MATCHING CROPS AND ENVIRONMENTS: QUANTIFYING PHOTOTHERMAL INFLUENCES ON REPRODUCTIVE DEVELOPMENT IN BAMBARA GROUNDNUT (VIGNA SUBTERRANEA (L.) VERDC.)

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STELLINGEN

1. De zon is de meest onderbenutte natuurlijke hulpbron.

2. Bij onderzoek naar de effecten van temperatuur en fotoperiode op de reproductieve ontwikkeling van peulvruchten moet zowel naar de bloei als naar de vruchtzetting worden gekeken.
   Dit proefschrift.

3. De effecten van temperatuur en fotoperiode op de vruchtzetting van bambara aardnoot kunnen op dezelfde wijze worden gekwantificeerd als hun effecten op de bloei.
   Dit proefschrift.

4. Een geleidelijke toename of afname van de fotoperiode heeft in bambara aardnoot geen invloed op de ontwikkelingssnelheid van bloei tot peulvorming, hetgeen betekent dat de ontwikkelingssnelheid per dag berekend kan worden op basis van de fotoperiode en temperatuur van die dag en dat deze dagelijkse ontwikkelingssnelheden kunnen worden geaccumuleerd.
   Dit proefschrift.

5. Wil de Landbouwuniversiteit een 'Werelduniversiteit' blijven, dan dient zij er zorg voor te dragen dat haar kennis en ervaring op het gebied van de landbouw in de tropen op peil worden gehouden.

6. In tegenstelling tot wat termen als 'natuurbescherming' en 'natuurbehoud' doen vermoeden, kan 'de natuur' niet worden vernietigd.

7. Het is een misverstand te menen dat natuurlijke geneesmiddelen per definitie minder schadelijk zijn dan synthetische medicijnen.

8. De mens is ook maar een dier.

Frans de Waal, 1996. Good natured: the origins of right and wrong in humans and other animals. Harvard University Press, Cambridge, U.S.A. 296 pp.

9. Pas als de politieke kleur van kandidaten en niet hun nationaliteit doorslaggevend is bij benoemingen voor Europese topfuncties, is er werkelijk sprake van Europese éénwording.

10. Het woord 'kinderachtig' heeft geheel ten onrechte een negatieve betekenis.

11. "Al ligt een boomstam nog zo lang in het water, hij wordt nooit een krokodil."

Mandinka spreekwoord.

Martin Brink

Matching crops and environments: quantifying photothermal influences on reproductive development in bambara groundnut (*Vigna subterranea* (L.) Verdc.)

Wageningen, 5 juni 1998

ABSTRACT

The extent to which crops are adapted to specific environments greatly depends on how their development is affected by climatic factors. Development in bambara groundnut (*Vigna subterranea* (L.) Verdc.) is known to be influenced by temperature and photoperiod. The objective of this study was to quantify the influence of these factors on reproductive development in selections from different origins. Models relating development rates to photoperiod and temperature with linear equations were made for different bambara groundnut selections on the basis of research in semi-controlled environments. The photoperiod and temperature responses could be explained very well by the photothermal conditions in the regions where the selections were obtained. Validation of the models with the results of glasshouse and field experiments showed good to reasonable agreement between observed and predicted times to flowering and podding. It is shown that the average photoperiod between flowering and podding determines the rate from flowering to podding, and that a gradual increase or decrease in photoperiod does not affect that rate. This means that photothermal models intended to predict bambara groundnut development in field situations with fluctuating photoperiods can be based on studies with constant photoperiods. It is also shown that growth and development in bambara groundnut are largely independent and that there are no strong direct photoperiod effects on dry matter partitioning. The usefulness of photothermal development models for identifying suitable selections for different locations and sowing dates is demonstrated in a simulation study for Botswana. It is concluded that the influence of photoperiod and temperature on bambara groundnut development can be quantified through descriptive linear models, using data from semi-controlled environment experiments with constant temperatures and photoperiods. These quantitative models, either on their own or incorporated into a crop growth model; can be useful instruments for matching bambara groundnut genotypes and specific environments.

Keywords: bambara groundnut (*Vigna subterranea*), photoperiod, temperature, development, phenology, flowering, podding, modelling.

Erratum

The text on p.88 should be:

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Dedicated to the memory of my brother Karel

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PREFACE

This thesis is the tangible result of five years of work on the relatively unknown African food crop bambara groundnut. The study was carried out in the framework of the international research programme *Evaluating the potential for bambara groundnut as a food crop in semi-arid Africa*, supported by the Life Sciences and Technologies for Developing Countries Programme of the European Union. I sincerely hope that this thesis will not only help to evaluate, but also help to fulfil the potential of this crop, and that it will make a contribution, however small, to increased food security in Africa.

Many people have been involved in the work that led to this thesis. First of all, I want to express my gratitude to my co-promotor Egbert Westphal for his day-to-day guidance from the earliest beginnings to the conclusion of this project. Egbert, I greatly appreciate that your door was always open for me to discuss what I had on my mind. Your continuous support, enthusiasm and optimism were very encouraging. I also want to thank my promotors Marius Wessel and Rudy Rabbinge for their patient and positive supervision. Both of you were always ready to discuss plans and papers. My predecessor, bambara groundnut pioneer Anita Linnemann, is gratefully acknowledged for sharing her extensive knowledge of the crop. Her help enabled me to make a flying start. My colleagues at the Department of Agronomy, TUPEA and PROSEA are thanked for their help and for the interest they showed.

Within the EU-programme, Wageningen Agricultural University co-operated with Botswana College of Agriculture (Botswana), Njala University College (Sierra Leone), Sokoine University of Agriculture (Tanzania) and the University of Nottingham (U.K.). I want to thank Dr Azam-Ali, Dr Collinson, Prof. Karikari, Mrs Kwerepe, Dr Munthali, Mr Ramolemana, Dr Sesay, Dr Sibuga, Dr Tarimo, Dr Wigglesworth and all others involved in the EU-programme for the pleasant cooperation and the hospitality during my visits to the partner institutions.

The heart of this thesis is a series of experiments carried out in Wageningen from 1993 to 1996. Several students participated in the experimental work: Saït Drammeh, Ana Cristina Garcez, Alwin Kamstra, Ralf Köhne and Sérgio Mateus are thanked for their commitment and enthusiasm, which persisted through many hours of tedious work. Joke Belde, Ildiko van de Linde and Sandra Bot were very helpful and patient in the execution of the experiments, observational work and harvesting. Anton Houwers, Tek-An Lie and Martin Muilenburg are acknowledged for supplying *Rhizobium* for the experiments. I am grateful to Willem Keltjens and Jeanne Dijkstra for their advice on matters regarding nutrient supply and plant diseases respectively. Many people of UNIFARM have been involved in the organization and execution of the experiments. I especially want to thank Ton Blokzijl, Theo Damen, Wim den Dunnen, Gerrit van Geerenstein, Jan van der Pal, Casper Pillen, Harry Scholten, Taede Stoker, Gerrit Timmer, Evert Verschuur and Rinus van de Waart. Jack van Zee provided technical assistance and made the cover photograph of the flower and the pods.

The information collected in the experiments had to be analysed and written up. I thank Gerrit Gort and Martin van Montfort for their assistance with the statistical analysis. Dr Craufurd (the University of Reading) is acknowledged for providing the RoDMoD computer programme and Dr Collinson (the University of Nottingham) for providing a programme to analyse reciprocal transfer experiments. Drafts of most chapters of this thesis were discussed in group 1 of the C.T. de Wit Graduate School for Production Ecology. The participants in this discussion group are sincerely thanked for their very useful contributions. The comments of Conny Almekinders, Joost Brouwer, Jan Goudriaan, Herman van Keulen, Anita Linnemann, Tjeerd Jan Stomph, Paul Struik, Jan Vos and Jan Wienk on parts of this thesis are also very much appreciated. Joy Burrough-Boenisch corrected most parts of this thesis, and Helen West and Joost Brouwer smaller sections. Any remaining language errors present in this thesis are certainly due to my incorrigible habit of making last-minute changes to 'final' versions.

Finally, I want to thank my family. My parents always encouraged me in my studies and helped me to arrive at where I am at the moment. Corry is thanked for her understanding and support during the past years, in which this thesis took up a large part of my time, thoughts and energy. My son Lukas has enriched and livened up my life in the past two years.

CHAPTER 1

GENERAL INTRODUCTION

1 GENERAL INTRODUCTION

1.1 Matching crops and environments

A substantial increase in food production has been achieved in the more humid parts of the tropics in the last 50 years, particularly in Asia, where crop yields have increased through the use of high-yielding cultivars, fertilizers, irrigation and improved cropping practices. In semi-arid Africa, on the other hand, food production has hardly increased. Here, the techniques that could overcome existing production constraints are not available or affordable for the large majority of farmers. Under these conditions, an alternative, more realistic approach to increase food production may be to grow crops and crop genotypes that are adapted to existing production constraints like low rainfall and poor soils, instead of trying to overcome these constraints by applying irrigation and fertilizers. In other words, a strategy of matching crops and environments instead of trying to control and change environments.

One crop considered to be adapted to semi-arid Africa, is the grain legume bambara groundnut (*Vigna subterranea* (L.) Verdc.). Bambara groundnut has the advantages of legumes in general (Smil, 1997): it is able to fix atmospheric nitrogen through symbiosis with *Rhizobium* bacteria, it has a high protein content, and it can be consumed in many ways. Additionally, it is reported to give reasonable yields in regions where soils are too poor and rainfall is too low for other legumes like groundnut (*Arachis hypogaea* L.), cowpea (*Vigna unguiculata* (L.) Walp.) and common bean (*Phaseolus vulgaris* L.) (Linnemann and Azam-Ali, 1993).

In 1992, the international research programme *Evaluating the potential for bambara groundnut as a food crop in semi-arid Africa* was started with funding from the European Union and involving institutions from Botswana, Tanzania, Sierra Leone, the United Kingdom and The Netherlands. The objectives of this programme were: (1) to identify suitable agro-ecological regions and seasons for the cultivation of bambara groundnut in Tanzania, Botswana and Sierra Leone; (2) to produce a validated model of bambara groundnut for predicting biomass and pod yields of different genotypes in contrasting environments; (3) to identify the physiological attributes associated with the ability of bambara groundnut to produce yields under semi-arid conditions; (4) to recommend suitable management practices to stabilise the yields of bambara groundnut under rainfed conditions; and (5) to outline a methodology for applying a similar approach to rapidly assess the potential of other underutilised species in tropical environments (Azam-Ali, 1997).

The present study, undertaken within the framework of this programme and carried out in The Netherlands, investigates environmental effects on development in bambara groundnut. Development is an important aspect of plant adaptation to environments, because a successful match of crops and environments requires that crops complete their reproductive development within the available growing season and have an optimal balance between vegetative and reproductive phases. Furthermore, critical stages of their development should not coincide with unfavourable conditions (Loomis and Connor, 1992). Quantification of the influence of environmental factors on development in different bambara groundnut genotypes is a step in the process of matching crops and crop genotypes to specific environments.

1.2 Bambara groundnut

Bambara groundnut is an indeterminate annual herb, with creeping stems carrying trifoliolate leaves with erect petioles. Flowers form at the base of the petioles, usually in pairs. Self-pollination is the rule. After pollination and fertilization, the peduncle grows and pods form on or under the ground. The pods usually contain one seed, which may be cream, white, red, black, purple or brown. Some genotypes have an eye around the hilum; the eye varies in colour and shape (IBPGR/IITA/GTZ, 1987).

The area of origin of bambara groundnut extends from northern Nigeria to Cameroon (Hepper, 1970). At present, the major producers are Nigeria, Niger, Ghana, Burkina Faso and Ivory Coast, but the crop is also widely grown in eastern and southern Africa and in Madagascar (Appa Rao et al., 1986; Linnemann and Azam-Ali, 1993). It is not important outside Africa. Reliable production figures are difficult to obtain, because the crop is mainly grown for home consumption and sale at local markets (Hepper, 1970; Goli et al., 1991). The annual world production is estimated to be around 330,000 MT, with 45-50% produced in West Africa (Coudert, 1982).

Bambara groundnut is primarily grown for the seeds, which are used as food, but the vegetative parts may be used as fodder (Hepper, 1970). An important advantage of bambara groundnut is that not only mature, but also immature seeds can be consumed by humans. These immature seeds can be used to fill the 'hungry gap' during the growing season, when stores are empty and the main crops are not yet harvestable. The time from sowing to maturity in the field is reported to range from 90 to 170 days (Doku and Karikari, 1971; Linnemann and Azam-Ali, 1993).

Farmers value bambara groundnut because it has multiple uses, tastes good, tolerates poor soils, is relatively free of diseases and pests, and tolerates drought (Linnemann and Azam-Ali, 1993). The drought tolerance of bambara groundnut has been confirmed in glasshouse experiments, where bambara groundnut gave seed yields equivalent to 300 kg ha^{-1} under levels of drought where groundnut failed to even produce pods (Linnemann and Azam-Ali, 1993).

1.3 Environmental influences on development in grain legumes

Photoperiod and temperature play an important role in the regulation of development in grain legumes (Summerfield and Wien, 1980). The most obvious example is soya bean (*Glycine max* (L.) Merrill), which has been a pioneer crop in photoperiod research. Early this century, it was found that flowering in soya bean may be delayed by long photoperiods and that genotypes differ in their response to photoperiod (Garner and Allard, 1920, 1923, 1930). It is now known that soya bean is sensitive to photoperiod and temperature in all phases from flowering to maturity (Johnson et al., 1960; Morandi et al., 1988; Grimm et al., 1993, 1994).

Groundnut, on the other hand, has long been considered a day-neutral plant (Fortanier, 1957). More recent research has shown that the appearance of the first flower may be unaffected by photoperiod, but that photoperiod does influence development after the onset of flowering: flower, peg and pod numbers are higher under short days than under long days (Wynne at al., 1973; Emery et al., 1981; Flohr et al., 1990; Bagnall and King, 1991a, 1991b; Bell et al., 1991).

With respect to cowpea, it has long been known that the appearance of flower buds and open flowers may be retarded under long photoperiods (Njoku, 1958; Wienk, 1963). Photoperiod effects on the appearance of flower buds, flowers and mature pods are modified by temperature (Hadley et al. 1983a).

In common bean, all stages of the life cycle may be sensitive to photoperiod (Evans, 1993). The onset of flowering has been found to be unaffected by photoperiod in some genotypes and retarded by long photoperiods in others (White and Laing, 1989). In mungbean (*Vigna radiata* (L.) Wilczek), lentil (*Lens culinaris* Medic.), chickpea (*Cicer arietinum* L.) and faba bean (*Vicia faba* L.), the time to flowering is reported to be sensitive to photoperiod and temperature (Roberts et al., 1985; Summerfield, et al., 1985; Ellis et al., 1990; Imrie and Lawn, 1990).

Development in bambara groundnut is known to be influenced by temperature and photoperiod, and there are large differences between genotypes in their response to these factors. Glasshouse experiments at Wageningen Agricultural University have shown that the onset of flowering in most genotypes is photoperiod-insensitive, but that long photoperiods retard the onset of pod growth ('podding'). Of the 13 genotypes studied by Linnemann (1994a), only 'Ankpa4' from Nigeria appeared to be photoperiod-sensitive with regard to flowering, while all were photoperiod-sensitive with regard to podding. The finding that the onset of flowering in bambara groundnut may be photoperiod-insensitive but the onset of podding photoperiod-sensitive has been confirmed in a field experiment in Botswana (Harris and Azam-Ali, 1993).

1.4 Quantifying the influence of environmental factors on development

Quantifying the influence of environmental factors on crop development can be very useful for the design of genotype-management combinations (Loomis and Connor, 1992) and is an important aspect of the development of crop growth simulation models (Jones et al., 1991). Multi-locational field trials or controlled environment experiments may be used to identify the influencing factors and to quantify their effects. One advantage of controlled-environment experiments is that they make it easier to separate the effects of photoperiod, temperature and other factors. Another advantage is that constant temperature and photoperiod conditions can be imposed. Whether multi-locational field trials or controlled-environment experiments are used, the range of photoperiod and temperature conditions included must be carefully chosen and sufficiently wide. Given that photoperiod response is genotype-specific, this response has to be quantified for each genotype.

Much work has been done to characterize the effects of photoperiod and temperature effects on development in soya bean. Different types of models have been developed, including linear models (Hadley et al., 1984; Mayers et al., 1991; Summerfield et al., 1993), linear-plateau models (Grimm et al., 1993) and logistic models (Sinclair et al., 1991). These models have been based on controlled-environment experiments (e.g. Hadley et al., 1984) or field experiments (Mayers et al., 1991; Sinclair et al., 1991; Grimm et al., 1993). Although much of the research on photoperiod effects in soya bean has focused on flowering, there have been some attempts to quantify the effects of environmental factors on development stages beyond flowering (Major et al., 1975; Hodges and French, 1985; Mayers et al., 1991; Grimm et al., 1994). The phenology part of the SOYGRO crop growth model includes all phases from flower initiation to maturity (Jones et al., 1991).

For groundnut, temperature effects on the onset of flowering have been quantified for several genotypes in glasshouse and growth chamber studies (Bagnall and King, 1991a; Nigam et al, 1994). Leong and Ong (1983) quantified the effects of temperature on flowering, pegging and podding of one cultivar ('Robut 33-1'), but they did not investigate photoperiod effects.

With respect to cowpea, the effects of photoperiod and temperature on the first appearance of flower buds, flowers and mature pods have been quantified with linear models based on controlled environment experiments (Hadley et al., 1983a). Linear flowering models have also been developed on the basis of field experiments (Ellis et al., 1994a).

Less work has been done on other legumes. For mungbean (Imrie and Lawn, 1990; Ellis et al., 1994b), chickpea (Roberts et al., 1985; Ellis et al., 1994c), lentil (Summerfield et al., 1985; Erskine et al., 1994) and faba bean (Ellis et al., 1990) the influence of photoperiod and temperature on flowering of different genotypes has been characterized through linear models based on controlled-environment or field experiments.

For bambara groundnut, a first attempt to quantify the influence of photoperiod and temperature on the onset of flowering and podding was carried out on three Nigerian genotypes (Linnemann and Craufurd, 1994). The present study builds further on this by quantifying the photothermal responses of selections from more diverse origins, validating the models with independent data and using the models in a field situation.

1.5 Research objective and methodology

The objective of this study is to quantify the influence of photoperiod and temperature on development in bambara groundnut selections from different origins on the basis of controlled environment research. The resulting quantitative models should be able to predict development in field situations, which would make them useful for identifying crop genotypes that would do well in specific environments. The study included the following elements:

1. experimentation to investigate the effects of photoperiod and temperature on development in different selections;
2. quantification of the effects of photoperiod and temperature on development through linear models;
3. validation of the models through (a) comparison of photothermal responses with temperatures and photoperiods in the regions where the selections were obtained and (b) comparison of model predictions with data from glasshouse experiments and field trials;
4. exploration of the potential of these models to identify well adapted genotypes for specific environments.

1.6 Outline of the thesis

First, temperature and photoperiod effects on the onset of flowering and the onset of podding of bambara groundnut selections from different origins are quantified with linear photothermal models (Chapter 2). It is then investigated whether the time from sowing to podding in bambara groundnut can be divided into photoperiod-sensitive and photoperiod-insensitive phases in the same way as the time between sowing and flowering in other crops (Chapter 3). Chapter 4 examines the applicability of the findings from controlled environment research with constant photoperiods in field situations with fluctuating photoperiods. Chapter 5 investigates the validity of some common assumptions in crop modelling: are development and growth independent and can development be modelled separately from crop growth? Are dry matter partitioning factors dependent on development stage and not directly influenced by photoperiod? In Chapter 6, photothermal models are developed for bambara groundnut selections from contrasting origins, near the equator (Tanzania) and near the Tropic of Capricorn (Botswana), and these models are validated. Chapter 7 presents a case-study for Botswana, which shows the implications of genotypic differences in responses to photoperiod and temperature in bambara groundnut and demonstrates the usefulness of photothermal development models for identifying suitable selections for different locations and sowing dates. In Chapter 8, the findings, methodology and implications of the whole study are discussed and evaluated.

CHAPTER 2

RATES OF PROGRESS TOWARDS FLOWERING AND PODDING IN BAMBARA GROUNDNUT (*VIGNA SUBTERRANEA*) AS A FUNCTION OF TEMPERATURE AND PHOTOPERIOD

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2. RATES OF PROGRESS TOWARDS FLOWERING AND PODDING IN BAMBARA GROUNDNUT (*VIGNA SUBTERRANEA*) AS A FUNCTION OF TEMPERATURE AND PHOTOPERIOD

M. Brink

Abstract

The influence of temperature and photoperiod on phenological development of three bambara groundnut (*Vigna subterranea*) selections from Botswana, Zimbabwe and Mali was investigated in a semi-controlled environment experiment with factorial combinations of three constant temperatures (20.9, 23.4, and 26.2 °C) and four constant photoperiods (10.0, 12.5, 13.5, and 16.0 h d^{-1}). In all three selections, the onset of flowering was influenced by temperature but not by photoperiod, while the onset of pod-growth ('podding') of all three selections was influenced by both factors. The influence of temperature and photoperiod was quantified by means of photothermal models, linking development rates to temperature and photoperiod with linear equations. The rate of progress from sowing to flowering of the three selections could be described very well ($r^2 \geq 95\%$) as a function of temperature; the rate of progress from flowering to podding was described reasonably well as a function of both temperature and photoperiod by a combination of one to three response planes (r^2 for the different selections ranging from 63% to 90%). Model testing with independent data sets showed good agreement between observed and predicted times to flowering and podding.

2.1 Introduction

The leguminous crop bambara groundnut (*Vigna subterranea* (L.) Verdc., syn. *Voandzeia subterranea* (L.) Thouars)) is an important secondary food crop in semi-arid Africa, where it is mainly grown by smallholders (Linnemann and Azam-Ali, 1993). It produces protein-rich seeds which are eaten unripe or ripe. Compared to groundnut (*Arachis hypogaea* L.), bambara groundnut performs relatively well under water stress and is less susceptible to diseases (Linnemann and Azam-Ali, 1993).

To explore the potential production of different bambara groundnut selections in various agro-ecological regions and assess the possibilities of transferring selections to other regions, it is necessary to know how development rates are influenced by environmental factors. In most crops, development rates are mainly determined by temperature and/or photoperiod (Roberts and Summerfield, 1987; Squire, 1990). Multi-locational field trials and/or controlled environment research are needed to identify the influencing factors and to quantify their effects. However, it is easier to separate the effects of photoperiod, temperature, and radiation in controlled environments than in field situations.

Quantification of the influence of temperature and photoperiod on development has been done with different types of models (Hodges, 1991; Sinclair et al., 1991). A relatively simple method, developed at the University of Reading, uses linear equations to relate the rate of progress from sowing to flowering (calculated as the inverse of the duration from sowing to flowering) to the mean pre-flowering photoperiod and temperature (Hadley et al., 1983b; Summerfield et al., 1991; Lawn et al., 1995). The main advantages of this method are that the responses to photoperiod and temperature become linear and that interactions between temperature and photoperiod influences often disappear (Summerfield et al., 1991). The method has been used to describe the flowering response to temperature and photoperiod in various leguminous crops: cowpea (*Vigna unguiculata* (L.) Walp.) (Hadley et al., 1983a; Ellis et al., 1994a); soya bean (*Glycine max* (L.) Merr.) (Hadley et al., 1984; Summerfield et al., 1993);

mungbean (*Vigna radiata* (L.) Wilczek) (Ellis et al., 1994b); chickpea (*Cicer arietinum* L.) (Roberts et al., 1985; Ellis et al., 1994c); lentil (*Lens culinaris* Medic.) (Summerfield, et al., 1985; Erskine et al., 1994); and faba bean (*Vicia faba* L.) (Ellis et al., 1990).

In the short-day species bambara groundnut, not only the onset of flowering, but also the onset of pod growth ('podding') is affected by photoperiod (Harris and Azam-Ali, 1993; Linnemann, 1993; Linnemann et al., 1995). Photoperiod usually has a stronger effect on the onset of podding than on the onset of flowering. Linnemann and Craufurd (1994) applied the Reading method to ascertain the rate of progress towards flowering and podding, but they did not validate their results with independent data sets.

The objectives of the present study were to assess the influence of temperature and photoperiod on flowering and podding in bambara groundnut selections from different origins; to quantify the temperature and photoperiod effects by means of photothermal models which relate development rates to photoperiod and temperature by means of linear equations; and to test whether these photothermal models adequately predict development rates in other situations.

2.2 Materials and methods

Experiments

The study involved eight different experiments: a main semi-controlled environment experiment used to construct development models and seven other experiments to test the models.

The main experiment was carried out from 16 May to 2 November 1994 in three identical glasshouses in Wageningen, The Netherlands (51°58' N). The experimental design was a split-split-plot with temperature (three levels) as first main factor, photoperiod (four levels) as second main factor, and selection (three selections) as subfactor. The bambara groundnut selections included were 'GabC92' from Botswana, 'NTSC92' from Zimbabwe, and 'Tiga Nicuru' from Mali.

Temperature in the three glasshouses was set at 20, 23, and 26 °C respectively. These temperatures were chosen, because preliminary experiments at the Department of Agronomy of Wageningen Agricultural University had indicated that bambara groundnut does not grow well at constant temperatures below 20 °C and that the optimum temperature for podding of some selections was lower than 28 °C (A.R. Linnemann, personal communication). It was not possible to keep the temperature in the glasshouses at these predetermined levels all the time, because of the warm, sunny weather during the experiment. Measured mean daily temperatures were 20.9, 23.4, and 26.2 °C respectively. Relative air humidity in the glasshouses was kept above 60%, and the glasshouses transmitted 52% of the outside photosynthetically active radiation (PAR).

The photoperiod treatments were constant photoperiods of 10, 12.5, 13.5, and 16 h d^{-1}. These photoperiod treatments were chosen, because earlier research had shown that at an average temperature around 25 °C, the main photoperiod response of 'Tiga Nicuru' occurs between photoperiods of 12 and 14 h d^{-1} (A.R. Linnemann personal communication; results have later been published in Linnemann et al. (1995)). A photoperiod of 10 h d^{-1} was expected to be below the critical photoperiod of 'Tiga Nicuru' in the temperature range of the experiment, and a photoperiod of 16 h d^{-1} above the ceiling photoperiod. A tent with lightproof tent-cloth (a double layer of LS100 from Ludvig Svensson Ltd Company) with four compartments, each 3.10 m wide, 1.50 m long, and 2.05 m high, was erected in each glasshouse. The photoperiod treatments were randomly allocated over the compartments. The tents were open from 08:00 h to 16:00 h, and closed from 16:00 h to 08:00 h. The plants in all compartments received natural daylight from 08:00 h to 16:00 h. The photoperiod was prolonged separately in each compartment by means of low intensity artificial light (two Philips TLD 36 W fluorescent tubes (colour no. 84) and two Philips 40 W bulbs in each compartment, together giving around 10 μmol m^{-2} s^{-1} PAR at plant height). Artificial light was on from 07:00 h to 8:00 h and from 16:00 h to 17:00 h, 19:30 h, 20:30 h, and 23:00 h for the 10, 12.5, 13.5, and 16 h d^{-1} photoperiod treatments respectively. From 16:00 h to 08:00 h, removable metal roofs were put over the glasshouses to exclude daylight and to prevent the temperature inside the tents from becoming too high. Each compartment contained a staging, on which 78 plants (26 plants per selection) were placed randomly. Within each compartment, the plants were circulated weekly.

Seeds were pre-germinated at 30 °C in a germination cabinet. When the root tips were visible, the seedlings were put singly in white plastic pots (upper diameter 20 cm; lower diameter 15 cm; height 20 cm; capacity 4.8 litres), filled with a 1:1 v/v mixture of sand and potting compost ('potting compost no.4' from Lentse potgrond b.v., consisting of 85% peat and 15% clay). A water extract of the sand/compost mixture (1:2 v/v soil and water) contained 66 mg l^{-1} N, 11 mg l^{-1} P and 35 mg l^{-1} K. At transplanting, the seedlings were inoculated with *Rhizobium* spp. strain CB 756, obtained from the Department of Microbiology, Wageningen Agricultural University. Fertilization was done with a standard complete nutrient solution which had proven to give good results in bambara research at Wageningen Agricultural University (A.R. Linnemann, personal communication). The standard solution was obtained by mixing 0.833 g 'Nutriflora-t' (supplied by Windmill Holland b.v.) and 1 g calcium nitrate in one litre water, resulting in a nutrient content of 172 mg l^{-1} N, 39 mg l^{-1} P, and 263 mg l^{-1} K. Nutrient solution was given at 28 (100 ml per plant), 39 (200 ml), 58 (200 ml) and 96 (200 ml) d after sowing. Water was applied manually when necessary. Predators were introduced preventively at regular intervals: *Amblyseius cucumeris* and *Orius insidiosus* against thrips (*Frankliniella occidentalis* and *Thrips tabaci*), and *Phytoseiulus persimilis* against spider mites (*Tetranychus urticae*).

Observations included dates of first flowering and onset of podding of each plant. The start of podding was defined as the moment the plant had a pod of at least 0.5 cm long. Direct podding observations were possible because the selections included in the experiment form pods on the soil surface and not below. Podding observations in a treatment combination were stopped when 50% of the plants in that treatment combination had started podding. The time to flowering in a treatment was defined as the time between the sowing date and the date when 50% of the plants in that treatment had started to flower ('50% flowering'). Similarly, the time from flowering to podding was defined as the time from the date of 50% flowering to the date when 50% of the plants had started podding ('50% podding').

Data sets from seven other experiments, carried out in Wageningen in 1993 and 1994 were used to test the models (Table 2.1). Experiments 1-5 were carried out in glasshouses, experiment 6 in a Heraeus growth cabinet, and experiment 7 in a growth chamber. In the experiments 1, 2, and 5, the photoperiod treatments were established as described for the main trial (8 h d^{-1} natural daylight, extended by low intensity artificial light). In the other experiments, there was no photoperiod extension by means of low intensity light, but high intensity natural and/or artificial light throughout the light period. Experiment 3 received natural daylight; experiment 4 natural daylight with supplementary lighting (Philips SON-T lamps giving 130 μmol m^{-2} s^{-1} PAR at plant height); experiment 6 received light from 16 fluorescent tubes (Philips TLD 58 W, colour no. 84) and two Philips 100 W incandescent bulbs (total PAR at plant height: 230 μmol m^{-2} s^{-1}); and experiment 7 light from Philips HPI and SON-T lamps, fluorescent tubes, and incandescent bulbs (total PAR at plant height: 210 μmol m^{-2} s^{-1}). In all test experiments plants were grown in white 5 l pots with a mixture of sand and potting compost, and crop management was as described for the main trial. The onset of flowering and podding was determined directly for individual plants in the same way as in the main experiment. For experiments 1 and 2 only flowering data were available.

Table 2.1. Characteristics of the seven validation experiments.

