

Quantifying the effects of temperature and photoperiod on phenological development to flowering in rice

Promotoren: dr. M.J. Kropff
hoogleraar in de onkruidkunde

dr. ir. J. Goudriaan
persoonlijk hoogleraar bij de vakgroep Theoretische Produktie-ecologie

PN08701, 2083

**Quantifying the effects of temperature and photoperiod
on phenological development to flowering in rice**

Xinyou Yin

Proefschrift
ter verkrijging van de graad van doctor
in de landbouw- en milieuwetenschappen
op gezag van de rector magnificus
dr. C.M. Karssen
in het openbaar te verdedigen
op woensdag 22 mei 1996
des namiddags te half twee in de Aula
van de Landbouwuniversiteit te Wageningen

Isn 925703

CIP-DATA KONINKLIJKE BIBLIOTHEEK, DEN HAAG

Yin, Xinyou

Quantifying the effects of temperature and photoperiod
on phenological development to flowering in rice /

Xinyou Yin. - [S.l. : s.n.]

Thesis Landbouwwuniversiteit Wageningen. - With ref.

- With summary in Dutch.

ISBN 90-5485-515-0

Subject headings: rice ; flowering / temperature /
photoperiod.

Printing: Grafisch Service Centrum Van Gils B.V., Wageningen

Propositions

1. The linear thermal time approach is invalid for predicting crop development over a wide range of environments; despite its simplicity, modellers should avoid to use it for quantifying crop phenology in a simulation model.

This thesis

2. While the night period is crucial for photoinduction, the light period may also play an important role in the photoperiodism of plants.

This thesis

3. The often reported conclusion that the night temperature is more important than the day temperature for crop development is the result of the difference in the temperature level between day and night.

This thesis

4. Developmental processes occurring simultaneously during plant growth can have different sensitivities to environmental factors.

This thesis

5. Phenological responses of plants to photoperiod are closely related to circadian phytochrome rhythms. All higher plants seem to have evolved with photoperiod sensitivity. However, the often reported varietal photoperiod insensitivity does not imply a lack of intrinsic circadian rhythms but simply that the genetic control of the phenological process is not responsive to daylength.

Major, D.J. and Kiniry, J.R., 1991. In: T. Hodges (ed.) Predicting crop phenology. CRC press, pp. 15-28.

6. Production economics tells us that the amount of resource application for the maximum use efficiency is lower than the amount that maximizes a yield of products. This theory also applies to crop phenology in that the temperature, at which the thermal time required for a crop to complete a phenophase is minimal, is lower than the temperature that maximizes crop development rate.

Yin, X., 1994. Acta Agronomica Sinica 20: 692-700.

7. With an improved, lodging-resistant rice variety, there is no optimum leaf area index (LAI) for dry matter production, but a critical LAI does exist in tropical environments. Beyond this critical value, grain yield does not benefit by a further increase in LAI.

Yoshida, S., 1981. Fundamentals of rice crop science. IRRI, 269 pp.

8. Many important traits in plants, such as yield and time to maturity, are quantitative in feature and are controlled by interactive multiple genes. Simulation models are powerful in that they can partition a quantitative trait into several genotypic parameters which correspond to individual characters that might be under separate genetic control.
9. Because plants are both complex in structure and plastic in behaviour, purely experimental approaches are generally limited to the generation of specific solutions and qualitative extrapolation; on the other hand, attempts at purely mathematical statements are similarly defected - the limitations of analytical mathematics force us very quickly towards only approximate representations of reality. Combining experimental work with modelling approach provides a way that can be used for integrative studies.

Loomis, R.S., Luo, Y. and Kooman, P.L., 1990. In: R. Rabbinge et al. (eds) Theoretical production ecology: reflections and prospects. Pudoc, pp. 105-124.

10. The additive law holds for material flows, but not for information flows.
11. Dynamic behaviour differs between closed and open systems in the course of time: the closed system tends to have a higher and higher entropy value as a consequence of degeneration; on the contrary, the open system tends to decrease its entropy value as a result of evolution.
12. Knowledge is the only instrument of production that is not subject to diminishing returns.
Clark, J.M., 1927. Journal of Political Economy, October.

Propositions accompanying the Ph.D. thesis 'Quantifying the effects of temperature and photoperiod on phenological development to flowering in rice', by Xinyou Yin, May 22, 1996.

水稻开花前期发育光温反应的定量研究

殷新佑

BIBLIOTHEEK
LANDBOUWUNIVERSITEIT
WAGENINGEN

Dedicated to my family

Abstract

Quantifying the effects of temperature and photoperiod on phenological development to flowering in rice

Accurate prediction of crop phenology is important not only for modelling purposes but also for crop improvement and management actions. The objective of this study was to develop a model for predicting phenological development to flowering in rice (*Oryza sativa* L.).

Data from the literature were analysed to evaluate a basic equation for crop development. The Beta function, commonly used as a skewed probability density function in statistics, was found to accurately describe responses of rice development rate to both temperature and photoperiod. Controlled-environment experiments were then conducted for detailed understanding of the physiological basis of photothermal responses of preflowering development in rice. Effects of day and night temperature on development to flowering were found to be different. The plants did not respond to photoperiod throughout the entire preflowering period; instead, the photoperiod-sensitive phase was sandwiched by two photoperiod-insensitive phases. It appeared that responses to both day and night temperature were stronger during the photoperiod-sensitive phase than during the two photoperiod-insensitive phases. The results also indicated that leaf appearance occurring simultaneously during the preflowering development had a different thermal response from that of the development *per se*.

Based on the experimental results, a detailed model for photothermal responses of flowering in rice was developed, using the Beta function. The model, referred to as the three-stage Beta (3s-Beta) model, describes different photothermal responses during the photoperiod-sensitive phase and the photoperiod-insensitive phases of preflowering ontogeny. Using parameter values derived from controlled-environment experiments, the 3s-Beta model adequately predicted rice flowering dates observed in field conditions. It performed better than several existing models over a wide range of environments.

In order to assist new plant type design, the 3s-Beta model was applied to determine optimal preflowering phenological traits of rice for an increased yield potential in three different irrigated environments in Asia.

The results of this thesis were discussed in view of the experimental findings, the methodology of phenology modelling and model applications.

Keywords: rice (*Oryza sativa* L.), phenology, flowering, modelling, temperature, photoperiod, thermoperiodism, developmental rate, yield potential.

水稻开花前期发育光温反应的定量研究

提要

准确预测作物发育进程,不仅对作物生长模拟而且对作物育种和栽培管理,均有十分重要意义。本研究之目的在于建立一个能准确预测水稻开花前期(即播种—开花)发育进程的定量模型。

首先,本研究基于文献资料,建立了作物发育的基本定量关系。结果表明:统计学中常用于描述非正态型概率密度函数的Beta模型,最准确地描述了水稻发育速度对温度和光周期(日长)的反应。

其次,本研究进行了气候箱和温室等控制环境试验,以阐明水稻花前期阶段发育的光温反应生理。就温度效应而言,水稻表现出明显的温周期现象:即对昼温和夜温有不同的反应。就光周期效应而言,稻株并不在整个花前期对光周期均敏感:光周期敏感期处于中间阶段,其前期和后期均为光钝感时期。稻株在光周期敏感期对昼温和夜温的反应,均比在两个光钝感期更强。试验也表明:与花前期阶段发育同时进行的出叶过程对温度的反应函数,不同于花前期阶段发育本身的温度反应函数。

基于以上试验结果,本研究建立了水稻花前期阶段发育光温反应的详细模型。由于以Beta模型作为基本方程描述花前期三个发育阶段的光温反应,该模型被称为三阶段Beta模型(3s-Beta)。利用控制环境试验获得的参数,该模型能较好地预测大田条件下水稻发育过程。它比现有的几个水稻发育模型更准确地预测不同田间条件下观察到的水稻开花日。

为协助设计新株型品种,本研究还利用3s-Beta模型确定了亚洲不同环境条件下水稻高产所需的花前期发育最适性状指标。

最后,就试验研究新发现,作物发育模拟方法,以及模型应用等方面作了讨论。

关键词: 水稻, 发育, 花前期, 模拟, 温度, 光周期(日长), 温周期现象, 产量潜力。

Acknowledgements

The work reported in this thesis was funded partly by The Netherlands' Ministry for Development Cooperation (DGIS) and partly by The US Environmental Protection Agency (EPA) under cooperative agreements with The International Rice Research Institute (IRRI). Research activities started during my first visit to IRRI (from September 1991 to March 1992) under the support of DGIS-funded project 'Simulation and Systems Analysis for Rice Production (SARP)', a collaboration between DLO-Research Institute for Agrobiological Sciences and Soil Fertility (AB-DLO), Department of Theoretical Production Ecology of the Wageningen Agricultural University (TPE-WAU) and IRRI. The work was continued during my second visit to IRRI (from December 1992 to December 1994) which was co-sponsored by the SARP project and an EPA-funded project 'Modelling the Impact of Climate Change on Rice Production in Asia'. The work was finalized during my stay in Wageningen (from January 1995 to February 1996) as a SARP-funded research fellow. I gratefully acknowledge the supports given by AB-DLO, TPE-WAU and IRRI through the two projects. I also thank my home institute Jiangxi Agricultural University for granting me the permission for an overseas study leave.

My two promotors Prof. Martin J. Kropff and Prof. Jan Goudriaan gave valuable advice on the work. Their interest in my research has been a constant source of inspiration. I am specifically grateful to Prof. Kropff for providing a solid basis in setting the whole framework of this thesis and for his day-to-day support and guidance. His systems approach to research has been extremely important for the progression and completion of this work. I also thank him for his critical comments on the manuscripts for all chapters of the thesis. I will not forget the hospitality I received from him and his wife Nynke.

Though thousands of kilometres separate Wageningen from IRRI, Prof. Goudriaan gave a lot of support and advice to the research when it was on-going at IRRI. His stimulating ideas were very useful for setting the experimentation plan. Also helpful were his comments on the manuscripts of the thesis. His critical attitude and alertness enabled me to gain more knowledge from the work throughout the program.

Many other people contributed to this thesis directly or indirectly. Dr. Hein ten Berge, the SARP project leader in Wageningen, gave very strong support. I thank Prof. F.W.T. Penning de Vries and Hein for providing excellent working facilities during my stay in Wageningen. Parts of this thesis received very valuable comments and suggestions from Prof. Rudy Rabbinge.

I acknowledge Profs R.J. Summerfield and E.H. Roberts (The University of Reading, UK) for providing published data, which helped to precipitate the ideas upon which parts of the research were formulated. I am grateful to Prof. R. H. Ellis (The University of Reading), Prof. T. Horie and Dr. H. Nakagawa (Kyoto University, Japan), Dr. C.G. McLaren (IRRI), Dr. P.K. Aggarwal (Indian Agricultural Research Institute), Dr. S. Peng (IRRI), Miss H.G.S. Centeno (IRRI), Mr. R.M. Visperas (IRRI), Mr. M.A. Ynalvez (IRRI) and Mr. D. Zhu (China National Rice Research Institute) for their contributions and co-authorship to one or more articles in this thesis. I thank Dr. M.J.W. Jansen (GLW-DLO) and J.C.M. Withagen (AB-DLO) for their

advice on the statistics used in Chapters 3 and 4, and Dr. Bas Bouman (AB-DLO) for giving the RIGAUS program used in Chapter 11.

I also thank Drs R. Booi (AB-DLO), A.J. Haverkort (AB-DLO), H. Jalink (CPRO-DLO), R.B. Matthews (Crandfield University, UK), M. van Oijen (TPE-WAU), S. Peng, T.L. Setter (IRRI) and L.J. Wade (IRRI) and all members of PE discussion group (I), from whom I received many comments for parts of this thesis. Dr. Jalink's keen awareness of the dimension issue in the Beta model used in this thesis is especially acknowledged. I thank Prem Bindraban (TPE-WAU) and Dr. E.C. Alocilja (Michigan State University, USA) for the discussions during early days of development. I express my gratitude to journal editors, Dr. R. Leuning (*Agricultural and Forest Meteorology*), Dr. D.W. Lawlor (*Annals of Botany*), Dr. V.S. Berg (*Crop Science*) and Prof. D.J. Connor (*Field Crops Research*) for their constructive suggestions on the manuscripts. The critical comments I received from referees were very important for improving the manuscripts. Unfortunately, I don't know most of their names, except Prof. D.J. Connor and Dr. R. Delecolle who openly refereed the *Annals of Botany* papers.

I am grateful to Mr. E. Manimtim and Mr. C. Diamante for their technical assistance and all IRRI phytotron staff for engineering assistance in conducting the experiments. I thank Mrs Say Calubiran-Badrina for improving most of the complicated figures in this thesis.

In the final stage of 'writing up', Gon van Laar spent a lot of time in checking several versions of the manuscripts. I am very much indebted to Gon for her help in setting the final layout of the thesis. I wish to thank Henriette Drenth, Lettie Berben and Alexandra Nagel who did a great job in the logistics or secretarial work. Helps from other friends in Wageningen are also acknowledged.

The Crop Simulation Modelling-Climate Unit (CSM-CU) at IRRI is an excellent group not only in doing scientific research but also in creating a pleasant work atmosphere. I enjoyed the time being a member in the CSM-CU office during my stay at IRRI. Rolly Torres and Jacque Dionora helped me to get familiar with computer software. Helen G. Centeno and Zeny Pascual provided the weather data used in this study. Susan Telosa helped with many administrative matters. Frank Abamu gave me another type of life outside work.

I wish to express my deep respect to my parents. They gave me full support to pursue my career abroad even when my only brother passed away just before my first visit to IRRI. My parents-in-law often wrote to me, providing another type of support.

Lastly, I like to extend my greatest love to my wife Yarong. She did everything possible for my well-being at home and took almost all responsibilities for raising our daughter Chiqi, who was born in China just after I departed China to start this research program. Without the morale I often received from them, at least I would have spent much longer time to complete this thesis. I highly adore her understanding of the fact that she and Chiqi were neglected during the last three years.

Account

Parts of this thesis have been included, in part or in whole, in the following publications:

- Chapter 2 Yin, X., Kropff, M.J., McLaren, G. and Visperas, R.M., 1995. A nonlinear model for crop development as a function of temperature. *Agricultural and Forest Meteorology* 77: 1-16.
- Chapter 3 Yin, X., Kropff, M.J. and Ellis, R.H., 1996. Rice flowering in response to diurnal temperature amplitude. *Field Crops Research*: in press.
- Chapter 4 Yin, X., Kropff, M.J. and Goudriaan, J., 1996. Differential effects of day and night temperature on development to flowering in rice. *Annals of Botany* 77: 203-213.
- Chapter 5 Yin, X. and Kropff, M.J., 1996. Use of the Beta function to quantify nonlinear effects of photoperiod on flowering and leaf number in rice. *Agricultural and Forest Meteorology*: in press.
- Chapter 6 Yin, X., Kropff, M.J. and Ynalvez, M.A., 1996. Photoperiodically sensitive and insensitive phases of preflowering development in rice. *Crop Science*: in press.
- Chapter 7 Yin, X., Kropff, M.J. and Goudriaan, J., 1996. Changes in developmental responses to temperature during preflowering ontogeny of rice. *Crop Science*: in press.
- Chapter 8 Yin, X. and Kropff, M.J., 1996. The effect of temperature on leaf appearance in rice. *Annals of Botany* 77: 215-221.
- Chapter 9 Yin, X., Kropff, M.J., Horie, T., Nakagawa, H., Centeno, H.G.S., Zhu, D. and Goudriaan, J., 1996. A model for photothermal responses of flowering in rice. I. Model description and parameterization. *Field Crops Research*: submitted.
- Chapter 10 Yin, X., Kropff, M.J., Horie, T., Nakagawa, H. and Goudriaan, J., 1996. A model for photothermal responses of flowering in rice. II. Model evaluation. *Field Crops Research*: submitted.
- Chapter 11 Yin, X., Kropff, M.J., Aggarwal, P.K., Peng, S. and Horie, T., 1996. Optimal preflowering phenology of rice for high yield potential in Asian irrigated environments. *Field Crops Research*: accepted.

Contents

Chapter 1	General introduction	1
Chapter 2	A nonlinear model for crop development as a function of temperature	7
Chapter 3	Rice flowering in response to diurnal temperature amplitude	21
Chapter 4	Differential effects of day and night temperature on development to flowering in rice	33
Chapter 5	Use of the Beta function to quantify the effect of photoperiod on flowering in rice	49
Chapter 6	Photoperiodically sensitive and insensitive phases of preflowering development in rice	57
Chapter 7	Changes in developmental responses to temperature during preflowering ontogeny of rice	73
Chapter 8	The effect of temperature on leaf appearance in rice	87
Chapter 9	A model for photothermal responses of flowering in rice I. Model description and parameterization	99
Chapter 10	A model for photothermal responses of flowering in rice II. Model evaluation	115
Chapter 11	Optimal preflowering phenology of rice for high yield potential in Asian irrigated environments	131
Chapter 12	General discussion	143
Summary		151
Samenvatting		155
References		159
Curriculum vitae		173

Abbreviations

3s-Beta	Three-stage Beta model
BLM	Bilinear model
BVP	Basic vegetative phase
DAS	Days after sowing
DR	Developmental rate
DS	Developmental stage
f	Days from sowing to flowering
f_o	Minimum value for f
GDD	Growing degree days procedure
HT	High temperature
LAI	Leaf area index
LAR	Leaf appearance rate
LD	Long day
LN _m	Leaf number on the main stem
LT	Low temperature
MD	Mean absolute predictive discrepancy
m-RCM	Modified rice clock model
PFP	Preflowering period
PI	Panicle initiation
P_o	Optimum photoperiod
PPP	Post-PSP phase
PSP	Photoperiod-sensitive phase
PTU	Photothermal unit
QFP	Quadratic relation between f and photoperiod
QRP	Quadratic relation between the rate, $1/f$, and photoperiod
RCM	Rice clock model
SD	Short day
SE	Standard error
T_b	Base temperature
T_c	Ceiling temperature
T_D	Day temperature
T_N	Night temperature
T_o	Optimum temperature
T_{oD}	Optimum day temperature
T_{oN}	Optimum night temperature
TU	Thermal unit

Chapter 1

General introduction

The yield formation of a crop involves a series of processes of growth and development. Growth refers to accumulation of biomass in the plant as a whole or in certain organs, whereas development refers to the life cycle of the plant related to initiation and occurrence of organs (Hodges, 1991a; Ritchie, 1993). The commonly used term 'phenology' refers to the progress of plants through identifiable stages of development (Summerfield et al., 1991). Both growth and phenological development are affected by environmental and genetic factors.

The biomass yield of a crop can be simply calculated as the product of the rate of biomass accumulation and the duration of development. Genetic variation among cultivars of a crop is usually most evident in the duration of development and least evident in the rate of growth (Ritchie, 1993). Therefore, adaptation of a crop to a particular environment is primarily determined by responses of crop development to environmental factors (Roberts et al., 1993).

Crop growth simulation models are increasingly being used to support field research and extension in agriculture (Penning de Vries et al., 1989). A simulation model for crop potential production (i.e. with ample water and nutrient supply and without pest, diseases and weeds) usually includes several components dealing with dry matter production, leaf area growth and phenological development, respectively. In many crop models, e.g. SUCROS (Goudriaan and van Laar, 1994), phenology provides a temporal framework for modelling assimilate partitioning into various growing organs, which, in turn, largely determines the accuracy of predicting crop productivity. Without precise prediction of the phenology, the crop simulation model will simulate growth processes at different times and under different conditions than they actually do. Modelling crop phenology is as critical as modelling the crop growth rate to predict crop productivity.

The ability to predict crop development is also important for management decisions related to such things as timing of pesticide application, scheduling of orderly crop harvest, selecting planting dates to avoid severe climatic stress at critical stages, or synchronizing flowering of cross-pollinated crops for hybrid seed production (Ritchie, 1993; Shaykewich, 1995). Despite these apparent needs, the accurate prediction of crop phenology under diverse environmental conditions remains a problem for modellers (Tollenaar, 1990; Shaykewich, 1995).

An overview of previous studies on modelling crop phenology

The time from sowing to flowering is a principal determinant of relative maturity of adaptiveness to the cropping environments (Summerfield et al., 1991). Thus the recording of days from sowing to flowering has predominated in studying phenology. Although crop development to flowering can be influenced to some extent by factors such as energy supply,

humidity, nutrients and water stress, it is principally controlled by temperature and photoperiod (Ritchie, 1993; Horie, 1994; Shaykewich, 1995). A short photoperiod accelerates flowering in short-day plants, but delays flowering in long-day plants. A high temperature generally promotes flowering and a low temperature delays flowering. However, many winter crops need a low temperature for vernalization during early growth periods (Goudriaan and van Laar, 1994; Horie, 1994).

Researches have been quantifying plant development in response to temperature for more than 200 years (Yoshida, 1981). It is widely accepted that Reaumur (1735) is the one who introduced a thermal unit (TU) concept for predicting plant development. This concept assumes that plants need a fixed number of temperature sum to fulfil a developmental phase. This assumption implies that the crop development rate (DR), expressed as the inverse of the duration in days for a given phase, is a linear function of temperature (Ellis et al., 1990). Since then, numerous attempts have been made to improve the TU method. Several studies have compared these different TU methods for predicting the time to flowering in various crops (e.g. Gilmore and Rogers, 1958; Cross and Zuber, 1972; Major et al., 1975a; Coelho and Dale, 1980; Kiniry and Keener, 1982; Bonhomme et al., 1994). The TU approaches are fairly reliable for a given cultivar. However, prediction with these TU methods was often more accurate for early than for late cultivars (Major et al., 1975a), suggesting that other factors such as photoperiod also affected flowering.

Since Garner and Allard (1920) reported the influence of photoperiod on plant growth and development, much attention has also been paid to the effect of photoperiod on crop phenology. Nuttonson (1948) found that the number of photothermal units (PTU), the multiple of thermal units by the average daylength over the period of observation, was more constant from station to station than the number of TU alone. The PTU concept implies a linear relationship between DR and photoperiod, and assumes an interaction between temperature and photoperiod, in agreement with the early work of Roberts and Struckmeyer (1938) on this interaction in many plant species.

Although both TU and PTU methods are attractive because of their simplicity, they are empirical and have no physiological basis. Moreover, the relationship between DR and temperature or photoperiod is nonlinear over a wide range of conditions (Ferguson, 1958; Horie, 1994; Loomis and Connor, 1992), in contrast with the assumption of linearity in both TU and PTU methods. Kiniry and Keener (1982) introduced an equation, which has a theoretical basis (based on the enzyme kinetic response) and accounts for a nonlinear response to temperature, to estimate DR of field-grown maize (*Zea mays* L.). However, this detailed physiological equation was not better than the traditional TU methods in terms of predictive ability. This was presumably due to the fact that the error involved in estimation of a large number of parameters of the equation exceeded the information gained from the underlying theory. More generally applicable models may be those intermediate equations which are rationally modelled on the basis of physiology of crop development (Horie, 1994).

Robertson (1968) was one of the first to develop such an intermediate model relating DR to temperature and photoperiod. He used a quadratic equation to describe nonlinear effects of both temperature and photoperiod on the DR of wheat (*Triticum aestivum* L.), which were multiplied together. The multiplicative model, implying existence of an interaction between

temperature and photoperiod, allows for situations without progression in development when either temperature or photoperiod is below its threshold. The multiplicative formulation was further used in many subsequent photothermal models for different crops (e.g. Major et al., 1975b; Angus et al., 1981; Hammer et al., 1989; Horie and Nakagawa, 1990; Gao et al., 1992; Grimm et al., 1993; Hiden and Larsen, 1994). Among these nonlinear multiplicative models, the model of Robertson (1968) is unique in that it considers responses to day and night temperature separately on the basis of results of Went (1944a,b; 1950 and 1956) who reported that some plants have a different response to night temperature than to day temperature. Coligado and Brown (1975b) also included a diurnal temperature range as a separate variable in their model for maize development; however, they assumed that the nonlinear effects of temperature and photoperiod on DR were additive, rather than multiplicative.

Roberts and Summerfield (1987) and Summerfield et al. (1991) presented a different philosophy on modelling the effects of temperature and photoperiod on DR. They emphasized that over a wide range of conditions, it is the mean daily temperature which controls crop development to flowering, rather than any specific effect of either day or night temperature. They indicated that once the data on days to flowering were transformed into the rate of development, the inverse of the number of days to flowering, the effects of temperature and photoperiod on development became linear and noninteractive over the range of temperatures between base and optimum values. They suggested a linear additive model to describe photothermal responses of flowering, in contrast with many other models. This additive model was subsequently shown to be useful for predicting flowering times in various annual crops (e.g. Summerfield et al., 1992, 1993; Ellis et al., 1994).

Despite the large difference in model structure, most of the models described the observations fairly well (Horie, 1994). For example, Sinclair et al. (1991) indicated that both the linear additive model and the logistic multiplicative models were able to predict accurately soybean [*Glycine max* (L.) Merr.] flowering dates observed in a single location. However, predictability of most models was often very weak when they were extrapolated beyond the environmental range from which their parameters were derived (Horie, 1994). One reason for this is that most existing models ignore the significant changes in developmental responses to environments during crop ontogeny. For example, annual crops usually only respond to photoperiod during a limited period between sowing and flowering (Roberts and Summerfield, 1987), whereas most models assume that photoperiod sensitivity does not change during the entire preflowering development.

Objectives and approach

The principal objective of this study was to develop an improved photothermal model that can be used to reliably predict rice (*Oryza sativa* L.) crop development under a wide range of environmental conditions. For this purpose, existing literature data were first analysed to evaluate basic equations that were introduced to describe responses of DR to temperature and photoperiod. Secondly, controlled-environment experiments were conducted to obtain physiological understanding of developmental responses to temperature and photoperiod in

rice. Experiments for the effects of temperature focused on whether there are differential effects of day and night temperature on DR and whether there is any variation in the sensitivity of response to temperature during preflowering development. Experiments for responses to photoperiod were conducted to estimate durations of photoperiodically sensitive and insensitive phases of development to flowering. The results of these experiments resulted in a detailed model which not only combines merits of many existing models but also accounts for which environmental factors most strongly modulate development at any point in time.

A large number of rice genotypes were tested in controlled-environment experiments to investigate genotypic variation in their photothermal responses. At the same time, most of these genotypes were also tested in a multilocational field experiment. The field observations were used to examine whether the model parameters derived from controlled environments can be extrapolated to predict crop performance in field conditions. The data from a wide range of photothermal environments were collected to evaluate the predictive superiority of the new model to typical existing models. Finally, the new model was used to determine optimal preflowering phenology for an increased yield potential of rice cultivars in different irrigated environments.

Outline of the thesis

The structure of this thesis is illustrated in Fig. 1.1.

A basic equation to describe the effect of a diurnally constant temperature on DR is introduced in Chapter 2. This equation is used in Chapter 3 to predict DR at diurnally fluctuating temperatures, to investigate whether there is any effect of diurnal temperature fluctuation on DR in rice. Based on the results in Chapter 3, a phytotron experiment was designed to analyse differential effects of day and night temperature on DR (Chapter 4).

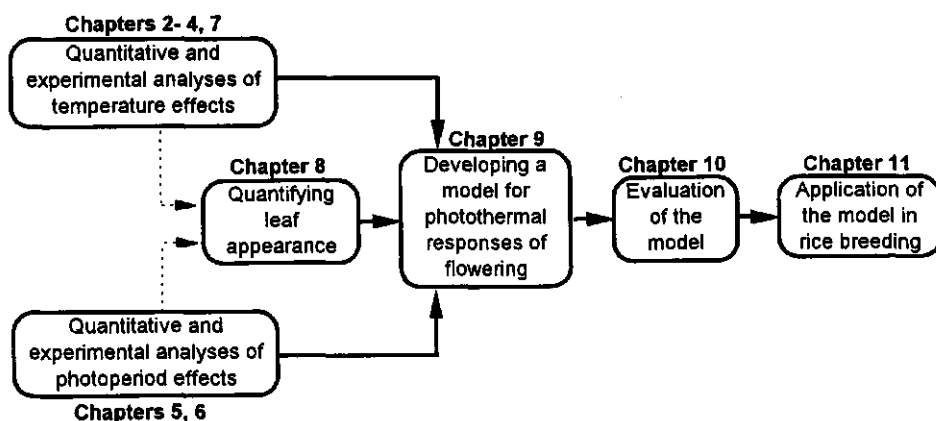


Fig. 1.1. Outline of the thesis.

In Chapter 5, the equation introduced in Chapter 2 for the effect of temperature was evaluated to describe the effect of photoperiod on development to flowering in rice. To estimate durations of photoperiodically sensitive and insensitive phases of preflowering period, an experiment of transferring plants at various times between two photoperiods was conducted for various rice cultivars (Chapter 6). The results of a similar experiment of transfers but between two temperatures are presented in Chapter 7 to examine the variation in sensitivity to temperature during preflowering ontogeny. Chapters 6 and 7 indicate that the critical times for changes in response to temperature and photoperiod are associated with the leaf number on the main stem. This results in inclusion of Chapter 8 in which a model for describing the main-stem leaf appearance is presented.

Based on the results of Chapters 2–8, a detailed photothermal model for predicting rice flowering dates was developed (Chapter 9). This new model was compared with several existing phenological models in the performance over a wide range of photothermal environments (Chapter 10). In Chapter 11, the model was coupled to ORYZA1, an ecophysiological model for irrigated rice production (Kropff et al., 1994b), to determine optimal preflowering phenology for an increased yield potential in strongly different Asian irrigated environments.

Chapter 2

A nonlinear model for crop development as a function of temperature

Abstract The Beta function, commonly used as a skewed probability density function in statistics, was introduced to describe the effect of temperature on the rate of crop development. The framework is set by three cardinal temperatures, namely the base (T_b), the optimum (T_o) and the ceiling (T_c) temperature. The model parameters T_b and T_c and three other coefficients μ , α and β can be used to derive the value of T_o and the maximum development rate. Parameter α also characterizes the curvature of the relationship with temperatures between T_b and T_o , and parameter β describes the curvature between T_o and T_c . The model has one parameter less than the Rice Clock Model (RCM); and in contrast to the RCM, it ensures that the maximum development rate occurs exactly at T_o . The model accurately described the response to temperature of several developmental processes, and was superior to two widely used thermal time approaches in predicting rice flowering time.

Introduction

Crop development is primarily affected by temperature and can be modified by other factors such as photoperiod (Hodges, 1991b). Within a range of temperatures below a certain value, crop development rate (DR) often increases proportionally with the temperature (Roberts and Summerfield, 1987). With the global warming due to the greenhouse effect, the response of DR to high temperatures has also posed particular concern to modellers for predicting crop development (Matthews et al., 1995).

The effect of temperature on DR is often described by using a thermal time concept. One widely used thermal time method (Tollenaar et al., 1979) is the Growing Degree Days (GDD) procedure, which relates DR linearly to temperatures above a crop- or cultivar-specific base temperature (T_b), at or below which DR is zero. In some applications of the GDD procedure, an upper limit of temperature is assumed above which DR remains constant (Hodges, 1991b).

Although the GDD system is attractive because of its simplicity and its higher accuracy in predicting phenological events than number of days *per se* (Kiniry and Keener, 1982), it has been subjected to much criticism over the years. The classical work of Lehenbauer (1914) on the elongation of maize (*Zea mays* L.) seedlings in relation to temperature showed a rapid decline of the elongation rate when the optimum temperature, T_o , was exceeded. The data of Lehenbauer (1914) have been used by many studies (e.g. Gilmore and Rogers, 1958; Coelho and Dale, 1980) to describe DR of crops. For example, based on these data, Gilmore and Rogers (1958) presented a bilinear model (BLM) that included a reversed linear function to

account for declining DR at temperatures higher than T_o . Roberts and Summerfield (1987) defined the maximum temperature at which the DR equals zero as a ceiling temperature (T_c). Garcia-Huidobro et al. (1982a) and Roberts and Summerfield (1987) described temperatures between T_b and T_o as sub-optimal and those between T_o and T_c as supra-optimal; and T_b , T_o and T_c were referred to as three cardinal temperatures.

Although the BLM describes Lehenbauer's (1914) data better than the GDD, it does not describe the pattern accurately. The data showed a skew bell-shaped curve: an accelerating increase of the rate at low temperatures, a linear section, an optimum, followed by a rapid fall-off beyond T_o . This response is qualitatively typical for the temperature effect on many biological processes (Ferguson, 1958; Orchard, 1975; Tyldesley, 1978; Johnson and Thornley, 1985).

Various nonlinear models have been developed to describe the temperature response of developmental processes in plants. Johnson and Thornley (1985) reviewed many nonlinear equations for biological processes based on their underlying theory. A detailed model, which is based on the response of enzymatic reactions to temperature, was found to fit Lehenbauer's (1914) data very well (Sharpe and DeMichele, 1977). However, when this model was introduced to predict maize development in the field, it did not perform better than the thermal time methods GDD and BLM (Kiniry and Keener, 1982). In addition, its large number of parameters prevented its use under field conditions (Kiniry and Keener, 1982; Hodges, 1991b). Most nonlinear approaches use descriptive equations (Robertson, 1968; Coligado and Brown, 1975b; Angus et al., 1981; Horie and Nakagawa, 1990; Gao et al., 1992). However, most descriptive equations do not account for the frequently observed decline of DR at supra-optimal temperatures (e.g. the power-law function (Coligado and Brown, 1975b), the exponential model (Angus et al., 1981) and the logistic model (Horie and Nakagawa, 1990)). A quadratic equation (e.g. Robertson, 1968) does account for this decline at supra-optimal temperatures. However, it assumes a symmetric response and does not allow for any concave curvature near T_b . These limitations were overcome in a model for rice (*Oryza sativa* L.), the Rice Clock Model (RCM) (Gao et al., 1992), which describes the response of DR to temperature as:

$$DR = \exp(k) \left(\frac{T - T_b}{T_o - T_b} \right)^\alpha \left(\frac{T_c - T}{T_c - T_o} \right)^\beta \quad (2.1)$$

where k , α and β are the model parameters, and $\exp(k)$ defines the maximum DR when $T = T_o$ (in the original RCM, T_b , T_o , α and β were respectively denoted as T_L , T_U , P and Q). However, the maximum DR does not always occur at T_o in Eq. 2.1. For example, using the parameters for an *indica* rice cultivar DTWX as derived by Gao et al. (1992), the temperature for the maximum DR based on Eq. 2.1 is 2.3°C higher than the prespecified T_o of 30°C (Fig. 2.1). To make the model have maximum DR at T_o , Gao et al. (1992) added the following restriction:

$$DR = \exp(k) \quad \text{if} \quad \left(\frac{T - T_b}{T_o - T_b} \right)^\alpha \left(\frac{T_c - T}{T_c - T_o} \right)^\beta > 1 \quad (2.2)$$

However, this restriction is artificial and can result in a nonsmooth curvilinear relationship (Fig. 2.1).

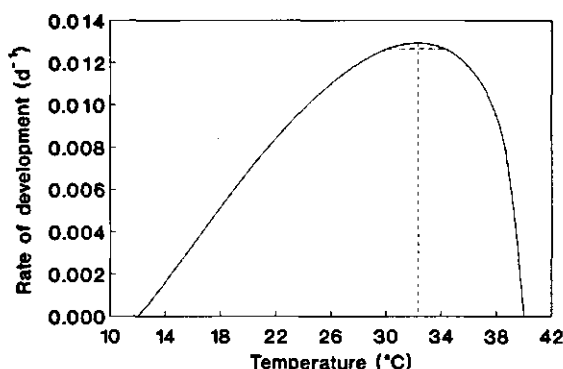


Fig. 2.1. Relation between temperature and rate of development from emergence to heading in rice cv. DTWX, based on the basic equation (Eq. 2.1) of Rice Clock Model (Gao et al., 1992). The horizontal line indicates the nonsmooth part given by Eq. 2.2. Note the discrepancy between the prespecified optimum temperature (30°C) and the temperature at which the rate calculated from Eq. 2.1 is maximal (shown by the vertical line).

In this Chapter, a nonlinear model, which is simpler than the RCM but overcomes the problem of the RCM, is introduced to describe crop development involving the three cardinal temperatures. The model was evaluated using published data sets on several developmental processes, and was compared with the RCM and the two thermal time methods GDD and BLM for predicting the time to flowering of the rice crop.

Materials and methods

The model

A well known nonsymmetric function, the Beta function (Abramowitz and Stegun, 1965), provides a model for the relationship between DR and temperature which has a form similar to that of the RCM, Eq. 2.1, but has fewer parameters and allows nonproblematic estimation of T_0 . The Beta function is commonly used to give a flexible family of nonsymmetric, unimodal probability density functions with fixed end points (Johnson and Leone, 1964) which allow points of inflexion on either side of the mode. Based on the Beta model, an equation for describing the response of the DR to temperatures between T_b and T_c can be expressed as:

$$DR = \exp(\mu)(T - T_b)^\alpha (T_c - T)^\beta \quad (2.3)$$

where μ , α and β are the model parameters.

In contrast to the RCM, Eq. 2.3 does not include T_0 and the maximum DR as its parameters; however, it can provide estimates of T_0 and the maximum DR. T_0 is the zero of the first-order derivative DR' of Eq. 2.3 which is:

$$DR' = \exp(\mu)(T - T_b)^{\alpha}(T_c - T)^{\beta} \left(\frac{\alpha}{T - T_b} - \frac{\beta}{T_c - T} \right). \quad (2.4)$$

Hence

$$T_o = \frac{\alpha T_c + \beta T_b}{\alpha + \beta} \quad (2.5)$$

Substituting T_o into Eq. 2.3 results in an estimate of R_o , the maximum DR:

$$R_o = \exp(\mu) \alpha^{\alpha} \beta^{\beta} \left(\frac{T_c - T_b}{\alpha + \beta} \right)^{\alpha + \beta} \quad (2.6)$$

Thus, the Beta model has one parameter less than the RCM; but, unlike the RCM, it can smoothly describe the nonlinear relationship between DR and temperature.

Experimental data

Three published experimental data sets for different crops were used to illustrate the ability of the Beta model to describe the shape of the response of crop development to temperature. The first data set gives the duration between sowing and emergence in two cassava (*Manihot esculenta* Crantz) cultivars MAus10 and MAus7 under a wide range of diurnally constant temperatures (Keating and Evenson, 1979). The second data set, on meristem temperature effect on the leaf development of maize (cv. 'Erliking' F1 hybrid), was published by Watts (1971). In this experiment, the temperature of the meristematic region was varied between 0 and 40°C, and the temperature of the root zone and the air around the leaves was kept at 25°C. The third data set, on the development from sowing to tassel initiation of maize, was published by Ellis et al. (1992b). In this experiment, plants of five cultivars (Tuxpeno Crema I C 18, Cravinhos 8445, B73 × Mo17, H-32, and Across 8201) were grown in growth chambers with 10 diurnally constant temperatures ranging from 12 to 37°C at a constant photoperiod of 12 h d⁻¹.

A fourth data set was used to compare the predictive capacity of the Beta model with the RCM and two widely-used thermal time methods GDD and BLM. This data set was obtained from a phytotron experiment on the effect of temperature on days from sowing to flowering in rice cultivar IR8 (IRRI, 1977). Treatments in the experiment included one diurnally constant temperature (24°C) and 11 diurnally alternating regimes with different day and night temperatures (Table 2.1). In all alternating temperature treatments, the day temperature was applied for 8 h d⁻¹ and the night temperature for 16 h d⁻¹. The four models were parameterized using an independent data set for IR8 from an experiment conducted in 1993 with five diurnally constant temperatures 22, 24, 26, 28 and 32°C at a photoperiod of 12 h d⁻¹ (see Chapter 4). Days to flowering at the common constant temperature treatment of 24°C were 98 d in the IRRI (1977) experiment and 97 d in the 1993 data set, indicating that the effective photoperiod was compatible between these two experiments.

To compare the performance of the models in predicting rice flowering, the mean absolute deviation (MD) was used to indicate the accuracy of the predictions. All models were run

Table 2.1. Treatments, observed days to flowering in the controlled-temperature experiment of IRRI (1977) on rice cv. IR8, and predicted days by each of the four models: the Growing Degree Days procedure (GDD), the bilinear model (BLM), the Rice Clock Model (RCM) and the Beta model (Beta), using the parameters (presented in Fig. 2.5) derived from an independent experiment with five diurnally constant temperatures.

Treatment No.	Temperature (°C)†			Observed (d)	Predicted (d)			
	Day	Night	Mean		GDD	BLM	RCM	Beta
a	24	24	24.0	98	100	100	99	99
b	26	23	24.0	84	100	100	99	99
c	28	22	24.0	112	100	100	102	102
d	30	21	24.0	118	106	100	108	108
e	32	20	24.0	130	112	112	117	117
f	36	18	24.0	>155	125	161	162	162
g	32	18	22.7	148	125	127	137	137
h	28	18	21.3	153	125	125	138	138
i	24	18	20.0	145	143	143	157	157
j	20	18	18.7	>155	167	167	195	195
k	24	22	22.7	106	112	112	112	112
l	24	20	21.3	129	125	125	131	131

† In the experiment of IRRI (1977), periods of day and night temperatures were 8 and 16 h d⁻¹, respectively.

with an 8-h time step to account for the difference in the duration of day and night temperatures in the data set of IRRI (1977).

Analytical Approaches

When values of T_b and T_c were given, the parameter values were determined by least squares regression after log-transforming Eq. 2.3 into its linear form:

$$\ln DR = \mu + \alpha \ln(T - T_b) + \beta \ln(T_c - T)$$

Otherwise the nonlinear optimization package PROC NLIN of the Statistical Analysis Systems Institute (SAS, 1988) was used to estimate parameter values when T_b and T_c were not given. The SAS procedure was also used to parameterize Eq. 2.1 of the RCM.

However, data from only five temperatures in the 1993 data set for rice cv. IR8 were not enough to estimate the six parameters in Eq. 2.1. Because the models were tested using data from experiments of IRRI (1977) where the temperatures were not close to the extremes of T_b and T_c , the model performance might not be sensitive to the values for T_b and T_c . To reduce the number of parameters to be estimated, values for T_b and T_c were predefined for the RCM and the Beta model based on sensitivity analysis by varying T_b and T_c within an adequate range.

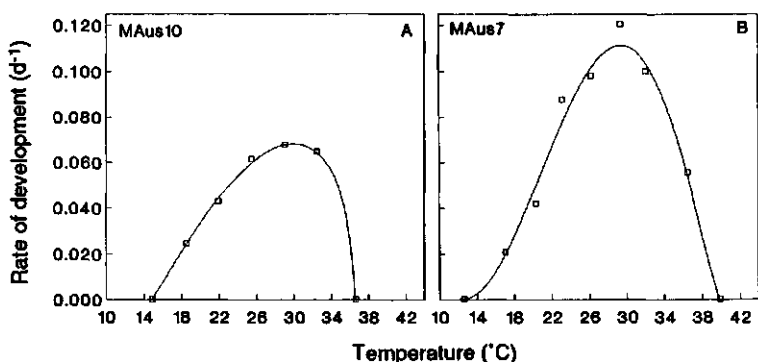


Fig. 2.2. Rate of development from sowing to emergence in two cassava cultivars as a function of temperature (data of Keating and Evenson, 1979). The curve was based on Eq. 2.3 with parameter values as in Table 2.2.

Results

Illustration of the descriptive ability of the Beta model

Keating and Evenson (1979) showed that cassava plants of MAus10 did not emerge below 14.8°C or above 36.6°C, whereas MAus7 did not emerge below 12.5°C or above 39.8°C. From these results, values of T_b and T_c for the two cultivars were determined. The other parameters of the Beta model, Eq. 2.3, were estimated by least squares regression of log-transformed data (Table 2.2). The model described the nonsymmetric response quite accurately, although DR of MAus7 around T_o was somewhat underestimated (Fig. 2.2).

In the data of Watts (1971) on meristem temperature effect on maize leaf development, no distinct value for either T_b or T_c was determined. All five parameters of the Beta model were then obtained from the nonlinear optimization package of SAS. The model adequately described the data (Table 2.2 and Fig. 2.3). The relatively low value for T_b can be explained by the fact that the temperature of air and root-zone was kept at 25°C which may have been high enough to trigger maize leaf extension even though the meristem temperature was below 0°C. However, this estimation for T_b was based on extrapolation far beyond the range of temperatures used in the experiment, resulting in a high standard error (Table 2.2). Watts (1971) fitted the data between 0 and 30°C with an exponential curve using a Q_{10} of 2.0, a factor by which the rate is increased as temperature rises 10°C. That approach does not account for the rapid decline of the rate above T_o (Fig. 2.3).

Ellis et al. (1992b) indicated that the value of T_c for maize cvs. H-32 and Across 8201 was about 37°C based on their experimental results that plants of these two cultivars grown at the constant temperature 37°C died before reaching tassel initiation whereas 37°C was not lethal to plants of other three cultivars. Based on these, the value of DR at 37°C for each of H-32 and Across 8201 was determined. The Beta model closely described the nonsymmetric temperature response for rate of development between sowing and tassel initiation in the five

Table 2.2. Values of the five parameters (with standard errors in parentheses) in the Beta model (Eq. 2.3) and the resultant estimates of the optimum temperature (T_o) and the maximum development rate (R_o).

Cultivar	Model Parameter					n^\dagger	r^2	T_o	R_o
	μ	α	β	T_b	T_c				

1. <i>Cassava</i> (sowing - emergence)§									
MAus10‡	-6.484 (0.301)	1.071 (0.066)	0.469 (0.070)	14.8	36.6	7	0.997	30.0	0.0683
MAus7‡	-11.035 (0.813)	2.077 (0.179)	1.268 (0.159)	12.5	39.8	9	0.975	29.5	0.1118
2. <i>Maize leaf extension</i> §									
Erliking	-9.683 (7.100)	2.563 (1.570)	0.132 (0.163)	-12.8 (14.8)	40.1 (0.01)	7	0.998	37.5	1.6118
3. <i>Maize</i> (sowing - tassel initiation)§									
Tuxpeno Crema I C 18	-4.876 (0.288)	0.504 (0.070)	0.207 (0.043)	11.0 (0.4)	37.1 (0.07)	10	0.994	29.5	0.0504
Cravinhos 8445	-5.743 (0.768)	0.754 (0.189)	0.308 (0.085)	9.7 (1.4)	37.2 (0.21)	10	0.990	29.2	0.0573
B73 × Mo17	-5.313 (0.598)	0.651 (0.148)	0.233 (0.070)	10.1 (1.1)	37.2 (0.16)	10	0.990	30.0	0.0546
H-32	-4.941 (0.286)	0.290 (0.058)	0.482 (0.064)	11.8 (0.2)	37.0 (0.01)	10	0.990	21.2	0.0518
Across 8201	-5.366 (0.726)	0.398 (0.160)	0.530 (0.137)	11.3 (0.9)	37.0 (0.02)	10	0.965	22.3	0.0505

† n is the number of environments fitted.

‡ T_b and T_c were determined as temperatures at which the cassava plants did not emerge.

§ Data source: 1. Keating and Evenson (1979); 2. Watts (1971); 3. Ellis et al. (1992b).

cultivars (Fig. 2.4). A clear varietal difference in the T_o was found to range from 21.2 to 30.0°C, whereas the varietal difference in either T_b or T_c was small (Table 2.2). Ellis et al. (1992b) fitted the data of each cultivar by the equation $DR = a + bT + cT^2 + dT^3$ (where a , b , c and d are constants), for the sub-optimal and supra-optimal ranges separately. They indicated the problem of determining a value for T_o by visual examination of the data, as the observed T_o often did not represent a specific value or even a narrow range (e.g. Fig. 2.4C). Eq. 2.3 can be used to explicitly estimate T_o for each cultivar.

Comparison of the Beta model with GDD, BLM, and RCM in predictive capability

Parameters of the models

From sensitivity analysis by varying T_b from 5 to 15°C and T_c from 35 to 45°C in 1°C steps, it was established that the values of T_b and T_c had little impact on goodness of fit of both the

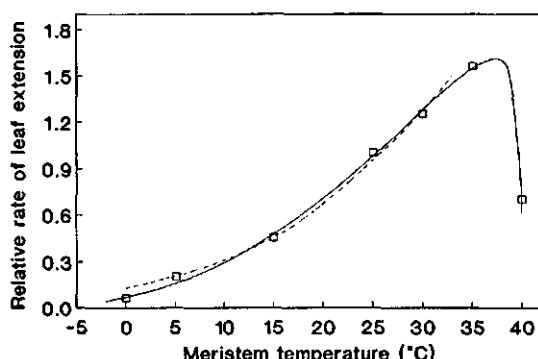


Fig. 2.3. Relative leaf extension rate in maize as affected by temperature at the meristem region (data of Watts, 1971). The solid curve was based on Eq. 2.3 with parameter values in Table 2.2, while the dashed one was drawn from the concept of Q_{10} of 2.0 used by Watts (1971).

RCM and the Beta model to the 1993 data set on development to flowering in rice cv. IR8. The r^2 value varied from 0.98 when $T_b = 5$ and $T_c = 35^\circ\text{C}$ to 0.97 when $T_b = 15$ and $T_c = 45^\circ\text{C}$ for both models. For each set of T_b and T_c values, the two models had the same r^2 value, indicating that one extra parameter in the RCM compared to the Beta model did not result in a higher descriptive ability. Since the r^2 value of both models hardly changed within a wide range of T_b and T_c , values for T_b and T_c were determined as 8 and 42°C . These values are commonly used in rice growth simulation models (Alocilja and Ritchie, 1991; Kropff et al., 1994b).

Based on visual inspection of the data, 28°C was assumed as the upper temperature (T_u) for the GDD model above which DR remains constant, and 32°C was assumed to be supra-optimal for the BLM model. Parameters for the range with the increasing DR in both GDD and BLM were then estimated by linear regression on the observations at 22, 24, 26 and 28°C . For the supra-optimal range of the BLM, parameters were estimated assuming that $T_c = 42^\circ\text{C}$.

The parameter values for the four models, including the maximum DR (R_o) estimated by each model, are given in Fig. 2.5. All models described the data accurately. The estimated R_o was highest in the BLM and lowest in the GDD model. The temperature for the maximum DR calculated from Eq. 2.1 of the RCM was 30.2°C , only 0.8°C higher than the generated value of T_o ; so the nonsmooth part of the RCM given by Eq. 2.2 is not obvious in Fig. 2.5C.

Performance of the models

Observed and predicted days to flowering are given in Table 2.1. The predicted days were exactly the same for the RCM and the Beta model. The comparisons between observed and predicted days for the four models are shown in Fig. 2.6. This figure does not include results of the regimes 36/18 and $20/18^\circ\text{C}$, at which observed days to flowering were recorded as >155 d. The nonlinear models performed better than the linear ones. The MD values were 12.3 d for the GDD, 12.7 d for the BLM and 9.4 d for the two nonlinear models (Fig. 2.6).

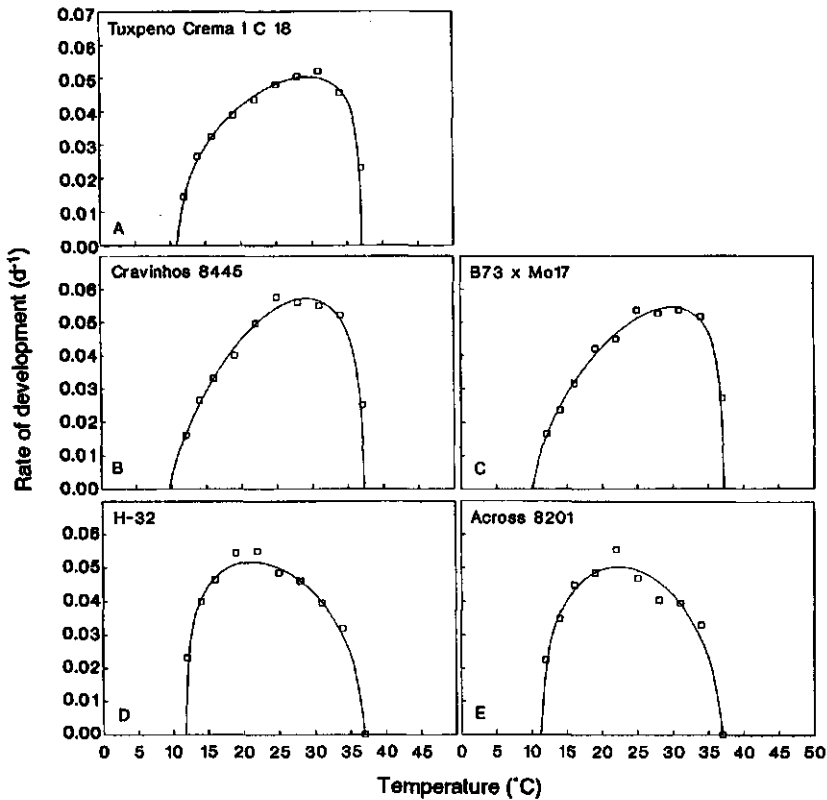


Fig. 2.4. Relations between temperature and the rate of development from sowing to tassel initiation in five maize cultivars at a photoperiod of 12 h d⁻¹ (data of Ellis et al., 1992b). The curves represent the relations of Eq. 2.3 with parameters shown in Table 2.2.

All models correctly predicted no flowering at 155 days for the regime of 20/18°C. However, the GDD model, which does not allow for the detrimental effect of high temperatures, underestimated days to flowering at 36/18°C (Table 2.1). Because the DR was assumed to be constant for $T > T_u$, the GDD also failed to predict the difference in the flowering date among 28/18, 32/18 and 36/18°C treatments. However, the MD value for the GDD was somewhat lower than that for the BLM (Fig. 2.6). This was because the BLM tended to overestimate the DR at temperatures close to T_o (Fig. 2.5), so the BLM underestimated days to flowering at 30/21°C (Table 2.1).

The superiority of the nonlinear models was particularly obvious for the 28/22, 30/21, 32/20, 32/18 and 28/18°C treatments, where the night temperature was relatively low. For these regimes, days to flowering were considerably underestimated by the linear models. This can be attributed to the fact that development rates at temperatures $< 22^\circ\text{C}$ were somewhat higher for the linear models than the nonlinear ones (Fig. 2.5).

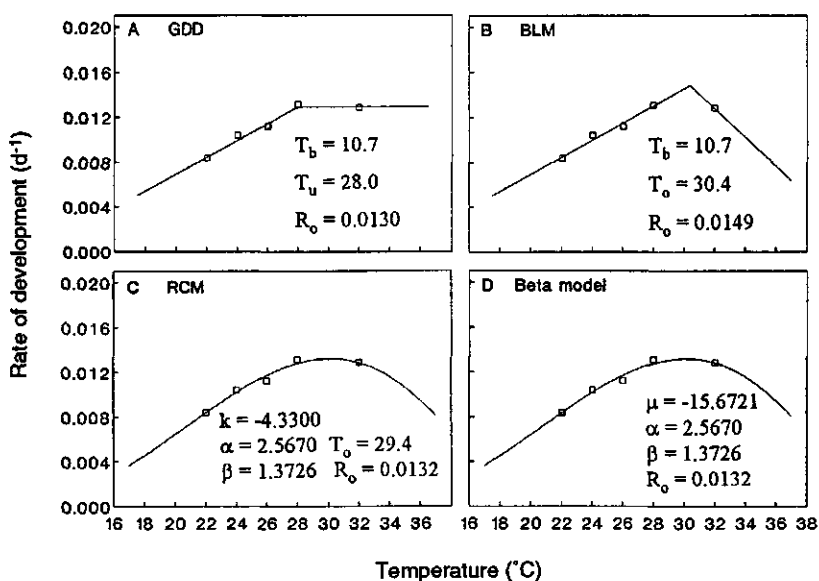


Fig. 2.5. Rate of development from sowing to flowering of rice (cv. IR8) at five diurnally constant temperatures (see Chapter 4), fitted respectively by the Growing Degree Days procedure (GDD), the bilinear model (BLM), the Rice Clock Model (RCM), and the Beta model. Values for T_b and T_c used in both RCM and the Beta model were 8 and 42°C, respectively.

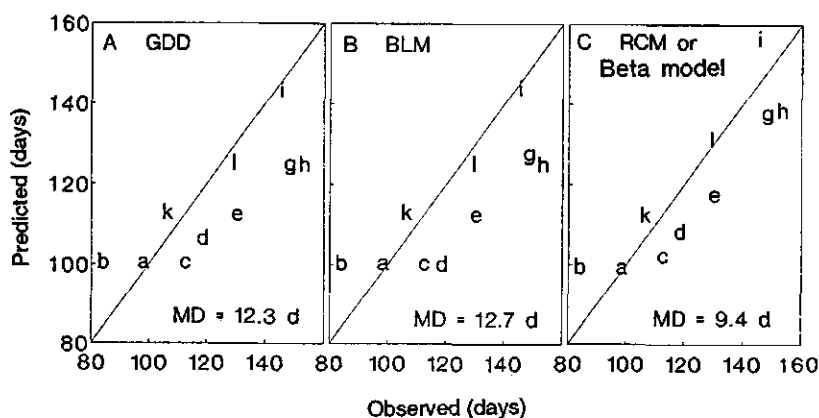


Fig. 2.6. Observed vs predicted days from sowing to flowering of rice (cv. IR8) (data of IRRI, 1977) for the four models. The predicted values were based on the parameters derived from an independent experiment with five diurnally constant temperatures (presented in Fig. 2.5). The letters correspond to the treatment numbers specified in Table 2.1. The solid line represents the 1:1 ratio. MD is the mean absolute derivation of predictions from the observed days.

A clear problem with the linear models is their inability to predict the observed difference in the flowering date between the treatments with the same mean daily temperature of 24°C but with different diurnal amplitudes. The GDD model had the same prediction for the treatments where the day temperature was lower than T_o , while the BLM had the same prediction for those where the day temperature was sub-optimal (Table 2.1). Actual difference in the flowering date among these treatments was predicted by the nonlinear models to some extent. A similar result also occurred for the comparison between 28/18 and 24/20°C, which had the same mean daily value of 21.3°C.

Discussion

Model performance

The thermal time approaches are often used to describe the effect of temperature on crop development, because the relationship between development and temperature becomes linear over a wide range of temperatures once the rate (inverse of the duration) is used (Roberts and Summerfield, 1987). However, evidence from several experiments showed that the rate also responds to temperature in a nonlinear way (e.g. Fig. 2.4). The two widely used thermal time methods GDD and BLM did not predict rice flowering dates as accurately as the two nonlinear models (Table 2.1, Fig. 2.6). Hodges (1991b) emphasized that a linear equation has to be reparameterized for applications outside the range of conditions for which the parameters were derived. However, this may result in different estimates of T_b for the same cultivar. For example, based on a linear function, Summerfield et al. (1992) reported that T_b for the development to panicle emergence in rice cultivar IR36 was 10.9°C, whereas Ellis et al. (1993) reported a T_b of 8.6°C for this cultivar. This is most probably due to the fact that temperatures used by Summerfield et al. (1992) included lower regimes than those used by Ellis et al. (1993).

Relationships between the Beta model and the RCM

Several nonlinear models have been developed to quantify the response of crop development to temperature (Robertson, 1968; Coligado and Brown, 1975b; Angus et al., 1981; Horie and Nakagawa, 1990; Gao et al., 1992). The RCM (Gao et al., 1992) shows some advantages over others, since it is flexible to handle nonsymmetric responses. However, the basic equation of the RCM, Eq. 2.1, does not necessarily predict a maximum DR at T_o (Fig. 2.1). Gao et al. (1992) attempted to overcome this problem by adding Eq. 2.2, which, however, can make the RCM take a nonsmooth form. By setting the first-order derivative of Eq. 2.1 equal to zero:

$$DR' = \exp(k) \left(\frac{T - T_b}{T_o - T_b} \right)^\alpha \left(\frac{T_c - T}{T_c - T_o} \right)^\beta \left(\frac{\alpha}{T - T_b} - \frac{\beta}{T_c - T} \right) = 0 \quad (2.7)$$

an expression for calculating T_o in the unconstrained RCM is derived; and this expression is the same as Eq. 2.5. Substituting this expression for T_o into Eq. 2.1 leads to a form of the Beta model similar to Eq. 2.1, but equivalent to Eq. 2.3:

$$DR = \exp(k^*) \left(\frac{T - T_b}{T_c - T_b} \right)^\alpha \left(\frac{T_c - T}{T_c - T_b} \right)^\beta \quad (2.8a)$$

where $k^* = k + \alpha \ln((\alpha + \beta)/\alpha) + \beta \ln((\alpha + \beta)/\beta)$. The form of the Beta model given in Eq. 2.3 results from placing the terms in $(T_c - T_b)$ of Eq. 2.8a in the constant, μ , so that $\mu = k^* - (\alpha + \beta) \ln(T_c - T_b)$. On the other hand, substituting expressions for α or β from Eq. 2.5 into Eq. 2.1 produces the Beta model in two other forms:

$$DR = \exp(k) \left[\left(\frac{T - T_b}{T_o - T_b} \right)^{\frac{T_o - T_b}{T_c - T_b}} \left(\frac{T_c - T}{T_c - T_o} \right) \right]^\beta \quad (2.8b)$$

$$DR = \exp(k) \left[\left(\frac{T - T_b}{T_o - T_b} \right) \left(\frac{T_c - T}{T_c - T_o} \right)^{\frac{T_c - T_o}{T_o - T_b}} \right]^\alpha \quad (2.8c)$$

Parameters in these two forms of the Beta model are explicitly biologically meaningful, if the factor $\exp(k)$ in Eq. 2.8b or Eq. 2.8c is replaced by R_o . Clearly, T_o , or α , or β in Eq. 2.1 of the RCM is superfluous; dropping one of them results in the Beta model. The RCM gives similar or identical estimates of DR to the Beta model when the difference between predetermined T_o and the calculated T_o from Eq. 2.7 is small (Table 2.1). However, this difference can be large in which case the Beta model will give a more reliable description than the RCM.

