveniliteit. Bij de oogst (135 dagen na zaai) was het totaal zaad drooggewicht per plant hoger voor planten die na 41 of 54 dagen waren overgezet dan voor planten waarvoor dit na 21 dagen geschiedde. Planten die na 28 dagen waren overgezet gaven een tussenliggende waarde.

De meeste (79-91%) peulen werden gevormd op de zijassen die zich op de knopen 1 tot en met 4 van de hoofdas ontwikkelden. Er waren geen verschillen in de fractionele verdeling van de peulen over de hoofdas bij planten die na 28 of meer dagen waren overgezet. De peulen van planten die na 21 of 28 dagen waren overgezet, waren gelijkmatiger verdeeld over de knopen van de eerste twee primaire zijassen dan de peulen van planten die na 41 of 54 dagen waren overgezet. Planten van de laatstgenoemde behandelingen vormden hun peulen meer naar het uiteinde van de zijassen en geconcentreerd op twee naburige knopen (knopen 5 en 6 bij planten die na 41 dagen waren overgezet; knopen 6 en 7 bij planten die na 54 dagen waren overgezet). Uitstel van de inductie van peulvorming leidde in dit experiment aldus tot hogere zaad opbrengsten per plant en een meer gesynchroniseerde ontwikkeling - en dus rijping - van de peulen.

Fotothermale regulering van de ontwikkeling (Hoofdstuk 6). De fotothermale respons van het begin van de bloei (*f*) en het begin van de peulvorming (*p*) werden voor drie herkomsten bepaald in een factorieel experiment met vier fotoperioden en drie gemiddelde etmaal temperaturen. Het begin van de bloei werd gedefinieerd als de dag waarop de eerste bloem openging. Het begin van de peulvorming werd bepaald door lineaire regressie van peul drooggewichten op het aantal dagen na zaai.

Ontwikkelingssnelheden werden verkregen uit de reciproke waarden van f en p. In twee herkomsten, 'Ankpa 2' en 'Yola', begon de bloei onafhankelijk van de fotoperiode en werd $1/f$ alleen door de temperatuur bepaald, waarbij bloei eerder optrad bij 28.1 °C dan bij 20.2 °C. De derde herkomst, 'Ankpa 4', was gevoelig voor zowel de fotoperiode als de temperatuur en f werd vertraagd door verlaging van de temperatuur, door fotoperioden $>$ 12,66 uur bij 20.2 °C, alsmede door fotoperioden $>$ 11,33 uur bij 24.1 en 28.1 °C. In tegenstelling hiermee werd p in alle drie herkomsten beïnvloed door de temperatuur en de fotoperiode.

Klaarblijkelijk nam de gevoeligheid voor de fotoperiode toe tussen het begin van de bloei en het begin van de peulvorming. De meest fotoperiode-gevoelige herkomst ten aanzien van *p* was 'Ankpa 4', gevolgd door 'Yola' en 'Ankpa 2'. Er bestonden ook verschillen in gevoeligheid voor temperatuur tussen de onderzochte herkomsten.