	Experiment						
	1	2	3	4	5	6	7
Sowing date	19 May 1993	6 Jul 1993	7 Jul 1993	3 Nov 1993	18 Apr 1994	16 May 1994	16 May 1994
Final harvest date	18 Oct 1993	10 Nov 1993	3 Nov 1993	7 Mar 1994	2 Nov 1994	24 Oct 1994	25 Oct 1994
Selections	'GabC92'	'GabC92'	'NTSC92' 'Tiga Nicuru'	'GabC92'	'GabC92' 'NTSC92'	'GabC92' 'NTSC92' 'Tiga Nicuru'	'GabC92' 'NTSC92' 'Tiga Nicuru'
Average daily temperature (°C)	24.8	24.5	24.4	23.9	25.7	22.1	23.4
Average minimum temperature (°C)	22.2	22.3	n.a.	21.4	22.9	21.6	23.1
Average maximum temperature (°C)	27.5	27.0	n.a.	28.1	29.5	22.5	23.7
Photoperiod treatments (h d^{-1})	10, 12	12, 14	11.5	12	11, 14	12.5	13.5
Number of replicates	3	2	3	3	1	1	1
No. of plants per selection per photoperiod treatment per replicate:							
- flowering observations	17	18	4	15	30-36	4	26
- podding observations	-	-	4	15	6	4	26

Modelling

The influence of temperature and photoperiod on the rate of progress from sowing to flowering and the rate of progress from flowering to podding of the three bambara groundnut selections was modelled according to the photothermal approach developed at the University of Reading (Hadley et al., 1984; Summerfield et al., 1991). In this approach, the rate of progress to flowering ($1/f$; with f being the number of days from sowing to flowering) is related quantitatively to photoperiod (P) and/or temperature (T) by means of one to three linear equations, assuming that temperatures are between the base and optimum temperatures for flowering. In the most complex situation three separate but intersecting planes, characterized by six parameters (a_1, b_1, a_2, b_2, c_2 and a_3) can be distinguished (Fig. 2.1):

A: a thermal plane, characterized by the equation:

$$1/f = a_1 + b_1 T \tag{1.1}$$

B: a photothermal plane:

$$1/f = a_2 + b_2 T + c_2 P \tag{1.2}$$

C: a plane of minimum development rate:

$$1/f = a_3 \tag{1.3}$$

Interactions between temperature and photoperiod effects only occur when plane boundaries are transgressed. Within the planes, there is no interaction. The boundary line between plane A and plane B gives the critical photoperiod (P_{cr}) as a function of temperature:

$$P_{cr} = ((a_1 - a_2) + (b_1 - b_2) T) / c_2 \tag{1.4}$$

The boundary line of plane B and plane C represents the ceiling photoperiod (P_{ce}):

$$P_{ce} = (a_3 - a_2 - b_2 T) / c_2 \tag{1.5}$$

When the actual photoperiod is shorter than P_{cr}, the development rate is influenced solely by temperature. At a photoperiod between P_{cr} and P_{ce}, $1/f$ is determined by P and T, and above P_{ce} the development rate is constant. For a given selection, $1/f$ can be described by one of five possibilities: (1) a thermal plane only; (2) a photothermal plane only; (3) a thermal plane and a photothermal plane; (4) a photothermal plane and a plane of minimum rate; (5) all three planes.

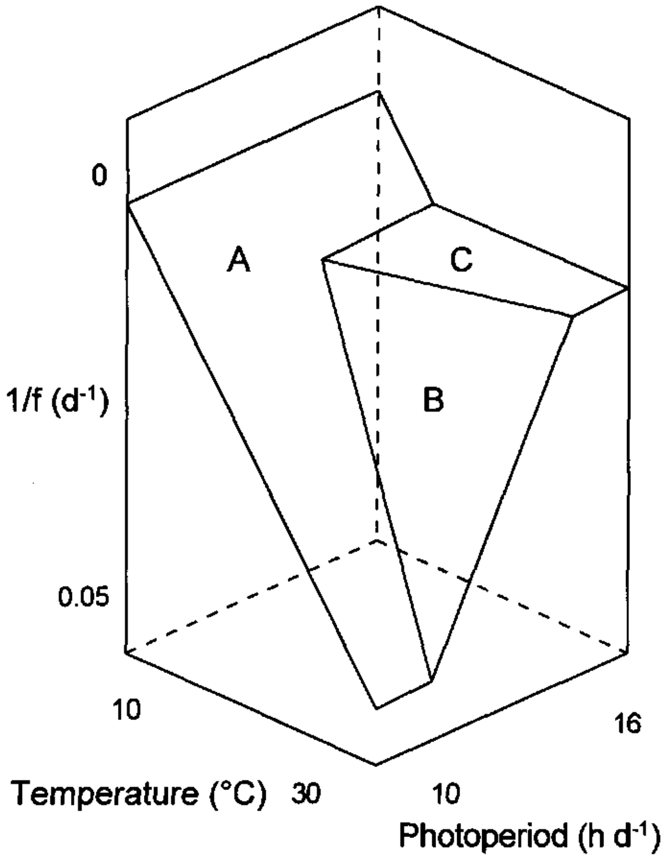

Fig. 2.1. Rate of progress to flowering (1/*f*, with *f* being the number of days from sowing to flowering) as a function of temperature and photoperiod (hypothetical example for a short-day plant at temperatures between the base and optimum temperature for flowering; after Linnemann and Craufurd, 1994). A, thermal plane; B, photothermal plane; C, plane of minimum development rate.

In the application of this approach to the results of the experiment, these five possibilities were examined not only for the rate of progress from sowing to flowering ($1/f$) of each of the three selections, but also for the rate of progress from flowering to podding ($1/(p\text{-}f)$). This is different from Linnemann and Craufurd (1994), who considered the rate from sowing to flowering and the rate from sowing to podding ($1/p$), and did not look at the rate of progress from flowering to podding. However, to study the photothermal effects on flowering and podding, it seems more appropriate to separate the two phases completely, and not include the time to flowering in the podding analysis.

The best fit was determined by means of the RoDMod computer program (Watkinson et al., 1994), which uses an iterative procedure to minimize the combined sums of squares of deviations of observed from estimated rates. The simplest model (only a thermal plane) is fitted first, followed by the more complex models. A more complex model is accepted only if it statistically significantly reduces the residual sums of squares of the deviations of model estimates from observations. The temperature values used in the equations were the measured average temperatures from sowing to flowering or flowering to podding.

Model testing

Predictions of the time from sowing to flowering and the time from flowering to podding in the seven test experiments in Table 2.1 were made with the PREDICTF routine of the RodMod computer program (Watkinson et al., 1994) on the basis of the average daily temperature and photoperiod data from the test experiments and the model parameters derived from the main experiment. The PREDICTF routine calculates the development rate in 1-day time-steps, on the basis of photoperiod and mean temperature of each day separately. The predictions were compared with the times from sowing to flowering and the times from flowering to podding observed in the experiments.

2.3 Results

Experiment

Flowers and pods were formed in all treatments. The time from sowing to 50% flowering varied from 35 to 53 d for 'Tiga Nicuru', from 40 to 55 d for 'NTSC92' and from 42 to 58 d for 'GabC92'. For all three selections, flowering was influenced by temperature, but photoperiod had no influence (Fig. 2.2).

The greatest differences in the time from 50% flowering to 50% podding were found for 'Tiga Nicuru': 25 to 82 d. For 'NTSC92' the time from 50% flowering to 50% podding ranged from 29 to 72 d, and for 'GabC92' from 32 to 74 d. Development from flowering to podding in all three selections was influenced by both temperature and photoperiod (Fig. 2.3).

Modelling

The rate of progress from sowing to flowering of the three selections could be adequately ($r^2 \geq 95\%$) described by thermal response planes (Table 2.2, Fig. 2.2). The fitted equations for the flowering responses of 'GabC92' and 'NTSC92' had very similar parameter values.

The influence of photoperiod and temperature on the rate of progress from flowering to podding of 'GabC92' and 'NTSC92' in the temperature range of the experiment could be described by a photothermal response plane, but the fit was much better for 'GabC92' than for 'NTSC92' (Table 2.3, Fig. 2.3). For both selections, the parameters b_2 and c_2 had negative values, reflecting that in the temperature and photoperiod range of the experiment, the rate of progress from flowering to podding decreased with both temperature and photoperiod.

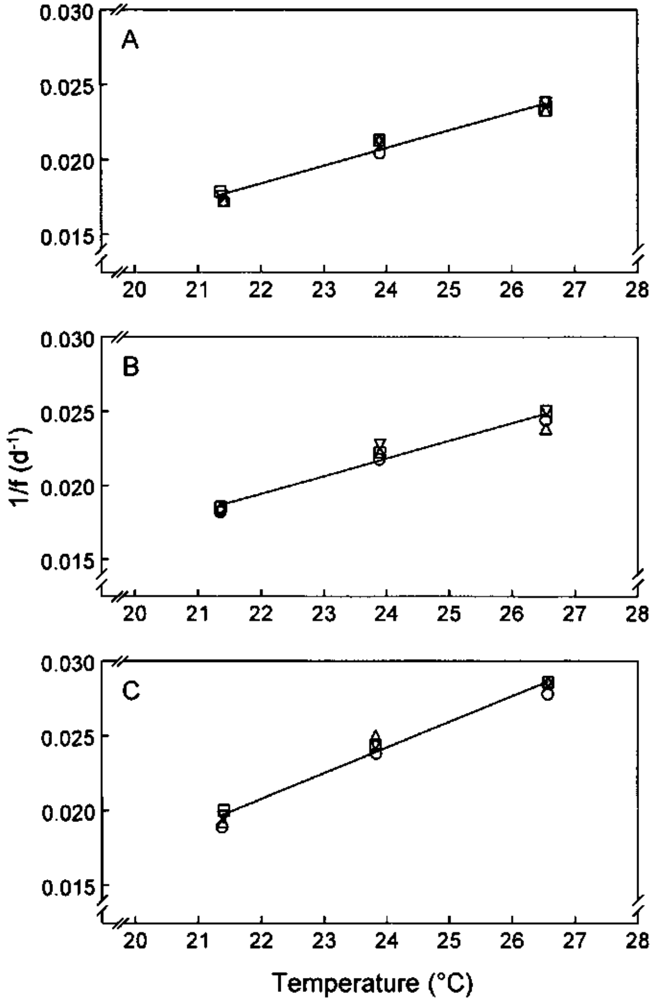

Fig. 2.2. Rate of progress from sowing to flowering (1/*f*, with *f* being the number of days from sowing to flowering) in bambara groundnut selections 'GabC92' (A), 'NTSC92' (B), and 'Tiga Nicuru' (C) as a function of temperature under constant photoperiods of 10 h d^{-1} (○), 12.5 h d^{-1} (▽), 13.5 h d^{-1} (△), and 16 h d^{-1} (□). The solid lines refer to the fitted models.

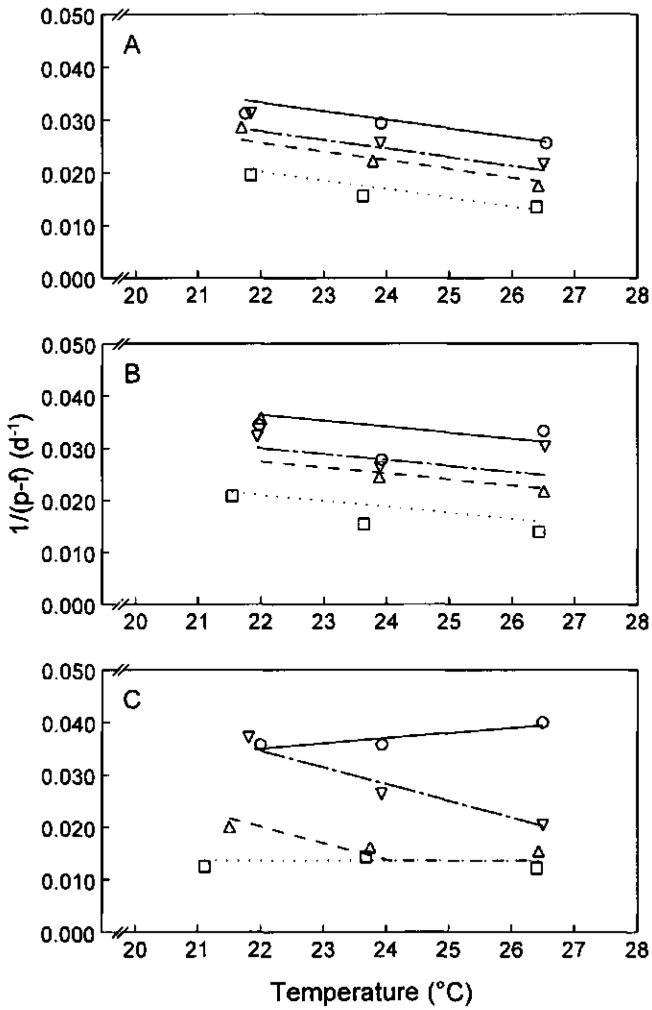

Fig. 2.3. Rate of progress from flowering to podding (1/(*p-f*); with (*p-f*) being the number of days from flowering to podding) in bambara groundnut selections 'GabC92' (A), 'NTSC92' (B), and 'Tiga Nicuru' (C) as a function of temperature under constant photoperiods of 10 h d^{-1} (○), 12.5 h d^{-1} (▽), 13.5 h d^{-1} (△), and 16 h d^{-1} (□). The lines are the fitted model values for 10 h d^{-1} (———), 12.5 h d^{-1} (— - —), 13.5 h d^{-1} (– – – –), and 16 h d^{-1} (· · · ·).

Table 2.2. Fitted relations between rate of progress towards flowering (1/*f*) and mean pre-flowering temperature (*T*) in three bambara groundnut selections grown in combinations of three constant temperatures (20.9, 23.4, and 26.2 °C) and four constant photoperiods (10.0, 12.5, 13.5, and 16.0 h d^{-1}).

Selection	Fitted equations	n	Parameter values		r^2 (%)
			a_1 (s.e.)	b_1 (s.e.)	
'GabC92'	$1/f = a_1 + b_1 T$	12	-0.007464 (0.001593) ***	0.001176 (0.000066) ***	96.6
'NTSC92'	$1/f = a_1 + b_1 T$	12	-0.006876 (0.001926) **	0.001195 (0.000080) ***	95.3
'Tiga Nicuru'	$1/f = a_1 + b_1 T$	12	-0.017104 (0.001904) ***	0.001721 (0.000079) ***	97.7

*** $P \leq 0.001$); ** $P \leq 0.01$; * $P \leq 0.05$; n.s. not significant.
n, number of temperature/photoperiod combinations.

Table 2.3. Fitted relations between rate of progress from flowering to podding ($1/(p\text{-}f)$) and mean temperature (T) and photoperiod (P) between flowering and podding in three bambara groundnut selections grown in combinations of three temperatures (20.9, 23.4, and 26.2 °C) and four constant photoperiods (10.0, 12.5, 13.5, and 16.0 h d^{-1}).

Selection	Method	Plane	Fitted equations	n	Parameter values			r^2 (%)
					a_1, a_2 or a_3 (s.e.)	b_1 or b_2 (s.e.)	c_2 (s.e.)	
'GabC92'	1	B	$1/(p\text{-}f) = a_2 + b_2\,T + c_2\,P$	12	0.091579 (0.007590) ***	-0.001650 (0.000278) ***	-0.002193 (0.000253) ***	90.4
'NTSC92'	1	B	$1/(p\text{-}f) = a_2 + b_2\,T + c_2\,P$	12	0.087653 (0.018293) ***	-0.001158 (0.000672) n.s.	-0.002572 (0.000593) **	63.4
'Tiga Nicuru'	1	B	$1/(p\text{-}f) = a_2 + b_2\,T + c_2\,P$	12	0.099451 (0.019967) ***	-0.000842 (0.000721) n.s.	-0.004268 (0.000667) ***	78.2
	2	A	$1/(p\text{-}f) = a_1 + b_1\,T$ (for $P \leq P_{cr}$)	3	0.013100 (0.011400) n.s.	0.000994 (0.000473) n.s.	-	63.1
		B	$1/(p\text{-}f) = a_2 + b_2\,T + c_2\,P$ (for $P_{ce} \geq P \geq P_{cr}$)	5	0.285300 (0.042600) *	-0.003177 (0.000704) *	-0.014470 (0.002570) *	89.9
		C	$1/(p\text{-}f) = a_3$ (for $P \geq P_{ce}$)	4	0.013591 (0.000755)	-	-	-

*** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$; n.s. not significant.

Method 1 refers to fitting with the RoDMoD computer program (Watkinson et al., 1994); method 2 refers to an alternative approach (see text). The letters A, B, and C refer to the planes in Fig. 2.1. P_{cr}, critical photoperiod; P_{ce}, ceiling photoperiod; n, number of temperature/photoperiod combinations.

According to the results of the RoDMod analysis, the rate of progress towards podding of 'Tiga Nicuru' was described by a photothermal plane as well. However, the experimental results indicate a different model, with a thermal plane, a photothermal plane, and a plane of maximum delay (model 5). Therefore, the results for 'Tiga Nicuru' were analyzed in an alternative way as well (method 2). The 12 temperature/photoperiod combinations were divided into three groups, with group 1 (the thermal plane) consisting of the 10.0 h d^{-1} treatments; group 2 (the photothermal plane) consisting of the 12.5 h d^{-1} and the 13.5 h d^{-1} treatments except the 26.2 °C / 13.5 h d^{-1} treatment; and group 3 (the plane of minimum development rate) of the 16.0 h d^{-1} treatments and the 26.2 °C / 13.5 h d^{-1} treatment. A regression analysis was carried out for each plane separately, using the GENSTAT statistical package (Payne et al., 1993). Results are shown in Table 2.3. This alternative model fits the experimental results very well (Fig. 2.3C). In this model, the critical photoperiod for the rate from flowering to podding in 'Tiga Nicuru' decreases from 12.47 h d^{-1} at 22 °C to 11.32 h d^{-1} at 26 °C, the ceiling photoperiod from 13.95 h d^{-1} at 22 °C to 13.07 h d^{-1} at 26 °C (Table 2.4).

In summary, within the temperature (20.9 - 26.2 °C) and photoperiod (10 - 16 h d^{-1}) ranges considered, the rates from flowering to podding of 'GabC92' and 'NTSC92' decrease with both temperature and photoperiod. The rate from flowering to podding of 'Tiga Nicuru' increases with temperature at short photoperiods, is constant at long photoperiods, and decreases with photoperiod and temperature at intermediate photoperiods.

Model testing

Application of the fitted models shown in Tables 2.2 and 2.3 to data sets from the test experiments showed that the time from sowing to flowering was well predicted: all deviations were within 10% of the predicted values (Fig. 2.4A). Predictions for the time from sowing to podding were less accurate (Fig. 2.4B), especially for experiment 5 (Table 2.5). For 'Tiga Nicuru', the podding model derived by method 2 gave better predictions than the method 1 model (Table 2.5). The values for 'Tiga Nicuru' in Fig. 2.4B are those derived with method 2. Predictions of the time from sowing to podding, calculated by adding the predictions of the time to flowering and the time from flowering to podding were in good agreement with observed data: deviations between predicted and observed times from sowing to podding were less than 10% (Fig. 2.4C), except for experiment 5 (Table 2.5).

Table 2.4. Critical (P_{cr}) and ceiling (P_{ce}) photoperiods of bambara groundnut selection 'Tiga Nicuru' at temperatures from 22 to 26 °C.

T (°C)	P_{cr} (h d^{-1})	P_{ce} (h d^{-1})
22	12.47	13.95
23	12.18	13.73
24	11.89	13.51
25	11.61	13.29
26	11.32	13.07

The model in Table 2.3 was used to calculate P_{cr} and P_{ce}.

2.4 Discussion

Temperature and photoperiod responses

The results of the main experiment clearly show that flowering in the three bambara groundnut selections in the temperature and photoperiod ranges of the experiment is influenced by temperature but not by photoperiod (Fig. 2.2). The onset of podding, on the other hand, is clearly influenced by both temperature and photoperiod (Fig. 2.3). This is a pattern which has been found in most of the bambara groundnut selections included in experiments to date, though some selections have been found for which not only podding, but also flowering is influenced by both temperature and photoperiod (Linnemann, 1991; Linnemann, 1993). Photoperiod research in other legumes has usually been confined to the flowering response, though the existence of photoperiod effects on development phases beyond flowering has also been reported for soya bean (*Glycine max*) (Grimm et al., 1994) and groundnut (*Arachis hypogaea*) (Flohr et al., 1990).

Modelling

For all three selections, the rates of progress from sowing to flowering of the 12 treatments in the experiment could adequately be quantified as a function of temperature only (Table 2.2; Fig. 2.2). The rate of progress from flowering to podding of 'GabC92' was well described by a photothermal response plane, and that of 'Tiga Nicuru' by a combination of a thermal response plane, a photothermal response plane, and a plane of minimum development rate (Table 2.3; Fig. 2.3). The rate from flowering to podding of 'NTSC92' could not be quantified well, which might be due to the greater heterogeneity of this selection.

The critical photoperiod for the rate from flowering to podding in 'Tiga Nicuru' decreased from 12.47 h d^{-1} at 22 °C to 11.32 h d^{-1} at 26 °C (Table 2.4). These critical photoperiods are comparable with those found in other studies. Linnemann and Craufurd (1994) found similar critical photoperiods for podding for the bambara groundnut selections 'Yola' and 'Ankpa4' from Nigeria: from 12.6 and 13.2 h d^{-1} at 20 °C to 11.4 and 11.8 h d^{-1} at 26 °C. The critical photoperiod for flowering in a cowpea genotype from Uganda ('TVu 1188') has been found to range from 16.0 h d^{-1} at 15 °C to 11.5 h d^{-1} at 25 °C (Ellis et al., 1994a). Reports on soya bean are contradictory: in a controlled environment study, critical photoperiods for flowering in eight cultivars have been found to increase with temperature (Hadley et al., 1984), while in field experiments, the critical photoperiods for flowering in nine different soya bean genotypes decreased with temperature (Summerfield et al., 1993). In the latter study, critical photoperiods of 12.6 to 13.6 h d^{-1} at 20 °C and 11.7 to 13.3 h d^{-1} at 25 °C have been found.

Table 2.5. Predicted (Pr) and observed (Ob) times from sowing to flowering (*f*), flowering to podding (*p-f*) and sowing to podding (*p*) for three bambara groundnut selections in various test experiments (experiment numbers refer to Table 2.1).

Selection		Exp.	Photop. (h d^{-1})	*f* (d)		*p-f* (d)		*p* (d)	
				Pr	Ob	Pr	Ob	Pr	Ob
'GabC92'		1	10	45	43	35	n.a.	80	n.a.
			12	45	44	41	n.a.	86	n.a.
		2	12	46	47	41	n.a.	87	n.a.
			14	46	47	49	n.a.	95	n.a.
		4	12	51	55	41	33	92	88
		5	11	46	47	42	49	88	96
			14	46	47	62	87	108	134
		6	12.5	55	57	37	41	92	98
		7	13.5	50	46	43	44	93	90
'NTSC92'		3	11.5	44	40	34	37	78	77
		5	11	44	46	34	44	78	90
			14	44	45	48	72	92	117
		6	12.5	52	52	34	33	86	85
		7	13.5	47	43	39	36	86	79
'Tiga N.'	Method 1	3	11.5	39	39	34	23	73	62
		6	12.5	48	50	37	34	85	84
		7	13.5	43	39	46	60	87	99
	Method 2	3	11.5			27	23	66	62
		6	12.5			30	34	78	84
		7	13.5			64	60	97	99

The predicted values of *f* and *p-f* were calculated with the models in Table 2.2 and Table 2.3, respectively; the predicted value of *p* was calculated by adding the values of *f* and *p-f*.

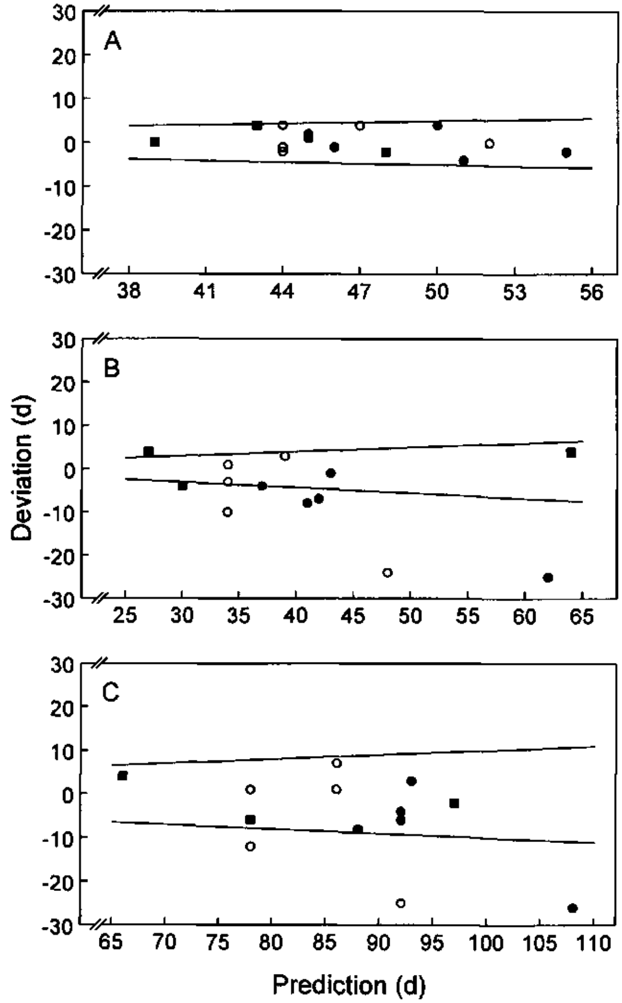

Fig. 2.4. Deviations (predicted number of days minus observed number of days in independent test experiments) of the time from sowing to flowering (A), the time from flowering to podding (B), and the time from sowing to podding (C) for bambara groundnut selections 'GabC92' (●), 'NTSC92' (○), and 'Tiga Nicuru' (■). Solid lines show the limits of ± 10% deviation. Predictions of the time from sowing to flowering and the time from flowering to podding are based on the models in Tables 2.2 and 2.3; the predicted time from sowing to podding was calculated by adding the predicted time from sowing to flowering and the predicted time from flowering to podding.

The ceiling photoperiod for the rate from flowering to podding in 'Tiga Nicuru' decreased from 13.95 h d^{-1} at 22 °C to 13.07 h d^{-1} at 26 °C (Table 2.4). Summerfield et al. (1993) found that ceiling photoperiods for the rate to flowering in soya bean increased with temperature. The difference is due to the fact that the parameter b_2 in the photothermal response plane of 'Tiga Nicuru' has a negative value ($1/(p-f)$ decreases with temperature), while this parameter has a positive value (development rate increasing with temperature) for the soya bean genotypes used by Summerfield et al. (1993). This means that the photothermal plane of 'Tiga Nicuru' is tilted differently than the photothermal plane in Fig. 2.1.

Model testing

Model testing showed that the predictions of the time from sowing to flowering, based on the linear models derived from the main experiment, agreed well with the observed times to flowering in the test experiments: deviations between predicted and observed values were always lower than 10% (Fig. 2.4A).

Predictions of the time from flowering to podding were less accurate. Deviations were often higher than 10% (Fig. 2.4B), but in all test experiments except experiment 5 the difference between predicted and observed times from flowering to podding was less than 10 d (Table 2.5). The extreme long times to podding of 'GabC92' and 'NTSC92' in experiment 5 might be a result of the maximum temperatures for podding being exceeded, because experiment 5 was carried out in a glasshouse without forced cooling, and maximum temperatures of 35-40 °C were common in the months after flowering. Deviations between predicted and observed times from sowing to podding were less than 10%, except for experiment 5 (Fig. 2.4C; Table 2.5).

In the main experiment, the photoperiod was prolonged beyond 8 h d^{-1} by means of low intensity artificial light. In the experiments 3, 4, 6, and 7, there was no photoperiod extension by means of low intensity light, but high intensity natural and/or artificial light throughout the light period. The good prediction of the times to flowering and podding in the experiments 3, 4, 6, and 7 with models based on the main experiment indicates that light integral has no effect on development.

2.5 Conclusion

This study has shown that the times from sowing to flowering and from flowering to podding in bambara groundnut may be predicted with simple linear models (relating the rates of progress from sowing to flowering and from flowering to podding in bambara groundnut to photoperiod and temperature), based on a semi-controlled environment experiment. Observed times from sowing to flowering and podding are between 90 and 110% of the predicted values.

CHAPTER 3

THE PHOTOPERIOD-SENSITIVE PHASE FOR PODDING IN BAMBARA GROUNDNUT (*VIGNA SUBTERRANEA*)

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3 THE PHOTOPERIOD-SENSITIVE PHASE FOR PODDING IN BAMBARA GROUNDNUT (*VIGNA SUBTERRANEA*)

M. Brink

Abstract

A glasshouse experiment was conducted to determine whether the period between sowing and the onset of podding in bambara groundnut (*Vigna subterranea*) can be divided in photoperiod-sensitive and photoperiod-insensitive phases. Treatments were established by transferring plants between 14 h d^{-1} (LD) and 11 h d^{-1} (SD) every two weeks. There were also control treatments of constant LD and SD. Flowering was not affected by photoperiod, but the onset of podding was delayed by long photoperiods. At an average temperature of 25.7 °C, the main photoperiod effect on podding occurred from 42 days after sowing onwards in 'NTSR94' and 'NTSC92', and from 57 days after sowing onwards in 'GabC92'. The time from sowing to podding could not be divided clearly into photoperiod-sensitive and photoperiod-insensitive periods, because in all three selections podding tended to be later in early transfers from SD to LD than in constant LD, and earlier in the early transfers from LD to SD than in constant SD. This phenomenon has been found in rice as well, but cannot satisfactorily be explained.

3.1 Introduction

Bambara groundnut (*Vigna subterranea* (L.) Verdc.) is an important leguminous food crop in tropical Africa (Linnemann and Azam-Ali, 1993). It is an indeterminate annual herb with creeping stems, carrying trifoliate leaves with erect petioles. Flowers appear at the base of the petioles, usually in pairs. After pollination, the peduncle grows out and pods form on or below the soil surface. Each pod usually contains one seed, and both the unripe and ripe seeds are consumed by humans (Duke, 1981; Linnemann and Azam-Ali, 1993). In many bambara groundnut genotypes, the onset of flowering is photoperiod-insensitive, but the onset of podding is retarded by long photoperiods (Linnemann, 1991; Linnemann and Craufurd, 1994). In some genotypes, both the onset of flowering and the onset of podding are delayed by long photoperiods (Linnemann, 1993; Linnemann and Craufurd, 1994).

In a previous study, the influence of temperature and photoperiod on development rates in three bambara groundnut selections has been quantified by means of photothermal models, based on a semi-controlled environment experiment with constant photoperiods and temperatures (Chapter 2). The rate of progress from sowing to flowering of these selections could be described as a function of the average temperature in the period from sowing to flowering; the rate of progress from flowering to podding as a function of the average temperature and photoperiod in the period from flowering to podding. Thus, it was assumed that photoperiod plays a role throughout the period from flowering to podding. However, plants which are photoperiod-sensitive with regard to the onset of flowering, such as many soya bean (*Glycine max* (L.) Merr.) genotypes, are often not sensitive throughout the entire pre-flowering period (Wilkerson et al., 1989; Collinson et al., 1993). Three phases are usually distinguished between sowing and flowering: (1) a pre-inductive phase (also referred to as the juvenile phase) in which plants are not sensitive to photoperiod; (2) an inductive phase, in which plants are sensitive to photoperiod and flower induction occurs; and (3) a post-inductive phase, in which flower buds develop into open flowers and the photoperiod does not play a role (Hodges and French, 1985; Roberts et al., 1986; Ellis et al., 1992). In some studies, the pre-inductive phase is defined to start at sowing (Ellis et al., 1992). In other studies (Hodges and French, 1985; Roberts et al., 1986), a fourth phase, the pre-emergence phase, is distinguished and the pre-inductive phase is defined to start at emergence. The duration of the different phases can be estimated on the basis of reciprocal transfer experiments, in which plants are transferred from long days to short days and vice versa at regular intervals (Van Dobben, 1957; Ellis et al., 1992).

