Yielding ability of potato crops as influenced by temperature and daylength

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ABSTRACT

Today, potato is grown commercially in almost all climates of the world, except in tropical lowlands. The highest tuber yields are obtained in areas with temperate climates in North-western Europe and the North-West of the United States. In tropical and subtropical climates tuber yields are lower and less stable. To determine if this is due to the lack of adaptation of potato to the conditions prevailing in the tropics, the effect of climate on potential yield was examined. The study presented in this thesis explored the potential and attainable yields of potato. It aimed to determine and quantify the effect of climate on potential tuber dry matter production and to assess the genetic variation in the sensitivity for this climate. Potential dry matter production in potato is governed by the genetic characteristics of a cultivar and the climatic factors, radiation, temperature and daylength. Hitherto, research into the effect of temperature and daylength on the potato crop has been done in two types of studies. The tuber yield was either correlated directly with these climate factors, or separate processes in the plant were related to temperature and daylength.

The general introduction demonstrates that to understand the behaviour of the crop and the variation in tuber yields, the crop and its relations with the environment must be studied as an integrated system. The subsequent chapters describe a study in which experimental data are incorporated into a simulation model. In the experiments the relations of the individual crop characteristics to temperature and daylength were obtained and the model was used to calculate the consequences of variation in daylength and temperature for tuber dry matter production. First a series of models constructed in the Netherlands was tested with weather data from a series of years in Scotland (Chapter 2). There appeared to be no difference in the ability of the models to simulate tuber dry matter production after reparameterization. It was easier to parameterize for simple models than complex models because the latter included more crop processes.

To improve the model's general applicability, the key processes determining tuber dry matter production had to be identified. In all previous models, dry matter allocation was driven by a temperature-dependent development. This was an oversimplification for the purposes of this study and therefore a new relation describing dry matter allocation had to be developed. It was hypothesized that dry matter allocation is governed by a dominant tuber sink and that this dry matter allocation determines the earliness and thus the yielding ability of a potato crop. This hypothesis was confirmed in a series of experiments on early

and late cultivars in the Netherlands (Chapter 3). The difference in dry matter allocation between cultivars however, was only partly explained by the differences in dry matter production. Leaf longevity also played a role in explaining earliness and yielding ability.

To assess the effect of temperature, daylength and radiation on yield formation in potato, field trials were carried out in Rwanda (2 altitudes), Tunisia (Spring, Autumn and Winter) and the Netherlands. To study the interaction between environment and genotype, eight cultivars differing in earliness when grown in the Netherlands were planted. Total dry matter production and tuber yields were analysed in terms of light interception and light use efficiency. Variation in total and tuber dry matter production was mainly explained by the differences in light interception. Light interception was divided into average light intensity, length of the growing period and in maximum proportion of light intercepted. The light use efficiency was found to be inversely related to an increased radiation intensity. Variation in length of the growing season was the most important factor explaining the differences in total light interception. Shorter days at emergence and higher temperatures throughout the season resulted in a shorter growth cycle. The extent of the response differed between cultivars and was mainly explained in terms of duration of ground cover.

To quantify the relation between tuber yield and the climatic factors; (temperature, daylength and radiation) the growth cycle of the potato crop was divided into three phases (Chapters 5). By relating the length of each phase to temperature, daylength and radiation, the influence of these factors on crop growth and development processes was determined. The variation in the length of all three phases contributed to the variation in the duration of the growth cycle and thus to the variation in tuber yield. Both higher temperatures and shorter daylengths hastened the development in the phase between emergence and tuber initiation, and the degree of the change depended on the cultivar. In the second phase, from start of tuber growth to end of leaf growth, temperature and daylength had similar effects but these were less than in phase 1. The last phase, from end of leaf growth to end of crop growth was shortened by high temperatures and high radiation. The shift in sink priorities between tubers and leaves in phase 1 affected phases 2 and 3, so part of the variation in these phases could be explained from the variation in phase 1. The information obtained in the experiments was combined with data from literature to obtain a complete overview of temperature and daylength reactions to the various growth and developmental processes. These relations were introduced in the simulation model developed in chapter 3. The model (LINTUL-POTATO described in Chapter 6) was used to explore different climate and temperature situations for a standard potato cultivar.

STELLINGEN

1: Knolinitiatie krijgt in verhouding tot begingroei van de aardappelknol te veel aandacht.
(dit proefschrift)

2: Eerder afsterven van een gewas uit fysiologisch oud pootgoed wordt vooral bewerkstelligd door een langzamere begingroei van het loof.
(Perennec, P. & P. Madec, 1980. Age physiologique du plant de pomme de terre. Incidence sur la germination et repercussions sur le comportement de plantes. *Potato Research* 23: 183-199.)
(dit proefschrift)

3: De vroegheidsschaal voor aardappelen in de beschrijvende rassenlijst wordt alleen in een Nederlands groeiseizoen bepaald, is relatief en daardoor onbruikbaar voor andere regios.
(dit proefschrift)

4: Het opbrengend vermogen van een cultivar hangt af van de mate waarin het groeiseizoen en de groeicyclus op elkaar zijn afgestemd.
(dit proefschrift)

5: De optimum temperatuur voor aardappelproduktie is locatie en rasafhankelijk.
(dit proefschrift)

6: In aardappel is eindopbrengst een slecht selectiecriterium.

7: Op korte termijn is met gewasfysiologie veel meer te bereiken dan met veredeling.

8: Warm weer is geen lekker weer.

9: Een werknemer moet niet geselecteerd worden op wat hij gedaan heeft maar op wat hij kan doen.

10: Het hedendaagse akkerbouwbeleid van de EU heeft voor de akkerbouwer grotere negatieve consequenties dan een natuurramp.

11: Het ontstaan van de landbouwuniversteit was te danken aan een landbouwcrisis, zo het nu laat aanzien zal het verdwijnen van de landbouwuniversiteit ook hieraan te danken zijn.

12: Een organisatie in het eind van zijn levenscyclus kenmerkt zich ondermeer door een groeiende overhead .

13: "Landbouw" in de naam en het hebben van "groene richtingen" rechtvaardigen het bestaan van een universiteit in Wageningen.

14: Het aantal mensen dat op vakantie gaat naar plaatsen die niet toeristisch zijn maakt het onwaarschijnlijk dat deze plaatsen bestaan.

15: Het standpunt van de dierenbescherming over paardesport leidt tot het verdwijnen van het paard uit Nederland.

Stellingen behorende bij het proefschrift:

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Integrating the effects of temperature and daylength of the separate processes resulted in simulated tuber dry matter production levels that were agreeing with those reported in the literature. It is shown that as daylength increases, potato can tolerate a broader range of temperatures. In chapter 7 the model is verified against the set of experiments used to build the model and validated against independent data. The model explains the differences in observed tuber dry matter production between locations by incorporating the effects of temperature and daylength. The differences between cultivars were smaller than the differences between location and therefore explained less well. The values observed in experiments carried out in climates that were most suitable for potato production were simulated better than those from experiments carried out in less suitable conditions.

Finally the yielding ability of a potato crop for a range of climates between the equator and 60°N was evaluated. The potential total dry matter production, potential tuber dry matter production and the ideotype were determined for each climate. The potential total dry matter was dependent on the length of the growing season. Tuber dry matter production was dependent on the length of the growing season and the length of the growth cycle: tuber yields were restricted when the growing season was too short to fit the growth cycle or when tuber initiation was too early and the conditions favoured tuber growth at the expense of leaf growth. In chapter 8 the advantages of the approach and the application of systems analysis in breeding and introduction of new cultivars are discussed. Combining observations at the process level with the explanatory capacity of the simulation model reveals how tuber dry matter production is affected by the climatic factors temperature, daylength and radiation. Temperature and daylength together affected the development before tuber initiation; further development was affected by temperature only. Radiation was found to influence growth rate only. Integrating the effects revealed that especially the period between emergence and tuber initiation were determinative for further growth and development of the crop. This insight can be used to design ideotypes in breeding, to improve the efficiency of selection procedures and to analyse yield gaps in potato production.

Aan mijn ouders
Voor Miriam

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CONTENTS

CHAPTER 1

GENERAL INTRODUCTION

Potato was first cultivated in the Andean highlands in South America. At the end of the 16th century potatoes were brought to Spain and in the following centuries the crop spread throughout Europe (Hawkes, 1992). It disseminated to most other parts of the world from Europe, rather than directly from South America. Missionaries and colonists introduced the crop into many tropical and subtropical areas from the 17th century onwards, where it was mostly eaten by Europeans. However, food shortages often encouraged local people to include potatoes in their diet (Horton, 1987).

Since the early sixties of the present century the area cultivated with potato in tropical and subtropical zones has increased by 70% and yields have doubled. This, in combination with a declining production in temperate areas has meant that the relative importance of tropical and subtropical areas in world potato production is increasing. Potato consumption per capita is still low in developing countries and is expected to increase only if the costs of production are reduced (Horton, 1992), which means reducing the unit costs of production (Midmore, 1992). However, the climate in these developing countries may be unfavourable for attaining high yields and therefore a constraint for the reduction of the production costs (Haverkort 1990).

POTATO AND CLIMATE

Today potato is grown commercially in almost all climates of the world, with the exception of the tropical lowlands (Midmore and Rhoades, 1988). The highest tuber yields are obtained in areas with temperate climates in North-western Europe and the North-West of the United States (van der Zaag 1984; Stol et al. 1991). In tropical and subtropical climates tuber yields are lower and less stable. There are various reasons for these lower yields. In these climates the pressure of pests and diseases is high, crops suffer from nutrient deficiencies and adequate irrigation is often not possible because of the absence of good quality irrigation water. But even under crop growth conditions not limited by water or nutrients and in the absence of pests, diseases and weeds (henceforth referred to as non-limiting conditions), the yields are still low in tropical climates. Under such conditions he potential dry matter production is completely governed by the genetic characteristics of a cultivar and the climatic factors, radiation, temperature and daylength (De Wit, 1968). The highest tuber yields have been reported at temperatures between 18 and 21°C (Bodlaender, 1960; Borah and Milthorpe, 1962). At temperatures above and below this, tuber dry matter production is lower. Short daylengths normally shorten the growth cycle of a potato crop and therefore they reduce final tuber yields (Haverkort,

1990) This sensitivity to daylength varies among cultivars (Menzel, 1985). Increased radiation normally leads to increased yields, but high radiation levels are often associated with high temperatures and high vapour pressure deficits, leading to low yields. The interaction between potato and climate is complex and not constant over the growing season. Therefore to understand how climatic factors influence potential tuber yield, the crop-environment system must be analysed in a way that integrates the effect of the three crucial climatic factors on the processes that determine this yield.

DRY MATTER PRODUCTION IN POTATO

Potato can produce large amounts of dry matter because it partitions only a small part of its production to parts that are not harvested. The harvest index of about 0.8 in potato is high compared to cereals (about 0.5) and oil seed crops (about 0.35). However, this same feature may lead to lower yields since it may reduce the amount of foliage formed and hence the amount of radiation intercepted. And since total crop dry matter production results from the amount of intercepted radiation and its efficiency for dry matter production (Monteith, 1969), tuber yields will be lower as well.