Fotoregulering van de ontwikkeling en de groei (Hoofdstuk 7). De herkomsten 'Tiga Nicuru' en 'Ankpa 4' werden opgekweekt bij constante fotoperioden van 10, 12, 14 en 16 uur om de accumulatie van droge stof te bestuderen. De fotoperiode beïnvloedde alleen het begin van de bloei in herkomst 'Ankpa 4', echter het begin van de peulvorming in beide herkomsten. Bij fotoperioden van 14 en 16 uur vormden de planten van 'Ankpa 4' geen peulen. De fotoperiode had geen effekt op de totale bovengrondse droge-stof produktie in 'Ankpa 4' en slechts een klein effekt in 'Tiga Nicuru'. De fotoperiode oefende een indirekte invloed uit op de droge-stof verdeling via zijn invloed op de ontwikkeling: in beide herkomsten veranderde de verdeling van assimilaten na het door de fotoperiode geïnduceerde begin van de peulvorming. Daarnaast werd er een direkt effekt van de fotoperiode op de droge-stof verdeling waargenomen. Ten eerste bezaten, kort na het begin van de bloei (40 dagen na zaai), planten van 'Tiga Nicuru' bij een fotoperiode van 10 of 12 uur meer droge stof in de vorm van bladschijven en minder in de vorm van stengelmateriaal dan planten bij fotoperioden van 14 of 16 uur. Ten tweede was de toename in het totale drooggewicht van de peulen per plant bij 'Ankpa 4' bij een fotoperiode van 10 uur bijna twee maal zo groot als die bij een fotoperiode van 12 uur. Dit verschil was gerelateerd aan een kleiner aantal groeiende peulen bij de fotoperiode van 12 uur. De fotoperiode had kennelijk een grote invloed op het aantal groeiende sinks en, als gevolg daarvan, op de totale sink-sterkte van de plant. Dit was niet afhankelijk van de aanwezigheid van talloze vruchtbeginsels aan de planten van alle behandelingen, de planten van 'Ankpa 4' bij fotoperioden van 14 en 16 uur inbegrepen.

Landbouwkundige gevolgen en onderwerpen voor verder onderzoek (Hoofdstuk 8). De waargenomen fotoperiode-gevoeligheid voor het begin van de peulvorming in bambara aardnoot heeft voordelen boven de aanpassing aan de lengte van het groeiseizoen door middel van fotoperiode-gevoeligheid voor het begin van de bloei alleen, zoals in andere gewassen. Herkomsten met een zwakke reaktie op fotoperiode (d.w.z. ongunstige fotoperioden vertragen het begin van de peulvorming in geringe mate) hadden een kortere inductieve periode nodig om peulen te vormen dan herkomsten met een sterke reaktie op fotoperiode (d.w.z. ongunstige fotoperioden vertragen het begin van de peulvorming in aanzienlijke mate). Vroege inductie van de peulvorming resulteerde in lagere zaad opbrengsten, doordat planten hun assimilaten gebruikten voor vroege reproduktieve groei ten koste van verdere vegetatieve groei. Vroege inductie leidde ook tot een minder gesynchroniseerde ontwikkeling - en

bijgevolg rijping - van de peulen dan late inductie. De fotoperiode beïnvloedde tevens de droge-stof verdeling. Bij korte fotoperioden (10 en 12 uur) werd er minder droge stof in de vorm van stengelmateriaal aangetroffen dan bij langere fotoperioden (14 en 16 uur). Planten komen bij korte fotoperioden snel in produktie en behoeven daarom geen verdere vertakking voor de voortzetting van hun vegetatieve groei.

De fotoperiode-gevoeligheid van de peulvorming zorgt voor een tijdige afrijping van herkomsten op hun breedtegraad van oorsprong. Direkt zaaien na het begin van de regens stelt het gewas in de gelegenheid optimaal gebruik te maken van de lengte van het groeiseizoen. Daarom kunnen onder deze omstandigheden de hoogste opbrengsten worden verwacht. Zaaizaad voor het volgende gewas dient te worden verzameld van planten die de diversiteit in het hele veld vertegenwoordigen. Hierdoor wordt de heterogeniteit gehandhaafd die het de herkomst mogelijk maakt om flexibel te reageren op verschillen in omgevingsfaktoren.

Fotoperiode-gevoeligheid brengt met zich mee dat het noodzakelijk is voor de karakterisering van herkomsten de groeiomstandigheden te standaardiseren teneinde vergelijkbare resultaten te verkrijgen op verschillende lokaties. Fotoperiode-gevoeligheid dient te worden gehandhaafd bij het selekteren en veredelen van nieuwe cultivars. Aan de hand van een hypothetisch voorbeeld worden de gevolgen van fotoperiode-gevoeligheid geïllustreerd voor de verspreiding van herkomsten.