Flexibility of the Beta model

Although the Beta model has one parameter less than Eq. 2.1 of the RCM, it has the same property as Eq. 2.1, that is, both low and high temperature effects have been considered in a single equation, and the nonsymmetric response can be flexibly handled (Figs 2.2-2.4). The flexibility of the Beta model is illustrated by the fact that the model can describe any inflexion of response in the sub-optimal or supra-optimal range. The temperatures at which the inflexion occurs can be calculated as the values at which the second-order derivative equals zero. These values can be derived as:

$$T_{f1} = \frac{\alpha T_c + \beta T_b}{\alpha + \beta} - \frac{T_c - T_b}{\alpha + \beta} \sqrt{\frac{\alpha \beta}{\alpha + \beta - 1}} \quad (2.9a)$$

$$T_{f2} = \frac{\alpha T_c + \beta T_b}{\alpha + \beta} + \frac{T_c - T_b}{\alpha + \beta} \sqrt{\frac{\alpha \beta}{\alpha + \beta - 1}} \quad (2.9b)$$

where T_{f1} and T_{f2} represent the temperatures of the inflexion points respectively at the sub-optimal and supra-optimal range. Eq. 2.9a shows that $T_{f1} = T_b$ if $\alpha = 1$, whereas Eq. 2.9b shows that $T_{f2} = T_c$ if $\beta = 1$. It can be further analysed that an inflexion occurs in the sub-optimal range only if $\alpha > 1$ (Fig. 2.2B, Fig. 2.3), and an inflexion occurs in the supra-optimal range

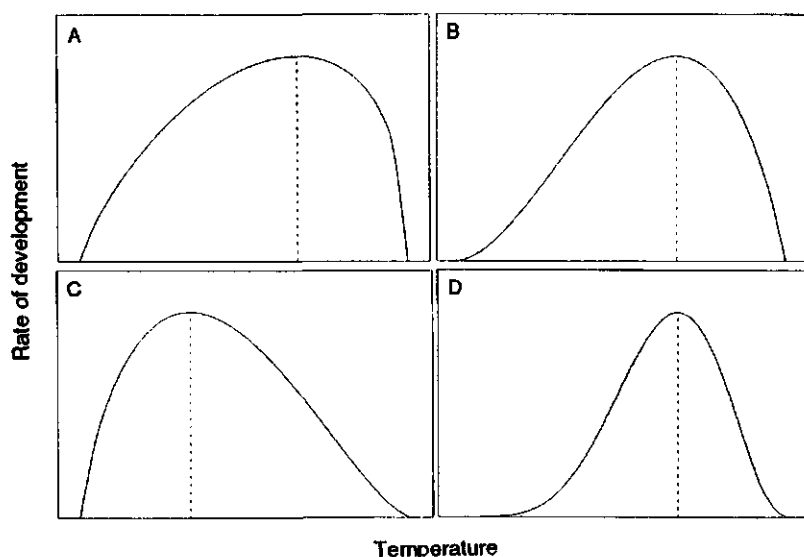


Fig. 2.7. Four theoretical nonsymmetric forms of the nonlinear curve for the temperature response of development rate as determined by parameters α and β in the Beta model: A: $\alpha < 1$ and $\beta < 1$, no inflexion within both sub-optimal and supra-optimal ranges; B: $\alpha > 1$ but $\beta < 1$, an inflexion with the sub-optimal range but no inflexion within the supra-optimal range; C: $\alpha < 1$ but $\beta > 1$, no inflexion with the sub-optimal range but an inflexion within the supra-optimal range; D: $\alpha > 1$ and $\beta > 1$, an inflexion within each of sub-optimal and supra-optimal ranges.

only if $\beta > 1$ (Fig. 2.2B). Parameter α , therefore, determines the curvature of the relationship over the sub-optimal range, whereas parameter β determines the curvature for supra-optimal range. Different combinations of parameters α and β make the model flexible to fit four possible nonsymmetric forms of the relationship between the DR and temperature (Fig. 2.7).

In addition, some of existing models can be generated from the Beta model. For example, the Beta model becomes a simple linear thermal time model if $\alpha = 1$ and $\beta = 0$, a power-law model if $\beta = 0$, a quadratic model if $\alpha = \beta = 1$, or a general symmetric model if $\alpha = \beta$.

Application of the Beta model and the need for further studies

Although the Beta model was introduced for crop development, it may apply to other biological processes. For example, according to the data of Tanaka (1976), effects of temperature on rice photosynthesis rate can be described by it. Many thermal response patterns, as presented by Ferguson (1958), Orchard (1975), Tyldesley (1978), and Johnson and Thornley (1985), coincide with the different forms of the model shown by Fig. 2.7. The simple form of the model, Eq. 2.3, can be easily parameterized if values of T_b and T_c are predetermined from the data or external sources. The form with biologically meaningful parameters, Eq. 2.8b or Eq.

2.8c where the factor $\exp(k)$ is expressed with parameter R_0 , can be used to characterize the difference among crops or among cultivars within a crop in the developmental response to temperature.

For application to crop development, this Chapter indicates that the Beta model describes the response to constant temperatures quite well (Figs 2.2-2.4). For the response to alternating temperatures, however, the mean deviation between observed and predicted days to flowering in rice was > 9 d (Fig. 2.6). In this Chapter, no difference in the effect of day and night temperature on DR was assumed. With the data on IR8 rice (Table 2.1), however, IRRI (1977) indicated a relatively more important role of night temperature than the day value. But that conclusion was based on a linear model which did not realistically describe the response of DR to temperature. The greater influence of night temperature can be due to the fact that in the experiment of IRRI (1977), night temperature was in the range where DR increases proportionally with the temperature whereas day temperature was often supra-optimal (Table 2.1). Nevertheless, Coligado and Brown (1975b) indicated an effect of diurnal temperature range on development in maize. As the Beta model tends to have a larger discrepancy for the treatments with a higher diurnal amplitude (Table 2.1), the approach might be improved by accounting for the effect of the diurnal temperature range. This gives an element that needs a further study.

Chapter 3

Rice flowering in response to diurnal temperature amplitude

Abstract Temperature is an important determinant of crop development rate (DR). Some reports have shown that the response of DR to temperature is nonlinear over a wide range of conditions. Others indicate that DR is affected by the amplitude of the diurnal temperature fluctuation. However, the nonlinearity between DR and temperature and the temperature amplitude effect are often confounded, as the amplitude effect can be explained by the nonlinearity. The objective of this Chapter is to determine whether there is an effect of the temperature amplitude *per se* on development to flowering in rice (*Oryza sativa* L.), based on a published controlled-environment data set for 16 cultivars. The response of DR to diurnally constant temperatures was quantified by a nonlinear model. This model was used to predict days to flowering at diurnally fluctuating temperatures. The often large discrepancies between predicted and observed days indicated an effect of the diurnal temperature amplitude *per se* on the DR. This effect was significant at different probability levels in 11 cultivars, but not in the other five ($P > 0.10$). The trend of this effect, where significant, also strongly differed among cultivars: temperature amplitude accelerated flowering in one cultivar but delayed it in others. The nonlinearity between DR and temperature and the effect of the temperature amplitude could explain a large part of the often observed variation among environments of thermal unit requirements for flowering.

Introduction

Temperature is one of the major environmental variables that determine the time to flowering in rice (Yoshida, 1981). The thermal time concept has been widely used to describe crop development in response to temperature. It is based on the assumption that a fixed amount of thermal units (TU) above a base temperature (T_b) is required to complete a specific developmental phase. However, the TU requirement for flowering in rice often varies considerably across environments (IRRI, 1977; Rice Photothermal Ecology Research Group (RPERG), 1978; Oldeman et al., 1987). For example, among ten cultivars tested at eight locations in China (latitude from 18°20' N to 47°07' N and altitude from 3.5 m to 1916.0 m) in 1962 and 1963, the TU requirement ($T_b = 8^\circ\text{C}$) for the period from emergence to flowering ranged from 737.4 to 1207.3°Cd in cv. Mei Xian Tu Mang and from 823.1 to 1477.5°Cd in cv. San Shi Zi (RPERG, 1978). This large variation can be partly attributed to the effect of photoperiod on development (Oldeman et al., 1987; Loomis and Connor, 1992). However, the largest variation in the TU requirement among the ten cultivars tested by RPERG (1978) was found in the photoperiod-insensitive cultivar San Shi Zi.

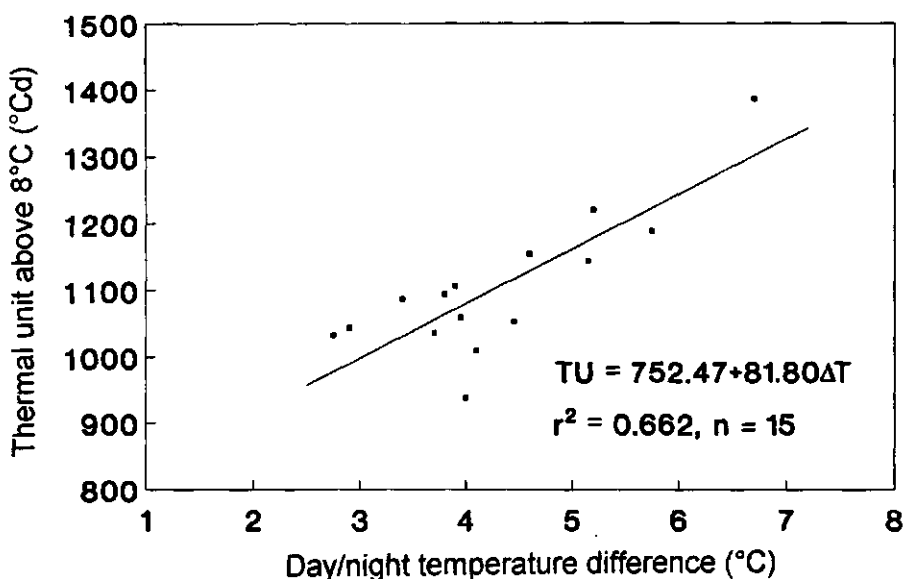


Fig. 3.1. The relation between the average day-to-night temperature amplitude (ΔT) and the thermal unit (TU) above 8°C required for the period from emergence to flowering for plants of photoperiod-insensitive rice cv. San Shi Zi grown in a multilocal field experiment in 1963 (data of RPERG, 1978).

A reason for the variation in the TU requirement could be the assumption, in the thermal time approach, of linearity in the relationship between development rate (DR, expressed as the inverse of the duration) and temperature. Several studies have indicated that this relationship is nonlinear if wide ranges of temperatures are considered (Angus and Zandstra, 1980; Yoshida, 1981; Haniu et al., 1983; Loomis and Connor, 1992; Shaykewich, 1995). For example, in maize (*Zea mays* L.), Ellis et al. (1992b) showed that the DR to tassel initiation increased nonlinearly with temperature above T_b up to an optimum temperature, T_o , beyond which DR decreased, again nonlinearly, until a ceiling temperature, T_c , was reached. This bell-shaped response was shown to be qualitatively typical of development in many crops (Watts, 1972; Keating and Evenson, 1979; Tollenaar et al., 1979; Hammer et al., 1989).

Another reason for the variation in the TU requirement could be the use of the daily mean temperature in the thermal time concept. Early work by Went (1944a) in tomato (*Lycopersicon esculentum* Mill.) has indicated that plant growth and development is also affected by a diurnal temperature change. Subsequent studies in different crops further confirmed Went's conclusion (Quinby et al., 1973; Coligado and Brown, 1975a; IRRI, 1977; Wallace and Enriquez, 1980; Garcia-Huidobro et al., 1982b; Sorrells and Myers, 1982). The amplitude of day and night temperature affected the development of bean (*Phaseolus vulgaris* L.) (Wallace and Enriquez, 1980) and of sorghum (*Sorghum bicolor* L. Moench) (Quinby et al., 1973; Sorrells and Myers, 1982). For pearl millet (*Pennisetum typhoides* S. & H.) seed germination, Garcia-Huidobro et al. (1982b) found that the TU requirement for 50% germination varied with the increase of

temperature amplitude. For rice, IRRI (1977) reported that the time interval from sowing to flowering varied greatly among plants growing in a phytotron with the same mean temperature but at different day and night values. All these suggest that the TU requirement may vary with the diurnal temperature amplitude. Indeed, preliminarily analysing the data from the multilocal field experiments in 1963 for photoperiod-insensitive rice cv. San Shi Zi (RPERG, 1978) indicated that the TU requirement for the period from emergence to flowering changed with the difference between average day and night temperature (Fig. 3.1).

However, the observed difference in DR between diurnally fluctuating and the equivalent constant temperatures could also be the consequence of the nonlinear relationship between DR and temperature. A wide amplitude around the optimum temperature results in a smaller daily advance than the optimum because the crop spends many hours at temperatures that limit development (Loomis and Connor, 1992). Ellis et al. (1992b) have indicated that when the nonlinearity between DR and temperature was considered, the development to tassel initiation in maize was indeed not affected by the diurnal change of temperature. Similar results in maize were reported for seedling emergence and anthesis as well (Warrington and Kanemasu, 1983a). But whether this is true for development to flowering in rice is not yet known.

This Chapter presents an analysis which aimed to determine whether the amplitude of the diurnal temperature fluctuation *per se* is important for development to flowering in rice.

Materials and methods

Experimental data

The published data set used in this Chapter came from a growth chamber experiment where 16 rice cultivars, including 11 *indica* cultivars, four *japonica* cultivars and one intermediate *japonica* × *indica* cultivar, were tested (Summerfield et al., 1992). Plants of all cultivars were grown in pots in 13 chambers with different photothermal treatments. The treatments were chosen to represent photothermal environments encountered in typical rice-growing environments. Among the 13 photothermal treatments, eight treatments which had a constant photoperiod of 11.5 h d⁻¹ were used here to avoid the effect of photoperiod. In four of these treatments, a constant temperature was maintained (i.e. 16, 20, 24 and 28°C). In the other four treatments, diurnally fluctuating temperatures were used (day/night: 20/16, 28/16, 28/20 and 32/20°C). In each of the fluctuating diurnal cycles, day and night temperature was imposed for 12 h d⁻¹. Pots were irrigated six times per day. Relative humidity was held constant at 70 ± 2% in each chamber. Three cultivars (Azucena, IR42 and TN1) had not flowered at the constant temperature of 16°C by 250 days after sowing when the experiment was terminated. No result was obtained for cv. Barkat at the constant 28°C nor for TN1 at 32/20°C.

Analytical approaches

The response of DR to diurnally constant temperatures was analysed by using a nonlinear model described in Chapter 2:

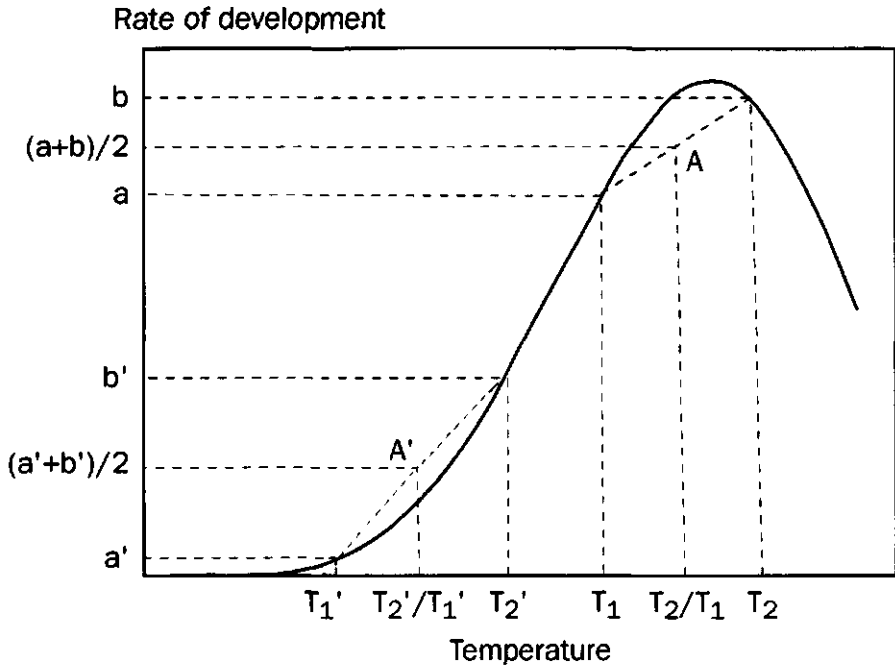


Fig. 3.2. Schematic representation of the method to predict crop development rate (DR) at diurnally fluctuating temperatures from a response of DR to diurnally constant temperatures. The value for the DR at the fluctuating temperature (day/night: T_2/T_1 or T_2'/T_1') can be estimated as the average for two corresponding diurnally constant temperatures T_1 and T_2 or T_1' and T_2' if the durations for day and night temperatures at the fluctuating regime are each 12 h d^{-1} . At point A, DR at the fluctuating temperature T_2/T_1 is lower than at the equivalent constant temperature, whereas at point A', DR at T_2'/T_1' is higher than at the equivalent constant temperature.

$$DR = R_o \cdot g(T) \quad (3.1)$$

where R_o is the maximum value for DR when temperature is optimum; $g(T)$, the function defining the nonlinear effect of temperature, T , on the DR, is calculated by:

$$g(T) = \left[\left(\frac{T - T_b}{T_o - T_b} \right) \left(\frac{T_c - T}{T_c - T_o} \right)^{\frac{T_c - T_o}{T_o - T_b}} \right]^\alpha$$

where α is a cultivar-specific coefficient, defining the curvature of the relationship; T_o is the optimum temperature at which $DR = R_o$; T_b and T_c are the base and ceiling temperature at which DR is zero.

The relation based on the constant temperatures was then used to predict days to flowering at diurnally fluctuating temperatures by separating day and night temperature. An illustration

for this method is given in Fig. 3.2, using a typical response curve shown in Chapter 2. The figure indicates that DR at a fluctuating temperature can differ from that at the equivalent constant temperature with the same mean daily value. When the mean temperature is higher than the inflection point on the curve, the DR at a fluctuating temperature is lower than at constant temperature (point A in Fig. 3.2); below the inflection point, DR under the fluctuating regime is higher than at constant temperature (point A' in Fig. 3.2) (Shaykewich, 1995). If days to flowering at the fluctuating temperature could not be predicted from this analysis, the discrepancies between predicted and observed days would be attributed to an additional effect of diurnal temperature fluctuation *per se*, which is independent of the nonlinearity. A separate model would then be needed to account for this additional effect.

Results and discussion

The response of DR to the eight temperature treatments in the 16 rice cultivars tested by Summerfield et al. (1992) is shown in Fig. 3.3. Because the temperatures used in the experiment was limited by typical thermal environments in rice-growing areas, only part of the response curve shown in Fig. 3.2 is presented in Fig. 3.3.

In the analysis, Eq. 3.1 was first used to describe the response of DR to the four constant temperatures. However, Eq. 3.1 has five parameters, which cannot be fully estimated from four observations at the constant temperatures. A sensitivity analysis in Chapter 2 by varying T_b between 5 and 15°C and T_c between 35 and 45°C in 1°C step for rice cv. IR8 has indicated that values for T_b and T_c are not important for goodness of fit of the model. A similar analysis with the data of Summerfield et al. (1992) indicated that for each cultivar the four data points at the constant temperatures were accurately described by the model if any two of the three parameters α , T_b and T_c were fixed beforehand. Since both T_b and T_c are often beyond the temperature range in rice-growing environments, they hardly affect the capacity of the model to describe the data in normal conditions. Thus, standard values for T_b (8°C) and T_c (42°C) (Alocilja and Ritchie, 1991; Kropff et al., 1994b) were used. Based on these standard values for T_b and T_c , values were determined for other parameters in Eq. 3.1 (Table 3.1). The model with three estimated parameters described the data with $r^2 > 0.98$ in all cultivars. However, values for T_b and R_0 are based on extrapolation beyond the temperature range of the data in some cultivars, especially for Azucena, Carreon and IR36 where the estimated T_b was higher than 35°C. An accurate estimation of parameter values for these cultivars would need experimental data at higher constant temperature regimes.

The DR at a diurnally fluctuating temperature was typically lower than the DR at the equivalent constant temperature (Fig. 3.3). However, the DR at 20/16°C was often somewhat higher than the interpolated value of DR at the equivalent constant temperature. To determine whether these differences in the DR between the fluctuating and the equivalent constant temperatures are due to the nonlinear relationship between DR and temperature, the actual days to flowering in fluctuating temperature regimes are compared in Fig. 3.4 with those predicted by Eq. 3.1 using parameter values given in Table 3.1. The agreement was generally good at the fluctuating temperature of 20/16°C (Fig. 3.4A). However, for the regimes where

Table 3.1. Values of parameters in Eq. 3.1 (established when T_b and T_c were set to be 8 and 42°C, respectively) for 16 rice cultivars derived from the data of Summerfield et al. (1992) at diurnally constant temperatures.

Ecotype	Cultivar	R_0 (d ⁻¹)	α	T_0 (°C)	r^2
<i>Indica</i>	BPI-76	0.0131	2.008	28.8	1.000
	Peta	0.0113	2.273	27.1	0.999
	Azucena†	0.0135	1.172	36.0	1.000
	Pinulot 330	0.0123	2.220	27.8	1.000
	Intan	0.0102	1.868	27.4	0.996
	Carreon	0.0210	1.726	35.3	0.988
	TN1†	0.0122	2.175	29.6	1.000
	IR5	0.0106	2.638	25.7	1.000
	IR8	0.0113	2.178	27.4	1.000
	IR36	0.0119	1.386	36.5	0.996
	IR42†	0.0107	0.994	30.5	1.000
<i>Japonica</i>	Jkau 450	0.0131	2.784	24.7	0.999
	Eiko	0.0161	2.252	29.4	1.000
	Barkat†	0.0124	4.046	23.6	1.000
	Stejaree 45	0.0213	2.213	32.1	1.000
<i>Intermediate</i>	Suweon 303	0.0162	3.000	27.1	0.993

† Parameter values were estimated from the data of three constant temperatures available for these cultivars.

the day/night temperature difference was 8–12°C, the discrepancies between predicted and observed days were often large, up to 60 d (Fig. 3.4B,D). These discrepancies in some cultivars (e.g. IR8) were more obvious than in others (e.g. IR36). The trends were also not consistent among cultivars. Plants of some cultivars (e.g. Jkau 450) reached flowering earlier than predicted, while most other cultivars generally flowered later than predicted.

The fact that nonlinearity between DR and temperature cannot fully explain the difference in the DR between fluctuating and constant temperatures indicates that there is an additional effect of diurnal temperature amplitude *per se* on the rate of rice development to flowering. Based on Eq. 3.1, a model accounting for this additional effect can be expressed as:

$$DR = R_0 \cdot g(T) \cdot \exp(\gamma \Delta T) \quad (3.2)$$

where ΔT is the diurnal temperature amplitude, i.e. the difference between day and night temperature; γ is the coefficient that defines the varietal responsiveness to the amplitude, with a large value of γ indicating that the cultivar is highly responsive to the amplitude. Eq. 3.2 becomes Eq. 3.1 if $\gamma = 0$, indicating that DR is not affected by the amplitude.

Eq. 3.2 was then compared with Eq. 3.1 for describing the data at all temperature treatments. Parameters of both Eq. 3.1 and Eq. 3.2 were estimated by using the nonlinear optimization package of the Statistical Analysis Systems Institute (SAS, 1988). To avoid

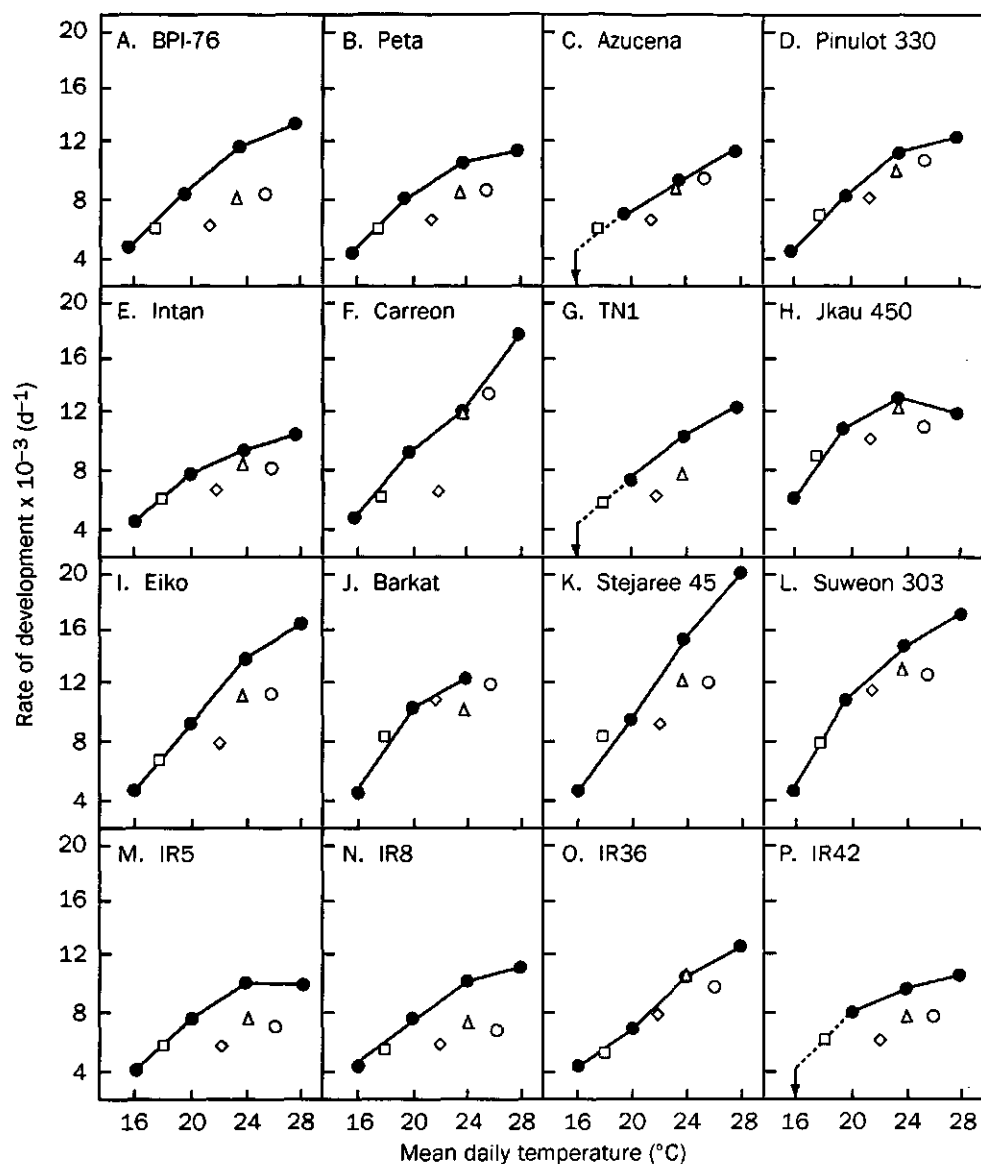


Fig. 3.3. Relations between daily mean temperature and rate of development to flowering in 16 rice cultivars at the photoperiod of 11.5 h d^{-1} (data of Summerfield et al., 1992). The solid curves were plotted from observations (\bullet) at diurnally constant temperatures. The open symbols indicate the observations at diurnally fluctuating temperatures (\square : $20/16^{\circ}\text{C}$, \diamond : $28/16^{\circ}\text{C}$, \triangle : $28/20^{\circ}\text{C}$, and \circ : $32/20^{\circ}\text{C}$). The dashed line with an arrow downwards in (C), (G) and (P) indicates that plants did not flower after 250 d of growth at the diurnally constant temperature of 16°C .

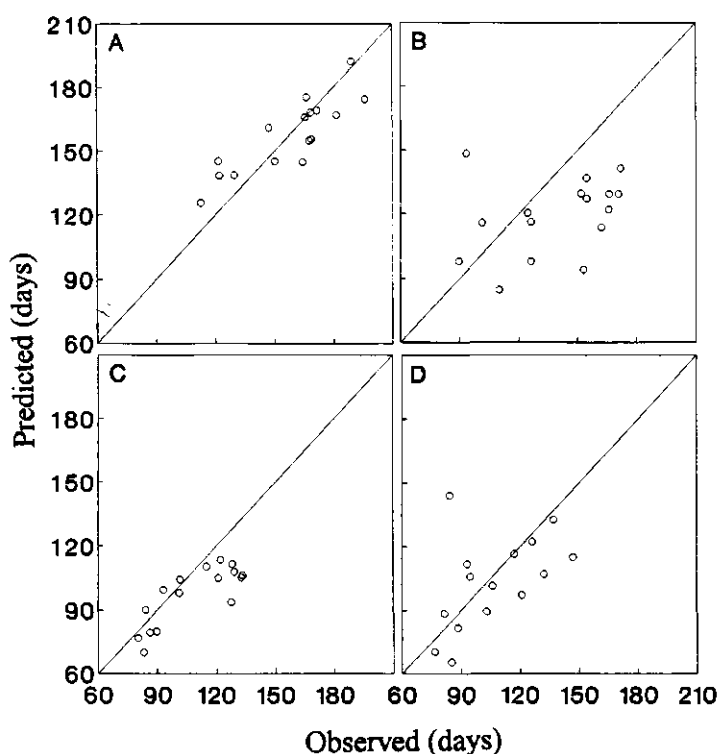


Fig. 3.4. Comparisons of observed days to flowering in the fluctuating temperature regimes 20/16°C (A), 28/16°C (B), 28/20°C (C) and 32/20°C (D) with those days predicted by the relations (quantified in Table 3.1) between temperature and rate of development to flowering from observations at diurnally constant temperatures in 16 rice cultivars (data of Summerfield et al., 1992).

confounding effects as a result of the nonlinear relationship between DR and temperature, day (T_D) and night temperatures (T_N) were used separately but with the same coefficients. That is, when the data from all treatments including fluctuating temperatures with equal day and night periods were used to parameterize the models, Eq. 3.1 was re-formulated as

$$DR = 0.5R_0[g(T_D) + g(T_N)]$$

and Eq. 3.2 became

$$DR = 0.5R_0[g(T_D) + g(T_N)]\exp(\gamma\Delta T)$$

Parameter values for Eqs 3.1 and 3.2 estimated from this approach are given in Table 3.2.

The F test was conducted to determine whether Eq. 3.2 led to a significant improvement over Eq. 3.1 in describing the data for each cultivar. The test showed that the model Eq. 3.2 was significantly better than Eq. 3.1 at different probability levels in most cultivars (Table 3.2). This indicated that besides the nonlinear relationship between DR and temperature, there was

Table 3.2. Values of parameters in Eqs 3.1 and 3.2 (established when T_b and T_c were set to be 8 and 42°C, respectively) for 16 rice cultivars derived from the data of both diurnally constant and fluctuating temperatures.

Cultivar	Eq. 3.1				Eq. 3.2					P^\dagger
	R_o (d ⁻¹)	α	T_o (°C)	r^2	R_o (d ⁻¹)	α	T_o (°C)	γ	r^2	
BPI-76	0.0118	2.909	26.5	0.844	0.0139	1.582	31.5	-0.030	0.983	0.0046
Peta	0.0109	2.307	26.9	0.943	0.0115	1.765	28.8	-0.012	0.977	0.0731
Azucena	0.0115	1.460	31.9	0.925	0.0184	0.935	41.9	-0.010	0.968	0.1413
Pinulot 330	0.0126	1.773	29.4	0.977	0.0127	1.726	29.7	-0.001	0.978	0.8446
Intan	0.0099	1.968	27.0	0.967	0.0104	1.597	28.6	-0.009	0.989	0.0453
Carreon	0.0177	2.080	32.5	0.884	0.0371	1.474	41.9	-0.020	0.952	0.0752
TN1	0.0111	3.329	27.0	0.939	0.0130	1.527	32.6	-0.027	0.994	0.0256
IR5	0.0103	2.902	25.3	0.940	0.0105	2.316	26.2	-0.013	0.978	0.0595
IR8	0.0106	3.122	25.7	0.889	0.0113	2.032	27.8	-0.024	0.997	0.0004
IR36	0.0130	2.151	29.9	0.978	0.0131	2.128	30.0	-0.001	0.978	0.9425
IR42	0.0101	2.440	26.0	0.849	0.0112	0.941	32.3	-0.022	0.988	0.0094
Jkau 450	0.0132	2.050	25.5	0.939	0.0130	2.560	24.7	0.011	0.988	0.0158
Eiko	0.0150	2.650	28.1	0.952	0.0171	1.896	31.4	-0.016	0.988	0.0260
Barkat	0.0141	1.635	29.5	0.842	0.0131	1.842	27.8	0.006	0.845	0.8169
Stejaree 45	0.0174	3.076	28.0	0.925	0.0208	2.017	32.1	-0.022	0.981	0.0271
Suweon 303	0.0163	2.370	28.3	0.982	0.0162	2.400	28.2	0.001	0.982	0.9031

† The probability level at which Eq. 3.2 described the data significantly better than Eq. 3.1.

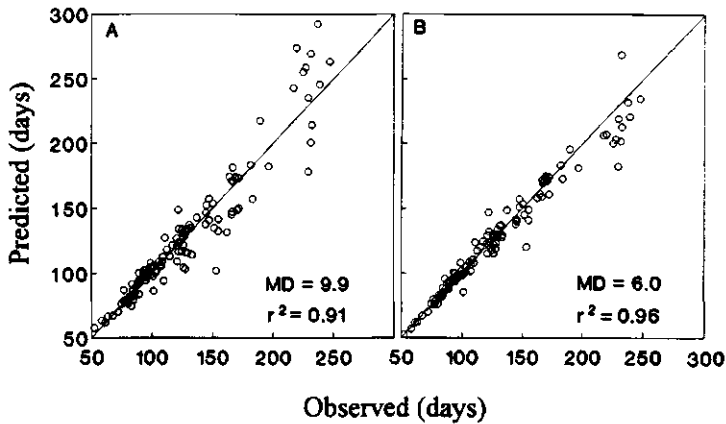


Fig. 3.5. Comparisons of observed days to flowering in 16 rice cultivars at all temperature regimes (data of Summerfield et al., 1992) with those predicted by Eq. 3.1 (A) and by Eq. 3.2 (B) with parameter values given in Table 3.2. MD is the mean absolute predictive discrepancy (days) and r^2 is the coefficient of determination for the linear regression between predicted and observed days to flowering.

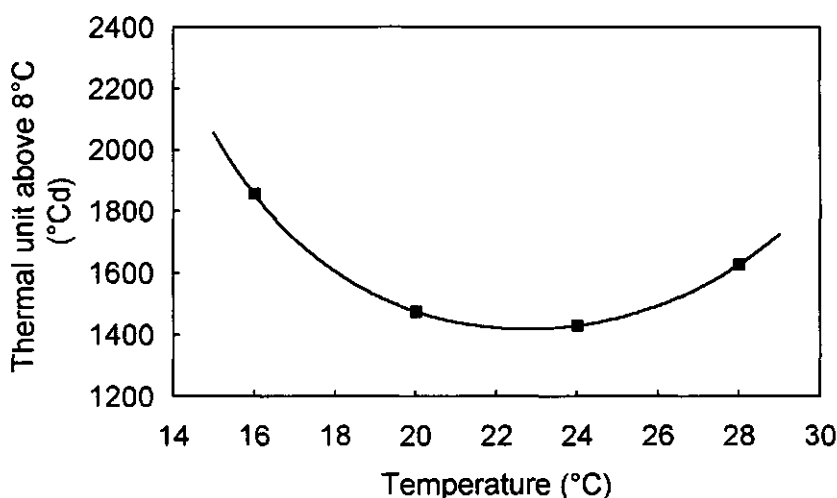


Fig. 3.6. The relation between temperature and the thermal unit (TU) above 8°C for days to flowering at diurnally constant temperatures in rice cv. Pinulot 330 (data of Summerfield et al., 1992). The curve is based on Eq. 3.3 with coefficients given in Table 3.1. The points are TU values calculated from the data in days to flowering.

an independent effect of the temperature amplitude *per se* on DR in these cultivars. However, for cvs Azucena, Pinulot 330, Barkat, Suweon 303 and IR36, Eq. 3.2 did not describe the data better than Eq. 3.1 ($P > 0.10$) (Table 3.2). In these five cultivars, differences in the DR between fluctuating and equivalent constant temperatures, which were often smaller than those in other cultivars (Fig. 3.3), could be due to nonlinearity between DR and temperature. To illustrate the overall descriptive ability of each of the two models, the observed and calculated days to flowering are compared in Fig. 3.5 with the data of all cultivars. The mean absolute discrepancy (MD) between observed and calculated days was 9.9 d for Eq. 3.1 and 6.0 d for Eq. 3.2. The value of r^2 for the linear regression between observed and calculated days was 0.91 for Eq. 3.1 vs 0.96 for Eq. 3.2.

The demonstration that the independent effect of the diurnal temperature amplitude *per se* occurs in most rice cultivars but not in others exhibits some of the conflict that exists in many species. When the nonlinearity between DR and temperature was considered, no specific effect of the amplitude *per se* was detected for growth and development in maize (Tollenaar et al., 1979; Warrington and Kanemasu, 1983a; Ellis et al., 1992b). However, only one or a few cultivars were used in these studies. Many other studies for different species (Went, 1944a; Quinby et al., 1973; Coligado and Brown, 1975a; IRRI, 1977; Wallace and Enriquez, 1980; Garcia-Huidobro et al., 1982b; Sorrells and Myers, 1982) indicated the effect of the diurnal temperature change. However, this effect was often confounded with the effect of the nonlinearity in those studies.

To what extent does the above analysis explain the often observed variation of the TU requirement for rice plants to reach flowering among environments? First, the nonlinearity

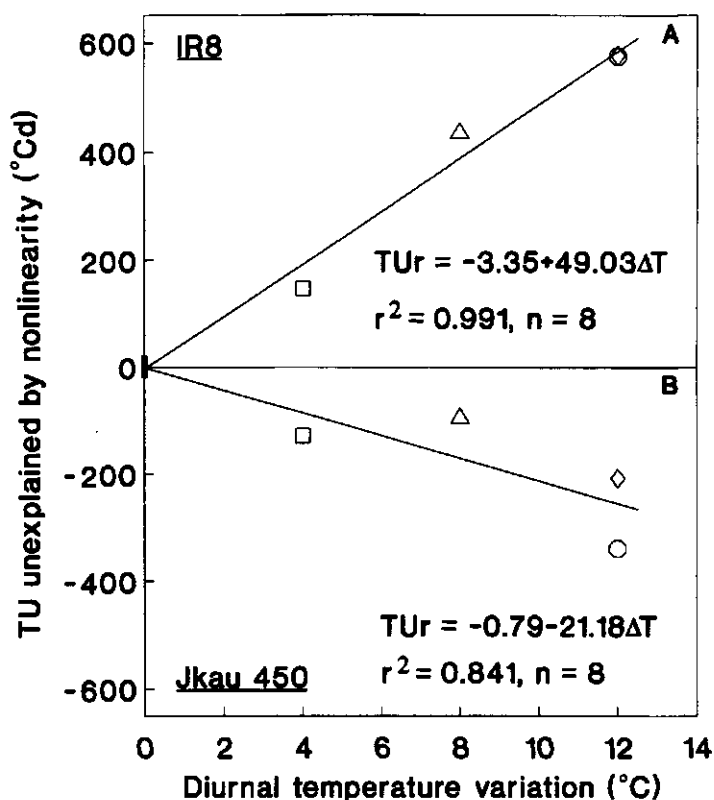


Fig. 3.7. The thermal unit unexplained by the nonlinear development rate-temperature relationship (TU_r , calculated from Eq. 3.4 with coefficients quantified in Table 3.1) as affected by the diurnal temperature amplitude (ΔT) at different temperatures (*: constant temperatures; \square : 20/16°C; \diamond : 28/16°C; Δ : 28/20°C; \circ : 32/20°C) in rice cvs IR8 and Jkau 450 (data of Summerfield et al., 1992).

between DR and temperature implies that the TU requirement varies with the temperature imposed on plants. The relation between the TU requirement and temperature *per se* can be derived from Eq. 3.1:

$$TU = (T - T_b) / [R_0 \cdot g(T)] \quad (3.3)$$

This relation is illustrated in Fig. 3.6 for cv. Pinulot 330 at diurnally constant temperatures. This figure indicates that the nonlinearity between DR and temperature accounts for part of the variation of the TU requirement among environments. This is the case for the cultivars in which the difference in DR between fluctuating and constant temperatures can be explained by the nonlinearity.

For those cultivars in which the difference in DR between fluctuating and constant temperatures cannot be fully explained by the nonlinearity, the effect of the diurnal temperature amplitude on the DR is an important factor for the variation of the TU requirement. Fig. 3.1

has shown the effect of the day/night temperature difference on the TU requirement under field conditions. However, the effect of the amplitude shown in Fig. 3.1 was confounded by the nonlinearity between DR and temperature. The effect of diurnal temperature amplitude *per se* on the TU requirement can be determined from controlled-environment data by removing the part of the TU variation due to the nonlinearity:

$$TU_r = (T - T_b) \left(f - \frac{1}{0.5R_0[g(T_D) + g(T_N)]} \right) \quad (3.4)$$

where T is the daily mean temperature, f is the observed days to flowering, TU_r is the thermal unit unexplained by the nonlinearity. This type of analysis with the data of Summerfield et al. (1992) demonstrated that the effect of the diurnal temperature amplitude *per se* on the TU requirement was cultivar-specific. Fig. 3.7 gives two contrasting responses for IR8 and Jkai 450, respectively. Here the temperature amplitude increases the TU requirement in IR8 but generally reduces it in Jkai 450. The strong effect of the temperature amplitude *per se* on IR8 (Fig. 3.7A) may explain the result in Chapter 2 that Eq. 3.1 accurately predicted flowering dates of this cultivar at diurnally constant temperatures but not at diurnally fluctuating regimes. Loomis and Connor (1992) also indicated a different TU requirement for a phenological phase of a crop at the same mean temperature but different diurnal amplitudes. However, they attributed it only to the nonlinearity between DR and temperature. Fig. 3.7 clearly indicates that the diurnal temperature amplitude can change the TU requirement.

If the effect of the nonlinearity between DR and temperature was not considered, one might conclude that the temperature amplitude delayed flowering in Jkai 450, since the DR at fluctuating temperatures were often lower than at equivalent constant temperatures (Fig. 3.3H). However, Fig. 3.7B indicated that the temperature amplitude reduced the TU requirement in Jkai 450, implying that the amplitude *per se* can accelerate development in this cultivar. This agrees with the interpretation by Eq. 3.2 in which the value of parameter γ was significantly positive in this cultivar ($P < 0.02$), in contrast with the negative value in most other cultivars (Table 3.2).

In conclusion, the reanalysis of data of Summerfield et al. (1992) for diverse cultivars has shown an effect of diurnal temperature amplitude *per se* on development from sowing to flowering in rice. This effect can explain a large part of the often observed variation of the TU requirement for development to flowering. However, it is difficult to find out the mechanism for this effect from the data set used here. One possible reason could be that in the experiment of Summerfield et al. (1992), the water temperature, which largely determines the growing-point temperature during the early developmental phase (Collinson et al., 1995), might deviate occasionally from the air temperature to different extents between day and night. However, the considerable difference in the response to the temperature amplitude among cultivars obtained in this Chapter warrants a further study with greater detail in a carefully designed controlled-environment experiment.

Chapter 4

Differential effects of day and night temperature on development to flowering in rice

Abstract There are conflicting reports with regard to the difference in effects of day temperature (T_D) and night temperatures (T_N) on plant development. The objective of this Chapter is to determine whether there are different effects of T_D and T_N on development from sowing to flowering in rice (*Oryza sativa* L.).

Plants of 24 rice cultivars were grown in naturally-lighted growth chambers at five diurnally constant (22, 24, 26, 28 and 32°C) and four diurnally fluctuating temperatures (26/22, 30/22, 22/26 and 22/30°C for T_D/T_N with 12 h d⁻¹ each) with a constant photoperiod of 12 h d⁻¹. The treatments were selected to enable the separation of effects of T_D and T_N on development rate (DR).

The response of DR to constant temperatures was typically nonlinear. This nonlinearity could not explain the difference in DR between fluctuating temperatures with the same mean daily value but opposite T_D/T_N differences. Differential effects of T_D and T_N on DR to flowering were detected in all but one cultivar. In most cases, T_D exerted a greater influence than T_N , in contrast with many previous reports based on the assumption of a linearity between DR and temperature. The data were further analysed by a nonlinear model which separated effects of T_D and T_N . The estimated value for the optimum T_N was generally 25–29°C, about 2–4°C lower than the estimated optimum T_D in most cultivars. The effects of T_D and T_N on DR were found to be interactive in some cultivars. These results form a new basis for modelling rice flowering dates.

Introduction

Crop development is primarily affected by temperature and can be modified by other factors such as photoperiod (Hodges, 1991b). Agronomists, agrometeorologists and crop modellers have attempted to quantitatively assess the effect of temperature on crop development rate (DR). Relationships have been found to vary in form from linear (e.g. Roberts and Summerfield, 1987) to variously nonlinear approaches (e.g. Horie and Nakagawa, 1990; Gao et al., 1992).

These approaches typically use the mean daily temperature, assuming that effects of day temperature (T_D) and night temperature (T_N) on DR are the same. However, several studies have indicated a different impact of T_D and T_N on plant growth and development. Based on observations in numerous species, Roberts (1943) suggested that the temperature during the night rather than the day largely determines the response of plants to temperature. Went (1944a) made detailed observations of the effect of T_N on stem extension rates of plants of tomato (*Lycopersicon esculentum* Mill.), and proposed the term 'thermoperiodicity' to describe

the apparently greater rate of plant growth and development in diurnally fluctuating temperatures compared to plants grown at constant temperatures. The subsequent work of Went (1944b) presented a general mechanism for thermoperiodicity, that is, the predominance of two different processes during the day and the night, of which the dark process has a much lower temperature optimum than the light process. The thermoperiodicity was shown to be a general phenomenon in other higher plants (e.g. Camus and Went, 1952). This phenomenon was further confirmed by many studies on seed germination (Thompson et al., 1977; Garcia-Huidobro et al., 1982b; Brown, 1987) and for many other horticultural crops (e.g. Mortensen, 1994). The studies of Went (1944a,b) also led several workers to analyse the effect of T_D and T_N on plant growth and development without considering the mean daily temperature. For example, Brown (1969) assumed two different responses of development to temperature, quadratic for the daily maximum temperature and linear for the minimum in the Ontario Corn Heat Unit equation. Robertson (1968) considered different responses to T_D and T_N in a model for predicting DR of wheat (*Triticum aestivum* L.). The model of Robertson (1968) was also used for other crops, e.g. barley (*Hordeum vulgare* L.) (Williams, 1974).

However, in all Went's (1944a) experiments, tomato plants were subjected to T_D for 8 h d⁻¹ and to T_N for 16 h d⁻¹. The relative importance of T_N could be attributed to the fact that plants stayed longer in the night regime. Ellis et al. (1990) re-examined the original data of Went (1944a) by taking the respective durations of T_D and T_N into account and indeed found little support for Went's theory in tomato. Other controlled-temperature experiments also showed that for many species, the optimum T_N is not necessarily lower than the optimum T_D and that a diurnal change in temperature is not essential for maximum growth. No evidence was found of a requirement for thermoperiodicity during growth of sugar cane (*Saccharum officinarum* L.) (Glasziou et al., 1965), for flowering in peanuts (*Arachis hypogaea* L.) (Wood, 1968), or for seedling emergence, tassel initiation and anthesis of maize (*Zea mays* L.) (Warrington and Kanemasu, 1983a). No specific effects of T_N as imposed to T_D could be detected for rice (*Oryza sativa* L.) seed germination and vegetative growth (Chaudhary and Ghildyal, 1969, 1971) or on development to flowering in both species *O. sativa* and *O. glaberrima* of rice (Roberts and Carpenter, 1965). Hopkinson (1967) did not find evidence for a different effect of T_N at any stage of growth in several tobacco (*Nicotiana tabacum*) cultivars. Jacobs (1951) found no parallel for flower or fruit development of peanuts with that of tomatoes reported by Went (1944a). Roberts and Summerfield (1987) suggested that within the range of conditions between a base and an optimum temperature, it is the mean diurnal temperature which is most important for the modulation of flowering rather than any specific or separate effects of either day or night value. Summerfield et al. (1992) indicated that this general rule as discussed by Roberts and Summerfield (1987) for annual crops also applies to rice.

The conclusion of Summerfield et al. (1992) for rice, however, was based on value for the optimum temperature for most rice cultivars between 24 and 26°C, which was derived from a bilinear model of Roberts and Summerfield (1987). This model assumes that DR was linearly related to temperature above a base value up to an optimum, beyond which DR decreases, again linearly, until a ceiling temperature is reached. Reanalysis of the data of Summerfield et al. (1992) using a nonlinear model showed that the optimum temperature was typically 27–32°C, obviously higher than the estimations of Summerfield et al. (1992) (Chapter 3). Within a

wide range of temperatures, it was found that the diurnal temperature amplitude affected the number of days from treatment to panicle emergence (Nagai, 1963) or to panicle initiation (Haniu et al., 1983), or from sowing to flowering (IRRI, 1977) in rice. IRRI (1977) further indicated that T_N affected DR more than T_D in rice and the effect was more significant in the tropically adapted cultivar IR8 than in the temperate cv. Fujisaka 5. Chang and Vergara (1971), Stewart and Langfield (1971) showed that the mean daily minimum temperature was a more important factor than the maximum temperature for the development from sowing to flowering in field-grown rice.

Because the relationship between temperature and DR is nonlinear over a wide range of conditions (Tollenaar et al., 1979; Loomis and Connor, 1992; Chapter 2), T_N is often in the range where DR increases strongly with temperature, whereas DR may change much less with changes in T_D . Based on the nonlinearity, Ellis et al. (1992b) indeed explained the difference in DR of maize between diurnally constant and fluctuating regimes with the same diurnal mean value reasonably well. However, for rice, the apparent difference in the impact of T_D and T_N can not be attributed to the nonlinearity alone (Chapter 3). It appears that the phenomenon of 'thermoperiodicity' found in the early work of Roberts (1943) and Went (1944a,b) for plant growth also applied to rice development.

The objective of this study was to determine experimentally whether there are different effects of T_D and T_N on development to flowering in rice.

Materials and methods

Plant materials and environmental conditions

Twenty-four cultivars of *O. sativa* of the *indica* and *japonica* types (Table 4.1) were selected on the basis of their origin, year of release and reported responsiveness to photoperiod (e.g. Vergara and Chang, 1985; Summerfield et al., 1992).

The experiment was conducted in nine naturally-lighted growth chambers at the International Rice Research Institute (IRRI). Treatments included five constant and four diurnally fluctuating temperatures (Table 4.2). Temperatures were maintained within $\pm 1^\circ\text{C}$. T_D and T_N were imposed for 12 h d⁻¹. To avoid confounding effects of an asynchrony between thermoperiod and photoperiod as reported by Morgan et al. (1987), T_D was maintained to match the photoperiod from 06:00 to 18:00 h. To maintain the constant photoperiod, each chamber was darkened by a metal cover when the natural daylength was longer than 12 h d⁻¹, and was illuminated with two 200 W incandescent lamps when it was < 12 h d⁻¹. Atmospheric CO₂ concentration and relative humidity were maintained at $340 \pm 10 \mu\text{mol mol}^{-1}$ and $70 \pm 5\%$, respectively. The experiment started on 13 Sep. 1993 and ended when all plants had flowered.

Plant husbandry and management

Five pre-germinated seeds were sown in 1-litre plastic pot (11 cm in diameter and 16 cm in height). There were three pot replicates for each cultivar at each temperature. Pots were filled

Table 4.1. Rice cultivars investigated in the experiment.

Cultivar	IRGC accession no. †	Origin	Sensitivity to photoperiod
<i>Indica</i>			
IR8 ‡	10320	IRRI	weak
IR36 ‡	30416	IRRI	weak
IR42 ‡	36959	IRRI	medium
IR64	66970	IRRI	weak
IR72	76330	IRRI	weak
Azucena ‡	00328	Philippines	medium
CO36	28556	India	strong
MR84	73077	Malaysia	medium
Guang Lu Ai 4	28480	China	weak
ADT36	64818	India	weak
Carreon ‡	05993	Philippines	strong
TN1 ‡	38845	China (Taiwan)	weak
Peta ‡	00035	Indonesia	medium
Shan You 63 §	—	China	weak
IR64616H §	—	IRRI	weak
<i>Japonica</i>			
Nipponbare	12731	Japan	medium
Koshihikari	08305	Japan	medium
Eiko ‡	09417	Japan	weak
Fujisaka 5	00244	Japan	weak
Lao Lai Qing	53396	China	strong
Xiu Shui 11	—	China	medium
Stejaree 45 ‡	46980	Korea	weak
Hwasong	—	Korea	medium
Illpoom	—	Korea	medium

† International Rice Germplasm Center at IRRI.

§ *Indica* hybrid cultivar.

— Not on IRGC listing.

‡ Cultivars also tested by Summerfield et al., (1992).

with medium loam soil, each blended with 0.042 g N, 0.010 g P₂O₅ and 0.024 g K₂O fertilizer. After sowing, the pots were kept in an open-sided greenhouse until the prophyll leaf emerged (about 48 h), and then transferred to the chambers. The chambers had 1.6 m² of floor space, and the 72 pots (three replicates × 24 cultivars) were arranged in a completely randomized design. Plants were thinned to one per pot at the three-leaf stage. At mid-tillering and panicle

Table 4. 2. Day and night temperature treatments imposed in separate chambers.

Treatment no.	Temperature (°C)		
	Day	Night	Mean
1	22	22	22
2	24	24	24
3	26	26	26
4	28	28	28
5	32	32	32
6	26	22	24
7	30	22	26
8	22	26	24
9	22	30	26

initiation, each pot was topdressed with 0.042 g N. From the five-leaf stage onwards, pots were rotated inside the chamber weekly to equalize any border or shading effects.

Plants were irrigated manually twice a day, at 06:00 and 18:00 h, respectively. Summerfield et al. (1992) showed that in their experiment, the temperature of water in pots often deviated from the air temperature and that day/night changeover phases for the water temperature in the diurnally fluctuating regimes were somewhat longer than those of the air temperature. Water temperature may affect rice development more than air temperature especially at early stages when the meristem is under water (Matsushima et al., 1964; Collinson et al., 1995). To avoid an effect of water temperature, plastic barrels with water were maintained at the different temperatures used in the experiment to enable fast adjustment of pot water temperature through irrigation in the morning or evening. The amount of water applied was based on consumption during the previous day.

The time of panicle emergence and flowering were recorded for individual tillers. Because plants of cv. Carreon did not flower and plants of cvs IR36 and TN1 flowered incompletely at a constant temperature of 22°C, the time of the main-stem panicle emergence (when panicle neck was at the same level as the auricle of the flag leaf) was used as the flowering time.

Results

The effect of constant diurnal temperature on rate of development to flowering

The response of DR to flowering, i.e. the inverse of the duration from sowing to flowering, to the five constant temperatures between 22 and 32°C was typically nonlinear (Fig. 4.1). The data on this response in each cultivar were fitted to a nonlinear model described in Chapter 2:

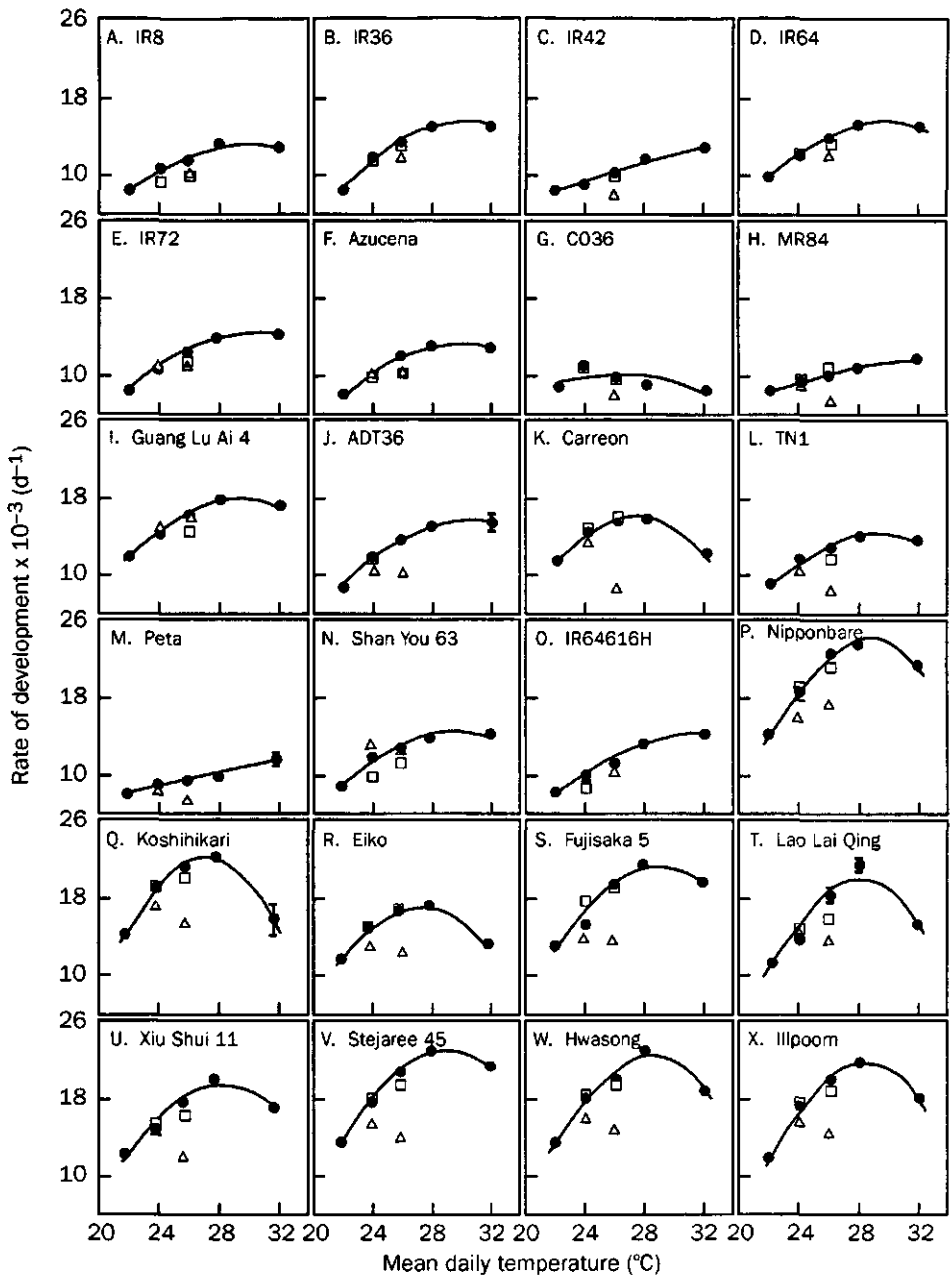


Fig. 4.1. Rates of development from sowing to flowering in 24 rice cultivars at five constant temperatures (\bullet), two diurnally fluctuating temperatures with warmer day than night (\square), and two fluctuating temperatures with cooler day than night (Δ). Vertical bars for the constant temperatures indicate means \pm standard errors (where larger than symbols). The curves show the relations of Eq. 4.1 (quantified in Table 4.3) determined from the observations at five constant temperatures.