This study aims to determine whether the time from sowing to podding in bambara groundnut can be divided into photoperiod-sensitive and photoperiod-insensitive phases in the same way as the time between sowing and flowering in other crops.

3.2 Material and methods

Experimental design and plant material

A reciprocal transfer experiment was conducted in a glasshouse in Wageningen, The Netherlands (51°58' N), in the period 18 April to 2 November 1994. The experiment included 14 photoperiod treatments (six transfer times of plants from long days (LD, 14 h d^{-1}) to short days (SD, 11 h d^{-1}) or vice versa and two control treatments of constant LD or SD). Three bambara groundnut selections were used: 'GabC92', collected in Gaborone, Botswana, and 'NTSR94' and 'NTSC92', obtained from 'National Tested Seeds' in Zimbabwe. The results of preliminary unpublished experiments by the author of the present study had shown that these three selections are insensitive to photoperiod with regard to the onset of flowering, but sensitive to photoperiod with regard to the onset of podding. Podding in 'GabC92' had been found to start later than in the other two selections, therefore the transfer dates in the present experiment were later for this selection than for the other two. The plants were arranged in six blocks, each containing one replicate plant per photoperiod treatment per selection. Each block consisted of two trolleys, one with SD and the other with LD. The treatments and selections were randomly placed on the trolleys. Within each trolley, the plants were circulated weekly. At the start of the experiment, half of the plants of each selection were placed in LD and the other half in SD. Every two weeks, one plant per selection per replicate was transferred from LD to SD, and one from SD to LD. One plant per selection per replicate remained under LD throughout the experiment (LD control), and one under SD (SD control). 'NTSR94' and 'NTSC92' were transferred at 29, 43, 57, 71, 85 and 99 days after sowing (DAS); 'GabC92' at 43, 57, 71, 85, 99 and 113 DAS. This experimental set-up has been used frequently for research on inductive phases in crops (Van Dobben, 1957; Ellis et al., 1992; Collinson et al., 1992, 1993; Yin et al., 1997) and is an intermediate between a completely randomized block design and a split plot design.

Environmental conditions

Throughout the experiment, the plants were exposed to natural daylight from 08:00 to 16:00. From 16:00 to 08:00, they were placed in sheds, where the photoperiod was prolonged by low-intensity artificial light (fluorescent tubes (Philips TLD 36 Watt, colour no. 84) and Philips 40 W bulbs). Therefore, all treatments received the same amount of photosynthetically active radiation. During the daylight period, the air temperature was set between 26 and 29 °C; the rest of the day between 22 and 25 °C. However, on sunny days maximum temperatures above 35 °C were recorded. The average daily temperature throughout the experimental period was 25.7 °C, with an average daily maximum of 29.6 °C and minimum of 22.9 °C.

Plant husbandry

The seeds were pre-germinated in a germination cabinet at 30 °C. When the root tips became visible, the plants were transplanted singly to white plastic pots (capacity 5 l), filled with a 1:1 v/v mixture of sand and potting compost (potting compost no.4 from Lentse potgrond b.v., consisting of 85% peat and 15% clay). At transplanting, the plants were inoculated with *Rhizobium* spp. strain CB 756, obtained from the Department of Microbiology, Wageningen Agricultural University. All plants were fertilised with a standard complete nutrient solution obtained by mixing 0.833 g Nutriflora-t (supplied by Windmill Holland b.v.) and 1 g calcium nitrate in one litre of tap water, resulting in a nutrient content of 172 mg l^{-1} N, 39 mg l^{-1} P, and 263 mg l^{-1} K. This nutrient solution (200 ml per plant) was applied at three-weekly intervals in the period 3 to 12 weeks after sowing. Water was applied manually, as needed. Biological pest control was used: the predators *Amblyseius cucumeris* and *Orius insidiosus* against thrips (*Frankliniella occidentalis* and *Thrips tabaci*), and *Phytoseiulus persimilis* against spider mites (*Tetranychus urticae*).

Observations

The onset of flowering and podding of each plant was recorded on the basis of daily observations. Flowering onset was defined as the day on which the plant had its first open flower, and podding onset as the first day the plant had a pod at least 0.5 cm long. This could be observed directly, because the three selections form pods on the soil surface. The number of unfolded leaves on each plant was counted weekly. A leaf was considered to be unfolded if the angle between the halves of the top leaflet was 90° or more.

Analysis

Results were analysed separately for each selection with a statistical method designed to fit a model of the type presented in Fig. 3.1 to results of reciprocal transfer experiments. This method has been used to determine the photoperiod-sensitive and photoperiod-insensitive phases for flowering in soya bean (Collinson et al., 1993) and rice (*Oryza sativa* L.) (Collinson et al., 1992; Yin et al., 1997). The parameters were fitted to the results with the FITNONLINEAR directive of the

GENSTAT statistical package (Payne et al., 1993). In this procedure, the estimates of the four parameters (a_1, I_S, I_L and a_3) are optimised to minimise the residual sum of squares of the regression model. Starting values have to be supplied for the parameters to be optimised. As indicated by Ellis et al. (1992), the choice of the starting values can influence the parameter estimates. Therefore, twenty runs with different starting values were carried out for each selection. If runs with different starting values led to different models, the model with the lowest residual sum of squares was selected.

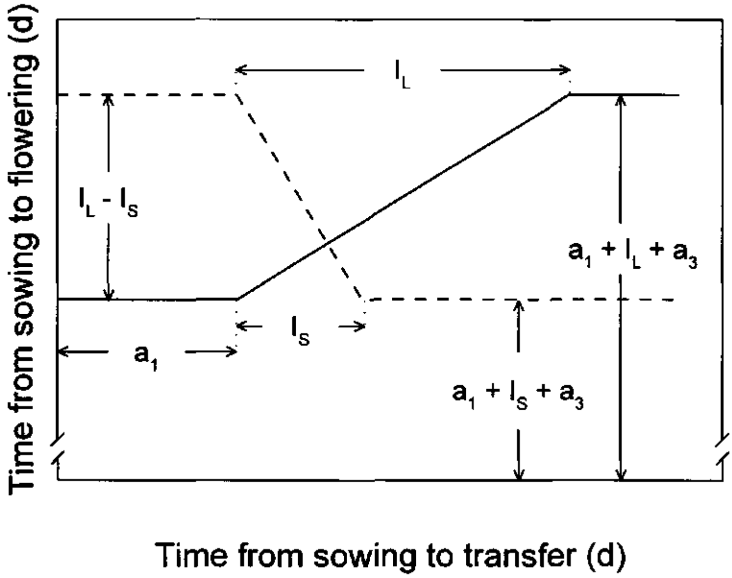

Fig. 3.1. Response model of the time from sowing to the onset of flowering for short-day plants transferred from short to long days (------) or long to short days (——) at different times after sowing (hypothetical example for a short-day plant). The model includes a pre-inductive phase (a_1), an inductive phase under short photoperiods (I_S), an inductive phase under long photoperiods (I_L), and a post-inductive phase (a_3). After Ellis et al. (1992).

3.3 Results

No significant ($p \leq 0.05$) effects of the treatments on the onset of flowering were found in the three selections. The average time from sowing to the first flower was 45 days for 'NTSR94', 47 days for 'NTSC92', and 49 days for 'GabC92'.

Treatment effects on the time to the onset of podding were significant ($p \leq 0.001$) for all three selections. The time from sowing to podding in the different treatments are presented in Fig. 3.2. The results were not exactly conform the expected pattern shown in Fig. 3.1. Podding in all three selections tended to be later in the early transfers from SD to LD than in constant LD, and earlier in the early transfers from LD to SD than in constant SD. The main photoperiod effect occurred from 57 DAS onwards in 'GabC92', and from 42 DAS onwards in 'NTSR94' and 'NTSC92'.

When the standard model of Fig. 3.1 was applied, the estimated durations of the pre-inductive phase (a_1), the inductive phase under SD (I_S), the inductive phase under LD (I_L), and the post-inductive phase (a_3) under the experimental temperature regime were 66, 21, 89, and 6 days respectively for 'GabC92', and 56, 17, 54, and 4 days for 'NTSR94' (Table 3.1). The overall fit of the model was better for 'GabC92' than for 'NTSR94' (Fig. 3.2). The model could not be fitted for the more heterogeneous selection 'NTSC92'.

The number of leaves per plant for six of the treatments is presented in Fig. 3.3. The other eight treatments were excluded to keep the figures legible, but they fall within the extremes of the treatments shown. The number of leaves per plant generally increased until the onset of podding. Plants under constant SD tended to have fewer leaves than plants which had been under LD for some weeks before transfer to SD conditions, especially 'NTSR94'. Similarly, the mean leaf number on plants under constant LD tended to be higher than that of plants which had been under SD for some time before transfer to LD.

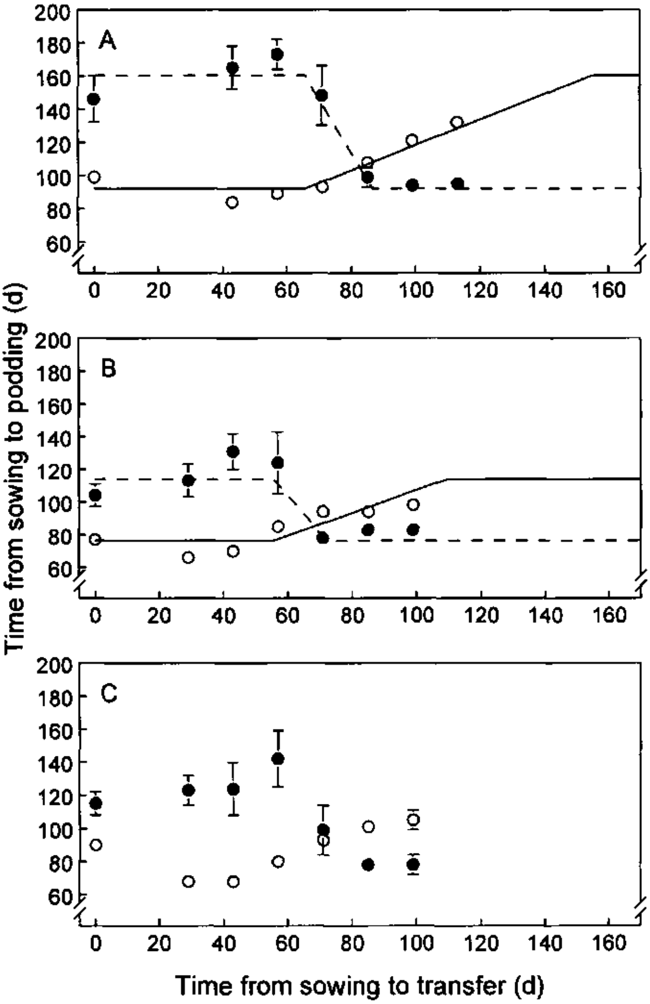

Fig. 3.2. Time (d) from sowing to the onset of podding for bambara groundnut selections 'GabC92' (A), 'NTSR94' (B) and 'NTSC92' (C) transferred from 11 to 14 h d^{-1} (●) or 14 to 11 h d^{-1} (○) at various times (d) after sowing. Vertical bars indicate means ± standard error (only visible where larger than the symbols). The lines (------ and ——) refer to the fitted model. It was not possible to fit a model for 'NTSC92'.

Table 3.1. Means and standard errors of the estimates of the durations (d) of the pre-inductive phase (a_1), the inductive phase under short photoperiods (I_S), the inductive phase under long photoperiods (I_L), and the post-inductive phase (a_3) at an average temperature of 25.7 °C for the bambara groundnut selections 'GabC92' and 'NTSR94'. It was not possible to fit a model for 'NTSC92'.

Parameter	'GabC92'	'NTSR94'
a_1	65.8 ± 3.2	55.6 ± 3.6
I_S	20.8 ± 4.3	16.6 ± 5.0
I_L	89.0 ± 8.4	54.1 ± 8.6
a_3	5.5 ± 3.2	4.1 ± 3.7
r^2	0.73	0.50

The values of r^2 refer to the overall model.

3.4 Discussion

The main photoperiod effect occurred from 42 days after sowing onwards in 'NTSR94' and 'NTSC92', and from 57 days after sowing onwards in 'GabC92'. Flowering started at 45, 47 and 49 DAS for 'NTSR94', 'NTSC92' and 'GabC92' respectively, so the difference between the onset of flowering and the beginning of the main photoperiod influence was small.

The results shown in Fig. 3.2 do not exactly follow the expected pattern shown in Fig. 3.1., but seem to indicate two separate effects. At first the time to podding increases when the pods have been longer under SD, but later the trend is reversed and the main photoperiod effect takes place. The breakpoint is earlier in plants transferred from LD to SD than in plants transferred from SD to LD.

Similar effects have been reported for rice. In reciprocal transfer experiments with four *indica* rice cultivars, 'Peta' showed delayed flowering at early transfers from SD to LD and accelerated flowering at early transfers from LD to SD at an average temperature of 28.7 °C but not at 23.8 °C (Collinson et al., 1992).

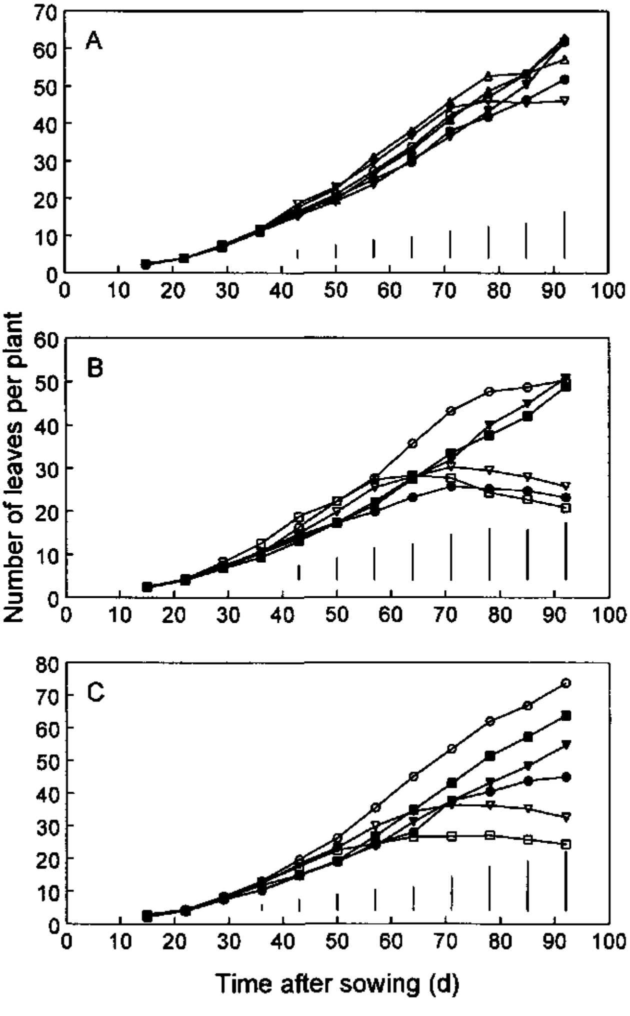

Fig. 3.3. Mean number of leaves per plant for bambara groundnut selections 'GabC92' (A), 'NTSR94' (B) and 'NTSC92' (C) under different photoperiod treatments: constant 11 h d^{-1} photoperiod (●); constant 14 h d^{-1} photoperiod (○); transfer from 11 to 14 h d^{-1} at 29 DAS (■), 43 DAS (▼) and 57 DAS (▲); and transfer from 14 to 11 h d^{-1} at 29 DAS (□), 43 DAS (▽) and 57 DAS (△). Data are shown for constant photoperiods and transfers at 29 and 43 DAS ('NTSR94' and 'NTSC92') or 43 and 57 DAS ('GabC92'). Vertical bars represent LSD at p=0.05 (no significant treatment effect before 37 DAS for 'NTSC92' and 43 DAS for 'GabC92' and 'NTSR94'; LSD based on all 14 treatments, which are not all shown).

In a reciprocal transfer experiment with 20 rice cultivars, Yin et al. (1997) found in seven (mainly *japonica*) cultivars that plants transferred early from SD (10 h d^{-1} or 12.5 h d^{-1}) to LD (14 h d^{-1}) flowered later than plants in the constant LD treatment. However, flowering was not found to be strongly accelerated by an early transfer from LD to SD compared to the constant SD treatment. Two of the seven cultivars were included in three different transfer experiments, and showed similar behaviour in all three experiments.

The results shown in Fig. 3.2 might indicate that the pre-inductive period is shorter under LD than under SD, which would imply a long-short day response. It is also possible that another factor was confounded with long photoperiods, for instance light intensity or temperature. This is unlikely, however, because the light levels used for photoperiod extension were very low and the sheds were well ventilated. Another reason why confounding with other factors is not probable, is that only part of the cultivars in the studies of Collinson (1992) and Yin et al. (1997) showed this pattern.

The effect could be related to differences in leaf number per plant. The mean number of leaves per plant (and hence leaf area) tended to be lower for plants under constant SD than for those under LD for some weeks before transfer to SD, and higher for constant LD plants than for those which had been under SD for some time (Fig. 3.3). A possible influence of leaf number on the onset of podding could be through the availability of assimilates, but, as photoperiod is perceived by the leaves (Thomas and Vince-Prue, 1997), it could also be through effects of leaf area or age on photoperiod perception and the subsequent production of promoting or inhibiting substances by the leaves.

Yin et al. (1997) also mention the possibility that plants may be sensitive to the direction of photoperiod change. In the present experiment, any effect of the direction of photoperiod change might have been enlarged by the sudden large change in photoperiod: from 11 h d^{-1} to 14 h d^{-1} in one single step.

If the standard response model of Fig. 3.1 is fitted, the estimated duration of the pre-inductive phase is 66 days in 'GabC92' and 56 days in 'NTSR94' (Table 3.1).

Flowering in 'GabC92' and 'NTSR94' started at 49 and 45 DAS respectively, so the time between the onset of flowering and the beginning of the inductive phase for podding would be 17 days for 'GabC92' and 11 days for 'NTSR94'.

The standard errors of the times to podding were relatively large in the treatments with constant LD and early transfers from SD to LD (Fig. 3.2). Similar results were obtained in a study on the inductive phase for flowering in the long-day species lentil (*Lens culinaris* Medic.): the standard error was relatively large in the constant SD treatment and the treatments with a transfer from a more inductive (LD) to a less inductive (SD) photoperiod, both for a local land race and for a cultivar (Roberts et al, 1986).

The main photoperiod effect occurred later in 'GabC92' than in 'NTSR94' (Fig. 3.2). Linnemann (1994b) reported that in selection 'Tiga Nicuru' from Mali podding was already induced before flowering started. Thus, the duration of the pre-inductive phase varies between bambara groundnut selections. Genotypic differences in the duration of the pre-inductive phase have also been found in crops which are photoperiod-sensitive with regard to flowering, for example soya bean (Wilkerson et al., 1989; Collinson et al., 1993), rice (Collinson et al., 1992; Yin et al., 1997) and maize (*Zea mays* L.) (Kiniry et al., 1983). Differences in the duration of the pre-inductive phase can be exploited when bambara groundnut selections from higher latitudes are transferred to lower latitudes, where photoperiods are shorter than the critical photoperiods for these selections. A choice can be made between selections with pre-inductive phases of different lengths to obtain a good match between the length of the growing season and the crop cycle.

3.5 Conclusion

At an average temperature of 25.7 °C, the main photoperiod effect on podding occurred from 42 days after sowing onwards in 'NTSR94' and 'NTSC92', and from

57 days after sowing onwards in 'GabC92'. The time from sowing to podding could not be divided clearly into photoperiod-sensitive and photoperiod-insensitive phases in the same way as the time between sowing and flowering in other crops. This was because podding in all three selections tended to be later in early transfers from SD to LD than in constant LD, and earlier in the early transfers from LD to SD than in constant SD. This phenomenon has been found in rice as well, but cannot satisfactorily be explained.

CHAPTER 4

EFFECTS OF CONSTANT, INCREASING AND DECREASING PHOTOPERIODS ON REPRODUCTIVE DEVELOPMENT AND YIELD IN BAMBARA GROUNDNUT (*VIGNA SUBTERRANEA*)

Submitted as:

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4 EFFECTS OF CONSTANT, INCREASING AND DECREASING PHOTOPERIODS ON REPRODUCTIVE DEVELOPMENT AND YIELD IN BAMBARA GROUNDNUT (*VIGNA SUBTERRANEA*)

M. Brink

Abstract

The influence of constant and gradually increasing or decreasing photoperiods on the reproductive development and yield of four bambara groundnut (*Vigna subterranea*) selections from eastern and southern Africa was studied in a glasshouse experiment. Treatments included constant photoperiods of 12, 13, and 14 h d^{-1}, a decreasing photoperiod (14 h d^{-1} decreasing to 11 h d^{-1} at a rate of 1 min d^{-1}), an increasing photoperiod (12 h d^{-1} increasing to 15 h d^{-1} at a rate of 1 min d^{-1}) and a photoperiod that first increased (from 13 h d^{-1} to 14 h d^{-1} at a rate of 1 min d^{-1}) and later decreased (from 14 h d^{-1} to 12 h d^{-1} at a rate of 1 min d^{-1}). No significant photoperiod effect on the rate of progress from sowing to flowering was found in any of the selections, but the rate of progress from flowering to podding was influenced by photoperiod in all four selections. The average photoperiod between flowering and podding determined the rate from flowering to podding, and a gradual increase or decrease did not affect that rate. Therefore, bambara groundnut models intended to predict development in field situations with fluctuating photoperiods may be based on studies with constant photoperiods. Final harvest results showed that a prolonged time from sowing to podding led to a higher total plant dry weight, but a lower seed yield, because of a lower harvest index. The harvest index and seed yield per plant seemed not to be affected by the photoperiod and the direction of change in photoperiod in the pod-filling phase.

4.1 Introduction

Crop development is mainly determined by temperature and/or photoperiod (Roberts and Summerfield, 1987; Squire, 1990). When the influence of photoperiod on development in legumes is modelled, direction and rate of change in photoperiod are usually ignored (e.g. Hodges and French, 1985; Sinclair et al., 1991; Summerfield et al., 1991; Grimm et al., 1994). The photoperiod reaction is assumed to be instantaneous, previous photoperiods are assumed to be irrelevant, and daily development rates may simply be accumulated. However, Constable and Rose (1988) found different development rates for similar average photoperiods and temperatures in spring and autumn sowings in soya bean (*Glycine max* (L.) Merr.) field experiments. They concluded that the interval from emergence to flowering and from flowering to maturity in soya bean was not only affected by temperature and photoperiod, but also by the rate at which the photoperiod changed. In contrast, Acock et al. (1994) found no effect of the direction of change in photoperiod on the time to flowering in soya bean in a controlled environment experiment.

In the leguminous food crop bambara groundnut (*Vigna subterranea* (L.) Verdc.), an indeterminate annual herb with pods on or below the soil surface, the onset of flowering and the onset of pod growth ("podding") can be affected by photoperiod. In some genotypes, both flowering and podding are delayed by long photoperiods, but in many others flowering is photoperiod-insensitive, and only podding is retarded by long photoperiods (Linnemann, 1991; Linnemann and Craufurd, 1994). The effects of photoperiod and temperature on rates of progress from sowing to flowering and flowering to podding have been quantified in linear models for different bambara groundnut selections on the basis of semi-controlled environment research with constant photoperiods (Chapter 2). These linear models, however, do not include effects of changing photoperiods. It has been found that bambara groundnut plants transferred from long (14 h d^{-1}) to short (11 h d^{-1}) days started podding earlier than plants kept under constant short days, and plants transferred from short to long days started podding later than plants kept under constant long days (Chapter 3). These effects may have been caused by changing photoperiods influencing development.

The objective of the present study was to assess the effect of gradual changes in photoperiod on development rates in bambara groundnut. It was expected that if there are any effects, these would be that a gradual increase in photoperiod retards development, whereas a gradual decrease accelerates it. If there are no effects, bambara groundnut development models can be based on results of studies with constant photoperiods.

4.2 Material and methods

Experiment

A glasshouse experiment was conducted from 25 April to 25 October 1995 at Wageningen Agricultural University, The Netherlands (51°58' N). The experimental design was a split-plot with photoperiod (six treatments) as main factor and bambara groundnut selections (four) as split factor, in two replicates. The selections, all cream coloured, were: 'GabC92' and 'GabC94', collected from markets in Gaborone, Botswana (24°40'S); 'DipC94', collected from a farmer at Diphiri, near Gaborone; and 'DodC94', collected from a market in Dodoma, Tanzania (6°10'S). The six photoperiod treatments were (Fig. 4.1): constant photoperiods of (1) 12, (2) 13 and (3) 14 h d^{-1}; (4) a continuously decreasing photoperiod (from 14 h d^{-1} at two days after sowing (DAS) to 11 h d^{-1} at 182 DAS); (5) a continuously increasing photoperiod (from 12 h d^{-1} at 2 DAS to 15 h d^{-1} at 182 DAS); and (6) a photoperiod initially increasing (from 13 h d^{-1} at 2 DAS to 14 h d^{-1} at 62 DAS at a rate of 1 min d^{-1}) and then decreasing (from 14 to 12 h d^{-1} at a rate of 1 min d^{-1}). The treatments were chosen such that the average photoperiod in the changing photoperiod treatments would remain between the lowest (12 h d^{-1}) and highest (14 h d^{-1}) constant photoperiod treatment. This range was selected because it was known that bambara groundnut is photoperiod sensitive in this range (Linnemann et al., 1995; Chapter 2).

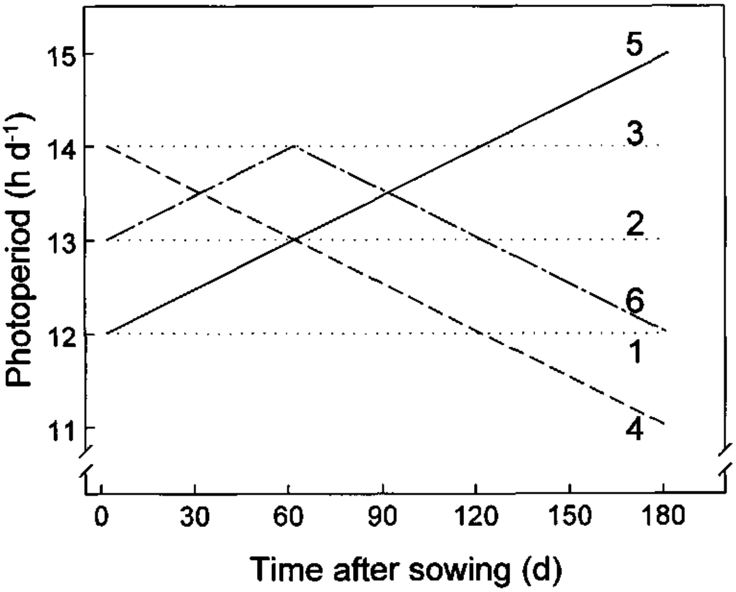

Fig. 4.1. Schematic overview of the six photoperiod treatments included in the experiment: (1) constant photoperiod of 12 h d^{-1}; (2) constant photoperiod of 13 h d^{-1}; (3) constant photoperiod of 14 h d^{-1}; (4) photoperiod decreasing at 1 min d^{-1} from 14 h d^{-1} at 2 DAS to 11 h d^{-1} at 182 DAS; (5) photoperiod increasing at 1 min d^{-1} from 12 h d^{-1} at 2 DAS to 15 h d^{-1} at 182 DAS; and (6) photoperiod increasing at 1 min d^{-1} from 13 h d^{-1} at 2 DAS until 62 DAS and decreasing at 1 min d^{-1} from 62 DAS to 12 h d^{-1} at 182 DAS.

A replicate consisted of six trolleys, each subjected to a separate photoperiod treatment and carrying six plants per selection, grouped by selection. Within each trolley, the plants were circulated weekly. From 08:00 to 16:00 h all plants were exposed to natural daylight, from 16:00 to 08:00 h the trolleys were placed inside sheds, where the photoperiod was prolonged by means of low intensity artificial light (fluorescent tubes (Philips TLD 36 Watt, colour no. 84) and Philips 40 W bulbs). Artificial light was on from 07:00 to 08:00 h and from 16:00 h to a time dependent on the photoperiod treatment. All photoperiod treatments received the same amount of photosynthetically active radiation.

From 08:00 to 16:00 h the glasshouse temperature was set between 26 and 29 °C; the rest of the day it was between 22 and 25 °C. However, on sunny days, maximum temperatures higher than 35 °C were recorded. Average daily glasshouse temperature during the experiment was 26.3 °C, with an average daily maximum of 31.3 and an average daily minimum of 21.7 °C.

Seeds were pre-germinated in a germination cabinet. Two days after sowing, the plants were transplanted singly in white plastic pots (4.8 l), filled with a 1:1 v/v mixture of sand and potting compost ('potting compost no.4' from Lentse potgrond b.v., consisting of 85% peat and 15% clay). At transplanting, *Rhizobium* spp. strain CB 756, obtained from the Department of Microbiology, Wageningen Agricultural University, was put in the planting hole. The plants were fertilized at three-weekly intervals from 5 to 14 weeks after sowing, with 200 ml of a standard complete nutrient solution obtained by mixing 0.833 g 'Nutriflora-t' (supplied by Windmill Holland b.v.) and 1 g calcium nitrate in one litre water, resulting in a nutrient content of 172 mg l^{-1} N, 39 mg l^{-1} P, and 263 mg l^{-1} K. The plants were kept well-watered. Pests were controlled by regular introduction of *Amblyseius cucumeris* and *Orius insidiosus* against thrips (*Frankliniella occidentalis* and *Thrips tabaci*), and *Phytoseiulus persimilis* against spider mites (*Tetranychus urticae*).

Non-destructive observations included the dates of onset of flowering and podding of each plant. The onset of flowering was defined as the day the plant had its first open flower; the onset of podding as the day the plant had a pod of at least 0.5 cm long. Direct podding observations were possible because the selections included in this study form pods on the soil surface. From the daily observations, the dates when 50% of the plants had started flowering ('50% flowering') and 50% of the plants had started podding ('50% podding') were calculated for each treatment in each replicate. At the final harvest (183 DAS), the dry weights of above ground vegetative parts, pods and seeds were determined for each plant.

Analysis

Results of the three constant photoperiod treatments were subjected to analysis of variance with the GENSTAT statistical package (Payne et al., 1993) to determine whether the rate of progress from sowing to flowering ($1/f$; with f being the number of days from sowing to flowering) and the rate of progress from flowering to podding ($1/(p-f)$; with $(p-f)$ being the number of days from flowering to podding) were influenced by photoperiod. Subsequently, the results of the changing photoperiod treatments were compared with those of the constant photoperiod treatments, to determine their possible effect on development. Final harvest results were also subjected to analysis of variance with the GENSTAT statistical package.