To obtain a maximum tuber yield, there must be optimal dry matter allocation to the leaves (assuring light interception and thus total dry matter production) and to the tubers (assuring that when the growth cycle is completed, most of the dry matter produced ends up in the tubers). However, the problem is that there many are interacting processes in the plant, each influenced by a series of climatic variables. To assess the key processes and how these processes are affected by the climate, the crop has to be analysed step by step at an increasing level of detail. By relating climatic variables to processes at each level of detail the variation in tuber dry matter production between cultivars and sites can be explained.

The explanation of the variation caused by the climate provides information about the yield potential at a certain location. Comparing this information with the actual yields obtained by farmers and in experiments should reveal if the lower yields in tropical and subtropical areas are the result of climatic constraints or of sub-optimal management, and from this it should be possible to identify ways of improving yields.

APPROACH AND OBJECTIVES OF THIS STUDY

The study presented in this thesis explores the potential yields of potato. It aimed to determine and quantify the effect of climate on potential tuber dry matter production and to assess the genetic variation in potatoes sensitivity to climate. To do this, field experiments were combined with simulation models. The experiments were intended to reveal which processes are influenced by temperature and daylength, when these processes are influenced, to what extent, and the variation between cultivars. Subsequently the influence of the environmental factors that determine potential dry matter production were quantified for a series of cultivars. A simulation model was used to integrate the effects of the individual crop processes and to explain the variation in tuber dry matter production. Finally the model was used to evaluate potato performance in different climates, with the aim of revealing influence the consequences of temperature, radiation and daylength on production potential under the various climatic conditions.

OUTLINE OF THESIS

In chapter 2 the state of the art in modelling potato growth and development is reviewed and evaluated. Potato models originating from the Netherlands and differing in complexity are parameterized for a Scottish location and tested against independent data from a different year at the same location. The adjustments during the parameterization and the ability of the different levels of complexity to predict dry matter production are discussed.

In chapter 3 the difference in earliness between cultivars in a series of experiments in the Netherlands is analysed with a simulation approach. The model hypothesises that tubers are a dominant sink once they start to grow. The various processes affecting earliness are evaluated.

To assess the effect of temperature, daylength and radiation on yield formation in potato, field trials were carried out at six different sites, chosen so that their climatic conditions covered a broad range of the temperatures and daylengths in which potatoes are grown (from the tropical to temperate climates). To study the interaction between environment and genotype, eight cultivars differing in earliness when grown in the Netherlands were included. First, total dry matter production and tuber yields are analysed in terms of light interception and light use efficiency. Subsequently these yield components are divided into the sub-components leaf area duration, light intensity and harvest index to assess the sources of variation between location and cultivars. These components and sub components are then related to temperature and daylength (chapter 4).

The growth cycle of the potato crop is discussed in chapter 5, using a classification into three phases. These phases coincide with the crucial plant processes leaf growth, competition between leaf growth and tuber growth and leaf senescence. By relating the length of each phase to climatic factors the implications of these factors for crop growth and development are determined.

Data obtained in the experiments were combined with data from the literature to obtain a complete overview of temperature and daylength reactions to the various growth and developmental processes. These relations are introduced in the simulation model described chapter 3 and the interaction between daylength and temperature is evaluated for a standard cultivar and the consequences on total tuber yield are studied (chapter 6).

In chapter 7 the model is verified against the set of experiments used to build it and is validated against independent data. The constraints for tuber production in a range of climate types are explored. Genetic characteristics and environmental conditions that may determine tuber dry matter production are indicated and ideotypes with respect to temperature and daylength are given.

The thesis concludes with a general discussion (chapter 8) in which the methodology of the study, scientific achievements and its implications for potato breeding and production are evaluated.

CHAPTER 2

A COHERENT SET OF MODELS TO SIMULATE POTATO GROWTH

P.L. Kooman and C.J.T. Spitters

ABSTRACT

Simulation models are useful tools for predicting tuber yields and gaining insight into crop growth processes. Which model to choose depends on the aim of a study. This chapter presents a coherent set of models for simulating potato crop growth at different levels of complexity. The models are first parameterized for Scottish conditions and subsequently tested against independent data from the same site. The level of complexity does not influence the accuracy of predictions of tuber yields. The complex models however, take more effort to parameterize than the simple models. The dry matter allocation needed to be adjusted because the dry matter partitioning relations originally used appeared to be cultivar- and site specific. The accuracy of the prediction of tuber yields was also affected by the data obtained from the calibration experiments.

INTRODUCTION

Crop growth models are used to predict yields or to gain insight into the processes determining crop growth. When a model is used as a research tool, the aspect of acquiring insight is the main objective of modelling and the accuracy of prediction is of secondary importance. Since the aims in modelling studies may vary considerably, models describing the different processes at different levels of detail have to be available.

If a single universal model describing all aspects of potato crop growth and able to answer any question were ever to be built, it would necessarily be very detailed. It would also have the disadvantage of an unpredictable error behaviour. It would have too much detail for any single research question, would require substantial effort from the user and it would be virtually impossible to parameterize for a particular condition. A more promising approach would be to develop a coherent set of models simulating the different processes of plant production at different levels of detail.

Objectives

The objective of the study described here was to compare and analyse the behaviour and performance of models, defined at different levels of detail. This paper describes how simulation at different levels of complexity can be approached, using two examples. The first example pertains to potential production of a potato crop under the prevailing weather conditions; i.e. its dry matter accumulation under ample supply of water and nutrients assuming absence of pests, diseases and weeds. Three major processes are then distinguished: (i) light interception, (ii) light utilization for dry matter production and (iii) dry matter distribution. A wide range of model descriptions of the various processes is available for each of these main processes. A limited, but coherent set is presented here.

More comprehensive models, that simulate the growth of single organs (Ng & Loomis, 1984) are available. However, they are to detailed to be used to illustrate the approach involving a coherent set of models. Below the performance of the combination of the coherent set of models is shown not only for the simulation of potential production, but also incorporating a stress factor that limits production. In this case the stress is drought.

Further description of the model

The models presented here have partly been described as separate models in more detail by Spitters (1987), Spitters et al. (1989), and Spitters (1990). They were originally applied under Dutch conditions but are not limited to those conditions. For a flexible use these models were placed in a FORTRAN shell that facilitated management and integration of data (van Kraalingen & Penning de Vries, 1990).

DESCRIPTION OF THE MODELS

General structure

In the situation of potential production the daily dry matter increment is mainly dependent on: (i) incoming PAR (photosynthetically active radiation, between 400 and 700 nm), (ii) the fraction of PAR intercepted by the foliage and (iii) the efficiency of its use for dry matter production. The phenological development of the plant is mainly driven by accumulated temperature. The development stage of the plant determines the distribution pattern of dry matter and consequently, through leaf growth, the pattern of interception of PAR. A sub optimal supply of water and nutrients and the presence of pests and diseases are referred to as 'stress'. In the presence of such stress factors, the growth rate is reduced and the dry matter distribution pattern alters in relation to the severity of the stress. The incidence and severity of stress is simulated in separate sub models. In this study an example of drought stress is given. The list of variables of the coherent set of models is given in Table 2.1.

Governing equations

Development of leaf area and interception of light

Interception of light by the foliage may be described at three levels of complexity (Table 2.2). The simplest approach is to describe the fractional interception of PAR as a function of the phenological development stage. This development stage is determined by the effective temperature sum starting at plant emergence. The increase of intercepted PAR is described by a logistic function, with thermal time as the driving variable (Eq. 2.1). The decrease towards maturity is assumed to be linearly inversely proportional to the increase in temperature sum (Eq. 2.2). The actual interception of PAR is the minimum of both functions:

$$F_{LINT} = \frac{N F_0 e^{R_0 t}}{N F_0 e^{R_0 t} + 1 - N F_0} \qquad \text{Equation 2.1}$$

$$F_{LINT} = 0.5 - \frac{t - t_{50}}{d} \qquad \text{Equation 2.2}$$

In both models of the second and third levels of complexity (Table 2.2) interception of PAR is calculated from the increase in leaf area resulting from leaf growth and from its decrease caused by ageing (Spitters et al., 1989). The increase in LAI is then the product of leaf dry matter increment and the specific leaf area of the new leaves:

$$\delta LAI = SLA * \delta W_{lv} \qquad \text{Equation 2.3}$$

Equation 2.3 assumes that the increase of leaf area is determined by the availability of assimilates and consequently by the level of daily solar radiation. Temperature rather than radiation determines development during the juvenile stage of leaf growth. The LAI can then can be described by an exponential function of the temperature sum from plant emergence:

$$LAI_t = NL_0 e^{R_l t} \qquad t \leq 450 \qquad LAI \leq 0.75 \qquad \text{Equation 2.4}$$

The decrease in leaf area in this most detailed approach is obtained by multiplying the amount of green leaf area by the relative death rate. Beyond a certain stage of development both the formation of new leaves and the death of old leaves contribute to the change in LAI. The decrease in LAI due to dying of leaves in the most detailed model is obtained by the product of green area and the relative death rate (RDR). Two factors determining RDR are development stage (RDR_{dv} see Table 2.3) and self shading (RDR_{sh}). The development is quantified by thermal time, and leaves die after 810 degree days. (Table 2.3). The leaves die due to self shading when the critical LAI (LAI_c) is exceeded (Table 2.3). In the model is the actual death rate the maximum of RDR_{dv} and RDR_{sh} (Eq. 2.5).

$$RDR = \max[RDR_{dv}, RDR_{sh}] \qquad \text{Equation 2.5}$$

The RDR is then multiplied with the green LAI to obtain the change in LAI.

$$\delta LAI = LAI * RDR \qquad \text{Equation 2.6}$$

The combination of Equations 3, 4 and 6 results in the actual increase of LAI. The fractional PAR interception of the canopy is then calculated from the simulated LAI (Eq. 2.7) as is done at level 2 (Table 2.2):

$$F_{LINT} = 1 - e^{-k\,LAI} \qquad \text{Equation 2.7}$$

Absorption of PAR may also be calculated from a light profile in the canopy which relates exponentially to LAI and is an extension of the approach used at the second level. In this third, most detailed photosynthesis model, a distinction is also made between profiles for the direct beam from the sun and for diffuse radiation (e.g. de Wit, 1965; Spitters, 1986; Goudriaan, this volume).

The use of intercepted PAR for dry matter production

Two methods were used to calculate light utilization: a summary approach in which daily growth is calculated from the amount of intercepted PAR, and a more detailed approach in which the increase in dry matter is calculated from simulated rates of photosynthesis and respiration.

Table 2.1. List of variables.