Voor verder experimenteel onderzoek naar de basisfaktoren die groei en ontwikkeling bepalen, wordt aanbevolen om genetisch homogener materiaal te gebruiken dan is gebeurd in de experimenten die in dit proefschrift worden beschreven. Bovendien dient er een methode te worden ontwikkeld waarmee op efficiënte en, bij voorkeur, niet-destructieve wijze het begin van de peulvorming kan worden vastgesteld. De teelt van bambara aardnoot onder volledig gecontroleerde omstandigheden zou aanzienlijk kunnen worden verbeterd door een lichtbron te ontwikkelen waarbij planten morfologisch gelijken op hun onder veldomstandigheden opgegroeide landrasgenoten.

Een onderwerp dat nader onderzoek behoeft betreft de invloed van de fotoperiode op de groeistadia na het begin van de peulvorming. Bovendien is het denkbaar dat de spreiding in de fotoperiode-gevoeligheid tussen bambara aardnoot herkomsten groter is dan in dit proefschrift wordt gerapporteerd. Tevens is onbekend of schemerlicht bijdraagt aan de lengte van de fotoperiode waaraan de plant wordt blootgesteld, en wat de invloed is van (de snelheid van) verandering in de fotoperiode. Kennis van temperatuurseffekten is schaars; de basis en optimum temperaturen voor ontwikkelings-processen moeten nog nader worden vastgesteld. Tenslotte dient de gewenste graad van heterogeniteit in landrassen te worden bepaald in relatie tot

mogelijke fluctuaties in de hoeveelheid en duur van de neerslag tussen de jaren. Deze heterogeniteit en de flexibiliteit in de ontwikkeling van de planten in relatie tot veranderingen in de fotoperiode verklaren grotendeels waarom het gewas kan produceren onder marginale omstandigheden in regen-afhankelijke gebieden.

References

Aiming, Q. (1990). Genetic characterisation of time to flowering in grain legumes. *Food Legume Newsletter* 13: 4-6.

Arnold, T.H. and K.J. Musil (1983). A preliminary survey of primitive crops cultivated in the northern Transvaal of South Africa. *Bothalia* 14: 595-601.

Bagnall, D.J. and R.W. King (1991a). Response of peanut (*Arachis hypogaea*) to temperature, photoperiod and irradiance. 1. Effect on flowering. *Field Crops Research* 26: 263-277.

Bagnall, D.J. and R.W. King (1991b). Response of peanut (*Arachis hypogaea*) to temperature, photoperiod and irradiance. 2. Effect on peg and pod development. *Field Crops Research* 26: 279-293.

Begemann, F. (1988). Ecogeographic Differentiation of Bambarra Groundnut (*Vigna subterranea*) in the Collection of the International Institute of Tropical Agriculture (I.I.T.A.). Wissenschaftlicher Fachverlag, Giessen. 153 pp.

Brooks, C.B.; R.B. Dadson and B.M. Green (1988). Evaluation of symbiotic effectiveness of elite and wild strains of *Bradyrhizobium* on cultivars of *Voandzeia subterranea* (L.) Thouars. *Tropical Agriculture* 65: 61-63.

Collinson, S.T.; R.J. Summerfield, R.H. Ellis and E.H. Roberts (1993). Durations of the photoperiod-sensitive and photoperiod-insensitive phases of development to flowering in four cultivars of soyabean [*Glycine max* (L.) Merrill]. *Annals of Botany* 71: 389-394.

Constable, G.A. and I.A. Rose (1988). Variability of soybean phenology response to temperature, daylength and rate of change in daylength. *Field Crops Research* 18: 57-69.

Coudert, J. (1984). Market openings in West Africa for cowpeas and bambara groundnuts. *International Trade Forum* 20(1): 14-15, 28-29.

Cure, J.D.; R.P. Patterson, C.D. Raper Jr., and W.A. Jackson (1982). Assimilate distribution in soybeans as affected by photoperiod during seed development. *Crop Science* 22: 1245-1250.

Dadson, R.B.; C.B. Brooks and J.G. Wutoh (1988). Evaluation of selected rhizobial strains grown in association with bambara groundnut (*Voandzeia subterranea* (L.) Thouars). *Tropical Agriculture* 65: 254-256.