Table 4.3. Values of parameters (with standard errors in parentheses) of Eq. 4.1 in 24 rice cultivars estimated from the data at diurnally constant temperatures when T_b and T_c were set to be 8 and 42°C, respectively.

Cultivar	R_o (d ⁻¹)	α	T_o (°C)	r^2 (df)
IR8	0.0132(0.0002)	2.55(0.26)	30.2(0.3)	0.963(14)
IR36	0.0159(0.0002)	3.14(0.30)	30.2(0.3)	0.971(13)
IR42	0.0132(0.0009)	1.09(0.30)	35.5(3.1)	0.942(14)
IR64	0.0158(0.0001)	2.86(0.09)	29.9(0.1)	0.996(14)
IR72	0.0146(0.0001)	2.75(0.17)	30.4(0.2)	0.987(14)
Azucena	0.0137(0.0002)	3.01(0.25)	30.0(0.3)	0.982(10)
CO36	0.0103(0.0003)	1.27(0.60)	25.7(1.0)	0.447(14)
MR84	0.0122(0.0004)	1.09(0.27)	33.9(2.1)	0.936(14)
Guang Lu Ai 4	0.0180(0.0002)	2.79(0.27)	29.6(0.3)	0.956(14)
ADT36	0.0159(0.0003)	2.75(0.38)	30.5(0.5)	0.944(14)
Carreon	0.0163(0.0001)	3.76(0.22)	27.3(0.1)	0.976(11)
TN1	0.0147(0.0001)	2.68(0.21)	29.7(0.2)	0.973(14)
Peta	0.0145(0.0192)	0.70(0.52)	41.8(18.2)	0.818(14)
Shan You 63	0.0149(0.0003)	2.42(0.40)	30.3(0.6)	0.913(14)
IR64616H	0.0148(0.0002)	2.19(0.25)	31.9(0.6)	0.976(14)
Nipponbare	0.0248(0.0002)	3.97(0.21)	28.9(0.1)	0.981(14)
Koshihikari	0.0224(0.0004)	4.91(0.46)	27.5(0.2)	0.921(13)
Eiko	0.0175(0.0002)	3.65(0.28)	27.7(0.2)	0.961(12)
Fujisaka 5	0.0222(0.0003)	3.48(0.29)	29.3(0.2)	0.962(14)
Lao Lai Qing	0.0215(0.0005)	5.56(0.55)	28.3(0.2)	0.919(14)
Xiu Shui 11	0.0199(0.0002)	3.81(0.26)	28.8(0.1)	0.967(14)
Stejaree 45	0.0240(0.0001)	3.52(0.10)	29.4(0.1)	0.996(13)
Hwasong	0.0236(0.0003)	4.18(0.30)	28.5(0.1)	0.958(14)
Illpoom	0.0231(0.0002)	4.65(0.21)	28.4(0.1)	0.985(13)

$$DR = 1/f = R_o \cdot \left[\left(\frac{T - T_b}{T_o - T_b} \right) \left(\frac{T_c - T}{T_c - T_o} \right)^{\frac{T_c - T_o}{T_o - T_b}} \right]^\alpha \tag{4.1}$$

where f is the number of days from sowing to flowering, T is the temperature (°C), R_o is the maximum value for DR, T_o is the optimum temperature at which $DR = R_o$; T_b and T_c are the base and ceiling temperature at which DR is zero; α is a cultivar-specific coefficient, defining the curvature of the relationship.

Although the five parameters in Eq. 4.1 can be derived from the data at constant temperatures, estimation of T_b and T_c by extrapolating the relation to lower or higher temperatures may not be reliable because values for T_b and T_c (Alocilja and Ritchie, 1991; Gao et al., 1992;

Kropff et al., 1994b) are far outside the range of the five constant temperatures selected in this study. Therefore, the standard values for T_b (8°C) and T_c (42°C) (Alocilja and Ritchie, 1991; Kropff et al., 1994b) were used to give more accurate estimation of the other parameters.

Values for parameters R_o , α and T_o , estimated by SigmaStat (Jandel Scientific, 1994) from the data of individual replicates of each treatment, varied among cultivars (Table 4.3). Eq. 4.1 adequately described the response of DR to the five constant temperatures (Fig. 4.1), with $r^2 > 0.91$ in most cultivars (Table 4.3). Because an optimum temperature was not observed for IR42, MR84 and Peta in the range of temperatures used in the present study (Fig. 4.1C,H,M), values for T_o in these cultivars are not reliably estimated.

Effects of day and night temperature on rate of development to flowering

The DR at four diurnally fluctuating temperatures often deviated from the values expected from the nonlinear relationships for the constant temperatures (Fig. 4.1). To determine whether there are different effects of T_D and T_N on DR, predicted days to flowering based on the results from the five constant temperatures were compared to the observations in the four fluctuating regimes. For the 26/22, 30/22 and 22/26°C treatments, observed and predicted days agreed; but for the 22/30°C treatment, the days to flowering were underestimated on the basis of the constant temperature data (Fig. 4.2).

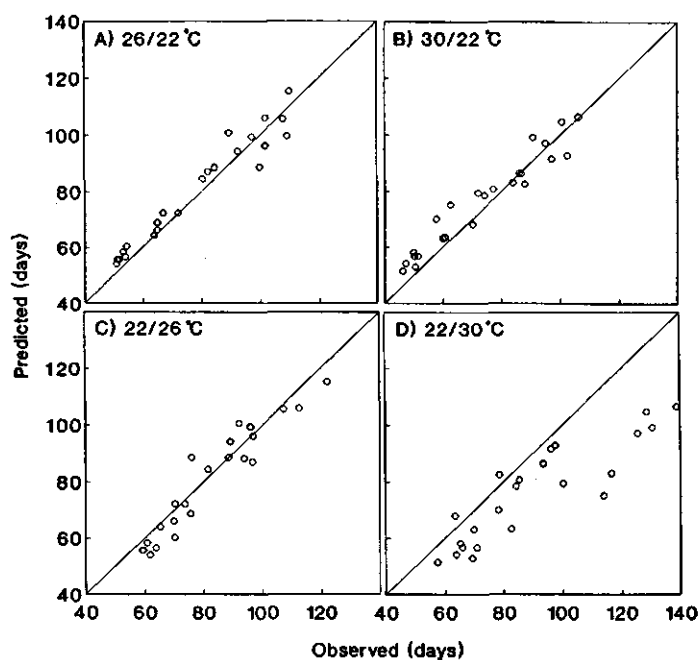


Fig. 4.2. Comparison of days to flowering observed at four diurnally fluctuating temperatures with those predicted by the relations of Eq. 4.1 (quantified in Table 4.3) determined from observations at five constant temperatures. The lines show the 1:1 relationship.

The results were further analysed to determine the difference in the response of DR to T_D and T_N by plotting the response to a change in T_D (or T_N) for treatments with the same T_N (or T_D) (Fig. 4.3). The response to changes in T_D at the same T_N was different from the response to changes in T_N at the same T_D in all cultivars except cv. Azucena in which the responses were essentially the same (Fig. 4.3F). This difference was more evident in *japonica* than *indica* cultivars. In most cases, plants grown at a lower T_N developed more rapidly than plants grown at a higher T_N at the same mean value. This resulted in a weak response of DR to T_N in most cultivars, e.g. Fujisaka 5 (Fig. 4.3S). However, a different trend was observed in cvs IR8, Guang Lu Ai 4 and Shan You 63 (Fig. 4.3A,I,N). For these three cultivars, T_N affected DR more than T_D .

In a second analysis, the results in Fig. 4.3 were used to predict the observations at the constant temperatures. This requires a model which separates effects of T_D and T_N on DR. To this end, both additive and multiplicative models for different effects of T_D and T_N were tested:

$$DR = R_{oD} \cdot g(T_D) + R_{oN} \cdot h(T_N) \quad (4.2)$$

$$DR = R_o \cdot g(T_D) \cdot h(T_N) \quad (4.3)$$

where R_{oD} , R_{oN} and R_o are development rate coefficients; $g(T_D)$ and $h(T_N)$ are functions defining the effects of T_D and T_N , respectively, and are quantified based on Eq. 4.1 as:

$$g(T_D) = \left[\left(\frac{T_D - T_b}{T_{oD} - T_b} \right) \left(\frac{T_c - T_D}{T_c - T_{oD}} \right)^{\frac{T_c - T_{oD}}{T_{oD} - T_b}} \right]^{\alpha_D}$$

$$h(T_N) = \left[\left(\frac{T_N - T_b}{T_{oN} - T_b} \right) \left(\frac{T_c - T_N}{T_c - T_{oN}} \right)^{\frac{T_c - T_{oN}}{T_{oN} - T_b}} \right]^{\alpha_N}$$

where T_{oD} and T_{oN} are the optimum values for T_D and T_N , respectively; α_D and α_N are coefficients characterizing the curvature of their respective relationship. Because little is known about the difference in either T_b or T_c between day and night, it is assumed that both T_b and T_c are the same for day and night responses.

The models were parameterized from the data of individual replicates of the five treatments shown in Fig. 4.3. No difference in goodness of fit was found between the two models. However, because of one more parameter in Eq. 4.2, parameters for this model derived from the data of the five treatments had large standard errors. Eq. 4.3 was then chosen for further analyses.

Table 4.4 gives the coefficients of Eq. 4.3 estimated with a standard T_b (8°C) and T_c (42°C). These coefficients were used to predict the flowering times at the constant temperatures. The model predicted well the flowering dates at constant temperatures 24, 26 and 28°C (Fig. 4.4A). The days to flowering were underpredicted by the model only for cv. CO36 at 26 and 28°C. However, when the model was extrapolated to predict the effect of a constant temperature of 32°C, the days to flowering were overpredicted in many *indica* cultivars (Fig. 4.4B).

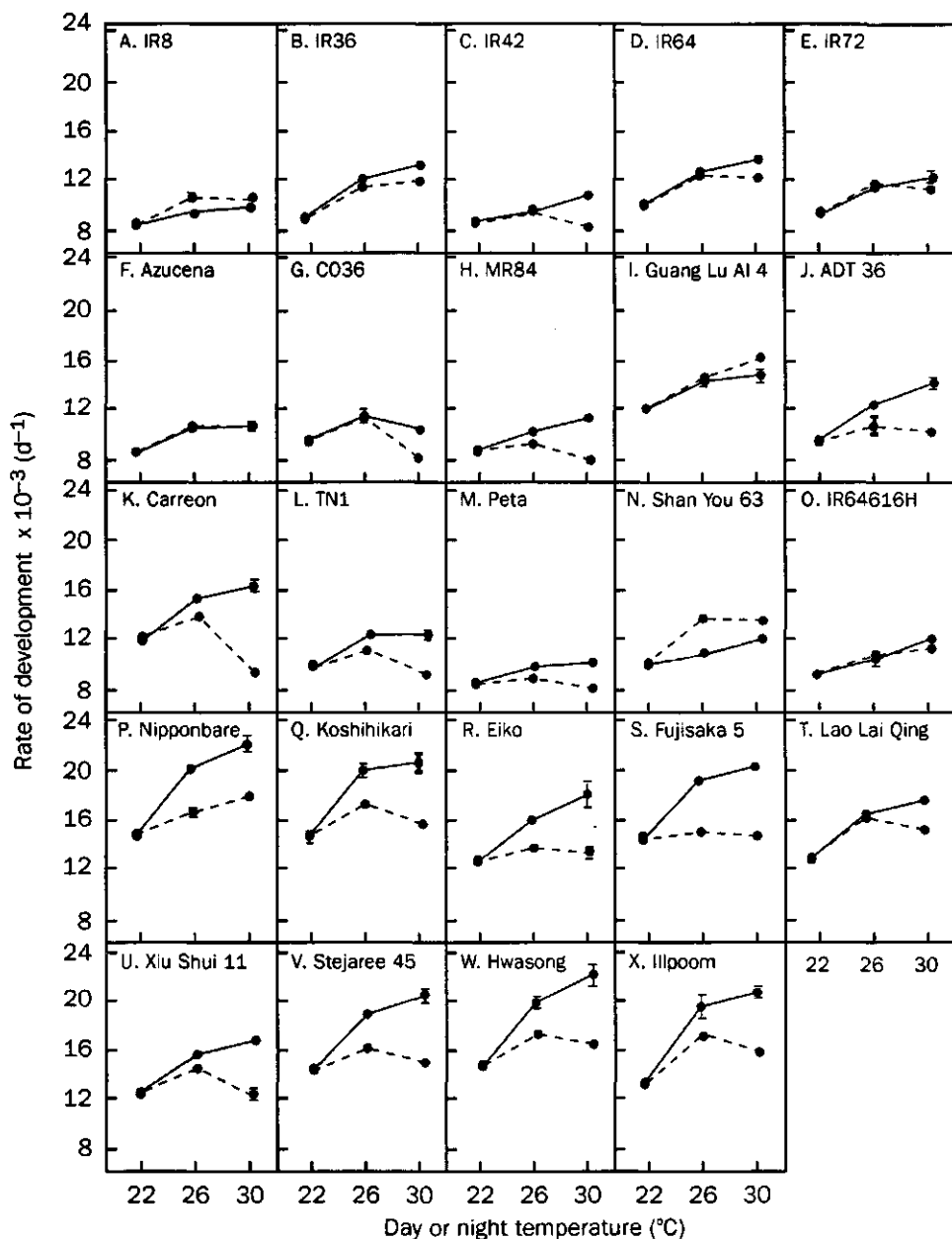


Fig. 4.3. Effects of day temperatures between 22 and 30°C with a constant night temperature of 22°C (—) and effects of night temperatures between 22 and 30°C with a constant day temperature of 22°C (---) on rates of development from sowing to flowering in 24 rice cultivars. Vertical bars indicate means \pm standard errors (where larger than symbols).

Table 4.4. Values of parameters (with standard errors in parentheses) of Eq. 4.3 in 24 rice cultivars estimated from the data at temperatures 22/22, 26/22, 30/22, 22/26 and 22/30°C (day/night) when T_D and T_c were set to be 8 and 42°C, respectively.

Cultivar	R_o (d ⁻¹)	α_D	T_{oD} (°C)	α_N	T_{oN} (°C)†	r^2 (df)
IR8	0.0130(0.0018)	0.47(0.42)	35.7(12.5)	2.50(0.38)	27.7(0.3)*	0.915(14)
IR36	0.0174(0.0004)	2.30(0.26)	29.8(0.5)	2.26(0.27)	28.7(0.4)+	0.983(14)
IR42	0.0141(0.0174)	0.46(0.25)	42.0(16.0)	2.34(0.26)	25.6(0.1)***	0.971(14)
IR64	0.0175(0.0004)	1.94(0.28)	29.9(0.7)	2.73(0.28)	27.6(0.2)***	0.974(14)
IR72	0.0151(0.0006)	1.69(0.52)	29.8(1.4)	3.00(0.51)	27.4(0.3)*	0.897(14)
Azucena	0.0137(0.0006)	2.29(0.51)	28.0(0.5)	2.39(0.63)	28.0(0.8) <i>ns</i>	0.905(11)
CO36	0.0135(0.0005)	3.11(0.47)	26.6(0.2)	4.58(0.50)	25.4(0.2)***	0.943(14)
MR84	0.0141(0.0024)	0.60(0.10)	40.8(4.6)	1.69(0.12)	25.0(0.1)***	0.997(14)
Guang Lu Ai 4	0.0198(0.0013)	1.66(0.67)	28.7(1.3)	1.27(0.65)	31.9(3.9) <i>ns</i>	0.850(14)
ADT36	0.0162(0.0012)	1.91(0.71)	31.4(2.5)	1.71(1.00)	27.1(1.2) <i>ns</i>	0.939(11)
Carreon	0.0192(0.0008)	2.14(0.49)	29.5(0.9)	5.22(0.65)	25.1(0.2)***	0.975(13)
TN1	0.0142(0.0004)	2.51(0.35)	28.2(0.4)	3.25(0.39)	25.6(0.2)***	0.969(14)
Peta	0.0100(0.0006)	1.35(0.70)	29.2(1.9)	1.55(0.92)	25.1(0.8)+	0.832(12)
Shan You 63	0.0212(0.0289)	0.50(0.33)	41.9(19.5)	4.26(0.28)	27.7(0.1)***	0.983(14)
IR64616H	0.0192(0.0416)	0.66(0.49)	41.9(21.8)	1.71(0.49)	28.9(1.0)*	0.914(14)
Nipponbare	0.0271(0.0028)	2.44(0.36)	29.8(0.7)	0.59(0.42)	34.8(8.7) <i>ns</i>	0.975(14)
Koshihikari	0.0246(0.0014)	3.08(0.51)	28.4(0.5)	2.56(0.86)	26.6(0.3)+	0.952(12)
Eiko	0.0193(0.0015)	1.52(0.74)	31.9(3.6)	1.15(0.86)	26.9(1.3) <i>ns</i>	0.899(13)
Fujisaka 5	0.0203(0.0005)	2.52(0.26)	29.0(0.3)	0.42(0.31)	27.1(1.3) <i>ns</i>	0.987(14)
Lao Lai Qing	0.0212(0.0004)	1.99(0.23)	29.5(0.5)	2.87(0.23)	27.1(0.1)***	0.981(14)
Xiu Shui 11	0.0191(0.0004)	1.75(0.23)	29.7(0.6)	2.90(0.29)	25.9(0.1)***	0.986(12)
Stejaree 45	0.0224(0.0008)	2.44(0.42)	29.2(0.6)	1.85(0.49)	26.4(0.4)**	0.965(13)
Hwasong	0.0255(0.0014)	2.44(0.64)	29.8(1.1)	2.34(0.72)	26.9(0.5)*	0.928(14)
Illpoom	0.0264(0.0014)	3.60(0.58)	28.7(0.5)	3.23(0.65)	27.1(0.3)*	0.945(14)

† +, *, **, *** indicate that T_{oN} is significantly different from T_{oD} at the probability levels of 0.10, 0.05, 0.01 and 0.001, respectively; *ns* means no significant difference between T_{oD} and T_{oN} ($P > 0.10$).

The overpredictions also occurred when Eq. 4.2 was used. This could arise because Eq. 4.2 or Eq. 4.3 does not account for some type of interaction between T_D and T_N , which was observed in several cultivars. For example, in cv. CO36 for which the predictive discrepancies were most evident (Fig. 4.4), there was a strongly negative interaction between T_D and T_N (Fig. 4.5).

The optimum temperature differed between day and night (Fig. 4.3). In many cultivars, the optimum T_D , T_{oD} , was not observed within the range between 22 and 30°C. For these cultivars, as DR increased proportionally with T_D , the model gave a high estimate of T_{oD} (Table 4.4). The optimum night value, T_{oN} , was typically 2–4°C lower than T_{oD} . However, the difference

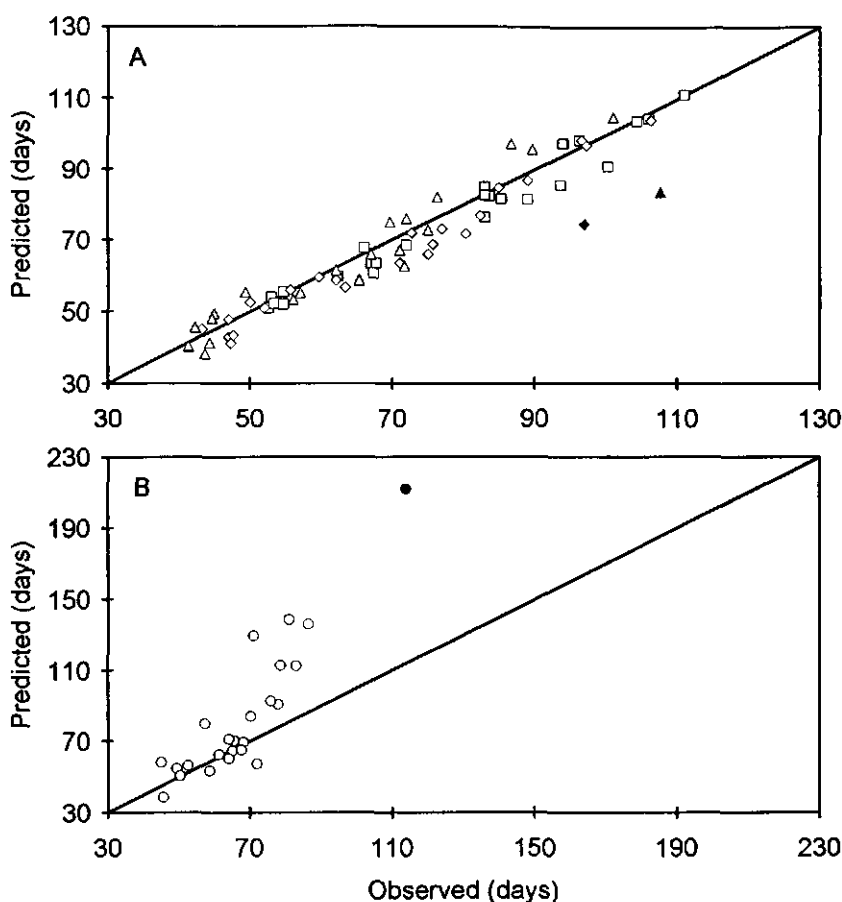


Fig. 4.4. Comparison of days to flowering observed at the constant temperatures of (A) 24°C (square), 26°C (diamond) and 28°C (triangle) and (B) 32°C with those predicted by the relations of Eq. 4.3 (quantified in Table 4.4) determined from observations at five diurnal temperatures (day/night) 22/22, 26/22, 30/22, 22/26 and 22/30°C. The lines show the 1:1 relationship. The closed symbols are for cv. CO36.

between T_{oD} and T_{oN} were not significant ($P > 0.10$) in cvs Azucena, Guang Lu Ai 4, ADT36, Nipponbare, Eiko and Fujisaka 5 (Table 4.4). Comparison with the optimum mean daily value, T_o , estimated from the data at the constant temperatures (Table 4.3), indicates that T_o was between T_{oD} and T_{oN} in most cultivars. In many others except cv. Peta, T_o was only slightly outside of the range limited by T_{oD} and T_{oN} .

An analysis of the combined data of constant and fluctuating temperatures

Eqs 4.1, 4.2 and 4.3 were further evaluated against the combined data of all nine treatments in 24 rice cultivars. To avoid confounding effects as a result of the nonlinearity between DR and

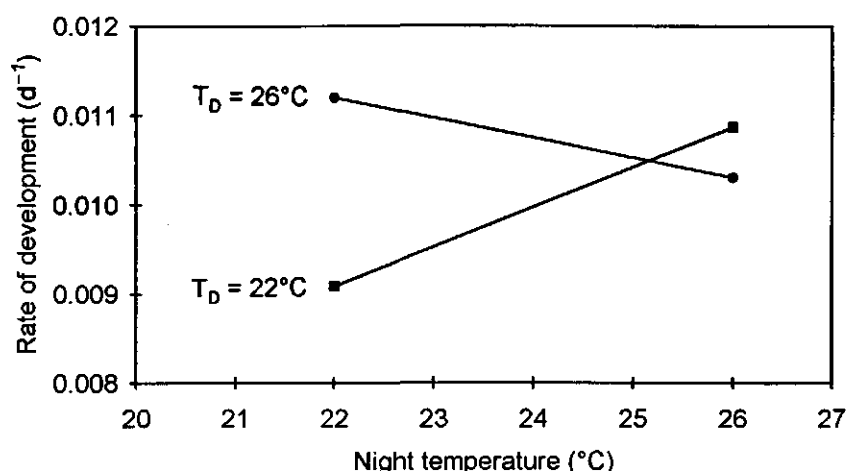


Fig. 4.5. Effects of two night temperatures on the rate of development from sowing to flowering in cv. CO36 at two different levels of day temperature (T_D).

temperature, the day and night periods were used separately but with the same coefficients in parameterizing Eq. 4.1 from the data including diurnally fluctuating temperatures. Not surprisingly, both Eq. 4.2 and Eq. 4.3 fitted to the data better than Eq. 4.1 in terms of either mean absolute discrepancy (MD) or r^2 for the linear regression between observed and predicted days (Fig. 4.6). However, no significant difference ($P > 0.10$) was found between Eq. 4.2 and Eq. 4.3, although Eq. 4.2 performed somewhat better than Eq. 4.3 (Fig. 4.6). Furthermore, Eq. 4.2 often had large standard errors for its parameters even though they were estimated from the data of all nine treatments.

Discussion

The data for rice presented in this Chapter support the conclusion from earlier studies that there are different effects of T_D and T_N on DR (Fig. 4.3), a phenomenon referred to as 'thermoperiodicity' or 'thermoperiodism' (Went, 1944a). Several workers have explained thermoperiodicity as a result of the nonlinearity of the relationship between temperature and DR (e.g. Tollenaar et al., 1979; Loomis and Connor, 1992). In most phytotron experiments, T_N was lower than T_D (e.g. IRRI, 1977; Summerfield et al., 1992). T_D was most probably beyond the optimum value whereas T_N was often in the range where DR increased proportionally with increasing temperature. In this Chapter, an attempt was made to exclude this effect of temperature level between T_D and T_N by comparing responses of plants to opposite diurnal temperature fluctuations at the same mean daily value (Table 4.2). If nonlinearity was the only reason for thermoperiodicity, plants would flower simultaneously in the 26/22 and 22/26°C treatments, and in the 30/22 and 22/30°C treatments. The results in Fig. 4.3 indicate that

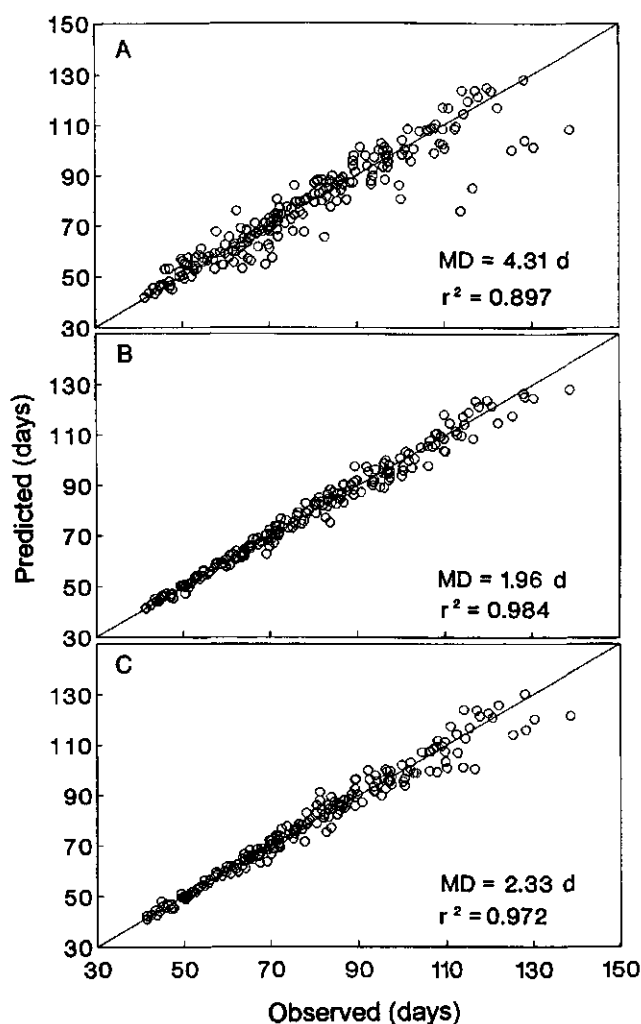


Fig. 4.6. Comparison of observed days to flowering for all rice cultivars at all nine temperatures with those predicted by Eq. 4.1 (A), Eq. 4.2 (B), and Eq. 4.3 (C). The linear regressions between predicted (y) and observed days (x) are: $y = 7.02(\text{SE } 1.69) + 0.90(\text{SE } 0.02)x$ for Eq. 4.1, $y = 1.56(0.69) + 0.98(0.01)x$ for Eq. 4.2, and $y = 2.13(0.91) + 0.97(0.01)x$ for Eq. 4.3, with the coefficients of determination (r^2) shown in the figure. MD is the mean absolute discrepancy of predictions by the models. The lines show the 1:1 relationship.

nonlinearity cannot explain the response. This agrees with the conclusion in Chapter 3 that the difference in DR of rice between diurnally fluctuating and equivalent constant temperature cannot be due to nonlinearity alone.

Many studies (Roberts, 1943; Went, 1944a,b; Chang and Vergara, 1971; Stewart and Langfield, 1971; IRRI, 1977; Littleton et al., 1979) concluded that T_N was more important

than T_D for plant growth and development. However, the results of this Chapter indicated that T_N promoted flowering more efficiently than T_D in three cultivars only, whereas the opposite effect was found in most other cultivars (Fig. 4.3). The results for cv. IR8 (Fig. 4.3A) agrees with the finding that DR for this cultivar from a phytotron experiment (IRRI, 1977) and field experiments (Chang and Vergara, 1971; Stewart and Langfield, 1971) is primarily determined by the night or minimum temperature. In contrast, we did not find a greater influence of T_N in cv. Fujisaka 5 (Fig. 4.3S), which IRRI (1977) showed to have. The consistent importance of T_N found by IRRI (1977) for both IR8 and Fujisaka 5 can be attributed to the longer duration for T_N (16 h d⁻¹) than for T_D (8 h d⁻¹) and the lower temperatures for T_N (18–24°C) than for T_D (20–36°C).

Based on the bilinear linear model, Summerfield et al. (1992) showed that the optimum temperature was 24–26°C in most rice cultivars and concluded that within the sub-optimal range of temperature, it was the mean daily temperature which largely determined DR to flowering in rice. Re-interpretation of the data of Summerfield et al. (1992) with a nonlinear model showed that the optimum temperature was generally in the range of 27–32°C (Chapter 3), which agrees with the values found in the present Chapter (Table 4.3). The optimum mean diurnal temperature identified by Summerfield et al. (1992) was similar to the optimum T_N established here, which is significantly lower than the optimum T_D in most cultivars (Table 4.4).

The central question is why rice development responds differently to T_D and T_N . Considerable evidence has been found for interactions between temperature and photoperiod (e.g. Roberts and Struckmeyer, 1938; Roberts and Carpenter, 1965; Major et al., 1990). The results for cvs IR8, Guang Lu Ai 4 and Shan You 63, which consistently flowered earlier when T_N was higher (Fig. 4.3A,I,N), could be explained by the stimulation of a high T_N on photoinduction in rice (Chen and Shao, 1981; Khan, 1982), because it is the dark period which is crucial in rice photoperiodism (Vergara and Chang, 1985). However, these three cultivars are all weakly photoperiod-sensitive (Table 4.1). Most cultivars, including strongly photoperiod-sensitive cultivars CO36, Carreon and Lao Lai Qing (Table 4.1), flowered earlier at treatments with a lower T_N (Fig. 4.3). This indicates that thermoperiodism may be a phenomenon independent from photoperiodism, or that the light period is also important during the photoinduction process. An additional reason for the different effects of T_D and T_N can be associated with the reduced supply of assimilates for growth of plants in the diurnally reversed temperature. The effect of assimilates on flower development of crops has been reported (Sachs, 1987; Bernier, 1988) and is supported by recent evidence for effects of CO₂ (Manalo et al., 1994; Mortensen, 1994) and light intensity (Sedighi and Jolliff, 1994) on plant development. However, the hypothesis related to the assimilate supply cannot explain the results in IR8, Guang Lu Ai 4 and Shan You 63. Innovative physiological studies are needed to elucidate the reason for the different effects of T_D and T_N .

Although many existing models for phenological development in rice (e.g. Horie and Nakagawa, 1990; Gao et al., 1992) use the mean daily temperature, the evidence in this study justifies models of Robertson (1968) and Brown (1969), in which effects of T_D and T_N on DR were considered to be different. However, while Robertson (1968) described effects of T_D and T_N on the DR in an additive way, this Chapter found that a multiplicative model with one less parameter also performed well (Fig. 4.6). The additive model ignores any possible interaction

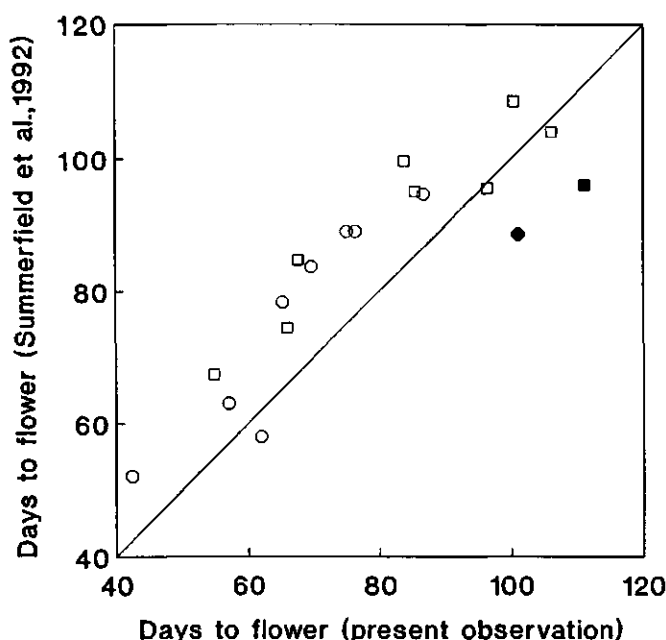


Fig. 4.7. Comparison in days from sowing to flowering for nine rice cultivars at 24 (square) or 28°C (circle) between the data of Summerfield et al. (1992) and the present observations. The line shows the 1:1 relationship. The nine cultivars common to both studies are identified in Table 4.1. The closed symbols are for cv. Peta.

between T_D and T_N , and had large standard errors for parameters derived from the data of the experiment reported in this Chapter. The multiplicative model allows for the situation of no development when plants grow at a temperature continuously lower than T_b during the day, or during the night (unpublished data).

Summerfield et al. (1992) indicated that the water temperature which surrounded the basal regions of rice stems were often lower than the ambient air. Nine of the cultivars used by Summerfield et al. (1992) were also examined in the present study (Table 4.1). The results of the two experiments in days to flowering at two diurnally constant temperatures 24 and 28°C common to both experiments are given in Fig. 4.7. In most cases except for cv. Peta, plants flowered earlier in the present experiment than that of Summerfield et al. (1992). This suggests that the control of water temperature in the present study effectively eliminated a large deviation from air temperature. Since it is water temperature which largely determines the development of rice plants during their early growth (Matsushima et al., 1964), the water temperature is the important element to be considered for predicting rice flowering dates.

Chapter 5

Use of the Beta function to quantify the effect of photoperiod on flowering in rice

Abstract The time of flowering in rice (*Oryza sativa* L.) is affected by photoperiod. A nonlinear response has been reported with an optimum photoperiod, either below or above which flowering can be delayed. Three equations which account for both short- and long-day nonlinear effects were compared to describe the response of rice to photoperiod. The Beta model is unique in that it can describe an asymmetric shape of the relation between days to flowering (f) or rate of development to flowering ($1/f$) and photoperiod (P). The other two models were the quadratic relation between f and P (QFP) and the quadratic relation between the rate, $1/f$, and P (QRP). The Beta model accurately described the flowering response to a wide range of photoperiods, and was superior to QFP and QRP in predicting the photoperiod effect on the flowering time as observed in several published data sets involving diverse rice cultivars.

Introduction

The time interval between sowing and flowering in rice is influenced by photoperiod. A large variation in photoperiod sensitivity among cultivars has been reported (Chandraratna, 1954; Best, 1959; Tang et al., 1978; Evans et al., 1984; Vergara and Chang, 1985). This wide range of photoperiod sensitivities reflects a mechanism of crop adaptation to cope with diverse environmental conditions (Major and Kiniry, 1991).

Rice is generally classified as a short-day plant (Vergara and Chang, 1985). However, a long-day response has often been reported as well (e.g. Misra, 1953). Such a discrepancy may be due to the qualitative way in which a single photoperiod is compared with the gradual change of natural daylength (Coolhaas and Wormer, 1953; Chandraratna, 1954). Chandraratna (1954) and Best (1959, 1960 and 1961) suggested a necessity to use a quantitative way for studying the effect of photoperiod on days to flowering (f). Many studies, where the quantitative way was used, demonstrated the existence of an optimum photoperiod (P_o), above or below which f would increase (Chandraratna, 1954; Best, 1960; Roberts and Carpenter, 1962; Roberts and Carpenter, 1965; Vergara et al., 1965; Vergara and Lilis, 1967; Ahn, 1968; Tang et al., 1978). In the supra-optimal range (i.e. photoperiods $> P_o$), rice behaves like a short-day plant; but, in the sub-optimal range (photoperiods $< P_o$), as a long-day plant (Best, 1959). Examples for this type of nonlinear flowering response curve are given in Fig. 5.1 based on the data of Best (1961) and Roberts and Carpenter (1962). The short-day response of rice flowering in the supra-optimal range is a well-known phenomenon, whereas the long-day response in the sub-optimal range was often attributed to a shortage of energy for development under short photoperiods (e.g. Horie, 1994). However, Best (1961) reported that the delay of

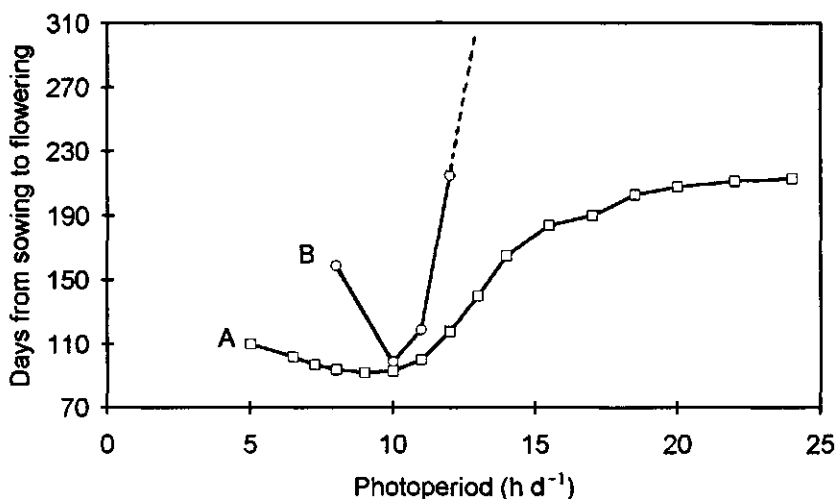


Fig. 5.1. Curves of photoperiodic response for days from sowing to flowering in two rice cultivars (curve A: data of Best (1961) for cv. Tjina; curve B: data of Roberts and Carpenter (1962) for cv. Lead 35). The dashed part of curve B indicates no flowering at photoperiods $> 12 \text{ h d}^{-1}$.

flowering at short photoperiods remained obvious when this 'non-photoperiodic' effect due to the shortage of energy was corrected (curve A in Fig. 5.1). The delay by a short photoperiod of 8 h d^{-1} , compared to the flowering time at 10 h d^{-1} , can be 60 d even when daily total amount of light radiation was uniform among the photoperiod treatments (curve B in Fig. 5.1).

The responses of curve A in Fig. 5.1 indicate that no single simple equation can be used to fit the nonlinear response over the whole range of photoperiods between 5 and 24 h d^{-1} as used by Best (1961). However, most studies on rice photoperiodism used photoperiods around the optimum, i.e. between 8 and 16 h d^{-1} (e.g. Vergara et al., 1965), which cover the main range of interest to agronomists and breeders (Chandraratna, 1954) and the photoperiod environments of world's principal rice-growing regions (Summerfield et al., 1992). Chandraratna (1954) used a quadratic equation $f = a + bP + cP^2$ (where P is photoperiod in h d^{-1} , and a , b and c are constants) to fit the photoperiod response of days to flowering. Based on this equation, he suggested that the flowering response of rice cultivars to photoperiod can be characterized by P_0 , minimum days to flowering (f_0) and photoperiod sensitivity. Values of P_0 and f_0 can be estimated by assuming that the first-order derivative equals zero; and an estimate of the photoperiod sensitivity is related to the gradient of the response curve (Chandraratna, 1954).

Robertson (1968) also considered the response of the long-day crop wheat (*Triticum aestivum* L.) to photoperiod as a nonlinear function using an optimum photoperiod. In contrast to Chandraratna (1954), however, Robertson (1968) used the quadratic equation to describe the development rate (DR), which is the inverse of the days to flowering, as a function of photoperiod. This model was subsequently tested by others (e.g. Angus et al., 1981) for wheat

and applied to barley (*Hordeum vulgare* L.) (Williams, 1974) and soybean [*Glycine max* (L.) Merr.] (Major et al., 1975).

In many rice cultivars like Tjina, the response to photoperiod is asymmetric (Fig. 5.1) (Best, 1960 and 1961). Therefore, the symmetric quadratic methods can be subjected to criticism and another approach is required. In Chapter 2, it was demonstrated that the Beta function, commonly used as a skewed probability density function in statistics (Johnson and Leone, 1964; Abramowitz and Stegun, 1965), can be used to describe an asymmetric response of DR to temperature. After transformation to the development rate, the Beta function can probably be used to adequately describe the response of DR to photoperiod as well.

The objective of this Chapter is to analyse the ability of the Beta function to describe the nonlinear response of DR to photoperiod in rice, in comparison with the quadratic models as proposed by Chandraratna (1954) and Robertson (1968).

Materials and methods

Experimental data

The data presented by Best (1961) on days from sowing to flowering in four rice cultivars with different photoperiod sensitivities were used to evaluate the ability of the Beta model to describe the shape of the photoperiod response of rice development. Plants of cvs Americano 1600, Tjina, Basmati 370 and Skrivimankoti were grown at photoperiods ranging from 5 to 24 h d⁻¹. The data covering the range of photoperiods from 8.0 to 15.5 h d⁻¹ were used in this study for testing the model.

Three other published data sets were used to compare the Beta model with the quadratic models as proposed by Chandraratna (1954) and Robertson (1968). The first data set gives days from sowing to flowering in 12 rice cultivars grown at six photoperiods of 8, 10, 12, 13, 14 and 16 h d⁻¹ (Vergara and Lilis, 1967). The second data set was published by Ahn (1968) where 15 Korean early, medium and late maturity cultivars were tested at six photoperiods: 8, 10, 12, 13, 14 and 16 h d⁻¹. The third data set on the responses of 38 rice cultivars to photoperiods of 10, 12, 13 and 14 h d⁻¹ was derived from a phytotron experiment with a diurnally constant temperature of 25°C (Tang et al., 1978).

Modelling methods

The quadratic relation between f and P (QFP)

Chandraratna (1954) proposed a quadratic equation to fit data on the relationship between days to flowering (f) and photoperiod (P):

$$f = a + bP + cP^2 \quad (5.1)$$

where a , b and c are constants. Based on Eq. 5.1, the value for P_0 can be derived as $-b/2c$, and the value for minimum days to flowering, f_0 , at P_0 is calculated by $a - b^2/4c$.

The quadratic relation between rate, 1/f, and P (QRP)

Robertson (1968) used the quadratic equation to describe the response of DR, inverse of the days, to photoperiod. This relation can be formulated as:

$$DR = 1/f = a' + b'P + c'P^2 \quad (5.2)$$

where a' , b' and c' are constants. Based on Eq. 5.2, P_o can be derived as $-b'/2c'$ and f_o is calculated by $4c'/(4a'c' - b'^2)$. Eq. 5.2 can also be used to derive values for lower and upper critical limits, i.e. base and ceiling photoperiods, at which DR is zero.

The Beta model

Based on the Beta function, a nonsymmetric and unimodal probability density functions in statistics (Johnson and Leone, 1964; Abramowitz and Stegun, 1965), an equation for the response of development rate to photoperiod can be expressed as

$$DR = 1/f = \exp(\mu)(P - P_b)^\delta (P_c - P)^\epsilon \quad (5.3)$$

where P_b and P_c are the base and ceiling photoperiods, respectively; μ , δ and ϵ are model parameters. By setting the first-order derivative of Eq. 5.3 at zero, P_o can be derived as:

$$P_o = \frac{\delta P_c + \epsilon P_b}{\delta + \epsilon} \quad (5.4)$$

and the value for f_o can be calculated by:

$$f_o = \exp(-\mu) \delta^\delta \epsilon^\epsilon \left(\frac{\delta + \epsilon}{P_c - P_b} \right)^{\delta + \epsilon} \quad (5.5)$$

Because little is known about accurate values of P_b and P_c in rice, a simple form of the Beta model was used, in which the extreme values of daylength, 0 and 24 h d⁻¹, were assigned to P_b and P_c , respectively:

$$DR = 1/f = \exp(\mu) P^\delta (24 - P)^\epsilon \quad (5.6)$$

This also reduces the number of parameters to be estimated in the Beta model.

Analytical approaches

The models were parameterized based on the data for the individual cultivars for all data sets. The mean value of absolute predictive discrepancies (MD) and the value of r^2 for the linear regression between observed and predicted days to flowering by each modelling method were calculated. The MD and r^2 values were taken as measures of accuracy for the models to describe the data.

Results

Illustration of the descriptive ability of the Beta model

The simplified Beta model, Eq. 5.6, was fitted to the data of Best (1961) in four rice cultivars at photoperiods from 8.0 to 15.5 h d⁻¹. The parameter values for the four cultivars are given in Table 5.1. The equation described the data with $r^2 \geq 0.95$. Fig. 5.2 shows the ability of the model to predict the general trend of the response, demonstrating the flexibility of the function.

Table 5.1. Values of parameters (with standard errors in parentheses) of Eq. 5.6 derived from the data of Best (1961) on days to flowering in four rice cultivars at photoperiods from 8 to 15.5 h d⁻¹, and resultant estimates of the optimum photoperiod, P_o , and the minimum number of days to flowering, f_o .

Cultivar	Model parameter			n^\ddagger	r^2	P_o (h d ⁻¹)	f_o (d)
	μ	δ	ϵ				
Americano 1600	-15.46(1.08)	2.06(0.21)	2.48(0.23)	8	0.970	10.9	64.6
Tjina	-15.27(3.10)	1.43(0.58)	2.81(0.68)	8	0.962	8.1	90.5
Basmati 370	-27.93(4.24)	3.93(0.79)	5.53(0.93)	8	0.952	10.0	72.7
Skrivimankoti	-51.08(9.63)	7.56(1.70)	11.19(2.20)	7	0.960	9.7	61.9

‡ n is the number of observations fitted.

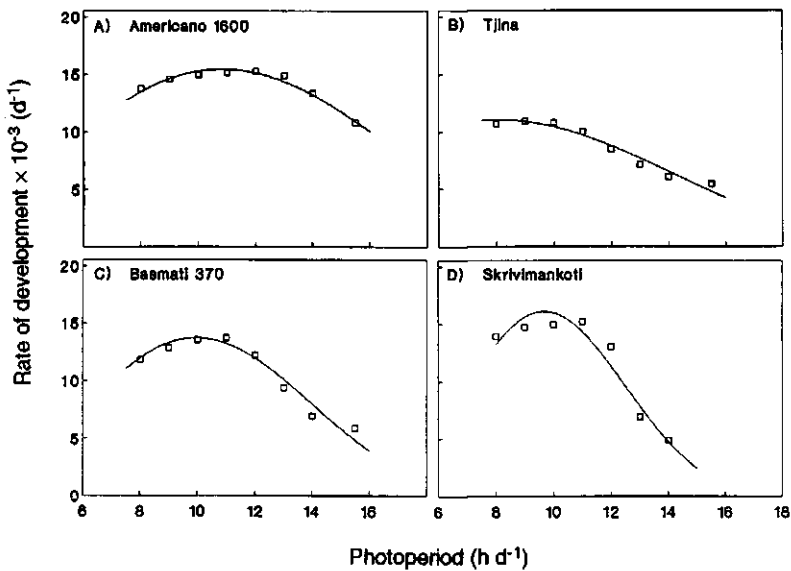


Fig. 5.2. Rate of development to flowering as affected by photoperiods between 8 and 15.5 h d⁻¹ in four rice cultivars (data of Best, 1961). The curves were based on Eq. 5.6 with parameters quantified in Table 5.1.

Table 5.2. Mean absolute predictive discrepancies in days (MD) and the r^2 value for the linear regression between observed and predicted days to flowering by the three models.

Data set	QFP (Eq. 5.1)		QRP (Eq. 5.2)		Beta (Eq. 5.6)	
	MD	r^2	MD	r^2	MD	r^2
Vergara and Lilis (1967)	2.92	0.980	5.54	0.920	2.89	0.980
Ahn (1968)	2.53	0.975	3.94	0.922	2.26	0.977
Tang et al. (1978)	2.42	0.985	4.73	0.939	1.93	0.990

Comparison of the Beta model with QFP and QRP in predictability

The simplified Beta model, Eq. 5.6, was further compared with the QFP and QRP methods. The performance of the models for the data sets of Vergara and Lilis (1967), Ahn (1968) and Tang et al. (1978) is illustrated in Table 5.2. Although all models described the data quite well with $r^2 \geq 0.92$, the Beta model performed better than QFP, and QFP was better than QRP in terms of either MD or r^2 value for all three data sets. However, the superiority of the Beta model to the QFP method was small for these data sets (Fig. 5.3).

Discussion

The concept of a 'critical photoperiod' has often been used to characterize the photoperiodic response of flowering in rice (e.g. Gao et al., 1992). Summerfield et al. (1992) indicated that photoperiods below this critical value have no delaying effect on floral development in rice. This concept contradicts the existence of an optimum photoperiod, which has been observed in rice (Chandraratna, 1954; Best, 1960; Roberts and Carpenter, 1962; Roberts and Carpenter, 1965; Vergara et al., 1965; Vergara and Lilis, 1967; Ahn, 1968; Tang et al., 1978). Because the natural daylength in rice-growing regions is normally in the supra-optimal range, the delay of flowering of rice at supra-optimal photoperiods makes it a short-day plant (Vergara and Chang, 1985). However, a long-day response was often observed at the sub-optimal photoperiods. This long-day response cannot be only attributed to a lack of energy for growth and development, as the delay by a short photoperiod was obvious even when daily total amount of light radiation was uniform among photoperiod treatments (Roberts and Carpenter, 1962). The long-day effect of sub-optimal photoperiods can be explained by the fact that the light period also plays an important role in the catena of photo-inductive reactions although the dark period is crucial in the photoperiod response (Chandraratna, 1963).

The quadratic method QRP has been successfully used for predicting development in several crops (Robertson, 1968; Williams, 1974; Major et al., 1975; Angus et al., 1981). Its performance in estimating the photoperiod effect in rice, however, was consistently inferior to

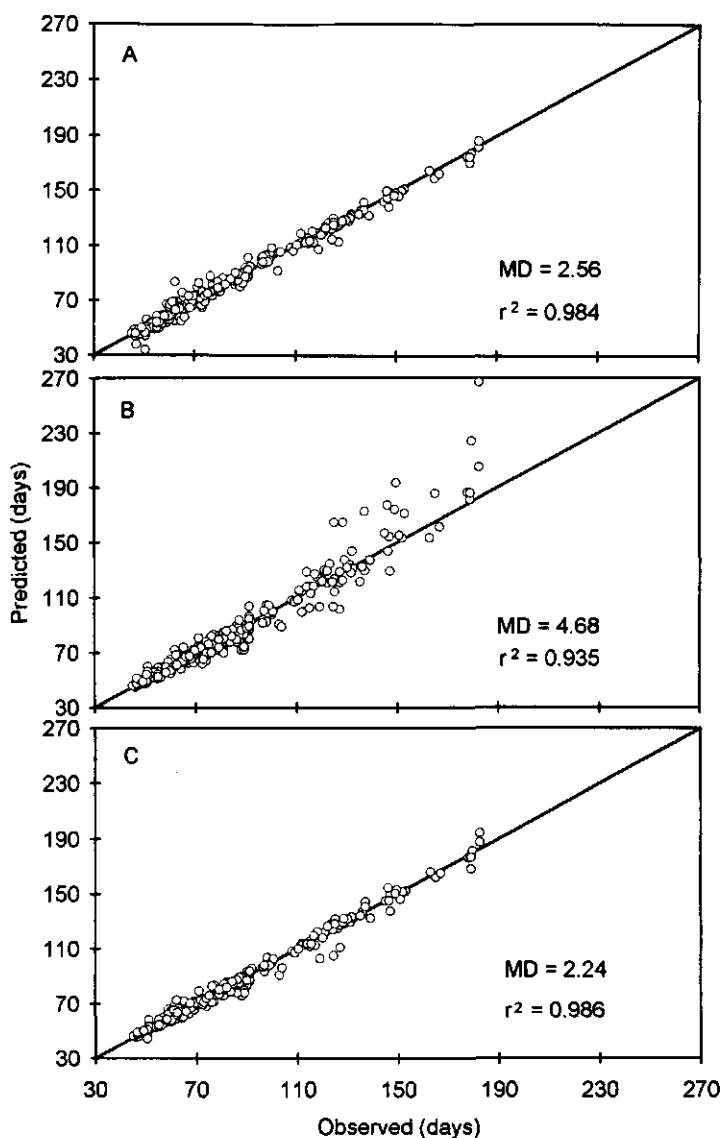


Fig. 5.3. The pooled result in three published data sets (see text) for comparison between observed days to flowering of rice and those predicted by three models (A: Eq. 5.1; B: Eq. 5.2; C: Eq. 5.6). The lines indicate the 1:1 relationship. MD is the mean absolute predictive discrepancy in days, and r^2 is for the linear regression between predicted and observed days.

that of the quadratic model QFP and the Beta model (Table 5.2, Fig. 5.3). Among the three models, the Beta model is unique since it describes the nonsymmetric shape of the relationship for f or $1/f$. This model with only three parameters, Eq. 5.6, adequately described the shape of

the relationship over the range of photoperiods in rice-growing environments (Fig. 5.2), and performed better than the two quadratic equations with the same number of parameters (Table 5.2, Fig. 5.3). Although Eq. 5.6 is empirical, it describes the response of development as an interaction between photoperiod, P , and dark period, $24 - P$, in agreement with the generally expressed viewpoint that photoperiod interacts with the dark period to control flowering (Blaney and Hamner, 1957; Hillman, 1969).

Substituting Eq. 5.4 and Eq. 5.5 into Eq. 5.3, the Beta model can be transformed into the form with biologically meaningful parameters, that is,

$$DR = \frac{1}{f_o} \left[\left(\frac{P - P_b}{P_o - P_b} \right)^{\frac{P_o - P_b}{P_c - P_b}} \left(\frac{P_c - P}{P_c - P_o} \right) \right]^{\epsilon} \quad (5.7)$$

If P_b and P_c are set to be 0 and 24 h d^{-1} , respectively, the other three parameters P_o , f_o and the photoperiod sensitivity as suggested by Chandraratna (1954) for characterizing varietal photoperiod response are clearly shown in Eq. 5.7. For the 69 rice cultivars involved in the four published data sets used in this Chapter, estimated values for P_o and f_o varied from 8.1 to 12.4 h d^{-1} and from 38.5 to 127.4 d , respectively, whereas the sensitivity parameter ϵ varied from 0.50 to 26.81. This result agrees with the conclusion of Chandraratna (1954) that rice cultivars strongly differ in the sensitivity, and, to a lesser extent, in P_o and f_o .

Based on the data of several controlled-photoperiod experiments, this Chapter shows that the simplified Beta function, Eq. 5.6, can accurately describe the overall effect of photoperiod on the rate of development from sowing to flowering in rice. However, to predict days to flowering under field conditions, it is necessary to first estimate the period during which plants are sensitive to photoperiod, since rice plants do not respond to photoperiod throughout the entire preflowering period (Vergara and Chang, 1985). This is a subject that will be addressed in Chapter 6.

Chapter 6

Photoperiodically sensitive and insensitive phases of preflowering development in rice

Abstract The time interval between sowing and flowering in rice (*Oryza sativa* L.) comprises three successive phases: a basic vegetative phase (BVP), a photoperiod-sensitive phase (PSP) and a post-PSP phase (PPP). The objective of this study was to estimate the lengths of the three phases in diverse rice cultivars to provide the basis for accurately predicting rice flowering dates. In greenhouse experiments, plants of 20 cultivars were transferred from short day (SD) (10 h d^{-1}) to long day (LD) (12.5 or 14 h d^{-1}) or from LD to SD at various times after sowing. The duration of BVP varied greatly among cultivars ranging from 16.7 to 45.4 d. The *indica* cultivars exhibited an apparently longer BVP than the *japonica* cultivars. The duration of PPP also varied among cultivars, but to a lesser extent, from 18.0 to 37.2 d. For all cultivars, the length of the intervening PSP was shorter in SD (3.6 to 24.1 d) than in LD (10.5 to 76.5 d); the difference in PSP between SD and LD depended on the photoperiod sensitivity of the cultivar. The PSP in both SD and LD did not necessarily end at panicle initiation (PI), but, on average, 4 to 5 d after PI. The result confirms the necessity to divide the entire preflowering period into the three phases for modelling purposes. Further studies are needed to elucidate the phenomenon in some cultivars of an unusual delay of flowering by early SD-to-LD transfers before PI.

Introduction

Although the time to flowering in rice is often delayed by a long photoperiod, rice cultivars do not respond to photoperiod during the entire period from sowing to flowering (Best, 1961; Vergara and Chang, 1985). Roberts and Summerfield (1987) divided the period from sowing to flowering into three phases: the pre-inductive, the inductive, and the post-inductive phase. Plants are sensitive to photoperiod only during the inductive phase. Vergara et al. (1965) described the pre-inductive phase as the basic vegetative phase (BVP), and the inductive phase as the photoperiod-sensitive phase (PSP). These two terms are widely used to describe the response of rice to photoperiod (Chang et al., 1969; Vergara and Chang, 1985).

The transition from BVP to PSP occurs rapidly in rice (Best, 1961). The time of this transition can be estimated from the response of plants exposed to an inductive photoperiod at various times after sowing (Chandraratna, 1948; Misra, 1955; Tang and Li, 1964; Misra and Khan, 1973; Zhang, 1985; Mimoto et al., 1989; Collinson et al., 1992). Although the onset of PSP varied widely among cultivars, the end of PSP was reported to vary less, i.e. the PSP ended approximately at panicle initiation (PI) (Tang and Li, 1964). Based on the assumption that PSP ends at PI and that the period between PI and flowering is constant, the length of BVP has been determined by subtracting 35 d from the number of days between sowing and

flowering at the optimum photoperiod, at which development to flowering is most rapid (Vergara et al., 1965; Chang et al., 1969; Vergara and Chang, 1985).

However, many workers have reported that the duration from PI to flowering is affected by photoperiod (Coolhaas and Wormer, 1953; Best, 1961; Janardhan and Murty, 1967). Plants subjected to insufficient photoinductive cycles sometimes formed panicles but the panicle did not emerge (Vergara et al., 1965). Based on results in one rice cultivar, Collinson et al. (1992) found that PI occurred when about 80% of PSP had elapsed.

The degree of photoperiod sensitivity of rice plants has been reported to vary with age (e.g. Noguchi et al., 1971; Misra and Khan, 1973; Hanyu and Chujo, 1987). However, this aging effect is probably the result of other factors such as seedling vigour (Vergara and Chang, 1985). The evidence from plants transferred from a less inductive to a more inductive photoperiod suggests that there is no change in photoperiod sensitivity *per se* during PSP (Roberts and Summerfield, 1987; Horie, 1994). This conclusion was found to apply to both *japonica* (Mimoto et al., 1989) and *indica* rices (Collinson et al., 1992).

Unlike photoperiod, which affects only a limited period of the crop life cycle, temperature modulates all successive stages of development (Roberts and Summerfield, 1987). For rice, Collinson et al. (1992) indicated that durations of all BVP, PSP and the post-PSP phase (PPP) varied with temperature. However, while the number of days for BVP depends on temperature, the leaf number on the main-stem (LN_m) at the end of BVP does not vary much with temperature for a given cultivar (Mimoto et al., 1989).

Reliable prediction of rice development in the field requires quantitative knowledge about which environmental factors modulate the development at any given time. An important step is to determine the period when the plant responds to photoperiod. The objective of this study was to estimate the durations of BVP, PSP and PPP of preflowering development in diverse rice cultivars. This was accomplished by moving plants between short-day (SD) and long-day (LD) photoperiods at regular intervals after sowing.