Variable	Meaning	Units
A_m	the light saturated photosynthesis rate	(g CO_2 m^{-2} leaf h^{-1})
A	CO_2 assimilation rate	(g m^{-2} d^{-1})
C_f	conversion efficiency	(g g^{-1} CH_20)
D	daylength	(h d^{-1})
d	duration of leaf senescence	(°C d)
E	soil evaporation	(mm d^{-1})
E_r	evaporation from short grass in the Netherlands	(mm d^{-1})
F_0	initial light interception capacity per plant	(MJ m^{-2})
F_{sm2}	factor reducing evapotranspiration because of drying out of top 2 cm	
F(t)	temperature function related to respiration	
F_{cr}	crop factor with a value of 1.1	
F_{LINT}	light interception	(MJ m^{-2})
HI_m	asymptotic maximum harvest index	
HI_t	harvest index at temperature sum t	
I	= (1-g)Id/D the incident flux averaged over the daylight period and corrected for canopy reflection	(J m^{-2} h^{-1})
I_n	infiltration from precipitation and irrigation	(mm d^{-1})
i	time of onset of tuber filling	(°C d)
k	extinction coefficient for PAR (Monsi & Saeki, 1953)	
L_0	initial leaf area at emergence	(m^2 $plant^{-1}$)
LAI	leaf area index	(m^2 m^{-2})
LAI_c	critical leaf area index for self shading	(m^2 m^{-2})
LAI(t)	LAI on time t (in day degrees after emergence)	(m^2 m^{-2})
ln	natural logarithm	
LUE	average light use efficiency	(g MJ^{-1})
LUE_{tb}	light use efficiency for tuber growth	(g MJ^{-1})
N	plant density	(m^{-2})
P	percolation to layers below the root zone	(mm d^{-1})
PAR	incoming photosynthetically active radiation	(MJ m^{-2} d^{-1})
Pi	partitioning factor for organ i	
P_{lv}	partitioning factor for leaves	
P_{rt}	partitioning factor for roots	

continue Table 2.1.

Variable	Meaning	Units
P_{st}	partitioning factor for stems	
P_{tb}	partitioning factor for tubers	
R_0	initial relative growth rate	(°$C^{-1}d^{-1}$)
RDR	relative death rate	(°$C^{1}d^{-1}$)
RDR_{dv}	death rate due to development	(°$C^{-1}d^{-1}$)
RDR_{sh}	death rate due to self shading	(°$C^{-1}d^{-1}$)
R_l	relative leaf area growth rate	(°$C^{-1}d^{-1}$)
R_m	maintenance respiration	(g CH_20 m^{-2} d^{-1})
s	initial slope of harvest index curve	
SLA	specific leaf area of a new leaf	(m^2 g^{-1})
SM	actual moisture content of the soil	(cm^3 cm^{-3})
SM_a	moisture content at air dryness	(cm^3 cm^{-3})
SM_f	moisture content at field capacity	(cm^3 cm^{-3})
t	thermal time	(°C d)
T	crop transpiration	(mm d^{-1})
t_{50}	thermal time when 50 % of the leaves has died	(°Cd)
W	total dry matter	(g m^{-2})
W_i	organ dry matter	(g m^{-2})
W_{lv}	dry matter of total leaves	(g m^{-2})
W_{lvg}	dry matter of green leaves	(g m^{-2})
W_{rt}	dry matter of roots	(g m^{-2})
W_{tb}	dry matter of tubers	(g m^{-2})
δLAI	daily increment of LAI	(m^2 m^{-2} d^{-1})
δS	daily rate of change in soil moisture	(mm d^{-1})
δW	daily growth of dry matter	(g m^{-2} d^{-1})
δW_i	dry matter growth of organ i	(g m^{-2} d^{-1})
δW_{lv}	dry matter growth of leaves	(g m^{-2} d^{-1})
δW_{tb}	dry matter growth of tubers	(g m^{-2} d^{-1})
ε	initial efficiency for single leaf	(g CO_2 J^{-1})

In the summary approach, total dry matter growth is calculated directly from the product of the incoming PAR, the fraction intercepted by the canopy and an average light use efficiency for dry matter production (LUE):

$$\delta W = LUE * F_{LINT} * PAR \qquad \text{Equation 2.8}$$

LUE changes with the development stage of the crop. Equation 2.8 is based on the generally observed proportionality between the dry matter growth rate and the amount of intercepted radiation (e.g.: Monteith, 1969; Gosse et al., 1986) and is used at levels 2 and 3 (Table 2.2).

The increase of tuber dry weight may also be calculated directly from the amount of intercepted radiation (Haverkort & Harris, 1987). In this short cut an apparent light use efficiency is used for tuber dry matter production:

$$\delta W_{tb} = LUE_{tb} * F_{LINT} * PAR \qquad \text{Equation 2.9}$$

In the second approach, as used at level 3 (Table 2.2), dry matter increase is calculated from photosynthesis and respiration. Rates of leaf photosynthesis are calculated at different depths in the canopy from the photosynthesis response curve (Spitters et al., 1989) and the amount of radiation intercepted by the separate leaf layers. The intensity of exposure to radiation varies within a canopy and changes during the day. The daily crop photosynthesis is calculated by integration of the photosynthesis of the individual leaves over the leaf layers and over the day.

Some of the assimilates produced are then used for maintenance of the standing biomass and the remainder are converted into structural dry matter. The daily dry matter growth rate is given by:

$$\delta W = C_f\left(\frac{30}{44}A - R_M\right) \qquad \text{Equation 2.10}$$

30/44 represents the ratio of the molecular weights of CH_2O and CO_2 (McCree, 1970). The conversion efficiency C_f accounts for growth respiration. It is not a constant but a weighted mean, determined by relative allocations of incremental dry matter to component plant parts: 1.46 units substrate are required per unit increment in dry leaf dry matter; likewise the units of substrate required by each unit of stem, root and tuber material are 1.51, 1.44 and 1.28 units of substrate (Spitters et al., 1989).

Table 2.2. Characterization of the models differing in complexity and detail (levels).

	level 1	level 2	level 3
Light interception	Fractional (Eq. 2.1)	Based on LAI (Eq. 2.7)	Based on LAI and light profile (Eq. 2.7)
Light utilization	Efficiency (Eq. 2.8)	Efficiency (Eq. 2.8)	Photosynthesis and Respiration (Eq. 2.9)
Dry matter distribution	Harvest Index (Eq. 2.12)	Distribution pattern (Eq. 2.13)	Distribution pattern (Eq. 2.13)

A numerical approach is used in the more comprehensive model for the calculation of daily crop photosynthesis. It consists of an asymptotic exponential function for the momentary photosynthesis light response of the individual leaves. The photosynthesis light response of individual leaves is characterized by its initial slope, the initial light use efficiency (ε) and its asymptote: the light saturated rate of photosynthesis (A_m) (Spitters et al., 1989). Light exposure within a canopy is further refined by differentiating between a shaded area that receives diffuse radiation only and a sunlit area that receives both direct and diffuse radiation. The calculated instantaneous assimilation rates are integrated over the daily sine wave of incident solar radiation in which the direct and diffuse radiation fluxes are separated. This is discussed in detail by Spitters (1986), Spitters et al. (1986), Goudriaan (1986), and Spitters et al. (1989) who gave a listing of the program.

A distinction is made between respiration needed to maintain the existing biostructures (maintenance respiration, R_m in Eq. 2.10) and respiration related to the conversion of assimilates into structural plant material (growth respiration $1\text{-}C_f$, Equation 2.10) (McCree, 1970). The maintenance respiration is calculated by multiplying the weights of the organs by a specific factor, and allowing for a temperature effect:

$$R_M = \left(0.03W_{lv} + 0.015W_{st} + 0.015W_{RT} + 0.0045W_{tb}\right)F(t)\frac{W_{lvg}}{W_{lv}} \qquad \text{Equation 2.11}$$

The maintenance respiration of the different organs per unit dry matter is given for a base temperature of 25 °C. At other temperatures respiration rates are calculated using a Q_{10} of 2, accounted for in the temperature function F(t). The respiration coefficients are derived from Penning de Vries & van Laar (1982), but those for the tubers from Spitters et al.

(1989). The ratio between green leaf weight and total leaf dry weight is included to take into account the decrease of the metabolic activity of plant tissue in older plants (Spitters et al., 1989).

Dry matter distribution

In the simplest model for dry matter distribution, tuber yields equal the product of total biomass produced and the harvest index (HI). The harvest index is a function of the temperature sum from emergence (Spitters, 1987):

$$HI_t = HI_m \left(1 - e^{\frac{-s(t-i)}{HI_m}}\right) \qquad \text{Equation 2.12}$$

At levels 2 and 3 (Table 2.2), the daily increase of dry matter δW is partitioned to leaves, stems, tubers and roots according to partitioning coefficients which are functions of the development stage of the crop. The growth rate of a particular organ is the result of the product of the total dry matter increase and the partitioning coefficient of this organ.

$$\delta W_i = P_i * \delta W \qquad \text{Equation 2.13}$$

In most experiments the root weight is not determined, so in our coherent set (levels 2 and 3 (Table 2.2)) the dry matter is initially distributed between the roots and the other plant parts. Dry matter not partitioned to the roots goes to the tubers, stems and leaves (Fig. 2.1, Table 2.3).

The effects of drought stress are accounted for in the model by relating the light interception, the crop dry matter growth rate and the dry matter distribution to the availability of water. The changes in the amount of available soil moisture in the rooted zone are therefore calculated in a sub model.

Crop growth under water limitation

Water balance Many models are published which calculate the amount of available soil water for the plant over time (Hanks et al., 1982). A simple method is used to model a freely draining soil profile, based on the continuity equations. More detailed approaches are easily included in the modular structure of the model.

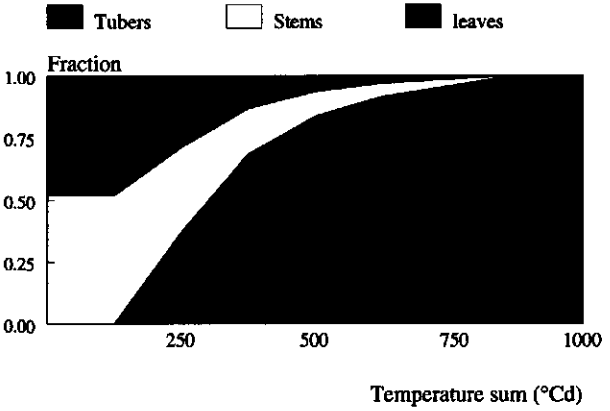

Figure 2.1. Schematic representation of the proportional distribution of the daily growth between tubers, stems and leaves in relation to the thermal time as used at levels 2 and 3.

In this version of the model the maximum rooting zone is regarded as one soil layer, a reservoir from which the crop receives water needed for growth and transpiration. The rate of change of soil moisture in this single layer is calculated as:

$$\delta S = I_n - P - E - T \qquad \text{Equation 2.14}$$

The percolation rate is calculated from the amount of water in excess of field capacity. The evaporation rate is calculated as:

$$E = E_r \left(e^{-0.7 \mathrm{kLAI}} \right) f_{sm2} \qquad \text{Equation 2.15}$$

where

E_r = reference evapotranspiration according to Makkink (1957)

The factor f_{sm2} accounts for the drying out of the top 2 cm of the soil, and is taken from van Keulen & Seligman (1987). To determine the value of f_{sm2}, the soil moisture within the upper 2 cm is calculated separately (Spitters, 1989). Crop transpiration rate is dependent on the LAI, using a reference transpiration when LAI equals 4. The rate diminishes concomitantly with the availability of water.

$$T = E_r F_{cr} \frac{1 - e^{-0.7 \mathrm{k\,LAI}}}{1 - e^{-0.7 \mathrm{k} 4}} \frac{SM - SM_a}{SM_f - SM_a} \qquad \text{Equation 2.16}$$

Crop - water relations Drought stress influences crop growth through a reduced transpiration rate resulting from closure of the stomata and consequently reduced photosynthesis rates. The ratio between actual and potential rate of transpiration (T/T_0) is assumed to decrease linearly with soil moisture suction from unity at the critical suction to zero at the wilting point. (Feddes et al., 1978; Spitters et al., 1989). The ratio T/T_0 is applied to the growth rate. It influences the specific leaf area and accelerates leaf senescence.