Doku, E.V. (1969). Growth habit and pod production in bambara groundnut (*Voandzeia subterranea*). *Ghana Journal of Agricultural Science* 2: 91-95.

Ellis, R.H.; R.J. Lawn, R.J. Summerfield, A. Qi, E.H. Roberts, P.M. Chay, J.B. Brouwer, J.L. Rose and S.J. Yeates (1994a). Towards the reliable prediction of time to flowering in six annual crops. III. Cowpea *Vigna unguiculata*. *Experimental Agriculture* 30: 17-29.

Ellis, R.H.; R.J. Lawn, R.J. Summerfield, A. Qi, E.H. Roberts, P.M. Chay, J.B. Brouwer, J.L. Rose, S.J. Yeates and S. Sandover (1994b). Towards the reliable prediction of time to flowering in six annual crops. IV. Cultivated and wild mung bean. *Experimental Agriculture* 30: 31-43.

Flohr, M.-L.; J.H. Williams and F. Lenz (1990). The effect of photoperiod on the reproductive development of a photoperiod sensitive groundnut (*Arachis hypogaea* L.) cv. NC Ac 17090. *Experimental Agriculture* 26: 397-406.

Goli, A.E. and N.Q. Ng (1988). Harvesting period of bambarra groundnut for maximum yield and seed quality in the humid tropics. *Agronomy Abstracts of the 1988 Annual Meetings*: 55.

Hadley, P.; E.H. Roberts, R.J. Summerfield and F.R. Minchin (1983). A quantitative model of reproductive development in cowpea [*Vigna unguiculata* (L) Walp.] in relation to photoperiod and temperature, and implications for screening germplasm. *Annals of Botany* 51: 531-543.

Harris, D. and S.N. Azam-Ali (1993). Implications of daylength sensitivity in bambara groundnut (*Vigna subterranea*) for production in Botswana. *Journal of Agricultural Science* 120: 75-78.

IBPGR/IITA/GTZ (1987). Descriptors for Bambara Groundnut. International Board for Plant Genetic Resources, Rome. 23 pp.

IITA (1987). IITA Annual Report and Research Highlights 1986. Ibadan. p. 138.

Johnson, D.T. (1968). The bambarra groundnut: a review. *Rhodesia Agricultural Journal* 65(1): 1-4.

Kay, D.E. (1979). Food Legumes. Crop and Product Digest 3. Tropical Products Institute, London. pp. 17-25.

Kowal, J.M. and D.T. Knabe (1972). An Agroclimatical Atlas of the Northern States of Nigeria, with Explanatory Notes. Ahmadu Bello University Press, Zaria. p. 23.

Lawn, R.J. (1989). Agronomic and physiological contraints to the productivity of tropical grain legumes and prospects for improvement. *Experimental Agriculture* 25: 509-528.

Linnemann, A.R. (1986). Bambara groundnut (*Vigna subterranea* (L.) Verdc.): an annotated bibliography. Tropical Crops Communication No. 11. Wageningen Agricultural University, Department of Tropical Crop Science, Wageningen. 39 pp.

Linnemann, A.R. (1987). Bambara groundnut (*Vigna subterranea* (L.) Verdc.) - a review. *Abstracts on Tropical Agriculture* 12(7): 9-25.

Linnemann, A.R. (1988). Cultivation of bambara groundnut (*Vigna subterranea* (L.) Verdc.) in Northern Nigeria. Report of a field study. Tropical Crops Communication No. 15. Wageningen Agricultural University, Department of Tropical Crop Science, Wageningen. 14 pp.

Linnemann, A.R. (1990). Cultivation of bambara groundnut (*Vigna subterranea* (L.) Verdc.) in Western Province, Zambia. Report of a field study. Tropical Crops Communication No. 16. Wageningen Agricultural University, Department of Tropical Crop Science, Wageningen. 34 pp.

Linnemann, A.R. (1991). Preliminary observations on photoperiod regulation of phenological development in bambara groundnut (*Vigna subterranea*). *Field Crops Research* 26: 295-304.