4.3 Results

All plants formed flowers during the experiment. The time from sowing to 50% flowering (f) in the different treatments varied from 43 to 50 days for 'GabC92', from 38 to 40 for 'GabC94', from 38 to 41 for 'DipC94' and from 43 to 57 for 'DodC94'. Analysis of variance on the constant photoperiod treatments showed that selection effects on the rate of progress from sowing to flowering ($1/f$) were significant ($p \leq 0.01$), but photoperiod effects and interaction effects of selection and photoperiod were not. The selections can be divided into two groups with regard to $1/f$: 'DodC94' and 'GabC92' on one hand, 'GabC94' and 'DipC94' on the other (Table 4.1). The rate of progress from sowing to flowering was similar in shifting photoperiods and constant photoperiods (Fig. 4.2).

Table 4.1. Rate of progress from sowing to flowering (1/*f*) and flowering to podding (1/(*p*-*f*)) for four bambara groundnut selections and three constant photoperiods. No interaction effects occurred between selection and photoperiod treatments.

		1/*f*	1/(*p*-*f*)
Selection	'GabC92'	0.0219	0.0196
	'GabC94'	0.0256	0.0263
	'DipC94'	0.0256	0.0277
	'DodC94'	0.0220	0.0188
Photoperiod (h d^{-1})	12	0.0241	0.0348
	13	0.0236	0.0210
	14	0.0235	0.0135
$LSD_{0.05}$ selection		0.00281	0.00371
$LSD_{0.05}$ photoperiod		n.s.	0.00579

Pods were formed on all plants except the 'DodC94' plants in the increasing photoperiod treatment. The time from 50% flowering to 50% podding (*p*-*f*) ranged from 34 to 94 days for 'GabC92', from 26 to 67 days for 'GabC94', from 23 to 70 days for 'DipC94' and 37 to >140 (no pods formed) for 'DodC94'. The rate of progress from flowering to podding (1/(*p*-*f*)) in the constant photoperiod treatments was significantly influenced by selection and photoperiod, but interaction effects were not significant. On the basis of the rate of progress from flowering to podding, the four selections can be divided into the same two groups as for the rate of progress from sowing to flowering: lower rates for 'GabC92' and 'DodC94', higher rates for 'GabC94' and 'DipC94' (Table 4.1). From Fig. 4.3, which shows 1/(*p*-*f*) as a function of the average photoperiod in the period between flowering and podding, it can be concluded that the increasing photoperiods do not have a retarding effect and that the decreasing photoperiods do not have an accelerating effect.

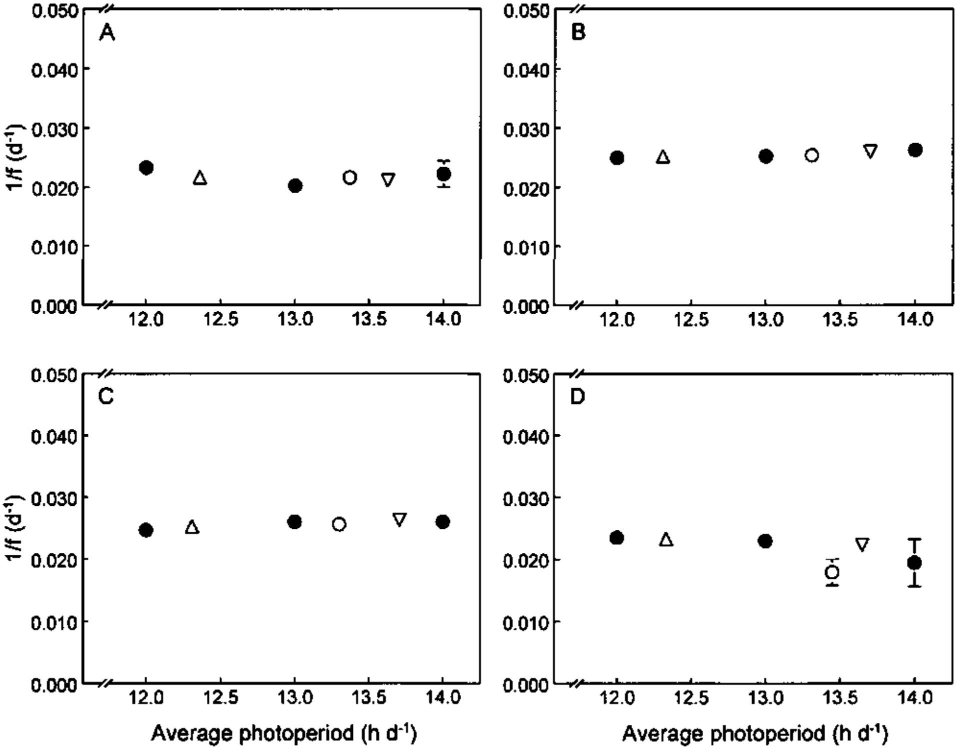

Fig. 4.2. Rate of progress from sowing to flowering (1/*f*; with *f* being the number of days from sowing to flowering) in bambara groundnut selections 'GabC92' (A), 'GabC94' (B), 'DipC94' (C), and 'DodC94' (D) as a function of the average photoperiod between sowing and flowering under different photoperiod regimes: constant photoperiods of 12, 13, or 14 h d^{-1} (●); photoperiod decreasing at 1 min d^{-1} from 14 h d^{-1} at 2 DAS (▿); photoperiod increasing at 1 min d^{-1} from 12 h d^{-1} at 2 DAS (▵); and photoperiod increasing at 1 min d^{-1} from 13 h d^{-1} at 2 DAS until 62 DAS and decreasing at 1 min d^{-1} from 62 DAS onwards (○). Vertical bars indicate means ± standard error (only visible where larger than the symbols).

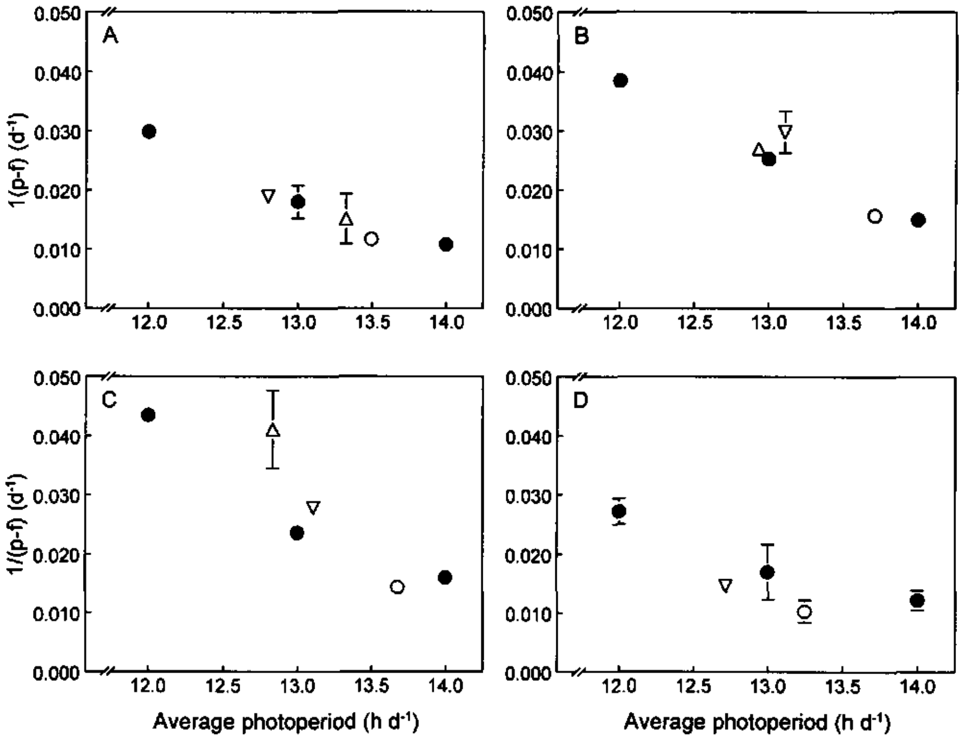

Fig. 4.3. Rate of progress from flowering to podding (1/(*p-f*); with (*p-f*) being the number of days from flowering to podding) in bambara groundnut selections 'GabC92' (A), 'GabC94' (B), 'DipC94' (C), and 'DodC94' (D) as a function of the average photoperiod between flowering and podding under different photoperiod regimes: constant photoperiods of 12, 13, or 14 h d^{-1} (●); photoperiod decreasing at 1 min d^{-1} from 14 h d^{-1} at 2 DAS (▽); photoperiod increasing at 1 min d^{-1} from 12 h d^{-1} at 2 DAS (△); and photoperiod increasing at 1 min d^{-1} from 13 h d^{-1} at 2 DAS until 62 DAS and decreasing at 1 min d^{-1} from 62 DAS onwards (○). Vertical bars indicate means ± standard error (only visible where larger than the symbols).

The total time from sowing to podding ranged from 77 to 140 days for 'GabC92', from 66 to 105 days for 'GabC94', from 64 to 109 days for 'DipC94' and from 80 to >183 days for 'DodC94'. Fig. 4.4 shows that the selections 'GabC94' and 'DipC94' had similar times from sowing to podding in all photoperiod treatments, but the third selection from Botswana, 'GabC92', always needed a longer time.

Total dry matter production (excluding roots) was higher for 'GabC92' and 'DodC94' than for 'GabC94' and 'DipC94' and higher under constant 13 and 14 h d^{-1} photoperiods than under constant 12 h d^{-1} (Table 4.2). The highest seed yield (17.2 g per plant) was obtained from 'GabC92' in the constant 12 h d^{-1} treatment. Total plant dry weight increased with increasing time from sowing to podding, whereas seed dry weight and harvest index were lower when podding occurred later (Fig. 4.5). The harvest index and seed yield per plant were not affected by the photoperiod and the direction of change in photoperiod in the pod-filling phase, though the harvest index tended to be slightly lower in the increasing photoperiod treatment than in other treatments with similar times to podding.

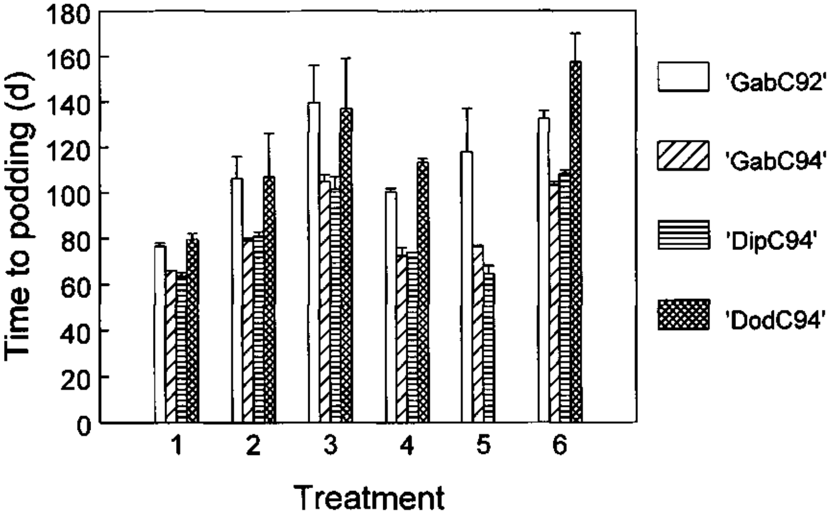

Fig. 4.4. Means and standard errors of the time from sowing to podding in four bambara groundnut selections in the six photoperiod treatments of Fig. 4.1. 'DodC94' in treatment 5 had not started podding when the experiment was terminated (183 DAS).

Table 4.2. Total plant (excluding roots), pod and seed dry weights and harvest index (seed weight as a fraction of total plant weight) at the final harvest (183 DAS) for four bambara groundnut selections in the six photoperiod treatments of Fig. 4.1.

Dry weight (g plant^{-1})	Selection	Treatment						
		1	2	3	4	5	6	Mean
Total	'GabC92'	37.8	45.0	41.7	37.8	47.3	48.2	43.0
	'GabC94'	28.2	31.7	37.2	30.8	31.1	38.7	33.0
	'DipC94'	25.7	32.4	32.5	33.0	28.3	35.9	31.3
	'DodC94'	28.6	38.6	41.6	37.7	45.6	43.9	39.3
	Mean	30.1	36.9	38.3	34.8	38.1	41.7	36.6
		$\mathrm{LSD}_{0.05}$ treatment: 5.38; $\mathrm{LSD}_{0.05}$ selection: 4.16; $\mathrm{LSD}_{0.05}$ interaction: n.s.						
Pods	'GabC92'	20.9	17.6	5.3	16.9	8.8	10.1	13.3
	'GabC94'	17.7	17.1	13.5	17.5	15.5	14.7	16.0
	'DipC94'	18.1	17.9	13.4	19.2	15.5	11.8	16.0
	'DodC94'	16.6	8.6	2.6	11.2	0.0	2.6	6.9
	Mean	18.3	15.3	8.7	16.2	10.0	9.8	13.1
		$\mathrm{LSD}_{0.05}$ treatment: 1.48; $\mathrm{LSD}_{0.05}$ selection: 2.07; $\mathrm{LSD}_{0.05}$ interaction: 4.54; $\mathrm{LSD}_{0.05}$ interaction (within same treatment): 5.06						
Seeds	'GabC92'	17.2	14.5	4.2	14.0	7.1	8.4	10.9
	'GabC94'	15.0	14.7	11.6	14.8	13.1	12.9	13.7
	'DipC94'	15.2	15.2	11.7	16.5	13.1	10.1	13.6
	'DodC94'	13.7	6.8	2.0	9.4	0.0	1.9	5.6
	Mean	15.3	12.8	7.4	13.7	8.3	8.3	11.0
		$\mathrm{LSD}_{0.05}$ treatment: 1.37; $\mathrm{LSD}_{0.05}$ selection: 2.06; $\mathrm{LSD}_{0.05}$ interaction: 4.51; $\mathrm{LSD}_{0.05}$ interaction (within same treatment): 5.05						
Harvest index	'GabC92'	0.46	0.32	0.10	0.37	0.16	0.17	0.26
	'GabC94'	0.53	0.46	0.31	0.48	0.42	0.33	0.42
	'DipC94'	0.59	0.47	0.36	0.50	0.46	0.28	0.44
	'DodC94'	0.48	0.18	0.05	0.25	0.00	0.04	0.17
	Mean	0.52	0.36	0.21	0.40	0.26	0.21	0.32
		$\mathrm{LSD}_{0.05}$ treatment: 0.043; $\mathrm{LSD}_{0.05}$ selection: 0.032; $\mathrm{LSD}_{0.05}$ interaction: 0.077; $\mathrm{LSD}_{0.05}$ interaction (within same treatment): 0.079						

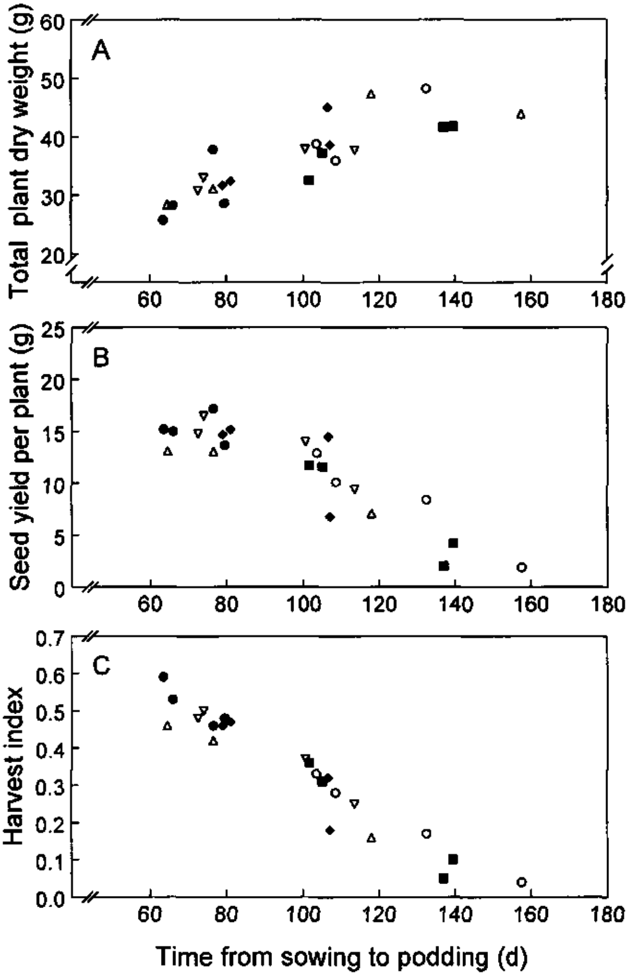

Fig. 4.5. Total dry weight per plant (excluding roots) (A), seed dry weight per plant (B) and harvest index (seed dry weight as a fraction of total plant dry weight) (C) at the final harvest (183 DAS) in the treatments 1 (●), 2 (♦), 3 (■), 4 (▿), 5 (▵) and 6 (○) of Fig. 4.1.

4.4 Discussion

It was shown that when the rate of progress from flowering to podding is plotted against the average photoperiod between flowering and podding, there are no indications that increasing photoperiods have a strong retarding effect or decreasing photoperiods a strong accelerating effect on the rate of progress from flowering to podding (Fig. 4.3). Hence, the average photoperiod determines the time to podding in bambara groundnut and a gradual change in photoperiod does not affect development rates. The assumption that the photoperiod reaction is instantaneous and that daily development rates may be accumulated appears to be valid for the period to podding in bambara groundnut. Therefore, it is possible to base photothermal models intended for prediction of bambara groundnut development in field situations on studies with constant photoperiods.

The findings of the present study are not in agreement with those of Constable and Rose (1988), who suggest that development rates in soya bean are affected by the rate of change in photoperiod. However, they confirm those of Acock et al. (1994), who found no effect of the direction of change in photoperiod on time to flowering in soya bean. There are contradictory reports for cereals too. In multilocation field experiments with maize (*Zea mays* L.), Bonhomme et al. (1991) did find a significant effect of rate of change in photoperiod on total leaf number. However, in a field experiment with wheat (*Triticum aestivum* L.) and an outdoor pot experiment with spring barley (*Hordeum vulgare* L.), both including constant and increasing photoperiod treatments, no effect of rate of change on development rates independent of the average photoperiod was found (Slafer et al., 1994; Kernich et al., 1995). Reports that rate of change in photoperiod does affect development rates are often based on field experiments with different sowing dates and natural photoperiods (Constable and Rose, 1988; Bonhomme et al., 1991), where rate of change in photoperiod might be confounded with other factors, such as temperature, radiation and availability of water and nutrients. In studies with simultaneous artificially constant and changing photoperiod treatments and the same sowing date for all treatments, no effects of rate of change in photoperiod on development rates are usually found (Acock et al., 1994; Slafer et al., 1994; Kernich et al., 1995; this study)

In all six photoperiod treatments, the time from sowing to podding was longer for 'GabC92' than for the other two selections from Botswana, 'GabC94' and 'DipC94' (Fig. 4.4). Therefore 'GabC92' can be characterized as a relatively late selection, and the other two as relatively early selections. The reason that no podding occurred in 'DodC94' in treatment 5 is probably that photoperiods longer than 14 h d^{-1} strongly retard or inhibit podding in this selection.

Final harvest results showed that a prolonged time from sowing to podding led to a higher total plant dry weight, which, however, did not translate into higher yields at six months after sowing. It is possible that the harvest index and yield of plants with a longer vegetative period would have been higher if the plants had been allowed to grow longer. In soya bean, for example, it has been found that reducing the vegetative period of late maturing cultivars did not lead to lower seed yields, because the harvest index became higher, whereas in two early maturing cultivars, a reduced vegetative phase led to lower seed yields (Schweitzer and Harper, 1985). The finding that seed yield and harvest index were strongly related to the time to podding and not to the photoperiod and the direction of change in photoperiod in the pod-filling phase, indicates that there is no influence of photoperiod on dry matter partitioning in the pod-filling phase.

4.5 Conclusion

The average photoperiod in the period between flowering and podding determines the rate from flowering to podding, and a gradual increase or decrease in photoperiod has no effect independent of the average photoperiod. Therefore, photothermal models intended to predict bambara groundnut development in field situations with fluctuating photoperiods may be based on studies with constant photoperiods. Final harvest results showed that a prolonged time from sowing to podding led to a higher total plant dry weight, but a lower seed yield, because of a lower harvest index. Harvest index and seed yield per plant seem not to be affected by the photoperiod and the direction of change in photoperiod in the pod-filling phase.

CHAPTER 5

DEVELOPMENT, GROWTH AND DRY MATTER PARTITIONING IN BAMBARA GROUNDNUT (*VIGNA SUBTERRANEA*) AS INFLUENCED BY PHOTOPERIOD AND SHADING

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5 DEVELOPMENT, GROWTH AND DRY MATTER PARTITIONING IN BAMBARA GROUNDNUT (*VIGNA SUBTERRANEA*) AS INFLUENCED BY PHOTOPERIOD AND SHADING

M. Brink

Abstract

A semi-controlled environment study was conducted to investigate the interaction between growth and development in bambara groundnut (*Vigna subterranea*) and the influence of photoperiod on dry matter partitioning. The experimental design was a split-plot with four photoperiods (10.5, 11.8, 13.2 and 14.5 h d^{-1}) and two light treatments: unshaded and shaded (42% light reduction). The selection used was 'DipC94' from Botswana. The dates of 50% flowering and 50% podding were determined, and samples of plants were harvested at 22, 36, 50, 64, 78, 92, 106, and 120 days after sowing. Total dry matter production was 41% lower in the shaded treatment than in the unshaded treatment, but the rates of progress from sowing to flowering and flowering to podding decreased by only 3 and 12 % respectively. This suggests that growth and development in bambara groundnut are largely independent. Photoperiod influenced dry matter partitioning indirectly, through its influence on the onset of podding. There were, however, no strong direct photoperiod effects on dry matter partitioning, either before or after the onset of podding.

5.1 Introduction

The leguminous crop bambara groundnut (*Vigna subterranea* (L.) Verdc.) is an important secondary food crop in Africa, mainly grown by smallholders in drier regions (Linnemann and Azam-Ali, 1993). Bambara groundnut is an indeterminate annual herb, with creeping stems carrying trifoliolate leaves with erect petioles. Flowers are formed at the base of the petioles, usually in pairs. After pollination, the peduncle grows out and pods form on or under the ground. The pods usually contain one seed. Unripe and ripe seeds are used for human consumption (Linnemann and Azam-Ali, 1993).

It is generally assumed that photoperiod and temperature are the main environmental factors influencing reproductive development in annual crops (Summerfield et al., 1991; Hodges, 1991; Sinclair et al., 1991). In most bambara groundnut genotypes investigated, the onset of flowering is photoperiod-insensitive and the onset of podding is retarded by long photoperiods (Linnemann, 1994a; Chapter 2 of this thesis). The effects of photoperiod and temperature on rates of progress from sowing to flowering and flowering to podding have been quantified in linear models for different bambara groundnut selections, using data from semi-controlled environment research (Chapter 2). These models operate under the widely held assumption that interaction between development and growth may be ignored and that crop development may be modelled separately from crop growth.

Another common assumption in crop growth modelling is that dry matter partitioning factors depend mainly on development stage and are not directly influenced by photoperiod. In bambara groundnut, photoperiod influences dry matter partitioning indirectly through its influence on reproductive development. The onset of podding coincides with a major shift in the assimilate distribution, which becomes mainly directed towards pod growth (Linnemann et al., 1995). Linnemann et al. (1995) suggested that the partitioning factors before this major switch from vegetative to pod growth may not be constant, but directly influenced by photoperiod. They found that the percentage of above ground matter partitioned to the leaf blades of selection 'Tiga Nicuru' was higher under short (10 or 12 h d^{-1}) than under long (14 or 16 h d^{-1}) photoperiods and the percentage partitioned to the stem parts (petioles and stems) lower. They also suggested that the partitioning factors after the onset of podding are directly influenced by photoperiod, because the pod growth rate in selection 'Ankpa4' was higher under a 10 h d^{-1} photoperiod than under a 12 h d^{-1} photoperiod. In soya bean (*Glycine max* (L.) Merr.), the proportion of dry matter increase partitioned to the reproductive structures has also been found to be greater under short days than under long days or treatment with interrupted nights (Cure et al., 1982; Morandi et al., 1988).

The two objectives of the present study on bambara groundnut were therefore to find out if there is any interaction between growth and development and whether photoperiod has a direct effect on dry matter partitioning.

5.2 Material and methods

A semi-controlled environment experiment was conducted in the period 26 May to 23 September 1996 in Wageningen, The Netherlands (51°58' N). The experimental design was a split-plot with photoperiod (four levels) as main factor and shading (two levels) as split factor, and two replicates. The experiment was carried out in two identical glasshouses with forced ventilation, which function as replicates.

A tent with four compartments was placed in each glasshouse, which made it possible to apply four different photoperiods. From 08:00 h to 16:00 h, the tents were removed and the plants received natural daylight. From 16:00 h to 08:00 h, the plants were covered by the tents, and the photoperiod in the compartments was prolonged to a different extent by means of low intensity artificial light (four Philips TLD 36 W fluorescent tubes (colour no. 84) and two 40 W bulbs per compartment). This ensured there was no difference in the amount of photosynthetically active radiation (PAR) received in different photoperiods. The constant photoperiods in the four compartments in each glasshouse were 10.5, 11.8, 13.2, and 14.5 h d^{-1}. Artificial light was supplied from 07:00 to 08:00 h and from 16:00 to respectively 17:30, 18:50, 20:10, and 21:30

h for the different photoperiods. Removable metal roofs were put over the glasshouses from 16:00 h to 08:00 h, to exclude daylight and to prevent the temperature inside the tents from becoming too high.

Each compartment contained a staging with 80 plants of bambara groundnut selection 'DipC94', a cream coloured selection collected from a farmer at Diphiri, near Gaborone, Botswana (24°40'S; 25°55'E). One half of each table (40 plants) was covered from 08:00 to 16:00 h with a frame of green shade netting. The nets were removed from 16:00 to 08:00 h, and both halves of each table received the same amount of low intensity artificial light. To estimate the light reduction by the glasshouse structure and the shading treatment, ceptometer measurements were carried out five times: in the morning and in the afternoon at the beginning and at the end of the experimental period, and in the afternoon in the second half of June, when outside radiation reached a peak. The PAR at plant level in the unshaded treatments was 52% of that outside the glasshouse. Shade netting caused a further average PAR reduction of 42%. The mean global radiation in the experimental period, measured in a meteorological station at about 500 m distance from the glasshouse, was 15.9 MJ m^{-2} d^{-1} (Department of Meteorology, Wageningen Agricultural University), which corresponds to about 8 MJ m^{-2} d^{-1} PAR. The radiation between 08:00 and 16:00 can be estimated on 77% of the daily radiation in the period June to September (Anon., 1989).

From 10:00 to 16:00 h, the temperature in the glasshouse was set at 27 °C; from 18:00 to 08:00 h at 23 °C. Between 08:00 and 10:00 h the temperature was set to increase gradually from 23 to 27 °C; from 16:00 to 18:00 h to decrease gradually from 27 to 23 °C. The average temperature over the whole experiment was 25.0 °C.

The seeds were pre-germinated in a germination cabinet at 30 °C. When the root tips became visible, the plants were transplanted (one plant per pot) in white plastic 5 l pots, filled with a 1:1 v/v mixture of sand and potting compost ('potting compost no.4' from Lentse potgrond b.v., consisting of 85% peat and 15% clay). At transplanting, *Rhizobium* spp. strain CB 756, obtained from the Department of

Microbiology, Wageningen Agricultural University, was put in the planting hole. The plants were fertilized with a complete nutrient solution obtained by mixing 0.833 g 'Nutriflora-t' (supplied by Windmill Holland b.v.) and 1 g calcium nitrate in one litre of tap water, resulting in a nutrient content of 172 mg l^{-1} N, 39 mg l^{-1} P, and 263 mg l^{-1} K. The solution (220 ml per plant) was applied four times at two-weekly intervals between 24 and 82 days after sowing. The plants were kept well-watered. Biological pest control was used: *Amblyseius cucumeris* and *Orius insidiosus* were introduced regularly against thrips (*Frankliniella occidentalis* and *Thrips tabaci*), and *Phytoseiulus persimilis* against spider mites (*Tetranychus urticae*). The plants were circulated weekly and earthed-up individually on the day they had a pod longer than 0.5 cm.

Non-destructive observations included dates of first flowering and onset of podding of each plant. Flowering onset was defined as the day on which the plant had its first open flower, and podding onset as the first day the plant had a pod at least 0.5 cm long. Direct podding observations were possible because the selection included in this study forms pods on the soil surface. On the basis of the individual plant observations, the dates when 50% of the plants in a treatment had started flowering ('50% flowering'), and 50% of the plants in a treatment had started podding ('50% podding') were determined. Daily flower counts were carried out on 6 plants per treatment per replicate from the onset of flowering to the onset of podding of these plants.

Eight harvests of five plants per photoperiod/radiation combination per replicate were carried out at two-weekly intervals, at 22 days after sowing (DAS). At each harvest, leaf area, number of leaves and pods, and dry weight of roots, leaf blades, petioles, stems and pods were determined. Fallen plant material was collected throughout the experiment. Dry matter partitioning factors were calculated by dividing the weight increases of the various organs between two successive harvests by the increase in total plant dry weight in the same period.

Statistical analysis (analysis of variance) of the results was done with the GENSTAT 5.3 statistical package (Payne et al., 1993).

5.3 Results

Growth

Total plant dry weight was significantly influenced by shading throughout the experimental period, but photoperiod and interaction effects between photoperiod and shading were not significant. The final total plant dry weight was 41% lower in the shaded treatment than in the unshaded treatment (Table 5.1). The average growth rate over the experimental period was 0.23 g d^{-1} for the unshaded treatment and 0.14 g d^{-1} for the shaded treatment. Dropped flowers, aborted ovaries and dead roots were not included in the total plant weight, so the actual total dry matter production must have been somewhat higher than given in Table 5.1.

Table 5.1. Mean plant dry weights (including roots) in the unshaded (Unsh.) and shaded (Sh.) treatments at different harvests, and the difference between the two treatments as a percentage of the dry weight in the unshaded treatment. The differences between the shaded and unshaded treatments were significant for all eight harvests. There were no significant photoperiod effects or interaction effects of photoperiod and shading on the mean plant dry weight.

Time (DAS)	Mean plant dry weight (g)		Difference (%)
	Unsh.	Sh.	
22	1.1	0.9	24.6
36	3.1	2.2	28.1
50	6.8	4.3	37.3
64	11.8	7.1	39.9
78	16.2	10.0	38.0
92	20.7	11.3	45.8
106	24.6	14.6	40.6
120	27.8	16.4	41.1

Development

The rate of progress from sowing to flowering (1/*f*, with *f* being the number of days from sowing to 50% flowering) was not influenced by photoperiod, but shading reduced the rate slightly (Table 5.2). No significant interaction was found between photoperiod and shading. The average time to flowering was 41.6 days for the unshaded and 42.9 days for the shaded treatments. In all treatments, the date of 50% flowering was between the second and third harvests. Therefore the flowering data are based on 30 plants per treatment per replicate.