In the water-restricted versions of the model the dry matter distribution pattern alters and increased drought stress favours the subterranean parts (Brouwer, 1983) as described by van Keulen et al. (1982).

Input and output of the model

The input parameters are summarized in Table 2.4. The potential version of the model required daily radiation and daily minimum and maximum temperature. The models with inbuilt water relations also require the early morning vapour pressure and the daily rainfall. The time step used during the simulation is 1 day and the integration method is Euler. The output of level 1 is the total dry matter and tuber dry matter. On the other levels each state or rate variable used in the model is also output.

PARAMETERIZATION AND CALIBRATION

Original parameterization and calibration

The set of models was initially parameterized for potato cv. Bintje under Dutch conditions. The data in Table 2.3 which did not change, were estimated under these conditions. Only the parameters dependent on variety and site had to be re-estimated for the present study.

The experimental data for the re-estimation were provided by the Scottish Crop Research Institute. The different treatments in the experiments are summarized in Table 2.5. The 240 kg N treatment in 1984 and the WET treatment in 1986 were used to parameterize the potential versions of the set. The WET and DRY treatments in 1986 were used to parameterize the versions in which water relations were included. The 240 N treatments in 1985 and the WET and DRY treatment in 1987 were to be predicted.

Table 2.3 Parameter estimates for the set of crop growth models.

1	2	3	4	5	6	7	8	9
process	eq. nr	parameter	description parameter	value of parameter	method of estimation	data source	method of re-estimation	new value
Light interception	2	d (°C d)	Duration of leaf senescence	600	Regression	Spitters (1987)	Regression	325
	1	F_0 (MJ d^{-1})	Initial light interception capacity per plant	0.014	Regression	Spitters (1990)	Regression	0.0139
	7	k	Extinction coefficient	1	Regression	Spitters (1987)	No change	
	1.4	N (m^{-2})	Plant number	-	-	-	Data	4
Leaf growth and senescence	2	t_{50} (°C d)	Time when light interception is reduced to 50 %	1308 for Bintje	Regression	Spitters (1987)	Regression	1505
	4	L_0 (m^2 $plant^{-1}$)	Initial leaf area at emergence	155		Spitters et al. (1989)	No change	

Continue Table 2.3

1	2	3	4	5	6	7	8	9
process	eq. nr.	parameter	description parameter	value of parameter	method of estimation	data source	method of re-estimation	new value
Leaf growth and senescence	1	R_o $(^{\circ}C^{-1}d^{-1})$	Initial relative leaf growth rate	0.014	Regression	Spitters (1990)	Regression	0.0119
	5	RDR_{dv} $(^{\circ}C^{-1}d^{-1})$	Relative death rate due to development	0.000968 * t * exp (0.002867* (t-725)) for Bintje		Spitters et al. (1989)	Calibration	0.000512 * t * exp (0.002867 *(t-810.))
	5	RDR_{sh} $(^{\circ}C^{-1}d^{-1})$	Relative death rate due to self shading	0.03 * (LAI-5.2) /5.2))	Calibration	Spitters unpublished	No change	
	4	R_1 $(C^{-1}d^{-1})$	Relative leaf area growth rate	0.012		Spitters et al. (1989)	No change	
	3	SLA $(m^2\ g^{-1})$	Specific leaf area of new leaf	0.3		Spitters et al. (1989)	calibration	(200+0.33) * 10^{-5}

Continue Table 2.3

1	2	3	4	5	6	7	8	9
process	eq. nr.	parameter	description parameter	value of parameter	method of estimation	data source	method of re-estimation	new value
Dry matter assimilation		A_m (g CO_2 m^{-2} leaf h^{-1})	Light saturated photosynthesis rate	30		Spitters et al. (1989)	Optimisation	30.85
Dry matter assimilation	8	LUE (g MJ^{-1})	Average light use efficiency	2.35 $t \le i$ 2.35 + 0.00092(t-i) $i < t < i+380$ 2.70 $t \le i+380$	Regression	Spitters (1990)	Regression	$2.94*(P_{tb}+ 0.7*(1-P_{tb}))$
		ε (g CO_2 J^{-1})	Initial efficiency for single leaf	0.45		Spitters et al. (1989)	Optimisation	0.4
Dry matter distribution	12	HI_m	Asymptotic maximum of the harvest index	0.84	Regression	Spitters (1987)	Regression	0.791
	12	i (°C d)	Time of onset of tuber filling	398 for Bintje	Estimated in field	Spitters (1987)	Estimated from curve	166.5

Continue Table 2.3

1	2	3	4	5	6	7	8	9
process	eq. nr.	parameter	description parameter	value of parameter	method of estimation	data source	method of re-estimation	new value
	13	P_{lv}	Partitioning factor for the leaves	0.75-(t-i/430) ($0<P_{lv}<0.75$)		Spitters et al. (1989)	Regression	0.48*exp (-0.0050 (t-158))
	13	P_{rt}	Partitioning factor for the roots	1-0.8 + 0.2 * P_{tb} ($0<P_{rt}<1$)			No change	
Dry matter distribution	13	P_{st}	Partitioning factor for the stems	1 - P_{lv} - P_{tb}		Spitters et al. (1989)	No change	1 - P_{lv} - P_{tb}
	13	P_{tb}	Partitioning factor for the tubers	(t-i/430) ($0<P_{tb}<1$)		Spitters et al. (1989)	Regression	1-exp (-0.00453 (t-158))
	12	s (°$C^{-1}d^{-1}$)	Initial slope of the harvest index curve	0.00322 for Bintje	Regression	Spitters (1987)	Regression	0.00272

Continue Table 2.3

1	2	3	4	5	6	7	8	9
process	eq'n no.	parameter	description parameter	value of parameter	method of estimation	data source	method of re-estimation	new value
Water relations	16	F_{cr}	Crop specific factor for transpiration	1.1			No change	
	-	SW_{fc} ($kg\ H_20\ m^{-3}$)	Volumetric soil moisture content at field capacity				Estimated	300
	-	SW_{wp} ($kg\ H_20\ m^{-3}$)	Volumetric soil moisture content at wilting point				Estimated	60
	-	SW_{ad} ($kg\ H_20\ m^{-3}$)	Volumetric soil moisture content at air dryness				Estimated	20

Parameterization and calibration for Scottish conditions

Firstly the light interception parameters were modified, since they are variety-specific (Spitters, 1987). Compared to Bintje, Maris Piper had a slower development of foliage in the beginning of the season. This resulted in a lower value of F_0 and R_0 at level 1 (Eq. 2.1) and a lower value of R_1 at levels 2 and 3 (Eq. 2.4). Maris Piper had a later senescence compared to Bintje, so the t_{50} at level 1 (Eq. 2.2) was raised and the RDR_{dv} function at levels 2 and 3 (Eq. 2.5) had to start later and had to progress more slowly. When the allocation of assimilates to the different plant organs was studied it was found that Maris Piper initiated the tubers later than Bintje. In the beginning of the season Maris Piper allocates a smaller fraction of dry matter to the tubers. Therefore the slope and the maximum of the harvest index function at level 1 (Eq. 2.12) were assigned a lower value. New relations had to be derived from the data for the partitioning to the tubers and leaves at levels 2 and 3. In the original model the partitioning of assimilates to tubers was a linear function of the temperature sum (Spitters et al., 1989). This linear function is here replaced by a negative exponential function (Table 2.3) which results in the partitioning pattern given in Figure 2.1 and in a better prediction of yield.

Table 2.4. Model characteristics.

Language	: Fortran		
Shell	: Fortran Simulation Environment.	(FSE)	
Time step	: 1 Day		
Time scale	: 1 season		
Input	: Daily values of weather data		
	Radiation		(kJ m^{-2}d^{-1})
	Temperature	MIN	(°C)
		MAX	(°C)
	Vapour pressure	(KPa)	
	Wind speed		(m s^{-1})
	Rain		(mm d^{-1})

Table 2.5. Experiments and treatments used in this study.

Year	Treatment	Parameterization/Prediction
1984	0 kg N	Not used
	240 kg N	Parameterization
1985	0 kg N	Not used
	240 kg N	Prediction
1986	WET	Parameterization
	DRY	Parameterization
1987	WET	Prediction
	DRY	Prediction

Finally, the conversion from light to assimilates was evaluated. At levels 1 and 2 the LUE was made sink-dependent (Table 2.3) because the presence of tubers increases the photosynthesis rate (Ng & Loomis, 1984). The parameters for this relation could be derived from regression analysis. At level 3 the A_m and δ could not be derived directly and were obtained with an optimization method based on the algorithm of Price (1978) as applied in crop growth models by Klepper & Rouse (1991). In the optimization procedure, the values to be estimated were chosen at random within a given range. After running the model with those values the result was compared with the experimental data. The run with the set of parameter values most closely approximating the experimental data was assumed to be the optimum set and used in the present study. The agreement between the models and the experimental data is illustrated in Figures 2a-c.

The difference between the simulations at the different levels is very small. The simulation of total dry matter and tuber dry matter in the year 1984 N4 treatment (Fig. 2a) matched the observed data well, especially early in the season. At levels 2 and 3 the model tended to underestimate the production towards the end of the season. At these levels (2 and 3), the leaf dry matter production was predicted well but the stem dry matter was slightly underestimated (data not shown). The model with different levels of complexity gave comparable result for the WET treatment in 1986, but the estimates were not as good as those for 1984. Figure 2.2b (1986 WET treatment) shows that at the beginning of the season the tuber dry matter was underestimated whereas the total dry matter was estimated rather well. The simulated tuber dry matter yields at the end of the season compared well