Linnemann, A.R. (1992). Bambara groundnut (*Vigna subterranea*) literature: A revised and updated bibliography. Tropical Crops Communication No. 17. Wageningen Agricultural University, Department of Tropical Crop Science, Wageningen. 124 pp.

Linnemann, A.R. (1993). Phenological development in bambara groundnut (*Vigna subterranea*) at constant exposure to photoperiods of 10 to 16 h. *Annals of Botany* 71: 445-452.

Linnemann, A.R. (in press). Phenological development in bambara groundnut (*Vigna subterranea*) at alternate exposure to 12 and 14 h photoperiods. *Journal of Agricultural Science*.

Linnemann, A.R. (submitted). Phenological development in bambara groundnut (*Vigna subterranea*) transferred from 14-h to 11-h photoperiods. *Journal of Agricultural Science*.

Linnemann, A.R. and S. Azam-Ali (1993). Bambara groundnut (*Vigna subterranea*). In: Williams, J.T. (Ed.). Pulses and Vegetables. Chapman & Hall, London. pp. 13-58.

Linnemann, A.R. and P.Q. Craufurd (in press). Effects of temperature and photoperiod on phenological development in three genotypes of bambara groundnut (*Vigna subterranea*). *Annals of Botany*.

Lipton, M. (1990). Foreword. In: Singh, I. The Great Ascent: The Rural Poor in South Asia. Johns Hopkins University Press, Baltimore. pp. xv-xxiii.

Major, D.J. and J.R. Kiniry (1991). Predicting daylength effects on phenological processes. In: Hodges, T. (Ed.). Predicting Crop Phenology. CRC Press, Boca Raton, Florida. pp. 15-28.

Mayers, J.D.; R.J. Lawn and D.E. Byth (1991). Adaptation of soybean (*Glycine max* (L.) Merrill) to the dry season of the tropics. I. Genotypic and environmental effects on phenology. *Australian Journal of Agricultural Research* 42: 497-515.

Morandi, E.N.; L.M. Casano and L.M. Reggiardo (1988). Post-flowering photoperiodic effect on reproductive efficiency and seed growth in soybean. *Field Crops Research* 18: 227-241.

Msekera Regional Research Station (1989). GRZ/UNDP/FAO food legumes research (ZAM/86/003). Annual Report 1988-89 (Part B). Chipata, Zambia. pp. 124-129.

Munsell Color Charts for Plant Tissues (1972). Second, revised edition. Munsell Color Division, Baltimore.

National Research Council (1979). Bambara groundnut. In: Tropical Legumes, Resources for the Future. National Academy of Sciences, Washington. pp. 47-53.

Nishitani, T.; K. Muraki and J. Inoue (1988). Effect of daylength on the flowering and fruiting in bambarra groundnut (*Vigna subterranea* (L.) Verdec.). *Japanese Journal of Tropical Agriculture* 32: 80-84.

Rachie, K.O. and P. Silvestre (1977). Grain legumes. In: Leakey, C.L.A. and J.B. Wills (Eds). Food Crops of the Lowland Tropics. Oxford University Press, Oxford. pp. 41-74.

Roberts, E.H. and R.J. Summerfield (1987). Measurement and prediction of flowering in annual crops. In: Atherton, J.G. (Ed.). Manipulation of Flowering. Butterworths, London. pp. 17-50.

Roberts, E.H.; R.J. Summerfield, P. Hadley and R.H. Ellis (1988). Research on the control of flowering at the Plant Environment Laboratory, Reading University, UK. *Flowering Newsletter* 5: 2-10.

Sass, J.E. (1964). Botanical Microtechnique. Iowa State University Press, Ames, Iowa. 228 pp.

Sellschop, J.P.F. (1962). Cowpeas, (*Vigna unguiculata* (L.) Walp. *Field Crop Abstracts* 15: 259-266.

Shanmugasundaram, S. and M.S. Lee (1981). Flower-inducing potency of different kinds of leaves in soybean, *Glycine max* (L.) Merr. *Botanical Gazette* 142: 36-39.