The rate of progress from flowering to podding (1/(*p*-*f*), with (*p*-*f*) being the number of days from 50% flowering to 50% podding) was strongly influenced by photoperiod and to a lesser extent by shading (Table 5.2). The interaction effect of both factors was not significant. The time from flowering to podding ranged from 20.5 days (10.5 h d^{-1}; unshaded) to 53.5 days (14.5 h d^{-1}; shaded).

Table 5.2. Rate of progress from sowing to flowering (1/*f*) and rate of progress from flowering to podding (1/(*p*-*f*)) in the unshaded (Unsh.) and shaded (Sh.) treatments under constant photoperiods of 10.5, 11.8, 13.2, and 14.5 h d^{-1}.

Photoperiod (h d^{-1})	1/*f*			1/(*p*-*f*)		
	Unsh.	Sh.	Mean	Unsh.	Sh.	Mean
10.5	0.0238	0.0230	0.0234	0.0488	0.0403	0.0445
11.8	0.0238	0.0233	0.0235	0.0438	0.0408	0.0423
13.2	0.0244	0.0234	0.0239	0.0357	0.0301	0.0329
14.5	0.0241	0.0235	0.0238	0.0193	0.0187	0.0190
Mean	0.0240	0.0233	0.0237	0.0369	0.0325	0.0347
Significance level:						
- shading effect		**			**	
- photoperiod effect		n.s.			**	
- interaction effect		n.s.			n.s.	
$LSD_{0.05}$ photoperiod:		-			0.00667	

In the unshaded treatments, the total time from sowing to podding was for the 10.5, 11.8, 13.2 and 14.5 h d^{-1} photoperiods respectively 62.5, 65.0, 69.0 and 93.5 days. The equivalent figures for the shaded treatments were 68.5, 67.8, 76.0 and 96.0 days, which is 3 to 7 days longer. Because of the intermediate harvests, the podding data are based on 20 plants per treatment per replicate for the 10.5, 11.8 and 13.2 h d^{-1} photoperiods, and on 10 plants per treatment per replicate for the 14.5 h d^{-1} photoperiod.

The number of flowers per plant between the onset of flowering and the onset of podding ranged from 60 to 251 and increased with photoperiod (Table 5.3). This effect is partly attributable to the longer interval between flowering and podding under longer photoperiods. However, the number of flowers per day was also influenced by photoperiod. It was lower under 10.5 or 11.8 h d^{-1} than under 13.2 or 14.5 h d^{-1} photoperiods (Table 5.3). Shading also influenced the number of flowers per day, which was lower in the shaded plants.

Table 5.3. Total number of flowers per plant between the onset of flowering and the onset of podding and the number of flowers per day in this period in the unshaded (Unsh.) and shaded (Sh.) treatments under constant photoperiods of 10.5, 11.8, 13.2, and 14.5 h d^{-1}.

Photoperiod (h d^{-1})	Total number of flowers			Number of flowers per day		
	Unsh.	Sh.	Mean	Unsh.	Sh.	Mean
10.5	69	60	64	3.05	2.50	2.78
11.8	67	62	64	3.10	2.55	2.83
13.2	128	132	130	4.25	3.75	4.00
14.5	251	207	229	4.80	3.65	4.23
Mean	129	115	122	3.80	3.11	3.46
Significance level:						
- shading effect		n.s.			**	
- photoperiod effect		***			***	
- interaction effect		n.s.			n.s.	
$LSD_{0.05}$ photoperiod:		17.4			0.265	

The number of leaves and the leaf area were significantly influenced by shading from the second harvest (36 DAS) onwards (Fig. 5.1). Leaf number was significantly influenced by photoperiod from the third harvest (50 DAS) onwards, leaf area from the fourth (64 DAS). Significant interaction effects between photoperiod and shading were found at the last two harvests (106 and 120 DAS) only. The mean number of pods was significantly lower in the shaded treatments from 78 DAS onwards. Photoperiod effects and interaction effects between photoperiod and shading were only significant at the harvests at 78 and 92 DAS. At the final harvest there was no significant difference between the photoperiod treatments in the mean number of pods per plant. Fig. 5.1 shows that the rapid increase in the number of pods per plant in the first few weeks after the onset of podding coincides with a slowing down of the increase in the number of leaves per plant.

Dry matter partitioning

The photoperiod effects on partitioning of the dry matter increase before the onset of podding were generally not significant. However, partitioning to the stems tended to be higher under longer photoperiods, and partitioning to the roots lower (Table 5.4). Significant shading effects were mainly found in the first three weeks after sowing. Partitioning to the leaf blades remained constant in the pre-podding period, but after 36 DAS partitioning to the roots decreased and partitioning to petioles and stems increased. The partitioning of the dry matter increase after the onset of podding was analysed using data on the 10.5, 11.8, and 13.2 h d^{-1} photoperiods. Data on the 14.5 h d^{-1} photoperiod were not used, because 50% podding occurred much later in that treatment. Partitioning after the onset of podding was not influenced by photoperiod (in the range from 10.5 to 13.2 h d^{-1}) or by shading. The vegetative plant parts still showed some growth in the first two weeks after the onset of podding, but thereafter dry matter was reallocated to the pods (Table 5.5). In the 14.5 h d^{-1} treatment, partitioning after the onset of podding showed the same trend (Table 5.6) as in the other photoperiods. At the final harvest, the pod dry weight per plant in the shaded treatments was half that in the unshaded treatments (Table 5.7). Pod dry weights under 10.5, 11.8 and 13.2 h d^{-1} photoperiods were very similar, but they were much lower under 14.5 h d^{-1}.

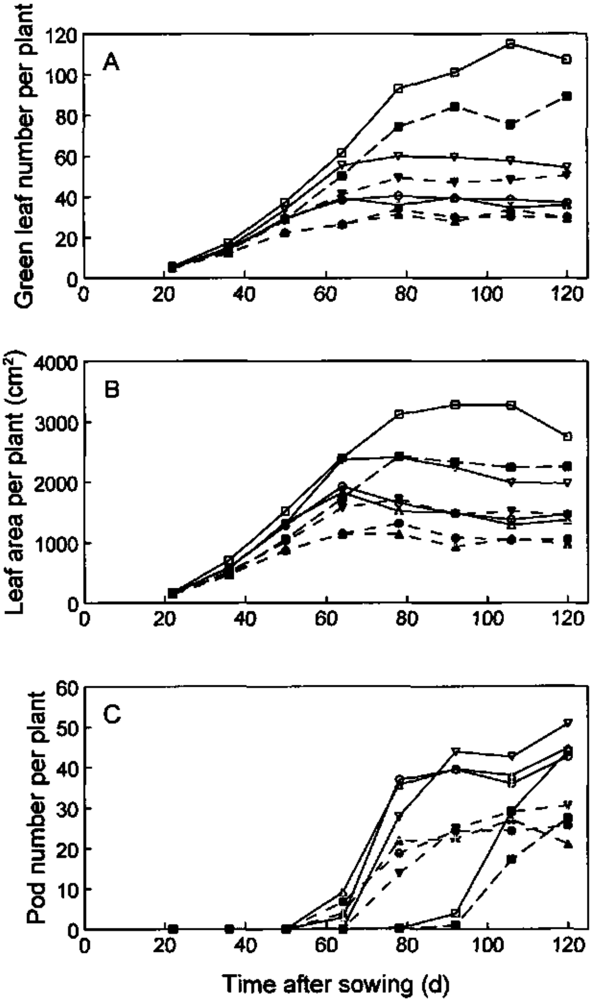

Fig. 5.1. Mean green leaf number (A), leaf area (B), and pod number (C) per plant against time after sowing for plants grown in the unshaded treatment under constant photoperiods of 10.5 (△), 11.8 (○), 13.2 (▽), and 14.5 h d^{-1} (□), and the shaded treatment under constant photoperiods of 10.5 (▲), 11.8 (●), 13.2 (▼), and 14.5 h d^{-1} (■).

Table 5.4. Fraction of the plant dry weight increase partitioned to different organs in the pre-podding period under different photoperiods and in the unshaded (Unsh) and shaded (Sh) treatments. There were no interaction effects between shading and photoperiod.

Plant part	Period (DAS)	Mean	Photoperiod ($h\ d^{-1}$)					Shading treatment		
			10.5	11.8	13.2	14.5	$LSD_{0.05}$	Unsh	Sh	Sign.
Roots	0-22	0.17	0.19	0.19	0.14	0.16	n.s.	0.20	0.13	***
	22-36	0.22	0.24	0.23	0.23	0.20	n.s.	0.23	0.21	n.s.
	36-50	0.09	0.11	0.09	0.09	0.06	n.s.	0.09	0.08	n.s.
	50-64	0.08	0.08	0.11	0.05	0.06	n.s.	0.06	0.09	n.s.
Stems	0-22	0.11	0.09	0.10	0.12	0.11	n.s.	0.09	0.12	**
	22-36	0.08	0.07	0.07	0.09	0.10	n.s.	0.07	0.09	n.s.
	36-50	0.12	0.10	0.10	0.13	0.14	0.013	0.11	0.12	**
	50-64	0.12	0.12	0.11	0.12	0.14	n.s.	0.12	0.12	n.s.
Petioles	0-22	0.17	0.17	0.17	0.18	0.18	0.007	0.16	0.19	***
	22-36	0.18	0.18	0.18	0.19	0.20	n.s.	0.18	0.19	n.s.
	36-50	0.25	0.25	0.24	0.24	0.26	n.s.	0.25	0.25	n.s.
	50-64	0.25	0.24	0.23	0.26	0.27	n.s.	0.27	0.24	n.s.
Leaf blades	0-22	0.55	0.55	0.53	0.57	0.56	n.s.	0.55	0.56	n.s.
	22-36	0.51	0.52	0.52	0.49	0.50	n.s.	0.51	0.51	n.s.
	36-50	0.55	0.54	0.56	0.55	0.54	n.s.	0.55	0.55	n.s.
	50-64	0.53	0.53	0.51	0.56	0.53	n.s.	0.54	0.53	n.s.
Pods	50-64	0.02	0.04	0.03	0.00	0.00	n.s.	0.01	0.02	n.s.

Table 5.5. Fraction of the plant dry weight increase partitioned to different organs after the onset of podding (based on all treatments except the 14.5 h d^{-1} treatment). The average onset of podding was 68 DAS.

Period (DAS)	Fraction					
	Roots	Leaf blades	Petioles	Stems	Pods	Total
64-78	0.00	0.15	0.08	0.06	0.72	1.00
78-92	-0.04	-0.09	-0.12	-0.02	1.27	1.00
92-106	-0.09	-0.12	-0.10	-0.04	1.34	1.00
106-120	-0.12	-0.04	-0.13	-0.01	1.29	1.00

Table 5.6. Fraction of the plant dry weight increase partitioned to different organs after the onset of podding in the 14.5 h d^{-1} treatment. The average onset of podding was 95 DAS.

Period (DAS)	Fraction					
	Roots	Leaf blades	Petioles	Stems	Pods	Total
92-106	0.08	0.12	0.00	0.06	0.74	1.00
106-120	-0.18	-0.26	-0.07	-0.03	1.54	1.00

5.4 Discussion

Interaction between growth and development

In this study, it was found that shading (42% light reduction) resulted in a lower plant dry matter production (41%) (Table 5.1). This was accompanied by a slight decrease in the rate of progress from sowing to flowering (3%) and the rate of progress from flowering to podding (12%) (Table 5.2). This suggests that there may be some interaction between growth and development in bambara groundnut, but that the effect is small. These results also imply that the onset of flowering and podding in bambara groundnut grown as an intercrop and shaded by taller cereals will not be very different from that in sole-cropped bambara groundnut.

The finding that photoperiod did not significantly affect total plant growth, is in accordance with Linnemann et al. (1995), who found no photoperiod influence on above ground dry matter accumulation in bambara groundnut selection 'Ankpa4' from Nigeria and only a slight influence in 'Tiga Nicuru' from Mali. The photoperiod effect on the rate of progress from flowering to podding was much more pronounced than the shading effect (Table 5.2).

Photoperiod and dry matter partitioning

The findings of this study confirm that the onset of podding coincides with a major shift in the assimilate distribution, which becomes mainly directed towards pod growth. As photoperiod has a strong influence on the onset of podding, the indirect effect of photoperiod on dry matter partitioning is obvious. Direct photoperiod effects on dry matter partitioning before the onset of podding were not significant, but partitioning to the stems tended to be higher under longer photoperiods (Table 5.4). This tendency is in agreement with earlier findings that the percentage of above ground matter partitioned to the leaf blades is higher under short photoperiods and the percentage partitioned to the stem parts lower (Linnemann et al., 1995). A direct effect of photoperiod on dry matter partitioning after the onset of podding was not found, which is in contrast with earlier findings in bambara groundnut (Linnemann et al., 1995) and soya bean (Cure et al., 1982; Morandi et al., 1988). However, it confirms the findings of Chapter 4, where it was found that seed yield in bambara groundnut is strongly related to the time to podding and not to the photoperiod regime in the pod-filling phase.

Table 5.7. Mean pod dry weight (g) per plant in the unshaded (Unsh.) and shaded (Sh) treatments and under different photoperiods. Shading and photoperiod effects were significant from 78 DAS onwards. There were no interaction effects.

Time (DAS)	Shading treatment		Photoperiod ($h\ d^{-1}$)				
	Unsh.	Sh.	10.5	11.8	13.2	14.5	$LSD_{0.05}$
22	0.0	0.0	0.0	0.0	0.0	0.0	n.s.
36	0.0	0.0	0.0	0.0	0.0	0.0	n.s.
50	0.0	0.0	0.0	0.0	0.0	0.0	n.s.
64	0.1	0.1	0.1	0.1	0.0	0.0	n.s.
78	2.2	0.7	2.9	1.8	1.1	0.0	1.57
92	5.0	2.1	4.8	5.1	4.1	0.1	2.00
106	8.4	4.4	8.1	7.7	7.9	2.0	2.81
120	12.5	6.3	10.1	11.0	11.2	5.3	2.66

Determinacy

Loomis and Connor (1992) distinguish determinate, indeterminate and facultative determinate crops. In determinate crops, vegetative growth ceases at flowering, because the shoot's apical meristem is converted to the reproductive structure. In indeterminate crops, flowering overlaps with vegetative growth and can continue for weeks or months. In this situation, the apical meristem continues to produce leaves, while flowers are formed from axillary meristems. The advantage of indeterminacy is that prolonged flowering enables the plant to compensate for loss of flowers or seed as a result of temporary adverse conditions (Loomis and Connor, 1992). Under certain conditions, reproductive growth in some indeterminate plants monopolizes all assimilates and apical activity ceases, resulting in facultative determinacy. In the present study it was found that the onset of podding in bambara groundnut coincides with a slowing down of the leaf appearance rate (Fig. 5.1). This suggests that though bambara groundnut is an indeterminate plant (leaf formation is not influenced by the onset of flowering), the onset of podding leads to facultative determinacy.

Podding observations

In the studies by Linnemann and Craufurd (1994) and Linnemann et al. (1995), the onset of flowering in bambara groundnut was determined in the same way as in the present study, but the onset of podding was not. In the present study, podding was observed directly, whereas Linnemann and Craufurd (1994) and Linnemann et al. (1995) determined the onset of podding through linear regression of pod weights at different harvests against time. Because intermediate harvests were carried out in the present study, it was possible to compare the two methods. The results obtained by the different methods do not differ much (Table 5.8), which implies that both methods can be used. An important advantage of observing podding directly is that far fewer plants are required. However, the method cannot be used on bambara groundnut selections that form pods underground or when plants are earthed-up before the onset of podding.

Table 5.8. Means and standard errors of the times from sowing to podding in the different treatment combinations as determined by direct podding observations (method 1) and by linear regression of the pod weights at intermediate and final harvests against time (method 2).

Photoperiod ($h\ d^{-1}$)	Non-shaded		Shaded	
	Method 1	Method 2	Method 1	Method 2
10.5	62.5 ± 1.5	61.5 ± 3.0	68.5 ± 2.5	65.7 ± 0.0
11.8	65.0 ± 3.0	65.6 ± 2.5	67.5 ± 1.5	66.7 ± 0.1
13.2	69.0 ± 1.0	72.1 ± 0.9	76.0 ± 0.0	77.0 ± 0.4
14.5	93.5 ± 2.5	92.4 ± 1.8	96.0 ± 1.0	93.7 ± 0.9

5.5 Conclusion

In the shaded treatments, total dry matter production was 41% lower than in the unshaded treatment, but the effects of shading on development were minor. The rates of progress from sowing to flowering and flowering to podding were reduced by only 3 and 12 % respectively. This suggests that growth and development in bambara groundnut are largely independent. Photoperiod influenced dry matter partitioning indirectly, through its influence on the onset of podding. Strong direct photoperiod effects of dry matter partitioning, either before or after the onset of podding, were not found.

CHAPTER 6

QUANTIFYING PHOTOTHERMAL INFLUENCES ON REPRODUCTIVE DEVELOPMENT IN BAMBARA GROUNDNUT (*VIGNA SUBTERRANEA*): MODELS AND THEIR VALIDATION

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6 QUANTIFYING PHOTOTHERMAL INFLUENCES ON REPRODUCTIVE DEVELOPMENT IN BAMBARA GROUNDNUT (*VIGNA SUBTERRANEA*): MODELS AND THEIR VALIDATION

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Abstract

The effects of photoperiod and temperature on reproductive development in two bambara groundnut (*Vigna subterranea*) selections from contrasting origins were quantified by means of linear models. The two selections were 'DodR94' from Tanzania, near the equator, and 'DipC94' from Botswana, near the Tropic of Capricorn. The models were based on a semi-controlled environment study with four constant photoperiods (10.5, 11.8, 13.2, and 14.5 h d^{-1}, covering the range of photoperiods in the tropics) and four constant temperatures (20, 23, 26, 29 °C). Higher temperatures were included as well, but plants died at constant temperatures of 33 and 36 °C. The rate of progress from sowing to flowering of both selections could be described by a thermal response plane. For 'DipC94', the rate of progress from flowering to podding could be described well by a combination of a thermal response plane and a photothermal response plane. In the case of the podding response of 'DodR94', the intervals between the experimental photoperiods were too large to allow quantification of the photoperiod effect. The photoperiod and temperature response of the selections could be explained very well by the photothermal conditions in the regions from which the selections came. Validation of the photothermal models with the results of glasshouse experiments in The Netherlands and field experiments in Tanzania and Botswana gave mixed results: predicted and observed time to flowering for 'DipC94' corresponded well, and predicted and observed time from flowering to podding reasonably well. Flowering predictions for 'DodR94' were not accurate,

possibly because this selection experiences photoperiod effects when temperatures are higher than those applied in the experiment on which the models were based.

6.1 Introduction

In semi-arid Africa, where rainfall is low, soil fertility poor and production conditions are difficult to control, increased food production requires crops and crop genotypes well adapted to local environments. An important aspect of plant adaption is the way reproductive development is influenced by environmental factors. Temperature and photoperiod are the main factors influencing the development of annual crops and there are often large genotypic differences in the response to these factors (Roberts and Summerfield, 1987). Quantification of the effects of photoperiod and temperature on reproductive development in crop genotypes is important when ascertaining the potential of genotypes for a particular agro-ecological region.

Bambara groundnut (*Vigna subterranea* (L.) Verdc.) is one of the crops that could be used to increase food production. It is a leguminous food crop, which is already widely cultivated in tropical Africa (Duke, 1981), with a reported high drought resistance (Linnemann and Azam-Ali, 1993). It is an indeterminate annual herb, which forms pods on or under the soil. In many bambara groundnut selections, the onset of flowering is photoperiod-insensitive, but the onset of pod growth ('podding') is retarded by long photoperiods. In some genotypes though, both the onset of flowering and the onset of podding are delayed by long photoperiods (Linnemann, 1991; Linnemann and Craufurd, 1994). The photoperiod influence on flowering and podding has been demonstrated in glasshouse (Linnemann, 1991) and field experiments (Harris and Azam-Ali, 1993). Recently, it has been shown that the time from sowing to flowering of bambara groundnut selections in independent experiments could be well predicted with photothermal models based on a semi-controlled environment experiment, and the time from flowering to podding reasonably well (Chapter 2).

However, that study included only temperatures up to 26 °C, and the results were not validated with field data.

The present study was intended to remedy this. Its aims were: (1) to quantify the influence of temperature and photoperiod on reproductive development of bambara groundnut selections from contrasting origins with linear models; and (2) to validate these models by: (a) comparing the photothermal responses of the selections with the photothermal conditions in the regions where they were obtained; and (b) comparing the model predictions with results from glasshouse experiments in The Netherlands and field experiments in Tanzania and Botswana.

6.2 Material and methods

The study included seven experiments: a main, semi-controlled environment experiment, used to derive photothermal development models, and six validation experiments.

Main experiment

The main experiment included four constant photoperiods (10.5, 11.8, 13.2, and 14.5 h d^{-1}) and six constant temperatures (20, 23, 26, 29, 33, and 36 °C), covering the range of photoperiods and temperatures in the tropics. Two bambara groundnut selections, collected from farmers, were used: 'DipC94', a cream coloured selection collected at Diphiri, near Gaborone, Botswana (24°40'S; 25°55'E); and 'DodR94', a red coloured selection collected near Dodoma, Tanzania (6°10'S; 35°46'E). Long-term climatic data for Dodoma and Gaborone are shown in Table 6.1.

Development at temperatures of 20, 23 and 26 °C was studied in three identical phytotron glasshouses in Wageningen, The Netherlands (51°58'N) in the period 9 May to 15 November 1995. The air temperature in the glasshouses was maintained by forced ventilation at 20, 23 and 26 °C respectively. A tent with four compartments, each with different constant photoperiod (10.5, 11.8, 13.2, or 14.5 h d^{-1}) was placed within each glasshouse. Every day, the tents were removed from 08:00 to 16:00 h and the plants were exposed to daylight. The radiation at plant level was 52% of the photosynthetically active radiation (PAR) outside the glasshouse. The tents were in position from 16:00 to 08:00 h, during which time the photoperiod was prolonged with low intensity artificial light (four Philips TLD 36 W fluorescent tubes (colour no. 84) and two 40 W incandescent bulbs per compartment). Low intensity light was used to ensure that plants in all photoperiod treatments received the same amount of PAR. To create the four photoperiods, artificial light was supplied daily from 07:00 to 08:00 h and from 16:00 to respectively 17:30, 18:50, 20:10, and 21:30 h. From 16:00 h to 08:00 h, the glasshouses were covered with removable metal roofs to exclude daylight and to prevent the temperature inside the tents from becoming too high. Each compartment contained twenty plants of both selections and the plants were circulated weekly. Relative air humidity was kept above 60%.

Development at higher temperatures was studied in three Heraeus growth cabinets. From 10 July to 2 October 1995, these were used to grow plants under a 10 h d^{-1} photoperiod at temperatures of 29, 33 and 36 °C. From 3 October 1995 to 12 March 1996, they were used to grow plants at 29 °C under photoperiods of 11.8, 13.2, and 14.5 h d^{-1}. Six plants of 'DipC94' and six plants of 'DodR94' were placed in each cabinet. Temperature and relative humidity in the growth cabinets were recorded with thermohygrographs. Light was provided by 16 fluorescent tubes (Philips TLD 58 W, colour no. 84) and four 100 W incandescent bulbs. The plants were circulated weekly.

Seeds were pre-germinated in a germination cabinet. After the root tips had emerged, the seedlings were put singly into white plastic pots (capacity 4.8 litres), filled with a 1:1 v/v mixture of sand and potting compost ('potting compost no.4' from Lentse potgrond b.v., consisting of 85% peat and 15% clay). At transplanting, *Rhizobium* spp. strain CB 756, obtained from the Department of Microbiology, Wageningen Agricultural University, was put in the planting hole. The plants were fertilized with a standard complete nutrient solution obtained by mixing 0.833 g 'Nutriflora-t' (supplied by Windmill Holland b.v.) and 1 g calcium nitrate in one litre of tap water, resulting in a nutrient content of 172 mg l^{-1} N, 39 mg l^{-1} P, and 263 mg l^{-1} K. This nutrient solution (220 ml per plant) was applied four times at three-weekly intervals in the period 28 to 90 days after sowing. Plants were kept well-watered. Biological pest control was used: the predators *Amblyseius cucumeris* and *Orius insidiosus* against thrips (*Frankliniella occidentalis* and *Thrips tabaci*), and *Phytoseiulus persimilis* against spider mites (*Tetranychus urticae*).

Table 6.1. Average photoperiod (P), daily maximum (T_{max}) and minimum temperature (T_{min}), and rainfall (R) for Dodoma (Tanzania, 6°10'S; 35°46'E; altitude 1120 m) and Gaborone (Botswana, 24°40'S; 25°55'E; altitude 980 m). Source of photoperiod data: Watkinson et al. (1994); source of temperature and rainfall data: Smith (1993). Temperature and rainfall data are based on 52 (Dodoma) or 30 (Gaborone) years.

Month	Dodoma				Gaborone			
	P^* ($h\ d^{-1}$)	T_{max} (°C)	T_{min} (°C)	R (mm)	P^* ($h\ d^{-1}$)	T_{max} (°C)	T_{min} (°C)	R (mm)
Jan	13.19	29.3	18.3	151	14.32	32.5	19.3	82
Feb	13.03	29.3	18.1	115	13.73	32.1	19.0	81
Mar	12.93	29.1	18.0	123	13.39	30.5	17.1	69
Apr	12.68	28.7	17.6	51	12.30	26.8	13.2	51
May	12.58	28.0	16.1	5	11.74	24.5	7.6	15
Jun	12.53	27.3	13.8	1	11.47	21.7	4.1	11
Jul	12.55	26.6	13.0	0	11.59	22.0	3.6	4
Aug	12.63	27.3	13.8	0	12.05	25.1	6.5	3
Sep	12.77	29.2	14.9	1	12.70	29.5	11.5	13
Oct	12.95	30.6	16.4	5	13.44	31.3	15.7	44
Nov	13.13	31.7	17.9	20	14.12	31.5	18.2	59
Dec	13.24	30.6	18.6	106	14.49	31.6	18.5	88
Total				578				520

* Civil twilight included

Observations included the onset of flowering and podding of each plant. The onset of flowering was defined as the day the plant had its first open flower; the onset of podding as the day the plant had a pod of at least 0.5 cm long. The dates when 50% of the plants in a treatment had started flowering ('50% flowering') and 50% of the plants in a treatment had started podding ('50% podding') were established from observations of individual plants.

Validation experiments

The photothermal models were validated with the data from two glasshouse experiments in Wageningen in 1995 and 1996, and four field experiments in the 1994/95 and 1995/96 rainy seasons in Tanzania and Botswana (Table 6.2). There were three experiments in Tanzania: one in Morogoro (6°49'S; 37°40'E) and two in Hombolo (5°54'S; 35°57'E), near Dodoma (Table 2). The Botswana experiment was conducted in Sebele (24°33'S; 25°54'E), near Gaborone. Daily photoperiods, minimum and maximum temperatures and rainfall data during the experimental period are shown in Fig. 6.1.

Management and observations in the glasshouse validation experiments were as described for the main experiment. For details on the 1995 and 1996 experiments, see Chapters 4 and 5, respectively.

The Tanzanian field experiments were conducted under rainfed conditions in a randomized complete block design with four replicates and a plot size of 5.6 by 5.6 m. The land was tractor-ploughed and ridges were made with hoes. Each plot contained 16 ridges, 35 cm apart. Before sowing, NPK-fertilizer (25:5:5) was applied equivalent to 40 kg N ha^{-1}. The crop was sown on the ridges with a within-row distance of 10 cm and thinned to a distance of 20 cm at 21 days after sowing (DAS). The date of first flowering was recorded for 25 (Morogoro) or 20 (Hombolo) individual plants per plot. The onset of podding was estimated through linear regression of pod weights at different harvests against time. Earlier research has shown that the results obtained with this method do not differ much from those obtained with the method described above for the main experiments (Chapter 5). Six plants per plot were harvested at 21, 34, 48, 62, 76, 97 and 118 days after sowing.

Table 6.2. Glasshouse (1-2) and field (3-6) experiments used to validate the development models.

No.	Location	Season	Selections	Photoperiod treatments	Sowing dates
1	Wageningen, The Netherlands	1995	'DipC94'	12 h d^{-1} 13 h d^{-1} 14 h d^{-1} 14-11 h d^{-1} * 12-15 h d^{-1} ** 13-14-12 h d^{-1} ***	25 Apr
2	Wageningen, The Netherlands	1996	'DipC94'	10.5 h d^{-1} 11.8 h d^{-1} 13.2 h d^{-1} 14.5 h d^{-1}	26 May
3	Morogoro, Tanzania	1994/95	'DodR94'	Natural	22 Dec 13 Jan 3 Feb 9 Mar 30 Mar 20 Apr
4	Hombolo, Tanzania	1994/95	'DodR94'	Natural	4 Jan 24 Jan 13 Feb
5	Hombolo, Tanzania	1995/96	'DipC94', 'DodR94'	Natural	4 Jan 21 Jan 7 Feb
6	Sebele, Botswana	1995/96	'DipC94'	Natural	18 Dec

* Photoperiod decreasing from 14 h d^{-1} at sowing to 11 h d^{-1} at 180 days after sowing (DAS), with a gradual decrease of 1 min d^{-1}.

** Photoperiod increasing from 12 h d^{-1} at sowing to 15 h d^{-1} at 180 DAS, with a gradual increase of 1 min d^{-1}.

*** Photoperiod first increasing (from 13 h d^{-1} at sowing to 14 h d^{-1} at 60 DAS, with a gradual increase of 1 min d^{-1}), and later decreasing (from 14 h d^{-1} at 60 DAS to 12 h d^{-1} at 180 DAS, with a gradual decrease of 1 min d^{-1}).

The Botswana experiment had a split-plot design with moisture level (rainfed and irrigated) as main plots and phosphorus levels (0, 10, 20, 40 and 80 kg ha^{-1}) as subplots. It had four replicates and the plot size was 6 x 6 m. Phosphorous (single superphosphate) was broadcast after the land had been ploughed and was worked into the soil. No other nutrients were applied. Seeds were sown 10 cm apart in rows 40 cm apart, and thinned to a within-row distance of 50 cm at 23 DAS. Weeding and pest control were done when necessary. The number of plants with at least one open flower was counted daily in each plot. The date of 50% flowering was defined as the date half of the plants in each plot had at least one open flower. Twelve plants per plot were used to monitor the onset of podding. The date of 50% podding was defined as the day six of these had at least one pod 0.5 cm long.