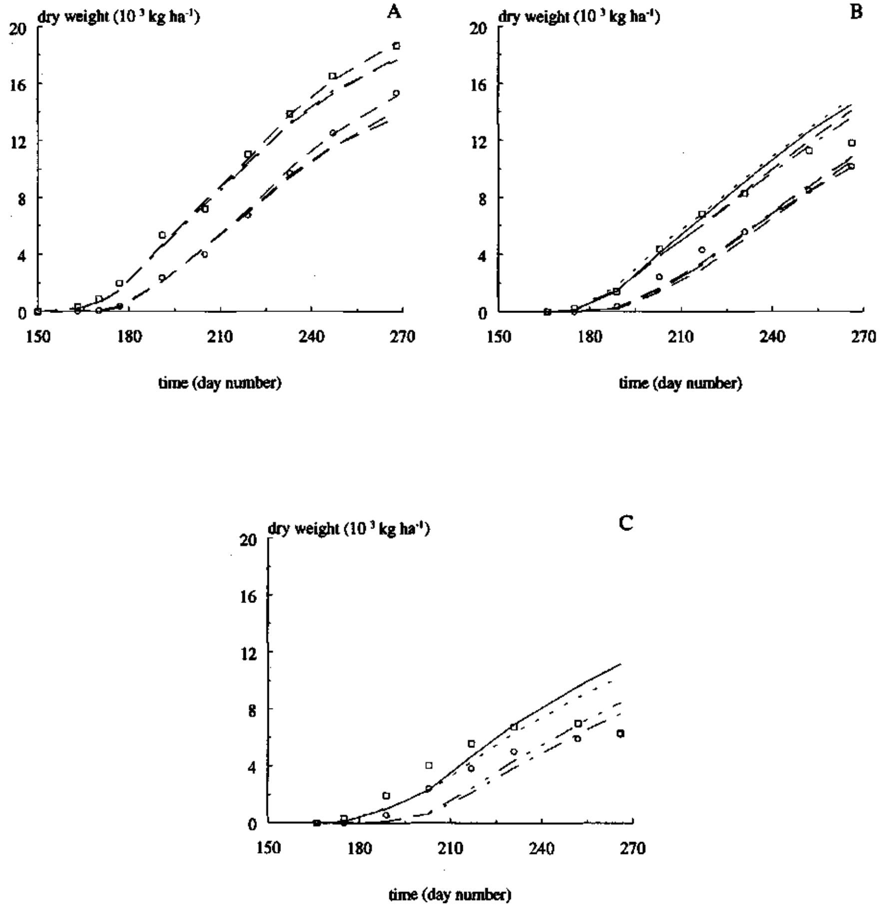

Figure 2.2. Simulated and observed production of total dry matter ((□) observed, (—·—) L 1, (·····) L 2, (— —) L 3) and tuber dry matter ((O) observed, (— —) L 1, (—— ——) L 2, (————) L 3, (—— -) L 2W, (— - -) L 3W) for the 1984 N4 (A), 1986 WET (B) and 1986 DRY (C) treatments. (Calibration)

with the measured data, but total dry matter simulations dropped below the measured values. More assimilates were partitioned to the foliage than was measured, resulting in an overestimation of dry matter in leaves and stem (data not shown). The LAI is directly related to the leaf dry matter, so overestimating the leaf dry matter led to an overestimation of the light interception and subsequently to an overestimation of the total biomass at the end of the season, especially at levels 2 and 3.

In the DRY treatment of 1986 (Fig. 2.2c) the effect of drought on total dry matter and tuber dry matter was underestimated at the beginning of the season. The simulated effect of drought reduced the growth at the beginning of the season too much, while at the end of the season the rate of senescence slowed down, which resulted in rather high light interception and too high a simulated total and tuber dry matter production.

RESULTS

This section illustrates the performance of the models when challenged to predict dry matter yields. Total crop dry weight as well as tuber dry weight simulations were in general reasonably close to the measured data for 1985 N4 treatment (Fig. 2.3a for levels 1, 2 and 3). The simulated deviations for level 1 were mainly due to a underestimated value for the light use efficiency. Figure 2.4a shows a large underestimation of simulated stem dry weight but a good agreement between simulated and measured leaf dry weight for levels 2 and 3.

The model predictions for the 1987 WET treatment remained below the measured data for both the total dry weight and tuber dry weight, as shown in Figure 2.3b (levels 1, 2 and 3 without water balance and levels 2 and 3 with a water balance) as explained in Section 2.2.4., with model level 1 showing the largest deviations from the observations. Figure 2.4b shows a large simulated deviation (underestimation) of stem dry weight and an equally large simulated deviation (overestimation) of leaf dry weight for the 1987 WET treatment. In general, levels 2 and 3 with water, balance performed the same as levels 2 and 3 without water, balance.

The 1987 DRY treatment was simulated with levels 2 and 3 with the water, balance. There was good agreement between simulated and observed values for both the total dry weight and tuber dry weight (Fig. 2.3c), whereas leaf and stem dry weights were largely overestimated by the model (Fig. 2.4c).

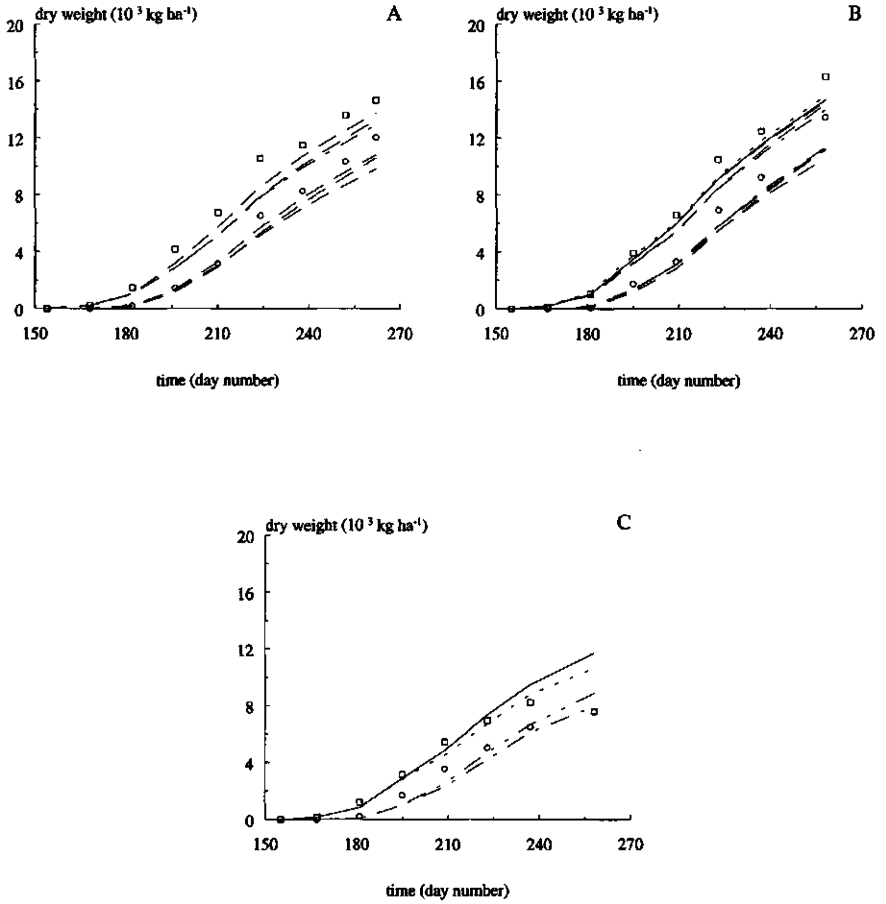

Figure 2.3. Simulated and observed production of total dry matter ((□) observed, (—·—) L 1, (·····) L 2, (– —) L 3, (······) L 2W, (——) L 3W) and tuber dry matter ((O) observed, (— —) L 1, (—— ——) L 2, (——— ———) L 3, (—— -) L 2W, (— - -) L 3W) for 1985 N4 (A), 1987 WET (B) and 1987 DRY (C) treatments

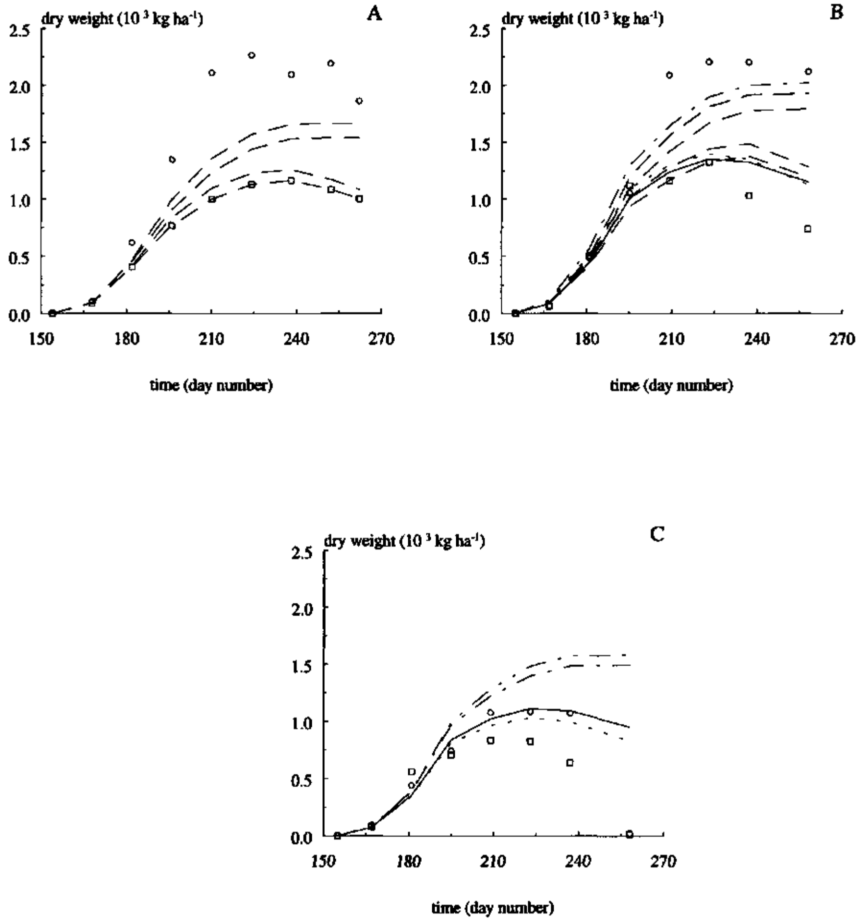

Figure 2.4. Simulated and observed production of leaf dry matter ((Δ) observed, (—·—) L 1, (·····) L 2, (— —) L 3, (······) L 2W, (——) L 3W) and Stem dry matter ((◊) observed, (— —) L 1, (—— ——) L 2, (———) L 3, (—— -) L 2W, (— - -) L 3W) for 1985 N4 (A), 1987 WET (B) and 1987 DRY (C) treatments

DISCUSSION

Modelling a crop has two important facets. The first facet is the model and its structure. In the model structure, the basic assumptions about growth and development are summarized. The second facet of modelling a crop is the parameterization of the model for a certain situation.

The model structure was varied in this study by using different levels of complexity for the main processes which determine crop growth. The level of complexity appeared to be unimportant for the prediction of dry matter production under conditions allowing potential growth. The more complex models (levels 2 and 3) took more effort to parameterize compared to the more simple one (level 1). This model (level 1) seems to be most suitable for predictions but the more complex models are needed when water relations are included.

Simulation of allocation of assimilates to the different plant organs proved to be less accurate. This is an important factor in the models because it influences the light interception and total growth through the partitioning to the leaves. In the models used in this study, partitioning is driven by development. Various authors have found that dry matter allocation in a potato crop is also influenced by source-sink relations (Fishman et al., 1984; Johnson et al., 1986) which when included in the models, may improve the performance.

The second facet of modelling is the parameterization of the models. Not all the parameters used in the models are independent of variety and site. In this study the parameters were estimated using the 1984 and 1986 data sets. Both the 1984 N4 treatment and the 1986 WET treatment were thought to have been stress-free. However, when the 1986 WET data were studied closely this appeared not to be the case, as at the beginning of season the partitioning to the tubers was high at the expense of leaf growth and total production. The total yield at the end of the 1986 season was also biased. This implies that there was stress at the beginning of the season. The parameters estimated using the 1986 data resulted in an underestimation of crop dry matter production. Drought had a large effect on the simulated results of 1986, probably because of an over-simplistic description of the soil water balance. It was assumed that there was a freely draining profile with no capillary rise from the ground water. Nevertheless, the predictions for total and tuber dry weight for the 1987 DRY treatment were satisfactory.