Siemonsma, J.S. (1982). La Culture du Gombo (*Abelmoschus* spp.), Légume-fruit tropical avec référence spéciale à la Côte d'Ivoire. Landbouwhogeschool, Wageningen. p. 272.

Sivakumar, M.V.K.; M. Konate and S.M. Virmani (1984). Agroclimatology of West Africa: Mali. Information Bulletin no. 19. International Crops Research Institute for the Semi-Arid Tropics, Patancheru. pp. 41-43.

Squire, G.R. (1990). The Physiology of Tropical Crop Production. C.A.B International, Wallingford. pp. 22-25.

Stanley, R.G. and H.F. Linskens (1974). Pollen. Springer Verlag, Berlin. p. 67-70.

Stanton, W.R.; J. Doughty, R. Orraca-Tetteh and W. Steele (1966). *Voandzeia subterranea* Thouars. In: Grain Legumes in Africa. Food and Agriculture Organization, Rome. pp. 128-133.

Steele, W.M.; D.J. Allen and R.J. Summerfield (1985). Cowpea (*Vigna unguiculata* (L.) Walp.). In: Summerfield, R.J. and E.H. Roberts (Eds). Grain Legume Crops. Collins, London. p. 520-583.

Summerfield, R.J.; R.J. Lawn, A. Qi, R.H. Ellis, E.H. Roberts, P.M. Chay, J.B. Brouwer, J.L. Rose, S. Shanmugasundaram, S.J. Yeates and S. Sandover (1993). Towards the reliable prediction of time to flowering in six annual crops. II. Soyabean (*Glycine max*). *Experimental Agriculture* 29: 253-289.

Summerfield, R.J. and E.H. Roberts (1987). Effects of illuminance on flowering in long- and short-day grain legumes: a reappraisal and unifying model. In: Atherton, J.G. (Ed.). Manipulation of Flowering. Butterworths, London. pp. 203-223.

Summerfield, R.J.; E.H. Roberts, R.H. Ellis and R.J. Lawn (1991). Towards the reliable prediction of time to flowering in six annual crops. I. The development of simple models for fluctuating field environments. *Experimental Agriculture* 27: 11-31.

Summerfield, R.J. and H.C. Wien (1980). Effects of photoperiod and air temperature on growth and yield of economic legumes. In: Summerfield, R.J. and A.H. Bunting (Eds). Advances in Legume Science. HMSO, London. pp. 17-35.

Swanevelder, C.J. (1991). Bambara groundnuts. In: Report on Research and other Activities of the Oil and Protein Seed Centre 1989/90. Grain Crops Research Institute, Potchefstroom, South Africa. p. 39.

Tanimu, B. and J.Y. Yayock (1990). Bambaranut agronomy. In: Cropping Scheme Report 1990. Legumes and oilseeds research programme. Ahmadu Bello University, Institute of Agricultural Research, Zaria, Nigeria.

Tieghem, Ph. van (1869). Recherches physiologiques sur la végétation libre du pollen et de l'ovule et sur la fécondation directe des plantes. Annales des Sciences Naturelles. Botanique 5, Serie 12, t., 312-329.

Wien, H.C. and R.J. Summerfield (1980). Adaptation of cowpeas in West Africa: effects of photoperiod and temperature response in cultivars of diverse origin. In:

Summerfield, R.J. and A.H. Bunting (Eds). Advances in Grain Legume Research. HMSO, London. p. 405-417.

Wallace, D.H. (1985). Physiological genetics of plant maturity, adaptation, and yield. In: Janick, J. (Ed.). Plant Breeding Reviews. Volume 3. Avi Publishing Company, Westport. pp. 21-167.

Wallace, D.H.; R.W. Zobel and K.S. Yourstone (1993). A whole-system reconsideration of paradigms about photoperiod and temperature control of crop yield. *Theoretical and Applied Genetics* 86: 17-26.