Materials and methods

Experiments

Three greenhouse experiments were conducted at the International Rice Research Institute (IRRI), Philippines. A total of 20 cultivars from contrasting rice growing environments (Table 6.1) were selected based on their photoperiod sensitivities reported elsewhere (e.g. Vergara and Chang, 1985).

In all experiments, pot plants were arranged in a randomized complete block design on mobile trolleys which were moved daily into the greenhouse between 08:00 and 17:00 h, after which they were distributed among darkrooms. The darkrooms were provided with different hours of $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ supplementary light to obtain the required photoperiods. The temperature in the darkrooms was maintained at $24 \pm 2^\circ\text{C}$, whereas the daytime temperature in the greenhouse fluctuated with seasons, typically in the range of $32 \pm 6^\circ\text{C}$.

Table 6.1. Rice cultivars investigated in this study.

Cultivar	Ecotype	Origin	Photoperiod sensitivity
Exp. 6.1			
IR42	<i>indica</i>	IRRI	intermediate
IR64	<i>indica</i>	IRRI	weak
IR72	<i>indica</i>	IRRI	weak
IR64616H†	<i>indica</i>	IRRI	weak
MR84	<i>indica</i>	Malaysia	intermediate
Xiu Shui 11	<i>japonica</i>	China	strong
Koshihikari	<i>japonica</i>	Japan	weak
Nipponbare	<i>japonica</i>	Japan	intermediate
Exp. 6.2			
IR5	<i>indica</i>	IRRI	intermediate
IR8	<i>indica</i>	IRRI	weak
IR36	<i>indica</i>	IRRI	weak
Carreon	<i>indica</i>	Philippines	strong
CO36	<i>indica</i>	India	strong
ADT36	<i>indica</i>	India	weak
Shan You 63†	<i>indica</i>	China	weak
Xiu Shui 11	<i>japonica</i>	China	strong
Lao Lai Qing	<i>japonica</i>	China	strong
Koshihikari	<i>japonica</i>	Japan	weak
Nipponbare	<i>japonica</i>	Japan	intermediate
Akihikari	<i>japonica</i>	Japan	weak
Hwasong	<i>japonica</i>	Korea	intermediate
Ilpoom	<i>japonica</i>	Korea	intermediate
Odea	<i>japonica</i>	Korea	weak
Exp. 6.3			
Koshihikari	<i>japonica</i>	Japan	weak
Nipponbare	<i>japonica</i>	Japan	intermediate

† *Indica* hybrid rice.

Seeds of each cultivar were pre-germinated and then planted in 1-litre plastic pots with five seeds per pot. Seedlings were thinned first to three and then to one plant per pot. The growing medium in pots was a loamy clay soil, which was blended with 0.042 g N, 0.010 g P₂O₅ and 0.024 g K₂O per pot. Additional 0.04 g N was top-dressed for each pot at mid-tillering and PI. Plants were irrigated daily to keep the soil saturated until 15 days after sowing (DAS), and were grown under continuously flooded conditions thereafter.

Table 6.2. Photoperiods and times from sowing to transfer from short day (SD, h d⁻¹) to long day (LD, h d⁻¹) and from LD to SD.

	SD	LD	Transfer times (days after sowing)
Exp. 6.1	10.0	14.0	12 16 20 24 28 35 42 49 56 63 70 77 84
Exp. 6.2			
Carreon and CO36	10.0	12.5	5 10 15 20 25 30 35 44 53 62 71 80 89 98 107
other cultivars	10.0	14.0	5 10 15 20 25 30 35 42 49 56 63 70 77 84 91
Exp. 6.3†	12.5	14.0	5 10 15 20 25 30 35 42 49

† Plants were transferred from SD to LD without corresponding moves from LD to SD in Exp. 6.3.

Initially, half of the pots for each cultivar were placed in SD, half in LD. Plants were transferred, two at a time for each cultivar, from one photoperiod to the other, i.e. two plants that had been in SD since potting were exchanged with the two that had been in LD. Transfers were made at 4 to 9 d intervals, starting between 5 and 12 DAS (Table 6.2). Once a plant was transferred, it was grown in the new photoperiod until flowering. Plants grown continuously at SD or LD were used as control, equivalent to the treatment of a transfer at 0 DAS.

In the first experiment (Exp. 6.1), plants of four *indica*, three *japonica*, and one *indica* hybrid cultivars (Table 6.1) were sown on 3 June 1993. The SD and LD regimes were 10 and 14 h d⁻¹, respectively; and transfers between SD and LD started at 12 DAS and ended at 84 DAS at different intervals (Table 6.2).

In the second experiment (Exp. 6.2), plants of 15 cultivars (three of them also tested in Exp. 6.1), including six *indica*, eight *japonica* and one *indica* hybrid cultivars (Table 6.1), were sown on 2 April 1994. The treatments were generally similar to those of Exp. 6.1. However, due to their strong photoperiod sensitivity, the LD regime for cvs CO36 and Carreon was 12.5 h d⁻¹ (Table 6.2) to avoid the unusual delay of flowering at LD. The transfers were conducted from 5 to 107 DAS for CO36 and Carreon, and to 91 DAS for other cultivars.

In addition to the above two experiments, a third experiment (Exp. 6.3) was conducted simultaneously with Exp. 6.2 using two *japonica* cultivars (Table 6.1). Plants were moved from SD (12.5 h d⁻¹) to LD (14 h d⁻¹) at 5 to 7 d intervals between 5 and 49 DAS (Table 6.2).

Plants were observed daily to obtain the flowering dates. Flowering was determined when 50% of the florets of the first panicle had flowered. In control treatments, more pots were added to provide enough plants to be dissected for determining the time of PI. PI was defined by the stage when apex appears to the naked eye as a fuzzed tip of 0.2 to 0.5 mm. When PI was first detected, two or more plants were further dissected to confirm the uniformity of development among plants. The main-stem leaf number was marked, starting with the first leaf with a complete leaf blade. The time for appearance of each main-stem leaf ligule was recorded for the plants in the control treatments.

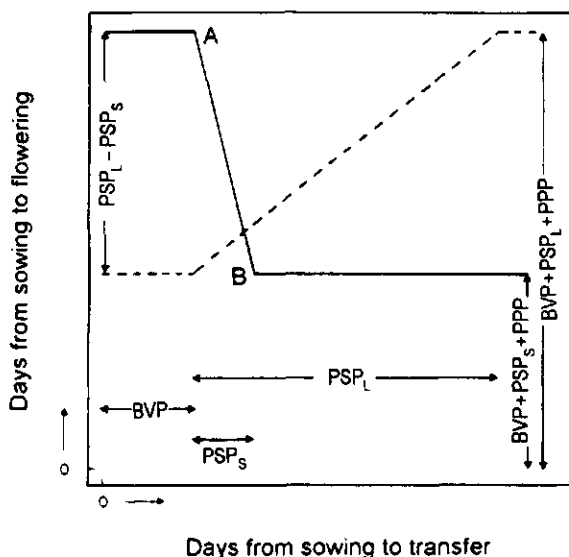


Fig. 6.1. Schematic representation of the response of days from sowing to flowering for plants transferred from short-day (SD) to long-day (LD) conditions (solid line) or from LD to SD conditions (broken line) at various times after sowing, if the period from sowing to flowering comprises three consecutive phases: basic vegetative phase (BVP), photoperiod-sensitive phase (PSP_s and PSP_L in SD and LD, respectively) and post-photoperiod-sensitive phase (PPP). In this figure, both axes have the same scale.

Analytical approach

The objective of the analysis was to estimate durations of BVP, PSP in SD (PSP_s) and in LD (PSP_L), and PPP from the data on days from sowing to flowering (f) in the transfer experiment. If the transition from one phase to another is abrupt and the photoperiod sensitivity of plants does not change with age during PSP, the relationship between f and time of transfer (t) are segmentedly linear (Fig. 6.1).

For plants transferred from LD to SD where $t \leq BVP$ and for those transferred from SD to LD where $t \geq BVP + PSP_s$, the days to flowering can be quantified by:

$$f = BVP + PSP_s + PPP \quad (6.1)$$

For plants transferred from SD to LD where $t \leq BVP$ and for LD to SD transfers where $t \geq BVP + PSP_L$, the days to flowering can be expressed as:

$$f = BVP + PSP_L + PPP \quad (6.2)$$

Less obvious is the description for those plants transferred during PSP. However, if photoperiod sensitivity does not change during PSP, the relation between f and t is linear (Horie, 1994), as shown in Fig. 6.1. This relation can be described by:

$$f = a + bt \quad (6.3)$$

where a and b are constants to be determined. For SD-to-LD transfers during PSP, where the relation is shown by the line segment AB in Fig. 6.1, Eq. 6.3 results in:

$$\text{point A:} \quad \text{BVP} + \text{PSP}_L + \text{PPP} = a + b\text{BVP} \quad (6.4)$$

$$\text{point B:} \quad \text{BVP} + \text{PSP}_S + \text{PPP} = a + b(\text{BVP} + \text{PSP}_S) \quad (6.5)$$

From Eq. 6.4 and Eq. 6.5, coefficients a and b in Eq. 6.3 can be determined as:

$$a = \text{BVP} \cdot \text{PSP}_L / \text{PSP}_S + \text{PSP}_L + \text{PPP} \quad (6.6a)$$

$$b = 1 - \text{PSP}_L / \text{PSP}_S \quad (6.6b)$$

Substituting a and b into Eq. 6.3 gives:

$$f = t + \text{PSP}_L - (t - \text{BVP})\text{PSP}_L / \text{PSP}_S + \text{PPP} \quad (6.7)$$

Similar logic for the transfers from LD to SD during PSP results in:

$$f = t + \text{PSP}_S - (t - \text{BVP})\text{PSP}_S / \text{PSP}_L + \text{PPP} \quad (6.8)$$

Ellis et al. (1992a) derived equations for analysis of this type of transfer experiment with the same form as Eq. 6.7 and Eq. 6.8, based on an additional assumption that the relation between rate of development to flowering (i.e. $1/f$) and photoperiod is linear. Eq. 6.7 and Eq. 6.8 were derived here without that assumption. In fact, the relation between $1/f$ and a wide range of photoperiods is nonlinear in rice (Chapter 5).

By introducing dummy variables: $Z_0 = 0$ and $Z_1 = 1$ for SD-to-LD transfers and $Z_0 = 1$ and $Z_1 = 0$ for LD-to-SD transfers, all linear relations in Fig. 6.1 can be summarized based on Eqs 6.1, 6.2, 6.7 and 6.8 as:

$$f = \text{BVP} + Z_0\text{PSP}_S + Z_1\text{PSP}_L + \text{PPP} \quad \text{if } t \leq \text{BVP} \text{ (including the control, i.e. } t=0) \quad (6.9)$$

$$f = t + Z_0\text{PSP}_S + Z_1\text{PSP}_L - Z_0(t - \text{BVP})\text{PSP}_S / \text{PSP}_L - Z_1(t - \text{BVP})\text{PSP}_L / \text{PSP}_S + \text{PPP} \quad (6.10)$$

if $\text{BVP} < t < \text{BVP} + Z_0\text{PSP}_L + Z_1\text{PSP}_S$

$$f = \text{BVP} + Z_0\text{PSP}_L + Z_1\text{PSP}_S + \text{PPP} \quad \text{if } t \geq \text{BVP} + Z_0\text{PSP}_L + Z_1\text{PSP}_S \quad (6.11)$$

The results of the transfer experiment can then be quantified by the four parameters BVP, PSP_S , PSP_L and PPP, which can be estimated using an iterative procedure of the PROC NLIN of the Statistical Analysis Systems Institute (SAS, 1988).

The model of Eqs 6.9 to 6.11 was used to estimate durations of BVP, PSP_S , PSP_L and PPP for each of the cultivars where the response followed the pattern in Fig. 6.1. However, there was a large delay in the flowering time for plants of early SD-to-LD transfers in many cultivars (see Results). For such cases, the model was used to estimate values of BVP, PSP_L and PPP by excluding several outliers due to the early SD-to-LD transfers. For these cultivars, the value for PSP_S was estimated as follows: (1) determining a linear relation which fits data from the maximal delay to the following one or two transfers; (2) extrapolating this relation to estimate the day for the onset of PPP in SD; (3) estimating PSP_S by subtracting the value of BVP from the day for the onset of PPP in SD.

Results and discussion

Response of flowering to the time of transfer

Plants of the eight cultivars tested in Exp. 6.1 flowered in all treatments (Fig. 6.2). The results for the five *indica* cultivars (Fig. 6.2A-E) followed the pattern as described in Fig. 6.1. However, there was an unexpected delay of flowering for plants of several early SD-to-LD transfers in three *japonica* cvs Xiu Shui 11, Koshihikari and Nipponbare (Fig. 6.2F-H), compared to their LD control plants.

To determine whether this phenomenon also occurs in other cultivars, 15 cultivars, including the three *japonica* cultivars of Exp. 6.1 and five other *japonica* cultivars, were extensively examined in Exp. 6.2 (Table 6.1). Transfers in Exp. 6.2 started earlier than in Exp. 6.1 (Table 6.2) to observe the earliest time of onset of the unexpected delay. All *japonica* cultivars exhibited a similar trend (Fig. 6.3H-O) as found in Exp. 6.1, although it was not obvious in the two weakly photoperiod-sensitive *japonica* cvs Akihikari (Fig. 6.3L) and Odea (Fig. 6.3O). Among the eight *indica* cultivars, the phenomenon was found in CO36 only (Fig. 6.3E). In most cases, this effect started significantly with plants transferred at 10 to 20 DAS and ended around the time of PI at SD. The delay of flowering also caused an increase in LN_m in both experiments (Fig. 6.4). This suggests that the time of PI was also delayed for plants of these transfers, compared to the LD control plants.

To analyse if the unexpected effect is photoperiod-specific, a third experiment was conducted with *japonica* cvs Koshihikari and Nipponbare, in which SD was changed to 12.5 h d^{-1} and plants were moved only from SD to LD during the critical period for the effect. In this experiment, a significant prolongation of the vegetative growth in the transferred plants compared with the LD control plants was observed as well (Fig. 6.5).

Several reports (Coolhaas and Wormer, 1953; Best, 1961; Noguchi et al., 1967) indicated that noninductive cycles with photoperiods of 18 to 24 h d^{-1} can negate the effect of photoinductive cycles in rice, which agrees with the phenomenon of the delay of flowering by the SD-to-LD transfers observed here. However, this phenomenon was not clearly shown in most similar studies for rice, because only transfers from LD to SD were used without the SD-to-LD transfers (Misra, 1955; Mimoto et al., 1989) or because only a few *indica* cultivars were tested (Collinson et al., 1992). Zhang (1985) indicated that there was a long-day response during some part of BVP. However, in the experiments reported in this Chapter, the early LD-to-SD treatments had little promotion of flowering relative to the SD control plants in those cultivars where the delay of flowering by the SD-to-LD transfers was large (Figs 6.2 and 6.3). Thus, the long-day response suggested by Zhang (1985) cannot explain the delay by early SD-to-LD transfers. Tang and Li (1964) emphasized the importance of the direction in the daylength change and indicated that strongly photoperiod-sensitive cultivars flowered earlier with shortening days. Although this may explain the delayed flowering due to a SD-to-LD transfer, detailed physiological studies are needed to elucidate the mechanism for the antagonistic action of LD on the SD induction.

The results for transfers from LD to SD in all cultivars agreed well with the pattern as described in Fig. 6.1 (Figs 6.2 and 6.3). A highly significant linear relationship between days of

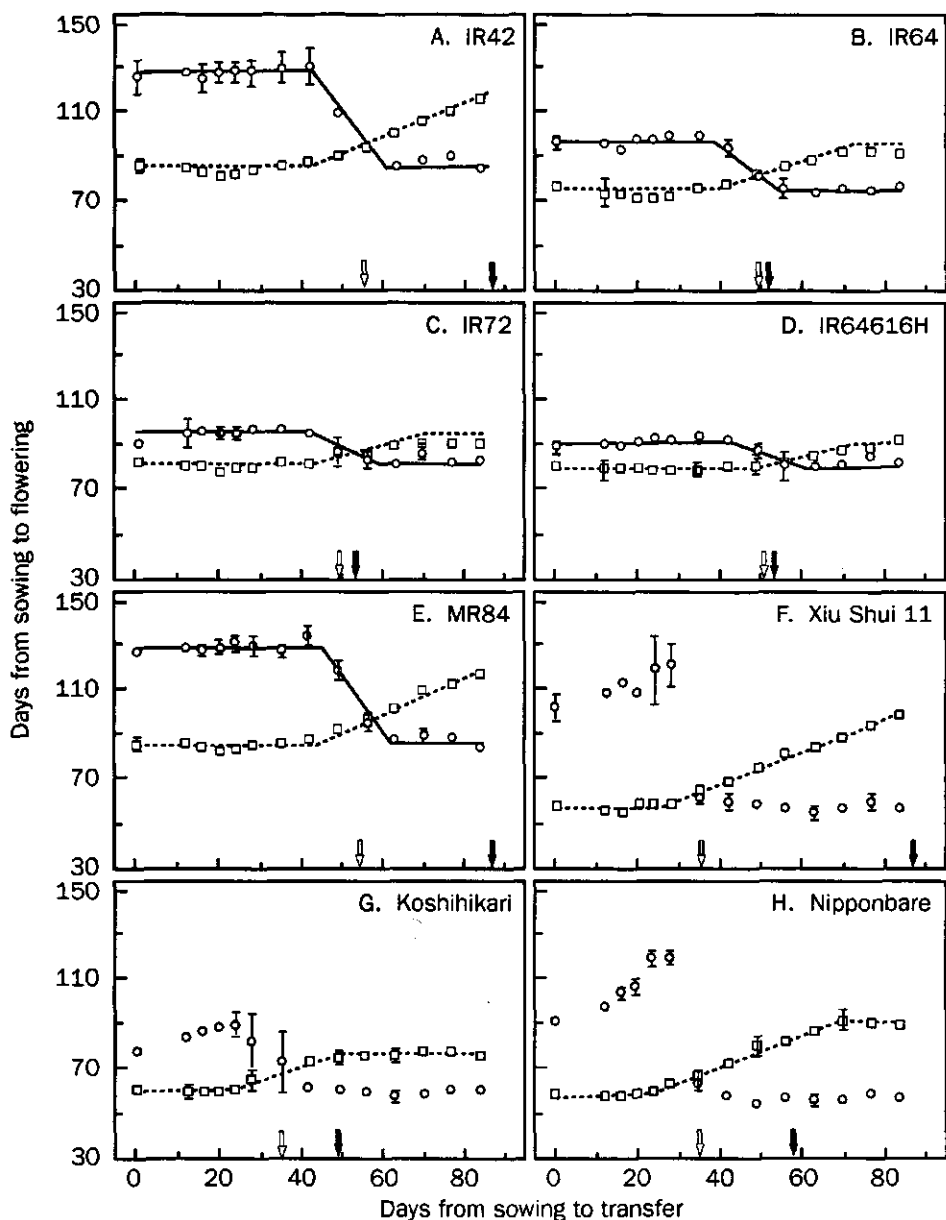


Fig. 6.2. Days from sowing to flowering for plants of eight rice cultivars transferred from short-day (SD) to long-day (LD) (circles) or from LD to SD (squares) at various times after sowing (Exp. 6.1). Vertical bars represent means \pm standard deviations (where larger than symbols). The open and closed arrows indicate the times of panicle initiation for plants continuously grown in SD and LD, respectively. The solid and broken lines showed the fitted relations (Tables 6.3 and 6.4) for transfers from SD to LD and from LD to SD, respectively.

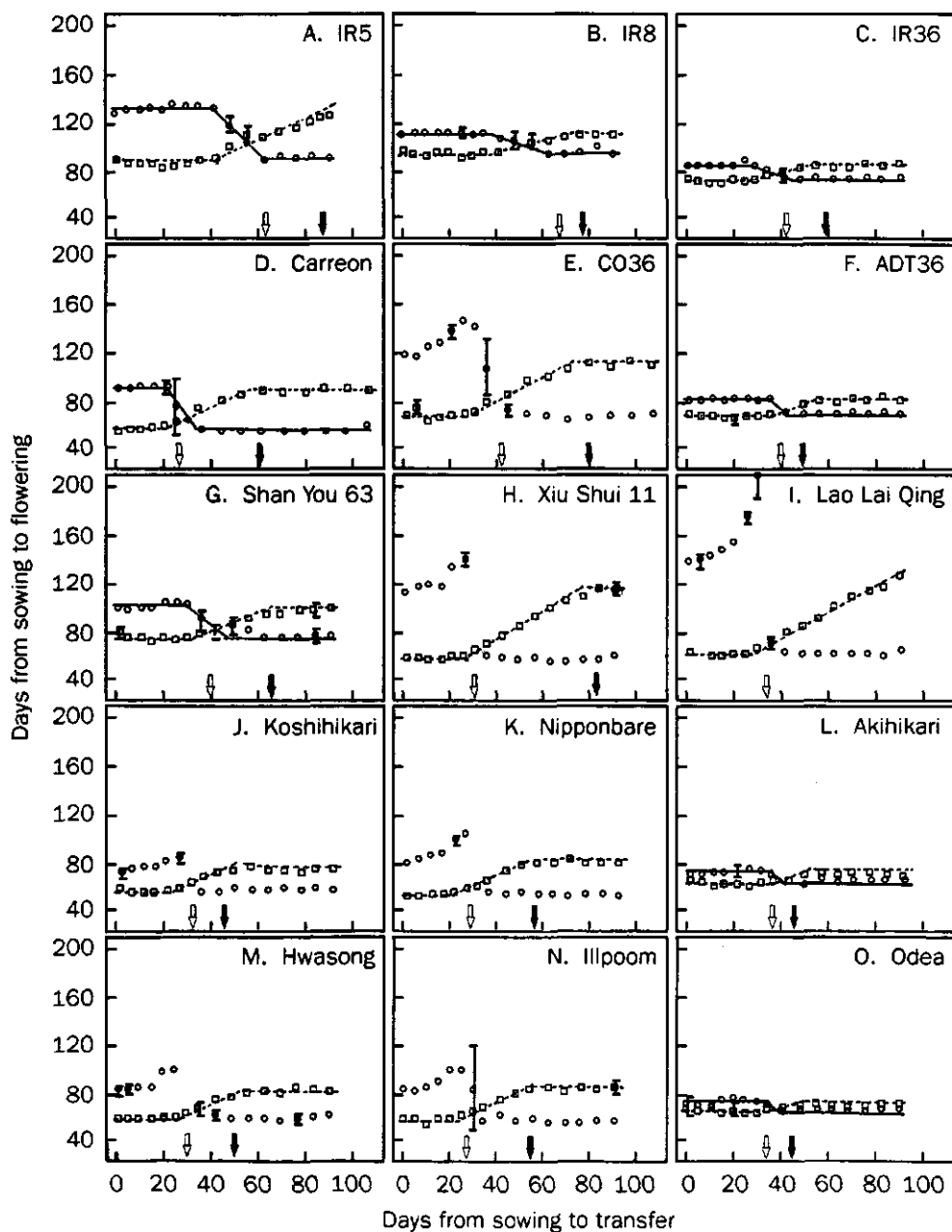


Fig. 6.3. Days from sowing to flowering for plants of 15 rice cultivars transferred at various times after sowing (Exp. 6.2). Further details as for Fig. 6.2. Panicle initiation of cv. Lao Lai Qing under the long-day photoperiod was observed to occur at 125 days after sowing, which is not shown in this figure.

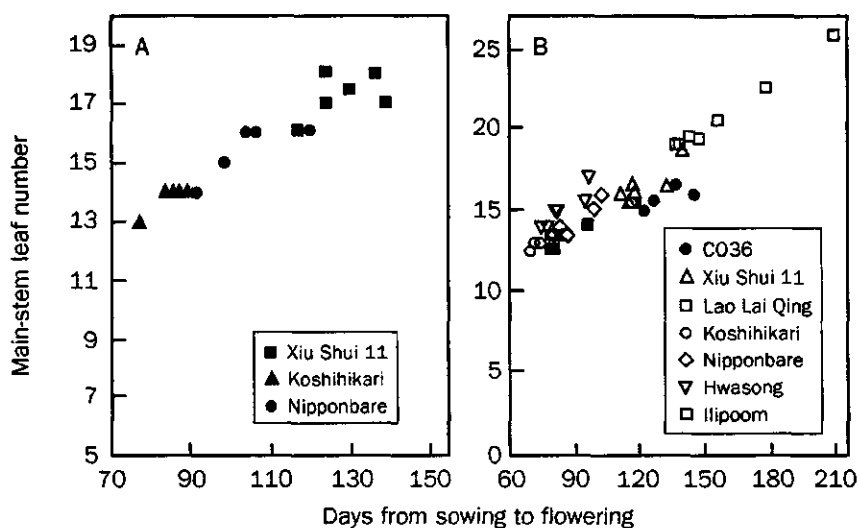


Fig. 6.4. The relation between final main-stem leaf number and days from sowing to flowering for those rice plants with large delays of flowering caused by early transfers from short-day to long-day photoperiods (A: Exp. 6.1; B: Exp. 6.2).

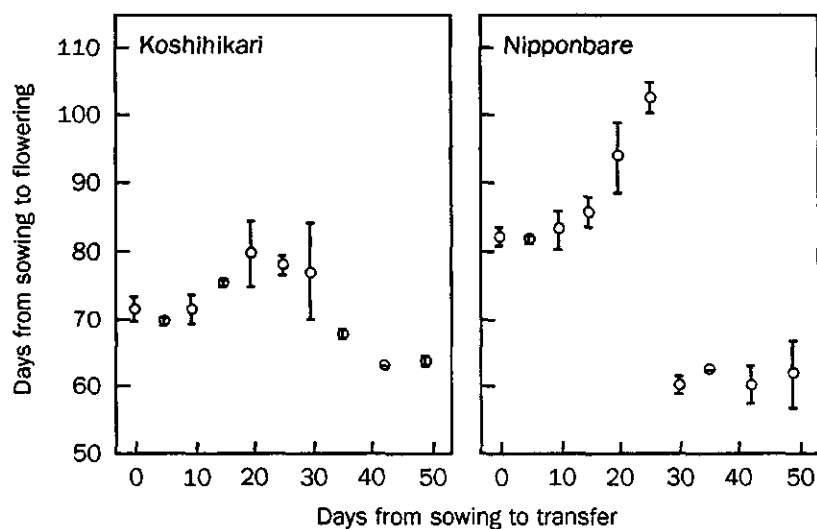


Fig. 6.5. Days from sowing to flowering for plants of two rice *japonica* cultivars transferred from short-day to long-day conditions at various times after sowing (Exp. 6.3). Vertical bars represent means \pm standard deviations.

flowering and day of transfer was obtained when plants were moved from LD to SD during PSP. Similar linearity has been observed by others for rice (Misra, 1955; Tang and Li, 1964; Mimoto et al., 1989; Collinson et al., 1992) and for other crops, e.g. lentil (*Lens culinaris* Medik.) (Roberts et al., 1986), barley (*Hordeum vulgare* L.) (Roberts et al., 1988), maize (*Zea mays* L.) (Kiniry et al., 1983) and soybean [*Glycine max* (L.) Merr.] (Wilkerson et al., 1989; Collinson et al., 1993; Acock et al., 1994). This linearity indicates that photoperiod sensitivity does not vary with age within PSP (Horie, 1994). The reported changes of sensitivity in rice (Noguchi et al., 1971; Mirsa and Khan, 1973; Hanyu and Chujo, 1987) was probably due to the fact that the treatments covered the transition from BVP to PSP, or from PSP to PPP.

Duration of photoperiodically sensitive and insensitive phases

Estimated values of BVP, PSP_s, PSP_L and PPP with the model of Eqs 6.9 to 6.11 for each of the cultivars where the responses followed the pattern as described in Fig. 6.1 are given in Table 6.3. For the cultivars which did not follow the pattern in Fig. 6.1 for early SD-to-LD transfers, the results of estimates are given in Table 6.4.

Table 6.3. Duration (d, SE in parentheses) of basic vegetative phase (BVP), photoperiod-sensitive phase in short days (PSP_s) and in long days (PSP_L), and post-photoperiod-sensitive phase (PPP) of development to flowering in 13 rice cultivars where the results in the experiments followed the pattern described in Fig. 6.1.

Cultivar	BVP	PSP _s	PSP _L	PPP	r ²	n†	BVP*‡
Exp. 6.1							
IR42	42.0(1.64)	17.2(2.68)	59.8(3.04)	25.6(1.49)	0.988	28	50.0
IR64	40.2(1.80)	13.9(3.65)	34.8(3.97)	20.5(2.43)	0.949	28	42.0
IR72	42.0(5.21)	15.6(7.91)	27.8(8.16)	23.4(3.70)	0.865	28	46.5
IR64616H	45.4(3.22)	15.3(5.80)	26.5(6.01)	20.2(3.35)	0.885	28	46.5
MR84	44.6(1.39)	14.1(2.34)	57.4(2.85)	27.1(1.49)	0.983	28	50.0
Exp. 6.2							
IR5	40.7(2.01)	23.3(3.42)	66.9(4.44)	23.2(2.48)	0.959	31	52.0
IR8	40.3(2.81)	24.1(4.74)	39.8(5.14)	28.0(2.89)	0.916	32	59.5
IR36	27.9(1.97)	16.5(3.42)	29.0(3.65)	23.8(2.10)	0.933	32	33.0
Carreon	20.0(2.42)	9.6(4.52)	43.6(4.71)	23.3(2.38)	0.978	32	16.5
ADT36	35.7(3.52)	6.1(6.52)	19.1(6.56)	23.9(3.73)	0.923	32	31.5
Shan You 63	30.0(2.95)	14.2(4.67)	38.0(5.07)	28.3(2.51)	0.928	32	41.5
Akihikari	32.2(4.24)	11.8(6.87)	18.4(7.07)	18.0(3.85)	0.728	32	30.0
Odea	34.1(1.85)	3.6(5.67)	10.5(5.72)	23.6(4.15)	0.776	32	29.5

† n is the number of treatments fitted;

‡ BVP* is the basic vegetative phase determined from the method of Vergara and Chang (1985), i.e. by subtracting 35 d from days to flowering in SD.

Table 6.4. Duration (d, SE in parentheses) of basic vegetative phase (BVP), photoperiod-sensitive phase in short days (PSP_s) and in long days (PSP_L), and the post-photoperiod-sensitive phase (PPP) of development to flowering in seven rice cultivars where the results in the transfers from SD to LD did not follow the pattern described in Fig. 6.1.

Cultivar	BVP	PSP _L	PPP	r^2	n^\dagger	PSP _s [‡]	BVP* [§]
Exp. 6.1							
Xiu Shui 11	25.6(1.69)	61.8(3.66)	29.6(1.62)	0.990	23	9.9	27.5
Koshihikari	20.7(1.57)	30.6(2.74)	26.0(1.57)	0.987	22	22.0	25.5
Nipponbare	21.3(1.71)	46.0(3.18)	24.2(1.81)	0.988	23	14.2	24.0
Exp. 6.2							
CO36	23.6(2.39)	52.2(4.54)	35.8(2.75)	0.981	26	17.6	28.5
Xiu Shui 11	22.3(1.34)	59.0(2.45)	33.6(1.38)	0.994	30	8.1	20.0
Lao Lai Qing	25.5(1.19)	76.5(2.50)	37.2(1.30)	0.996	27	9.7	26.0
Koshihikari	18.4(2.17)	30.0(3.30)	22.6(1.52)	0.971	28	12.5	21.0
Nipponbare	16.7(1.63)	42.8(2.32)	20.6(0.93)	0.989	28	13.8	15.0
Hwasong	23.0(2.42)	31.5(3.35)	24.1(1.22)	0.966	30	7.4	19.5
Illpoom	19.6(1.71)	32.6(3.19)	27.9(1.98)	0.981	28	15.7	22.0

† n is the number of treatments fitted;

‡ PSP_s is determined by subtracting the value for BVP from the day for the onset of PPP under SD conditions (see text);

§ BVP* is the basic vegetative phase determined from the method of Vergara and Chang (1985), i.e. by subtracting 35 d from days to flowering under SD conditions.

The model described the data in strongly and moderately sensitive cultivars more accurately than in weakly sensitive ones. The duration of BVP varied greatly among cultivars (Tables 6.3 and 6.4). In general, *indica* cultivars had a longer BVP than *japonica* cultivars, 20.0 to 45.4 d in the *indica* vs 16.7 to 34.1 d in the *japonica* cultivars. The duration of PPP varied somewhat less among cultivars, ranging from 18.0 to 37.2 d. As expected, in all cultivars, the duration of PSP_L was longer than that of PSP_s, depending on the photoperiod sensitivity of the cultivar. The value for PSP_L was much longer in highly sensitive than weakly sensitive cultivars. The value for PSP_s varied from 3.6 to 24.1 d, agreeing well with Vergara and Chang (1985) who indicated that the minimum number of photoinductive cycles required to initiate panicle primordia varied from 4 to 24 d.

The duration of BVP in rice (Table 6.3) is relatively long when compared to long-day crops such as lentil (Roberts et al., 1986) and barley (Roberts et al., 1988) and other short-day crops such as maize (Kiniry et al., 1983) and soybean (Wilkerson et al., 1989; Collinson et al., 1993; Acock et al., 1994). Vergara and Chang (1985) reported that the length of BVP in rice ranged from 3 to 88 d. This result was often cited by others (e.g. Horie, 1994) to emphasize the large variation of BVP in rice. The experimental results in this Chapter showed that the genotypic

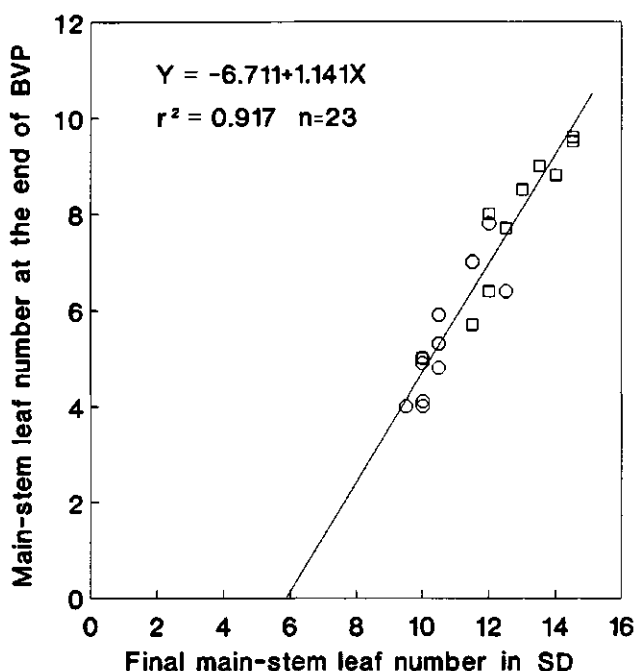


Fig. 6.6. The relation between the main-stem leaf number at the end of the basic vegetative phase (BVP) and the final main-stem leaf number of rice plants (squares: *indica* cultivars; circles: *japonica* cultivars) grown under short-day (SD) conditions. The line is the regression line.

variation in BVP is rather less than the estimations based on the method of Vergara and Chang (1985) (Table 6.3), agreeing with the analysis of Collinson et al. (1992) with four rice *indica* cultivars. The method of Vergara and Chang (1985) assumes that the PI-flowering interval is a constant 35 d and that the PSP in the SD photoperiod (often at 10 h d⁻¹) is zero. In fact, the PSP has a finite value even at 10 h d⁻¹ (Table 6.3) and the PI-flowering interval at 10 h d⁻¹ was often less than 35 d (Figs 6.2 and 6.3). Because the overestimation of the PI-flowering duration can cancel out the underestimation of PSP_s, the estimation of BVP by that method was sometimes coincident with the estimated value given in this Chapter (Tables 6.3 and 6.4).

Estimated values for BVP, PSP_s, PSP_L and PPP in cvs Xiu Shui 11, Koshihikari and Nipponbare were generally smaller in Exp. 6.2 when compared to Exp. 6.1 (Table 6.4). This may be due to a difference in the daytime temperature between the two experiments which were conducted in different seasons, since the length of BVP for a given cultivar varied with temperature (Tang and Li, 1964; Mimoto et al., 1989; Collinson et al., 1992; Horie, 1994). However, Mimoto et al. (1989) indicated that the LN_m at the end of BVP was less affected by temperature. The LN_m at the end of BVP were 5.9, 4.8 and 4.9 in Exp. 6.1 vs 5.0, 4.0 and 4.0 leaves in Exp. 6.2 for Xiu Shui 11, Koshihikari and Nipponbare, respectively. The LN_m at the end of BVP in Koshihikari was 4.0–4.8 in the experiments reported in this Chapter, vs 3.8–4.3

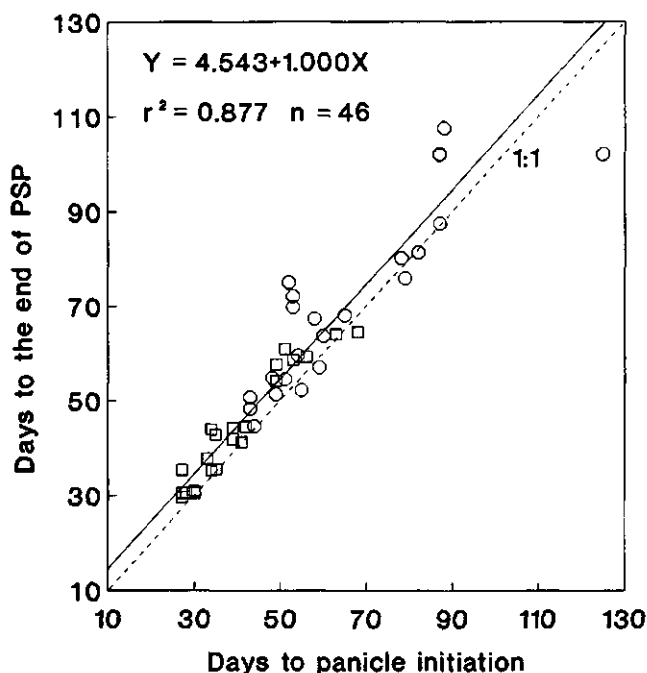


Fig. 6.7. Comparison between days from sowing to the end of the photoperiod-sensitive phase (PSP) and days from sowing to panicle initiation under both short-day (squares) and long-day (circles) conditions. The broken line represents the 1:1 relationship; the solid line is the regression line.

reported by Mimoto et al. (1989) for this cultivar. A similar result was also found for cv. Lao Lai Qing tested by Tang and Li (1964) who reported that the LN_m at the end of BVP was 5.7, vs 6.4 found in Exp. 6.2 reported here. In general, rice plants appeared to first become photoperiod-sensitive at the leaf stage of at least 4.0. Most IR-cultivars selected at IRRI, appeared to become sensitive at a quite late stage, i.e. the leaf stage of about 9.0. Further analysis based on Exp. 6.1 and Exp. 6.2 indicated that the leaf stage when rice plants become sensitive to photoperiod was linearly related to the final LN_m in SD (Fig. 6.6). This linearity supports the relative importance of BVP in determining the length of the total vegetative period under SD conditions (Vergara and Chang, 1985).

Dissection of the control plants showed that PI occurred before, at, or after the end of the PSP, depending on the cultivar or photoperiod treatment (Figs 6.2 and 6.3, Fig. 6.7). This agrees with some reports (e.g. Coolhaas and Wormer, 1953; Janardhan and Murty, 1967) that PI-flowering duration can be affected by photoperiod to some extent. Based on the result in one cultivar, Collinson et al. (1992) concluded that PI occurred after about 80% of the PSP had elapsed in rice. The results with diverse cultivars obtained from both Exps 6.1 and 6.2 reported in this Chapter indicated that, on average, the photoperiod sensitivity ends at about 4–5 d after PI (Fig. 6.7).

Conclusions

Rice plants gave a uniform response when moved from LD to SD and a non-uniform response when moved from SD to LD. The uniform response of all cultivars was illustrated by a highly linear relation between days to flowering and day of LD-to-SD transfer within the PSP. The non-uniform response was reflected by significant delays of flowering due to early SD-to-LD transfers in some cultivars but not in others.

The results generally support the division of the preflowering development in rice into three successive phases: BVP, PSP and PPP. There were large variations among cultivars for the length of each phase, although the PPP varied less. The variation of BVP among cultivars was apparently less than the previous estimates that were based on incorrect assumptions. The analysis also demonstrated that the PSP did not necessarily end at PI. These combined results provided a basis to model the photoperiod-sensitive interval of development to flowering in rice. A further study is required to determine temperature sensitivity during each of these three phases.

Chapter 7

Changes in developmental responses to temperature during preflowering ontogeny of rice

Abstract To accurately predict the time of flowering, it is essential to determine effects of environmental factors on crop development at different stages. The objective of this study was to examine the variation in developmental responses to day and night temperature during preflowering ontogeny of rice (*Oryza sativa* L.). Three controlled-environment experiments were conducted in which plants of three contrasting cultivars, CO36, Shan You 63 and Nipponbare, were transferred at various days after sowing (DAS) between two diurnally constant temperatures (26 and 21°C), between two night temperatures with the same day temperature (day/night: 26/26 and 26/16°C), and between two day temperatures with the same night temperature (28/19 and 19/19°C). In all experiments, the response of the time to flowering to the time of transfer varied with phenological stage, indicating that the sensitivity to both day and night temperature varies with plant age during ontogeny. The period from sowing to flowering can be divided into three phases. The onset of the second phase, the highly temperature sensitive phase, varied largely among cultivars: about 20 DAS in the *japonica* cv. Nipponbare vs 35–60 DAS in the two *indica* cultivars. However, the end of the highly sensitive period varied much less, about 20–25 d before flowering. For modelling purposes, functions for the effects of both day and night temperature in the second phase have to be different from those in the first and third phase.

Introduction

The time interval between sowing and flowering in rice comprises three successive phases: the basic vegetative phase (BVP), the photoperiod-sensitive phase (PSP) and the post-PSP phase (PPP) (Chapter 6). Unlike photoperiod, which affects only the duration of the PSP in photoperiod-sensitive cultivars, temperature affects the duration of all three developmental phases of all cultivars in annual crops (Roberts and Summerfield, 1987). In general, high temperature accelerates and low temperature delays flowering; but extremely high temperatures can delay flowering of rice as well (Haniu et al., 1983; Vergara and Chang, 1985). Many models for predicting rice flowering dates have been developed to account for this effect of temperature.

Although most models assume rice plants have the same response to temperature throughout preflowering ontogeny, it is not known if temperature has the same effect in the different phases leading to flowering (Vergara and Chang, 1985). Wang (1960) pointed out that crops responded differently to the same environmental factor during the various phases of their life cycle. The optimum temperature, at which the crop developed most rapidly, was found to differ among different developmental stages in tomato (*Lycopersicon esculentum* Mill.) (Went, 1945, 1950 and 1956), in faba bean (*Vicia faba* L.) (Ellis et al., 1988), and in wheat (*Triticum*

aestivum L.) (Slafer and Rawson, 1995a). The base temperature, at or below which crop development stops, was also shown to vary throughout the life cycle in wheat (Angus et al., 1981; Slafer and Rawson, 1995a) and in sorghum [*Sorghum bicolor* (L.) Moench] (Hammer et al., 1989). Many modelling studies in different crops showed that model parameters for temperature sensitivity differed among developmental phases (Robertson, 1968; Williams, 1974; Major et al., 1975b; Angus et al., 1981; Weir et al., 1984; Hammer et al., 1989; Grimm et al., 1994; Nakagawa and Horie, 1995). Experimental work also demonstrated that relative effects of temperature on phenology varied among different stages in many crops (Seddigh and Jolliff, 1984; Seddigh et al., 1989; Cockshull and Kofranek, 1994). The importance of plant age was also observed for the temperature effect on leaf number (Arnold, 1969; Tollenaar and Hunter, 1983; Booiij and Meurs, 1993), which in turn largely determines crop phenology.

For rice, Owen (1971) indicated that the base and optimum temperatures varied among developmental stages. Shibata et al. (1973) showed that development to heading was most sensitive to temperature at about 10 days before panicle initiation (PI). Ahn (1968) reported that high temperature reduced the BVP but had little effect on the PSP, whereas Vergara and Lilis (1968) found that night temperature during the PSP altered days to flowering. The duration of the period from PI to flowering is about 35 days in tropics (Vergara and Chang, 1985), implying that the length of this period is hardly affected by temperature. However, Collinson et al. (1992) showed that the length of all BVP, PSP and PPP was strongly affected by temperature in four tested rice cultivars.

Variation in the base and optimum temperatures or temperature sensitivity with plant age in rice has often been suggested (Best, 1959; Oka, 1959; Noguchi, 1960; Owen, 1972; Suge and Nishizawa, 1982; Haniu et al., 1983; Nakagawa and Horie, 1995). However, changes in thermal response of preflowering development with the stage in rice have not been quantified. The study reported in this Chapter aimed to experimentally analyse variation in developmental responses to temperature during preflowering ontogeny in rice. In Chapter 4, different effects of day and night temperature on development in rice were found. In the study reported here, experiments were designed to analyse the response to both day and night temperature.

Materials and methods

Plant material

Three rice cultivars were selected on the basis of their contrasting ecotypes, origins, and photoperiod sensitivity (Table 7.1). Day temperature affects development to flowering more than night temperature in cvs CO36 and Nipponbare, whereas night temperature affects development more than day temperature in cv. Shan You 63 (Chapter 4).

Environmental conditions

Three experiments were conducted in six indoor growth chambers of the phytotron unit of the International Rice Research Institute, Philippines. In the first experiment (Exp. 7.1), plants

Table 7.1. Rice cultivars investigated in this study.

Cultivar	Ecotype	Origin	Photoperiod sensitivity
CO36	<i>indica</i>	India	strong
Shan You 63†	<i>indica</i>	China	weak
Nipponbare	<i>japonica</i>	Japan	intermediate

† F1 hybrid rice

were transferred between two diurnally constant temperatures (high temperature (HT) = 26°C and low temperature (LT) = 21°C) at various times after sowing to examine the general response of plants to temperature. Since the effect of temperature on development to flowering in rice differs between day and night periods (Chapter 4), the second (Exp. 7.2) and the third (Exp. 7.3) experiments were designed to examine possible specific responses to night and day temperature, respectively. In Exp. 7.2, plants were transferred between chambers with different night temperature and the same day temperature (HT = 26/26°C and LT = 26/16°C for day/night). In Exp. 7.3, plants were transferred between chambers with different day temperature and the same night temperature (HT = 28/19°C and LT = 19/19°C). For the chambers with a diurnally varying temperature, the duration of both day and night temperature was 12 h d⁻¹, with an abrupt transition between day and night. Temperatures varied by $\pm 0.5^\circ\text{C}$ in each chamber. The combination of cool white fluorescent lamps supplemented with tungsten incandescent lamps provided an irradiance of 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at plant height. Photoperiod was controlled as 12 h d⁻¹, agreeing with the period of day temperature. Atmospheric CO₂ concentration ($340 \pm 10 \mu\text{mol mol}^{-1}$) and relative humidity ($80 \pm 2\%$) were maintained constant in each chamber.

Plant husbandry and management

Five pre-germinated seeds were sown into 11 cm diameter (one litre) plastic pots. The growing medium was a loamy clay soil, blended with 0.042 g N, 0.010 g P₂O₅ and 0.024 g K₂O for each pot. Additional 0.04 g N was topdressed for each pot at mid-tillering and PI. After sowing, the pots were kept in an open-sided greenhouse for 2 d until the prophyll leaf emerged, and then moved into the chambers. The chambers had 1.6 m² of floor space, and pots were arranged in a completely randomized design. Pots were thinned first to three and then to one plant per pot. Plants were irrigated twice a day using the method described in Chapter 4.

Initially, half of the pots for each cultivar were placed in HT, half in LT. Plants were transferred from one temperature to the other at different times after sowing in two replicates, i.e. two plants that had been in LT were exchanged with the two that had been in HT. However, only one plant was transferred at a time in Exp. 7.3 for Shan You 63. Transfers were executed with an interval of 6 d in Exps 7.1 and 7.2, and of 5 d in Exp. 7.3. After a plant was transferred, it was grown in the new chamber until flowering was observed or the experiment

was terminated. A control treatment involved plants continuously exposed to either HT or LT, equivalent to the treatment with a transfer at 2 days after sowing (DAS). Due to the reported difference in development rate (Chapter 4), the number of transfers differed among cultivars. In Exps 7.1 and 7.2, transfers ended at 122, 110 and 86 DAS for CO36, Shan You 63 and Nipponbare, respectively; in Exp. 7.3, the transfers ended at 112, 107 and 97 DAS for these three cultivars, respectively. Height of the pots was adjusted to maintain a constant distance from the lamps to the top of the plants (about 80 cm).

Plants were observed twice a day to determine when flowering and panicle emergence occurred on individual tillers. Those plants on which panicles had failed to emerge by 175 DAS were discarded when the experiment was terminated. In Exps 7.1 and 7.2, the main-stem leaves were marked for each plant and the final main-stem leaf number was determined at panicle emergence. Because at the constant temperature of 19°C in Exp. 7.3, plants of CO36 and Shan You 63 never flowered and the panicles often did not fully emerge, the time of emergence of the earliest panicle tip was used as the flowering time.

Results

Days from sowing to flowering

The relationships between days from sowing to flowering and days from sowing to transfer in the three cultivars are given in Figs 7.1, 7.2 and 7.3 for Exps 7.1, 7.2 and 7.3, respectively. The period to flowering in all cultivars was greatly affected by the time of transfer in all experiments. Some plants had flowered before the transfer was conducted (Figs 7.1-7.3). Plants of CO36 which were transferred from HT to LT before 56 DAS in Exp. 7.2 had not flowered when the experiment was terminated at 175 DAS (Fig. 7.2A). There was sometimes large plant-to-plant variation for each treatment in the flowering time. This variation was least in Nipponbare in all experiments.

Transfers from low to high temperature

There were one (Fig. 7.2A,B) or two (Fig. 7.1, Fig. 7.2C, Fig. 7.3C) critical times of transfer, where the relationship between days to flowering and day of LT-to-HT transfer changed. These critical times were most clearly shown for Nipponbare in all experiments (Figs 7.1C, 7.2C, 7.3C) and for CO36 and Shan You 63 in Exp. 7.2 (Fig. 7.2A,B). This indicates that the temperature sensitivity of preflowering development changed with plant age. Based on these changes, preflowering development was visually divided into two or three different phases. Within each phase, the relationship between days to flowering and day of transfer was linear. However, these linear relations cannot be clearly shown from the results of CO36 and Shan You 63 in Exp. 7.3 (Fig. 7.3A,B).

The slopes of the linear relationship between days to flowering and day of transfer differed among the phases (Table 7.2). The value of the slope in the second phase significantly differed from zero, whereas in the first and third phase, a small, often not significant, slope was found.

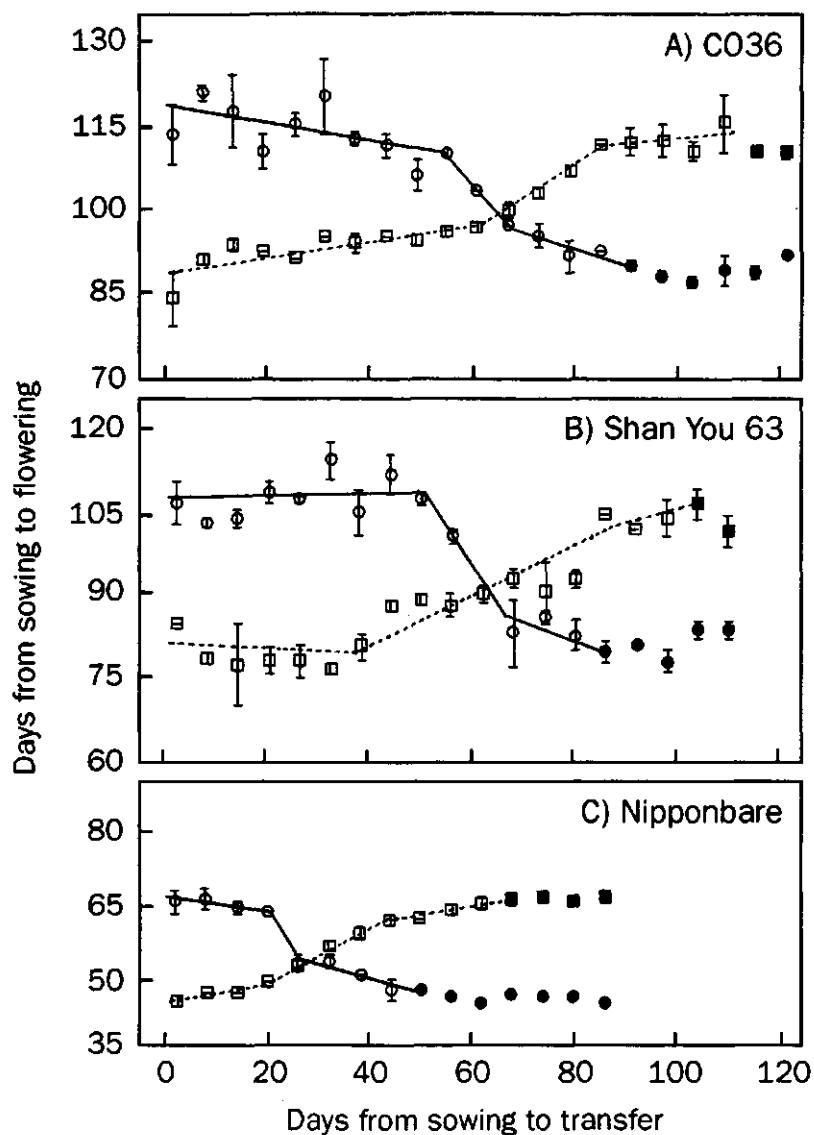


Fig. 7.1. Days from sowing to flowering for plants of three rice cultivars transferred from constant low (LT, 21°C) to constant high (HT, 26°C) temperature (squares) or from HT to LT (circles) at various times after sowing (Exp. 7.1). Vertical bars represent means \pm standard errors. The closed symbols refer to the observations from those plants which flowered before transfer. The dashed and solid segmented lines represented the relations visually fitted to the observations of LT-to-HT and HT-to-LT transfers, respectively, where flowering occurred after transfer.

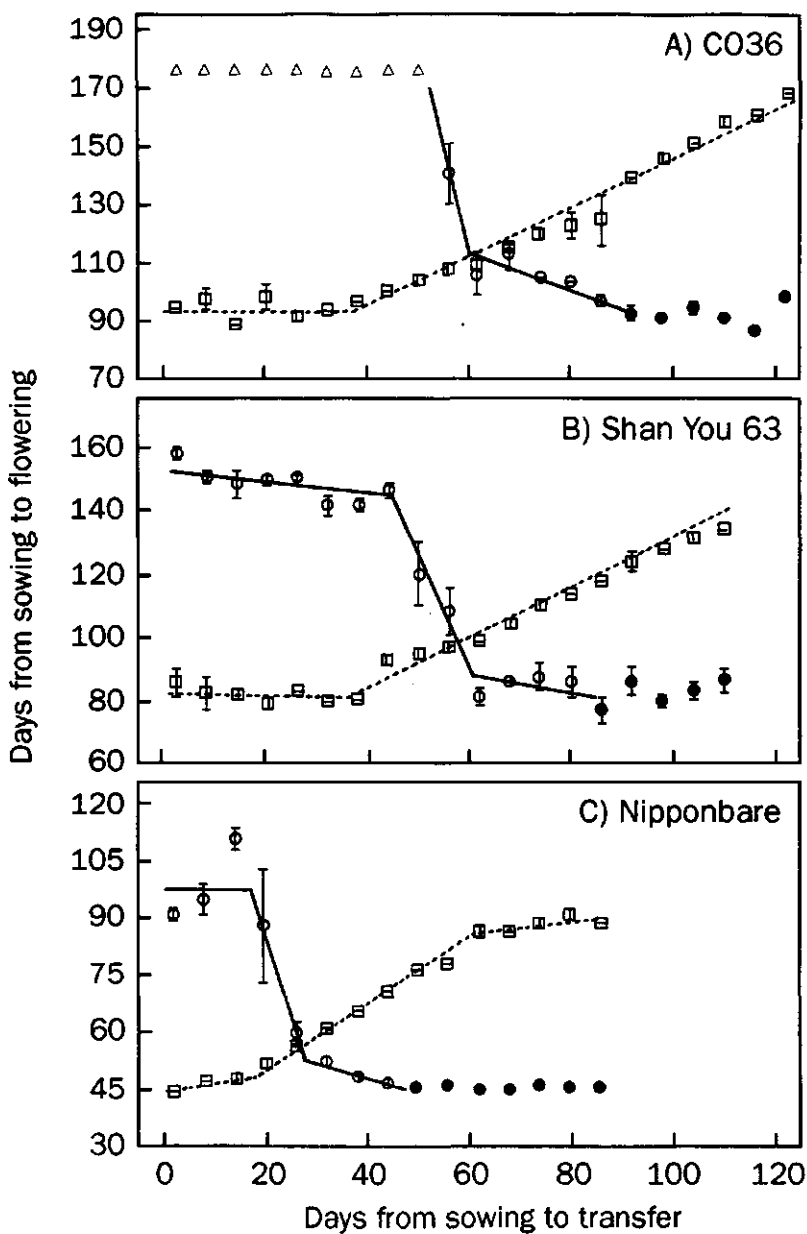


Fig. 7.2. Days from sowing to flowering for plants of three rice cultivars transferred from low (LT, 26/16°C for day/night) to high (HT, 26/26°C) night temperature (squares) or from HT to LT (circles) at various times after sowing (Exp. 7.2). The triangles indicate that those plants transferred from HT to LT had not flowered when the experiment terminated at 175 days after sowing. For further details see Fig. 7.1.

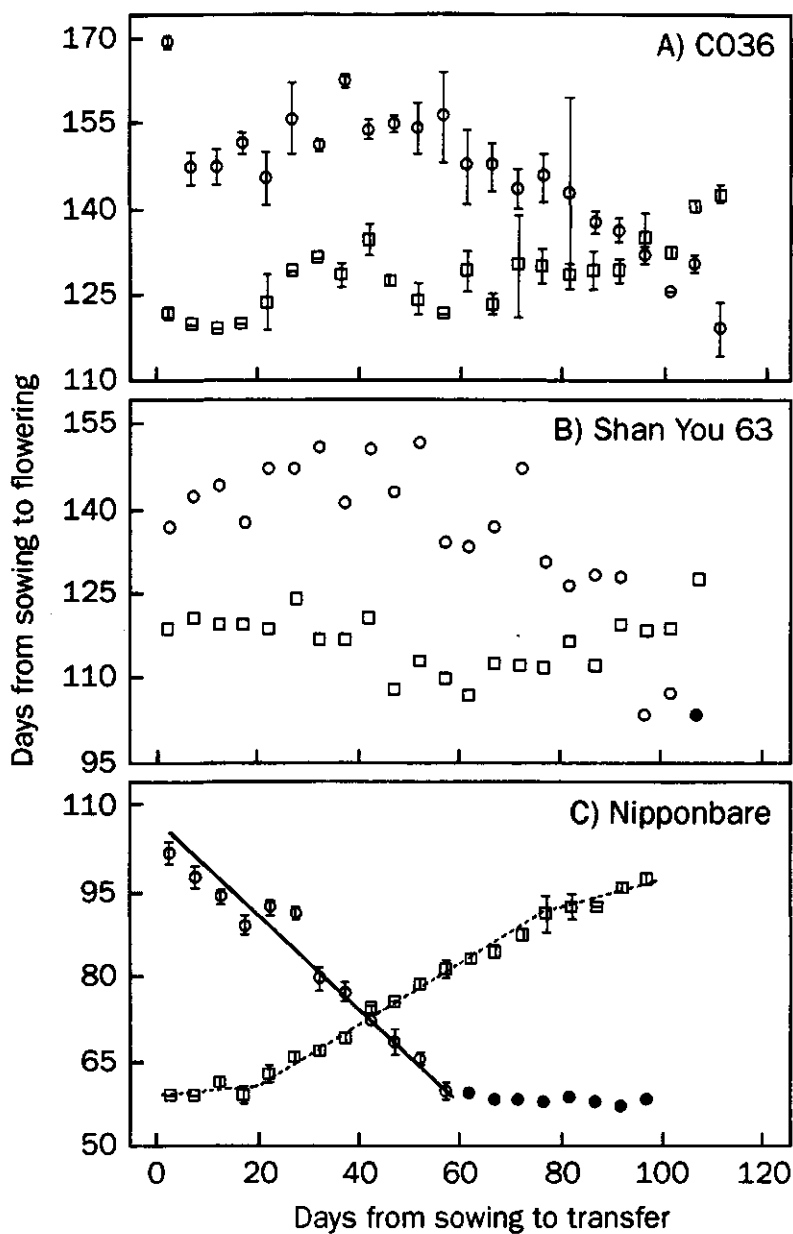


Fig. 7.3. Days from sowing to flowering for plants of three rice cultivars transferred from low (LT, 19/19°C for day/night) to high (HT, 28/19°C) day temperature (squares) or from HT to LT (circles) at various times after sowing (Exp. 7.3). For further details see Fig. 7.1.