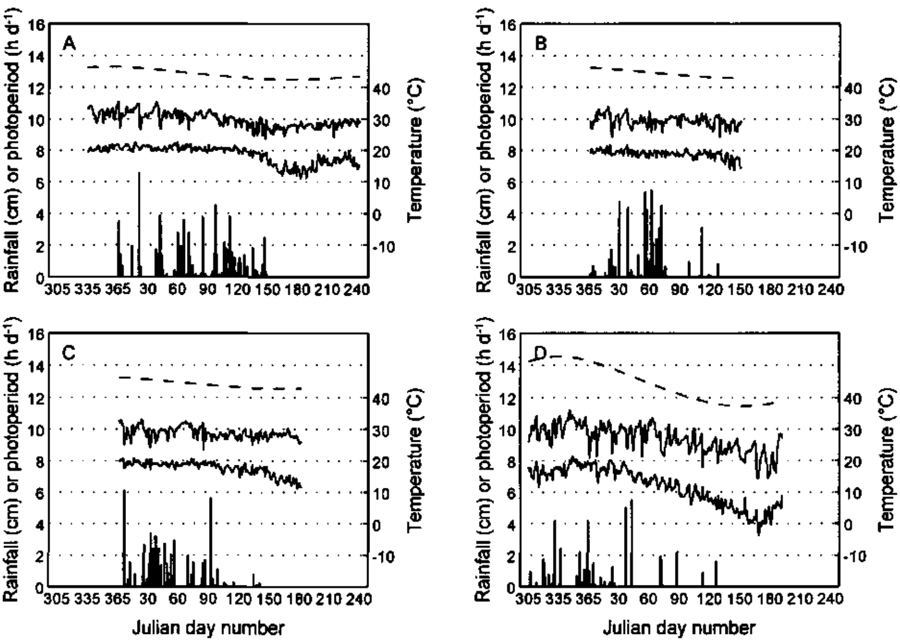

Fig. 6.1. Daily photoperiod (dashed line), maximum (upper solid line) and minimum temperature (lower solid line), and rainfall (vertical bars) during the four field experiments: Morogoro 1994/95 (A); Hombolo, 1994/95 (B) and 1995/96 (C); and Sebele, 1995/96 (D).

Modelling approach

The results of the main experiment were used to quantify the influence of temperature and photoperiod on development rates with the photothermal approach (Hadley et al., 1983b; Roberts and Summerfield, 1987), which has been applied to quantify temperature and photoperiod effects on the time to flowering in a range of annual legumes (Lawn et al., 1995). In this approach, linear equations are used to relate development rates to mean photoperiod and temperature.

In the absence of photoperiod effects, the development rate ($1/x$; with x being the number of days from sowing to development stage x) increases linearly with temperature from zero at the base temperature (T_b) to a maximum rate at the optimum temperature (T_o); beyond T_o, the development rate decreases linearly with temperature to zero at the ceiling (or maximum) temperature (T_{ce}) (Fig. 6.2A).

When photoperiod effects play a role, the development rate is related to photoperiod (P) and/or temperature (T) by means of response planes. Most published studies have considered photothermal effects between T_b and T_o only, and in that case a maximum of three planes can be distinguished (Fig. 6.2B):

(1) a below-optimum thermal response plane:

$$1/x = a_1 + b_1 T \tag{6.1}$$

(2) a photothermal plane:

$$1/x = a_2 + b_2 T + c_2 P \tag{6.2}$$

(3) a plane of minimum development rate:

$$1/x = a_3 \tag{6.3}$$

A slight temperature effect may be found in plane 3 (Watkinson et al., 1994), which would give an alternative third plane:

$$1/x = a_3 + b_3 T \tag{6.4}$$

The parameter b_2 in Eq. 6.2 usually has a value of zero or higher, but earlier bambara groundnut research (Chapter 2) has shown that it may assume a negative value, which means that the development rate decreases with temperature in the photothermal plane.

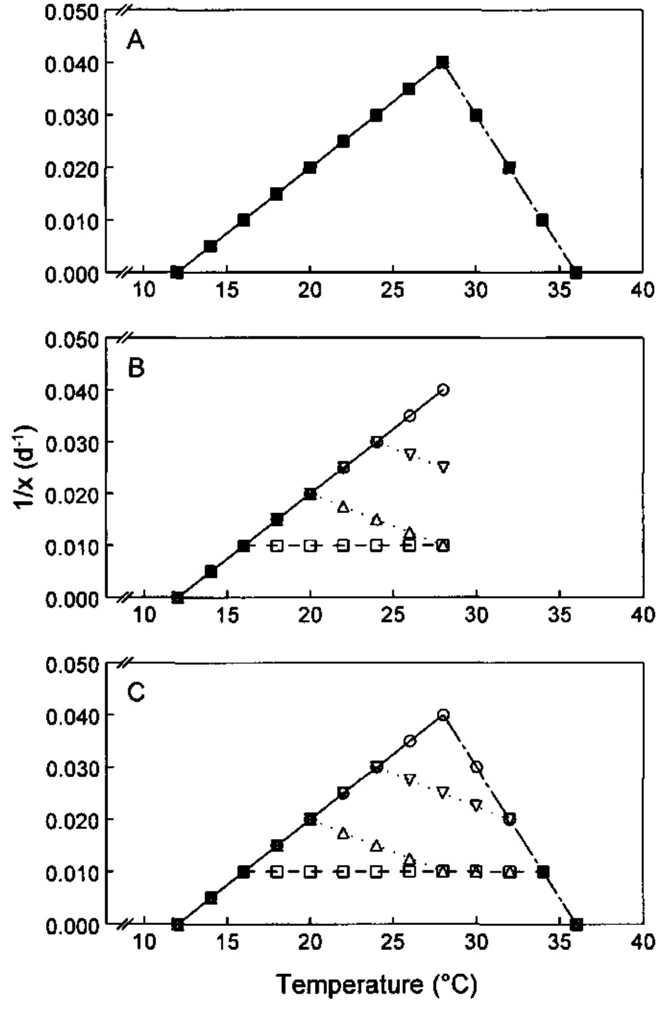

Fig. 6.2. Theoretical model of the effects of temperature and photoperiod on development rate (1/*x*; with *x* being the number of days from sowing to development stage x) in a short-day plant. Temperature effects only (A); temperature and photoperiod effects between base and optimum temperature (B); and temperature and photoperiod effects between base and ceiling temperature (C). The symbols refer to photoperiods (■: all photoperiods; ○: 11 h d^{-1}; ▽: 12 h d^{-1}; △: 13 h d^{-1}; □: 14 h d^{-1}); the lines refer to planes in photothermal models: a below-optimum thermal response plane (———); an above optimum thermal response plane (— - —); a photothermal plane (· · · ·); and a plane of minimum development rate (– – – –).

Complete photothermal models over the temperature range from T_b to T_{ce} are scarce in the literature. However, the two models outlined above can be combined to give a four-plane model (Fig. 6.2C), consisting of the three planes mentioned above (Eq. 6.1, 6.2 and 6.3 or 6.4) and:

(4) an above-optimum thermal response plane:

$$1/x = a_4 + b_4\,T. \qquad (6.5)$$

In the present study, models were fitted with the RoDMod computer program (Watkinson et al., 1994). This program starts with fitting the simplest model (only a thermal plane, Eq. 6.1) and subsequently fits more complex models. A more complex model is accepted only if it statistically significantly reduces the residual sums of squares of the deviations of model estimates from observations. The RoDMoD program can fit models with three planes at most (Fig. 6.2B). If results in the present study indicated a more complex model than could be fitted with the program, an alternative model was fitted by grouping the data by eye and carrying out linear regression for each group separately with the GENSTAT statistical package (Payne et al., 1993).

Model validation

The models were validated in two ways: (a) by comparing the photothermal responses of the selections with the photothermal conditions in the regions where they were obtained; and (b) by comparing model predictions with results from glasshouse experiments in The Netherlands and field experiments in Tanzania and Botswana.

Predictions of the time from sowing to flowering and the time from flowering to podding in the validation experiments were calculated in one-day time-steps on the basis of model parameters and the daily photoperiod and average temperature. Average daily temperatures in the field experiments were obtained by averaging the measured daily maximum and minimum temperatures. Daily photoperiods in the field experiments were calculated on the basis of latitude and day of the year. The photoperiod was assumed to include civil twilight, which means that the photoperiod is defined to start and end when the centre of the sun is 6° below the horizon. This assumption is common practice and seems to be justified for soya bean (*Glycine max* (L.) Merrill), common bean (*Phaseolus vulgaris* L.) and chickpea (*Cicer arietinum* L.) (Summerfield and Roberts, 1987). At a latitude of 5°, civil twilight (morning and afternoon together) ranges from 42 to 46 minutes; at a latitude of 25°, from 46 to 52 minutes (List, 1958). The model predictions were compared with the times from sowing to flowering and flowering to podding observed in the different validation experiments.

6.3 Results

Main experiment and models

The plants kept at constant temperatures of 33 and 36 °C died, so results were only available for the 20, 23, 26 and 29 °C treatments. The results for 'DodR94' in the 14.5 h d^{-1}/ 29 °C treatment were not included in the analysis because differences between individual plants were very large: in some plants flowering was very late and podding did not occur in the experimental period.

The time from sowing to 50% flowering (f) ranged from 34 to 56 days in 'DipC94' and 36 to 57 days in 'DodR94'. In both selections, the rate of progress from sowing to flowering ($1/f$) increased with temperature (Fig. 6.3). The rate of progress from sowing to flowering of both selections could be described by a thermal response plane (Eq. 6.1) (Table 6.3). However, in 'DodR94', there was a tendency for longer photoperiods at the highest temperature included in the experiment to induce a slight delay (Fig. 6.3B). If only the results under 10.5 h d^{-1} were analysed, the thermal response plane was characterized by the equation: $1/f = -0.006742 + 0.001182\ T$.

The time from 50% flowering to 50% podding (p-f) ranged from 15 to 112 days in 'DipC94' and from 13 to 76 days in 'DodR94'. The rate of progress from flowering to podding (1/(*p*-*f*)) in 'DipC94' was affected by both temperature and photoperiod (Fig. 6.3C). In 'DodR94' there was a clear division between the 10.5 and 11.8 h d^{-1} treatments on one hand, and the 13.2 and 14.5 h d^{-1} treatments on the other. At photoperiods below 11.8 h d^{-1} or above 13.2 h d^{-1}, the rate of progress from flowering to podding was influenced by temperature only (Fig. 6.3D). The temperature effect was much stronger at short photoperiods than at long.

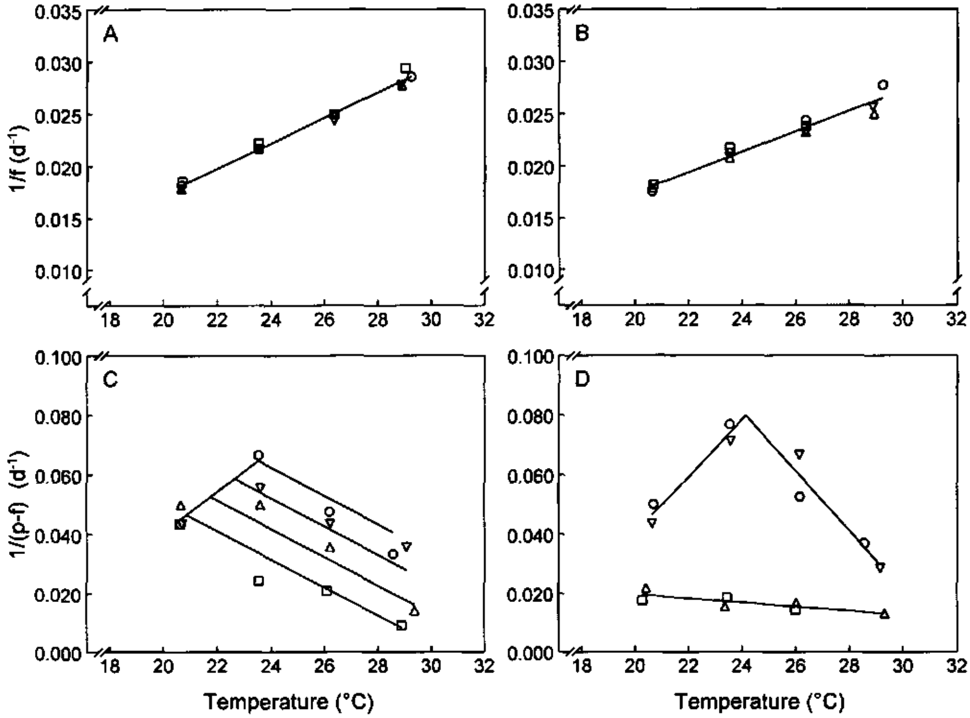

Fig. 6.3. Rate of progress from sowing to flowering (1/*f*) in bambara groundnut selections 'DipC94' (A) and 'DodR94' (B), and rate of progress from flowering to podding (1/(*p*-*f*)) in 'DipC94' (C) and 'DodR94' (D) as a function of temperature under constant photoperiods of 10.5 (○), 11.8 (▽), 13.2 (△), and 14.5 (□) h d^{-1}. The solid lines refer to the fitted models of Table 6.3.

Table 6.3. Fitted models describing the rate of progress from sowing to flowering (1/*f*) and from flowering to podding (1/(*p*-*f*)) as a function of temperature (*T*) and photoperiod (*P*) for the bambara groundnut selections 'DipC94' and 'DodR94'. The models for 'DipC94' and the flowering model for 'DodR94' were fitted with the RoDMoD computer program (Watkinson et al., 1994). For the 'DodR94' podding model, the observations were divided into three groups by eye, and regression analysis was carried out for each group separately.

Selection	Fitted models	n	Parameter values			r^2 (%)†
			a_1, a_2, a_3 or a_4 (s.e.)	b_1, b_2, b_3 or b_4 (s.e.)	c_2 (s.e.)	
'DipC94'	$1/f = a_1 + b_1 T$	16	-0.006948 (0.000881) ***	0.001215 (0.000035) ***	-	98.8
	$1/(p\text{-}f) = a_1 + b_1 T$ (for $P \leq P_{cr}$)	4	-0.096623 (0.006864) $^{n.s.}$	0.006864 (0.085304) $^{n.s}$	-	87.5
	$1/(p\text{-}f) = a_2 + b_2 T + c_2 P$ (for $P \geq P_{cr}$)	12	0.258885 (0.022688) ***	-0.004788 (0.000710) ***	-0.007751 (0.001054) ***	
'DodR94'	$1/f = a_1 + b_1 T$	15	-0.002035 (0.001375) $^{n.s.}$	0.000976 (0.000055) ***	-	95.7
	$1/(p\text{-}f) = a_1 + b_1 T$ (for $P \leq 11.8$ h d^{-1} and $T \leq 24.2$ °C)	4	-0.150400 (0.032200) *	0.009530 (0.001450) *	-	96.7
	$1/(p\text{-}f) = a_3 + b_3 T$ (for $P \geq 13.2$ h d^{-1})	7	0.033860 (0.005710) **	-0.000709 (0.000235) *	-	
	$1/(p\text{-}f) = a_4 + b_4 T$ (for $P \leq 11.8$ h d^{-1} and $T \geq 24.2$ °C)	4	0.322300 (0.070400) *	-0.010040 (0.002560) $^{n.s.}$	-	

† r^2 refers to the overall model, consisting of 1, 2 or 3 planes.

*** $P \leq 0.001$; ** $P \leq 0.01$; * $P \leq 0.05$; n.s. not significant.

P_{cr}, critical photoperiod; P_{ce}, ceiling photoperiod; n, number of temperature/photoperiod combinations.

The rate of progress from flowering to podding in 'DipC94' could be described well by a combination of a below-optimum thermal response plane (Eq. 6.1) and a photothermal response plane (Eq. 6.2), in which photoperiod and temperature effects are additive (Table 6.3). In the case of the podding response of 'DodR94', the experimental photoperiods were outside the range in which the photoperiod effect occurred (Fig. 6.3D) and the photoperiod response could not be quantified. The temperature model for $1/(p-f)$ in Table 6.3 was fitted by dividing the observations into three groups by eye and carrying out linear regression for each group separately with the GENSTAT statistical package (Payne et al., 1993). The model consists of a below-optimum response plane (Eq. 6.1), a plane of minimum development rate with a slight temperature effect (Eq. 6.4) and an above-optimum thermal response plane (Eq. 6.5).

Validation

The photoperiod responses of the two selections show their adaptation to the environment where they come from. In 'DipC94', the rate of progress from flowering to podding generally decreases with photoperiod in the range 10.5 to 14.5 h d^{-1}, while the natural photoperiod (including civil twilight) in the region of origin of 'DipC94' (near Gaborone) ranges from 11.5 to 14.5 h d^{-1} (Table 6.1). In the case of 'DodR94', the main photoperiod response occurs between 11.8 and 13.2 h d^{-1} photoperiods, while in the region where 'DodR94' comes from (Dodoma) the photoperiod ranges from 12.5 to 13.2 h d^{-1}.

The flowering models imply base temperatures for flowering of 6 °C for 'DipC94' and 2 °C for 'DodR94'. The optimum temperature for the rate of progress from sowing to flowering of both selections is higher than 29 °C (Fig. 6.3A). The base, optimum and ceiling temperatures for the rate of progress from flowering to podding in 'DodR94' would be respectively 16, 24 and 32 °C. The base temperature for the rate from flowering to podding in 'DipC94' is around 14 °C. The optimum and ceiling temperatures of 'DipC94' cannot be calculated, because the above-optimum thermal response plane (Eq. 6.5) could not be determined. Though the base and ceiling temperatures were obtained by extrapolating beyond the temperature range of the main experiment, they give an indication of the temperature requirements of the selections involved. Comparison with temperature data for the Dodoma region (Table 6.1) shows that the interval between the base and ceiling temperature for the rate from flowering to podding in 'DodR94' roughly coincides with the interval between the mean daily minimum and maximum temperature in the rainy season in the region of origin.

The predicted and observed times from sowing to flowering and flowering to podding, and the resulting times from sowing to podding of 'DipC94' in the validation experiments are shown in Table 6.4.

The time to podding in the field experiments was predicted under the assumption that civil twilight is included in the photoperiod. If the photoperiod was defined as the time from sunrise to sunset only, the predicted time from flowering to podding was 3 or 4 days shorter (data not shown). It was not possible to predict the time from flowering to podding for 'DodR94', because no complete photothermal model was available. No flowering data were available for the third sowing date in experiment 5. In the Botswana field experiment (experiment 6), phosphorus application had no effect on the time to flowering, but significant ($P<0.001$) differences were found between rainfed and irrigated treatments. Because of practical difficulties it was not possible to carry out daily podding observations in experiment 6. Therefore, the date of 50% podding for the different treatments could not be determined exactly, but it was between 64 and 73 DAS. The time to flowering of 'DipC94' in both the glasshouse and the field experiments was predicted well: the deviation between observed and predicted values did not exceed 10%, except for the second sowing date in experiment 5. Flowering predictions for 'DodR94' in the field were not accurate. The predicted time to flowering increased with sowing date, whereas the observed time to flowering decreased with sowing date. Predicted and observed times from flowering to podding in 'DipC94' corresponded reasonably well in the glasshouse experiments, but the observed times tended to be longer than the predicted times, with the difference larger at longer photoperiods. Validation with data from field experiments showed good agreement between predicted and observed times to podding for this selection.

6.4 Discussion

The flowering response of 'DipC94' found in the present study is very similar to that of the two bambara groundnut selections from Botswana ('GabC92') and Zimbabwe ('NTSC92') described earlier (Chapter 2) (Table 6.5). The flowering response of 'DodR94' is different, but this could be due to photoperiod effects at higher temperatures. When only the results under a photoperiod of 10.5 h d^{-1} are considered, the response is similar to that of 'DipC94', 'GabC92' and 'NTSC92'. The selections 'Ankpa2' and 'Yola' (Linnemann and Craufurd, 1994) have similar values for b_f as 'DipC94', 'GabC92' and 'NTSC92', but the values for a_f and the base temperatures are lower. The parameter values for 'Tiga Nicuru' are very different from those for all other selections and the base temperature is considerably higher. Note that the base temperatures in Table 6.5 are only indicative; they were obtained by extrapolation beyond the temperature range of the main experiment.

The general trend in the podding response of 'DipC94', a declining rate of progress from flowering to podding with increasing temperature and photoperiod at temperatures higher than 21-23 °C (Fig. 6.3C), is similar to the response found for 'GabC92' and 'NTSC92' in Chapter 2, though rates were higher in the present study. In 'DodR94', the intervals between photoperiods in the main experiment were too large, because the photoperiod response occurred between 11.8 and 13.2 h d^{-1} (Fig. 6.3D). Therefore the central photothermal plane for 'DodR94' could not be determined and no useful photothermal model could be made.

Table 6.4. Predicted (Pr) and observed (Ob) times from sowing to flowering (*f*), flowering to podding (*p-f*), and sowing to podding (*p*) in the validation experiments described in Table 6.2. The models in Table 6.3 were used to make the predictions. No comparison was made for *p-f* and *p* for selection 'DodR94', because no complete photothermal podding model was available.

Experiment	Selection	Photoperiod ($h\ d^{-1}$)	Sowing date	*f* (d)		*p-f* (d)		*p* (d)	
				Pr	Ob	Pr	Ob	Pr	Ob
1	'DipC94'	12	25 Apr	41	41	26	23	67	64
		13		41	39	32	42	73	81
		14		41	39	45	63	86	102
		14-11		41	38	33	36	74	74
		12-15		41	40	31	25	72	65
		13-14-12		41	39	43	70	84	109
2	'DipC94'	10.5	26 May	44	42	18	21	62	63
		11.8		44	42	21	23	65	65
		13.2		44	41	27	28	71	69
		14.5		44	42	37	52	81	94
3	'DodR94'	Natural	22 Dec	43	59				
			13 Jan	43	50				
			3 Feb	44	51				
			9 Mar	44	47				
			30 Mar	46	48				
			20 Apr	49	43				
4	'DodR94'	Natural	4 Jan	46	55				
			24 Jan	47	52				
			13 Feb	47	45				
5	'DodR94'	Natural	4 Jan	47	43				
			21 Jan	47	37				
			7 Feb	46	na				
	'DipC94'								
			4 Jan	45	43	26	30	71	73
			21 Jan	45	36	24	30	69	66
			7 Feb	45	na	21	na	66	na
6	'DipC94'	Natural	18 Dec	45	45*	28	na	73	na
				45	49**	28	na	73	na

* Irrigated treatment; ** Rainfed treatment

A possible explanation for the disparity between the observed time to flowering of 'DodR94' in the field and the prediction is, that maximum temperatures in the field experiments were higher than those in the experiment on which the model was based (Fig. 6.1), and that photoperiod plays a role at higher temperatures. In the (field) experiments 3 and 4, daily maximum temperatures during the first three months of the experiment were generally above 30 °C (Fig. 6.1), and deviations between predicted and observed times to flowering are more pronounced in this experiment than in experiment 5, where temperatures were lower.

Table 6.5. Parameter values for the thermal response plane ($1/f = a_l + b_l T$) and calculated base temperature (T_b) for the rate of progress from sowing to flowering of different bambara groundnut selections.

Selection	Origin	Parameter values		T_b (°C)	Source
		a_l	b_l		
'DipC94'	Botswana	-0.006948	0.001215	5.7	This chapter
'DodR94'*	Tanzania	-0.002035	0.000976	2.1	"
'DodR94'**	Tanzania	-0.006742	0.001182	5.7	"
'GabC92'	Botswana	-0.007464	0.001176	6.3	Chapter 2
'NTSC92'	Zimbabwe	-0.006867	0.001195	5.7	"
'Tiga Nicuru'	Mali	-0.017104	0.001721	9.9	"
'Ankpa2'	Nigeria	-0.0039	0.0013	3.0	Linnemann and Craufurd (1994)
'Ankpa4'	Nigeria	-0.0013	0.0009	1.4	"
'Yola'	Nigeria	-0.0038	0.0012	3.2	"

* All photoperiod treatments included.

** Only 10.5 h d^{-1} treatments included.

The fact that the observed time to flowering in experiments 3 and 4 decreased with sowing date (Table 6.4) does indeed suggest that photoperiod effects that could not be determined in the temperature range of the main semi-controlled environment experiment do play a role at higher temperatures. The results from experiment 6 indicate that the rate of progress to flowering in bambara groundnut may be influenced by moisture availability. Glasshouse experiments in the U.K. have shown that podding may also be delayed under drought conditions (Collinson et al., 1996). Further research to investigate the influence of water stress on development rates in bambara groundnut seems justified.

The predicted and observed times from flowering to podding in 'DipC94' corresponded reasonably well in the glasshouse experiments (Table 6.4). A possible explanation for the larger deviations in experiment 1 might be the lack of forced cooling in the glasshouse, which resulted in maximum temperatures of 35-40 °C on warm, sunny days. The model predictions were based on the average daily temperature (which was around 25 °C, near the optimum temperature for the rate from flowering to podding) without taking into account minimum (around 22 °C) and maximum temperatures (up to 40 °C), which makes it probable that $1/(p\text{-}f)$ was overestimated. The overestimate will be larger under long photoperiods, where the ceiling temperature is lower (Fig. 6.3C). Another explanation might be that the relative humidity of the air in this glasshouse could not be kept above 60% on hot, sunny days, when all windows were open for cooling purposes. It has been found that flowering in cowpea can be delayed by high pre-flowering saturation deficits of the air (Craufurd et al., 1996). Validation with data from field experiments showed good agreement between predicted and observed times to podding for 'DipC94', but the range in observed data was small.

The finding that the time from sowing to flowering of 'DipC94' in the validation experiments was predicted better than the time from flowering to podding agrees with an earlier study on other bambara groundnut selections (Chapter 2). It may partly be due to the fact that flowering in the selections concerned is influenced by temperature only, whereas podding depends on both photoperiod and temperature. Also, the models are based on a limited number of photoperiod/temperature combinations (16 in the present study; 12 in Chapter 2). To derive quantitative photothermal models which can be used to predict the time from flowering to podding more accurately, a larger number of photoperiod and temperature treatments may be needed. It is also possible that other factors than temperature and photoperiod, such as relative humidity, have a stronger effect on the onset of podding than on the onset of flowering.

6.5 Conclusion

This study has demonstrated that photoperiod and temperature effects on the rates of progress from sowing to flowering and flowering to podding may be quantified by means of linear models on the basis of semi-controlled environment experiments. Responses to photoperiod and temperature in bambara groundnut selections from different latitudes could be explained very well by the prevailing photothermal environment in the regions where the selections were obtained. Validation of the photothermal models with the results of glasshouse experiments in The Netherlands and field experiments in Tanzania and Botswana gave mixed results: predicted and observed time to flowering for 'DipC94' corresponded well, and predicted and observed time from flowering to podding reasonably well. Flowering predictions for 'DodR94' were not accurate, possibly because this selection experiences photoperiod effects when temperatures are higher than those applied in the experiment on which the models were based.

CHAPTER 7

USING PHOTOTHERMAL DEVELOPMENT MODELS TO IDENTIFY SUITABLE BAMBARA GROUNDNUT (*VIGNA SUBTERRANEA*) SELECTIONS FOR DIFFERENT SOWING DATES AND LOCATIONS IN BOTSWANA

7 USING PHOTOTHERMAL DEVELOPMENT MODELS TO IDENTIFY SUITABLE BAMBARA GROUNDNUT (*VIGNA SUBTERRANEA*) SELECTIONS FOR DIFFERENT SOWING DATES AND LOCATIONS IN BOTSWANA

M. Brink

Abstract

A simulation study was carried out to investigate the implications of genotypic differences in photothermal responses in bambara groundnut (*Vigna subterranea*) and to demonstrate the usefulness of photothermal development models in identifying suitable selections for different locations and sowing dates in Botswana. Times to flowering and podding for different selections were calculated for different sowing dates at two locations (Sebele and Francistown) in two rainy seasons (1992/93 and 1993/94). Calculations were made with photothermal development models for the selections 'DipC94' and 'GabC92' from Botswana and 'Tiga Nicuru' from Mali and actual daily minimum and maximum temperatures and photoperiods (with or without civil twilight). The simulation results indicate that for early sowing dates 'GabC92' and 'Tiga Nicuru' may be used to prolong the time to podding and thus to promote vegetative growth. For later sowing dates, the risk of water shortage in the pod-filling phase is greater for these selections than for 'DipC94'. When sown very late, the differences between the three selections become very small, but pod yields will be absent or very low because of water shortage. Differences between the two locations were small, which implies that photoperiod differences within Botswana are probably not large enough to merit using selections with different photoperiod sensitivities for different locations. Early sowing resulted in longer predicted times to podding than late sowing, but not to such an extent that podding always occurred at the same date,

irrespective of the sowing date. The inclusion or exclusion of civil twilight in the photoperiod did affect the simulated time to podding, especially for 'Tiga Nicuru'. Therefore, determination of the responsiveness of bambara groundnut to dim light would increase the usefulness of the photothermal models.

7.1 Introduction

Bambara groundnut (*Vigna subterranea* (L.) Verdc.) is a leguminous food crop, widely cultivated in tropical Africa (Duke, 1981). It is mainly grown for the seeds, which are used as food, but the vegetative parts may be used as fodder (Hepper, 1970). An important advantage of bambara groundnut is that immature seeds are suited for human consumption and can be used to fill the 'hungry gap' during the growing season, when stores are empty and the main crops are not yet harvestable. Bambara groundnut performs better under dry conditions than groundnut (*Arachis hypogaea* L.) and other legumes, and is relatively free of pests and diseases (Linnemann and Azam-Ali, 1993).

In most bambara groundnut selections, the onset of flowering is photoperiod-insensitive, whereas the onset of podding is retarded under long photoperiods (Linnemann, 1994). In some selections, both the onset of flowering and the onset of podding are delayed by long photoperiods (Linnemann and Craufurd, 1994). The onset of podding is the most important event in the phenology of bambara groundnut, because it coincides with a major shift in assimilate partitioning and the end of vegetative growth (Chapter 5). Maturity is less important, because highly valued food is produced even if the crop does not reach maturity. The influence of temperature and photoperiod on the rates of progress from sowing to flowering and flowering to podding of selections from various origins has been quantified on the basis of semi-controlled environment research (Chapters 2 and 6).

The objectives of this simulation study are to investigate the implications of genotypic differences in photothermal responses in bambara groundnut and to demonstrate the usefulness of photothermal development models for identifying suitable bambara groundnut selections for different locations and sowing dates. The study focuses on Botswana, a country in southern Africa between 17 and 27 °S, with low rainfall and poor soils. Most rains fall in the rainy season of October/November-March/April. In Botswana, 75% of the population live in rural areas and a large majority of them practise arable farming in addition to other economic activities such as livestock keeping or commercial activities (Radcliffe et al., 1992). At present, the most important crops are sorghum (*Sorghum bicolor* (L.) Moench), maize (*Zea mays* L.) and cowpea (*Vigna unguiculata* (L.) Walp.) (Baker, 1987; Brink et al., 1996). Bambara groundnut is a secondary crop, mainly grown by women both for home consumption and for sale, with low use of external inputs (Brink et al., 1996). However, the importance of bambara groundnut in Botswana may increase, because of its tolerance to low soil fertility and drought (Linnemann and Azam-Ali, 1993).

7.2 Methodology

Photothermal development models for three bambara groundnut selections ('DipC94' and 'GabC92' from Botswana and 'Tiga Nicuru' from Mali) were used to predict the times to flowering and podding for different sowing dates at two locations in the 1992/93 and 1993/94 rainy seasons in Botswana. The models have been developed using semi-controlled environment experiments (Chapters 2 and 6) and link the rate of progress from sowing to flowering ($1/f$, with f being the number of days from sowing to flowering) and the rate of progress from flowering to podding ($1/(p-f)$, with $(p-f)$ being the number of days from flowering to podding) to mean photoperiod and temperature by means of linear equations, following the photothermal approach (Hadley et al., 1983b; Roberts and Summerfield, 1987). In all three selections, the rate of progress from sowing to flowering is influenced by temperature but not by photoperiod, whereas the rate of progress from flowering to podding is influenced by both temperature and photoperiod (Table 7.1).