Wareing, P.F. (1987). Juvenility and cell determination. In: Atherton, J.G. (Ed.). Manipulation of Flowering. Butterworths, London. pp. 83-92.

Witzenberger, A. (1987). Einfluss unterschiedlich gestalteter Photoperiode- und "Kylar"-Behandlungen auf das vegetative und reproduktive Wachstum mehrerer Erdnuss-Genotypen (*A. hypogaea* L.). Ph.D. Thesis. Rheinischen Friedrich-Wilhelms-Universität, Bonn, Germany. 203 pp.

Witzenberger, A.; J.H. Williams and F. Lenz (1988). Influence of daylength on yield-determining processes in six groundnut cultivars (*Arachis hypogaea*). *Field Crops Research* 18: 89-100.

List of publications and reports

1981 Linnemann, A.R. Preservation of certain tropical root and tuber crops. *Abstracts on Tropical Agriculture* 7(1): 9-20.

1985 Linnemann, A.R.; A. van Es and K.J. Hartmans. Changes in the content of L-ascorbic acid, glucose, fructose, sucrose and total glycoalkaloids in potatoes (cv. Bintje) stored at 7, 16 and 28 °C. *Potato Research* 28: 271-278.

1986 Linnemann, A.R. Agriculture in the semi-arid tropics; a review of current research and developments. International Course on Development Oriented Research in Agriculture, Wageningen. 48 pp.

Linnemann, A.R. Bambara groundnut (*Vigna subterranea* (L.) Verdc.): an annotated bibliography. Tropical Crops Communication No. 11. Department of Tropical Crop Science, Wageningen Agricultural University. 39 pp.

Linnemann, A.R.; S. Hitipeuw, B. Kruiger and E. Westphal. Influence of potassium fertilizer on yield of upland kangkong (*Ipomoea aquatica* Forsk.). *Netherlands Journal of Agricultural Science* 34: 503-505.

Linnemann, A.R.; J.M. Louwen, G.H.M.B. Straver and E. Westphal. Influence of nitrogen on sown and ratooned upland kangkong (*Ipomoea aquatica* Forsk.) at two planting densities. *Netherlands Journal of Agricultural Science* 34: 15-23.

1987 Linnemann, A.R. Bambara groundnut (*Vigna subterranea* (L.) Verdc.) - a review. *Abstracts on Tropical Agriculture* 12(7): 9-25.

Linnemann, A.R. and G.H. de Bruijn. Traditional seed supply for food crops. *ILEIA Newsletter* 3(2): 10-11.

1988 Bruijn, G.H. de, en A.R. Linnemann. Boerenmethoden zaaizaad-voorziening verdienen meer aandacht. *Landbouwkundig Tijdschrift* 100(1): 29-31.

Bruijn, G.H. de, en A.R. Linnemann. Caput-werkcollege Zaaizaad- en plantgoedvoorziening in de tropen (F400-100). Vakgroep Tropische Plantenteelt, Landbouwuniversiteit Wageningen. 51 pp.

Groosman, T.; A. Linnemann and H. Wierema. Technology Development and Changing Seed Supply Systems. Seminar proceedings, 22-23 June 1988. Research Report No. 27. Instituut voor Ontwikkelingsvraagstukken, Tilburg. 86 pp.

Linnemann, A.R. Cultivation of bambara groundnut (*Vigna subterranea* (L.) Verdc.) in Northern Nigeria. Report of a field study. Tropical Crops Communication No. 15. Department of Tropical Crop Science, Wageningen Agricultural University. 14 pp.

1989 Linnemann, A.R. *Vigna subterranea* (L.) Verdc. In: Van der Maesen, L.J.G. and Sadikin Somaatmadja (eds). Plant Resources of South-East Asia. 1.Pulses. Pudoc, Wageningen. p. 74-75.

Linnemann, A.R. and J.S. Siemonsma. Variety choice and seed supply by smallholders. *ILEIA Newsletter* 5(4): 22-23.