Table 7.2. Coefficients (standard errors in parentheses) for regression lines relating days to flowering to day of transfer from low to high temperature.

Cultivar	Phase	Intercept	Slope†	r^2	Transfer dates‡
Exp. 7.1					
CO36	1	88.6(1.4)	0.142(0.042)B	0.584**	2-56
	2	60.8(3.1)	0.575(0.042)A	0.984***	62-86
	3	99.0(17.8)	0.129(0.176)B	0.212ns	92-110
Shan You 63	1	81.2(2.0)	-0.100(0.085)B	0.217ns	2-38
	2	70.6(4.9)	0.322(0.076)A	0.718**	38-86
	3	91.8(12.5)	0.129(0.131)AB	0.327ns	86-104
Nipponbare	1	44.9(0.6)	0.200(0.049)B	0.893*	2-20
	2	38.3(0.9)	0.542(0.029)A	0.994***	20-38
	3	51.3(1.2)	0.217(0.022)B	0.980**	44-62
Exp. 7.2					
CO36	1	93.8(2.8)	0.015(0.121)B	0.003ns	2-38
	2	55.5(3.6)	0.900(0.042)A	0.975***	44-122
Shan You 63	1	83.3(1.4)	-0.100(0.062)B	0.340ns	2-38
	2	56.0(1.8)	0.716(0.024)A	0.988***	38-110
Nipponbare	1	43.8(0.9)	0.292(0.096)B	0.902+	2-14
	2	35.4(1.2)	0.784(0.029)A	0.992***	20-62
	3	76.5(5.3)	0.146(0.071)B	0.581ns	62-86
Exp. 7.3					
Nipponbare	1	58.0(1.1)	0.180(0.082)B	0.615+	2-22
	2	51.6(0.9)	0.510(0.017)A	0.990***	22-77
	3	66.2(6.4)	0.320(0.074)B	0.863*	77-97

+, *, **, and *** indicate significance of regression (i.e. slope $\neq 0$) at 0.10, 0.05, 0.01 and 0.001 probability levels, respectively; ns: not significant ($P > 0.05$).

† The different letter indicates the slope significantly different between phases within each cultivar in each experiment according to t tests ($\alpha = 0.01$).

‡ Data for plants moved from low to high temperature during this time period were used in calculation of the regression equations.

Table 7.3. Significance of the difference among cultivars in the value of the slope for the linear relationship between days to flowering and day of transfer for each identified phase in both Exp. 7.1 and Exp. 7.2. For a given phase in each experiment, the same letter indicates that the slopes of the two cultivars were not significantly different according to pairwise *t* tests ($\alpha = 0.05$).

	Transfers from low to high temperature†			Transfers from high to low temperature†		
	Phase 1	Phase 2	Phase 3	Phase 1	Phase 2	Phase 3
Exp. 7.1						
	CO36 a	CO36 a	CO36 a	CO36 a	CO36 a	CO36 a
	SY63 b	SY63 a	SY63 a	SY63 b	SY63 ab	SY63 a
	NPB ab	NPB a	NPB a	NPB ab	NPB b	NPB a
Exp. 7.2						
	CO36 a	CO36 a			CO36 a	CO36 a
	SY63 a	SY63 b		SY63 a	SY63 a	SY63 a
	NPB a	NPB ab		NPB a	NPB a	NPB a

† Cultivar abbreviations: SY63 = Shan You 63; NPB = Nipponbare.

For a given phase, the value of the slope did not differ significantly among cultivars within the experiment (Table 7.3). But there was a large difference among cultivars in the length of each phase; and this difference was more obvious in the first and second phase than in the third phase which started about 20–25 d before flowering (Figs 7.1–7.3). The second phase started earlier in *japonica* cv. Nipponbare (about 20 DAS) than in two *indica* cultivars (35–60 DAS).

Transfers from high to low temperature

Three different phases with a different temperature sensitivity during the preflowering period were also observed in transfers from HT to LT in Exps 7.1 and 7.2 (Figs 7.1 and 7.2). However, the different phases could not be distinguished in the HT-to-LT transfers in Exp. 7.3 (Fig. 7.3), either because there was no clear relationship between flowering and date of transfer (Fig. 7.3A,B) or because the linear relationship was smooth (Fig. 7.3C).

Because plants of these transfers initially experienced in HT, the length of the second phase was very short, compared to its length identified from the LT-to-HT transfers. However, the first and third phases were not necessarily shorter than those identified from the LT-to-HT transfers. Absolute values of the negative slopes for the linear relation in the second phase were significantly larger than those in the first and third phases, which did not differ significantly (Table 7.4). There was generally no significant difference among cultivars in the slope for a given phase (Table 7.3). However, there was a large difference among cultivars in the length of the first phase, which was shorter in Nipponbare than in the other two cultivars (Figs 7.1 and 7.2).

Table 7.4. Coefficients (standard errors in parentheses) for regression lines relating days to flowering to day of transfer from high to low temperature.

Cultivar	Phase	Intercept	Slope†	r ²	Transfer dates‡
Exp. 7.1					
CO36	1	118.2(2.5)	-0.163(0.073)ab	0.384+	2-56
	2	167.8(1.5)	-1.042(0.024)a	0.999*	56-68
	3	116.7(5.1)	-0.296(0.064)b	0.878*	68-92
Shan You 63	1	105.2(2.1)	0.091(0.071)a	0.192ns	2-50
	2	179.8(10.1)	-1.438(0.180)b	0.984*	50-62
	3	101.1(12.5)	-0.242(0.161)a	0.529ns	68-86
Nipponbare	1	66.5(0.7)	-0.146(0.055)a	0.778+	2-20
	2	98.5(0.0)	-1.750(0.000)b	1.000***	20-26
	3	62.8(2.8)	-0.346(0.077)a	0.909*	26-44
Exp. 7.2					
CO36	2	462.3(0.0)	-5.750(0.000)b	1.000***	56-62
	3	139.2(16.5)	-0.471(0.221)a	0.602ns	62-86
Shan You 63	1	154.5(2.5)	-0.291(0.091)a	0.628*	2-44
	2	295.3(18.1)	-3.438(0.339)b	0.981**	44-62
	3	93.7(18.0)	-0.150(0.242)a	0.114ns	62-86
Nipponbare	1	95.0(11.6)	0.058(0.898)ab	0.002ns	2-20
	2	181.4(0.0)	-4.708(0.000)b	1.000***	20-26
	3	62.5(2.8)	-0.367(0.068)a	0.935*	32-50
Exp. 7.3					
Nipponbare§		104.5(1.7)	-0.749(0.050)	0.958***	2-57

†, *, **, and *** indicate significance of regression (i.e. slope $\neq 0$) at 0.05, 0.01, and 0.001 probability levels, respectively; ns: not significant ($P > 0.05$).

† The same letter indicates the slope not significantly different between phases within each cultivar in each experiment according to *t* tests ($\alpha = 0.05$).

‡ Data for plants moved from low to high temperature during this time period were used in calculation of the regression equations.

§ Only one phase was identified because the linear relationship between days to flowering and day of transfer was smooth (see Fig. 7.3C).

Final leaf number on the main stem

Compared to the strong influence of temperature on days to flowering, the effect of temperature on the final main-stem leaf number was relatively small (Tables 7.5 and 7.6). In Exp. 7.1 where plants were moved between two diurnally constant temperatures, the leaf number did not change with changing transfer date (Table 7.5). However, in Exp. 7.2 where plants were moved between two night temperatures, the leaf number, especially in CO36 and Nipponbare, was altered significantly by temperature for plants transferred during the middle period of development (Table 7.6).

Table 7.5. The final main-stem leaf number (standard error in parenthesis if not zero) of plants of moving between constant low (LT) and constant high temperature (HT) regimes of three rice cultivars in Exp. 7.1.

Transfer (DAS†)	CO36		Shan You 63		Nipponbare	
	HT to LT	LT to HT	HT to LT	LT to HT	HT to LT	LT to HT
2	12.5(0.5)	13.0	12.5(0.5)	13.5(0.5)	10.0	10.0
8	13.0	13.0	12.0	12.0	9.5(0.5)	10.0
14	12.5(0.5)	13.5(0.5)	12.5(0.5)	12.5(0.5)	10.0	9.0
20	11.5(0.5)	13.5(0.5)	13.0	12.0	10.0	9.0
26	13.0	13.0	13.5(0.5)	11.5(0.5)	9.0	9.5(0.5)
32	13.0	13.0	13.5(0.5)	12.0	9.0	10.0
38	12.5(0.5)	13.5(0.5)	12.5(0.5)	12.0	10.0	9.5(0.5)
44	12.5(0.5)	13.0	13.5(0.5)	13.0	9.5(0.5)	10.0
50	12.5(0.5)	12.5(0.5)	13.5(0.5)	12.0	9.5(0.5)	10.0
56	13.0	12.0	13.0	12.0	10.0	10.0
62	13.0	13.0	13.0	12.0	9.0	10.0
68	13.0	12.5(0.5)	12.5(0.5)	12.5(0.5)	10.0	10.0
74	12.5(0.5)	13.0	12.5(0.5)	12.5(0.5)	9.5(0.5)	10.0
80	12.5(0.5)	13.0	13.0	12.0	9.5(0.5)	9.0
86	13.0	13.0	12.5(0.5)	13.5(0.5)	9.0	10.0
92	13.0	13.0	13.0	12.0		
98	12.5(0.5)	13.0	12.0	12.5(0.5)		
104	12.0	12.5(0.5)	13.5(0.5)	12.0		
110	13.5(0.5)	13.5(0.5)	13.0	12.0		
116	13.5(0.5)	12.5(0.5)				
122	13.5(0.5)	12.5(0.5)				

† DAS = days after sowing

Table 7.6. The final main-stem leaf number (standard error in parentheses if not zero) of plants of moving between low (LT) and high (HT) night temperature regimes of three rice cultivars in Exp. 7.2.

Transfer (DAS†)	CO36		Shan You 63		Nipponbare	
	HT to LT‡	LT to HT	HT to LT	LT to HT	HT to LT	LT to HT
2	13.3	14.0	14.5(0.5)	14.0	12.0	9.0
8	13.3	13.5(0.5)	14.0	13.5(0.5)	12.0	9.0
14	14.1	13.0	14.0	12.5(0.5)	13.0	9.0
20	13.8(0.3)	13.5(0.5)	14.0	12.5(0.5)	10.0(1.0)	10.5(0.5)
26	13.6(0.1)	13.0	14.0	12.0	9.0	10.0
32	13.9(0.2)	13.0	14.0	12.0	9.5(0.5)	10.5(0.5)
38	14.3(0.2)	13.0	14.5(0.5)	12.0	9.0	11.5(0.5)
44	14.0(0.1)	13.0	14.0	13.0	9.0	11.5(0.5)
50	14.5(0.1)	13.5(0.5)	14.0	13.0	9.0	12.0
56	13.0	14.0	12.5(0.5)	13.0	9.0	12.0
62	13.0	14.0	12.0	13.0	9.0	11.5(0.5)
68	14.0	14.5(0.5)	12.5(0.5)	13.5(0.5)	9.0	12.0
74	13.5(0.5)	14.5(0.5)	12.5(0.5)	14.0	9.0	12.0
80	14.0	14.0	12.5(0.5)	13.0	9.0	12.0
86	13.0	14.0	12.0	14.0	9.0	12.0
92	13.5(0.5)	15.0	12.5(0.5)	14.0		
98	13.5(0.5)	15.0	12.5(0.5)	14.0		
104	14.0	15.0	12.5(0.5)	14.0		
110	13.0	16.0	13.5(0.5)	14.0		
116	12.0	16.0				
122	13.0	16.0				

† DAS = days after sowing.

‡ For plants of HT-to-LT transfers at 2 to 50 DAS in which the flag leaf had not emerged when the experiment terminated at 175 DAS, the data given in the table are the main-stem leaf number at 175 DAS.

Discussion

The most striking observation from the experiments described in this Chapter was the significant change in sensitivity of the phenological response to temperature with plant age during preflowering ontogeny of rice, from slightly sensitive to highly sensitive and then to slightly sensitive again (Figs 7.1-7.3; Tables 7.2 and 7.4). This result agrees with the report of Shibata et al. (1973) who indicated that rice was most temperature-sensitive at about 10 days before PI, but sharply contrasts the report of Ahn (1968) that high temperature reduced the duration of the BVP but had little effect on the subsequent PSP. Several other studies in

various crops (Went, 1945, 1950 and 1956; Owen, 1971; Angus et al., 1981; Ellis et al., 1988; Hammer et al., 1989; Slafer and Rawson, 1995a) have indicated that the base or the optimum temperature for phenological response varies with plant age. The present study demonstrated that it was the temperature sensitivity *per se* which strongly varied with plant age in rice.

Rice plants are responsive to photoperiod only during the PSP (Collinson et al., 1992; Chapter 6). The strong temperature sensitivity of plants during the middle phase might be attributed to an additional effect of temperature during the PSP on the photoinduction process besides a direct effect on development rate. This can be substantiated by the fact that often the sensitivity value for the second phase in both Exps 7.1 and 7.2 was largest in the most photoperiod-sensitive cv. CO36 and smallest in the weakly sensitive cv. Shan You 63 (Tables 7.2 and 7.4). The first slightly temperature-sensitive period was shorter in *japonica* cv. Nipponbare than in the two *indica* cultivars (Figs 7.1 and 7.2), agreeing with the result that the BVP was shorter in *japonica* than *indica* cultivars (Chapter 6). Therefore, the present Chapter further justifies the division of the entire preflowering period into three phases, namely BVP, PSP and PPP for modelling purposes. The results also imply that both dark and light periods might be important for the photoinduction, since responses to both night and day temperature were stronger during the PSP than during the BVP or PPP (Fig. 7.2, Fig. 7.3C).

The effect of temperature on the final leaf number in cereal crops was small compared to the effect of photoperiod (Major and Kiniry, 1991). However, this Chapter indicated that the final leaf number was different among treatments with different night temperatures but the same day temperature (Table 7.6), although little variation was observed in the treatments with two diurnally constant temperatures (Table 7.5). This contradicts the report of Vergara and Lilis (1968) who found that the final leaf number was constant across night temperatures. In addition, the final leaf number did not respond to temperature throughout the preflowering period but only during the middle period (Table 7.6), agreeing with the results of Arnold (1969) and Tollenaar and Hunter (1983) on the temperature sensitive period for final leaf number in maize. Thus, the critical time for both photoperiod and temperature to affect the final leaf number in rice is during PSP.

The results for the two *indica* cultivars CO36 and Shan You 63 in Exp. 7.3 did not show a clear relationship between days to flowering and day of transfer (Fig. 7.3A,B). This might be due to the effect of the low temperature of 19°C on the response, since temperatures lower than 20°C often lead to the chilling damage in rice, especially in *indica* cultivars (Yoshida, 1981). The plants of CO36 and Shan You 63 grown at 19°C showed several signs of chilling damage including stunted growth, chlorotic leaves and abnormal panicles. The large plant-to-plant variation with respect to the time to flowering of these two cultivars in both Exp. 7.1 (Fig. 7.1A,B) and Exp. 7.3 (Fig. 7.3A,B) can also be attributed to the chilling damage from the LT regimes used in these two experiments.

Conclusions

The results of this Chapter showed that the responses of preflowering development to both day and night temperature changed with plant age, from slightly sensitive to highly sensitive and

then to slightly sensitive again. The highly sensitive phase started at about 20 DAS in the *japonica* cultivar Nipponbare, and at 35–60 DAS in the two *indica* cultivars, depending on temperature. However, less variation among cultivars was found in the timing of the end of the highly sensitive period, which occurred at 20–25 d before flowering. The highly temperature-sensitive period for development to flowering was also the critical period for the effect of temperature on the final main-stem leaf number.

The higher temperature sensitivity during the middle period of preflowering ontogeny was presumably due to an additional effect of temperature on the photoinduction process during PSP, which is sandwiched by two photoperiod-insensitive phases BVP and PPP. Therefore, for accurate modelling of rice flowering dates, functions for temperature effects on development rate during PSP have to be different from those on development rate during BVP or PPP.

Chapter 8

The effect of temperature on leaf appearance in rice

Abstract Temperature is the principal environmental determinant of crop leaf appearance. The objective of this Chapter is to analyse whether there are different effects of day temperature (T_D) and night temperature (T_N) on main-stem leaf appearance in rice (*Oryza sativa* L.).

Plants of 12 rice cultivars were grown at five constant temperatures (22, 24, 26, 28 and 32°C) and four diurnally fluctuating temperatures (T_D/T_N : 26/22, 30/22, 22/26 and 22/30°C) with a constant photoperiod of 12 h d⁻¹. The leaf appearance on the main stem was measured.

A constant change in leaf appearance rate was observed during ontogeny. The relation between the number of emerged leaves and days from seedling emergence was described by a power-law equation with only one cultivar-specific parameter. Values for this parameter were estimated for the five constant temperature treatments, and the relation between this parameter and temperature was quantified by a nonlinear model. On the basis of these relations, leaf appearance for the four fluctuating temperature treatments could be accurately predicted in each cultivar. This indicated that there were no specific effects of T_D and T_N on leaf appearance in rice, in contrast with the different effects of T_D and T_N on phenological development to flowering as found in Chapter 4. The optimum temperature for leaf appearance was found to be substantially higher than for development to flowering.

The final main-stem leaf number differed with diurnal temperature conditions. When a diurnal temperature delayed flowering, it increased the leaf number as well. This might explain why T_D and T_N had a different effect on development to flowering but not on leaf appearance.

Introduction

Leaf appearance is one of the important aspects of development in rice (Gao et al., 1992; Ellis et al., 1993), which can be used to determine the response of development to temperature (Ritchie and NeSmith, 1991). In cereal crops, panicle emergence immediately follows the full appearance of the flag leaf. Thus, if the final leaf number is known, flowering time can be predicted on the basis of leaf appearance (e.g. Grant, 1989; Miglietta, 1991a,b; Miller et al., 1993). In addition, quantification of leaf appearance is also important for predicting leaf area development of a crop (Slafer et al., 1994). Many studies (Klepper et al., 1982; Dwyer and Stewart, 1986; Hammer et al., 1987; Alm et al., 1988; Cao et al., 1988; Muchow and Carberry, 1989, 1990) have successfully predicted leaf area development from the leaf number.

Many studies in controlled-environment experiments (Tollenaar et al., 1979; Thiagarajah and Hunt, 1982; Cao and Moss, 1989; White et al., 1990; Ellis et al., 1993) quantified leaf appearance by using a linear model for the relation between the number of emerged leaves and the time from seedling emergence. In contrast, other studies reported a sudden decrease in leaf

appearance rate (LAR) at the time of transition from the vegetative to the reproductive growth stage, for example, at about panicle initiation in rice (Nagai, 1963; Baker et al., 1990) or at the stage of double ridge formation in wheat (*Triticum aestivum* L.) (Baker et al., 1986; Boone et al., 1990). However, Warrington and Kanemasu (1983b) reported an increased LAR after leaves 10–12 emerged in maize (*Zea mays* L.) in a controlled environment. Similarly, Muchow and Carberry (1989) found that the thermal time interval between appearance of successive leaves decreased gradually with increasing leaf position for field-grown maize. But Zur et al. (1989) indicated that the response curve for maize LAR vs leaf position was quadratic. In rice, Gao et al. (1992) used a power-law equation to describe the increase of leaf number as a function of time after emergence and showed that LAR decreased as time progressed.

Although the different findings can be due to a qualitative difference between cereals, an additional reason can be that different criteria for counting leaf number were used. Warrington and Kanemasu (1983b) noticed that LAR in maize could vary three to four fold due to different definitions for leaf appearance. Some workers counted the leaf once its tip was visible (e.g. Tollenaar et al., 1979; Baker et al., 1980; Kirby et al., 1985; Ellis et al., 1993), whereas others considered a leaf only when the ligule at the base of the lamina was visible above the enclosing sheath of the preceding leaf (e.g. Warrington and Kanemasu, 1983b; Muchow and Carberry, 1989, 1990). However, most researchers (Klepper et al., 1982; Baker et al., 1986; Cao and Moss, 1989; Baker et al., 1990; Boone et al., 1990; White et al., 1990; Slafer et al., 1994) used the Haun growth scale (Haun, 1973), where the leaf number is determined from the number of fully expanded leaves plus the ratio of the lamina length of the last visible growing leaf to that of the preceding leaf. For example, a stem with 6.2 leaves has six fully developed leaves and a seventh leaf one-fifth as long as the sixth. Although the Haun scale provides a more precise measure of leaf appearance than the method of simply counting number of visible leaves (Baker et al., 1986), it assumes that the tip of a leaf does not emerge earlier than the ligule of its predecessor. Kiniry et al. (1991) and Ritchie (1993) indicated that the rate of leaf tip appearance was often constant whereas the rate of full leaf expansion decreased with the thermal time from seedling emergence in maize. This implies that a leaf tip may appear earlier than the ligule of the preceding leaf.

Temperature is a principal environmental determinant of LAR (Ritchie, 1993). Many studies show that leaf number is linearly related to accumulated thermal units (TU, °Cd) from seedling emergence (Gallagher, 1979; Baker et al., 1980; Klepper et al., 1982; Kirby et al., 1985; Baker et al., 1986; Dwyer and Stewart, 1986; Boone et al., 1990; Muchow and Carberry, 1990; White et al., 1990; Kiniry et al., 1991; Slafer et al., 1994). The inverse of the slope of this linear relation provides an estimate of the phyllochron, the interval (°Cd) between the opening of two successive leaves. Thus, the TU system assumes a fixed phyllochron among environmental conditions. However, Cao and Moss (1989) found that the phyllochron increased exponentially with increasing temperature for all tested wheat and barley (*Hordeum vulgare* L.) genotypes, suggesting that LAR increased nonlinearly with the temperature. Indeed, Tollenaar et al. (1979) and Warrington and Kanemasu (1983b) described the relationship between LAR in maize and temperature by using third and fourth-degree polynomial equations, respectively, with an optimum temperature (T_o) of 30–35°C. For rice, Ellis et al. (1993) used a quadratic equation to describe this relationship and showed that T_o for

LAR of cv. IR36 was about 26°C, at least 2°C lower than the optimum for phenological development to flowering. Different temperature responses for foliar and floral development were also reported by Nakagawa and Horie (1991) for rice, and by Slafer and Rawson (1995b) for wheat. However, Gao et al. (1992) assumed that the value of T_0 for floral development also applied to leaf appearance in rice.

With regard to the impact of day temperature (T_D) and night temperature (T_N) on leaf appearance, Warrington and Kanemasu (1983b) reported that where temperature regimes had means lower than 20°C, LAR in maize was higher in differential diurnal temperatures than in constant temperatures but the same daily mean. However, they found that this difference can be attributed to the curvilinear nature of the leaf appearance response to temperature. Tollenaar et al. (1979) also reported no difference in effects of T_D and T_N on maize leaf appearance. In Chapter 4, a different impact of T_D and T_N on phenological development to flowering in rice was found. Whether there is a different effect of T_D and T_N on leaf appearance in rice is not known.

The objective of this Chapter is to quantify the effect of temperature on main-stem leaf appearance in rice by analysing whether T_D and T_N have a different impact on leaf appearance.

Materials and methods

An experiment was conducted in nine naturally-lighted growth chambers at the International Rice Research Institute (IRRI). Full experimental details were given in Chapter 4. Treatments included five constant (22, 24, 26, 28 and 32°C) and four diurnally fluctuating (T_D and T_N : 26/22, 30/22, 22/26 and 22/30°C) temperatures. In each diurnally fluctuating regime, T_D and T_N were imposed for 12 h d⁻¹. The photoperiod was maintained throughout the experiment at 12 h d⁻¹, agreeing with the period of T_D . Relative humidity was maintained at 70 ± 5%. Plants were grown in pots at each thermal environment from seedling emergence to flowering. The pot water temperature was controlled to be the same as the air temperature.

Each of the 24 tested rice cultivars had three replicate pots for each temperature. However, only two replicate plants in 12 cultivars were selected for leaf counting. These plants included seven *indica* (IR36, IR42, IR64, IR72, Azucena, MR84 and Guang Lu Ai 4), two *indica* hybrid (Shan You 63 and IR64616H) and three *japonica* (Nipponbare, Koshihikari and Hwasong) cultivars.

Two different approaches were used for counting the leaves on the main-stem. First, plants of four representative cultivars (IR36, IR72, IR64616H and Nipponbare) were observed daily to determine the dates of appearance of both tip and ligule of each main-stem leaf. The leaf tip was counted when it was visible above the enclosing sheath of the preceding leaf. The leaf ligule was counted when it was at the same level as its predecessor. Secondly, Haun leaf scale units (Haun, 1973) were used for all 12 cultivars. Plants were observed every 3 d for the first five leaves, every 4 d for leaves 6–10 and every 5 d for the remaining leaves. The leaf count started with the first leaf with a complete leaf lamina, i.e. the prophyll leaf without lamina (Yoshida, 1981) was not included in leaf counting. The final main-stem leaf number was obtained at panicle emergence.

Results and discussion

Leaf tip vs leaf ligule appearance

The relationship between the time of appearance of a leaf tip ($t_{\text{tip},n}$) and its preceding leaf ligule ($t_{\text{ligule},n-1}$) observed in the nine temperature treatments for four cultivars IR36, IR72, IR64616H and Nipponbare is:

$$t_{\text{ligule},n-1} = -0.153(0.017) + 1.0093(0.0005)t_{\text{tip},n} \quad r^2 = 0.9998, \text{df} = 724$$

where the figure in parentheses is the standard error of the regression coefficient. Nearly perfect agreement for appearance of a leaf tip and its preceding ligule suggests that the tip of a leaf generally appeared at the same day as the preceding leaf ligule. Thus, the Haun leaf units (Haun, 1973) can be used for measuring rice leaf appearance.

The number of leaves vs days from seedling emergence

An example of the relation of the number of leaf tips on the main stem over days from seedling emergence is given for cv. IR36 (Fig. 8.1). This response was typical for all cultivars at all temperatures. The response showed a continuous decrease of LAR during ontogeny (Fig. 8.1A). However, a nearly linear relation was found if the data were transformed into a logarithmic scale (Fig. 8.1B). Thus, a power-law equation was used to describe the relationship between leaf tip number (Y_t) and days from emergence (X)

$$Y_t = aX^b \quad (8.1)$$

where a and b are coefficients. Because there is already one leaf tip at emergence (i.e. $X=1$), the value for coefficient a in Eq. 8.1 has to be 1.0. Thus, only parameter b was used to quantify cultivar-specific characteristics at a given temperature.

The nonlinear relationship between leaf tip number and days from emergence contradicts the linear relationship reported by Tollenaar et al. (1979), Thiagarajah and Hunt (1982), Cao and Moss (1989), White et al. (1990) and Ellis et al. (1993) in the controlled-temperature experiments, and also contradicts the linearity between leaf number and accumulated TU reported by Gallagher (1979), Baker et al. (1980), Kirby et al. (1985), Dwyer and Stewart (1986), Muchow and Carberry (1990) and Slafer et al. (1994) for cereal crops grown in the field. The data did not indicate evidence of a distinct break point in the relationship at any temperatures (Fig. 8.1A), in contrast to the observations of Nagai (1963) and Baker et al. (1990) of a sudden decrease of leaf appearance rate. Gao et al. (1992) also used a power-law equation to describe the relationship between rice leaf number and the time from emergence:

$$Y = k \cdot \left(\frac{T}{T_o} \right)^p X^b \quad (T = T_o \text{ for } T > T_o)$$

where Y is main-stem leaf number, X is days from seedling emergence, T is temperature, T_o is optimum temperature, k , p and b are coefficients. Clearly, Gao et al. (1992) assumed that

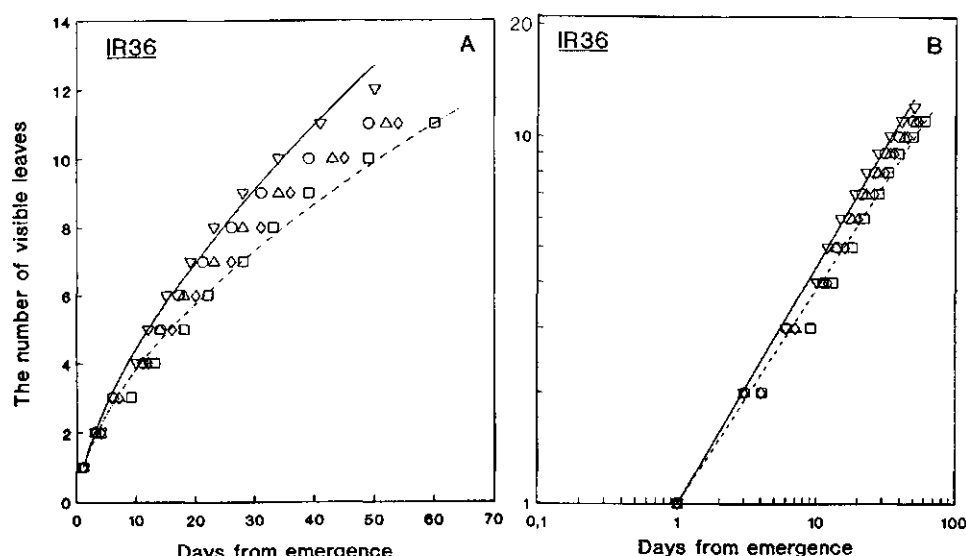


Fig. 8.1. The relation (A: normal scale; B: logarithmic scale) between the number of main-stem visible leaves (i.e. the number of leaf tips) and days from seedling emergence in plants of rice cv. IR36 at five constant temperatures (\square : 22°C; \diamond : 24°C; Δ : 26°C; \circ : 28°C; ∇ : 32°C). The dashed and solid lines represent fitted relations of Eq. 8.1 with $\alpha = 1.0$ to observations at 22 and 32°C, respectively.

coefficient α in Eq. 8.1 varied with temperature. However, the fact that the relationship between logarithm of leaf number and that of days from emergence at different temperatures was characterized by different slopes (Fig. 8.1B) suggested that it is coefficient b , rather than α , which strongly depended on temperature.

The value of parameter b in Eq. 8.1 for each cultivar at each temperature was derived by nonlinear optimization (SAS, 1988). To fit the data in Haun leaf growth units, Eq. 8.1 was adapted by accounting for one unit difference in the number between leaf tip and ligule, that is,

$$Y_h = X^b - 1 \quad (8.2)$$

where Y_h is the number of leaves in Haun units. There was a good agreement between values of parameter b estimated from the data in Haun units ($b_{(\text{Haun})}$) and from the data in leaf tip number ($b_{(\text{tip})}$) in cvs IR36, IR72, IR64616H and Nipponbare:

$$b_{(\text{Haun})} = 0.009(0.018) + 0.9872(0.0290)b_{(\text{tip})} \quad r^2 = 0.971, \text{df} = 35$$

where the figure in parentheses is the standard error of the regression coefficient. This further supports the use of Haun leaf units for leaf appearance measurement in rice. Because plants of cv. Azucena, a traditional *indica* cultivar, have very long leaves, the estimated b value at a given temperature in this cultivar was appreciably lower than those in other cultivars (Fig. 8.2).

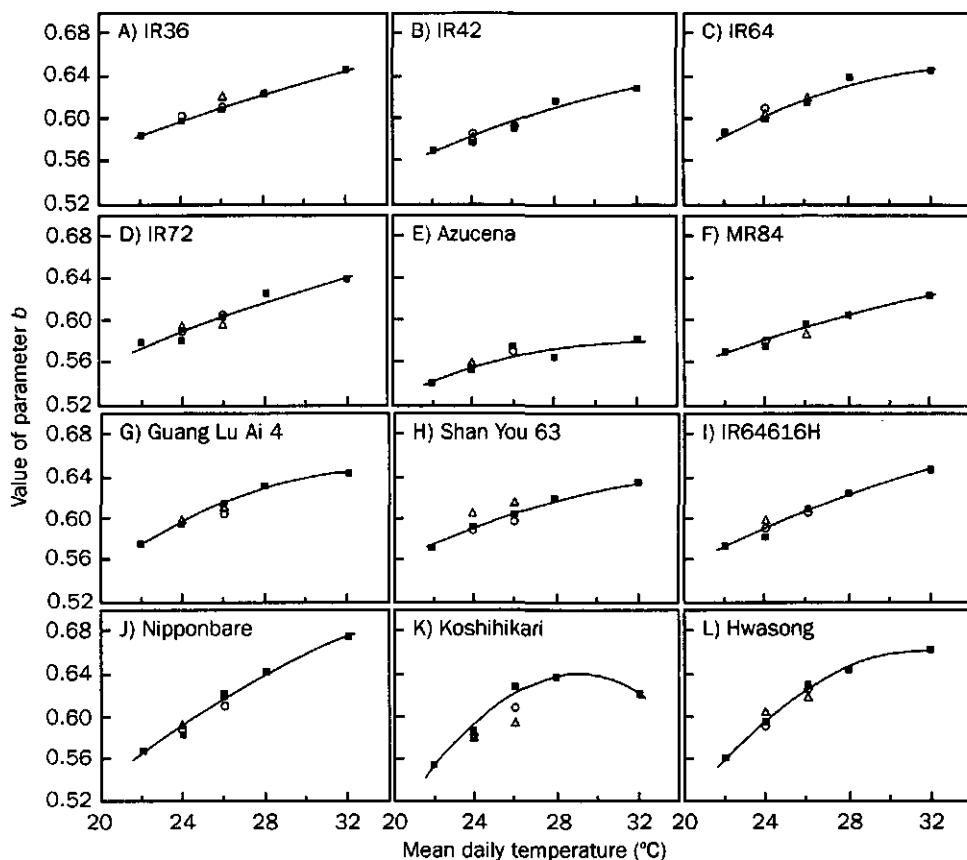


Fig. 8.2. The relations between the value of parameter b in Eq. 8.2 and the mean daily temperature in 12 rice cultivars. The curves represent Eq. 8.3 derived from the relation between parameter b and five diurnally constant temperatures (■). The open symbols indicate the values of parameter b at four diurnally fluctuating temperatures (○: 26/22 or 30/22°C; △: 22/26 or 22/30°C).

Effect of constant diurnal temperature on leaf appearance

For all cultivars, the value of parameter b in Eq. 8.2 varied among the five constant temperatures (Fig. 8.2). Because observations were limited to the range of temperatures between 22 and 32°C, an optimum temperature was not found in most cultivars. Nevertheless, the relation between the value of b and temperature was nonlinear in cvs Guang Lu Ai 4, Koshihikari and Hwasong (Fig. 8.2G,K,L). Thus, the relationship between the value of b and constant temperatures, T , was quantified by a nonlinear model described in Chapter 2:

Table 8.1. Values of parameters of Eq. 8.3 (with standard errors in parentheses) in 12 rice cultivars, derived from the data at five diurnally constant temperatures when T_b and T_c were set to be 8 and 42°C, respectively.

Cultivar	b_o	α	T_o (°C)	r^2
IR36	0.69(0.11)	0.19(0.03)	42.0(4.0)	0.998
IR42	0.66(0.08)	0.22(0.15)	39.6(13.7)	0.960
IR64	0.65(0.01)	0.32(0.14)	34.2(4.1)	0.967
IR72	0.67(0.11)	0.23(0.20)	39.6(17.5)	0.935
Azucena	0.58(0.01)	0.26(0.22)	32.7(6.2)	0.841
MR84	0.66(0.40)	0.18(0.11)	42.0(16.5)	0.972
Guang Lu Ai 4	0.65(0.00)	0.42(0.06)	32.9(1.1)	0.995
Shan You 63	0.64(0.00)	0.29(0.03)	35.1(1.1)	0.998
IR64616H	0.68(0.08)	0.26(0.14)	39.6(10.3)	0.976
Nipponbare	0.70(0.05)	0.41(0.15)	37.8(5.8)	0.985
Koshihikari	0.64(0.00)	1.06(0.13)	29.1(0.3)	0.984
Hwasong	0.66(0.00)	0.71(0.07)	31.7(0.6)	0.996

$$b = b_o \cdot \left[\left(\frac{T - T_b}{T_o - T_b} \right) \left(\frac{T_c - T}{T_c - T_o} \right)^{\frac{T_o - T_c}{T_o - T_b}} \right]^\alpha \tag{8.3}$$

where T_b and T_c are base and ceiling temperatures, respectively, at which leaf appearance ceases; T_o is optimum temperature at which parameter b reaches its maximal value, b_o ; and α is a coefficient defining the curvature of the relationship.

The standard values of T_b (8°C) and T_c (42°C) (Alocilja and Ritchie, 1991; Kropff et al., 1994b) were used to derive values for other coefficients in Eq. 8.3. Eq. 8.3 described the relation with $r^2 > 0.94$ in most cultivars (Table 8.1), even though the shape of the relation differed considerably among cultivars (Fig. 8.2). The estimated value of T_o for leaf appearance was not lower than 29°C in all cultivars (Table 8.1). However, because the estimated T_o was often outside the range of temperatures used in the experiment, which resulted in a large standard error in some cultivars, these values must be regarded as tentative. Nevertheless, the results indicate that T_o for leaf appearance was at least $> 32^\circ\text{C}$ in most tested cultivars. The value of T_o for leaf appearance was higher than that for development to flowering reported in Chapter 4 (Fig. 8.3). This contrasts with the assumption of Gao et al. (1992) that the value of T_o is the same for both foliar and floral development in a given type of rice cultivars. Ellis et al. (1993) also showed different temperature responses on foliar and floral development in cv. IR36 rice. However, they found that T_o was lower for foliar (about 26°C) than floral ($> 28^\circ\text{C}$) development, in contrast with the results reported here. The reason for such discrepancy is not clear; it could be that Ellis et al. (1993) considered a leaf as mature once its tip was visible, whereas the Haun leaf units were used in the present study.

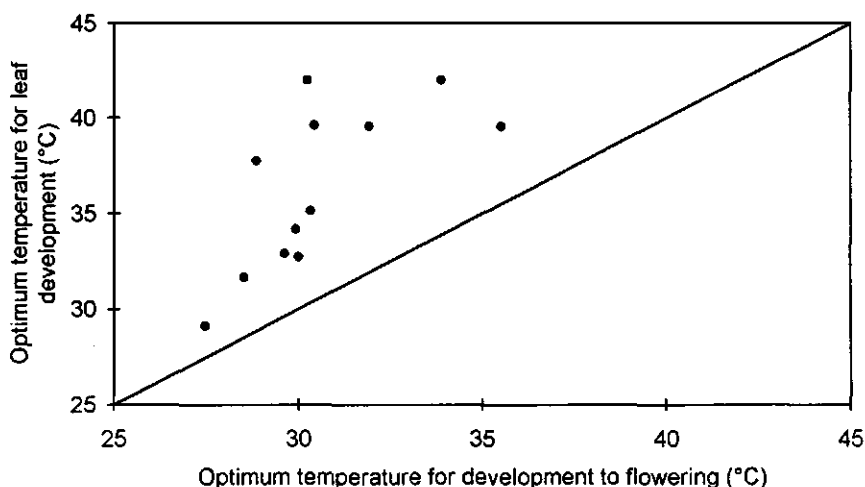


Fig. 8.3. Comparison between the value of the optimum temperature (T_o) for leaf development derived in this Chapter and the value of T_o for development to flowering derived in Chapter 4 from the data observed at five constant temperatures in 12 rice cultivars. The line shows the 1:1 relationship.

Predicting leaf appearance at diurnally fluctuating temperatures

In a second analysis, the relations established for constant temperatures were used to predict the leaf appearance at four diurnally fluctuating temperatures, with a time step of 0.5 d to separate effects of T_D and T_N . For this purpose, an expression for calculating LAR was derived on the basis of Eq. 8.2:

$$LAR = \frac{dY_h}{dX} = b \cdot (Y_h + 1)^{\frac{b-1}{b}} \quad (8.4)$$

Based on Eq. 8.4, the number of emerged leaves can be predicted as an integration of LAR over successive time steps. The predicted time course of leaf appearance agreed well with that observed for all cultivars in all diurnally fluctuating regimes. Examples are given in Fig. 8.4 for cvs MR84 and Nipponbare which had maximum and minimum final main-stem leaf numbers, respectively, among the 12 cultivars.

Good agreement between predictions and observations (Fig. 8.4) indicates that there is no different effect of T_D and T_N on LAR in rice. The value of parameter b in Eq. 8.2 for each cultivar at the four fluctuating temperatures was also derived (Fig. 8.2). No consistent evidence of any specific effects of T_D and T_N on the value of parameter b was found. The negligible difference in the effects of T_D and T_N on rice leaf appearance agreed with similar reports on leaf appearance in maize (Tollenaar et al., 1979; Warrington and Kanemasu, 1983b), but contrasts with the result of Chapter 4 on the significant difference in the effects of T_D and T_N on the rate of development to flowering. This indicates that developmental processes

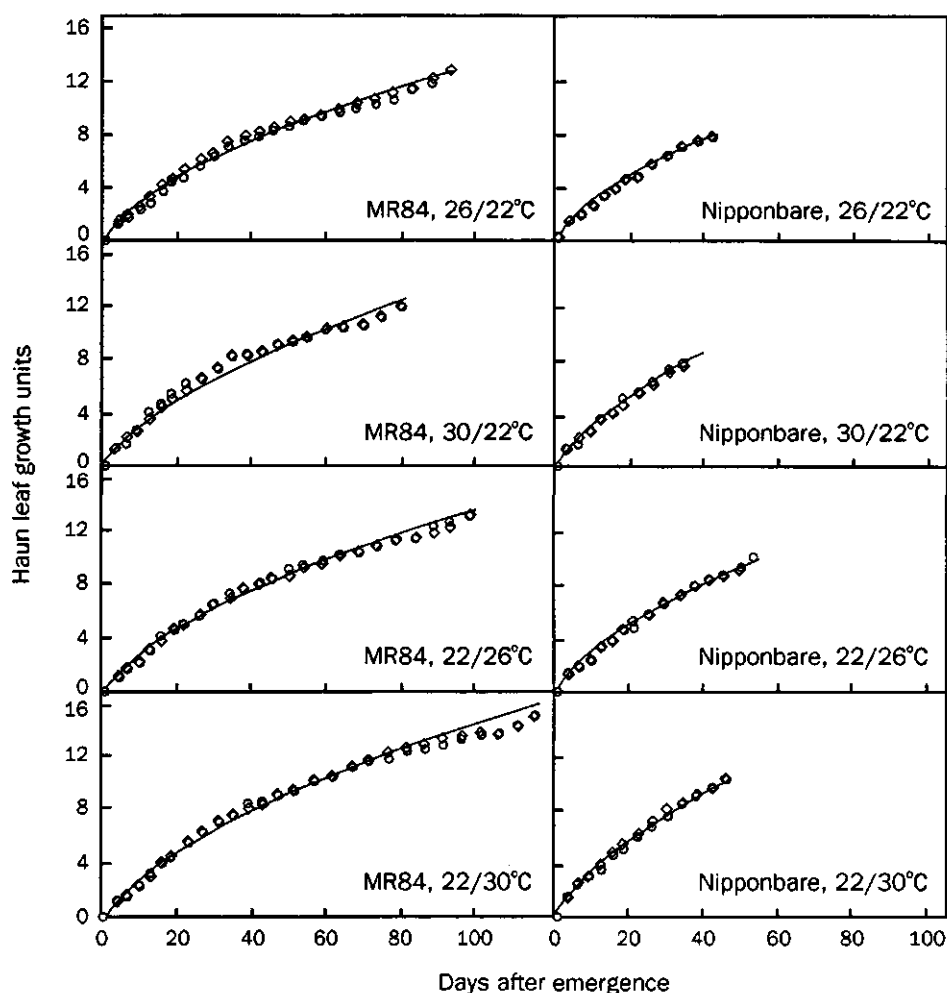


Fig. 8.4. Haun leaf growth units vs days from seedling emergence for two replicate plants (shown by different symbols) of rice cvs MR84 and Nipponbare grown at four diurnally fluctuating temperatures. The curves represent the time courses of leaf appearance predicted from Eq. 8.4 with the value of parameter b derived from the data at five constant temperatures (quantified in Table 8.1).

occurring simultaneously during plant growth (here leaf appearance and floral development) can have different sensitivities to T_D and T_N .

Since there is little evidence for specific effects of T_D and T_N on LAR in rice, quantification of the temperature effect on LAR is simpler than on the rate of development to flowering, for which the effects of T_D and T_N have to be differentiated (Chapter 4). Thus, a relatively simple approach for predicting rice flowering dates can be based on leaf appearance, given that LAR

Table 8.2. The final main-stem leaf number (with standard error in parentheses if not zero) at nine diurnal temperature treatments in three rice cultivars representing three different groups with respect to their temperature responses of development to flowering (Chapter 4): plants of Azucena had the same flowering time between two diurnal temperatures with the same daily mean value, those of Guang Lu Ai 4 flowered earlier at cool days with warm nights, and those of MR84 flowered earlier at warm days with cool nights.

Temperature (day/night, °C)	Final main-stem leaf number in three cultivars		
	Azucena	Guang Lu Ai 4	MR84
22/22	11.7(0.33)	10.0	12.0
24/24	11.0	10.0	12.0
26/26	11.0	10.0	13.0
28/28	11.0	10.0	12.0
32/32	10.0	11.3(0.33)	13.0
26/22	11.7(0.67)	10.7(0.33)	12.3(0.33)
30/22	12.3(0.33)	11.0	12.0
22/26	11.5(0.50)	10.0	13.0
22/30	12.0	10.0	15.0

is not greatly affected by photoperiod in cereal crops (Migletta, 1991a; Kiniry et al., 1991; Slafer et al., 1994). However, to predict flowering dates from leaf appearance, it is necessary to know the final main-stem leaf number that the crop will produce (Migletta, 1991b).

The effect of temperature on final main-stem leaf number

Table 8.2 shows the final main-stem leaf number in cvs Azucena, Guang Lu Ai 4 and MR84 at the nine temperature treatments. These three cultivars were shown here to represent three types of response for floral development to T_D and T_N (Chapter 4).

In general, the variation in leaf number was often small among constant temperature treatments and normal diurnally fluctuating temperatures (i.e. warm days following cool nights), agreeing with many reports (e.g. Migletta, 1991b) that the leaf number is not strongly affected by temperature. However, the variation in leaf number due to a change in the diurnal pattern of temperature was often great. When a diurnally fluctuating temperature delayed flowering compared to the treatment with the same daily mean value, it increased the number of main-stem leaves as well. For example, in MR84, plants at 22/30°C produced three more leaves on the main stem than those at 30/22°C. Similar results were also observed for other cultivars.

The parallelism in the change of final main-stem leaf number and days to flowering explains why there is no difference in the effect of T_D and T_N on LAR in rice. Since the final leaf number is determined at panicle initiation in cereal crops (Ritchie, 1993), this parallelism also indicates that the previous finding for rice on a difference in the effect of T_D and T_N on

development from sowing to flowering (Chapter 4) may apply to the development from sowing to panicle initiation.

Conclusions

This study confirmed that the Haun leaf growth units can be used to reliably measure the main-stem leaf appearance in rice. There was no abrupt change in LAR during ontogeny; instead, a constantly gradual decrease of LAR with increasing leaf position was observed and this was adequately described by a power-law model. This model was used to explain the response of leaf appearance to constant temperatures. The leaf appearance at diurnally fluctuating temperatures was accurately predicted on the basis of the relationships established from the constant temperatures. This indicates that there is no specific effects of T_D and T_N on leaf appearance in rice.

The framework established in this Chapter can be used to predict leaf appearance under field conditions where temperature varies both diurnally and seasonally. However, since leaf appearance is controlled by temperature near the apical meristem (Ritchie and NeSmith, 1991; Ritchie, 1993), a procedure to estimate the paddy water temperature is needed if parameter values provided in this study are used for field-grown rice.

Chapter 9

A model for photothermal responses of flowering in rice I. Model description and parameterization

Abstract While many models have been developed to predict crop development based on temperature and photoperiod, nearly all models ignore critical changes in photothermal responses during ontogeny. Based on experiments reported in previous Chapters, a detailed model was developed for predicting development to flowering in rice (*Oryza sativa* L.). As the model uses the Beta function as a basic equation for describing different photothermal responses of three successive phases during preflowering ontogeny, it was referred to as the three-stage Beta model. The model was parameterized for 17 rice cultivars using data of two controlled-environment experiments. The step-wise processes of parameterization identified the model parameters which do not vary strongly among cultivars and the parameters which can be estimated from values of other parameters. This analysis reduced the number of parameters to be estimated to five. The parameters from the controlled-environment experiments were then used to predict rice development as observed for 12 cultivars in an independent three-location field experiment. The model adequately predicted varietal and locational variation in rice flowering dates.

Introduction

An accurate prediction of crop phenology is a major requirement for crop growth simulation models (Penning de Vries et al., 1989). In rice, the interval between sowing and flowering strongly varies among cultivars and also largely depends on the growing environment, while the ripening phase from flowering to maturity is relatively constant (Vergara and Chang, 1985). Therefore, it is necessary to accurately quantify the effects of environmental variables that determine the interval between sowing and flowering of rice cultivars.

Temperature and photoperiod are the major environmental factors that determine time to flowering in crops (Roberts et al., 1993). Many models have been developed to describe phenological events of crops in relation to temperature and photoperiod (e.g. Robertson, 1968; Angus et al., 1981; Weir et al., 1984; Roberts and Summerfield, 1987; Horie and Nakagawa, 1990; Alocilja and Ritchie, 1991; Gao et al., 1992; Matthews and Hunt, 1994). Roberts and Summerfield (1987) described the rate of progress towards flowering using a linear additive function of temperature and photoperiod. Others (Robertson, 1968; Angus et al., 1981; Horie and Nakagawa, 1990; Gao et al., 1992) used a multiplicative formula which integrates nonlinear effects of temperature and photoperiod on crop development rate.

Nearly all previous photothermal models have one thing in common: they were developed based on the assumption that response of crop development towards flowering to temperature and photoperiod is constant throughout the entire period. So far, it has been difficult using

existing models to predict phenological development under a wide range of field conditions based on controlled-environment studies (Roberts et al., 1993; Lawn et al., 1995). Extensive controlled-environment experiments have been conducted recently for physiological understanding of photothermal responses of flowering in rice (Chapters 4, 6 and 7). These experiments revealed considerable quantitative insight into the mechanism of photothermal responses of rice and would be useful for deriving a model to predict rice flowering dates in a wide range of field conditions.

The objective of this Chapter is to present an experimentally-based photothermal model for calculating the daily rate of development to flowering in rice. The model was used to predict rice flowering dates in field conditions on the basis of parameters derived from physiological studies in controlled environments.

Materials and methods

The model

Major results from previously reported experiments revealed that:

(1) Besides the daily mean temperature, the diurnal temperature amplitude *per se* was found to affect development to flowering in rice (Chapter 3). This effect of the temperature amplitude can be due to a difference in effects of day and night temperature on development to flowering (Chapter 4).

(2) With regard to the photoperiod sensitivity, the entire period of development from sowing to flowering can be subdivided into three successive phases: basic vegetative phase (BVP), photoperiod-sensitive phase (PSP) and post-PSP phase (PPP); rice plants are sensitive to photoperiod only during PSP (Chapter 6).

(3) Rice plants are more responsive to both day and night temperature during PSP than during BVP or PPP; but, the sensitivity to either day or night temperature does not differ significantly between BVP and PPP (Chapter 7).

(4) The influence of day and night temperature on phenological development to flowering was associated with the main-stem leaf number. When a diurnally fluctuating temperature delayed flowering compared to the treatment with the same mean daily value, it increased the main-stem leaf number as well (Chapter 8).

(5) The critical period for the effect of temperature on the main-stem leaf number was the PSP (Chapter 7).

(6) As a consequence of (4) and (5), the critical period for the difference in the impact of day and night temperature on preflowering development is the PSP.

(7) However, different effects of day and night temperature may also occur during BVP and PPP, because the main-stem leaf stage at the end of BVP varied, although slightly, with the change in temperature (Chapter 6) but the rate of main-stem leaf appearance was not affected by the diurnal pattern of temperature (Chapter 8).

Based on the above experimental conclusions, the general structure of a model for estimating rice development rate (DR, d^{-1}) to flowering can be described as:

$$DR = \begin{cases} g'(T_D) \cdot h'(T_N) / f_o & \text{if } DS \leq \theta_1 \text{ or } DS \geq \theta_2 \\ g(T_D) \cdot h(T_N) \cdot r(P) / f_o & \text{if } \theta_1 < DS < \theta_2 \end{cases} \quad (9.1)$$

where DS is the developmental stage, calculated as an accumulation of the daily DR, with DS = 0.0 at sowing and DS = 1.0 at flowering; θ_1 and θ_2 are values of DS at the end of BVP and PSP, respectively (here $0.0 < \theta_1 < \theta_2 < 1.0$); f_o is the minimum number of days to flowering when photothermal conditions are optimal for the development; $g'(T_D)$ and $h'(T_N)$ are the functions describing the effects of day and night temperature, respectively, on DR during both BVP and PPP; $g(T_D)$, $h(T_N)$ and $r(P)$ are functions for the effects of day temperature, night temperature and photoperiod, respectively, on DR during PSP.

To account for the optimum response and any asymmetry in the relationship between DR and temperature or photoperiod, the Beta function commonly used as a skewed probability density function in statistics, which can flexibly describe responses of DR to either temperature (Chapter 2) or photoperiod (Chapter 5), was used. The Beta functions to describe these relationships are:

$$g'(T_D) = \left[\left(\frac{T_D - T_b}{T_{oD} - T_b} \right) \left(\frac{T_c - T_D}{T_c - T_{oD}} \right)^{\frac{T_c - T_{oD}}{T_{oD} - T_b}} \right]^{\alpha_D} \quad (9.2a)$$

$$h'(T_N) = \left[\left(\frac{T_N - T_b}{T_{oN} - T_b} \right) \left(\frac{T_c - T_N}{T_c - T_{oN}} \right)^{\frac{T_c - T_{oN}}{T_{oN} - T_b}} \right]^{\alpha_N} \quad (9.2b)$$

$$g(T_D) = \left[\left(\frac{T_D - T_b}{T_{oD} - T_b} \right) \left(\frac{T_c - T_D}{T_c - T_{oD}} \right)^{\frac{T_c - T_{oD}}{T_{oD} - T_b}} \right]^{\alpha_D} \quad (9.2c)$$

$$h(T_N) = \left[\left(\frac{T_N - T_b}{T_{oN} - T_b} \right) \left(\frac{T_c - T_N}{T_c - T_{oN}} \right)^{\frac{T_c - T_{oN}}{T_{oN} - T_b}} \right]^{\alpha_N} \quad (9.2d)$$

$$r(P) = \left[\left(\frac{P - P_b}{P_o - P_b} \right) \left(\frac{P_c - P}{P_c - P_o} \right)^{\frac{P_c - P_o}{P_o - P_b}} \right]^{\delta} \quad (9.2e)$$

where T_D = day temperature ($^{\circ}\text{C}$); T_{oD} is the optimum value for T_D ;
 T_N = night temperature ($^{\circ}\text{C}$); T_{oN} is the optimum value for T_N ;
 T_b , T_c = base and ceiling temperature ($^{\circ}\text{C}$), respectively, at which DR = 0;
 P = daily photoperiod (h d^{-1});
 P_b , P_o and P_c = base, optimum and ceiling photoperiod (h d^{-1}), respectively;
 α'_D , α'_N , α_D , α_N and δ = the sensitivity parameters that characterize the curvature of their respective relationship.

The cardinal temperatures may change with stages of preflowering development. However, no direct evidence was found for this change (Chapter 7); therefore, values for the cardinal temperatures were assumed to be the same for the three developmental phases. Although the value for either T_b or T_c can differ between day and night, it was assumed that they were equal for day and night to reduce the number of parameters to be estimated (Chapter 4). Values for T_b , T_c , P_b and P_c was also fixed since they are usually far beyond the range of rice-growing photothermal environments (Chapters 2 and 5). Values for T_b and T_c have been set at 8 and 42°C, respectively (Alocilja and Ritchie, 1991; Kropff et al., 1994b; Chapters 2, 3 and 4); and values for P_b and P_c have been set at 0.0 and 24.0 h d⁻¹, respectively (Chapter 5). Therefore, Eq. 9.1 has 11 parameters to be estimated: f_o , T_{oD} , T_{oN} , α'_D , α'_N , α_D , α_N , P_o , δ , θ_1 and θ_2 . In this study, experimental data were analysed to determine which parameters are most important to characterize different responses of cultivars. Because the model uses Beta functions as a basic equation to describe photothermal responses at three different developmental stages, it is referred to as the three-stage Beta model.

Experimental data

Photoperiod experiment

Details on the experiment were given in Chapter 6. Plants in 20 rice cultivars were serially transferred between short (10.0 h d⁻¹) and long photoperiods (12.5 or 14.0 h d⁻¹) at various times after sowing to determine the length of the PSP in each cultivar. Plants were kept in an open-sided greenhouse between 08:00 and 17:00 h of each day, after which they were distributed among darkrooms. The darkrooms were provided with different hours of supplementary light (10 $\mu\text{mol m}^{-2}\text{s}^{-1}$) to obtain the required photoperiods. The temperature in the darkrooms was maintained at $24 \pm 2^\circ\text{C}$, whereas the daytime temperature in the greenhouse fluctuated with seasons, typically within $32 \pm 6^\circ\text{C}$. In addition to the experiment involving these successive transfers, another experiment was conducted simultaneously in which plants were grown continuously from sowing to flowering in several constant photoperiods with an interval of 1 h d⁻¹ between the short and long photoperiod treatments. The data from these experiments were used to determine the model parameters related to the photoperiod response. However, the observations in some cultivars with unusual delays by early transfers from short to long photoperiods (see Chapter 6) were not included for analyses.

Temperature experiment

Plants of 24 rice cultivars were grown in naturally-lighted growth chambers at five diurnally constant (22, 24, 26, 28 and 32°C) and four fluctuating (day/night: 26/22, 30/22, 22/26 and 22/30°C) temperatures with a constant photoperiod of 12.0 h d⁻¹. The day and night temperatures were imposed for 12.0 h d⁻¹, with the day temperature period corresponding to the photoperiod from 06:00 to 18:00 h of each day. Full experimental details were presented in Chapter 4. Data from this experiment were used to determine the parameters for the effects of day and night temperature.

Validation experiments

To validate the model, a multilocal field experiment was conducted at three locations in Asia: Los Baños in Philippines (Latitude 14.18°N), Hangzhou in China (30.23°N) and Kyoto in Japan (35.02°N). These three locations were selected to represent tropical, subtropical and temperate climatic environments, respectively. Among 17 rice cultivars which had been studied in the photoperiod and temperature experiments, 12 cultivars were tested in the validation field experiment. However, not every cultivar was included in each location. Experiments at Los Baños and Hangzhou included both direct seeded and transplanted rice for each cultivar; while, at Kyoto, only five cultivars had a direct seeded treatment. To avoid the effect of the transplanting shock on phenological development (Kropff et al., 1994b), the data from direct seeded rice were used in the present study to evaluate the model because the model was parameterized from the data of the controlled-environment experiments where rice plants were direct seeded. However, little difference in the flowering time was found between transplanted and direct seeded plants at Kyoto. Thus, the data for the transplanted rice at Kyoto were also used to evaluate the model.