It can be concluded that this study illustrates the advantages of using a coherent set of models for simulating potato crop growth and development for particular purposes. Models using only a few parameters seem to be most appropriate for prediction purposes and more complicated models which describe individual crop growth processes in detail are needed when the influence of the environment on crop growth needs to be explained.

CHAPTER 3

AN ANALYSIS OF THE RELATION BETWEEN DRY MATTER ALLOCATION TO THE TUBER AND EARLINESS OF A POTATO CROP

P.L. Kooman and R.Rabbinge

ABSTRACT

Compared with early cultivars, late potato cultivars allocate a larger part of the available assimilates to the tubers early in the growing season, leading to shorter growing periods and lower yields. A dynamic simulation model integrating temperature and source-sink relations of the crop was used to analyse this relation, using data from experiments conducted in the Netherlands in five years. Dry matter allocation to the tuber in these field experiments was simulated well when the tuber was considered as a dominant sink that affects earliness of a potato crop in two ways: early allocation of assimilates to the tubers stops foliage growth early in the season and reduces the longevity of individual leaves. In a sensitivity analysis the influence of tuber initiation, leaf longevity and the relative tuber growth rate (rgr_{tb}) on assimilate allocation and crop earliness was evaluated. It was found that the relative tuber growth rate can influence crop earliness more than the other two factors, but when conditions for tuber growth are optimal, the leaf longevity is most important.

INTRODUCTION

Potato contributes significantly to the quality and quantity of the diet because of its high vitamin C and protein content and it is grown in various sites and climates throughout the world (Haverkort, 1990). Potato is now being grown successfully in the tropical and subtropical climates; potato production has doubled in these regions since late sixties (van der Zaag and Horton, 1983). However, the crop is mainly grown in relatively cool temperate or tropical highland climates and seems to be poorly adapted to warm climates. Tuber yields in warm regions still vary widely (Haverkort, 1986). The poor adaptation of potato may be caused by an unfavourable allocation of assimilates within the plant, since temperatures above 23 °C favour allocation of dry matter to the foliage at the cost of tuber growth (Haverkort and Harris, 1987).

Differences in assimilate allocation in potato are often referred to as earliness, because a difference in life span of the crop is observed in the field (Van Heemst, 1986, Spitters, 1987). Assimilate allocation results from the interaction of climatic conditions, cultural practices and genotype. Bodlaender (1960) showed that short photoperiod and low temperatures promote crop earliness. Van Heemst (1986) demonstrated that reduced nitrogen application rates and larger seed size make a crop earlier and Perrenec and Madec (1980) showed that older seed tubers have a similar effect. The cultivars in the existing gene pool exhibit a great diversity of assimilate allocation patterns (van Heemst 1986).

Assimilate allocation is the result of growth and development, which are mutually dependent and are difficult to analyse separately in experiments. Lateral stems, for example, will not develop when there is a shortage of available carbohydrate, in this case, development is restricted by growth. On the other hand, unless the appropriate conditions have been met, tubers will not be initiated even though sufficient assimilates are available for tuber growth. Here growth is restricted by development.

A quantitative approach using a combination of models and experiments allows the interaction between growth and development of the potato crop to be studied. The growth of the potato crop has been studied extensively, and various models are available to describe or predict the total biomass when environmental parameters are known (Ng and Loomis 1984, Spitters 1987, Ingram and McCloud, 1984). However, the influence of external factors and genotype on assimilate allocation and earliness in potato is being investigated and is therefore not included in these models.

The aim of the study described in this paper was to analyse the influence of assimilate allocation on the earliness of potatoes grown in field experiments. This relation was studied with a dynamic simulation model, integrating temperature and source-sink relations at the crop level.

MATERIAL AND METHODS

Some definitions

A daily leaf class is the amount of leaves (kg ha^{-1}) formed in one day. Leaf longevity is the maximum life span of a daily leaf class in °Cd and crop earliness is the life span of a crop (d). Tuber initiation date is defined as the date on which actual tuber growth starts. In the model an initial value of 1.0 g m^{-2}, estimated from tuber growth curves is taken as the starting point. The sink strength of the tuber (kg ha^{-1} d^{-1}) is defined as the ability to compete for assimilates compared to other organs. Assimilate allocation is the part of the daily assimilate production allocated to a particular organ.

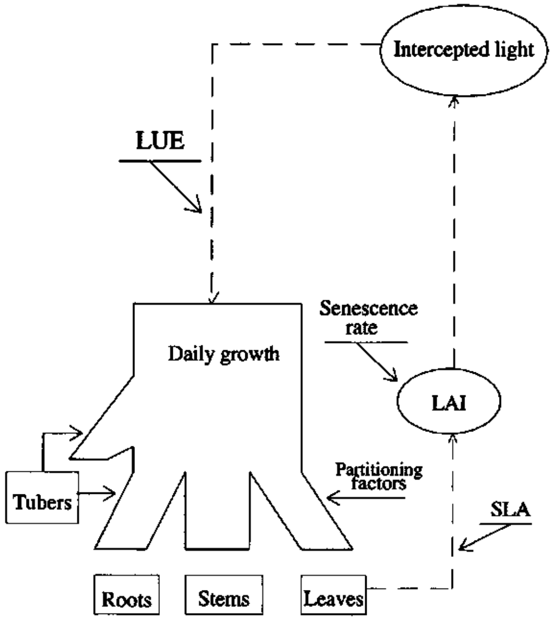

Figure 3.1. Schematic representation of the crop growth model in which the main processes are light interception, conversion to dry matter and assimilate allocation.

The data

Experimental data sets to evaluate assimilate allocation should meet the following prerequisites: the experiments must be carried out under conditions which do not limit growth. There should be no shortage of water and fertilizer, as assimilate allocation is influenced by water and nutrient shortage (Spitters and Schapendonk, 1990). Periodic harvests should be carried out during the growing season to monitor dry matter accumulation and allocation during the season. Cultivars of different maturity classes should be included, so that the influence of assimilate allocation on crop earliness can be evaluated. Data from two such sets of experiments were available at the DLO Research Institute for Agrobiology and Soil Fertility; they have been extensively described by Gmelig Meyling and Bodlaender (1981, Set 1) and Caesar et al. (1981, Set 2).

Both sets of data are from cultivar trials, carried out on a sandy soil with a high organic matter content at Varsseveld (East Netherlands). Set 1 is from trials carried out in 1968 and 1969 and involving the cultivars Alpha, Irene, Mentor, Pimpernel and Prudal. These cultivars ranged from very early (Prudal) to very late (Pimpernel). Set 2 is from trials carried out in 1971, 1972 and 1973 with four cultivars: the early cultivars Rheinhort and Ostara and the late Alpha and Condea. Nitrogen was applied at a rate of 200 kg ha^{-1} before planting and the planting density was 6 plants per m^2 in set 1 and 4 plants per m^2 in set 2. The distance between the rows was 75 cm in both sets. Periodic harvests of 10 plants were carried out at two-weekly intervals from May through September. Plants were divided into 4 fractions: tubers, stems, leaves and underground parts, and the fresh and dry weights of each fraction were determined separately.

The model

The model used in this study was relatively simple and focused on assimilate allocation, regulated by a dominant tuber sink (Moorby 1970, Sale, 1973, Gawronska et al.,1984). This led to the model as summarized in Figure 3.1, which is based on the model described by Spitters and Schapendonk (1990). Crop/water relations were not included and the parts dealing with dry matter allocation and leaf senescence were replaced by the equations given below.

Dry matter production was calculated from the amount of photosynthetically active radiation intercepted by the canopy and its conversion efficiency for dry matter production. The light-use efficiencies (Table 3.1) were estimated from field data with the help of the model, by minimizing the sum of squared differences between measured and calculated total biomass at the periodic harvests (Klepper and Rouse, 1991).

Assimilate allocation

The model calculations of the fraction of total dry matter produced, allocated to the tuber were based on the assumption that the tubers are the dominant sink in the potato crop. Three phases of dominance of the tubers can be distinguished; the initial phase when tuber growth is sink-limited, the second phase when there is competition for assimilates between tubers and other organs, and the third phase when tubers are such a strong sink that all assimilates are allocated to them.

The potential sink strength of the tubers (P_{tb}) is described by their size (W_{tb}) and their relative growth rate (rgr_{tb}) which is influenced by the effect of temperature (E_{tb}) as described by equation 3.1a.

$$P_{tb} = W_{tb} * rgr_{tb} * E_{tb} \qquad t \geq TI \qquad \text{Equation 3.1a}$$

The effective temperature function for tubers is taken from Van Heemst (1986) and normalized between 0 and 1. In the initial phase when tubers are still small and where growth is sink-limited, the growth rate of tubers (ΔW_{tb}) is equal to its potential sink strength.

$$\Delta W_{tb} = P_{tb} \qquad \text{Equation 3.1b}$$

The fraction of total assimilates allocated to the tubers (f_{tb}) is the daily tuber growth divided by the daily total growth (ΔW).

$$f_{tb} = \frac{\Delta W_{tb}}{\Delta W} = \frac{P_{tb}}{\Delta W} \qquad \text{Equation 3.1c}$$

The second phase of tuber growth is characterized by competition for assimilates between tubers and the rest of the plant. Tubers in this phase are not strong enough a sink to acquire all assimilates, but the source (availability of assimilates) is too small to enable all organs to grow at their potential rate. If it is assumed that the competition increases with increased potential sink strength of the tuber, the allocation can be described by equation 3.1d.

$$f_{tb} = \frac{P_{tb}}{\Delta W + P_{tb}} \qquad \text{Equation 3.1d}$$

When equation 3.1a is substituted in equation 3.1d equation 3.1e is obtained.

$$f_{tb} = \frac{W_{tb} * rgr_{tb} * E_{tb}}{\Delta W + W_{tb} * rgr_{tb} * E_{tb}} \qquad \text{Equation 3.1e}$$

The result is 1 equation which describes all phases of dry matter allocation to the tubers. Initially P_{tb} is very small compared to ΔW and tuber growth approaches exponential growth. Gradually W_{tb} increases, resulting in a greater sink strength and competition between tubers and foliage. Finally when W_{tb} becomes very large f_{tb} approaches 1 and all assimilates are allocated to the tubers.

The maximum relative growth rate for tubers use in this study (0.37 g g^{-1} d^{-1}) was derived by Ingram and McCloud(1984) from experiments in Florida , USA. The value they reported is slightly higher than the highest values of whole plants of wild plant species and crops as reported by Poorter and Remkes (1990) and Potter and Jones (1977). The use of the relatively high value of 0.37 g g^{-1} d^{-1} is justified by the fact that tubers consist of compounds with a more favourable conversion coefficient compared to whole plants.

Assimilates not partitioned to the tuber are allocated to the shoot and divided between the leaves and stems (Eq. 2. to Eq. 4.). In the model, root biomass is ignored because root measurements in the field experiments were not sufficiently accurate.

$$f_{sh} = 1 - f_{tb} \qquad \text{Equation 3.2}$$

$$f_{lv} = (f_{lv0} - (f_{sl} * f_{tb})) * f_{sh} \qquad \text{Equation 3.3}$$

$$f_{st} = (1 - f_{lv}) * f_{sh} \qquad \text{Equation 3.4}$$

Where f is the fraction of total daily growth allocated to an organ and the subscripts lv, sh and st represent leaves, shoot and stems respectively. f_{lv0} is the initial partitioning to the leaves and f_{sl} is the slope of the partitioning within the shoot. Based on the 1968 data the value of f_{lv0} was set at 0.75 and the value of f_{sl} was set at 0.5.