Table 7.1. Models describing the rate of progress from sowing to flowering ($1/f$) and from flowering to podding ($1/(p\text{-}f)$) as a function of temperature (T) and photoperiod (P) for the bambara groundnut selections 'DipC94', 'GabC92', and 'Tiga Nicuru'. The models were developed in Chapters 2 and 6.

Selection	Model
'DipC94'	$1/f = -0.006948 + 0.001215\ T$
	$1/(p\text{-}f) = -0.096623 + 0.006864\ T$ (for $P \leq P_{cr}$)
	$1/(p\text{-}f) = 0.258885 - 0.004788\ T - 0.007751\ P$ (for $P \geq P_{cr}$)
'GabC92'	$1/f = -0.007464 + 0.001176\ T$
	$1/(p\text{-}f) = 0.091579 - 0.001650\ T - 0.002193\ P$
'Tiga Nicuru'	$1/f = -0.017104 + 0.001721\ T$
	$1/(p\text{-}f) = 0.013100 + 0.000994\ T$ (for $P \leq P_{cr}$)
	$1/(p\text{-}f) = 0.285300 - 0.003177\ T - 0.014470\ P$ (for $P_{ce} \geq P \geq P_{cr}$)
	$1/(p\text{-}f) = 0.013591$ (for $P \geq P_{ce}$)

P_{cr}, critical photoperiod; P_{ce}, ceiling photoperiod

Based on the linear photothermal models of Table 7.1 and daily mean temperature and photoperiod, the time from sowing to flowering (f) and the time from flowering to podding ($p\text{-}f$) was predicted for different sowing dates, years and locations. From the simulated sowing date onwards, the daily rates of progress to flowering were accumulated until the date on which the accumulated daily rates of progress from sowing to flowering reached the value 1, which is, by definition, the predicted flowering date. From this date onwards, the daily rates of progress from flowering to podding were accumulated until the date on which the sum of daily rates of progress from flowering to podding reached the value 1, which is, by definition, the predicted podding date. Actual daily maximum and minimum temperatures for the different locations and seasons were obtained from the Botswana Meteorological Services. Mean daily temperatures were calculated by averaging measured daily minimum and maximum temperatures. Daily photoperiods were calculated on the basis of latitude and date. The photoperiod is usually assumed to include civil twilight, which means that the photoperiod is defined to start and end when the centre of the sun is 6° below the horizon (List, 1958). This assumption seems justified for soya bean (*Glycine max* (L.) Merrill), common bean (*Phaseolus vulgaris* L.) and chickpea (*Cicer arietinum* L.), but not for lentil (*Lens culinaris* Medic.) (Summerfield and Roberts, 1987). Because it is not known whether this assumption is valid for bambara groundnut, two sets of simulations were carried out, the first under the assumption that photoperiod includes civil twilight, the second under the assumption that photoperiod only includes the time from sunrise to sunset. In the latter case, the photoperiod is defined to start and end when the centre of the sun is 0.833° below the horizon (List, 1958).

The locations included were Sebele (24°33'S; 25°54'E), near Gaborone, the capital of Botswana, and Francistown (21°13'S; 27°30'E). The two locations are about 400 km apart and located respectively at the southern and northern ends of the main arable farming zone of the country (Brink et al., 1996). Long-term meteorological observations for Gaborone and Francistown are shown in Table 7.2. For both locations, predictions were made for the 1992/93 and 1993/94 rainy seasons. Photoperiod, temperature and rainfall characteristics of the different locations and seasons are shown in Fig. 7.1. Temperature and rainfall data were available from 1 October onwards for Sebele 1993/94, from 1 November onwards for Francistown 1993/94 and from 1 December onwards for both locations in 1992/93. Model predictions were made from these dates onwards at two-weeks intervals.

Table 7.2. Long-term (30-31 years) average daily maximum temperature (T_{max}), average daily minimum temperature (T_{min}) and average amount of rainfall (R) per month for Gaborone (24°40'S; 25°55'E) and Francistown (21°13'S; 27°30'E). Source: Smith (1993).

Month	Gaborone			Francistown		
	T_{max} (°C)	T_{min} (°C)	R (mm)	T_{max} (°C)	T_{min} (°C)	R (mm)
Jan	32.5	19.3	82	31.0	19.1	85
Feb	32.1	19.0	81	30.0	18.5	87
Mar	30.5	17.1	69	29.7	17.1	54
Apr	26.8	13.2	51	27.7	14.1	22
May	24.5	7.6	15	25.7	8.8	7
Jun	21.7	4.1	11	22.6	5.8	4
Jul	22.0	3.6	4	23.0	5.7	1
Aug	25.1	6.5	3	25.6	8.3	0
Sep	29.5	11.5	13	29.1	12.5	3
Oct	31.3	15.7	44	31.8	16.8	19
Nov	31.5	18.2	59	31.3	18.7	62
Dec	31.6	18.5	88	30.2	18.8	92
Total			520			436

7.3 Results

The effect of sowing date on reproductive development in the three selections is best shown in the results for the 1993/94 rainy season in Sebele, which started early (Fig 7.1B). For early sowing dates (October to December), 'Tiga Nicuru' always has the longest time to podding, and 'DipC94' the shortest (Fig. 7.2B). For sowing dates from January onwards, the time to podding decreases for all three selections, but most for 'Tiga Nicuru', and the differences between the selections become smaller at later sowing dates. However, the time to podding remains several weeks longer for

'GabC92' than for 'DipC94' until sowing date 1 March, when the time to podding is very similar for the three selections.

In the range of sowing dates studied, the general trend in the 1992/93 Sebele rainy season was roughly the same as in the 1993/94 season: the later the sowing date, the smaller the genotypic differences and the shorter the time to podding (Fig. 7.2). Because temperatures dropped earlier in the 1992/93 than in the 1993/94 season (Fig. 7.1), the time to flowering of all three selections starts to increase at sowing dates from sowing date 1 January 1993 onwards. The model predictions for Francistown were very similar to those for Sebele in the corresponding seasons (Fig. 7.2).

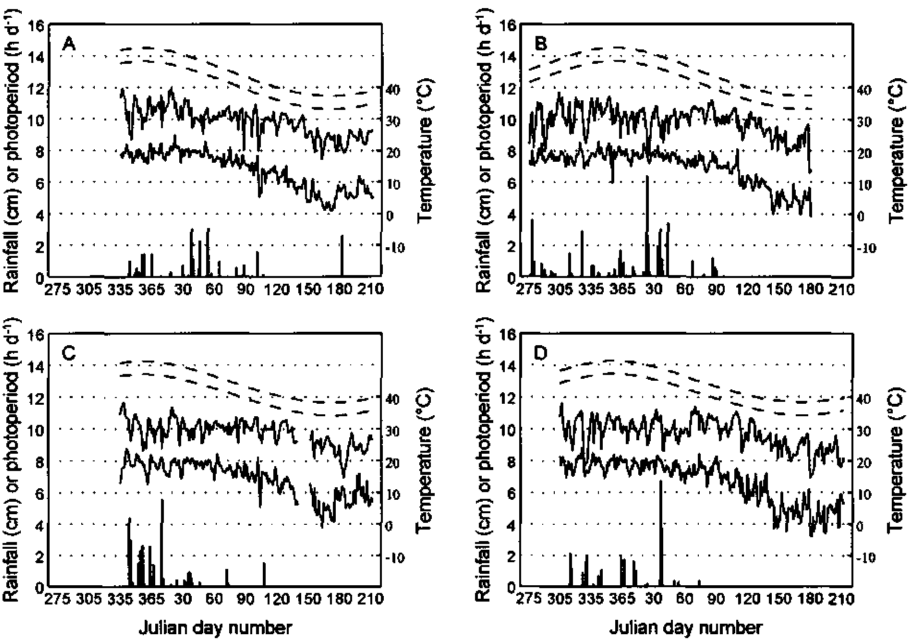

Fig. 7.1. Daily photoperiod with (upper dashed line) and without (lower dashed line) civil twilight, maximum temperature (upper solid line), minimum temperature (lower solid line) and rainfall (vertical bars) in the 1992/93 (A) and 1993/94 (B) rainy season in Sebele, and the 1992/93 (C) and 1993/94 (D) rainy season in Francistown.

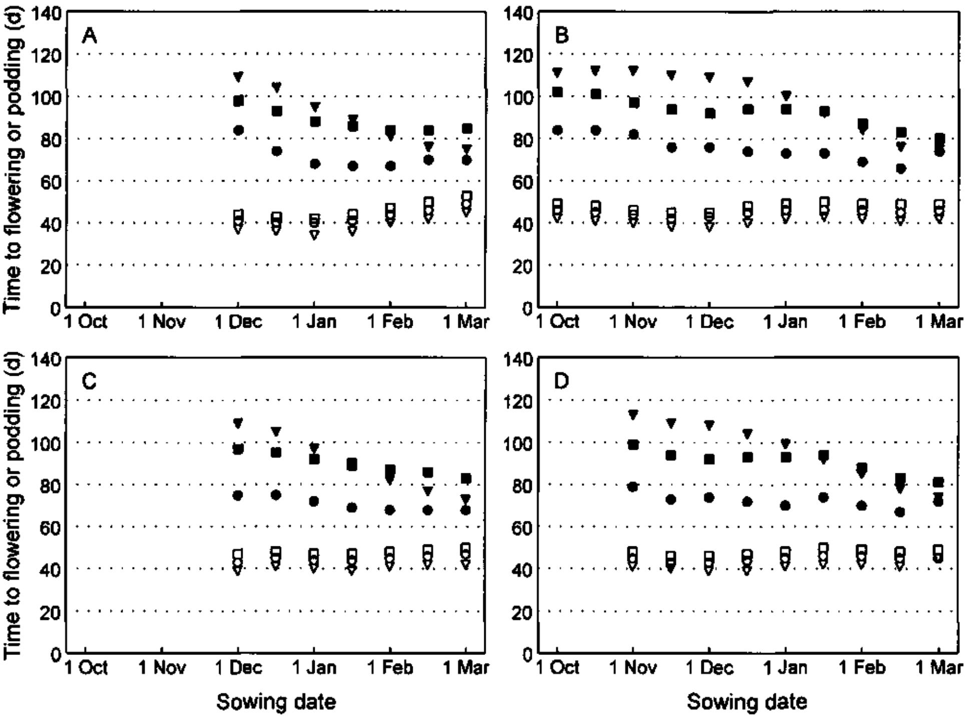

Fig. 7.2. Predicted times from sowing to flowering (open symbols) and to podding (closed symbols) for bambara groundnut selections 'DipC94' (○,●), 'GabC92' (□,■) and 'Tiga Nicuru' (▽,▼) in the 1992/93 (A) and 1993/94 (B) rainy season in Sebele, and the 1992/93 (C) and 1993/94 (D) rainy season in Francistown. Times from sowing to flowering and flowering to podding were calculated with the models in Table 7.1 and were based on the photoperiod including civil twilight.

When civil twilight is assumed not to be included in the photoperiod, the simulated times to podding become shorter (Fig. 7.3). The difference between the predictions based on photoperiods including and excluding civil twilight is usually less than a week for 'DipC94' and 'GabC92', but is greater for 'Tiga Nicuru'. The greatest difference, 20 days, is found for 'Tiga Nicuru' sown on 16 December in the 1993/94 season in Francistown.

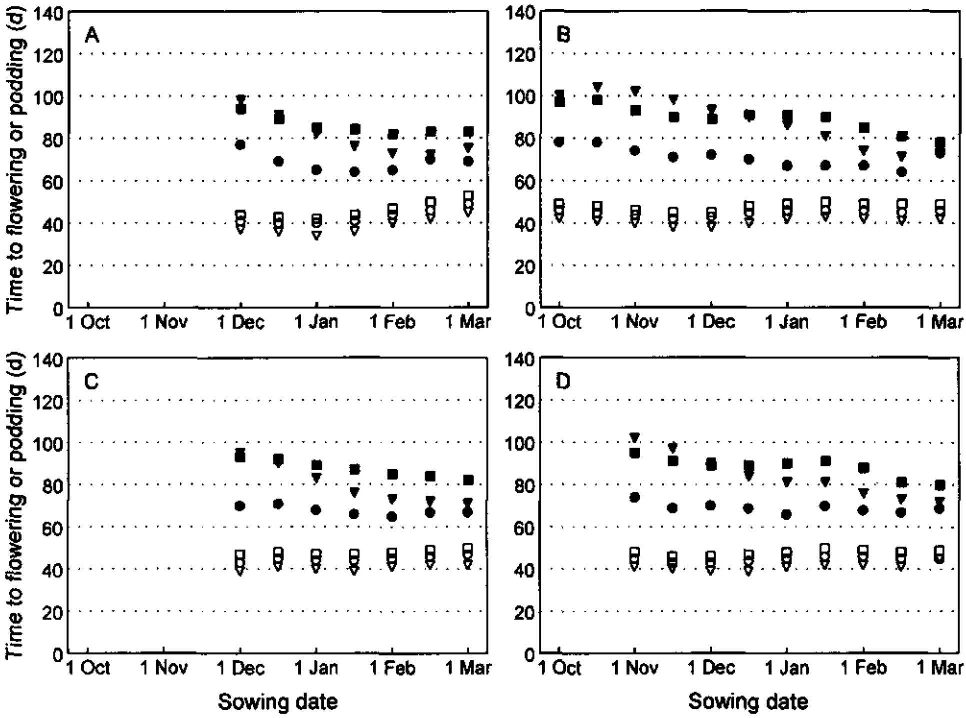

Fig. 7.3. Predicted times from sowing to flowering (open symbols) and to podding (closed symbols) for bambara groundnut selections 'DipC94' (○,●), 'GabC92' (□,■) and 'Tiga Nicuru' (▿,▾) in the 1992/93 (A) and 1993/94 (B) rainy season in Sebele, and the 1992/93 (C) and 1993/94 (D) rainy season in Francistown. Times from sowing to flowering and flowering to podding were calculated with the models in Table 7.1 and were based on the duration of daylight only (civil twilight not included).

7.4 Discussion

The simulation results indicate that at early sowing dates, genotypic differences in photothermal responses may be used to choose the time to podding. The use of 'DipC94' instead of 'Tiga Nicuru' would reduce the time to podding with 30-40 days, yielding food earlier (Fig. 7.2). At intermediate sowing dates, the differences between the selections may have important implications for moisture availability in the pod-filling phase. The 1993/94 rainy season in Sebele ended by the end of March, which implies that 'DipC94' sown later than mid-January would have to rely on residual soil moisture in the pod filling phase. The same applies to 'GabC92' and 'Tiga Nicuru' sown after 16 December. In the 1993/94 Francistown rainy season, the rains had ended by the end of February, which implies that 'DipC94' planted after mid-December, 'GabC92' planted after mid-November and 'Tiga Nicuru' planted after early November would have to rely on residual soil moisture in the pod-filling phase. These results indicate that for the two locations, the selections 'GabC92' and 'Tiga Nicuru' may be used to prolong the time to podding and thus vegetative growth at very early sowing dates, e.g in October. At later sowing dates, the risk of water shortage in the pod-filling phase is greater for these selections than for 'DipC94'. The effects of water shortage in the pod-filling stage of bambara groundnut have not yet been investigated, but in groundnut and cowpea this is the stage in which water shortage has the largest effects on seed yield (Nageswara Rao et al., 1985; Turk et al., 1980). At very late sowing dates, the differences between the selections become very small, but pod yields will be absent or very low because of lack of moisture.

Differences between the two locations were small. As Sebele (near Gaborone) and Francistown are located at respectively the southern and northern ends of the major cropping region in Botswana, it is probable that photoperiod differences within Botswana are not large enough to make it worthwhile using selections with different photoperiod sensitivities for different locations.

In cowpea (*Vigna unguiculata* (L.) Walp.), it has been found that the flowering of local West African cultivars is regulated by photoperiod in such a way that they flower at the end of the rains at their latitude of origin, irrespective of the sowing date (Wien and Summerfield, 1980). In the present study, early sowing resulted in longer predicted times to podding than late sowing, but not to such an extent that podding always occurred at the same date, irrespective of the sowing date. This finding is in agreement with the results of a field experiment carried out in Botswana in 1991 (Harris and Azam-Ali, 1993), in which the time from sowing to podding was found to range from 98 days for plants sown at the end of October to 52 days for plants sown at the beginning of January. Thus, a difference in sowing date of 9-10 weeks led to a difference in time to podding of only 46 days. This implies that the photothermal regulation of reproductive development in bambara groundnut selections from Botswana is probably less strict than that reported for West African cowpea cultivars. A possible explanation is that the end of the rainy season is more variable in Botswana than in West Africa.

The results of the present study are in agreement with the results of a farmers' survey carried out in Botswana in February 1995 (Brink et al., 1996), in which most farmers said that bambara groundnut should ideally not be sown later than December. Most farmers also said that the harvest date varies between years, depending on sowing date and rainfall, which confirms the finding that photoperiod sensitivity in bambara groundnut does not ensure that podding always occurs at the same date, irrespective of the sowing date.

It is much easier and cheaper to use models to study reproductive development of different bambara groundnut selections for a range of sowing dates and locations than to conduct field experiments at each location for several rainy seasons. The present study was intended to illustrate the use of models, and calculations were only made for two years. For a better assessment of the suitability of different selections, predictions for more years will be necessary, covering the variation between rainy seasons for a given location. To assess the risk of water shortage during specific development phases, photothermal models could be used in combination with rainfall probabilities for different months, based on long-term rainfall data.

A difficulty in the application of the models is, that it is not known to what extent twilight should be included in the photoperiod. It is common practice to include civil twilight in the photoperiod (Summerfield and Roberts, 1987). This study has shown that exclusion of civil twilight leads to shorter simulated times to podding, especially for 'Tiga Nicuru'. Investigations on the responsiveness of bambara groundnut to dim light would help to determine to what extent twilight should be included in the photoperiod. This knowledge would improve the applicability of photothermal development models. As long as it is not known whether the photoperiod should include civil twilight, it seems appropriate to carry out simulations for both cases and to indicate the range of simulated flowering and podding dates.

The models used in this study consider only the photothermal regulation of reproductive development. To make yield predictions under different circumstances, growth processes have to be taken into account as well. This could be done by incorporating the development models used in this study into crop growth models.

7.5 Conclusion

Photothermal development models can be a useful tool to find well adapted crop genotypes for specific environments. The simulation results indicate that for early sowing dates in Botswana the selections 'GabC92' and 'Tiga Nicuru' may be used to prolong the time to podding and thus vegetative growth. For later sowing dates, the risk of water shortage in the pod-filling phase is greater for these selections than for 'DipC94'. Early sowing resulted in longer predicted times to podding than late sowing, but not to such an extent that podding always occurred at the same date, irrespective of the sowing date. The inclusion or exclusion of civil twilight in the photoperiod affected the simulated time to podding, especially for 'Tiga Nicuru'. Therefore, determination of the responsiveness of bambara groundnut to dim light would increase the usefulness of the photothermal models.

CHAPTER 8

GENERAL DISCUSSION

8 GENERAL DISCUSSION

8.1 Quantifying photothermal influences on reproductive development in bambara groundnut

In this chapter, the findings presented in earlier chapters are discussed and evaluated in the context of the objective of the study, which was to quantify the influence of photoperiod and temperature on reproductive development in bambara groundnut (*Vigna subterranea* (L.) Verdc.) selections from different origins on the basis of controlled environment research. The resulting quantitative models had to be able to predict bambara groundnut development in field situations, so they could be used to identify crop genotypes that would do well in specific environments.

Model development

In this study, photoperiod and temperature effects on flowering and podding were quantified for five bambara groundnut selections: 'GabC92' and 'DipC94' from Botswana, 'DodR94' from Tanzania, 'NTSC92' from Zimbabwe and 'Tiga Nicuru' from Mali. The resulting photothermal models were based on the assumption that there is no interaction between development and growth and that crop development can be modelled separately from crop growth. In Chapter 5 it was shown that a light reduction of 42 % by shading led to total dry matter production being 41% less, but that the effects on development were relatively small: the rates of progress from sowing to flowering and flowering to podding were decreased by only 3 and 12% respectively. From this, it was inferred that growth and development in bambara groundnut are indeed largely independent.

In all five selections, the rate of progress from sowing to flowering increased with temperature in the temperature range of the experiments (21-27 °C and 20-29 °C) and this rate could be quantified very well ($r^2 \geq 95\%$) as a linear function of temperature only. In four of the five selections, photoperiod had no influence on the onset of flowering, but in 'DodR94' there seemed to be a slight photoperiod effect on flowering at an average temperature of 29 °C. Base temperatures for flowering in the five selections ranged from 5.7 to 9.9 °C, but these base temperatures were obtained by extrapolating beyond the temperature range of the main experiments. The base temperatures found in the present study were higher than those reported earlier for the Nigerian selections 'Ankpa2', 'Ankpa4' and 'Yola', which were 3.0, 1.4 and 3.2 °C respectively (Linnemann and Craufurd, 1994). They compare well with those reported for mung bean (*Vigna radiata* (L.) Wilczek), which range from 6.5 to 8.6 °C (Ellis et al., 1994b), soya bean (*Glycine max* (L.) Merrill), which were found to range from 4.6 to 10.0 °C in a controlled-environment study (Hadley et al., 1984) and from 5.5 to 12.5 °C in field experiments (Summerfield et al., 1993) and cowpea (*Vigna unguiculata* (L.) Walp.), which range from 7.2 to 10.8 (Hadley et al., 1983a; Ellis et al., 1994a; Craufurd et al., 1997). Base temperatures for flowering in bambara groundnut are lower than those reported for groundnut (*Arachis hypogaea* L.), which range from 9.6 to 14.0 °C (Leong and Ong, 1983; Bagnall and King, 1991a; Nigam et al., 1994).

The rate of progress from flowering to podding in all five selections was influenced by both temperature and photoperiod. The general trend was that this rate declined with increasing temperature and photoperiod at temperatures higher than 21-23 °C, the exception being 'Tiga Nicuru'. The rate of progress from flowering to podding could be quantified reasonably well (r^2 for the different selections ranging from 63% to 90%) as a function of both temperature and photoperiod by a photothermal response plane ('GabC92', 'NTSC92'), a combination of a thermal and a photothermal response plane ('DipC94') or a combination of a thermal response plane, a photothermal response plane and a plane of minimum development rate ('Tiga Nicuru'). In the case of 'DodR94', the intervals between the experimental photoperiods were too large to allow the photoperiod effect on podding to be quantified. In this selection, a strong photoperiod response occurred between 11.8 and 13.2 h d^{-1} in the whole temperature range of the experiment. A complete, three-plane model was obtained for 'Tiga Nicuru' only. In this selection, the critical photoperiod, which is the photoperiod below which the development rate is not influenced by photoperiod, for the rate of progress from flowering to podding decreased from 12.47 h d^{-1} at 22 °C to 11.32 h d^{-1} at 26 °C. The ceiling photoperiod, which is the photoperiod above which the development rate is not influenced by photoperiod decreased from 13.95 h d^{-1} at 22 °C to 13.07 h d^{-1} at 26 °C (Table 2.4). It is difficult to make comparisons with the photothermal podding responses of other legumes, because most efforts to quantify photothermal influences on reproductive development in legumes have focused solely on flowering.

The development models were based on semi-controlled environment experiments under constant photoperiods. In field situations, however, the photoperiod changes. In Chapter 4 it was shown that the average photoperiod between flowering and podding determined the rate of progress from flowering to podding, and that a gradual increase or decrease in photoperiod did not affect that rate. This implies that studies with constant photoperiods can be used to make models that predict bambara groundnut development in field situations with changing photoperiods. It also confirms that the rate of progress from flowering to podding can be modelled as a function of the average temperature and photoperiod in the period from flowering to podding.

Model validation

The photothermal models were validated by: (a) comparing the photothermal responses of the selections with the ecological conditions in the regions where they were obtained (Chapter 6); and (b) comparing the model predictions with results from glasshouse experiments in The Netherlands (Chapters 2 and 6) and field experiments in Tanzania and Botswana (Chapter 6). As shown in Chapter 6, responses to photoperiod and temperature in bambara groundnut selections from near the equator and near the Tropic of Capricorn could be explained very well by the photothermal environment prevailing in the regions where the selections were obtained. The time to flowering in glasshouse and field validation experiments could be predicted well, except for selection 'DodR94', possibly because this selection experiences photoperiod effects when temperatures exceed those applied in the experiment on which the models were based. The time from flowering to podding in the validation experiments was not always predicted well. This may be caused by podding being less predictable than flowering, but it may also be that there were too few photoperiod/temperature combinations to obtain accurate podding models, which include more parameters than the flowering models. Another explanation may be that some of the validation experiments were conducted in glasshouses without forced cooling in which maximum temperatures were very high (35-40 °C) on warm, sunny days. As model predictions were based on the average daily temperature (around 25 °C), development rates may have been overestimated. Furthermore, relative humidity of the air in the glasshouse experiments could not always be kept at the preset level on hot, sunny days. This may have affected development rates, because it has been found that flowering in cowpea can be delayed by high pre-flowering saturation deficits of the air (Craufurd et al., 1996).

Model use

The photothermal development models developed in this study are intended to be used to identify crop genotypes that are well adapted to specific environments. Chapter 7 presented an example of how the models can be used to simulate reproductive development as a function of sowing date in different years and for different locations. It was shown that at early sowing dates, differences in photothermal responses between the selections 'GabC92', 'DipC94' and 'Tiga Nicuru' may be used to select the desired length of the crop cycle. If it is important for farmers to have some yield as early as possible in the season, a selection that sets pods early may be sown. However, if the farmer prefers to have more vegetative growth, for instance to obtain fodder, a selection that sets pods later is preferable. At later sowing dates, the risk of drought stress in the pod-filling stage can be reduced by using 'DipC94', because of its faster development.

When daily meteorological data are available for a range of years, simulations can be carried out for typical early, average and late years to obtain general recommendations for a given location. To assess the risk of water stress during specific development phases, photothermal models can be used in combination with rainfall probabilities for different months, based on long-term rainfall data.

A difficulty in the application of the models in field situations is, that it is not known whether in the case of bambara groundnut twilight should be included in the photoperiod. The photoperiod is usually assumed to include civil twilight. This assumption seems justified for soya bean, common bean (*Phaseolus vulgaris* L.) and chickpea (*Cicer arietinum* L.), but not for lentil (*Lens culinaris* Medic.) (Summerfield and Roberts, 1987). In the Botswana case-study (Chapter 7), it was shown that the predicted time to podding in bambara groundnut may become considerably shorter when civil twilight is not included and the photoperiod is assumed to include only daylight. As long as it remains unknown whether or not the photoperiod perceived by bambara groundnut includes civil twilight, simulations should be conducted for both cases, and the range of simulated flowering and podding dates should be indicated.

8.2 Methodological issues

The development stages considered

The study addressed photothermal effects on flowering and podding. The onset of podding is the most important event in bambara groundnut development, as it coincides with a major shift in assimilate partitioning (Chapter 5). Photothermal effects on maturity could not be quantified, because development in the long photoperiod treatments was delayed to such an extent that the plants did not reach maturity before the experiments ended, not even in the long experiments of Chapters 3 (198 days), 4 (183 days) and 6 (190 days). Furthermore, there are no clear criteria for defining maturity in bambara groundnut. Criteria such as brown patches appearing on the pods (Doku and Karikari, 1970) were difficult to apply, because the plants were earthed-up after the onset of podding to mimic common practice among bambara groundnut farmers in Africa (Linnemann, 1988; Linnemann; 1990; Brink et al., 1996). The maturity criteria used by farmers are yellowing and falling of the leaves (Doku and Karikari, 1971; Linnemann, 1990; Brink et al., 1996). However, these criteria seem rather arbitrary for exact quantification in a research context, and leaf yellowing and shedding may also be affected by factors such as light intensity and water and nutrient availability.

Temperature range

The narrow range of constant temperatures in which bambara groundnut can be grown was an important constraint. Earlier research had shown that the crop does not grow well at temperatures below 20 °C (Linnemann, personal communication), and in the present study it appeared that the plants died at constant temperatures of 33 and 36 °C (Chapter 6). An alternative is to grow the plants at higher day and lower night temperatures, but then the optimum temperature for flowering may be exceeded during part of the day. In that case, the relation between rate of progress from sowing to flowering and average temperature will not be assessed correctly.

Photoperiod extension

Photoperiod levels in most experiments described in this study were established by extending an 8 h d^{-1} natural daylight period with low intensity artificial light to ensure that all treatments received the same amount of photosynthetically active radiation. The low-intensity artificial light was a combination of fluorescent tubes and incandescent bulbs, so that the light spectrum resembled natural daylight. In soya bean, it has been found that light with a relatively low red/far-red (R/FR) ratio causes stronger photoperiod responses than light with a higher R/FR ratio. Fluorescent light alone (high FR/R) gave the smallest photoperiod response, incandescent light (low R/FR) the largest (Cober et al., 1996b). Experiments that directly compare the effect of different light qualities on photoperiod responses in bambara groundnut might reveal whether photoperiod effects in bambara groundnut are influenced by light quality. However, no such experiments were conducted in the present study.

Other influences on reproductive development

Though it is generally accepted that photoperiod and temperature are the major factors controlling reproductive development in annual crops, other factors such as water and nutrient availability may also have influence. In pea (*Pisum sativum* L.), short-term drought stress led to an earlier end of flowering and fewer flowering nodes, but it did not affect the rate of progress to flowering, beginning of seed filling and physiological maturity. Long-term water stress, however, did advance the beginning and end of seed filling (Jeuffroy and Ney, 1997). In soya bean, it has been found that non-nodulating isolines flowered later and matured earlier than their nodulating counterparts because of nitrogen shortage (George et al., 1990). The effects of water and nutrient availability were not included in the present study, because they are investigated by other partners within the research programme *Evaluating the potential for bambara groundnut as a food crop in semi-arid Africa*. The effects of moisture availability on growth, development and yield are studied at the University of Nottingham, U.K., where glasshouse experiments have shown that the onset of podding may be delayed under severe drought (Collinson et al., 1996). Effects of both nutrient and water availability are investigated in Botswana (Ramolemana et al., 1997).

In the field experiment which was used for validation in Chapter 6, phosphorus application had no effect on the time to flowering, but plants in the rainfed treatment flowered later than plants in the irrigated treatment.

Empirical and mechanistic models

The development models presented in this thesis do not explain the underlying mechanisms of the effects of photoperiod and temperature on reproductive development. They can be classified as empirical models and not as mechanistic ones (Hodges, 1991). This applies to most efforts to model the influence of environmental factors on crop development to date, because the physiological mechanisms underlying development regulation are complicated and not well understood. However, some aspects are known, and the next section attempts to integrate these with the available information on bambara groundnut.

8.3 Mechanisms underlying photothermal influences on reproductive development

It is probable that photoperiod and temperature influence the activity of genes that affect assimilate partitioning to different organs. In soya bean, five genes, each with two alleles (E_1/e_1, E_2/e_2, E_3/e_3, E_4/e_4 and E_5/e_5), have been reported to control time to flowering and maturity (Upadhyay et al., 1994; Cober et al., 1996a). Under short days, the *E* alleles do not affect development and act similar to *e* alleles; under long days, they respond by delaying flowering and maturity (Cober et al., 1996a). In a study with eight isolines of the E_1/e_1, E_2/e_2 and E_3/e_3 genes, the isolines showed no difference in their flowering response to temperature, but their photoperiod sensitivity was different, which implies that temperature sensitivity and photoperiod sensitivity are under different genetic control (Upadhyay et al., 1994). It has been postulated that lack of photoperiod gene activity allows assimilates to be partitioned to potential buds, flowers, pod or seeds, whereas photoperiod gene activity leads to partitioning to vegetative organs (Wallace et al., 1993).