Siemonsma, J.S. and A.R. Linnemann. Seed supply and variety choice in low-input agriculture; a case study of soybean in Pasuruan, East-Java, Indonesia. In: Groosman, T. (Ed.). Seed industry development; developing coutries' experiences in different crops. Research Report No. 34. Instituut voor Ontwikkelingsvraagstukken, Tilburg. p. 67-76.

1990 Linnemann, A.R. Cultivation of bambara groundnut (*Vigna subterranea* (L.) Verdc.) in Western Province, Zambia. Report of a field study. Tropical Crops Communication No. 16. Department of Tropical Crop Science, Wageningen Agricultural University. 34 pp.

1991 Groosman, T.; A. Linnemann and H. Wierema. Seed industry development in a north/south perspective. Pudoc, Wageningen. 107 pp.

Linnemann, A.R. Preliminary observations on photoperiod regulation of phenological development in bambara groundnut (*Vigna subterranea*). *Field Crops Research* 26: 295-304.

Linnemann, A.R. Influence of photoperiod on development of bambara groundnut (*Vigna subterranea* (L.) Verdc.). *Acta Botanica Neerlandica* 40(4): 374.

1992 Linnemann, A.R. Bambara groundnut (*Vigna subterranea*) literature. A revised and updated bibliography. Department of Tropical Crop Science, Wageningen Agricultural University, Wageningen. 124 pp.

1993 Linnemann, A.R. Phenological development in bambara groundnut (*Vigna subterranea*) at constant exposure to photoperiods of 10 to 16 h. *Annals of Botany* 71: 445-452.

Linnemann, A.R. and S. Azam-Ali. Bambara groundnut (*Vigna subterranea*). In: Williams, J.T. (Ed.). Pulses and Vegetables. Chapman & Hall, London. pp. 13-58.

in press Linnemann, A.R. Phenological development in bambara groundnut (*Vigna subterranea*) at alternate exposure to 12 and 14 h photoperiods. *Journal of Agricultural Science*.

Linnemann, A.R. and P.Q. Craufurd. Effects of temperature and photoperiod on phenological development in three genotypes of bambara groundnut (*Vigna subterranea*). *Annals of Botany*.

accepted Linnemann, A.R.; M. Wessel and E. Westphal. Photoperiod regulation of development and growth in bambara groundnut (*Vigna subterranea*). *Field Crops Research*.

Curriculum vitae

Anita Rachel Linnemann was born on 19 December 1957 in Rotterdam, The Netherlands. She obtained her Gymnasium-ß diploma at the Christelijke Scholengemeenschap 't Loo in Voorburg in 1976, and, in the same year, started her studies in Tropical Crop Science at Wageningen Agricultural University, The Netherlands. After obtaining her 'kandidaats' diploma (cum laude) in 1980, she spent her practical training period on research on tomato and Chinese cabbage at the Asian Vegetable Research and Development Centre in Taiwan. She obtained her 'ingenieurs' diploma in 1985 with specializations in Tropical Crop Science, Food Technology and Phytopathology.

During the last years (1983-84) of her degree studies she worked as a course assistant for the International Course on Vegetable Growing and the International Course on development-oriented Research in Agriculture (ICRA). The Department of Tropical Crop Science, Wageningen Agricultural University employed her in this period to prepare of two scientific publications on the leaf vegetable kangkong (*Ipomoea aquatica* Forsk.), and she wrote lecture notes on agriculture in semi-arid areas for the ICRA curriculum.

In 1985, she contributed to the development of the problem-oriented course 'Praktijksimulatie Tropen' for first-year students of the Department of Tropical Crop Science. In 1986, she was asked to collaborate part-time in a research project called "Technology Development and the Seed Industry in a North-South Perspective". This project involved institutes in India (Indian Agricultural Research Institute), Kenya (Institute of Development Studies), Thailand (Thailand Development Research Institute) and two institutions in The Netherlands (Development Research Institute, Tilburg, and the Department of Tropical Crop Science). In 1987, she was appointed as a trainee research assistant at the Department of Tropical Crop Science for the research on the bambara groundnut which resulted in this thesis.