Parameter estimation for predicting flowering dates

A FORTRAN program for estimating parameters of a logistic model (Horie et al., 1986; Horie and Nakagawa, 1990; Sinclair et al., 1991) was adapted to parameterize the three-stage Beta model. A similar procedure has also been used by Hammer et al. (1989) and Grimm et al. (1993 and 1994). The program uses an iteration procedure of the simplex method (Haga and Hashimoto, 1980). In the procedure, the daily values of photoperiod and temperature are used to calculate daily DR beginning with the sowing date. In each iteration step of the simplex method, the sum of squares of the errors (SSE) (i.e. observed days minus predicted days from sowing to flowering) was calculated for $m+1$ different sets of the parameters (where m is the number of parameters to be estimated). The iteration was continued until the criterion for convergence $|SSE_{\max} - SSE_{\min}| < \varepsilon$ (where SSE_{\max} and SSE_{\min} are the maximum and the minimum of the sum squares of errors among the $m+1$ sets of parameters) was satisfied. A value of 3 was adopted for the criterion ε .

There is no guarantee that the solution obtained is unique and optimal. On many runs, there was a series of solutions with similar SSE but different parameter estimates. This can be due to the fact that the parameters obtained are locally rather than globally optimal (Haga and Hashimoto, 1980). In such a situation, the optimal solution is, to some extent, dependent on the initial values assigned to the parameters and the initial step sizes. To obtain the best values of parameters, the initial parameter values were presented in terms of their biological meaning and the step size was set to be adequately large (about 40% of the initial value) for those parameters whose values are not certain. By making several runs for each case using estimates of the previous run as the initial values of the next run, a fairly consistent result can be obtained.

The data in the 17 cultivars commonly tested in the photoperiod and temperature experiments were used to parameterize the model. To minimize an influence of the temperature

fluctuation in the photoperiod experiment, parameterization was first done with the photoperiod experiment using the following equation:

$$DR = \begin{cases} 1/f_{op} & \text{if } DS \leq \theta_1 \text{ or } DS \geq \theta_2 \\ r(P)/f_{op} & \text{if } \theta_1 < DS < \theta_2 \end{cases} \quad (9.3)$$

where f_{op} is the minimum days from sowing to flowering estimated from the photoperiod experiment, $r(P)$ is the photoperiod effect function as defined by Eq. 9.2e. Then using parameters θ_1 , θ_2 and photoperiod sensitivity parameter δ obtained from Eq. 9.3 and Eq. 9.2e as inputs, parameters for the temperature-effect component and the final value for f_o in Eq. 9.1 can be estimated with the data from the temperature experiment, given that the photoperiod in that experiment was fixed as 12.0 h d⁻¹.

The coefficients of the model derived from the photoperiod and temperature experiments were then used to predict the flowering dates in the three-location field experiment. The model was run on an hourly basis for the effect of temperature since the temperature under field conditions fluctuates diurnally. Hourly temperature (T_i) was computed from daily maximum (T_{max}) and minimum (T_{min}) temperature assuming that T_{max} occurs at 14:00 h according to (Kropff et al., 1994b; Matthews and Hunt, 1994):

$$T_i = \frac{T_{max} + T_{min}}{2} + \frac{T_{max} - T_{min}}{2} \cos\left(\frac{\pi}{12}(i-8)\right) \quad (9.4)$$

where i is the number of hours of a day ($i = 1, 2, \dots, 24$), starting with 1 for the hour of 07:00. The day temperature was assumed to correspond to the period from 06:00 to 18:00 h of each day and the night temperature then corresponded to the period from 18:00 to 06:00 h of the next day. The daily effects of day and night temperature on DR were calculated based on the hourly temperature. Based on this procedure, for example, the temperature effects on DR during the PSP were calculated as:

$$g(T_D) = \frac{1}{12} \sum_{i=1}^{12} g(T_i) \quad (9.5a)$$

$$h(T_N) = \frac{1}{12} \sum_{i=13}^{24} h(T_i) \quad (9.5b)$$

The daily photoperiod was calculated from the equation proposed by Goudriaan and van Laar (1978). Under field conditions, twilights may contribute to the daylength for crop photoperiodism (Angus et al., 1981; Vergara and Chang, 1985). It was often assumed that the daylength for the photoperiodic induction is the period during which the sun is at inclinations $> -4^\circ$ (Penning de Vries et al., 1989) or even lower sun angle (e.g. Weir et al., 1984; Roberts et al., 1993). There are other studies, however, which calculated the effective photoperiod as the period from sunrise to sunset assuming a 0° sun angle (e.g. Robertson, 1968; Sinclair et al., 1991). To determine the most appropriate sun angle for the photoperiod calculation, it was varied between 0° and -4° in a step of 0.5° .

Results and discussion

Parameters of the model

Parameters for the response to photoperiod

Parameter values of the model component for the photoperiod effect, i.e. Eq. 9.3 and its adherent Eq. 9.2e, estimated from the data of the photoperiod experiment, are given in Table 9.1. Indicators of the accuracy for the model to fit the data of each cultivar are the standard error (SE) and the coefficient of determination (r^2) for the linear regression between observed and predicted days from sowing to flowering. The model successfully described the data obtained from the experiment involving successive transfers of plants between the short and long photoperiods, with $r^2 > 0.87$.

Table 9.1. Values for the five parameters of Eq. 9.3 and its adherent Eq. 9.2e in 17 rice cultivars estimated from the photoperiod experiment.

Cultivar	f_{op} (d)	P_o (h d ⁻¹)	δ	θ_1	θ_2	SE	r^2 †	n §
IR8	92.53	9.92	3.3289	0.438	0.719	2.51	0.906	33
IR36	67.97	9.96	4.4898	0.394	0.612	1.65	0.936	33
IR42	84.53	9.41	6.2815	0.463	0.693	2.31	0.986	31
IR64	73.21	9.12	3.4252	0.479	0.747	2.62	0.939	31
IR72	80.59	9.75	3.4026	0.507	0.728	2.27	0.876	31
IR64616H	81.35	9.87	2.7374	0.502	0.754	2.07	0.875	31
MR84	84.96	8.98	5.2143	0.470	0.686	2.92	0.980	31
ADT36	65.04	9.77	4.3497	0.471	0.688	2.55	0.889	34
CO36	63.67	9.33	15.7126	0.327	0.572	3.81	0.972	27
Carreon	51.38	9.05	12.1521	0.329	0.563	3.10	0.972	33
Shan You 63	71.41	9.87	5.6171	0.378	0.652	2.83	0.945	34
Xiu Shui 11	61.55	9.64	9.6809	0.331	0.562	3.62	0.967	26
Lao Lai Qing	59.92	9.95	15.3079	0.326	0.516	3.25	0.990	28
Nipponbare	57.22	9.67	7.0510	0.331	0.595	3.66	0.943	26
Koshihikari	59.35	9.66	4.5117	0.332	0.592	1.93	0.946	26
Hwasong	54.03	9.90	8.1160	0.346	0.550	2.33	0.962	32
Illpoom	53.94	10.07	8.5163	0.329	0.575	2.49	0.966	32

† r^2 is for the linear regression between predicted and observed days.

§ n is the number of environments fitted.

Table 9.2. Values for the four parameters f_{op} , δ , θ_1 and θ_2 of Eq. 9.3 and its adherent Eq. 9.2e in 17 rice cultivars estimated from the photoperiod experiment when the value for P_o was fixed to be 10.0 h d⁻¹ (the number of environments fitted for each cultivar is the same as in Table 9.1).

Cultivar	f_{op} (d)	δ	θ_1	θ_2	SE	r^2 †	$\theta_2 - \theta_1$
IR8	92.61	4.0870	0.441	0.658	2.29	0.919	0.217
IR36	67.68	5.3209	0.428	0.614	1.73	0.929	0.186
IR42	84.91	9.4427	0.477	0.656	2.44	0.984	0.179
IR64	74.11	6.1739	0.510	0.726	2.41	0.948	0.216
IR72	80.63	4.2559	0.490	0.705	2.26	0.874	0.215
IR64616H	81.01	2.9923	0.505	0.761	1.97	0.882	0.256
MR84	85.99	9.1447	0.476	0.687	3.17	0.975	0.211
ADT36	65.30	5.1557	0.470	0.680	2.48	0.891	0.210
CO36	64.29	30.2918	0.333	0.532	3.38	0.978	0.199
Carreon	52.47	26.1834	0.325	0.562	2.66	0.976	0.237
Shan You 63	73.70	6.4117	0.445	0.659	3.97	0.888	0.214
Xiu Shui 11	62.56	12.6577	0.344	0.536	3.02	0.977	0.192
Lao Lai Qing	59.88	15.3466	0.350	0.548	3.66	0.986	0.198
Nipponbare	56.86	9.2754	0.350	0.592	3.25	0.951	0.242
Koshihikari	59.55	5.6478	0.332	0.587	1.82	0.949	0.255
Hwasong	54.04	9.0572	0.366	0.558	2.28	0.962	0.192
Illpoom	53.95	9.2965	0.364	0.563	2.43	0.967	0.199

† r^2 is for the linear regression between predicted and observed days.

There was largest genotypic variation in the value of the photoperiod sensitivity parameter δ and the least variation in the value of the optimum photoperiod P_o (Table 9.1), agreeing with a previous result based on other literature data (Chapter 5). The estimated value of P_o in each cultivar was very close to the widely used value for rice, i.e. 10 h d⁻¹ (Vergara and Chang, 1985). To reduce the number of parameters to be estimated, the value for P_o can be fixed to 10.0 h d⁻¹. This would not affect the predictive capacity of the model under field conditions since the photoperiods in rice-growing environments are > 10 h d⁻¹ (Summerfield et al., 1992).

Based on the fixed value of P_o as 10.0 h d⁻¹, estimates for other parameters of Eq. 9.3 and its adherent Eq. 9.2e are given in Table 9.2. The model with the fixed P_o also described the data well. It resulted in an even better fit than the model with the nonfixed P_o in some cultivars. The possible reason for this is that the fewer number of parameters may make it easier for the procedure of the simplex method to access the globally optimal solution (Horie et al., 1986). Although values of all parameters varied greatly among cultivars, the difference between values of θ_1 and θ_2 was fairly constant among cultivars, slightly deviating from 0.2 (Table 9.2). This suggests that the physiological time period for PSP at P_o has little genotypic variation.

Table 9.3. Values for the three parameters f_{op} , δ and θ_1 of Eq. 9.3 and its adherent Eq. 9.2c in 17 rice cultivars derived from the photoperiod experiment when the value for P_o was fixed to be 10.0 h d^{-1} and the value for θ_2 was set to be $(\theta_1 + 0.2)$ (the number of environments fitted for each cultivar is the same as in Table 9.1).

Cultivar	f_{op} (d)	δ	θ_1	SE	$r^2 \ddagger$
IR8	91.82	4.6465	0.455	2.30	0.915
IR36	67.34	5.4194	0.416	1.69	0.930
IR42	84.94	9.3444	0.477	2.40	0.984
IR64	73.92	6.5414	0.510	2.33	0.947
IR72	80.51	4.4203	0.506	2.23	0.873
IR64616H	80.23	4.1182	0.524	1.91	0.881
MR84	85.87	9.4930	0.468	3.11	0.976
ADT36	65.08	5.4547	0.461	2.40	0.894
CO36	64.82	29.4145	0.292	3.06	0.980
Carreon	53.96	26.5220	0.333	2.70	0.979
Shan You 63	72.40	7.3466	0.391	3.23	0.922
Xiu Shui 11	62.12	12.4434	0.348	3.01	0.977
Lao Lai Qing	59.48	15.2206	0.316	3.17	0.990
Nipponbare	56.21	10.6121	0.322	3.00	0.957
Koshihikari	59.54	6.5873	0.325	1.67	0.955
Hwasong	54.01	9.2360	0.356	2.24	0.962
Illpoom	53.50	9.5386	0.307	2.13	0.973

\ddagger r^2 is for the linear regression between predicted and observed days.

Considering the difference between θ_1 and θ_2 as 0.2 for all cultivars, the number of parameters to be derived in Eq. 9.3 can be reduced to three: f_{op} , δ and θ_1 ; and the results are given in Table 9.3. Again, one parameter reduction did not decrease the descriptive ability of the model. Therefore, parameters that are important for characterizing the varietal difference in the response to photoperiod are the photoperiod sensitivity δ and the developmental stage (θ_1) when plant first becomes sensitive to photoperiod.

Parameters for the response to temperature

Using the values of parameters δ and θ_1 given in Table 9.3 and the assumptions of ($P_o = 10.0 \text{ h d}^{-1}$) and ($\theta_2 = \theta_1 + 0.2$) as inputs for Eq. 9.1, other parameters, including f_o , α'_D , α'_N , α_D , α_N , T_{oD} and T_{oN} for the response of DR to temperature, can be estimated from the temperature experiment. Likewise, the step-wise analyses were conducted to determine the parameters which do not change strongly among cultivars.

Table 9.4. Values for the seven parameters f_o , T_{oD} , T_{oN} , α'_D , α'_N , α_D and α_N of Eq. 9.1 and its adherent Eq. 9.2a-d in 17 rice cultivars derived from the temperature experiment when values for parameters δ and θ_1 in Table 9.3 were used as inputs and P_o was fixed to be 10.0 h d^{-1} and the value for θ_2 was set to be $(\theta_1 + 0.2)$.

Cultivar	f_o (d)	T_{oD} (°C)	T_{oN} (°C)	α'_D	α'_N	α_D	α_N	SE	r^2 †	n §
IR8	72.39	31.3	28.6	0.8830	1.0179	0.6360	5.0723	5.87	0.948	9
IR36	57.76	31.9	28.9	1.0578	0.7956	2.1257	2.8781	1.58	0.996	9
IR42	73.25	32.8	27.2	0.9046	0.6073	1.4208	1.9729	10.77	0.821	9
IR64	57.14	30.3	28.4	1.0812	0.9977	2.8560	3.0168	3.74	0.975	9
IR72	65.41	29.9	28.4	0.8778	1.1658	3.1050	3.4009	5.52	0.946	9
IR64616H	64.57	30.4	28.9	1.0290	1.0185	2.7479	3.7411	7.14	0.927	9
MR84	70.60	33.1	25.8	0.8692	0.6340	2.1548	2.5053	11.66	0.845	9
ADT36	56.85	31.7	27.0	1.0851	0.8659	3.4927	2.5585	5.66	0.959	9
CO36	61.96	30.1	25.1	0.7187	1.1224	1.1526	2.9496	17.15	0.582	9
CO36†	63.18	25.5	24.5	0.7729	1.4254	2.0661	5.1121	9.59	0.931	8
Carreon	39.11	30.4	25.5	1.1244	1.3631	4.2397	5.3189	11.60	0.884	9
Shan You 63	61.85	30.6	28.8	0.5902	1.4699	0.6307	4.3934	5.24	0.949	9
Xiu Shui 11	44.61	30.0	27.0	1.2456	0.8892	3.4815	3.7150	5.79	0.926	9
Lao Lai Qing	41.76	28.1	27.9	1.0899	1.3989	5.6312	3.2570	4.36	0.947	9
Nipponbare	34.82	29.1	28.0	1.4984	0.7794	5.6554	3.7950	2.55	0.990	9
Koshihikari	40.55	28.5	26.3	1.6749	1.1187	4.9637	5.3122	1.73	0.991	9
Hwasong	36.47	29.3	26.9	1.3099	1.0434	5.0843	5.0430	2.45	0.984	9
Illpoom	37.28	29.3	26.8	1.2313	1.2277	5.1248	5.1826	1.87	0.992	9

† r^2 is for the linear regression between predicted and observed days.

§ n is the number of environments fitted.

† The observation at the constant temperature of 32°C excluded (see text).

First, all seven parameters were estimated from the data of the experiment (Table 9.4). The minimum days to flowering (f_o) varied by more than two folds, from 34 d in cv. Nipponbare to 73 d in cvs IR8 and IR42. For each cultivar, values for parameters α'_D and α'_N were generally lower than those for α_D and α_N , respectively, supporting the finding in Chapter 7 that rice plants are less sensitive to temperature during BVP or PPP than during PSP for development to flowering. The estimated value for T_{oD} were consistently higher than the value for T_{oN} , agreeing with the previous analysis from these data (Chapter 4). The model described the data with $r^2 > 0.82$ in all cultivars except cv. CO36 (Table 9.4). The poor fit for CO36 can be due to the observation of DR at 32°C which is higher than expected for this cultivar (see Fig. 4.1G in Chapter 4). Exclusion of this observation resulted in a much better fit of the data (Table 9.4). To show the range of variation for parameters of this cultivar, results of estimation based on the data both with and without 32°C observation are presented in further analysis.

Table 9.5. Values for the five parameters f_o , T_{oD} , T_{oN} , α_D and α_N of Eq. 9.1 and its adherent Eq. 9.2a-d in 17 rice cultivars derived from the temperature experiment when α'_D and α'_N were fixed to be 1.0. Further details as for Table 9.4 (the number of environments fitted for each cultivar is the same as in Table 9.4).

Cultivar	f_o (d)	T_{oD} (°C)	T_{oN} (°C)	α_D	α_N	SE	r^2_{\dagger}
IR8	71.41	31.2	28.8	0.6335	4.8881	3.81	0.958
IR36	56.77	32.6	28.7	2.1008	2.5006	1.12	0.997
IR42	73.29	32.5	27.4	1.5642	0.9928	7.61	0.820
IR64	58.07	31.2	28.3	2.2557	2.4434	2.00	0.982
IR72	65.44	30.7	28.7	2.1735	3.0687	2.74	0.973
IR64616H	63.14	32.9	29.8	0.9798	2.6081	2.55	0.980
MR84	71.27	33.8	25.4	1.5398	0.7940	7.09	0.871
ADT36	57.52	32.0	27.2	3.2794	1.0011	3.16	0.973
CO36	62.16	29.4	25.1	1.2039	3.1926	12.49	0.575
CO36†	63.40	25.6	24.2	2.5195	4.6216	5.77	0.921
Carreon	40.11	31.0	25.1	3.5287	4.2209	6.91	0.913
Shan You 63	60.70	29.6	28.8	0.4169	5.8392	4.15	0.939
Xiu Shui 11	41.94	31.1	26.6	3.5271	4.5316	3.71	0.943
Lao Lai Qing	41.05	29.9	27.2	3.1234	5.5391	2.87	0.955
Nipponbare	34.52	29.2	27.7	6.1144	3.8228	2.29	0.982
Koshihikari	41.07	28.1	26.4	6.7924	4.1789	1.12	0.992
Hwasong	36.77	29.5	26.8	5.1066	5.0854	1.80	0.981
Illpoom	37.67	29.1	26.8	5.6169	5.4445	1.32	0.994

‡ r^2 is for the linear regression between predicted and observed days.

† The observation at the constant temperature of 32°C excluded (see text).

All seven parameters varied, depending on cultivars; however, the variation in both α'_D and α'_N was very small (Table 9.4). Since the average value of either α'_D or α'_N among the 17 cultivars was very close to 1.0, they were fixed as 1.0. This resulted in an interpretation that the varietal difference in the response for preflowering development to temperature occurs only during PSP. The results of parameter values based on this interpretation are given in Table 9.5. The model with fixed values for α'_D and α'_N had a similar goodness of fit as the model with nonfixed values for α'_D and α'_N .

In many existing photothermal models for rice development (e.g. Horie and Nakagawa, 1990; Gao et al., 1992; Summerfield et al., 1992), only five or six parameters were used. Sensitivity analysis indicated that in most cultivars, the goodness of fit of the three-stage Beta model was more sensitive to the change in the value of the optimum temperature than to the change in the temperature sensitivity value of α_D or α_N . Evidence from other crops (e.g.

Table 9.6. Values for the parameters f_o , T_{oD} , T_{oN} and α_D of Eq. 9.1 and its adherent Eq. 9.2a-d in 17 cultivars derived from the temperature experiment when α_N was set equal to α_D . Further details as for Table 9.5.

Cultivar	f_o (d)	T_{oD} (°C)	T_{oN} (°C)	α_D	SE	r^2 †
IR8	73.66	31.5	29.3	1.3482	5.89	0.816
IR36	57.63	31.7	28.9	2.4820	1.00	0.996
IR42	72.94	33.1	27.0	1.0645	6.87	0.815
IR64	57.53	30.7	28.4	2.7256	2.00	0.979
IR72	66.67	31.5	29.7	1.3285	2.65	0.972
IR64616H	64.14	32.1	30.8	1.3894	2.41	0.978
MR84	68.89	35.6	25.4	0.9347	6.23	0.874
ADT36	55.93	33.5	26.9	2.2341	3.03	0.970
CQ36	67.35	28.1	24.1	0.7619	10.18	0.608
CO36†	64.37	25.5	23.4	2.6814	5.05	0.912
Carreon	39.55	31.9	24.4	3.0616	5.87	0.922
Shan You 63	62.49	29.9	28.7	2.2677	7.25	0.653
Xiu Shui 11	44.83	30.8	26.4	3.1492	3.61	0.934
Lao Lai Qing	41.58	28.9	27.6	4.3463	2.57	0.957
Nipponbare	35.40	30.5	27.5	3.9929	1.55	0.981
Koshihikari	40.39	28.4	26.4	5.8537	1.18	0.989
Hwasong	36.76	29.7	26.8	4.8802	1.48	0.984
Illpoom	37.81	29.2	26.8	5.2739	1.10	0.994

‡ r^2 is for the linear regression between predicted and observed days.

† The observation at the constant temperature of 32°C excluded (see text).

Grimm et al., 1993) indicates that the temperature sensitivity parameter could be fixed for all genotypes to predict flowering. Assuming that the difference in the effects of day and night temperature as found in Chapter 4 could be only due to the difference in values of T_{oD} and T_{oN} while the temperature sensitivity could be the same for day and night (i.e. $\alpha_D = \alpha_N$), the number of parameters of the model could be reduced. Based on this, values of the four parameters for the temperature effect estimated from the temperature experiment are given in Table 9.6. For most cultivars, the assumption of $\alpha_D = \alpha_N$ did not reduce the descriptive ability of the model. Only in cvs IR8 and Shan You 63 where the difference between values of α_D and α_N was large (Table 9.5), the assumption led to a poorer fit of the data.

Final estimation of parameters of the model

From the above step-wise analyses, the number of model parameters has been reduced to six, i.e. f_o , T_{oD} , T_{oN} , α_D , δ and θ_1 . To further explore the possibility to reduce parameters, the result

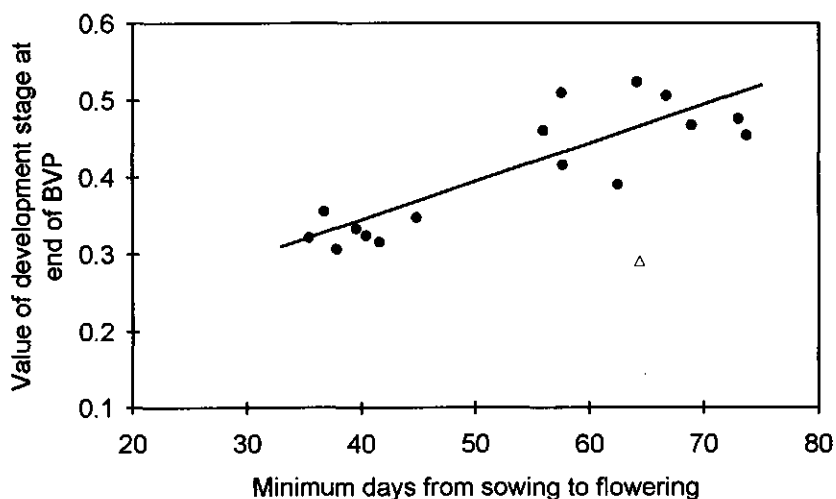


Fig. 9.1. The relation between the value of developmental stage at the end of the basic vegetative phase (BVP) (θ_1) and the minimum number of days from sowing to flowering in 17 rice cultivars. The open triangle is for cv. CO36. The line shows the linear regression given by Eq. 9.6.

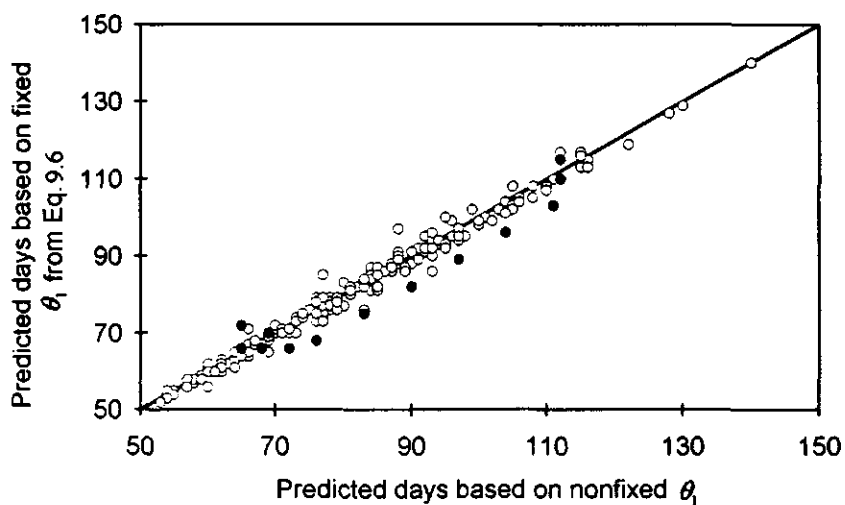


Fig. 9.2. Comparison between days from sowing to flowering predicted based on fixed θ_1 from Eq. 9.6 and those based on nonfixed θ_1 for the 17 rice cultivars tested in the photoperiod experiment. The closed symbols are for cv. CO36. The line shows the 1:1 relationship.

in Chapter 6 that the length of BVP was linearly related to the preflowering period at the short-day photoperiod was used. Indeed, the analysis with values of the 17 rice cultivars indicated a significant positive correlation between values of θ_1 and f_o , if cv. CO36 was excluded (Fig. 9.1):

$$\theta_1 = 0.145(0.0431) + 0.005(0.0008)f_o \quad r^2 = 0.735^{***} \quad (9.6)$$

where the figures in parentheses are the standard errors of the regression coefficients. If the value of θ_1 estimated from Eq. 9.6 was used as an input in Eq. 9.3, the data in the photoperiod experiment can be described by Eq. 9.3 with only two parameters to be estimated (i.e. f_{op} and δ). In fact, excluding CO36, fixing θ_1 by Eq. 9.6 did not much reduce goodness of fit of Eq. 9.3 to the data of the photoperiod experiment (Fig. 9.2). Therefore, the model parameters can be reduced to five. Based on Eq. 9.6 and resulting estimated δ from the photoperiod experiment, the second-round estimation for f_o , T_{oD} , T_{oN} , and α_D was obtained from the temperature experiment. The final estimates for the five model parameters are given in Table 9.7.

Table 9.7. Final estimated values for the five parameters f_o , T_{oD} , T_{oN} , α_D and δ of Eq. 9.1 and its adherent Eq. 9.2a-e in 17 rice cultivars.

Cultivar	f_o (d)	T_{oD} (°C)	T_{oN} (°C)	α_D	δ
IR8	73.69	30.9	30.5	1.0864	4.6809
IR36	58.79	31.8	29.1	2.2411	4.5926
IR42	71.41	33.5	27.5	1.1043	9.3443
IR64	57.70	31.0	28.4	2.4547	6.3779
IR72	65.89	31.0	29.4	1.8823	4.4854
IR64616H	63.84	32.3	31.1	1.2917	4.0372
MR84	69.86	34.9	25.3	1.0457	9.3340
ADT36	56.26	33.4	27.1	2.3656	5.6728
CO36	65.52	29.4	22.7	0.1000	30.3560
CO36†	64.10	25.7	23.4	2.5575	30.3560
Carreon	38.81	32.0	24.0	2.8517	28.0046
Shan You 63	62.44	30.1	29.6	2.0203	7.2179
Xiu Shui 11	43.82	30.0	26.7	3.9561	12.6164
Lao Lai Qing	42.50	29.0	27.9	3.7264	15.5437
Nipponbare	35.27	30.6	27.7	3.8769	10.9733
Koshihikari	40.50	28.5	26.4	5.5603	6.7207
Hwasong	36.81	29.7	26.8	5.0229	8.7803
Illpoom	38.94	29.3	27.0	4.7570	9.4246

† The observation at the constant temperature of 32°C excluded (see text).

Predicting flowering dates in field conditions: model validation

With the data of the 12 cultivars (IR36, IR64, IR72, IR64616H, MR84, ADT36, Shan You 63, Nipponbare, Koshihikari, Xiu Shui 11, Hwasong and Illpoom) in the three-location field experiment, a wide range of flowering dates was obtained. The days from sowing to flowering varied from 45 d for Nipponbare, Koshihikari and Hwasong at Los Baños to 168 d for MR84 at Kyoto.

The mean difference in number of days (MD_{day}), the mean absolute value for the difference (MD_{abs}), and the r^2 value for the linear regression between observed and predicted days based on the five-parameter model are given in Table 9.8 when various sun angles were used to calculate the daily effective photoperiod. The predictions based on -2° sun angle resulted in the least discrepancy of prediction by the model. This sun angle is the average of 0° used by Robertson (1968) and Sinclair et al. (1991) and -4° suggested by Penning de Vries et al. (1989). This result may imply an effect of light intensity on rice photoperiodism as indicated in some studies (Vergara and Chang, 1985) and appears to support the observation that the twilight in the morning can delay flowering but the twilight in the evening may not delay flowering (Yoshida, 1981; Vergara and Chang, 1985). To illustrate the model performance, a plot of days from sowing to flowering predicted with the -2° sun angle against the observed days for the 12 cultivars is presented in Fig. 9.3. In general, the model adequately predicted varietal and locational variation of rice flowering dates. Only one large predictive discrepancy was found for plants of MR84, a cultivar from tropical Malaysia, when grown in temperate Kyoto (see the triangle at the higher end in Fig. 9.3). The remaining discrepancies may be due to other factors such as the difference between air and water temperatures.

Table 9.8. The mean difference in number of days (MD_{day}), the mean absolute value for the difference (MD_{abs}), and the r^2 value for the linear regression between observed days to flowering and those predicted by the five-parameter model (with parameter values given in Table 9.7) when different sun angles were used to calculate the effective daylength for plants in 12 rice cultivars grown in the three-location experiment.

Sun angle	MD_{day} (d)	MD_{abs} (d)	r^2
0.0°	4.09	6.21	0.930
-0.5°	2.94	5.59	0.937
-1.0°	1.94	5.12	0.942
-1.5°	0.85	4.85	0.945
-2.0°	-0.41	4.85	0.946
-2.5°	-1.62	4.97	0.946
-3.0°	-3.03	5.56	0.945
-3.5°	-4.35	6.18	0.945
-4.0°	-6.03	7.09	0.947

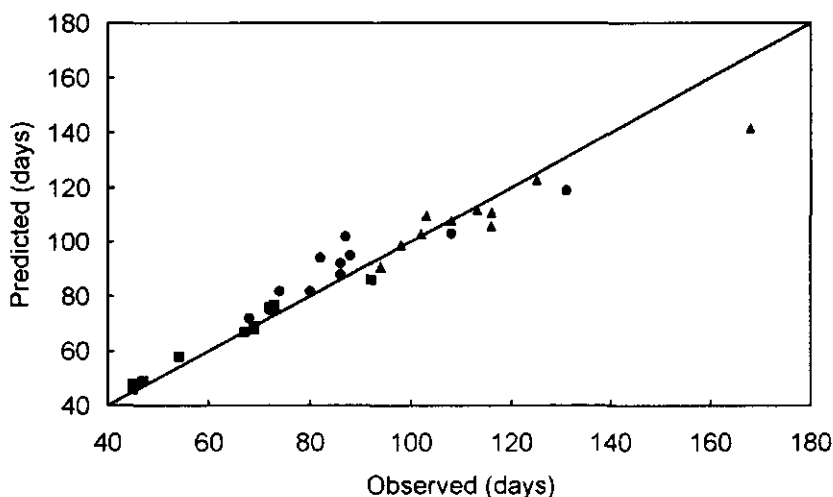


Fig. 9.3. Comparison between days from sowing to flowering predicted by the three-stage Beta model with parameters (given in Table 9.7) estimated from controlled-environment experiments using a -2° sun angle for photoperiod calculation (see text) and those observed in an independent three-location (squares for Los Baños in Philippines, circles for Hangzhou in China, and triangles for Kyoto in Japan) field experiment. The line shows the 1:1 relationship.

Conclusions

Based on experimental findings described in Chapters 2–8, a new model has been developed for photothermal responses of rice flowering in this Chapter. The model was parameterized using two controlled-environment experiments with 17 diverse rice cultivars. The step-wise processes of parameterization identified the model parameters which did not vary strongly among cultivars, and the parameters which can be estimated from values of other parameters. The remaining five parameters that are important for characterizing varietal responses are minimum days to flowering, photoperiod sensitivity, optimum day temperature, optimum night temperature, and temperature sensitivity during PSP.

The model was validated using the parameters from the controlled-environment experiments to predict rice flowering dates obtained in a multilocal field experiment. The model adequately predicted varietal and locational variations of the flowering times. However, the best performance of the model was achieved when the -2° sun angle was used to include the civil twilight for the effective photoperiod. A further study is required to evaluate whether this model is superior to existing models for predicting rice development over a wide range of field environments.

Chapter 10

A model for photothermal responses of flowering in rice II. Model evaluation

Abstract A detailed nonlinear model, the 3s-Beta model, for responses of flowering in rice (*Oryza sativa* L.) to temperature and photoperiod has been developed based on several controlled-environment experiments. The objective of this study was to evaluate this model for predicting rice flowering dates under field conditions. Other models used were a three-plane linear model and two nonlinear models, i.e. modified rice clock model (m-RCM) and the logistic model. Two existing data sets for photoperiod sensitive and nearly insensitive genotypes, respectively, were used to evaluate each model. For a photoperiod-sensitive cultivar, nonlinear models described the data more accurately than the linear one; but the performance of the three nonlinear models was similar although the 3s-Beta model best explained the variation of days to flowering across environments. For nearly photoperiod-insensitive genotypes, the models were evaluated first using the data from experiments in 1984. The 3s-Beta model performed better than m-RCM, m-RCM better than the logistic model, and the logistic model better than the linear model. When the coefficients derived from the 1984 experiments were used to predict flowering dates observed in experiments of a separate year, relative performance of the models remained the same although the difference among the models became smaller. Issues related to the model performance were discussed.

Introduction

The ability to predict development stage as a function of specific environmental variables is a basic requisite for crop growth models. Rice phenology is dependent on temperature and photoperiod. Several models (e.g. Horie and Nakagawa, 1990; Gao et al., 1992; Summerfield et al., 1992) have been presented to predict development to flowering in rice based on temperature and photoperiod. However, most existing models do not fully account for changes in developmental responses to these factors during ontogeny of rice.

Based on the results of several experiments under controlled environments, a detailed phenological model for predicting rice flowering dates has been derived (Chapter 9). This model is different from existing phenological models in that its structure is based on the experimental understanding of photothermal responses of flowering in rice. However, whether this model is superior to existing models in predictive performance has not been tested. The objective of the present Chapter is to evaluate the performance of this model in comparison to three existing models reported by Horie and Nakagawa (1990), Gao et al. (1992) and Summerfield et al. (1992), respectively, in predicting rice flowering dates under a wide range of field conditions.

Materials and methods

Description of the models

3s-Beta model

The three-stage Beta (3s-Beta) model presented in Chapter 9 uses the Beta function as a basic equation and divides the entire preflowering period into three phases. The model describes photothermal responses of flowering as:

$$DR = \begin{cases} g'(T_D) \cdot h'(T_N) / f_o & \text{if } DS \leq \theta_1 \text{ or } DS \geq \theta_2 \\ g(T_D) \cdot h(T_N) \cdot r(P) / f_o & \text{if } \theta_1 < DS < \theta_2 \end{cases} \quad (10.1)$$

where DR is the development rate (d^{-1}); DS is the development stage, calculated as an accumulation of daily DR; f_o is the minimum number of days to flowering; θ_1 and θ_2 are values of DS for the beginning and end of photoperiod-sensitive phase, respectively. The value for θ_2 was found to be set as $(\theta_1 + 0.2)$ for all rice cultivars, and the value for θ_1 was found to correlate to the value for f_o as: $\theta_1 = 0.145 + 0.005 f_o$ (Chapter 9).

The Beta functions in Eq. 10.1 that describe the responses to day and night temperature and photoperiod for the photoperiod-sensitive phase are:

$$g(T_D) = \left[\left(\frac{T_D - T_b}{T_{oD} - T_b} \right) \left(\frac{T_c - T_D}{T_c - T_{oD}} \right)^{\frac{T_c - T_{oD}}{T_{oD} - T_b}} \right]^\alpha \quad (10.2a)$$

$$h(T_N) = \left[\left(\frac{T_N - T_b}{T_{oN} - T_b} \right) \left(\frac{T_c - T_N}{T_c - T_{oN}} \right)^{\frac{T_c - T_{oN}}{T_{oN} - T_b}} \right]^\alpha \quad (10.2b)$$

$$r(P) = \left[\left(\frac{P - P_b}{P_o - P_b} \right) \left(\frac{P_c - P}{P_c - P_o} \right)^{\frac{P_c - P_o}{P_o - P_b}} \right]^\delta \quad (10.2c)$$

where T_D = day temperature ($^{\circ}C$); T_{oD} is a parameter for the optimum value of T_D ;
 T_N = night temperature ($^{\circ}C$); T_{oN} is a parameter for the optimum value of T_N ;
 T_b = the base temperature ($^{\circ}C$), at or below which the DR equals zero;
 T_c = the ceiling temperature ($^{\circ}C$), at or above which the DR is zero;
 P = photoperiod ($h d^{-1}$);
 P_b , P_o and P_c = the base, optimum and ceiling photoperiod ($h d^{-1}$), respectively;
 α = sensitivity coefficient to characterize the response to temperature;
 δ = sensitivity coefficient to characterize the response to photoperiod.

The functions $g'(T_D)$ and $h'(T_N)$ in Eq. 10.1, which are for effects of T_D and T_N on photoperiod-insensitive phases, have the same expression as Eq. 10.2a and Eq. 10.2b, respectively, but with the value of coefficient α as 1.0 (Chapter 9). To reduce the number of parameters to be estimated, the standard values, 8°C for T_b , 42°C for T_c , 0.0 h d⁻¹ for P_b , 10.0 h d⁻¹ for P_o , and 24.0 h d⁻¹ for P_c , were used (Chapter 9). Therefore, there are five model parameters for characterizing varietal photothermal responses of flowering: f_o , T_{oD} , T_{oN} , α and δ .

Modified rice clock model

Rice clock model (RCM) presented by Gao et al. (1992) describes the DR of preflowering development as a function of daily mean temperature and photoperiod:

$$DR = f(T) \cdot r(P) / f_o \quad (10.3)$$

where f_o is the minimum number of days to flowering. The function in the RCM for the effect of temperature, $f(T)$, has a similar form as the Beta equation. However, the original RCM does not ensure that the maximum DR occurs at T_o , and this problem can be overcome by the Beta model (Chapter 2). Therefore, an equation for the effect of temperature, T , can be modified based on the Beta function as:

$$f(T) = \left[\left(\frac{T - T_b}{T_o - T_b} \right) \left(\frac{T_c - T}{T_c - T_o} \right)^{\frac{T_c - T_o}{T_o - T_b}} \right]^\alpha \quad (10.4)$$

where α is a coefficient for the sensitivity of the DR to temperature. In the RCM, the effect of photoperiod is defined as:

$$r(P) = \exp[\beta(P - P_{mo})] \quad (10.5)$$

where P_{mo} is the maximal optimum photoperiod, at or below which $r(P)$ equals 1.0; β is a coefficient defining the photoperiod sensitivity of a cultivar.

Since the effect of temperature in the RCM was modified according to the Beta function, this model is referred to as a modified RCM (m-RCM). Values for T_b and T_c in the m-RCM were also fixed to be 8 and 42°C, respectively.

The logistic model

Horie and Nakagawa (1990) presented a model to describe DR of rice for the development to flowering as a function of daily mean temperature and photoperiod:

$$DR = \begin{cases} f(T) / f_o & \text{if } DS \leq \theta \\ f(T) \cdot r(P) / f_o & \text{if } DS > \theta \end{cases} \quad (10.6)$$

where f_o is the minimum number of days to flowering; DS is the developmental stage, calculated as accumulation of daily DR; θ is the value of DS at the end of the juvenile phase,

during which DR is not affected by photoperiod. The logistic function was used to define the effect of temperature on DR:

$$f(T) = \frac{1}{1 + \exp[-A(T - T_h)]} \quad (10.7)$$

where T_h is the temperature at which $f(T) = 0.5$, A is a coefficient defining the curvature of the response to temperature. The photoperiod effect on the development following the juvenile phase is quantified by:

$$r(P) = 1 - \exp[B(P - P_{\alpha})] \quad (10.8)$$

where B is a coefficient defining the responsiveness of a cultivar to photoperiod, P_{α} is the critical photoperiod, at or above which $r(P)$ equals zero.

Three-plane linear model

Hadley et al. (1984), Roberts and Summerfield (1987) and Summerfield et al. (1991) presented a modelling method in which they used a set of linear and additive equations relating DR to the mean temperature and photoperiod to describe a response surface including three planes.

The thermal plane, where the DR is sensitive only to temperature, is described by:

$$DR = a_1 + b_1 T \quad (10.9)$$

where a_1 and b_1 are genotype-specific coefficients.

The second (photothermal) plane, where DR is affected by both temperature and photoperiod, is described by:

$$DR = a_2 + b_2 T + c_2 P \quad (10.10)$$

where a_2 , b_2 and c_2 are genotype-specific coefficients.

A third plane defines a maximum delay of development, where the DR is not sensitive to any change of either photoperiod or temperature, that is,

$$DR = a_3 \quad (10.11)$$

where a_3 is a coefficient defining a minimum value for the DR.

This model with six coefficients can be applied to environments with temperatures limited by T_b and T_o . In a particular set of observations or for a particular genotype, not all parts of the response may necessarily be represented. This model, initially presented by Hadley et al. (1984) for soybean [*Glycine max* (L.) Merr.] and subsequently discussed by Roberts and Summerfield (1987) and Summerfield et al. (1991) for the general use in annual crops, was also found to be applied to rice (Summerfield et al., 1992).

Experimental data

Two data sets were used to evaluate the models. The first data set was largely derived from the data of Horie and Nakagawa (1990) on development from emergence to flowering for a

Table 10.1. Experiments used for a photoperiod-sensitive cultivar Nipponbare (Data source: Experiments 1-31 from Horie and Nakagawa, 1990; and Experiments 32-34 from Chapter 9).

Exp. no.	Country	Location	Latitude	Sowing date (day-month-year)
1	Japan	Tsukuba	36°01'N	28 Feb. 1982
2				14 Mar. 1982
3				28 Mar. 1982
4				10 Apr. 1982
5				24 Apr. 1982
6				9 May 1982
7				22 May 1982
8				5 Jun. 1982
9				14 Mar. 1983
10		Kyoto	35°03'N	10 Apr. 1983
11				10 May 1983
12				6 Jun. 1983
13				16 May 1985
14				25 May 1985
15				3 Jun. 1985
16				17 Jun. 1985
17				18 Mar. 1986
18				3 Apr. 1986
19				19 Apr. 1986
20				3 May 1986
21				21 May 1986
22				3 Jun. 1986
23				20 Jun. 1986
24				14 Jul. 1986
25				26 Mar. 1987
26				13 Apr. 1987
27				14 May 1987
28				23 May 1987
29				24 Jun. 1987
30				22 Mar. 1988
31				24 Apr. 1988
32				18 May 1993
33	China	Hangzhou	30°14'N	21 May 1993
34	Philippines	Los Baños	14°10'N	20 Jul. 1993

Table 10.2. Experiments in the International Rice Weather Yield Nursery (Data source: Oldeman et al., 1987).

Exp. no.	Country	Location	Latitude	Date (day-month-year)	
				Sowing	Transplanting
1	Korea	Suweon	37°16'N	7 May 1983	8 Jun. 1983
2				3 May 1983	15 Jun. 1983
3				15 Apr. 1984	24 May 1984
4				5 May 1984	14 Jun. 1984
5		Milyang	35°29'N	7 May 1983	8 Jun. 1983
6				17 May 1983	18 Jun. 1983
7				15 Apr. 1984	25 May 1984
8				5 May 1984	14 Jun. 1984
9	China (Taiwan)	Pingtung	22°40'N	5 May 1983	18 May 1983
10				27 Aug. 1983	12 Sep. 1983
11				7 Dec. 1983	13 Jan. 1984
12				27 Aug. 1984	13 Sep. 1984
13	China	Nanjing	32°03'N	14 Jun. 1983	9 Jul. 1983
14				1 May 1984	1 Jun. 1984
15				5 Jun. 1984	5 Jul. 1984
16	Burma	Yezin	21°57'N	17 Jun. 1983	16 Jul. 1983
17				17 Oct. 1983	8 Nov. 1983
18				2 May 1984	29 May 1984
19				2 Oct. 1984	2 Nov. 1984
20	Indonesia	Muara	6°36'S	12 Jan. 1984	3 Feb. 1984
21				11 Apr. 1984	2 May 1984
22				29 Aug. 1984	19 Sep. 1984
23		Sukamandi	6°15'S	19 Dec. 1983	9 Jan. 1984
24				28 Apr. 1984	19 May 1984
25				11 Oct. 1984	1 Nov. 1984
26	Philippines	Los Baños	14°10'N	5 May 1983	27 May 1983
27				11 Feb. 1984	2 Mar. 1984
28				5 Jun. 1984	25 Jun. 1984
29		Masapang	14°10'N	6 Nov. 1984	26 Nov. 1984
30				28 Dec. 1983	17 Jan. 1984
31				5 Jul. 1984	25 Jul. 1984
32	Thailand	Sanpatong	18°45'N	7 Jul. 1983	2 Aug. 1983
33				16 Jan. 1984	13 Feb. 1984
34				9 Jul. 1984	31 Jul. 1984

(To be continued)

35	Bangladesh	Joydebpur	23°54'N	26 Jun. 1983	31 Jul. 1983
36				31 Oct. 1984	5 Dec. 1984
37				11 Nov. 1983	20 Dec. 1983
38				16 Jul. 1984	17 Aug. 1984
39	India	Hyderabad	17°25'N	14 Jul. 1983	23 Aug. 1983
40				13 May 1984	12 Jun. 1984
41				25 Jun. 1984	26 Jul. 1984
42		Pattambi	10°48'N	25 Aug. 1983	23 Sep. 1983
43				9 Jun. 1984	3 Jul. 1984
44				20 Jul. 1984	14 Aug. 1984
45		Cuttack	20°30'N	11 Jul. 1983	5 Aug. 1983
46				28 Dec. 1983	3 Feb. 1984
47				23 Apr. 1984	16 May 1984
48				4 Aug. 1984	22 Aug. 1984
49		Kapurthala	30°56'N	11 May 1984	20 Jun. 1984
50				18 Jun. 1984	19 Jul. 1984
51		Coimbatore	11°02'N	12 Jul. 1983	6 Aug. 1983
52				3 Jun. 1984	28 Jun. 1984
53	Nepal	Parwanipur	27°04'N	19 Jul. 1983	12 Aug. 1983
54				15 Jul. 1984	6 Aug. 1984
55	Sri Lanka	Paranthan	8°59'N	27 Oct. 1983	5 Dec. 1983
56				29 Mar. 1984	24 Apr. 1984
57				23 Nov. 1984	20 Dec. 1984
58	Egypt	Sakha	31°05'N	15 Jun. 1984	12 Jul. 1984
59	Nigeria	Ibadan	7°34'N	25 Nov. 1983	22 Dec. 1983
60	Colombia	Palmira	3°31'N	12 Sep. 1983	11 Oct. 1983
61				12 Mar. 1984	12 Apr. 1984

photoperiod-sensitive cultivar Nipponbare (Table 10.1). These data came from field experiments conducted at Tsukuba and Kyoto in Japan from 1982 to 1988. To expand the range of the photothermal environment, additional observations from a three-location field experiment conducted in 1993 (Chapter 9) were included (Table 10.1). The combination of these data provided 34 observations with a range from 41 d at Los Baños in Philippines to 155 d of the first experiment in 1982 at Tsukuba in Japan.

The second data set was from a trial of the International Rice Weather Yield Nursery (IRWYN) (Oldeman et al., 1987). The trial was conducted in a wide range of environments in different countries, with 25 experiments started in 1983 and 36 experiments in 1984 (Table 10.2). The data on days from sowing to flowering in nine nearly photoperiod-insensitive genotypes (BG35-2, BG367-4, MRC603-303, IR13429-196-1, IR36, IR50, IR9729-67-3, IR9828-91-2-3 and Taichung sen yu) were observed in the trial.

Parameter estimation

A FORTRAN program developed by Horie et al. (1986) was adapted to estimate parameters for all models. This program uses an iteration procedure of the simplex method. Details about the use of the program were given by Horie et al. (1986), Horie and Nakagawa (1990), Sinclair et al. (1991) and Chapter 9. In the procedure, daily values of photoperiod and temperature are used to calculate daily DR. Therefore, all models were parameterized based on the daily mean values of photothermal variables. The daily photoperiod was calculated from an equation proposed by Goudriaan and van Laar (1978), assuming a -2° sun angle to account for the effect of twilights on rice photoperiodism (Chapter 9). For the 3s-Beta model, the mean day and night temperature was estimated from the daily maximum (T_{\max}) and minimum (T_{\min}) temperature according to (Penning de Vries et al., 1989; Kropff et al., 1994b):

$$T_D = 0.75T_{\max} + 0.25T_{\min} \quad (10.12)$$

$$T_N = 0.25T_{\max} + 0.75T_{\min} \quad (10.13)$$

Because not necessarily all three planes in the linear model exist for a particular genotype, the model was parameterized using a five-step procedure described by Watkinson et al. (1994). Each step resulted in a model of a single equation or a combination of Eqs 10.9-10.11. The model that gives the best fit of data is the most appropriate one for a given genotype. The five model steps are: 1) a simple regression for Eq. 10.9 involving temperature only was fitted to the data; 2) a multiple regression for Eq. 10.10 involving both temperature and photoperiod was fitted to the data; 3) a model having the first and second planes, i.e. the combination of Eq. 10.9 and Eq. 10.10, was fitted to the data by an iteration procedure, with the initial values which were the regression parameters obtained from steps 1 and 2; 4) a model having the second and third planes, i.e. the combination of Eq. 10.10 and Eq. 10.11, was fitted to the data by the iteration with the initial values for coefficients of Eq. 10.10 obtained in step 3; 5) a model having all three planes was fitted to the data with initial values for a_1 , b_1 , a_2 , b_2 and c_2 obtained from step 3 and the initial value for a_3 from step 4.

Once the coefficients in the models were obtained for each cultivar, a linear regression was done between predicted and observed days. The r^2 value for this linear regression and the mean absolute predictive deviation (MD) were used to indicate the accuracy of each model. For the IRWYN data set, the models were first parameterized using the experiments started in 1984. Then, the parameters derived from the 1984 data were used to predict the flowering times for the experiments started in 1983.

Results

Model performance for the photoperiod-sensitive cultivar

Table 10.3 gives parameter values of each model for the photoperiod-sensitive cultivar Nipponbare derived from the data set for the time interval between emergence and flowering as described in Table 10.1. The best fit for the linear model was achieved in step 3 of

Table 10.3. Values of parameters of the four models for development from emergence to flowering in the photoperiod-sensitive rice cultivar Nipponbare derived from the experiments described in Table 10.1.

Model	Model Parameters					r^2 †	MD§
3s-Beta model	f_o	T_{oD}	T_{oN}	α	δ		
	33.59	26.9	23.5	3.4259	11.2573	0.985	2.53
m-RCM	f_o	T_o	α	P_{mo}	β		
	35.15	26.8	3.6406	12.0	-0.3343	0.981	2.79
Logistic model	f_o	T_h	A	P_{α}	B	θ	
	41.76	17.6	0.5311	15.7	0.3786	0.343	2.29
Linear model	a_1	b_1	a_2	b_2	c_2		
	-0.01180	0.00112	0.01875	0.00085	-0.00197	0.948	4.65

† r^2 is for the linear regression between predicted and observed days.

§ MD is the mean absolute discrepancy between predicted and observed days.

parameterization as described earlier; thus, coefficients of the model with the combination of Eq. 10.9 and Eq. 10.10 are presented in Table 10.3.

All models described the data quite well with the r^2 value > 0.94 . However, the performance among the models was appreciably different. Three nonlinear models performed better than the linear one (Fig. 10.1): the nonlinear models described the data with $r^2 > 0.98$, while the linear model described the data with $r^2 = 0.948$ (Table 10.1).

The performance of the three nonlinear models was similar, although, in terms of the value of r^2 , the 3s-Beta model described the data somewhat better than m-RCM and the logistic model. The minimum MD value was obtained for the logistic model (MD = 2.29 d); however, this model had an overprediction of 14 d for the observed days in the tropics (i.e. Los Baños in Philippines), considerably larger than the overpredicted by m-RCM or 3s-Beta model (Fig. 10.1). This can be due to the fact that the logistic model underestimated the value of DR at temperatures around the optimum, as the minimum number of days, f_o , estimated by the logistic model was higher than the estimated by m-RCM or 3s-Beta model (Table 10.3).

Model performance for nearly photoperiod-insensitive genotypes

Among the 61 IRWYN experiments for nine nearly photoperiod-insensitive genotypes, 36 experiments were started in 1984 (Table 10.2). Values of parameters of each model for each genotype derived from these 36 observations in days from sowing to flowering are given in Table 10.4. Again, for the linear model, the best fit was achieved in step 3 of parameterization

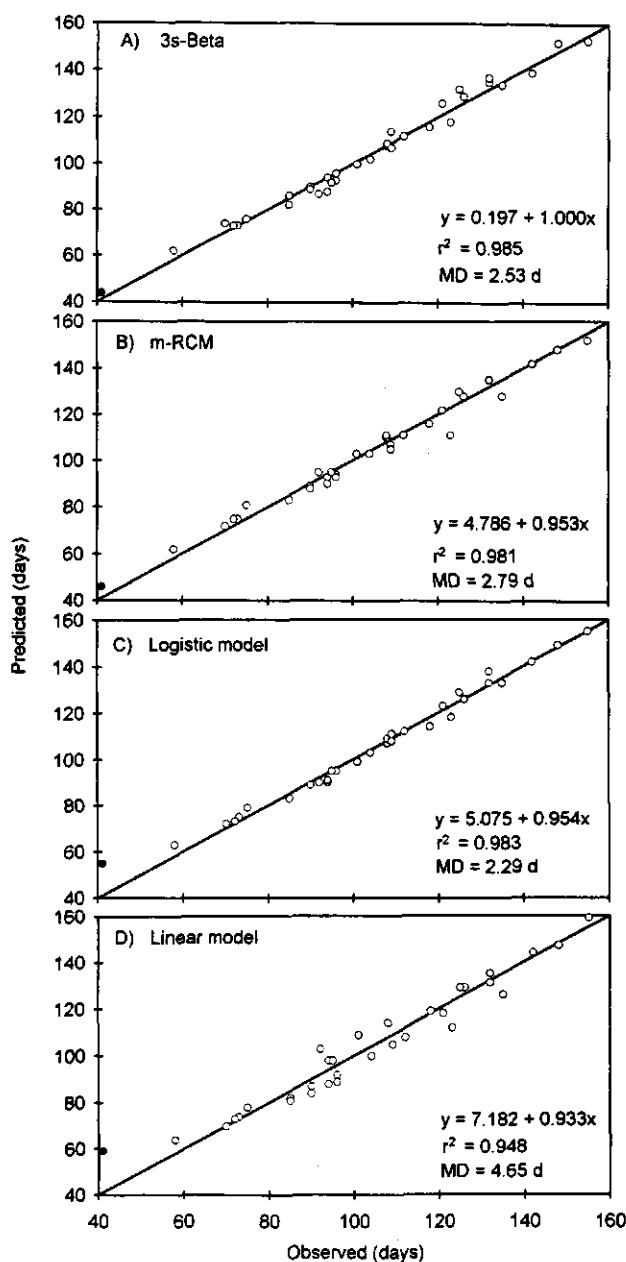


Fig. 10.1. Comparison of days from emergence to flowering in the photoperiod-sensitive cultivar Nipponbare observed in the experiments described in Table 10.1 with those predicted by four models with parameter values presented in Table 10.3. The closed 'circle' is for the data in Los Baños in Philippines (see text). The line indicates the 1:1 relationship. The r^2 represents the coefficient of determination for the linear regression (shown by equation) between predicted (y) and observed (x) days. The MD is the mean absolute predictive discrepancy.

Table 10.4. Values of parameters of the four models for development from sowing to flowering in nine nearly photoperiod-insensitive rice genotypes derived from the data of the 36 experiments started in 1984 described in Table 10.2.

Genotype	Model Parameters					r^2_{\dagger}	MD§
1. 3s-Beta model							
	f_o	T_{oD}	T_{oN}	α	δ		
BG35-2	77.49	29.7	25.7	3.2279	3.3411	0.876	4.61
BG367-4	78.44	30.1	25.9	2.4275	1.7569	0.823	4.89
MRC606-303	82.42	29.6	25.6	4.9200	1.2521	0.884	4.25
IR13429-196-1	81.70	29.2	25.0	4.0552	0.3241	0.785	5.22
IR36	80.87	29.3	25.1	4.6699	2.0242	0.872	4.53
IR50	77.59	29.7	25.7	2.3102	0.6452	0.845	4.11
IR9729-67-3	71.24	29.9	24.3	2.6760	1.7248	0.828	4.37
IR9828-91-2-3	80.59	28.5	26.1	3.4445	1.5859	0.839	4.97
Taichung sen yu	83.85	29.9	25.2	2.9956	1.5758	0.835	4.49
2. m-RCM model							
	f_o	T_o	α	P_{mo}	β		
BG35-2	80.56	27.7	3.3554	13.4	-0.0742	0.850	5.31
BG367-4	79.78	28.0	3.3469	16.8	-0.0562	0.801	5.39
MRC606-303	83.98	27.4	3.9195	18.7	-0.0716	0.824	5.03
IR13429-196-1	80.45	27.1	3.8019	16.3	-0.0472	0.734	5.56
IR36	82.80	27.6	3.8247	16.2	-0.0555	0.836	5.36
IR50	77.59	27.6	3.2589	9.9	-0.0003	0.816	4.47
IR9729-67-3	71.44	27.2	3.6592	11.8	-0.0045	0.791	4.51
IR9828-91-2-3	82.63	27.5	3.6444	15.6	-0.0679	0.791	5.78
Taichung sen yu	85.87	27.5	3.3624	16.0	-0.0529	0.804	5.14
3. Logistic model							
	f_o	T_h	A	P_{α}	B	θ	
BG35-2	76.69	19.4	0.4754	17.1	0.5243	0.414	0.792 6.39
BG367-4	77.62	19.3	0.4586	18.1	0.5305	0.446	0.745 6.33
MRC606-303	81.79	19.2	0.4076	18.2	0.5464	0.449	0.752 6.31
IR13429-196-1	81.07	18.9	0.5126	19.1	0.4849	0.459	0.646 7.17
IR36	81.55	19.6	0.5199	18.1	0.5015	0.419	0.757 6.86
IR50	78.97	19.0	0.4793	20.3	0.6537	0.417	0.732 5.64
IR9729-67-3	74.10	18.9	0.5685	18.9	0.4522	0.381	0.730 5.63
IR9828-91-2-3	78.92	19.5	0.4706	18.3	0.4322	0.449	0.746 6.83
Taichung sen yu	85.56	18.8	0.4432	18.8	0.5823	0.438	0.738 6.29

(To be continued)

4. Linear model							
	a_1	b_1	a_2	b_2	c_2		
BG35-2	-0.00614	0.00067	0.00139	0.00059	-0.00045	0.638	8.42
BG367-4	-0.00391	0.00059	0.00448	0.00047	-0.00041	0.659	7.36
MRC606-303	-0.00260	0.00051	0.00518	0.00041	-0.00042	0.623	7.78
IR13429-196-1	-0.00524	0.00064	0.00895	0.00013	-0.00006	0.609	7.72
IR36	-0.00360	0.00056	0.00432	0.00048	-0.00049	0.586	8.64
IR50	-0.00294	0.00055	0.00378	0.00069	-0.00006	0.531	7.47
IR9729-67-3	-0.00343	0.00061	0.00361	0.00051	-0.00037	0.543	7.43
IR9828-91-2-3	-0.00373	0.00057	0.00518	0.00044	-0.00044	0.605	8.19
Taichung sen yu	-0.00223	0.00050	0.00455	0.00037	-0.00029	0.607	7.37

‡ r^2 is for the linear regression between predicted and observed days.

§ MD is the mean absolute discrepancy between predicted and observed days.