Many common bean genotypes are photoperiod-insensitive for flower bud initiation, but photoperiod-sensitive for continued development of flower buds. The delay in flowering under long days is a result of the buds growing slower and/or aborting (Wallace et al., 1993). The photoperiod effect on podding in bambara groundnut is probably basically similar. A microscope study on a Nigerian selection (Linnemann, 1993) revealed that under short (11.5 h d^{-1}) and long (>14 h d^{-1}) days embryo development was identical up to 17 days after flowering, with all embryos growing slowly. Thereafter, some embryos in plants grown under short days increased rapidly in size, reaching their ultimate size at about 41 days after flowering. In plants grown under long days, all embryos stopped growing at about 17 days after flowering and began to shrivel at about 32 days after flowering. This suggests that photoperiod does influence assimilate partitioning to embryos in bambara groundnut in the same way that it influences partitioning to flower buds in common bean. In groundnut too, the greatest photoperiod response was found in the development of pegs to pods, whereas pollen production and fertilization were insensitive to photoperiod (Bagnall and King, 1991b).

Photoperiodic signals are perceived by the leaves, where promoting or inhibiting substances are formed (Thomas and Vince-Prue, 1997). It is this release of plant growth substances which may cause a shift in assimilate partitioning. In an experiment with soya bean, plants were kept under short days until 11 days after anthesis, after which half of the plants were transferred to a night interruption treatment, which is comparable to a long-day treatment. The concentration of abscisic acid (ABA) in the seeds of soya bean plants kept under short days increased more rapidly than that in plants transferred to the long-day treatment. Sucrose accumulated in embryos after the ABA concentration had peaked, which suggests that ABA stimulates sucrose transport to the seeds (Morandi et al., 1990).

8.4 Agronomic implications

Photoperiod sensitivity

The present study confirms earlier findings that the onset of flowering in most bambara groundnut selections is photoperiod-insensitive and the onset of podding is retarded by long photoperiods (Linnemann, 1994a). This phenomenon is not unique for bambara groundnut, because it has been shown that photoperiod may have strong effects on pod formation in groundnut genotypes with photoperiod-insensitive flowering (Flohr et al., 1990; Bagnall and King, 1991a; Bell et al., 1991). It is not clear why soya bean and cowpea are photoperiod-sensitive for the onset of flowering, whereas bambara groundnut and groundnut are photoperiod-sensitive for later development stages. According to Linnemann (1994a) the advantage of photoperiod regulation of podding instead of flowering is that it increases the flexibility of the crop, because the period of flexible duration is extended: from sowing to podding instead of from sowing to flowering.

It has been argued that photothermal effects on post-flowering growth and development of cowpea are not of major importance, because in most of the environments where the crop is grown podding occurs at shortening photoperiods (Craufurd et al., 1997). However, the present study has shown that flowering in bambara groundnut may occur before the photoperiod reaches its maximum (Chapter 7) and that photothermal influences on post-flowering development cannot be ignored. It seems probable that this will also hold for cowpea, especially for genotypes which are photoperiod-insensitive for flowering and which may flower as soon as 35 days after sowing under West African field conditions (Craufurd et al., 1997). Therefore, the quantification of photothermal effects on development in cowpea and other grain legumes should not remain restricted to the flowering response.

Onset of podding and harvest index

If the reproductive phase starts early, little vegetative matter is produced, which may limit the production potential of the crop. If the reproductive phase starts later, more vegetative dry matter is produced, but seed yields will be high only when the growing season is long enough for the harvest index to be high. In Chapter 4 it was shown that the harvest index in four bambara groundnut selections was inversely related to the time from sowing to podding and that pod and seed yields at 183 days after sowing were not higher in plants which had a long vegetative period and a high total biomass production, because the harvest index was very low.

Differences in the time to podding and thus in the length of the vegetative phase and in total biomass production can be exploited when designing appropriate cropping systems. To secure a high harvest index, it may be decided to sow selections that will start podding early under the prevailing photothermal conditions. The reduced biomass and light interception per plant can be compensated for by using higher plant densities (Lawn and Williams, 1987). However, sowing at higher densities implies the use of more seed and thus higher risk for the farmer.

Choice of genotypes

Bambara groundnut is usually not sown immediately after the first rains, because other crops (cereals) tend to get priority. This is illustrated by the great variation in bambara groundnut sowing dates encountered in field surveys in Botswana (Brink et al., 1996) and Zambia (Linnemann, 1990). In both countries, sowing dates ranged from November to February. A large variation in sowing date has also been reported for Nigeria: the bambara fields are usually prepared when the main food crops have been planted (Linnemann, 1988). It is agronomically sensible to sow cereals at the beginning of the rainy season and legumes later, because the nitrogen flux after the onset of the rainy season is more important for cereals than for legumes, which are able to fix atmospheric nitrogen. As shown in Chapter 7, model predictions of the time from sowing to podding can be used to choose appropriate selections and sowing dates for particular locations. It is much cheaper to use models based on controlled-environment experiments with carefully chosen photoperiod and temperature treatments than to conduct field experiments at a range of locations during several rainy seasons.

The study considered only the photothermal regulation of development. For predicting yield, however, growth processes also have to be taken into account. This could be done by incorporating the development models into crop growth models such as the bambara groundnut PARCH model (Collinson, 1997), which is being developed at the University of Nottingham, U.K., in the framework of the international research programme *Evaluating the potential for bambara groundnut as a food crop in semi-arid Africa*. The PARCH (Predicting Arable Resource Capture in Hostile environments) model is a combination of a crop growth module, based on light and water capture and the efficiency of conversion of light and water into dry matter, and a soil profile divided into layers (Bradley and Crout, 1992). The bambara groundnut PARCH model was developed on the basis of glasshouse studies and is in the process of being validated with field data (Collinson, 1997).

The finding that shading led to a lower total dry matter production, but only a small delay in development (Chapter 5) implies that the onset of flowering and podding in bambara groundnut intercropped with taller cereals will not be very different from that in sole-cropped bambara groundnut. Therefore, the development models can be used to for both intercropped and sole-cropped bambara groundnut.

Adaptation through photothermal regulation

It has been reported that the flowering of local West African cowpea cultivars is regulated by photoperiod in such a way that they generally flower at the end of the rains at their latitude of origin, irrespective of the sowing date (Wien and

Summerfield, 1980). In the simulation study for Botswana (Chapter 7), it was shown that early sowing of bambara groundnut in Botswana resulted in longer predicted times to podding than late sowing, but not to such an extent that podding always occurred at the same date, irrespective of the sowing date. This finding was in agreement with the results of a field experiment carried out in Botswana in 1991, in which difference in sowing date of 9-10 weeks led to a difference in time to podding of 46 days (Harris and Azam-Ali, 1993). Thus, the present study indicates that photothermal regulation of development in bambara groundnut is somewhat less strict than has been reported for cowpea in West Africa, which may be due to the end of the rainy season being more variable in Botswana than in West Africa.

Phenological plasticity

A good match between crops or crop genotypes and specific environments can be achieved by different strategies (Loomis and Connor, 1992). Soya bean cultivars have been classified into maturity groups, each of them best adapted to a certain production zone in the United States (Evans, 1993). Cultivars grown south of their zone flower too soon, cultivars grown north of their zone too late (Loomis and Connor, 1992). In other crops, such as wheat (*Triticum aestivum* L.), photoperiodicity has been suppressed or eliminated by breeding, which has led to improved cultivars with a wide geographic suitability. Breeding for day neutrality in bambara groundnut would eliminate its phenological plasticity. This phenological plasticity is one of the typical traits of tropical grain legumes, which enables the crop to compensate for stress and to respond to the environment (Lawn, 1989). Therefore, the use of development models to classify genotypes and to match bambara groundnut genotypes to specific locations, sowing dates and farmers' objectives seems a better approach than breeding for day neutrality.

8.5 Conclusion

This study has confirmed that the onset of flowering in most bambara groundnut selections is dependent on temperature, but is not photoperiod-sensitive, whereas the onset of podding is influenced by both temperature and photoperiod. The onset of podding coincides with the major shift in the assimilate distribution from vegetative to reproductive growth, and the timing of the onset of podding determines the length of the vegetative phase. This implies that for given locations and sowing dates genotypes can be selected which will have an optimal balance between vegetative and reproductive phases, taking into account farmers' objectives. The influence of photoperiod and temperature on the rate of progress from sowing to flowering and the rate of progress from flowering to podding in different selections can be quantified through descriptive linear models, using data from semi-controlled environment experiments with constant temperatures and photoperiods. The models predicted the time to flowering in validation experiments generally well, but the time from flowering to podding was not always predicted accurately. Nevertheless, the models did characterize the photothermal response of the selections reasonably well. Therefore, these quantitative models, either on their own or incorporated into a crop growth model, can be useful instruments for matching bambara groundnut genotypes to specific environments.

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SUMMARY

Introduction and objective

It seems likely that it is more realistic to increase food production in semi-arid Africa by growing crops and crop genotypes that are adapted to existing production constraints like low rainfall and poor soils, than by trying to overcome these constraints by applying irrigation and fertilizer. The extent to which plants are adapted to their environments is largely dependent on the way their development is affected by climatic factors. Crops should be able to complete their reproductive development within the growing season, have an optimal balance between vegetative and reproductive phases, and critical stages of their development should not coincide with unfavourable conditions. Reproductive development in bambara groundnut (*Vigna subterranea* (L.) Verdc.), a crop considered to be adapted to semi-arid Africa because it tolerates drought and low soil fertility, is known to be influenced by temperature and photoperiod. The objective of this study was to quantify the influence of photoperiod and temperature on reproductive development in selections from different origins on the basis of controlled environment research. The resulting quantitative models had to be able to predict reproductive development in field situations, which would make them useful for identifying crop genotypes that would do well in specific environments.

Quantifying photothermal effects on flowering and podding

Temperature and photoperiod effects on the onset of flowering and the onset of podding of bambara groundnut selections 'GabC92' (Botswana), 'NTSC92' (Zimbabwe) and 'Tiga Nicuru' (Mali) were quantified with the photothermal approach that has been used to quantify photoperiod and temperature influences on flowering in other leguminous crops (Chapter 2). In this approach, development rates are linked

to photoperiod and temperature with linear equations. This was done on the basis of a semi-controlled environment experiment with factorial combinations of three constant temperatures (20.9, 23.4, and 26.2 °C) and four constant photoperiods (10.0, 12.5, 13.5, and 16.0 h d^{-1}). In all three selections, the onset of flowering was influenced by temperature but not by photoperiod, whereas the onset of pod growth ('podding') was influenced by both factors. The rate of progress from sowing to flowering of the three selections could be modelled very well as a function of temperature; the rate of progress from flowering to podding could be modelled reasonably well as a function of both temperature and photoperiod. Model testing with independent data sets showed good agreement between observed and predicted times to flowering and podding.

The photoperiod-sensitive phase for podding

Chapter 3 describes an experiment to investigate whether the time from sowing to podding in bambara groundnut can be divided into photoperiod-sensitive and photoperiod-insensitive phases in the same way as the time between sowing and flowering in other crops. The reciprocal transfer experiment was done with three selections: 'GabC92' from Botswana and 'NTSR94' and 'NTSC92' from Zimbabwe. Treatments were established by transferring plants between 14 h d^{-1} (LD) and 11 h d^{-1} (SD) every two weeks. There were also control treatments of constant LD and SD. Flowering was not affected by photoperiod, but the onset of podding was delayed by long photoperiods. At an average temperature of 25.7 °C, the main photoperiod effect on podding occurred from 42 days after sowing onwards in 'NTSR94' and 'NTSC92', and from 57 days after sowing onwards in 'GabC92'. The time from sowing to podding could not be divided clearly into photoperiod-sensitive and photoperiod-insensitive phases, because in all three selections podding tended to be later in early transfers from SD to LD than in constant LD, and earlier in the early transfers from LD to SD than in constant SD.

Effects of constant, increasing and decreasing photoperiods

In Chapter 4 it is examined whether information obtained from experiments with constant photoperiods can be used in field situations where photoperiods fluctuate. This was investigated in a glasshouse experiment with four selections: 'GabC92', 'GabC94' and 'DipC94' from Botswana and 'DodC94' from Tanzania. Treatments included three constant photoperiods (12, 13, and 14 h d^{-1}) and three gradually changing photoperiods: a decreasing photoperiod (14 → 11 h d^{-1}), an increasing photoperiod (12 → 15 h d^{-1}) and a photoperiod that first increased and later decreased (13 → 14 → 12 h d^{-1}). No photoperiod effect on the rate of progress from sowing to flowering was found in any of the selections, but in all four selections the rate of progress from flowering to podding was influenced by photoperiod. The average photoperiod between flowering and podding determined the rate from flowering to podding, and a gradual increase or decrease did not affect that rate. Therefore, it is concluded that models intended to predict bambara groundnut development in field situations with fluctuating photoperiods can be based on studies with constant photoperiods.

Development, growth and dry matter partitioning

Chapter 5 discusses the validity of some common assumptions in crop modelling. The first assumption is that development and growth are independent and that crop development can be modelled separately from crop growth; the second that dry matter partitioning factors are dependent on development stage and not directly influenced by photoperiod. An experiment was conducted with four photoperiods (10.5, 11.8, 13.2 and 14.5 h d^{-1}) and two light treatments: unshaded and shaded (42% light reduction). The selection used was 'DipC94' from Botswana. Total dry matter production was 41% lower in the shaded treatment than in the unshaded treatment, but the rates of progress from sowing to flowering and flowering to podding decreased by only 3 and 12 % respectively. This led to the conclusion that growth and development in bambara groundnut are largely independent. Photoperiod influenced dry matter partitioning indirectly, through its influence on the onset of podding. There were, however, no strong direct photoperiod effects on dry matter partitioning, either before or after the onset of podding.

Models and validation

In chapter 6, linear photothermal models are developed for bambara groundnut selections from contrasting origins: 'DodR94' from Tanzania, near the equator, and 'DipC94' from Botswana, near the Tropic of Capricorn. The models were based on a semi-controlled environment study with four constant photoperiods (10.5, 11.8, 13.2, and 14.5 h d^{-1}), covering the range of photoperiods in the tropics) and four constant temperatures (20, 23, 26, 29 °C). Higher temperatures were included, but plants died at constant temperatures of 33 and 36 °C. The models were validated by comparing the photothermal responses of the selections with the photothermal conditions in the regions where they were obtained, and by comparing model predictions with results from glasshouse experiments in The Netherlands and field experiments in Tanzania and Botswana. The photoperiod and temperature response of the two selections could be explained very well by the photothermal conditions in the regions from which the selections came. Validation of the photothermal models with the results of glasshouse and field experiments gave mixed results: predicted and observed time to flowering for 'DipC94' corresponded well, and predicted and observed time from flowering to podding reasonably well. Flowering predictions for 'DodR94' were not accurate, possibly because this selection is sensitive to photoperiod when temperatures are higher than in the experiment on which the models were based.

Using photothermal development models

The implications of genotypic differences in responses to photoperiod and temperature in bambara groundnut and the usefulness of photothermal development models for identifying suitable selections for different locations and sowing dates are demonstrated in a simulation study for Botswana (Chapter 7). Times to flowering and podding for the selections 'DipC94', 'GabC92' and 'Tiga Nicuru' were calculated for different sowing dates at two locations (Sebele and Francistown) in two rainy seasons. Calculations were made with photothermal development models developed in Chapters 2 and 6 and with actual daily minimum and maximum temperatures and photoperiods (with or without civil twilight). The simulation results indicate that for early sowing dates 'GabC92' and 'Tiga Nicuru' may be used to prolong the time to podding and thus to promote vegetative growth. For later sowing dates, the risk of water shortage in the pod-filling phase is greater for these selections than for 'DipC94'. When sown very late, the differences between the three selections become very small, but pod yields will be absent or very low because of water shortage. Differences between the two locations were small, which implies that photoperiod differences within Botswana are probably not large enough to merit using selections with different photoperiod sensitivities for different locations. Longer photoperiods early in the rainy season resulted in longer predicted times to podding, but not to such an extent that podding always occurred on the same date, irrespective of the sowing date. When civil twilight was assumed not to be included in the photoperiod as perceived by bambara groundnut plants, the simulated times to podding became shorter, especially for 'Tiga Nicuru'. Therefore, determination of the responsiveness of bambara groundnut to dim light would increase the usefulness of the photothermal models.

Discussion and conclusion

In Chapter 8, the main findings, methodological issues and agronomic

implications of the study are discussed, together with some physiological mechanisms underlying the photothermal regulation of reproductive development. It is concluded that the influence of photoperiod and temperature on the rate of progress from sowing to flowering and the rate of progress from flowering to podding in different bambara groundnut selections can be quantified through descriptive linear models, using data from semi-controlled environment experiments with constant temperatures and photoperiods. Though predictions in validation experiments, especially of the time from flowering to podding, were not always accurate, the models did characterize the photothermal response of the selections reasonably well. It is therefore concluded that these quantitative models, either on their own or incorporated into a crop growth model, can be useful instruments for matching bambara groundnut genotypes and specific environments.

SAMENVATTING

Inleiding en doelstelling

Bij het streven naar verhoging van de voedselproductie in semi-aride Afrika, is het waarschijnlijk realistischer om te proberen gebruik te maken van gewassen en genotypen die aangepast zijn aan beperkingen zoals geringe regenval en lage bodemvruchtbaarheid, dan om te proberen dergelijke beperkingen op te heffen door het gebruik van irrigatie en kunstmest. De mate waarin gewassen aangepast zijn aan hun omgeving wordt grotendeels bepaald door de wijze waarop hun ontwikkeling wordt beïnvloed door klimaatsfactoren. Gewassen moeten in staat gesteld worden hun reproductieve ontwikkeling te voltooien en een optimaal evenwicht te handhaven tussen vegetatieve en reproductieve fasen, waarbij kritieke momenten in hun ontwikkeling niet mogen samenvallen met ongunstige omstandigheden. De ontwikkeling van bambara aardnoot (*Vigna subterranea* (L.) Verdc.), een gewas dat is aangepast aan semi-aride Afrika, wordt met name beïnvloed door temperatuur en fotoperiode.

Het doel van dit onderzoek was het kwantificeren van de invloed van temperatuur en fotoperiode op de reproductieve ontwikkeling van selecties van verschillende herkomst op basis van onderzoek onder gecontroleerde omstandigheden. Met de te ontwikkelen kwantitatieve modellen zou de reproductieve ontwikkeling onder veldomstandigheden moeten kunnen worden voorspeld, waardoor deze modellen een nuttig instrument zouden zijn om geschikte genotypen te identificeren voor specifieke locaties.

Het kwantificeren van de effecten van fotoperiode en temperatuur op de bloei en peulvorming

De effecten van temperatuur en fotoperiode op het begin van zowel de bloei als de peulvorming van de bambara aardnoot selecties 'GabC92' (Botswana), 'NTSC92' (Zimbabwe) en 'Tiga Nicuru' (Mali) werden gekwantificeerd met behulp van een benadering die eerder was gebruikt om de invloed van temperatuur en fotoperiode op de bloei van andere vlinderbloemigen te kwantificeren (Hoofdstuk 2). In deze benadering worden ontwikkelingssnelheden gerelateerd aan temperatuur en fotoperiode door middel van lineaire vergelijkingen. De vergelijkingen werden gebaseerd op een experiment onder semi-gecontroleerde omstandigheden met factoriële combinaties van drie constante temperaturen (20.9, 23.4 en 26.2 °C) en vier constante fotoperioden (10.0, 12.5, 13.5 en 16.0 uur per dag). Het begin van de bloei van alle drie selecties bleek te worden beïnvloed door de temperatuur, maar niet door de fotoperiode. Het begin van de peulvorming, echter, werd door zowel temperatuur als fotoperiode beïnvloed. De ontwikkelingssnelheid van zaai tot bloei van de drie selecties kon uitstekend worden gekwantificeerd als een functie van temperatuur; de ontwikkelingssnelheid van bloei tot peulvorming kon goed tot redelijk gekwantificeerd worden als een functie van zowel temperatuur als fotoperiode. Bij het toetsen van de modellen met onafhankelijke datasets kwamen de voorspelde en waargenomen tijdstippen van bloei en peulvorming goed met elkaar overeen.

De voor fotoperiode gevoelige fase

In Hoofdstuk 3 wordt onderzocht of de periode van zaai tot peulvorming in bambara aardnoot op dezelfde manier in voor fotoperiode gevoelige en ongevoelige fasen kan worden onderverdeeld als de periode van zaai tot bloei in andere gewassen. Een overzet-experiment werd uitgevoerd met drie selecties: 'GabC92' uit Botswana en 'NTSR94' en 'NTSC92' uit Zimbabwe. De behandelingen werden gecreëerd door elke twee weken een aantal planten over te zetten van een fotoperiode van 14 uur per dag (LD) naar een fotoperiode van 11 uur per dag (KD) en vice versa. Er waren ook controle-behandelingen met een vaste LD of KD. De bloei bleek niet te worden beïnvloed door fotoperiode, maar het begin van de peulvorming werd vertraagd door lange fotoperioden. Bij een gemiddelde temperatuur van 25.7 °C vond het belangrijkste fotoperiode-effect op de peulvorming plaats vanaf 42 dagen na de zaai in 'NTSR94' en 'NTSC92', en vanaf 57 dagen na de zaai in 'GabC92'. De tijd van zaai tot peulvorming kon niet duidelijk worden verdeeld in voor fotoperiode gevoelige en ongevoelige fasen, omdat de peulvorming in de drie selecties later plaatsvond bij vroeg overzetten van KD naar LD dan in constante LD, en eerder bij vroeg overzetten van LD naar KD dan in constante KD.

Effecten van constante, toenemende en afnemende fotoperioden

In Hoofdstuk 4 wordt nagegaan of informatie verkregen uit experimenten met constante fotoperioden gebruikt kan worden in veldsituaties waarin de fotoperiode fluctueert. Dit werd onderzocht in een kasproef met vier selecties: 'GabC92', 'GabC94' en 'DipC94' uit Botswana en 'DodC94' uit Tanzania. De behandelingen omvatten drie constante fotoperioden (12, 13 en 14 uur per dag) en drie geleidelijk veranderende fotoperioden: een afnemende fotoperiode (14 → 11 uur per dag), een toenemende fotoperiode (12 → 15 uur per dag) en een fotoperiode die eerst toenam en later afnam (13 → 14 → 12 uur per dag). Voor geen van de selecties werd een fotoperiode-effect op de ontwikkelingssnelheid van zaai tot bloei gevonden, maar in alle selecties werd de ontwikkelingssnelheid van bloei tot peulvorming wel beïnvloed door de fotoperiode. De gemiddelde fotoperiode tussen het begin van de bloei en het begin van de peulvorming bepaalde de ontwikkelingssnelheid van bloei tot peulvorming; een geleidelijke toename of afname had geen invloed. Er wordt daarom geconcludeerd dat modellen die bedoeld zijn om in veldsituaties met een fluctuerende fotoperiode de ontwikkeling van bambara aardnoot te voorspellen, gebaseerd kunnen worden op studies met constante fotoperioden.

Ontwikkeling, groei en droge stof verdeling

Hoofdstuk 5 behandelt de geldigheid van enkele gangbare aannames in de gewasmodellering. De eerste is dat ontwikkeling en groei onafhankelijk zijn en dat de ontwikkeling van een gewas afzonderlijk van de gewasgroei kan worden gemodelleerd; de tweede dat de droge-stof verdeling afhankelijk is van het ontwikkelingsstadium en niet direct door de fotoperiode wordt beïnvloed. Er werd een experiment uitgevoerd met vier fotoperioden (10.5, 11.8, 13.2 en 14.5 uur per dag) en twee lichtbehandelingen: onbeschaduwd en beschaduwd (42% lichtreductie). De gebruikte selectie was 'DipC94' uit Botswana. In de beschaduwde behandeling was de totale droge-stofproductie 41% lager dan in de onbeschaduwde, maar de ontwikkelingssnelheden van zaai tot bloei en van bloei tot peulvorming waren slechts respectievelijk 3 en 12 % lager. Dit leidde tot de conclusie dat groei en ontwikkeling van bambara aardnoot grotendeels onafhankelijk zijn. De fotoperiode had een indirecte invloed op de droge-stofverdeling, via de invloed op het begin van de peulvorming. Noch vóór, noch na het begin van de peulvorming werd echter een duidelijk direct effect van de fotoperiode op de droge-stofverdeling gevonden.

Modellen en validatie

Hoofdstuk 6 beschrijft hoe lineaire fotothermale modellen werden ontwikkeld voor bambara aardnoot selecties van uiteenlopende oorsprong: 'DodR94' uit Tanzania, dichtbij de evenaar, en 'DipC94' uit Botswana, dichtbij de steenbokskeerkring. De modellen werden gebaseerd op een experiment onder semi-gecontroleerde omstandigheden met vier constante fotoperioden (10.5, 11.8, 13.2 en 14.5 uur per dag), die de spreiding van fotoperioden in de tropen omvatten, en vier constante temperaturen (20, 23, 26 en 29 °C). In het experiment werden ook hogere temperaturen gebruikt, maar de planten gingen dood bij constante temperaturen van 33 en 36 °C. De modellen werden gevalideerd door de fotothermale respons van de selecties te vergelijken met de fotothermale omstandigheden in de gebieden van herkomst en door modelvoorspellingen te vergelijken met resultaten van kasproeven in Nederland en veldproeven in Tanzania en Botswana. De fotoperiode- en temperatuur-respons van de selecties kon zeer goed worden verklaard met de fotothermale omstandigheden in de gebieden van herkomst. Validatie van de fotothermale modellen met de resultaten van kas- en veld-proeven gaf wisselende resultaten: de voorspelde en gevonden tijden van zaai tot bloei van 'DipC94' kwamen goed overeen, en de voorspelde en gevonden tijden van bloei tot peulvorming redelijk goed. De voorspellingen met betrekking tot de bloei van 'DodR94' waren niet nauwkeurig, mogelijk doordat deze selectie fotoperiode-gevoelig is als de temperatuur hoger is dan in de proef waarop de modellen werden gebaseerd.

Het gebruik van fotothermale ontwikkelingsmodellen

Een simulatiestudie voor Botswana (Hoofdstuk 7) toont de implicaties van genotypische verschillen in de fotoperiode- en temperatuurs-reactie van bambara aardnoot en de bruikbaarheid van fotothermale ontwikkelingsmodellen om geschikte selecties te identificeren voor verschillende locaties en zaaidata. De tijd tot bloei en peulvorming van de selecties 'DipC94', 'GabC92' en 'Tiga Nicuru' werd berekend voor verschillende zaaidata op twee locaties (Sebele en Francistown) in twee regenseizoenen. De berekeningen werden gemaakt met fotothermale ontwikkelingsmodellen uit Hoofdstuk 2 en 6 en met werkelijke dagelijkse minimum en maximum temperaturen en fotoperioden (met of zonder schemering). De resultaten van de simulatie wijzen erop dat voor vroege zaaidata 'GabC92' en 'Tiga Nicuru' gebruikt kunnen worden om de tijd tot het begin van de peulvorming te verlengen en zodoende de vegetatieve groei te vergroten. Voor latere zaaidata is het risico van watertekort in de peulvormingsfase voor deze selecties groter dan voor 'DipC94'. Bij erg late zaai worden de verschillen tussen de drie selecties zeer klein, maar in dit geval zal de peulopbrengst laag zijn vanwege watertekort. De verschillen tussen de twee locaties zijn klein, hetgeen betekent dat de verschillen in fotoperiode binnen Botswana waarschijnlijk niet groot genoeg zijn selecties met een verschillende fotoperiode-gevoeligheid te gebruiken op verschillende locaties. Langere fotoperioden in het begin van het regenseizoen leidden tot een langere voorspelde tijd tot peulvorming, maar niet in die mate dat de peulvorming altijd omstreeks dezelfde datum plaats zou vinden, onafhankelijk van de zaaidatum. Indien aangenomen werd dat schemering niet meegeteld moest worden bij het berekenen van de daglengte, werd de gesimuleerde tijd tot peulvorming korter, met name voor 'Tiga Nicuru'. Daarom zal bepaling van de gevoeligheid van bambara aardnoot voor schemerlicht de bruikbaarheid van de fotothermale modellen vergroten.

Discussie en conclusie

In Hoofdstuk 8 worden de belangrijkste bevindingen, methodologische kwesties en agronomische implicaties van het onderzoek besproken. Tevens wordt er aandacht besteed aan de fysiologische mechanismen die ten grondslag liggen aan de fotothermale regulering van reproductieve ontwikkeling. Er wordt geconcludeerd dat de invloed van fotoperiode en temperatuur op de ontwikkelingssnelheid van zaai tot bloei en de ontwikkelingssnelheid van bloei tot peulvorming in bambara aardnoot selecties gekwantificeerd kan worden met behulp van beschrijvende lineaire modellen. Deze modellen kunnen gebaseerd worden op proeven onder semi-gecontroleerde omstandigheden met constante temperaturen en fotoperioden. Hoewel voorspellingen in validatie-experimenten, met name voor wat betreft de tijd van bloei tot peulvorming, niet altijd accuraat waren, karakteriseerden de modellen de fotothermale respons van de verschillende selecties redelijk goed. Er kan daarom worden geconcludeerd dat dergelijke kwantitatieve modellen, hetzij op zichzelf staand, hetzij als onderdeel van een gewasgroeimodel, een nuttig instrument kunnen zijn om geschikte bambara aardnoot genotypen te identificeren voor specifieke locaties.

CURRICULUM VITAE

Martin Brink was born on 2 October 1962 in Haarlem, The Netherlands. In 1980, he completed his secondary education (V.W.O.) at the Willem de Zwijger College in Bussum and in the same year he entered Wageningen Agricultural University to study Tropical Crop Science. From December 1984 to June 1985 he spent his practical training period in Sri Lanka and from January 1987 to January 1988 he was in Costa Rica, doing fieldwork on maize cropping systems for his MSc. He graduated in May 1988, with specializations in Tropical Crop Science, Development Economics, Tropical Animal Husbandry and Extension Education. From August 1988 to January 1992 he worked for the Netherlands Development Organization (SNV) at the Sahelian Centre of the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) in Niger, where he participated in on-farm research on cropping systems and agroforestry. After his return to The Netherlands, he worked at the former Department of Tropical Crop Science and the Department of Agronomy of Wageningen Agricultural University on the analysis of Costa Rican maize experiments. From May 1993 to May 1996 he was employed by the Department of Agronomy to participate in the international research programme *Evaluating the potential for bambara groundnut as a food crop in semi-arid Africa*, sponsored by the European Union. It was during this period that he conducted the research presented in this thesis. From September 1996 to June 1997 he worked part-time as an information specialist for the Wageningen Agricultural University Library. Since November 1996 he has been employed part-time by the Plant Resources of South-East Asia (PROSEA) Foundation to assist in the writing and editing of *Medicinal and poisonous plants*, volume 12 of the PROSEA handbook series.