Light interception, critical LAI and maximum leaf longevity

Light interception was calculated from the leaf area index, calculated as the product of leaf dry weight and its specific leaf area (Spitters and Schapendonk, 1990). The moment at which leaves senesced was dependent on temperature and self-shading (Eq. 5).

$$\Delta W_{ld} = W_{lv,i} \qquad \begin{array}{l} \sum t_{lv,i} \geq T_{lv} \\[2ex] \sum \dfrac{LAI - LAI_{cr}}{LAI_{cr}} * R_{sh} \geq 1 \end{array} \qquad \text{Equation 3.5}$$

Where ΔW_{ld} is the daily increase of dead leaves; $W_{lv,i}$ the weight of leaves formed on day i, henceforth referred to as daily leaf class; $t_{lv,i}$ (°C) effective temperature for the daily leaf class i; t_{lv} the leaf longevity in °Cd; LAI the leaf area index; LAI_{cr} the critical leaf area index and R_{sh} (d^{-1}) the relative death rate due to shading.

When the temperature sum of a daily leaf class exceeded the leaf longevity, the leaves in that leaf class were considered dead. When the LAI exceeds the critical LAI the oldest leaves die after 10 to 20 days, dependent on the actual LAI (Eq. 5). This critical LAI was set at 7.5 on the basis of the 1968 data. Leaf longevity was derived with the help of the simulation model. The leaf longevity values given in Table 3.1 were acquired by first calculating the light interception over the growing season from the measured amount of leaf dry matter and the specific leaf area. Subsequently the leaf longevity was set at the value that minimized the difference between the calculated and measured duration of the light interception.

RESULTS

Parameter estimation

The Julian day numbers at plant emergence and tuber initiation were estimated from the growth curves of the field experiments of set 1 and set 2. The emergence date varied between day 128 and 139 (Table 3.1). The time of tuber initiation also varied between the years. The difference between 1968 and 1969 was 10 days in set 1 and in set 2 there was a maximum difference of 11 days (Table 3.1). The time between emergence and tuber initiation differed markedly between years. In Set 1 the time between emergence and tuber initiation was longer in 1968 than in 1969 and in Set 2 this time was longer in 1972 than in 1971 or 1973. In all experiments, cultivars classified as early in the Netherlands List of Recommended Cultivars (1968-1976) also showed the earliest tuber initiation.

The light-use efficiencies differed between years and cultivars. In agreement with Spitters (1987), it was found that the difference in light-use efficiency between years was larger than between cultivars within a given year. This may be partly attributable to the differences in rainfall, resulting in a relatively low light-use efficiency in the dry years 1973 and 1969.

Leaf longevity was cultivar-dependent and systematically shorter (up to 700 °Cd) in early cultivars than in late cultivars.

Table 3.1: Light-use efficiency (LUE; g MJ^{-1}), emergence day (d), tuber initiation day (d), days between emergence and tuber initiation (d) and leaf duration(°Cd) as estimated from the experiments for the varieties used in the two sets of experiments.

			LUE g MJ^{-1}	Emergence day	Tuber initiation day	Emergence-Tuber initiation	Leaf longevity °Cd
Set 1	1968	Prudal	3.2	128	148	20	1100
		Mentor	3.5	128	150	22	1400
		Alpha	3.4	130	156	26	1500
		Irene	3.1	129	160	31	1200
		Pimpernel	3.2	131	165	34	1500
	1969	Prudal	2.4	125	140	15	1100
		Mentor	2.4	126	147	21	1500
		Alpha	2.3	128	149	21	1600
		Irene	2.2	126	149	23	1400
		Pimpernel	2.1	128	154	26	1600
	Average	Prudal	2.8	126.5	144	17.5	1100
		Mentor	3.0	127	148.5	21.5	1450
		Alpha	2.9	129	152.5	23.5	1550
		Irene	2.7	127.5	154.5	27	1300
		Pimpernel	2.7	129.5	159.5	30	1550
Set 2	1971	Ostara	2.5	134	149	15	1200
		Rheinhort	2.5	132	149	17	1200
		Alpha	2.6	136	159	23	1600
		Condea	2.3	135	162	27	1500
	1972	Ostara	2.5	128	153	25	1000
		Rheinhort	2.4	133	159	26	1000
		Alpha	2.5	135	168	33	1500
		Condea	2.2	133	169	36	1600
	1973	Ostara	1.9	135	150	15	1000
		Rheinhort	1.9	136	153	17	1000
		Alpha	2	139	158	19	1700
		Condea	1.8	136	161	25	1600
	Average	Ostara	2.3	132	151	18	1067
		Rheinhort	2.3	134	154	20	1067
		Alpha	2.4	137	162	25	1600
		Condea	2.1	135	164	29	1567

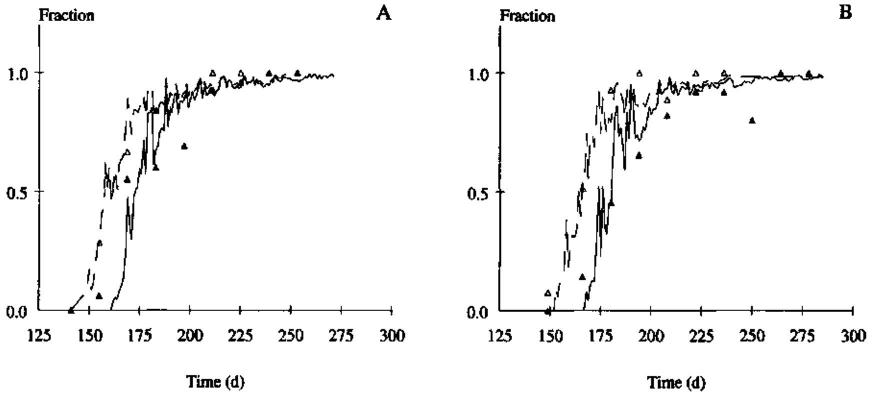

Figure 3.2. Fraction of the daily assimilate production allocated to the tubers in 1968 (a) and 1972 (b). Observed values for an early variety (△) (1968, Prudal and 1972, Ostara) a late variety (▲) (Alpha) and the simulated values for early (— —) and late (—) varieties.

Performance of the model

The total dry matter production part of the model had been validated in previous studies. (e.g. Spitters, 1987., Spitters et al., 1989). The dry matter distribution and leaf senescence sections were new in the model and investigated for the first time in the present study. There were many experiment-cultivar combinations in this study and therefore only a selection is shown in Figs. 3.2 and 3.3. Data on an early and a late cultivar of both experimental sets are given. The early cultivar in Set 1 was Prudal (1968) and in Set 2 it was Ostara (1972), the late cultivar in both sets was Alpha (1968, 1972).

Figure 3.2 shows the comparison of the observed fraction of dry matter produced allocated to the tubers between two consecutive harvests, and the simulated daily allocation. The simulation of early and late cultivars in both set 1 (Fig. 3.2a) and set 2 (Fig. 3.2b) corresponded well with the measured values and justifies the conclusion that the relation given in Equation 3.1e performed well for the given conditions.

Figs. 3.3a and 3.3b show the comparison of the observed light interception and the simulated values for Set 1 and Set 2. The simulation of leaf growth and LAI increase

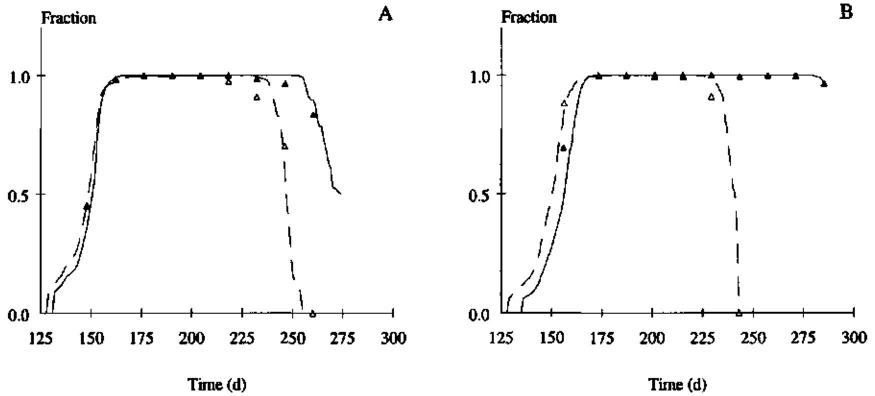

Figure 3.3. Light interception during the season in 1968 (a) and 1972 (b).
Observed values for an early variety (△) (1968, Prudal and 1972,Ostara) a late variety (▲) (Alpha) and the simulated values for early (— —) and late (—) varieties.

apparently agreed well with the experimental data. For each cultivar a constant value was taken for the leaf longevity, and no distinction was made between leaves formed early or late in the season. For the early cultivars this constant value simulated the decrease of LAI well (data not shown). For the late cultivars, however, the longevity of individual leaves differed considerably, leading to the LAI at the end of the season being overestimated. This did not influence the total production, because the time of crop senescence matched well and light interception mainly takes place in the uppermost four leaf layers (Haverkort et al. 1991).

Sensitivity analysis

The influence of the maximum leaf longevity, tuber initiation day and relative growth rate of tubers (rgr_{tb}) on crop earliness were evaluated by varying them in the model for a standard early and a standard late cultivar. The early cultivar was defined by tuber initiation at day 144 and a leaf longevity of 1100°Cd. For the late cultivar these values were day 160 and 1500°Cd. Weather data were the daily average values of solar radiation, minimum and maximum temperatures at Wageningen from 1960 to 1990. The emergence date of the crop was set to be 10 May and the season lasted until the fraction of light intercepted was reduced to zero or until 31 December at the latest. The light-use efficiency was set at 2.7 g MJ^{-1} and plant density was 4 plants per m^2.