Table 10.5. The performance of the models when coefficients determined from the 1984 experiments (presented in Table 10.4) were used to predict rice flowering dates observed in the 1983 experiments.

Cultivar	3s-Beta		m-RCM		Logistic		Linear	
	r^2 ‡	MD§	r^2	MD	r^2	MD	r^2	MD
BG35-2	0.854	5.28	0.838	5.80	0.794	6.44	0.693	8.16
BG367-4	0.783	6.40	0.772	6.60	0.728	7.36	0.653	7.76
MRC603-303	0.751	6.92	0.725	7.08	0.674	7.33	0.655	7.54
IR13429-196-1	0.810	5.33	0.833	5.29	0.795	6.04	0.713	7.21
IR36	0.836	5.29	0.835	5.54	0.789	6.42	0.728	7.08
IR50	0.750	6.13	0.716	6.67	0.701	6.63	0.640	7.25
IR9729-67-3	0.711	6.42	0.696	6.88	0.654	6.75	0.589	7.13
IR9829-91-2-3	0.845	5.08	0.819	5.75	0.756	6.79	0.716	7.13
Taichung sen yu	0.775	5.50	0.762	6.17	0.721	6.62	0.695	7.50

‡ r^2 is for the linear regression between predicted and observed days.

§ MD is the mean absolute discrepancy between predicted and observed days.

in all genotypes; therefore, Eq. 10.11 is not needed for the linear model to describe the photothermal responses of these rice genotypes.

Among the four models, the 3s-Beta model most successfully described the data in all genotypes, in terms of the value of either r^2 or MD (Table 10.4). The r^2 value for this model ranged from 0.785 in IR13429-196-1 to 0.884 in MRC603-303. Results for other three models

were also consistent among nine genotypes: m-RCM ($r^2 = 0.734-0.850$) was better than the logistic model ($r^2 = 0.646-0.792$), the logistic model was better than the linear model ($r^2 = 0.531-0.659$). The pooled data of all genotypes indicated that the 3s-Beta model explained 85.4%, m-RCM 81.8%, the logistic model 75.6% and the linear model 62.6% of the observed variation in the period from sowing to flowering which ranged from 65 to 158 d across environments and genotypes (Fig. 10.2). A problem with the linear model is clearly shown at the higher end in Fig. 10.2 which shows the data from a cool environment at Joydebpur, Bangladesh (Exp. no 36 in Table 10.2) when the plants were sown in the winter time.

The coefficients developed based on the 1984 data were used to predict flowering dates observed in the 25 experiments started in 1983 (Table 10.2). Values of r^2 and MD of the models for each of the nine genotypes are presented in Table 10.5. The 3s-Beta model outperformed the other three models for all genotypes, except for IR13429-196-2 for which the largest r^2 and lowest MD value resulted from the use of m-RCM. The results for the composite data of all genotypes are given in Fig. 10.3. Although the relative superiority of the models was the same, the difference among the models became smaller when compared to their performance shown in Fig. 10.2. This can be partly due to the fact that the range of flowering dates in the 1983 experiments (68–147 d) was somewhat smaller than in the 1984 experiments (64–158 d).

Discussion

One of the consistent results in this Chapter is that the best fit for the linear model was achieved in step 3 of parameterization, and thus, Eq. 10.11 is not needed for the model to describe photothermal responses of flowering for rice genotypes involved. This is in agreement with the result of Summerfield et al. (1992) that the third plane of the linear model, as described earlier, was not exhibited even at a long photoperiod of 15 h d⁻¹ in three rice cultivars. This Chapter also indicated that the linear model consistently performed worse than nonlinear ones. This contradicts the result of Summerfield et al. (1993) for soybean who reported that the linear model was more accurate than the logistic model, but agrees with the result of Sinclair et al. (1991) that the logistic model predicted soybean flowering dates somewhat better than the linear one. The poor performance of the linear model also highlights its main weakness that the model does not apply to the environments with temperatures $> T_0$ (Lawn et al., 1995). Then, part of the difficulty in using this model is that the high temperatures precluded the expression of temperature sensitivity for a genotype, at least part of the time (Sinclair et al., 1991).

In contrast to the 3s-Beta model and m-RCM, the logistic model assumes a level-off of DR at high temperatures. Considerable evidence (e.g. Haniu et al., 1983) has indicated that DR decreases with an increase of temperature when the temperature is higher than the optimum value for rice development. This may explain why the m-RCM, which has one parameter less than the logistic model, consistently performed better than the logistic model for the nine nearly photoperiod-insensitive genotypes tested in the IRWYN (Table 10.4 and Table 10.5). However, because the m-RCM ignores any changes of photoperiod sensitivity of rice plants

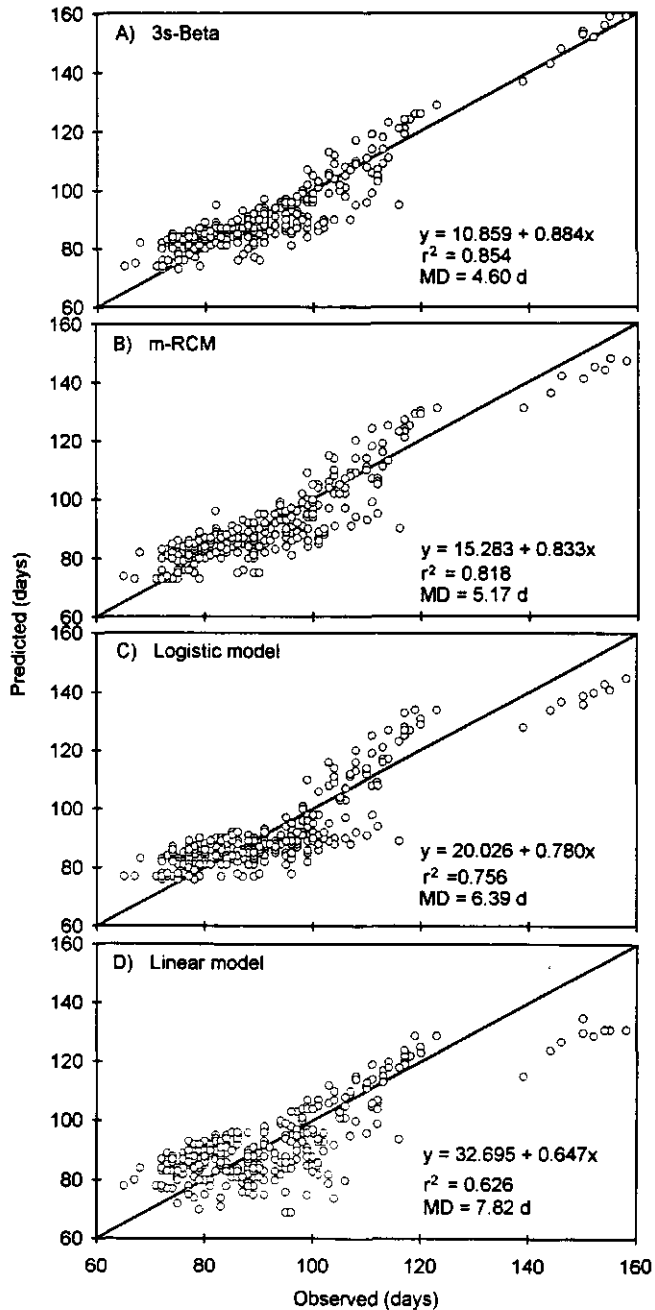


Fig. 10.2. Comparison of days from sowing to flowering in nine nearly photoperiod-insensitive rice genotypes observed in the experiments of 1984 (see Table 10.2) with those predicted by four different models with parameter values quantified in Table 10.4 (Data of Oldeman et al., 1987). Further details as for Fig. 10.1.

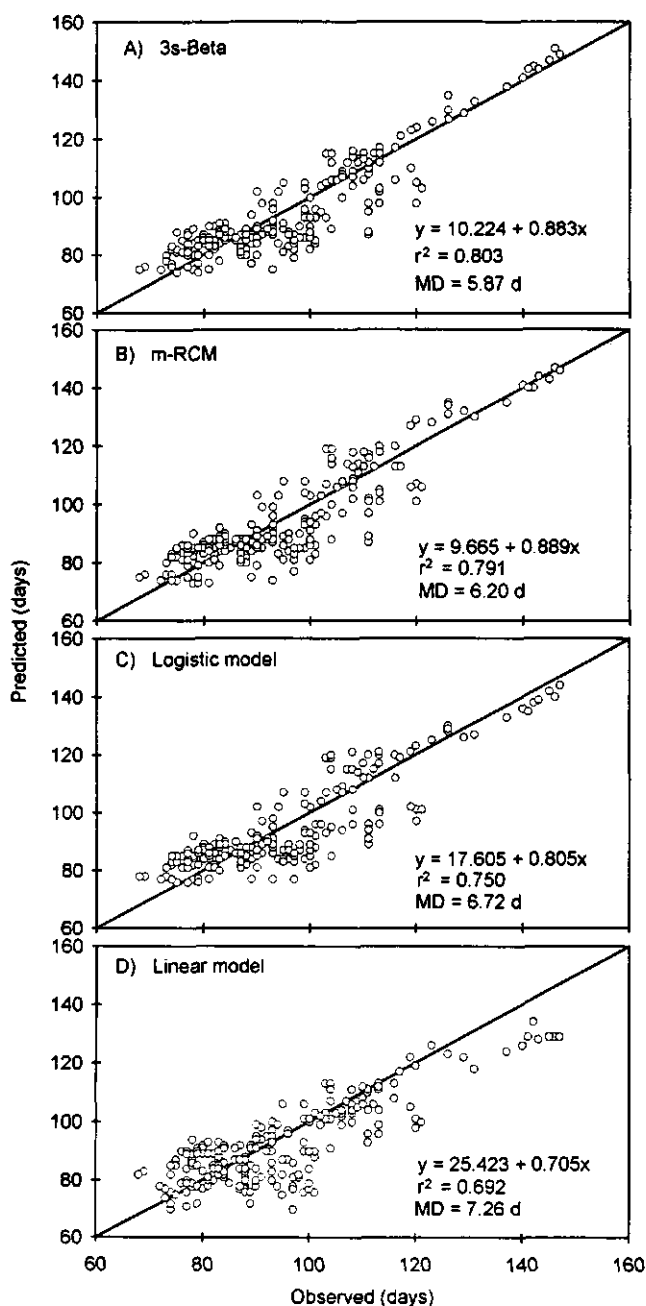


Fig. 10.3. Comparison of days from sowing to flowering in nine nearly photoperiod-insensitive rice genotypes observed in the experiments of 1983 (see Table 10.2) with those predicted by four different models with the parameter values (quantified in Table 10.4) estimated from the 1984 experiments (Data of Oldeman et al., 1987). Further details as for Fig. 10.1.

during preflowering development, the logistic model performed somewhat better than the m-RCM for the photoperiod-sensitive cultivar Nipponbare (Table 10.3, Fig. 10.1).

The 3s-Beta model incorporates most of the features of m-RCM and the logistic model. Furthermore, it uses day and night temperatures as separate variables and accounts for a change of the sensitivity to both day and night temperatures during preflowering development. However, even with this detailed model, considerable discrepancies between observed and predicted days remained for the data set of the IRWYN (Fig. 10.2 and Fig. 10.3). This can be partly due to a difference in the transplanting time among individual experiments of the IRWYN (Table 10.2), since there is a delay of development by transplanting (Dua et al., 1990). For a tropical environment, this delay (expressed in temperature sum) was found to be about 40% of the temperatures accumulated during the seed-bed period (Kropff et al., 1994b). However, it is difficult to quantify the effect in individual experiments of the IRWYN, because the effect of the transplanting shock varies with environments (Chapter 9).

Among genotypes involved in this study, two cultivars (Nipponbare and IR36) were analysed in Chapter 9 with the 3s-Beta model from controlled-environment experiments. Values for optimum day and night temperature estimated for the two cultivars in the present Chapter are about 3°C lower than those estimated in Chapter 9. The value for the minimum days, f_o , estimated for IR36 in the present Chapter is 80.9 d (Table 10.4), considerably higher than 57.6 d estimated in Chapter 9. These discrepancies can be attributed partly to the effect of transplanting shock as mentioned earlier, and partly to the fact that temperatures in the phytotron experiment used in Chapter 9 were fixed over day or night period of a diurnal cycle, in contrast to field conditions where temperatures are diurnally fluctuating. The discrepancies might be reduced by using temperature data over relatively short periods (e.g. 1 h) for field conditions. This should be done at the cost of a considerable increase of complexity for model parameterization.

Chapter 11

Optimal preflowering phenology of rice for high yield potential in Asian irrigated environments

Abstract One of the critical traits of rice ideotypes with an increased yield potential is the length of the period from sowing to flowering. The objective of this study was to determine the optimal preflowering phenology of rice (*Oryza sativa* L.) for high yield potential in different Asian irrigated environments.

A well evaluated ecophysiological model for irrigated rice production, ORYZA1, was used in this study. This model was coupled to the 3s-Beta model for preflowering phenology, which accounts for critical changes in photothermal responses of rice during ontogeny. Using a random number generator programme, a large number of combinations of parameter values of the 3s-Beta model, each equivalent to a hypothetical plant type, were created. The yield potential of these plant types was estimated by ORYZA1 for three locations, representing tropical, subtropical and temperate climatic environments, respectively.

For each environment there was an optimal preflowering period (PFP) which resulted in the highest yield. However, this PFP was not practically suitable in the subtropical and tropical environments from a cropping system viewpoint. In the subtropical environment, rice yield potential was restricted by the available growing season. In the tropical location, a critical flowering time was found, beyond which yield did not increase much by extending PFP. This critical value can be determined as the practically optimum PFP for the location as it allows a minimum growth duration without sacrificing yield potential. Yield was not sensitive to changes in individual phenological characteristics at the same PFP. As current standard cultivars in the different environments have a PFP which is very close to the optimum, further improvement of yield potential by manipulating preflowering phenology is limited.

Introduction

The yield potential of rice in irrigated environments in Asia has to be increased to cope with growing populations (IRRI, 1989). Therefore, new plant types with an increased yield potential have to be developed for different environments. Simulation models can be used to design plant types through evaluation of critical traits needed for high yield potential (Penning de Vries, 1991; Dingkuhn et al., 1993; Kropff et al., 1994a; Aggarwal, 1995; Kooman and Haverkort, 1995).

One key aspect for improved plant types is to match their phenology to the resources and constraints of target environments (Lawn et al., 1995). Of all phenological events, flowering is most important since it is the time of this stage which determines the climatic conditions to which the crop will be exposed during subsequent ripening growth (Roberts et al., 1993). In

rice, the genetic variation in the length of the postflowering period (from flowering to maturity) is relatively small for a given environment; it is the preflowering phase (i.e. from sowing to flowering) which varies greatly and largely determines the length of total growth duration of a cultivar (Vergara and Chang, 1985).

Genetic characteristics and environmental conditions determine the length of the preflowering period (PFP) in rice. Under irrigated conditions, PFP is determined almost exclusively by genetically controlled responses to temperature and photoperiod (Yoshida, 1981; Roberts et al., 1993). Recently, controlled-environment studies have been conducted to understand photothermal responses of preflowering development in rice (Chapters 4, 6 and 7). With regard to the response to photoperiod, the PFP can be divided into three successive subphases, i.e. the basic vegetative phase (BVP), the photoperiod-sensitive phase (PSP) and the post-PSP phase (PPP) (Chapter 6). With regard to the response to temperature, effects of day and night temperature were found to be different (Chapter 4), and responses to both day and night temperature were stronger during PSP than during BVP or PPP (Chapter 7). Based on these recent experimental findings, a quantitative model has been developed for photothermal responses of rice preflowering phenology (Chapter 9). As the model uses the Beta function as a basic equation to describe different photothermal responses of rice during the three subphases of PFP, it was referred to as the three-stage Beta (3s-Beta) model (Chapter 9).

One of the most important phenological events during PFP in rice is panicle initiation (PI), which marks the transition of the crop from vegetative growth to a reproductive development. After PI, rice plants allocate assimilates increasingly to the reproductive organs. A change in the time of PI may affect yield, because the distribution of a greater portion of assimilates to developing panicles may produce larger panicles if the period of panicle growth is extended (Yoshida, 1981). It has been shown that PI occurs some days before the end of PSP in rice (Chapter 6). The 3s-Beta model can represent the time when PSP ends for a given genotype; accordingly, it also predicts the time of PI.

Several studies emphasized the lengthening of postflowering duration as the main option to increase the yield plateau in rice (Penning de Vries, 1991; Dingkuhn et al., 1993; Kropff et al., 1994a; Aggarwal, 1995). Much less work has been done on the role of preflowering duration on the yield potential. However, changes in preflowering phenology, including the absolute length of PFP and the relative length of the three subphases, may affect the yield level in a specific environment. The objective of this study was to determine the optimal preflowering phenology of rice with respect to high yield potential in several Asian irrigated environments.

Materials and methods

Model description

ORYZA1

The rice simulation model ORYZA1 (Kropff et al., 1994b) was used in this study. The model simulates yield based on the responses of ecophysiological processes to the environments.

Under irrigated conditions, radiation, temperature and nitrogen (N) are the main factors determining crop growth rate. Leaf photosynthesis is calculated based on leaf N concentration and light intensity. The vertical N distribution in the canopy profile is accounted for by a generic exponential distribution derived from field experiments. Total daily CO₂ assimilation is obtained by integrating the instantaneous rates of CO₂ assimilation over the leaf area index (LAI) and over the day. Net daily growth rate is calculated after subtraction of maintenance and growth respiration requirements. The dry matter produced is distributed among various plant organs based on partitioning coefficients that depend on the phenological stage.

In the model, LAI is modelled in two phases. Before canopy closure, LAI development is a function of temperature. After canopy closure, the increase in LAI is obtained from the increase in leaf dry matter. For transplanted rice, ORYZA1 simulates the effect of transplanting shock on both phenological and LAI development. The delay of development by transplanting (°Cd), is calculated as a linear function of the age (°Cd) of seedlings that are transplanted. The number of spikelets per unit area is determined by crop growth rate between PI and flowering. Adverse temperature at the time of meiosis and pollination may result in spikelet sterility.

In the model, grains accumulate dry matter until the crop reaches phenological maturity, or until maximum grain weight is reached (sink limitation), or when the period with an average temperature < 12°C exceeds three days. ORYZA1 accurately predicted yields ranging from 5.7 to 14.7 t ha⁻¹ in a wide range of climatic environments (Kropff et al., 1994b).

3s-Beta phenological submodel

Based on the results of several controlled-environment studies (Chapters 4 and 6-8), the 3s-Beta model for rice preflowering phenology has been developed (Chapter 9). The model describes the development rate (DR, d⁻¹) as affected by temperature and photoperiod as:

$$DR = \begin{cases} g'(T_D) \cdot h'(T_N) / f_o & \text{if } DS \leq \theta_1 \text{ or } DS \geq \theta_2 \\ g(T_D) \cdot h(T_N) \cdot r(P) / f_o & \text{if } \theta_1 < DS < \theta_2 \end{cases} \quad (11.1)$$

where DS denotes the development stage (dimensionless), calculated as an accumulation of daily DR, with DS = 0.0 at sowing and DS = 1.0 at flowering; θ_1 and θ_2 are values of DS at beginning and end of PSP, respectively; f_o is the basic PFP (d), i.e. the minimum number of days to flowering which can be achieved if photothermal conditions are optimal; $g'(T_D)$ and $h'(T_N)$ are functions describing the responses to day and night temperature, respectively, during BVP or PPP; $g(T_D)$, $h(T_N)$ and $r(P)$ are functions for the responses to day and night temperature and photoperiod, respectively, during PSP.

The functions in Eq. 11.1 for the responses of DR to day and night temperature and photoperiod during different subphases were quantified by the Beta equation. For example, the Beta function for the effect of day temperature (T_D) on DR during PSP is:

$$g(T_D) = \left[\left(\frac{T_D - T_b}{T_{oD} - T_b} \right) \left(\frac{T_c - T_D}{T_c - T_{oD}} \right)^{\frac{T_c - T_{oD}}{T_{oD} - T_b}} \right]^\alpha \quad (11.2)$$

where T_{oD} is the optimum day temperature ($^{\circ}\text{C}$), at which $g(T_D)$ has its maximal value 1.0; T_b is the base temperature ($^{\circ}\text{C}$), at or below which DR equals zero; T_c is the ceiling temperature ($^{\circ}\text{C}$), at or above which DR is zero; α is sensitivity coefficient to characterize the response to temperature. The other functions in Eq. 11.1 have the same form as Eq. 11.2, but with different coefficients. Details about these functions and their coefficients are given in Chapters 9 and 10. To reduce the number of parameters to be estimated, values of some parameters were fixed since they vary little among cultivars (Chapter 9). The remaining five parameters for characterizing varietal responses were: f_o , T_{oD} , T_{oN} (optimum night temperature), α , and δ (sensitivity coefficient for the response to photoperiod) (see Chapters 9 and 10).

The five parameters have been estimated for the 17 diverse rice cultivars with different origins from two controlled-environment experiments; and these parameter values can be used to accurately predict rice flowering dates over a wide range of field conditions (Chapter 9).

Linking 3s-Beta model to ORYZA1

For this study, the 3s-Beta model was coupled to ORYZA1 for simulating preflowering phenology. The original phenological submodel of ORYZA1 was only used to estimate the transplanting shock on both phenological and leaf area development. For postflowering development, the procedure is the same as the original in ORYZA1.

Locations

Three locations in Asia, Los Baños in Philippines, Hangzhou in China, and Kyoto in Japan (Table 11.1), were selected here to represent tropical, subtropical and temperate environments, respectively. In Los Baños, rice is grown typically twice a year, i.e. in the dry and wet season (Centeno et al., 1995). The dry season lasts from January to May, and the wet season from June to December. In Kyoto, only one rice crop can be grown in a year because of the low temperature during winter time (Horie et al., 1995). In Hangzhou, two rice-based cropping systems exist, i.e. double-rice cropping (early-season rice immediately followed by late-season rice, and then followed by a winter crop) and one-season rice cropping (rice is grown in one season only, followed by a winter crop) (Zhu and Min, 1995). Standard cultivars and planting times for different seasons of the three locations (Table 11.1) were determined based on Centeno et al. (1995), Horie et al. (1995) and Zhu and Min (1995). Parameter values of the 3s-Beta model were determined for these cultivars in Chapter 9, except for cv. Guang Lu Ai 4, the standard cultivar for the early season in Hangzhou, for which parameters are not available.

Determining optimal preflowering phenology

To examine opportunities for increased yield potential by changing preflowering phenology, hypothetical plant types were generated in which the five parameters of the 3s-Beta model were varied simultaneously. This was achieved by using a random number generator programme, RIGAUS (Bouman and Jansen, 1993). By specifying the lower and upper limits of

Table 11.1. Rice growing seasons, normal planting dates, standard cultivars at the three locations, and development rate constants of the standard cultivars for postflowering period.

Location	Latitude	Season	Planting time (day number)	Standard cultivar	Development rate constant for post- flowering period ($^{\circ}\text{Cd}^{-1}$) [†]
Hangzhou	30°14'N	Early	79	Guang Lu Ai 4	0.00192
		Late	175	Xiu Shui 11	0.00184
		One-season	145	Shan You 63	0.00160
Kyoto	35°03'N		138	Nipponbare	0.00151
Los Baños	14°11'N	Wet	180	IR72	0.00178
		Dry	4	IR72	0.00178

[†] Based on the original phenological submodel of ORYZA1 (Kropff et al., 1994b), the bilinear model, in which the developmental rate is assumed to be linearly related to temperature above 8°C up to 30°C, beyond which the rate decreases, again linearly, until 42°C is reached.

parameter values and information on distribution properties of these values, RIGAUUS can create a wide array of 'hypothetical varieties'.

From values of the five parameters of the 3s-Beta model for the 17 rice cultivars (Table 9.7 in Chapter 9), it was found that the parameter f_0 followed the uniform distribution and parameters T_{OD} , T_{ON} , α and δ followed a Beta distribution. The upper limit for each parameter was determined as 10% higher than the actual highest value among the 17 cultivars, and the lower limit was 10% lower than the lowest value among those cultivars (Table 11.2). For δ , the parameter for photoperiod sensitivity, the lower limit was set to be zero, since absolute photoperiod-insensitivity has been observed (e.g. Tang et al., 1978).

A total of 999 hypothetical plant types were created with a random mix of the five parameters with the specified limit. However, those plant types for which the generated T_{ON} was higher than T_{OD} were not included in the analysis, because T_{OD} is $\geq T_{ON}$ in rice (Chapter 4). Accordingly, the remaining 808 hypothetical plant types were analysed for the different environments.

The yield potential of the 808 generated hypothetical plant types was estimated by ORYZA1 for each season at the three locations, using 1993 daily weather data. Except for phenology parameters, all simulations were run based on standard parameter values given by Kropff et al. (1994b) for cv. IR72. However, the LAI was underestimated for the early-season rice in Hangzhou if the standard value of relative LAI growth rate during the first phase of leaf area development was used. Therefore, the value adapted by Zhu and Min (1995) for this environment was used. The development rate constant for postflowering of the hypothetical

Table 11.2. The lower and upper limit of input parameters of the 3s-Beta model for RIGAUSS to generate hypothetical plant types.

Parameter	Description	Unit	Distribution	Lower limit	Upper limit
f_o	Basic preflowering period	d	Uniform	32	80
T_{oD}	Optimum day temperature	°C	Beta	23	38
T_{oN}	Optimum night temperature	°C	Beta	21	34
α	Temperature sensitivity	Dimensionless	Beta	1.0	6.0
δ	Photoperiod sensitivity	Dimensionless	Beta	0.0	33.0

plant types was set as that of the standard cultivar for each environment (Table 11.1) which was derived from a local field experiment as reported in Chapter 9.

The optimal PFP was determined based on the simulated yield of all hypothetical plant types. The duration of plant types with high yield potential was compared to that of the local standard cultivars. The performance of these plant types were further evaluated by using long-term weather data from 1959 to 1994 for Los Baños, from 1980 to 1989 for Hangzhou, and from 1985 to 1994 for Kyoto.

Results and discussion

The yield of all 808 hypothetical plant types was simulated for all three environments. For Hangzhou and Kyoto, often no yield was simulated for plant types with a strong photoperiod sensitivity (i.e. with a large value of δ) because plants were not predicted to flower during the available growing season. For such cases, only those plant types for which a yield was simulated were used for analysis.

Optimal preflowering period

The relation between simulated grain yield (14% moisture content) and PFP is given in Fig. 11.1. In general, for each environment, there was a PFP which resulted in a maximum yield. For Kyoto, the PFP determined from the available growing season agreed with the PFP at which the highest yield was simulated (Fig. 11.1D). For Hangzhou where two or three crops are grown in one year, the available time for rice, and therefore, the available season for PFP, is limited (Zhu and Min, 1995) (Fig. 11.1A-C). Thus, if the prevailing cropping system is taken into account, the maximum yield of rice cannot be achieved. Unlike other environments where a unimodal response was obtained, the simulated yield exhibited a bimodal response for early-season rice in Hangzhou (Fig. 11.1A). The yield decline after the first peak may be due to the shortened grainfilling period by high temperatures during that period. Nevertheless, the first

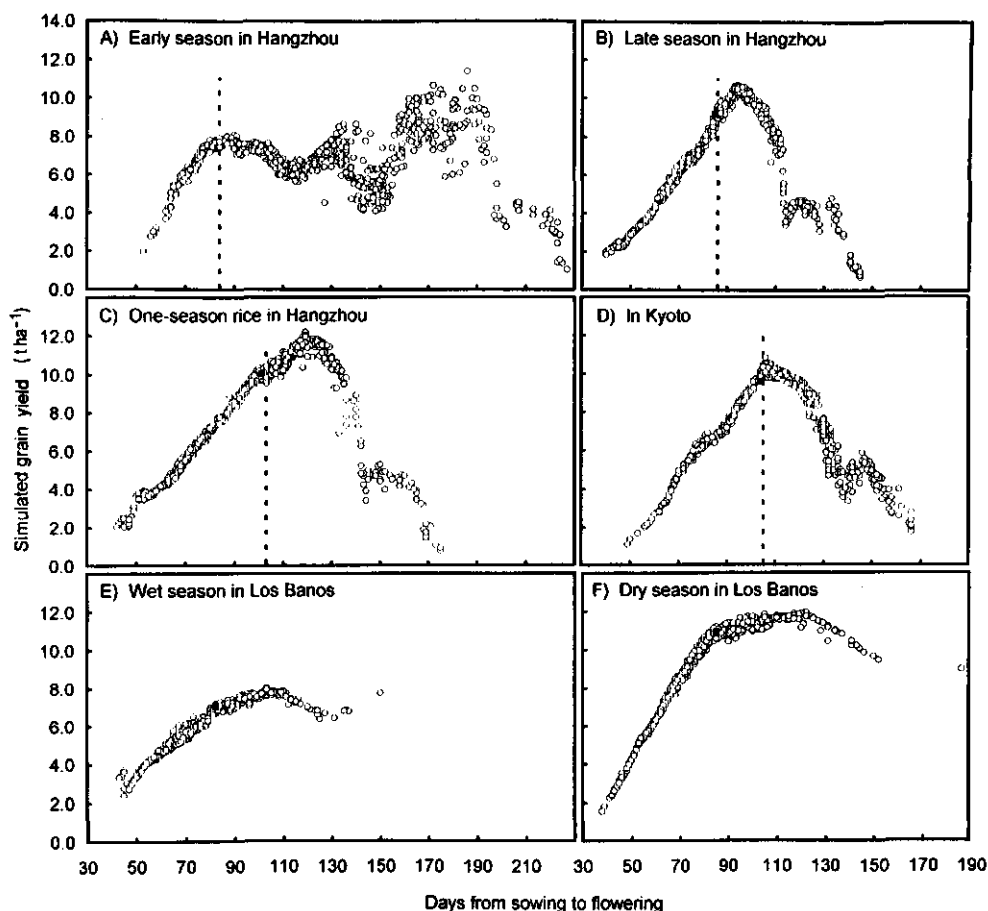


Fig. 11.1. Relation between simulated grain yield (14% moisture content) and preflowering period in rice for different seasons in three locations. Vertical dashed lines indicate the maximum preflowering period as determined by the length of available growing season. The black points represent current standard cultivars for the locations if available.

peak of the response for the early-season rice agrees well with the maximum PFP determined by the length of the growing season (Fig. 11.1A), indicating that an appropriate time has been determined for the early-season rice in the current cropping system of this location.

For Los Baños where the climatic conditions are suitable for rice growth all the year round, there was also a PFP for the highest yield (Fig. 11.1E,F). However, this PFP is not practical because it is too long, unavoidably resulting in an excessive vegetative growth which may cause lodging (Yoshida, 1981). Moreover, to facilitate the cultivation of 2-3 crops per year, the growth duration of rice has to be as short as possible (Centeno et al., 1995). In fact, for both wet and dry seasons, there was a critical PFP (about 82 d for the wet season and 85 d for

Table 11.3. The optimum preflowering period (PFP) and the corresponding total crop duration for different seasons at three locations.

Location	Season	Optimum PFP (d)	Total duration (d)
Hangzhou	Early	84	115
	Late	86	135
	One-season	103	145
Kyoto		104	157
Los Baños	Wet	82	113
	Dry	85	116

the dry season), below which the yield increases rapidly with increasing PFP, but beyond which the yield did not respond much to further extension of PFP (Fig. 11.1E,F). This critical point was more obvious in the dry season than in the wet season. These results show that the duration of PFP cannot be further shortened without largely sacrificing yield potential. It may also explain why the recently released semi-dwarf cv. IR72 has a similar yield potential as IR8 (released in 1964) which has a much longer duration (about 15 days) than IR72 (Kropff et al., 1994a,b).

Considering the available season and the critical flowering time, the optimum PFP practically suitable for a specific environment and the resultant total growth duration was determined as given in Table 11.3.

Response of yield to relative length of three subphases

The optimum PFP can be achieved by varying individual phenological characteristics, i.e. values of the five parameters of the 3s-Beta model. At a given length of PFP, various combinations of values for the five parameters resulted in different relative lengths of BVP, PSP and PPP. For a specific environment, there were 10–19 plant types generated by RIGAUSS with the optimum PFP (Table 11.4). Because of differences in the timing of PI among these plant types, different yields were simulated. The two plant types which resulted in the minimum and maximum yield, respectively, are given in Table 11.4. For each environment, there was a large difference in each parameter value among the two plant types. This difference was most evident in values of f_0 and δ , and least evident in the value of α . This suggests that the most important traits for breeders to manipulate flowering are the basic PFP and the photoperiod sensitivity. Table 11.4 further indicates that under irrigated conditions, both long basic PFP and weak photoperiod sensitivity are desirable for a higher yield potential in all environments. This

Table 11.4. Parameter values of the 3s-Beta model of the two hypothetical plant types with the optimum preflowering period which result in the minimum and maximum yields.

Season			Parameters				
			Yield (t ha ⁻¹)	f_o (d)	T_{oD} (°C)	T_{oN} (°C)	α δ
Hangzhou							
Early (12)†	Minimum	7.45	34.3	27.8	26.1	1.83	12.17
	Maximum	7.93	43.7	29.9	26.7	3.16	1.96
Late (14)†	Minimum	9.02	47.4	35.0	29.2	4.55	7.81
	Maximum	9.63	73.1	29.7	24.0	3.83	1.70
One-season (10)†	Minimum	9.64	44.4	32.5	27.5	2.18	12.80
	Maximum	10.44	77.4	30.5	28.7	3.42	3.31
Kyoto (11)†	Minimum	9.62	50.4	33.9	26.4	3.01	5.69
	Maximum	10.11	75.1	32.3	26.2	1.34	1.71
Los Baños							
Wet (19)†	Minimum	6.68	52.3	34.0	28.6	2.11	15.28
	Maximum	7.18	66.5	28.6	26.4	1.80	7.04
Dry (11)†	Minimum	10.55	58.0	35.3	29.2	2.23	2.67
	Maximum	11.20	78.3	29.0	24.4	1.72	0.99

† Figures in brackets indicate the number of hypothetical plant types with the optimum preflowering period.

supports the view that the strong photoperiod sensitivity is not required for the irrigated rice (Yoshida, 1981; Vergara and Chang, 1985).

However, the yield difference was very small among these hypothetical plant types in a specific environment (Table 11.4). This difference ranged from 0.38 t ha⁻¹ for Kyoto to 0.80 t ha⁻¹ for the one-season rice in Hangzhou. The small difference suggests that relative length of subphases of PFP is less important than the absolute length of PFP *per se* with respect to yield potential. In fact, the effect of the relative length of the subphases on yield is reflected by the effect of timing of PI, which might affect source-sink relationships. In this study, no sink limitation was simulated in the normal growing season in any specific environment, unless PFP was too short, or too long, which resulted in scattered responses of yield to PFP (e.g. Fig. 11.1A).

Comparison with current standard cultivars

With parameter values of the 3s-Beta model given in Chapter 9, the yield potential of standard cultivars was simulated for each environment (Fig. 11.1), except for the early season in

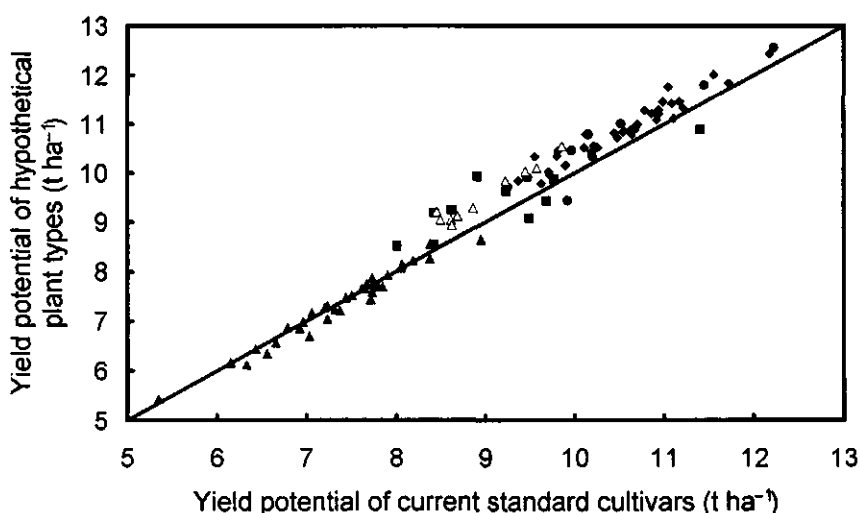


Fig. 11.2. Comparison of simulated yield (14% moisture content) potential between current standard cultivars and hypothetical plant types with an optimized preflowering phenology for the different locations and growing seasons (squares for the late season in Hangzhou, circles for one-season rice in Hangzhou, open triangles for Kyoto, closed triangles for the wet season in Los Baños, and diamonds for the dry season in Los Baños).

Hangzhou for which parameter values of the standard cultivar were not available. The PFP of the standard cultivar in Kyoto and those for late-season and one-season rice in Hangzhou is very close to the PFP set by the available growing season which determines the optimum PFP in those environments (Fig. 11.1B-D). For Los Baños, the standard cv. IR72 has the PFP which exactly agrees with the critical flowering time (Fig. 11.1E,F). Therefore, no significant difference was found between standard cultivars' PFP and the optimum PFP as given in Table 11.3. This indicates that selection pressure for a short crop duration has unconsciously identified the optimum PFP for each irrigated environment in rice breeding programs.

The performance of the hypothetical plant types with the optimum PFP which resulted in the maximum yield (Table 11.4) was further evaluated using long-term weather data. The simulated yields of these plant types are compared in Fig. 11.2 with those of the standard cultivars. Although the simulated yields of the optimal plant types were generally higher than those of the standard cultivars, the yield difference was very small. This further corroborates the conclusion that once the optimum PFP is determined, the yield improvement by manipulating preflowering phenology is limited.

Conclusions

This analysis has shown the importance of the length of PFP in determining rice yield potential under irrigated environments. Although there was a PFP in each environment which resulted in

the maximum simulated yield, often this PFP can not be practically used, except for Kyoto where only one crop of rice is grown per year. In Hangzhou, rice yield potential is restricted by the length of the available growing season if multiple cropping systems are used. For Los Baños, a critical PFP was identified, beyond which the yield did not increase very much with further extension of PFP. This critical point can be used as the practically optimum PFP for this tropical location, which is about 82–85 d.

Once the optimum PFP was determined, the yield did not respond much to changes in individual phenological traits although a long basic PFP and weak photoperiod sensitivity resulted in the highest yield. Because current standard cultivars have a PFP which is close to the optimum one, opportunities for further improvement of yield potential by manipulating preflowering phenology seem to be limited.

Chapter 12

General discussion

Much experimental and modelling work has been conducted for many years to analyse the effects of temperature and photoperiod on crop phenology. Experimental work involved both field and controlled-environment studies, and modelling methods varied from simple thermal unit approaches (e.g. Cross and Zuber, 1972) to complex theory-based nonlinear equations (e.g. Kiniry and Keener, 1982; Johnson and Thornley, 1985). Despite much effort, accurate prediction of crop phenology under diverse environments remains a problem for crop modellers (Tollenaar, 1990; Summerfield et al., 1991; Shaykewich, 1995).

Horie (1994) stated that a generally applicable model should be developed on the basis of physiological understanding of crop development. To understand photothermal responses of crop development, controlled-environment experiments are essential, because under field conditions effects of temperature and photoperiod are often confounded (Roberts et al., 1993). For example, in temperate climates the seasonal increase in photoperiod is closely associated with the rise in temperature. In this thesis, a model for predicting phenological development to flowering in rice (*Oryza sativa* L.) was developed on the basis of quantitative insights obtained from several controlled-environment studies on responses of rice flowering to temperature and photoperiod.

Experimental findings on photothermal responses of flowering

Considerable information on the effect of temperature on crop phenology was provided for different cereal crops in controlled-environment studies (Tollenaar et al., 1979; Warrington and Kanemasu, 1983a,b; Cao and Moss, 1989; Ellis et al., 1992b). Published controlled-environment studies on phenology, however, were rare for rice, relative to other cereal crops such as maize (*Zea mays* L.). One complete data set for rice came from an experiment using different combinations of day temperature (T_D) and night temperature (T_N) (IRRI, 1977). With this data set, IRRI (1977) concluded that T_N was a more important factor than T_D for development to flowering. However, that conclusion was derived on the basis of the assumption of a linear relation between crop development rate (DR) and temperature, in contrast to findings in many studies that the relation between DR and temperature was nonlinear (Chapter 2). Whether the use of a different temperature response for day and night is warranted has long puzzled phenologists since Went (1944a,b) reported an effect of diurnal temperature change and different impacts of T_D and T_N on plant growth and development. To clarify this point, a special controlled-temperature experiment was designed, in which the confounding effect due to the nonlinearity between DR and temperature was excluded (Chapter 4). The results supported existence of a difference in the impact of T_D and T_N on DR

in rice. In contrast to the results of IRRI (1977) on the relative importance of T_N , however, Chapter 4 illustrated that T_D affected DR more than T_N in most tested rice cultivars.

Many studies estimated phenological development based on the time required to fulfil a specific developmental phase (e.g. Robertson, 1968; Angus et al., 1981; Warrington and Kanemasu, 1983a; Chapters 1-3). Others expressed development rate by determining leaf initiation or appearance rate (Tollenaar et al., 1979; Thiagarajah and Hunt, 1982; Warrington and Kanemasu, 1983b; Grant, 1989; Miglietta, 1991a). The analysis of this thesis showed that the phasic development rate and leaf appearance rate in rice are differently affected by temperature. First, there are differential effects of T_D and T_N on the phasic development rate (Chapter 4), whereas T_D and T_N have no different effect on leaf appearance (Chapter 8). Secondly, the optimum temperature for leaf appearance was substantially higher than for phasic development (Chapter 8). Different functions for quantifying effects of temperature on the phasic development and leaf appearance have also been indicated by Warrington and Kanemasu (1983a,b) for maize, and by Slafer and Rawson (1995b) for wheat (*Triticum aestivum* L.). Therefore, an attempt to estimate the phasic development rate using a temperature-effect function for leaf appearance in some studies, e.g. Bonhomme et al. (1994) who used a function of Tollenaar et al. (1979) for maize leaf appearance to evaluate the thermal time required for development from sowing to silking, might cause a serious error.

The possibility that there is a variation in the phenological response of rice plants to temperature during ontogeny has been indicated by many reports (e.g. Owen, 1972; Haniu et al., 1983). However, this variation had not been proven experimentally until a study of transferring rice plants between low and high temperatures at various times after sowing was conducted (Chapter 7). The study clearly demonstrated that the response to both T_D and T_N during preflowering ontogeny changed from slightly sensitive to highly sensitive and then to slightly sensitive again. This is in contrast with the assumption in most existing models for predicting rice flowering dates (e.g. Horie and Nakagawa, 1990; Gao et al., 1992; Summerfield et al., 1992) that rice plants have the same temperature sensitivity throughout preflowering ontogeny. In describing crop phenology, a term 'juvenile phase' (Vergara and Chang (1985) defined it as the basic vegetative phase, BVP) is often used for the initial vegetative growth period during which plants do not respond to any changes in photoperiod (Roberts and Summerfield, 1987; Ritchie, 1993). Ritchie (1993) and Horie (1994) indicated that DR of the juvenile phase is strongly controlled by temperature. The evidence presented in this thesis suggests that the juvenile phase would better be defined as the initial phase with only slight thermal sensitivity.

Vergara and Chang (1985) published a well-known review based on numerous studies on the flowering response of rice plants to photoperiod. They developed a method to estimate the length of the juvenile phase or BVP, and photoperiod-sensitive phase (PSP) for a given rice cultivar, and reported that the duration of BVP varied widely among cultivars from 3 to 88 d. Several rice models were parameterized using the data of Vergara and Chang (1985). However, the results for a large number of cultivars reported in Chapter 6 of this thesis indicated that the genetic variation in the length of BVP was much smaller than the estimate by the method of Vergara and Chang (1985) which was based on incorrect assumptions (see Chapter 6). This thesis further shows that the most significant genotypic variation of flowering

response is the photoperiod sensitivity, rather than the length of BVP or the optimum photoperiod (Chapters 5 and 6).

This thesis generally supported Roberts et al. (1993) who emphasized the importance of controlled-environment studies in understanding flowering responses of a crop to temperature and photoperiod. However, because controlled-environment facilities are costly and are not always available, many modellers take a simple view of developmental rate and employ linear temperature units (TU) to advance their models (Loomis et al., 1990). It is clear now that for modelling purposes, the TU approach is too simple because it ignores: (1) any effects of photoperiod on DR (Chapters 5 and 6), (2) the optimum response of DR to temperature (Chapter 2), (3) the response of DR to the diurnal temperature amplitude *per se* (Chapter 3) or a difference in the impact of T_D and T_N on DR (Chapter 4), and (4) significant changes in the sensitivity of response to temperature with plant age (Chapter 7).

Modelling photothermal responses of flowering

There are various ways to quantify photothermal responses of crop development. The simplest (and historically probably the first) of these is the TU system. To use the TU system for defining crop development, accurate determination of the base temperature, T_b , at or below which DR equals zero, is critical (Shaykewich, 1995; Yang et al., 1995). Because the TU approach lacks a physiological basis and has problems as discussed above, the so-called genetic coefficient T_b defined by the TU method also varied with environments (Chapter 2). Further evaluating various TU methods (e.g. Bonhomme et al., 1994) and improving them, for example, by changing the value of T_b , may not be an area where efforts are likely to be productive (Shaykewich, 1995). For the same reasons, the use of the photothermal unit concept (Nuttonson, 1948) should also be avoided although it accounts for the effect of photoperiod.

The DR-temperature relation follows a nonsymmetrical optimum curve (Chapter 2). This response is the consequence of several biochemical processes including a threshold related to activation of key enzymes, an autocatalytic phase, a saturation phase limited by enzyme capacity and an injury phase (Loomis et al., 1990). Although this optimum curve can be described by an enzyme kinetic equation (Sharpe and DeMichele, 1977; Kiniry and Keener, 1982; Johnson and Thornley, 1985), it can be accurately described by a much simpler equation, the Beta function (Eq. 2.3), commonly used for describing a skewed probability distribution in statistics (Chapter 2). The function describes the temperature response of DR as an interaction between a temperature stimulation $(T - T_b)^\alpha$ and a temperature inhibition $(T_c - T)^\beta$. This function is also appropriate for the photoperiod effect on development to flowering in rice (Chapter 5). It may be applicable to describing the photoperiod effect on all short-day crops, as a nonlinear response to photoperiod in other short-day plants, e.g. soybean [*Glycine max* (L.) Merr.] (Cregan and Hartwig, 1984), has often been observed with an optimum photoperiod, either below or above which flowering can be delayed.

To quantitatively integrate effects of temperature and photoperiod, Robertson (1968) proposed a multiplicative formulation in his pioneering work on modelling wheat development. This formulation has been used by many subsequent photothermal models (Major et al., 1975b;

Angus et al., 1981; Hammer et al., 1989; Horie and Nakagawa, 1990; Gao et al., 1992; Grimm et al., 1993; Hiden and Larsen, 1994). On the contrary, Roberts and Summerfield (1987) considered the effect of photoperiod on DR should be added to, rather than multiplied by, that of temperature. Given the often observed interaction between temperature and photoperiod on DR (e.g. Tang, 1984), it appears that the more appropriate form is the multiplicative one, which allows for situations of no development when either temperature or photoperiod is below its threshold (Angus et al., 1981).

In terms of critical changes in developmental responses to temperature and photoperiod (Chapters 6 and 7), it is necessary to divide preflowering development of rice plants into three phases for modelling purposes. In the model of Robertson (1968) for wheat, the dependence of development upon temperature and photoperiod was allowed to change with physiological age of the plant. He divided the entire growth period into five phases of development and the same equation but with a different coefficient was used for each of the phases. A similar approach for wheat was also used by Angus et al. (1981). In the three-stage Beta (3s-Beta) model presented in Chapter 9 of this thesis, however, an overall equation, Eq. 9.1, was given for rice preflowering development, by using a common developmental rate constant, $1/f_0$ (where f_0 is the minimum number of days for the preflowering period), for all subphases, similar to the approach of Horie and Nakagawa (1990). This approach not only accounts for the changes in photothermal sensitivities during ontogeny but also simulates the entire preflowering phenology with a reduced total number of parameters to be estimated.

Despite that, the 3s-Beta model has a large number of parameters because the Beta function was used for describing the effects of T_D and T_N and photoperiod, and the experimental findings reported in Chapters 4 and 6–8 were fully incorporated. Fortunately, some parameters did not vary much among cultivars and some parameters can be estimated from values of others (Chapter 9). The number of remaining parameters which are most important for characterizing photothermal responses of flowering was five (Chapter 9). This five-parameter model accurately predicted rice flowering dates under field conditions with parameter values estimated from independent controlled-environment experiments (Chapter 9). It also performed better than existing five- or six-parameter models in predicting rice flowering dates over a wide range of field conditions (Chapter 10). Some models include the optimum photoperiod as a model parameter (e.g. Gao et al., 1992). Because the model parameters are often determined by fitting data of field experiments, some nonsense values for the optimum photoperiod can occasionally be obtained, e.g. 18.7 h d^{-1} for rice cv. MRC 606-303 (Table 10.4). A similarly inadequate value was also obtained by Angus et al. (1981) for wheat. This type of dilemma could be avoided by prefixing the values of those parameters with only slight variation among cultivars, especially when model parameters are estimated from field data.

Applications of the model

Hodges (1991a) and Shaykewich (1995) summarized several areas of applying a phenological model. Here, the possible application of the 3s-Beta model in plant breeding and crop improvement will be discussed.

Genotypic characterization

The parameters of the 3s-Beta model for individual genotypes (i.e. f_0 , T_{oD} , T_{oN} , α and δ) are genotypic characteristics. The value of f_0 provides an estimate of the 'inherent earliness or tendency to flower' for a genotype. The entities α and δ are direct estimates of the sensitivity of DR to temperature and photoperiod, respectively. The parameters T_{oD} and T_{oN} are optimum day and night temperature, respectively, which also varied among genotypes (Chapter 9). As such, the 3s-Beta model may provide an informative means of characterizing genotypes in germplasm collections, and can be used by breeders to select more efficiently, for hybridization, parents that have phenological traits appropriate for their target environments.

Comparison of the ranges in the parameter constants among diverse genotypes potentially provides useful information on the relative importance of photoperiod and temperature in conditioning flowering responses. This comparison also provides information on the genotypic variation in sensitivities to temperature and photoperiod, available to the breeder for manipulating time to flowering in rice. Evidence shown in this thesis (Table 9.7) indicates that temperature responses have not been directly subjected to the pressure of selection, when compared to photoperiod responses, since there was a much larger variation in the photoperiod sensitivity parameter δ than in the temperature sensitivity parameter α .

Improving genotypic adaptation

To be adapted to a specific environment, a genotype must flower sufficiently early for grain to be ripened while favourable conditions (e.g. suitable day and night temperature, high solar radiation, and adequate water supply) persist. However, if flowering is too early, plant vegetative growth may be insufficient to sustain large grain yields. First, the likely adaptation of individual rice genotypes to target locations can be obtained by matching seasonal variation at those locations with the photothermal domain around the optimum conditions defined by the model for a given rice genotype. Accurate information to judge if a genotype can be adapted in the target location can be obtained by the model from the daily weather data of an average year at that location. With the three-plane linear model (Roberts and Summerfield, 1987; also see Chapter 10), Roberts et al. (1993) and Lawn et al. (1995) demonstrated that this type of analysis was useful in soybean.

Synchronizing flowering of parent plants in hybrid seed production

The yield of hybrid rice seed production is often low, largely due to poor outcrossing as a result of asynchronous flowering of male and female parents. Temperature and photoperiod are factors determining the time of flowering of parent plants. Other environmental factors, such as wind speed and rainfall at the time of flowering play an important role in determining outcrossing percentage. In order to synchronize flowering of male and female parent plants and to have their flowering period at optimal weather conditions, a program for decision-making about sowing calendar of parents in different environments has been developed (Xu, 1995). However, that program was developed using a less accurate model, m-RCM (see Chapter 10).

The accuracy of the program can be improved using the 3s-Beta model, which would make it possible to more reliably choose planting dates of parent plants.

Designing 'ideotypes' for a target environment

In designing an 'ideotype' of a crop in a target environment, the key aim is to optimize productivity by matching the ontogeny to the weather of the target environment and where unfavourable extremes are unavoidable, to minimize their coincidence with more vulnerable stages (Roberts et al., 1993; Lawn et al., 1995). The 3s-Beta model uses several key parameters to characterize varietal responses to photothermal environments. Information on the genotypic range for these parameters might well be used to construct 'ideotypes' comprising novel parameter recombinations chosen to ensure desired responses in target environments.

A methodological framework for using crop simulation models in the design of plant types has recently been proposed (Aggarwal, 1995). If the 3s-Beta model is incorporated into a rice growth simulation model, it can be used to optimize the phenology parameters, with respect to a specific breeding goal for different target environments. An example for this type of analysis was given in Chapter 11 where the 3s-Beta model was coupled to the rice growth simulation model ORYZA1 (Kropff et al., 1994b) to optimize preflowering phenology for an increased yield potential in Asian irrigated environments.

Global changes will require changes in phenological response of plants (Matthews et al., 1995). The 3s-Beta model can be used to design new plant types which would make the optimal use of evolving changes in specific climates.

Future research needs

Experimental work reported in this thesis for rice has shown several phenomena which lay the groundwork for further physiological studies on regulation of flowering in rice. These include: (1) the difference in the effect of T_D and T_N on development to flowering (Chapter 4), (2) the unusual delay in flowering time for plants in some cultivars transferred before panicle initiation from short- to long-day photoperiod (Chapter 6), and (3) significant changes in the temperature sensitivity with plant age during preflowering ontogeny (Chapter 7). Physiological studies could elucidate the mechanisms behind these observed phenomena.

The modelling work presented in this thesis predicted flowering based on phasic development from sowing to flowering. This gives the estimate of developmental stage at a particular time as a decimal fraction of the entire preflowering period. The other models evaluated in Chapter 10 also belong to this type. The decimal value of the developmental stage provides a temporal framework for modelling partitioning of assimilates to various growing organs (e.g. Goudriaan and van Laar, 1994). Another type of methods for predicting the flowering time in cereal crops is to determine the leaf appearance rate given that the final leaf number is known (Shaykewich, 1995). It is generally recognized that for cereals, temperature is the major factor determining leaf appearance rate and photoperiod is the factor controlling

the leaf number (Warrington and Kanemasu, 1983b,c; Miglietta, 1991a,b). For rice, a method to quantify the temperature effect on leaf appearance has been developed based on controlled-environment data (Chapter 8). The equation for calculating the leaf number as influenced by photoperiod in rice has also been available (Yin and Kropff, 1996). However, leaf appearance depended on leaf temperature more than on air temperature (Ritchie, 1993; Jamieson et al., 1995). Furthermore, this thesis indicated that the final leaf number of rice is also affected by a diurnal pattern of temperature (Chapter 8). Some more work would be needed to develop a framework for predicting flowering times of field-grown rice on the basis of leaf appearance and leaf number. This model would be especially useful to link morphological and phenological events with management actions (Miller et al., 1993).

Summary

Crop growth simulation models are increasingly being used to support field research and extension in agriculture. A simulation model for crop potential production (i.e. with ample water and nutrient supplies and without pest and disease damages) usually includes modelling components dealing with dry matter production, leaf area growth and phenological development. Because phenology provides a temporal framework for modelling partitioning of assimilates to various growing organs, accurate modelling of phenology is essential for the accuracy of predicting crop yield. The objective of this study was to develop a model that can be used to reliably predict rice (*Oryza sativa* L.) crop development under diverse environmental conditions.

Temperature and photoperiod are the major environmental factors determining rice phenology. Of all phenological events, flowering is most important because it is the time period before this stage that varies the most among cultivars and that is most sensitive to changes in photothermal environments. Therefore, this study was confined to establish a quantitative relationship for the effects of temperature and photoperiod on the rate of development to flowering in rice. For this purpose, existing literature data were first collected to quantitatively analyse general responses of crop development rate to temperature and photoperiod. Secondly, controlled-environment experiments were conducted to obtain a better physiological understanding of photothermal responses of flowering. These quantitative analyses and experimental work were directly used in the development of a detailed phenological model.

To quantify the effect of temperature on crop development, the thermal time approach has been widely used. This approach assumes a linear relationship between developmental rate and temperature. However, many studies on crop development have observed a nonlinear response curve of the rate to temperature. The Beta function, well-known as a skewed probability density function in statistics, was therefore introduced to describe this nonlinear relationship based on the framework set by three cardinal temperatures, namely, the base, optimum and ceiling temperature (Chapter 2). The function was evaluated for several published data sets in different crops. It satisfactorily described the asymmetric response of development rate to diurnally constant temperatures, and was superior to two widely used thermal time approaches in predicting rice flowering time. However, an average predictive discrepancy of over 9 d remained for rice flowering at diurnally fluctuating temperatures.

The results of Chapter 2 indicated that diurnal temperature fluctuation might affect crop development. Therefore, the effect of diurnal temperature amplitude on development to flowering in rice was analysed, based on a published data set of Summerfield et al. (1992) (Chapter 3). This data set gives the flowering dates of plants of 16 diverse rice cultivars grown at four diurnally constant temperatures and four diurnally fluctuating temperatures at a constant photoperiod of 11.5 h d^{-1} . Development rates at diurnally constant temperatures were described by the nonlinear equation given in Chapter 2. This equation was then used to predict days to flowering at the diurnally fluctuating temperatures. The often large discrepancies between predicted and observed number of days indicated an effect of diurnal temperature

amplitude *per se* on rice development. This effect was statistically significant in 11 cultivars but not in five others. The direction of the effect differed among cultivars. Further study will be needed to analyse the mechanism of the temperature amplitude effect.

To this end, an experiment was conducted with 24 rice cultivars (Chapter 4). The plants were grown in nine naturally-lighted growth chambers at five diurnally constant temperatures (22, 24, 26, 28 and 32°C) and four diurnally fluctuating temperatures (day/night: 26/22, 30/22, 22/26 and 22/30°C) with a constant photoperiod of 12 h d⁻¹. Again, the relation between rate of development to flowering and diurnally constant temperatures was quantified by the nonlinear equation described in Chapter 2. This nonlinear model could not explain the observed difference in flowering dates between 26/22 and 22/26°C, and between 30/22 and 22/30°C. Different effects of day and night temperature on the rate of development to flowering were detected in all but one cultivar. In most cases, day temperature exerted a greater influence than night temperature, in contrast with previous reports on the relative importance of night temperature based on the assumption of a linear temperature response. In general, the optimum night temperature was about 2–4°C lower than the optimum day temperature. The difference of the impact of day and night temperature may explain the effect of diurnal temperature amplitude as found in Chapter 3. The results in Chapter 4 suggest the necessity to separate effects of day and night temperature, rather than just using the mean daily temperature, in a model for accurate prediction of rice flowering dates.

To quantify the overall effect of photoperiod on development to flowering, three nonlinear models, i.e. the Beta function, quadratic relation between days to flowering and photoperiod, and the quadratic relation between the rate of development to flowering and photoperiod, were compared (Chapter 5). All three models account for the often reported decline of development rate at photoperiods either lower or higher than the optimum. The simplified Beta model, where the base and the ceiling photoperiod was assumed to be 0 and 24 h d⁻¹, respectively, was superior to the two quadratic models.

However, when applied under field conditions, it is necessary to first estimate the period during which the plants are sensitive to photoperiod. The length of the photoperiod-sensitive phase and its variation among genotypes were analysed in Chapter 6. Three greenhouse experiments were conducted in which plants of 20 diverse rice cultivars were serially transferred between long-day (LD, 12.5 or 14.0 h d⁻¹) and short-day (SD, 10.0 h d⁻¹) photoperiods. It was shown that the photoperiod-sensitive phase (PSP) in each cultivar was sandwiched by the pre-sensitive basic vegetative phase (BVP) and the post-PSP phase (PPP). A model was developed to enable the complete data of this transfer experiment to be analysed simultaneously to estimate the lengths in BVP, PSP at both SD and LD, and PPP of each cultivar. The estimated value in all these four parameters differed strongly among cultivars; however, the PPP varied less. The result forms a reasonable database for modelling the photoperiod-sensitive period of rice.

These experiments in which plants were transferred between two photoperiods reported in Chapter 6 demonstrated that the response to photoperiod varied from insensitive to sensitive and then to insensitive again. A similar experiment of transfer but between two temperatures was conducted to examine whether there is any variation in the sensitivity of preflowering development to temperature (Chapter 7). Plants of three contrasting rice cultivars were

transferred between two diurnally constant temperatures, between two night temperatures with the same day value, and between two day temperatures with the same night value. The response of development to both day and night temperature changed with the advance of ontogeny, from slightly sensitive to highly sensitive and then to slightly sensitive again. Thus, the period from sowing to flowering can be divided into three phases. The sensitivity value of the first phase differs significantly from the second phase, but not from the third phase. The stronger sensitivity to temperature during the second phase is presumably due to an additional effect of temperature on the photoinduction process during PSP. Therefore, functions in models for effects of both day and night temperature in PSP have to be different from those in BVP and PPP.

The results in Chapters 6 and 7 indicate that critical moments for changes in the responses to temperature and photoperiod are associated with the leaf number on the main stem. In Chapter 8, the effect of temperature on the main-stem leaf appearance was analysed. Among the 24 cultivars tested in the controlled-environment experiment described in Chapter 4, plants of 12 cultivars were observed periodically to monitor leaf appearance on the main stem. A model for describing the effect of temperature on the leaf appearance was presented. First, the model parameters were derived from the data from five diurnally constant temperatures. These parameters were used to predict leaf appearance at four diurnally fluctuating temperatures. Good agreement between observed and predicted leaf number indicated that there were no specific effects of day and night temperature on leaf appearance. This result contrasts with the earlier observation of separate effects on rate of development to flowering as reported in Chapter 4. The optimum temperature for leaf appearance was substantially higher than for development to flowering.

Based on the results of Chapters 2–8, a detailed photothermal model for predicting rice flowering dates was developed in Chapter 9. As the model uses the Beta function as the basic equation for describing different photothermal responses of three successive phases (namely, BVP, PSP and PPP) during preflowering ontogeny, it was referred to as the three-stage Beta (3s-Beta) model. The model was parameterized for the 17 rice cultivars commonly tested in the two controlled-environment experiments as reported in Chapters 4 and 6, respectively. A step-wise processes of parameterization reduced the number of parameters to be estimated to five, i.e. the minimum days for preflowering period, the optimum day temperature, the optimum night temperature, the coefficient for temperature sensitivity and the coefficient for photoperiod sensitivity. The parameters from the controlled-environment experiments were then used to predict development as observed for 12 rice cultivars in an independent three-location field experiment. The model adequately predicted varietal and locational variation in flowering dates.

The predictive capability of the 3s-Beta model was further evaluated for field conditions by comparing it with three existing photothermal models for rice phenology (Chapter 10). The models used were the three-plane linear model (Summerfield et al., 1992) and two nonlinear models, i.e. the modified rice clock model (Gao et al., 1992) (m-RCM) and the logistic model (Horie and Nakagawa, 1990). Two published data sets, respectively for photoperiodically sensitive and nearly insensitive genotypes, were used to evaluate each model. For both situations, the three nonlinear models performed better than the linear one. Among the

nonlinear models, the 3s-Beta model always explained most of the variation of days to flowering across environments although its advantage over the m-RCM was small.

In Chapter 11, an application of the 3s-Beta model was illustrated, in which the 3s-Beta model was coupled to ORYZA1, an ecophysiological model for irrigated rice production (Kropff et al., 1994b), to determine optimal preflowering phenology for increased yield potential of irrigated rice in three locations in Asia with different climatic environments.

In Chapter 12, the results were discussed in view of the experimental findings of this study, the methodology of phenology modelling, and other possible applications of the 3s-Beta model. On the basis of the results of different studies, questions for future research were identified.

Samenvatting

Gewasgroeimodellen worden in toenemende mate gebruikt ter ondersteuning van gewasonderzoek en landbouwvoorlichting. Een simulatiemodel voor de potentiële gewasproductie (dat wil zeggen bij ruime voorziening met water en nutriënten en het gewas vrij van ziekten en plagen) omvat gewoonlijk modelcomponenten voor de productie van droge stof, voor groei van bladoppervlak en voor fenologische ontwikkeling. Aangezien de fenologie een tijdsbasis verschaft voor het modelleren van de verdeling van assimilaten naar de verschillende groeiende organen, is nauwkeurige modellering van fenologie essentieel voor de nauwkeurigheid van oogstvoorspelling. De doelstelling van dit onderzoek was een model te ontwikkelen dat gebruikt kan worden voor een betrouwbare voorspelling van de gewasontwikkeling van rijst (*Oryza sativa* L.) onder uiteenlopende omgevingsomstandigheden.

Temperatuur en fotoperiode zijn de belangrijkste omgevingsfactoren voor de fenologie. Van alle fenologische tijdstippen is die van bloei het belangrijkste, aangezien het de tijdsperiode vóór dit stadium is dat het meest van alle varieert over verschillende cultivars, en het meest gevoelig is voor veranderingen in de fotothermische omgeving. Daarom heb ik me in deze studie beperkt tot vaststelling van het kwantitatieve effect van temperatuur en fotoperiode op de ontwikkelingssnelheid tot bloei bij rijst. Met dit doel voor ogen werden eerst bestaande literatuurgegevens verzameld om in het algemeen de reacties van gewasontwikkeling op temperatuur en fotoperiode te analyseren. Vervolgens zijn fytotronproeven gedaan om een beter fysiologisch inzicht te krijgen. Deze kwantitatieve analyses en het experimentele werk werden rechtstreeks gebruikt bij de ontwikkeling van een gedetailleerd fenologisch model.

Voor de kwantificering van het effect van temperatuur op gewasontwikkeling wordt de temperatuursom methode veel gebruikt. Bij deze methode wordt een lineair verband aangenomen tussen ontwikkelingssnelheid en temperatuur. Echter, bij veel studies over gewasontwikkeling is een niet-lineaire respons van de ontwikkelingssnelheid op temperatuur waargenomen. Daarom werd de Betafunctie, bekend van scheve waarschijnlijkheidsverdelingen in de statistiek, ingevoerd om dit niet-lineaire verband te beschrijven, gebaseerd op een schema met drie kardinale temperaturen, namelijk de basistemperatuur, de optimumtemperatuur en de maximumtemperatuur (hoofdstuk 2). Deze functie werd getoetst voor verscheidene gepubliceerde datasets voor verschillende gewassen. De asymmetrische respons van ontwikkelingssnelheid op dagtemperatuur werd goed beschreven, en was superieur aan twee veel gebruikte temperatuursom methodes bij het voorspellen van het bloeitijdstip bij rijst. Echter, er bleef gemiddeld een verschil bestaan van negen dagen tussen het voorspelde en waargenomen tijdstip van bloei bij een dagelijks schommelende temperatuur.

De resultaten van hoofdstuk 2 gaven reeds aan dat temperatuurschommeling binnen de dag de fenologische ontwikkeling beïnvloedt. Daarom werd het effect van de dagelijkse temperatuuramplitude op de ontwikkeling tot bloei geanalyseerd met behulp van een gepubliceerde dataset van Summerfield et al. (1992) (hoofdstuk 3). Deze dataset geeft de bloeidata van planten van 16 verschillende rijstrassen, opgekweekt bij vier constante temperaturen en bij vier dagelijks schommelende temperaturen, alle bij een fotoperiode van

11,5 uur per dag. De ontwikkelingssnelheid bij constante temperaturen werd beschreven met de niet-lineaire vergelijking uit hoofdstuk 2. Deze formule werd vervolgens ook gebruikt om het aantal dagen tot bloei te voorspellen bij de dagelijks schommelende temperaturen. De vaak grote verschillen tussen het verwachte en waargenomen aantal dagen gaf aan dat er een effect moet zijn van de temperatuurwisseling zelf op de ontwikkelingssnelheid. Dit effect was statistisch significant bij elf rassen, maar niet bij vijf andere. De richting van het effect verschilde per cultivar. De conclusie was dat verdere studie nodig is om het mechanisme van het effect van de temperatuuramplitude te analyseren.

Daartoe werd een experiment opgezet met 24 rassen (hoofdstuk 4). De planten werden opgekweekt in negen groeikamers (bij daglicht) bij vijf verschillende maar constante temperaturen (22, 24, 26, 28 en 32°C) en bij vijf dagelijks schommelende temperaturen (dag/nacht: 26/22, 30/22, 22/26 en 22/30°C) bij een constante fotoperiode van 12 uur per dag. Ook hier werd de relatie tussen ontwikkelingssnelheid tot bloei en temperatuur gekwantificeerd door middel van de niet-lineaire relatie uit hoofdstuk 2. Dit niet-lineaire model kon de verschillen tussen bloeidata voor 26/22 en 22/26°C en tussen 30/22 en 22/30°C niet verklaren. Bij slechts één cultivar was het effect van dag- en nachttemperatuur op de ontwikkelingssnelheid tot bloei hetzelfde. Meestal had de dagtemperatuur een sterker effect dan de nachttemperatuur, dit in tegenstelling tot vroegere verslagen over het relatieve belang van de nachttemperatuur. Daarin was echter een lineaire temperatuurrespons aangenomen. In het algemeen was de optimale nachttemperatuur zo'n 2 tot 4°C lager dan de optimale dagtemperatuur. Het verschil tussen de invloed van dag- en nachttemperatuur kan het effect van de dagelijkse temperatuurgang, zoals gevonden in hoofdstuk 3, wellicht verklaren. De resultaten van hoofdstuk 4 geven een sterke aanwijzing dat het in een model voor nauwkeurige voorspelling van het bloeitijdstip bij rijst noodzakelijk is om de effecten van dag- en nachttemperatuur te scheiden, in plaats van eenvoudigweg de gemiddelde dagtemperatuur te gebruiken.

Voor de volledige kwantificering van het effect van fotoperiode op ontwikkeling tot bloei zijn drie niet-lineaire modellen vergeleken, namelijk de Betafunctie, een kwadratisch verband tussen duur tot bloei en fotoperiode en de kwadratische relatie tussen ontwikkelingssnelheid tot bloei en fotoperiode (hoofdstuk 5). Alle drie modellen houden rekening met het feit dat de ontwikkelingssnelheid minder wordt naarmate de fotoperiode meer afwijkt van zijn optimale waarde. Het vereenvoudigde Betamodel, met een minimum en een maximum fotoperiode van respectievelijk 0 en 24 uur per dag, deed het beter dan de beide kwadratische modellen.

Echter, voor gebruik onder veldomstandigheden is het noodzakelijk om eerst te weten gedurende welke periode de planten gevoelig zijn voor de fotoperiode. De lengte van de fotoperiodegevoelige fase en de variatie daarvan over genotype wordt geanalyseerd in hoofdstuk 6. Er zijn drie kasproeven gedaan, waarbij planten van 20 verschillende rijstrassen serieel werden omgewisseld tussen een langedagbehandeling (LD, 12,5 of 14 uur per dag) en een kortedagbehandeling (SD, 10 uur per dag). Het bleek dat elke cultivar een fotoperiodegevoelige fase (PSP) heeft die in ligt tussen een nog ongevoelige jeugdfase (BVP) en een postgevoelige fase (PPP). Een model werd ontwikkeld om de volledige dataset van dit experiment tegelijkertijd te analyseren, ten einde de tijdsduur van de BVP, PSP en PPP fases voor elke cultivar te schatten, zowel voor de kortedag- als voor de langedagbehandeling. De

parameterschattingen liepen sterk uiteen voor de verschillende cultivars, waarbij echter de PPP periode het minst varieerde. Er is zo een behoorlijke dataset beschikbaar om de fotoperiodegevoelige periode bij rijst te modelleren.

Deze experimenten, waarbij planten werden overgezet tussen twee fotoperiodes, hebben laten zien dat de respons op daglengte veranderde van ongevoelig naar gevoelig en weer terug naar ongevoelig. Een soortgelijke seriële verwisselproef, maar nu ten aanzien van temperatuur, is gedaan om te zien of er een verandering is in de temperatuurgevoeligheid van de ontwikkelingssnelheid (hoofdstuk 7). Planten van drie sterk verschillende rijstrassen werden serieel omgewisseld tussen twee verschillende maar vaste etmaaltemperaturen, tussen twee verschillende nachttemperaturen bij gelijke dagtemperatuur, en tussen twee verschillende dagtemperaturen bij gelijke nachttemperatuur. De reactie van ontwikkelingssnelheid op zowel dag- als nachttemperatuur veranderde met het ontwikkelingsstadium, van weinig gevoelig tot zeer gevoelig en weer terug naar weinig gevoelig. De periode van zaai tot bloei kan dus in drie fases worden verdeeld. De gevoeligheid in de eerste fase verschilt van die in de tweede fase, maar niet van die in de derde fase. De grotere gevoeligheid voor temperatuur gedurende de tweede fase is kennelijk een bijkomend effect van temperatuur op de fotoperiodegevoeligheid gedurende de PSP fase. Daarom moeten functies in modellen voor het effect van zowel dag- als nachttemperatuur voor de PSP fase verschillen van die voor de BVP en de PPP fases.

De resultaten van hoofdstuk 6 en 7 geven aan dat kritieke tijdstippen van verandering in de temperatuur- en fotoperiodesrespons samenhangen met het bladaantal op de hoofdstengel. In hoofdstuk 8 wordt het effect geanalyseerd van temperatuur op de bladverschijningsnelheid aan de hoofdstengel. Aan planten van twaalf van de 24 cultivars die getest waren in het fytotronexperiment zoals beschreven in hoofdstuk 4, zijn periodieke waarnemingen verricht om de bladverschijning aan de hoofdstengel vast te stellen. Een model voor het effect van temperatuur op de bladverschijning werd gepresenteerd. Eerst zijn modelparameters afgeleid uit de gegevens bij vijf verschillende stabiele etmaaltemperaturen. Deze parameters werden vervolgens gebruikt om de bladverschijning te voorspellen bij planten die opgroeiden bij vier verschillende dagelijkse temperatuurregimes. Waargenomen en voorspeld bladaantal kwamen goed overeen waaruit geconcludeerd kan worden dat er geen specifieke effecten waren van dag- en nachttemperatuur op bladverschijning. Dit resultaat verschilt van de eerdere waarneming van uiteenlopende effecten van dag- en nachttemperatuur op ontwikkeling tot bloei, vermeld in hoofdstuk 4. De optimumtemperatuur voor bladverschijning was aanzienlijk hoger dan die voor ontwikkeling tot bloei.

Op basis van de resultaten van de hoofdstukken 2 tot en met 8 werd een gedetailleerd fotothermisch model ontwikkeld om bloeitijdstip bij rijst te voorspellen (hoofdstuk 9). Aangezien het model de Betafunctie gebruikt als uitgangspunt om de verschillende fotothermische reacties in de drie opeenvolgende fases (en wel BVP, PSP en PPP) van de ontwikkeling tot bloei te beschrijven, werd dit model aangeduid als het 3-stadia Betamodel (3s-Beta). Het model is geparameteriseerd voor de zeventien verschillende rijstrassen die zijn getest in de twee fytotronexperimenten uit hoofdstuk 4 en 6. Door een stapsgewijze parameterisatie kon het aantal te schatten parameters worden teruggebracht tot vijf, namelijk het minimum aantal dagen van de periode tot bloei, de optimum dagtemperatuur, de optimum nachttemperatuur, de coëfficiënt voor de temperatuurgevoeligheid en de coëfficiënt voor de

fotoperiodegevoeligheid. De parameters uit de fytronexperimenten worden vervolgens gebruikt om de ontwikkeling te voorspellen bij twaalf rijstcultivars in een onafhankelijke veldproef op drie lokaties. Het model was in staat een goede voorspelling te geven van de variatie in bloeitijdstip over cultivar en lokatie.

De voorspellende kracht van het 3s-Betamodel voor veldomstandigheden is verder onderzocht door het te vergelijken met drie bestaande fotothermische modellen voor de fenologie van rijst (hoofdstuk 10). De gebruikte modellen waren het lineaire 3-vlaks model van Summerfield et al. (1992) and twee niet-lineaire modellen, namelijk het gemodificeerde rijstklokmodel (Gao et al., 1992) (m-RCM) en het logistische model (Horie en Nakagawa, 1990). Elk model werd geëvalueerd met twee gepubliceerde datasets, één voor daglengtegevoelige en één voor bijna dagneutrale genotypen. Voor elk van beide situaties deden de drie niet-lineaire modellen het beter dan het lineaire model. Van de niet-lineaire modellen bleek het 3s-Beta model steeds de meeste variantie te verklaren in de duur tot bloei voor de verschillende omstandigheden, ook al was het verschil met het m-RCM model gering.

In hoofdstuk 11 wordt een illustratie gegeven van een toepassing van het 3s-Beta model, waarbij het 3s-Betamodel gekoppeld werd aan ORYZA1, een ecofysiologisch model voor geïrrigeerde rijstproductie (Kropff et al., 1994b), om zo de optimale fenologie vòòr de bloei te bepalen voor het opbrengstpotentieel van geïrrigeerde rijst op drie plaatsen in Azië met verschillende klimatologische omstandigheden.

In hoofdstuk 12 worden de proefresultaten van deze studie besproken, naast de methodologie van het modelleren van fenologie, en andere mogelijke toepassingen van het 3s-Beta model. Op grond van de resultaten van de verschillende studies zijn vragen voor verder onderzoek aangegeven.

References

- Abramowitz, M. and Stegun, I.A., 1965. *Handbook of mathematical functions with formulas, graphs, and mathematical tables*. Dover Publications, Inc., New York, USA, 1045pp.
- Acock, M.C., Bunce, J.A. and Acock, B., 1994. Effect of changing daylength on flower initiation and development in two soybean cultivars. *Biotronics* 23: 93-104.
- Aggarwal, P.K., 1995. Plant type designs for increased yield potential of irrigated rice: a simulation analysis. In: Aggarwal, P.K., Matthews, R.B., Kropff, M.J. and van Laar, H.H. (Eds), *SARP Research Proceedings: Applications of systems approaches in plant breeding*. IRRI, Los Baños, Philippines, 59-66.
- Ahn, S.B., 1968. Studies on flowering response of Korean rice varieties and their optimum and critical photoperiods. *Res. Rep. Off. Rural Dev. Korea* 11(1): 59-64.
- Alm, D.M., Pike, D.R., Hesketh, J.D. and Stoller, E.W., 1988. Leaf area development in some crop and weed species. *Biotronics* 17: 29-39.
- Alocilja, E.C. and Ritchie, J.T., 1991. A model for the phenology of rice. In: T. Hodges (Ed.), *Predicting crop phenology*. CRC Press, Boca Raton, Florida, USA, 181-190.
- Angus, J.F. and Zandstra, H.G., 1980. Climatic factors and the modelling of rice growth and yield. In: R.L. Cowell (Ed.), *Agrometeorology of the rice crop*. IRRI, Los Baños, Philippines, 189-200.
- Angus, J.F., Mackenzie, D.H., Morton, R. and Schafer, C.A., 1981. Phasic development in field crops. II. Thermal and photoperiodic responses of spring wheat. *Field Crops Res.* 4: 269-283.
- Arnold, C.Y., 1969. Environmentally induced variations of sweet corn characteristics as they relate to time required for development. *J. Am. Soc. Hortic. Sci.* 94: 115-118.
- Baker, C.K., Gallagher, J.N. and Monteith, J.L., 1980. Daylength change and leaf appearance in winter wheat. *Plant Cell Environ.* 3: 285-287.
- Baker, J.T., Pinter Jr., P.J., Reginato, R.J. and Kanemasu, E.T., 1986. Effects of temperature on leaf appearance in spring and winter wheat cultivars. *Agron. J.* 78: 605-613.
- Baker, J.T., Allen Jr., L.H., Boote, K.J., Jones, P. and Jones, J.W., 1990. Developmental responses of rice to photoperiod and carbon dioxide concentration. *Agric. For. Meteorol.* 50: 201-210.
- Bernier, G., 1988. The control of floral evocation and morphogenesis. *Ann. Review Plant Physiol.* 39: 175-219.
- Best, R., 1959. Photoperiodism in rice. *Field Crop Abs.* 12: 85-93.
- Best, R., 1960. Photoperiodism in plants as studied by means of response curves. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen* 63C: 676-691.
- Best, R., 1961. *Some aspects of photoperiodism in rice (Oryza sativa L.)*. Elsevier Publishing Company, Amsterdam, The Netherlands, 87pp.
- Blaney, L.T. and Hamner, K.C., 1957. Interactions among effects of temperature, photoperiod, and dark period on floral initiation of Biloxi soybean. *Bot. Gaz.* 119: 10-24.

- Bonhomme, R., Derieux, M. and Edmeades, G.O., 1994. Flowering of diverse maize cultivars in relation to temperature and photoperiod in multilocation field trials. *Crop Sci.* 34: 156-164.
- Booij, B., and Meurs, E.J.J., 1993. Flower induction and initiation in celeriac (*Apium graveolens* L. var. *rapaceum* (Mill.) DC.): effects of temperature and plant age. *Sci. Hortic.* 55: 227-238.
- Boone, M.Y.L., Rickman, R.W. and Whisler, F.D., 1990. Leaf appearance rates of two winter wheat cultivars under high carbon dioxide conditions. *Agron. J.* 82: 718-724.
- Bouman, B.A.M. and Jansen, M.J.W., 1993. *RIGAUUS: Random input generator for the analysis of uncertainty in simulation*. Simulation Reports 34, CABO-TT, Wageningen, The Netherlands, 26pp.
- Brown, D.M., 1969. Heat units for corn in southern Ontario. *Ontario Dep. Agric. Food Info. Leaflet* 113/31: 1-4.
- Brown, R.F., 1987. Germination of *Aristida armata* under constant and alternating temperatures and its analysis with the cumulative Weibull distribution as a model. *Aus. J. Bot.* 35: 581-591.
- Camus, G.C. and Went, F.W., 1952. The thermoperiodicity of three varieties of *Nicotiana tabacum*. *Am. J. Bot.* 39: 521-528.
- Cao, W. and Moss, D.N., 1989. Temperature effect on leaf emergence and phyllochron in wheat and barley. *Crop Sci.* 29: 1018-1021.
- Cao, J., Hesketh, J.D., Zur, B. and Reid, J.F., 1988. Leaf area development in maize and soybean plants. *Biotronics* 17: 9-15.
- Centeno, H.G.S., Balbarez, A.D., Fabellar, N.G., Kropff, M.J. and Matthews, R.B., 1995. Rice production in the Philippines under current and future climates. In: R.B. Matthews, M.J. Kropff, D. Bachelet and H.H. van Laar (Eds), *Modeling the impact of climate change on rice production in Asia*. CAB International, Wallingford, UK and IRRI, Los Baños, Philippines, 237-250.
- Chandraratna, M.F., 1948. The effect of daylength on heading time in rice. *Trop. Agric.* 104: 130-140.
- Chandraratna, M.F., 1954. Photoperiod response in rice (*Oryza sativa* L.): I. Effects on inflorescence initiation and emergence. *New Phytol.* 53: 397-405.
- Chandraratna, M.F., 1963. Physiology and genetics of photoperiodism in rice. *Int. Rice Comm. Newsl.*, Special issue: 97-105.
- Chaudhary, T.N. and Ghildyal, B.P., 1969. Germination response of rice seeds to constant and alternating temperatures. *Agron. J.* 61: 328-330.
- Chaudhary, T.N. and Ghildyal, B.P., 1971. Response of rice plants to constant and cyclic submerged soil temperature regimes. *Plant and Soil* 34: 493-496.
- Chang, T.T., Li, C.C. and Vergara, B.S., 1969. Component analysis of duration from seeding to heading in rice by the basic vegetative phase and the photoperiod-sensitive phase. *Euphytica* 18: 79-91.

- Chang, T.T. and Vergara, B.S., 1971. Ecological and genetic aspects of photoperiod-sensitivity and thermo-sensitivity in relation to the regional adaptability of rice varieties. *Int. Rice Comm. Newsl.* 20: 1-10.
- Chen, Z. and Shao, Q., 1981. Effect of temperature in dark period on development of different ecotypes of rice. *Int. Rice Comm. Newsl.* 30: 31-35.
- Cockshull, K.E., and Kofranek, A.M., 1994. High night temperatures delay flowering, produce abnormal flowers and retard stem growth of cut-flower chrysanthemums. *Sci. Hortic.* 56: 217-234.
- Coelho, D.T. and Dale, R.F., 1980. An energy-crop growth variable and temperature function for predicting corn growth and development: Planting to silking. *Agron. J.* 72: 503-510.
- Coligado, M.C. and Brown, D.M., 1975a. Response of corn (*Zea mays* L.) in the pre-tassel initiation period to temperature and photoperiod. *Agric. Meteorol.* 14: 357-367.
- Coligado, M.C. and Brown, D.M., 1975b. A bio-photo-thermal model to predict tassel initiation time in corn (*Zea mays* L.). *Agric. Meteorol.* 15: 11-31.
- Collinson, S.T., Ellis, R.H., Summerfield, R.J. and Roberts, E.H., 1992. Durations of the photoperiod-sensitive and photoperiod-insensitive phases of development to flowering in four cultivars of rice (*Oryza sativa* L.). *Ann. Bot.* 70: 339-346.
- Collinson, S.T., Ellis, R.H., Summerfield, R.J. and Roberts, E.H., 1995. Relative importance of air and flood water temperatures on the development of rice (*Oryza sativa*). *Exp. Agric.*, 31: 151-160.
- Collinson, S.T., Summerfield, R.J., Ellis, R.H. and Roberts, E.H., 1993. Durations of the photoperiod-sensitive and photoperiod-insensitive phases of development to flowering in four cultivars of soyabean [*Glycine max* (L.) Merrill]. *Ann. Bot.* 71: 389-394.
- Coolhaas, C. and Wormer, T.M., 1953. Developmental differences in rice plants in relation to photoperiodism. *Neth. J. Agric. Sci.* 1: 202-216.
- Cregan, P.B. and Hartwig, E.E., 1984. Characterization of flowering response to photoperiod in diverse soybean genotypes. *Crop Sci.* 24: 659-662.
- Cross, H.Z. and Zuber, M.S., 1972. Prediction of flowering dates in maize based on different methods of estimating thermal units. *Agron. J.* 64: 351-355.
- Dingkuhn, M., Penning de Vries, F.W.T. and Miezan, K.M., 1993. Improvement of rice plant type concepts: systems research enables interaction of physiology and breeding. In: F.W.T. Penning de Vries, P.S. Teng and K. Metselaar (Eds), *Systems approaches for agricultural development*. Kluwer Academic Publishers, Dordrecht, The Netherlands, 19-35.
- Dua, A.B., Penning de Vries, F.W.T. and Seshu, D.V., 1990. Simulation to support evaluation of the production potential of rice varieties in tropical climates. *Transactions ASAE* 33: 1185-1194.
- Dwyer, L.M. and Stewart, D.W., 1986. Leaf area development in field-grown maize. *Agron. J.* 78: 334-343.
- Ellis, R.H., Roberts, E.H. and Summerfield, R.J., 1988. Variation in the optimum temperature for rates of seedling emergence and progress towards flowering amongst six genotypes of faba bean (*Vicia faba*). *Ann. Bot.* 62: 119-126.

- Ellis, R.H., Hadley, P., Roberts, E.H. and Summerfield, R.J., 1990. Quantitative relations between temperature and crop development and growth. In: M.T. Jackson, B.V. Ford-Lloyd and M.L. Parry (Eds), *Climatic change and plant genetic resources*. Belhaven Press, London, UK, 85-115.
- Ellis, R.H., Collinson, S.T., Hudson, D., and Patefield, W.M., 1992a. The analysis of reciprocal transfer experiments to estimate the durations of the photoperiod-sensitive and photoperiod-insensitive phases of plant development: An example in soya bean. *Ann. Bot.* 70: 87-92.
- Ellis, R.H., Summerfield, R.J., Edmeades, G.O. and Roberts, E.H., 1992b. Photoperiod, temperature and the interval from sowing to tassel initiation in diverse cultivars of maize. *Crop Sci.* 32: 1225-1232.
- Ellis, R.H., Qi, A., Summerfield, R.J. and Roberts, E.H., 1993. Rates of leaf appearance and panicle development in rice (*Oryza sativa* L.): a comparison at three temperatures. *Agric. For. Meteorol.* 66: 129-138.
- Ellis, R.H., Lawn, R.J., Summerfield, R.J., Qi, A., Roberts, E.H., Chay, P.M., Brouwer, J.B., Rose, J.L. and Yeates, S.J., 1994. Towards the reliable prediction of time to flowering in six annual crops. III. Cowpea (*Vigna unguiculata*). *Exp. Agric.* 30: 17-29.
- Evans, L.T., Visperas, R.M. and Vergara, B.S., 1984. Morphological and physiological changes among rice varieties used in the Philippines over the last seventy years. *Field Crops Res.* 8: 105-124.
- Ferguson, J.H.A., 1958. Empirical estimation of thermoreaction curves for the rate of development. *Euphytica* 7: 140-146.
- Gallagher, J.N., 1979. Field studies of cereal leaf growth. I. Initiation and expansion in relation to temperature and ontogeny. *J. Exp. Bot.* 30: 625-636.
- Gao, L.Z., Jin, Z.Q., Huang, Y. and Zhang, L.Z., 1992. Rice clock model - a computer simulation model of rice development. *Agric. For. Meteorol.* 60: 1-16.
- Garcia-Huidobro, J., Monteith, J.L. and Squire, G.R., 1982a. Time, temperature and germination of pearl millet (*Pennisetum typhoides* S. & H.) I. Constant temperature. *J. Exp. Bot.* 33: 288-296.
- Garcia-Huidobro, J., Monteith, J.L. and Squire, G.R., 1982b. Time, temperature and germination of pearl millet (*Pennisetum typhoides* S. & H.) II. Alternating temperature. *J. Exp. Bot.* 33: 297-302.
- Garner, W.W. and Allard, H.A., 1920. Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. *J. Agric. Res.* 18: 553-606.
- Gilmore, E.C. and Rogers, J.S., 1958. Heat units as a method of measuring maturity in corn. *Agron. J.* 50: 611-615.
- Glasziou, K.T., Bull, T.A., Hatch, M.D. and Whiteman, P.C., 1965. Physiology of sugar cane. VII. Effects of temperature, photoperiod duration, and diurnal and seasonal temperature changes on growth and ripening. *Aus. J. Biol. Sci.* 18: 53-66.
- Goudriaan, J. and van Laar, H.H., 1978. Calculation of daily totals of the gross assimilation of leaf canopies. *Neth. J. Agric. Sci.* 26: 373-382.

- Goudriaan, J. and van Laar, H.H., 1994. *Modelling potential crop growth processes*. Kluwer Academic Publishers, Dordrecht, The Netherlands, 238pp.
- Grant, R.F., 1989. Simulation of maize phenology. *Agron. J.* 81: 451-457.
- Grimm, S.S., Jones, J.W., Boote, K.J. and Hesketh, J.D., 1993. Parameter estimation for predicting flowering dates of soybean cultivars. *Crop Sci.* 33: 137-144.
- Grimm, S.S., Jones, J.W., Boote, K.J. and Herzog, D.C., 1994. Modeling the occurrence of reproductive stages after flowering for four soybean cultivars. *Agron. J.* 86: 31-38.
- Hadley, P., Roberts, E.H., Summerfield, R.J. and Minchin, F.R., 1984. Effects of temperature and photoperiod on flowering in soyabean [*Glycine max* (L.) Merrill]: A quantitative model. *Ann. Bot.* 53: 669-681.
- Haga, T. and Hashimoto, S., 1980. *Regression and principal component analysis*. Jpn. Sci. & Technol. Assoc. Publ., Tokyo, Japan.
- Hammer, G.L., Hill, K. and Schrodter, G.N., 1987. Leaf area production and senescence of diverse grain sorghum hybrids. *Field Crops Res.* 17: 305-317.
- Hammer, G.L., Vanderlip, R.L., Gibson, G., Wade, L.J., Henzell, R.G., Younger, D.R., Warren, J. and Dale, A.B., 1989. Genotype-by-environment interaction in grain sorghum. II. Effects of temperature and photoperiod on ontogeny. *Crop Sci.* 29: 376-384.
- Haniu, Y., Chujo, H. and Yoshida, S., 1983. Effect of air temperature on floral induction by short day in rice plants. *Jpn. J. Crop Sci.* 52: 135-142 (in Japanese with English abstract).
- Hanyu, Y. and Chujo, H., 1987. Temperature and age effect on floral induction of rice. *Jpn. J. Crop Sci.* 56 (Extra issue 1): 206-207 (in Japanese).
- Haun, J.R., 1973. Visual quantification of wheat development. *Agron. J.* 65: 116-119.
- Hiden, C. and Larsen, R.U., 1994. Predicting flower development in greenhouse grown chrysanthemum. *Sci. Hortic.* 58: 123-138.
- Hillman, W.S., 1969. Photoperiodism and vernalization. In: M.B. Wilkins (Ed.), *The physiology of plant growth and development*. McGraw-Hill Publishing Company Ltd., Maidenhead, Berkshire, UK, 559-601.
- Hodges, T., 1991a. Crop growth simulation and the role of phenological model. In: T. Hodges (Ed.), *Predicting crop phenology*. CRC Press, Boca Raton, Florida, USA, 4-6.
- Hodges, T., 1991b. Temperature and water stress effects on phenology. In: T. Hodges (Ed.), *Predicting crop phenology*. CRC Press, Boca Raton, Florida, USA, 7-13.
- Hopkinson, J.M., 1967. Effects of night temperature on the growth of *Nicotiana tabacum*. *Aus. J. Exp. Agri. Animal Husb.* 7: 78-82.
- Horie, T., 1994. Crop ontogeny and development. In: K.J. Boote, J.M. Bennett, T.R. Sinclair and G.M. Paulsen (Eds), *Physiology and determination of crop yield*. Madison, Wisconsin, USA, 153-180.
- Horie, T. and Nakagawa, H., 1990. Modelling and prediction of development process in rice. I. Structure and method of parameter estimation of a model for simulating development process toward heading. *Jpn. J. Crop Sci.* 59: 687-695 (in Japanese with English abstract).
- Horie, T., Nakagawa, H. and Kira, T., 1986. Modelling and prediction of the developmental processes of rice. I. Dynamic model for predicting the flowering date. *Jpn. J. Crop Sci.* 55: 214-215 (in Japanese).

- Horie, T., Nakagawa, H., Ohnishi, M. and Nakno, J., 1995. Rice production in Japan under current and future climates. In: R.B. Matthews, M.J. Kropff, D. Bachelet and H.H. van Laar (Eds), *Modeling the impact of climate change on rice production in Asia*. CAB International, Wallingford, UK and IRRI, Los Baños, Philippines, 143-164.
- IRRI (International Rice Research Institute), 1977. *Annual report for 1976*. Los Baños, Philippines, 113-120.
- IRRI (International Rice Research Institute), 1989. *IRRI towards 2000 and beyond*. IRRI, Los Baños, Philippines, 66pp.
- Jacobs, W.P., 1951. The growth of peanut plants at various diurnal and nocturnal temperatures. *Science* 114: 205-206.
- Jamieson, P.D., Brooking, I.R., Porter, J.R. and Wilson, D.R., 1995. Prediction of leaf appearance in wheat: a question of temperature. *Field Crops Res.* 41: 35-44.
- Janardhan, K.V. and Murty, K.S., 1967. Effect of photoperiod on panicle emergence in rice. *Current Sci.* 36: 382-383.
- Jandel Scientific, 1994. *SigmaStat statistical software for windows, user's manual*. San Rafael, CA.
- Johnson, I.R. and Thornley, J.H.M., 1985. Temperature dependence of plant and crop processes. *Ann. Bot.* 55: 1-24.
- Johnson, N.L. and Leone, F.C., 1964. *Statistics and experimental design in engineering and the physical sciences* (Vol.1). John Wiley & Sons, Inc., New York, USA, 523pp.
- Keating, B.A. and Evenson, J.P., 1979. Effect of soil temperature on sprouting and sprout elongation of stem cuttings of cassava (*Manihot esculenta* Crantz). *Field Crops Res.* 2: 241-251.
- Khan, P.A., 1982. Interaction of date of planting and photoperiod on flowering behaviours in rice. *Acta Bot. Indica* 10: 72-78.
- Kiniry, J.R. and Keener, M.E., 1982. An enzyme kinetic equation to estimate maize development rates. *Agron. J.* 74: 115-119.
- Kiniry, J.R., Ritchie, J.T., Musser, R.L., Flint, E.P. and Iwig, W.C., 1983. The photoperiod sensitive interval in maize. *Agron. J.* 75: 687-690.
- Kiniry, J.R., Rosenthal, W.D., Jackson, B.S. and Hoogenboom, G., 1991. Predicting leaf development of crop plants. In: T. Hodges (Ed.), *Predicting crop phenology*. CRC Press, Boca Raton, Florida, USA, 29-42.
- Kirby, E.J.M., Appleyard, M. and Fellowes, G., 1985. Effect of sowing date and variety on main shoot leaf emergence and number of leaves of barley and wheat. *Agronomie* 5: 117-126.
- Klepper, B., Rickman, R.W. and Peterson, C.M., 1982. Quantitative characterization of vegetative development in small cereal grains. *Agron. J.* 74: 789-792.
- Kooman, P.L. and Haverkort, A.J., 1995. Modelling development and growth of the potato crop influenced by temperature and daylength: LINTUL-POTATO. In: A.J. Haverkort and D.K.L. MacKerron (Eds), *Potato ecology and modelling of crops under conditions limiting growth*. Kluwer Academic Publishers, Dordrecht, The Netherlands, 41-60.

- Kropff, M.J., Peng, S., Setter, T.L., Matthews, R.B. and Cassman, K.G., 1994a. Quantitative understanding of rice yield potential. In: K.G. Cassman (Ed.), *Breaking the Yield Barrier*. Proceedings of a workshop on rice yield potential in favourable environments. IRRI, Los Baños, Philippines, 5-20.
- Kropff, M.J., van Laar, H.H. and Matthews, R.B., 1994b. ORYZA1: An ecophysiological model for irrigated rice production. *SARP Research Proceedings*. IRRI, Los Baños, Philippines, 110pp.
- Lawn, R.J., Summerfield, R.J., Ellis, R.H., Qi, A., Roberts, E.H., Chay, P.M., Brouwer, J.B., Rose, J.L. and Yeates, S.J., 1995. Towards the reliable prediction of time to flowering in six annual crops. VI. Applications in crop improvement. *Exp. Agric.* 31: 89-108.
- Lehenbauer, P.A., 1914. Growth of maize seedlings in relation to temperature. *Physiol. Res.* 1: 247-288.
- Littleton, E.J., Dennett, M.D., Monteith, J.L. and Elston, J., 1979. The growth and development of cowpea (*Vigna unguiculata*) under tropical field conditions. 2. Accumulation and partition of dry weight. *J. Agric. Sci. Camb.* 93: 309-320.
- Loomis, R.S. and Connor, D.J., 1992. *Crop ecology: productivity and management in agricultural systems*. Cambridge University Press, Cambridge, 104-128.
- Loomis, R.S., Luo, Y. and Kooman, P.L., 1990. Integration of activity in the higher plant. In: R. Rabbinge, J. Goudriaan, H. van Keulen, F.W.T. Penning de Vries and H.H. van Laar (Eds), *Theoretical production ecology: reflections and prospects*. Pudoc, Wageningen, The Netherlands, 105-124.
- Major, D.J. and Kiniry, J.R., 1991. Predicting daylength effects on phenological processes. In: T. Hodges (Ed.), *Predicting crop phenology*. CRC Press, Boca Raton, Florida, USA, 16-28.
- Major, D.J., Johnson, D.R. and Luedders, V.D., 1975a. Evaluation of eleven thermal unit methods for predicting soybean development. *Crop Sci.* 15: 172-174.
- Major, D.J., Johnson, D.R., Tanner, J.W. and Anderson, I.C., 1975b. Effects of daylength and temperature on soybean development. *Crop Sci.* 15: 174-179.
- Major, D.J., Rood, S.B. and Miller, F.R., 1990. Temperature and photoperiod effects mediated by the sorghum maturity genes. *Crop Sci.* 30: 305-310.
- Manalo, P.A., Ingram, K.T., Pamplona, R.R. and Egeh, A.O., 1994. Atmospheric CO₂ and temperature effects on development and growth of rice. *Agric. Ecosys. Environ.* 51: 339-347.
- Matsushima, S., Tanaka, T. and Hoshino, T., 1964. Analysis of yield-determining process and its application to yield-prediction and culture improvement of lowland rice. LXXI. Combined effects of air-temperatures and water-temperatures at different stages of growth on the growth and morphological characteristics of rice plants. *Proc. Crop Sci. Soc. Jpn* 33: 135-140.
- Matthews, R.B. and Hunt, L.A., 1994. GUMCAS: a model describing the growth of cassava (*Manihot esculenta* L. Crantz). *Field Crops Res.* 36: 69-84.

- Matthews, R.B., Kropff, M.J., Bachelet, D. and van Laar, H.H., 1995. *The impact of global climate change on rice production in Asia: a simulation study*. CAB International, Wallingford, UK and IRRI, Los Baños, Philippines, 289pp.
- Miglietta, F., 1991a. Simulation of wheat ontogenesis. I. Appearance of main stem leaves in the field. *Climate Res.* 1: 145-150.
- Miglietta, F., 1991b. Simulation of wheat ontogenesis. II. Predicting dates of ear emergence and main stem final leaf number. *Climate Res.* 1: 151-160.
- Miller, B.C., Foin, T.C. and Hill, J.E., 1993. CARICE: A rice model for scheduling and evaluating management actions. *Agron. J.* 85: 938-947.
- Mimoto, H., Yanase, M. and Chujo, H., 1989. Varietal differences of juvenile phase duration and photoperiodic sensitivity in paddy rice. *Jpn. J. Crop Sci.* 58: 628-634 (in Japanese with English abstract).
- Misra, G., 1953. Photoperiodic behavior of medium-early varieties of rice. *Science* 118: 552-553.
- Misra, G., 1955. Photoperiodism in rice. V. Response of two early-winter varieties to short-day photoperiods given after transplantation. *J. Ind. Bot. Soc.* 34: 53-66.
- Misra, G. and Khan, P.A., 1973. Interaction of photoperiodic dosage and plant age on rice. I. Effects of short photoperiod on a late-winter rice. *Bot. Gaz.* 134: 93-99.
- Morgan, P.W., Guy, L.W. and Pao, C-I., 1987. Genetic regulation of development in *sorghum bicolor*. III. Asynchrony of thermoperiods with photoperiods promotes floral initiation. *Plant Physiol.* 83: 448-450.
- Mortensen, L.M., 1994. Effects of day/night temperature variations on growth, morphogenesis and flowering of *Kalanchoe blossfeldiana* v. Poelln. at different CO₂ concentrations, daylengths and photon flux densities. *Sci. Hortic.* 59: 233-241.
- Muchow, R.C. and Carberry, P.S., 1989. Environmental control of phenology and leaf growth in a tropically adapted maize. *Field Crops Res.* 20: 221-236.
- Muchow, R.C. and Carberry, P.S., 1990. Phenology and leaf-area development in a tropical grain sorghum. *Field Crops Res.* 23: 221-237.
- Nagai, I., 1963. Growth and performance of rice varieties under controlled temperature and photoperiod conditions. *Int. Rice Comm. Newsl.*, Special issue: 71-85.
- Nakagawa, H. and Horie, T., 1991. Modeling and prediction of developmental process in rice. 10. Model for predicting development in leaf number. *Jpn. J. Crop Sci.* 60, Extra Issue 2: 272-273 (in Japanese).
- Nakagawa, H. and Horie, T., 1995. Modelling and prediction of developmental process in rice. II. A model for simulating panicle development based on daily photoperiod and temperature. *Jpn. J. Crop Sci.* 64: 33-42 (in Japanese with English abstract).
- Noguchi, Y., 1960. Studies on the control of flower bud formation by temperature and daylength in rice plants. IV. Flower bud formation in response to alternation of temperature conditions. *Jpn. J. Breed.* 10: 101-106.
- Noguchi, Y., Nakajima, T. and Yamaguchi, T., 1967. Studies on the control of flower bud formation by temperature and daylength in rice plants. VII. Elimination of photoinductive effects by keeping under long-day conditions. *Jpn. J. Breed.* 17: 20-24.

- Noguchi, Y., Nakajima, T. and Yamaguchi, T., 1971. Studies on the control of flower bud formation by temperature and daylength in rice plants. XI. Aging effect in relation to photoperiodic induction. *Jpn. J. Breed.* 21: 81-86.
- Nuttonson, M.Y., 1948. Some preliminary observations of phenological data as a tool in the study of photoperiodic and thermal requirements of various plant material. Vernalization and Photoperiodism – A Symposium. *Chronica Botanica*. Waltham Mass, 129-143.
- Oka, H.I., 1959. Variations in temperature responses among cultivated rice varieties. *Phyton* 12: 1-11.
- Oldeman, L.R., Seshu, D.V. and Cady, F.B., 1987. Response of rice to weather variables. In: *Weather and rice*. IRRI, Los Baños, Philippines, 5-39.
- Orchard, T.J., 1975. Calculating constant temperature equivalents. *Agric. Meteorol.* 15: 405-418.
- Owen, P.C., 1971. The effects of temperature on the growth and development of rice. *Field Crop Abs.* 24: 1-7.
- Owen, P.C., 1972. Effects of night temperature on growth and development of IR8 rice. *Exp. Agric.* 8: 213-218.
- Quinby, J.R., Hesketh, J.D. and Voigt, R.L., 1973. Influence of temperature and photoperiod on floral initiation and leaf number in sorghum. *Crop Sci.* 13: 243-246.
- Penning de Vries, F.W.T., 1991. Improving yields: designing and testing VHYVs. In: *Systems simulations at IRRI*. IRRI Research Paper Series nr. 151: 13-19. Los Baños, Philippines.
- Penning de Vries, F.W.T., Jansen, D.M., ten Berge, H.F.M. and Bakema, A., 1989. *Simulation of ecophysiological processes of growth in several annual crops*. Pudoc, Wageningen, The Netherlands and IRRI, Los Baños, Philippines, 271pp.
- Reaumur, R.A.F., 1735. Thermetric observations made at Paris during the year 1735, compared to those made below the equator on the Isle of Mauritius, at Algiers and on a few American islands. *Acad. Sci. Memoirs Acad. Sci. Paris.* 545.
- Ritchie, J.T., 1993. Genetic specific data for crop modeling. In: F.W.T. Penning de Vries, P.S. Teng and K. Metselaar (Eds), *Systems Approaches for Agricultural Development*. Kluwer Academic Publishers, Dordrecht, The Netherlands, 77-93.
- Ritchie, J.T. and NeSmith, D.S., 1991. Temperature and crop development. In: R.J. Hanks and J.T. Ritchie (Eds), *Modeling plant and soil systems*. Madison, Wisconsin, USA, 5-29.
- Roberts, E.H. and Carpenter, A.J., 1962. Flowering response of rice to different photoperiods of uniform daily amounts of light radiation. *Nature* 196: 1077-1078.
- Roberts, E.H. and Carpenter, A.J., 1965. The interaction of photoperiod and temperature on the flowering response of rice. *Ann. Bot.* 29: 359-364.
- Roberts, E.H. and Summerfield, R.J., 1987. Measurement and prediction of flowering in annual crops. In: J.G. Atherton (Ed.), *Manipulation of flowering*. Butterworths, London, UK, 17-50.
- Roberts, E.H., Summerfield, R.J., Muehlbauer, F.J. and Short, R.W., 1986. Flowering in lentil (*Len culinaris* Medic.): The duration of the photoperiodic inductive phases as a function of accumulated daylength above the critical photoperiod. *Ann. Bot.* 58: 235-248.

- Roberts, E.H., Summerfield, R.J., Cooper, J.P. and Ellis, R.H., 1988. Environmental control of flowering in barley (*Hordeum vulgare* L.). I. Photoperiod limits to long-day responses, photoperiod-insensitive phases and effects of low-temperature and short-day vernalization. *Ann. Bot.* 62: 127-144.
- Roberts, E.H., Summerfield, R.J., Ellis, R.H. and Qi, A., 1993. Adaptation of flowering in crops to climate. *Outlook Agric.* 22: 105-110.
- Roberts, R.H., 1943. The role of night temperature in plant performance. *Science* 98: 265.
- Roberts, R.H. and Struckmeyer, B.E., 1938. The effects of temperature and other environmental factors upon the photoperiodic responses of some of the higher plants. *J. Agric. Res.* 56: 633-677.
- Robertson, G.W., 1968. A biometeorological time scale for a cereal crop involving day and night temperature and photoperiod. *Int. J. Biometeorol.* 12: 191-223.
- RPERG (Rice Photothermal Ecology Research Group), 1978. *Photothermal ecology in Chinese rice varieties*. Science Press, Beijing, China, 156pp (in Chinese).
- Sachs, R.M., 1987. Roles of photosynthesis and assimilate partitioning in flower initiation. In: J.G. Atherton (Ed.), *Manipulation of flowering*. Butterworths, London, UK, 317-340.
- SAS (Statistical Analysis Systems Institute, Inc.), 1988. *SAS User's Guide: Statistics*. Version 6.04 edn. SAS, Cary, NC, 1028pp.
- Seddigh, M. and Jolliff, G.D., 1984. Night temperature effects on morphology, phenology, yield and yield components of indeterminate field-grown soybean. *Agron. J.* 76: 824-828.
- Seddigh, M. and Jolliff, G.D., 1994. Light intensity effects on meadowfoam growth and flowering. *Crop Sci.* 34: 497-503.
- Seddigh, M., Jolliff, G.D. and Orf, J.H., 1989. Night temperature effects on soybean phenology. *Crop Sci.* 29: 400-406.
- Sharpe, P.J.H. and DeMichele, D.W., 1977. Reaction kinetics of poikilotherm development. *J. Theor. Biol.* 64: 649-670.
- Shaykewich, C.F., 1995. An appraisal of cereal crop phenology modelling. *Can. J. Plant Sci.* 75: 329-341.
- Shibata, M., Sasaki, K. and Shimazaki, Y., 1973. Effects of air-temperature and water-temperature at each stage of the growth of lowland rice. II. Effect of air-temperature and water-temperature on the heading date. *Proc. Crop Sci. Soc. Jpn.* 42: 267-274.
- Sinclair, T.R., Kitani, S., Hinson, K., Bruniard, J. and Horie, T., 1991. Soybean flowering date: linear and logistic models based on temperature and photoperiod. *Crop Sci.* 31: 786-790.
- Slafer, G.A. and Rawson, H.M., 1995a. Base and optimum temperatures vary with genotype and stage of development in wheat. *Plant Cell Environ.* 18: 671-679.
- Slafer, G.A. and Rawson, H.M., 1995b. Rates and cardinal temperatures for processes of development in wheat: effects of temperature and thermal amplitude. *Aust. J. Plant Physiol.* 22: 913-926.
- Slafer, G.A., Connor, D.J. and Halloran, G.M., 1994. Rate of leaf appearance and final number of leaves in wheat: Effects of duration and rate of change of photoperiod. *Ann. Bot.* 74: 427-436.

- Sorrells, M.E. and Myers, O., 1982. Duration of developmental stages of 10 milo maturity genotypes. *Crop Sci.* 22: 310-314.
- Stewart, G.A. and Langfield, E.C.B., 1971. Temperature response of IR8 rice. *J. Aus. Inst. Agric. Sci.* 37: 252-254.
- Suge, H. and Nishizawa, T., 1982. Sensitivity of rice plant to temperature. *Agric. Hortic.* 57: 493-498 (in Japanese).
- Summerfield, R.J., Roberts, E.H., Ellis, R.H. and Lawn, R.J., 1991. Towards the reliable prediction of time to flowering in six annual crops. I. The development of simple models for fluctuating field environments. *Exp. Agric.* 27: 11-31.
- Summerfield, R.J., Collinson, S.T., Ellis, R.H., Roberts, E.H. and Penning de Vries, F.W.T., 1992. Photothermal responses of flowering in rice (*Oryza sativa*). *Ann. Bot.* 69: 101-112.
- Summerfield, R.J., Lawn, R.J., Qi, A., Ellis, R.H., Roberts, E.H., Chay, P.M., Brouwer, J.B., Rose, J.L., Shanmugasundaram, S., Yeates, S.J. and Sandover, S., 1993. Towards the reliable prediction of time to flowering in six annual crops. II. Soyabean (*Glycine max*). *Exp. Agric.* 29: 253-289.
- Tanaka, I., 1976. Climatic influence on photosynthesis and respiration of rice. In: *Climate and rice*. IRRI, Los Baños, Philippines, 223-245.
- Tang, S. and Li, W., 1964. Studies on photoperiod-sensitive phase in rice: I. The beginning and end of rice photoperiod-sensitive phase. *Acta Bot. Sinica* 12: 166-189 (in Chinese with Russian abstract).
- Tang, S., Ni, P., Tung, P. and Shen, J., 1978. Flowering response of rice cultivars to different photoperiods and temperatures in phytotron. *Acta Phytophysiol. Sinica* 4: 153-168 (in Chinese with English abstract).
- Tang, S.X., 1984. *Flowering response of rice varieties to photoperiod and temperature*. M.S. thesis, University of Philippines at Los Baños, Philippines.
- Thiagarajah, M.R. and Hunt, L.A., 1982. Effects of temperature on leaf growth in corn (*Zea mays*). *Can. J. Bot.* 60: 1647-1652.
- Thompson, K., Grime, J.P. and Mason, G., 1977. Seed germination in response to diurnal fluctuations of temperature. *Nature* 267: 147-149.
- Tollenaar, M., 1990. The influence of development patterns on grain yield of maize. In: S.K. Sinha, P.V. Sane, S.C. Bhargava and P.K. Aggarwal (Eds), *Proc. Intl. Cong. Plant Physiol.*, New Delhi, India, 181-193.
- Tollenaar, M. and Hunter, R.B., 1983. A photoperiod and temperature sensitive period for leaf number of maize. *Crop Sci.* 23: 457-460.
- Tollenaar, M., Daynard, T.B. and Hunter, R.B., 1979. Effect of temperature on rate of leaf appearance and flowering date in maize. *Crop Sci.* 19: 363-366.
- Tyldesley, J.B., 1978. A method of evaluating the effect of temperature on an organism when the response is nonlinear. *Agric. Meteorol.* 19: 137-153.
- Vergara, B.S. and Lilis, R., 1967. Response to photoperiod of reported long-day and intermediate varieties of rice. *Nature* 216: 168.
- Vergara, B.S. and Lilis, R., 1968. Studies on the responses of the rice plant to photoperiod. IV. Effect of temperature during photoinduction. *Philipp. Agric.* 51: 66-71.

- Vergara, B.S. and Chang, T.T., 1985. *The flowering response of the rice plant to photoperiod*. 4th edn, IRRI, Los Baños, Philippines, 61pp.
- Vergara, B.S., Puranabhang, S. and Lilis, R., 1965. Factors determining the growth duration of rice varieties. *Phyton* 22: 177-185.
- Wallace, D.H. and Enriquez, G.A., 1980. Daylength and temperature effects on days to flowering of early and late maturing beans (*Phaseolus vulgaris* L.). *J. Am. Soc. Hortic. Sci.* 105: 583-591.
- Wang, J.Y., 1960. A critique of the heat unit approach to plant response studies. *Ecology* 41: 785-790.
- Warrington, I.J. and Kanemasu, E.T., 1983a. Corn growth response to temperature and photoperiod. I. Seedling emergence, tassel initiation, and anthesis. *Agron. J.* 75: 749-754.
- Warrington, I.J. and Kanemasu, E.T., 1983b. Corn growth response to temperature and photoperiod. II. Leaf-initiation and leaf-appearance rates. *Agron. J.* 75: 755-761.
- Warrington, I.J. and Kanemasu, E.T., 1983c. Corn growth response to temperature and photoperiod. III. Leaf number. *Agron. J.* 75: 762-766.
- Watkinson, A.R., Lawn, R.J., Ellis, R.H., Qi, A. and Summerfield, R.J., 1994. *RoDMod: A computer program for characterising genotypic variation in flowering responses to photoperiod and temperature*. CSIRO Division of Tropical Crops & Pastures, Australia, 49pp.
- Watts, W.R., 1971. Role of temperature in the regulation of leaf extension in *Zea mays*. *Nature* 229: 46-47.
- Watts, W.R., 1972. Leaf extension in *Zea mays*. II. Leaf extension in response to independent variation of the temperature of the apical meristem, of the air around the leaves, and of the root-zone. *J. Exp. Bot.* 23: 713-721.
- Weir, A.H., Bragg, P.L., Porter, J.R. and Rayner, J.H., 1984. A winter wheat crop simulation model without water or nutrient limitations. *J. Agric. Sci. Camb.* 102: 371-382.
- Went, F.W., 1944a. Plant growth under controlled conditions. II. Thermoperiodicity in growth and fruiting of the tomato. *Am. J. Bot.* 31: 135-149.
- Went, F.W., 1944b. Plant growth under controlled conditions. III. Correlation between various physiological processes and growth in the tomato plant. *Am. J. Bot.* 31: 537-596.
- Went, F.W., 1945. Plant growth under controlled conditions. V. The relation between age, light, variety and thermoperiodicity of tomatoes. *Am. J. Bot.* 32: 469-479.
- Went, F.W., 1950. The response of plants to climate. *Science* 112: 489-494.
- Went, F.W., 1956. The role of environment in plant growth. *Am. Scientist* 44: 378-399.
- White, P.J., Cooper, H.D., Earnshaw, M.J. and Clarkson, D.T., 1990. Effects of low temperature on the development and morphology of rye (*Secale cereale*) and wheat (*Triticum aestivum*). *Ann. Bot.* 66: 559-566.
- Wilkerson, G.G., Jones, J.W., Boote, K.J. and Buol, G.S., 1989. Photoperiodically sensitive interval in time to flower of soybean. *Crop Sci.* 29: 721-726.
- Williams, G.D.V., 1974. Deriving a biophotothermal time scale for barley. *Int. J. Biometeorol.* 18: 57-69.

- Wood, I.M.W., 1968. The effect of temperature at early flowering on the growth and development of peanuts (*Arachis hypogaea*). *Aus. J. Agric. Res.* 19: 241-251.
- Xu, Q., 1995. A model for simulation of hybrid rice seed production. In: Aggarwal, P.K., Matthews, R.B., Kropff, M.J. and van Laar, H.H. (Eds), *SARP Research Proceedings: Applications of systems approaches in plant breeding*. IRRI, Los Baños, Philippines, 97-106.
- Yang, S., Logan, J. and Coffey, D.L., 1995. Mathematical formulae for calculating the base temperature for growing degree days. *Agric. For. Meteorol.* 74: 61-74.
- Yin, X. and Kropff, M.J., 1996. Use of the Beta function to quantify nonlinear effects of photoperiod on flowering and leaf number in rice. *Agric. For. Meteorol.*: in press.
- Yoshida, S., 1981. *Fundamentals of rice crop science*. IRRI, Los Baños, Philippines, 269pp.
- Zhang, W., 1985. A preliminary study on the response to different combinations of 16-hour long day and 10-hour short day in rice. *Acta Agron. Sinica* 11: 207-214 (in Chinese with English abstract).
- Zhu, D. and Min, S., 1995. Rice production in China under current and future climates. In: R.B. Matthews, M.J. Kropff, D. Bachelet and H.H. van Laar (Eds), *Modeling the impact of climate change on rice production in Asia*. CAB International, Wallingford, UK and IRRI, Los Baños, Philippines, 217-235.
- Zur, B., Reid, J.F. and Hesketh, J.D., 1989. The dynamics of a maize canopy development 1. Leaf ontogeny. *Biotronics* 18: 55-66.

Curriculum vitae

Xinyou Yin was born on 27 August 1963 in Hukou county, Jiangxi Province, the People's Republic of China. He obtained his BSc diploma in Agronomy at Jiangxi Agricultural University in 1984; and in the same year, he started his MSc studies at the same university with specialization in Agricultural Systems Analysis. After obtaining his Master degree in 1987, he worked at that university as a teaching associate and assistant professor, respectively. He joined the Crop Modelling Group at the International Rice Research Institute (IRRI) in Philippines as a research scholar from September 1991 to March 1992 and from December 1992 to December 1994. Since January 1995, he has been at DLO-Research Institute for Agrobiology and Soil Fertility and Department of Theoretical Production Ecology of Wageningen Agricultural University, The Netherlands, as a visiting research fellow. The research conducted both at IRRI and in Wageningen resulted in this thesis.