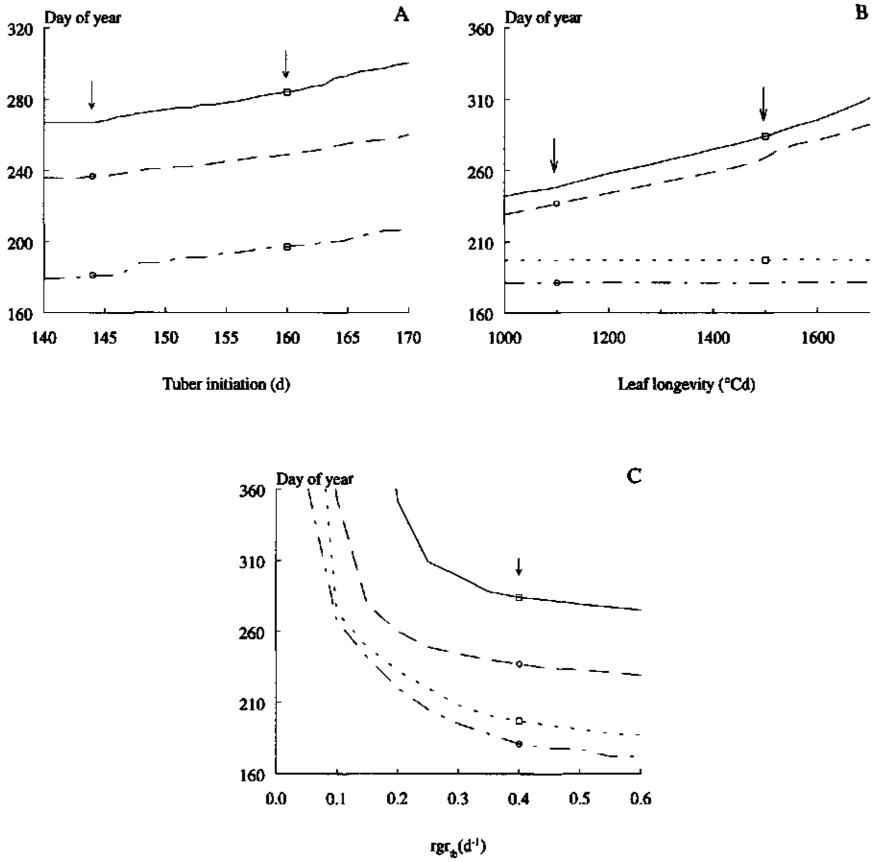

Figure 3.4. The effect of tuber initiation date (4a), leaf longevity (4b) and relative tuber growth rate (4c) on the day that 90 % of the daily assimilate production is allocated to the tubers (D_{90}) in a standard early (— -) and a late (· · · · ·) variety and on the day that the light interception is reduced to 50 % (D_{50}) in an early (— —) and a late (—) variety. Values for the standard early (O) and late (□) variety are given in the figures.

For the evaluation, crop earliness was divided into two components; leaf growth and leaf senescence. Leaf growth occurs in the period between emergence and the moment when leaf growth stops, defined here as the day on which 90 % of the daily assimilate production is allocated to the tubers (D_{90}). After this day no substantial leaf growth occurs. The timing of leaf senescence can be evaluated by the moment when crop growth stops, defined as the moment at which the fraction light intercepted is reduced to 50 % of full light interception (D_{50}); after this day no marked production takes place.

Tuber initiation and leaf longevity were varied between the minimum and maximum values in the experiments (Table 3.1.) The relative tuber growth rate in the experiment was constant, although when growing conditions are less optimal this is not necessarily the case. This parameter was varied between 0.1 and 0.6 g g^{-1} d^{-1} to ascertain its effect.

The results of the sensitivity analysis for tuber initiation are given in Figure 3.4a, with the value of the parameter on the abscissa and the Julian day number of D_{90} and D_{50} on the ordinate . Figure 3.4b shows the effect of leaf longevity, and Figure 3.4c shows the effect of relative growth rate.

When tuber initiation was delayed, leaf growth was prolonged, resulting in a later crop (Fig. 3.4a.). The tuber initiation dates studied ranged from day 140 to day 169. This range of 29 days was also found again in D_{90} and D_{50}. The early and late cultivars reacted similarly, indicating that with a fixed leaf longevity a delay of one day in tuber initiation date results in a delay of one day in crop senescence date.

Leaf longevity (Fig. 3.4b) did not affect leaf growth, resulting in a horizontal line for D_{90} in both the early and the late cultivar, with a difference of 16 days caused by the difference in tuber initiation. The influence of leaf longevity on D_{50} is large. When leaf longevity is increased from 1000 to 1700 °Cd there was a shift in D_{50} of 65 days for the early cultivar and of 68 days for the late cultivar. The additional 3 days for late cultivars resulted from its growing later in the season under lower temperatures.

The relative tuber growth rate can influence crop earliness more than the other two factors (Fig. 3.4c). Moreover, the nature of the reaction is different. With tuber initiation and leaf longevity the reaction is constant and has an equal sensitivity over the whole range. Crop earliness is sensitive to a change in rgr_{tb} when rgr_{tb} lies between 0.1 and 0.3, and is less sensitive at values of rgr_{tb} above 0.4. The small values are found when growing conditions for tubers are sub optimal. The rgr_{tb} mainly affects leaf growth which even continued until the end of the season at rgr_{tb} values below 0.2 g g^{-1} d^{-1}.

DISCUSSION

The simplicity of the model used here has the advantage that all processes can be verified easily and that information in the model is accessible to the reader (Spitters 1990). Despite its simplicity, the model presented here enabled the central processes such as light interception and assimilate allocation to be studied in relation to each other and to the environmental factors. Crop earliness can be divided into two components. The first component, leaf growth, is the result of crop growth and the allocation of assimilates to the leaves. The second component is the longevity of the formed leaves. It appears that factors which influence the strength of the tuber sink affect both assimilate allocation and the leaf longevity.

Assimilate allocation

The tuber sink strength in the initial growth phase is determined by the weight of the tubers, a result of their time of initiation, initial weight and relative growth rate. (Engels and Marschner, 1986). The growing conditions were nearly optimal and therefore the relative growth rate was set at a constant maximum value. The initial weight was also assumed to be constant in this study. The change in assimilate allocation is therefore determined by the time of initiation only, which on its own is a relatively insensitive parameter with respect to assimilate allocation and consequently to crop earliness (Fig. 3.4a). On the other hand, the relative growth rate has a large influence on the assimilate allocation of a crop, especially when a crop is grown under sub optimal conditions and the value of rgr_{tb} is low (Fig. 3.4c). This is probably why crops with a mild water stress at the beginning of the growing season persist longer (van Loon, 1981) or why a mulched crop under above-optimal temperatures dies sooner than an unmulched crop (Midmore, 1988).

Leaf longevity

The simulation of assimilate allocation could explain part of the variation in crop earliness. The rest of the variation was the result of a systematic extension of leaf longevity, up to 700 °Cd (Table 3.1) of late cultivars. This explained most of the variation in crop earliness; a small part was explained by the change in tuber initiation date and tuber growth in the sink-limited phase (i.e. the phase before D_{90}). In the sensitivity analysis, D_{50} was shifted 29 days for a standard cultivar by changing the tuber initiation date. However, when the leaf longevity was lengthened from 1000 °Cd to 1700 °Cd, D_{50} was 65 days later for an early cultivar and 68 days for a late cultivar, so the change in longevity seems more important. The differences in crop earliness found here correspond with experimental data for early cultivars that senesced in mid-August and for very late cultivars that senesced at the end of October. Late cultivars had a leaf longevity of about 1500 to 1700°Cd, or about 110 days. Vos and Biemond (1992) found similar values in a greenhouse experiment with the mid-late cultivar Bintje well supplied with nitrogen. When leaves do not attain the maximum longevity, factors other than temperature shorten their life span. The relation between crop earliness and leaf longevity suggests that the sink strength of the tubers not only limits the production of leaves but also their longevity.

Harris (1983) postulated that in the internal competition between the different organ groups of the crop the tuber is the dominant sink and that roots are the first to be subjected to this competition, causing root growth to decrease, which results in a concomitant reduction in the uptake of nutrients, especially nitrogen. A shortage of nitrogen is involved in the senescence of the crop. Considerable reallocation of carbon (Moorby 1970) and nitrogen (Millard et al. 1989) from the foliage to the tubers at the end of the growing season has been found under experimental conditions. It is assumed that at the end of the season, when the rooted soil is depleted, tubers withdraw nitrogen from the foliage. This reallocation will exhaust the nitrogen pool in the foliage faster in an early cultivar with a smaller amount of foliage than in a late cultivar with a larger amount of foliage. In early cultivars this will result in a shorter leaf longevity. Such a process, called self destruction, has also been described by Sinclair and De Wit (1976) in soybean.

This study supports the self destruction hypothesis in several ways. Firstly, because we found that early cultivars have a shorter leaf longevity than late cultivars, secondly because of the variability in the individual leaf longevity in late cultivars. The lower leaves in the canopy of late cultivars senesce faster than simulated with the model in which leaves have a fixed longevity and it is precisely these lower leaves that are influenced first by reallocation. Both phenomena can be attributed to redistribution of nitrogen to the tuber. A third argument in favour of the hypothesis is that fast growing crops have a shorter leaf longevity than slower growing crops (Table 3.1). In fast growing crops tubers grow faster and therefore need more nitrogen at the expense of leaves, thus reducing the leaf longevity.

In conclusion, the tuber initiation date in itself is not the only factor determining crop earliness. In this study the effect of tuber sink strength on leaf longevity was more important to crop earliness. This suggests that more study is needed of the relation between nitrogen uptake and distribution and the earliness of a potato crop.

Appendix: List of symbols

	Meaning	units
ΔW	Daily total growth	kg $ha^{-1}d^{-1}$
ΔW_{ld}	Increase of weight of dead leaves	kg $ha^{-1}d^{-1}$
ΔW_{lv}	Leaf growth rate	kg $ha^{-1}d^{-1}$
f_i	Fraction allocated to organ j	-
f_{lv}	Fraction allocated to leaves.	-
f_{sh}	Fraction allocated to the shoot.	-
f_{st}	Fraction allocated to stems.	-
f_{tb}	Fraction of total dry matter partitioned to the tubers	-
LAI	Leaf area index	m^2 m^{-2}
LAI_{cr}	Critical LAI for self shading.	m^2 m^{-2}
rgr_{tb}	Relative growth rate of tubers.	kg $kg^{-1}d^{-1}$
R_{sh}	Death rate of leaves due to self shading.	d^{-1}
t_{lv}	Effective shoot temperature.	^oC
$t_{lv}max$	Maximum leaf longevity for a daily leaf class.	^oC
t_{tb}	Effective tuber temperature.	^oC
$W_{lv,i}$	Weight of daily leaf class i.	kg ha^{-1}

CHAPTER 4

GENOTYPE-ENVIRONMENT INTERACTION IN POTATO 1: LIGHT INTERCEPTION, TOTAL DRY MATTER PRODUCTION AND TUBER YIELD

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ABSTRACT

The potential and actual dry matter production of potato crops in tropical and subtropical environments were found to be lower than in a temperate climate. In eleven field trials in Rwanda, Tunisia and the Netherlands, the total dry matter production and tuber yield of eight cultivars were analysed. The light-use efficiency correlated negatively with light intensity. Variation in length of the growing season appeared to be the most important factor explaining the differences in both total and tuber yield. The harvest index was of minor importance. The variation in length of the growing season between sites was related to daylength and temperature such that shorter days at emergence and higher temperatures throughout the season resulted in a shorter growth cycle. The extent of these effects differed between cultivars and could partly be explained in terms of ground cover duration, length of the growing season and average seasonal weather data.

INTRODUCTION

Potatoes are grown in a wide range of environments (Haverkort, 1990). The highest potential and actual tuber yields are obtained in areas with temperate climates in North-western Europe and the North-west of the United States (van der Zaag 1984, Stol et al. 1991), thanks to long growing seasons combined with adequate cropping practices. The potential production and the ratio between actual and potential production are lower in tropical and subtropical climates. Part of this difference originates from the use of cultivars that are high yielding in temperate regions but are not adequately adapted to the high temperatures and short daylength in tropical and subtropical climates. Another cause of the lower yields may be the shorter growth cycles due to unsuitable weather conditions in these climates.

The yielding ability of cultivars in different climates can be assessed in various ways. Tai and Young (1989) analysed tuber yields statistically in a wide range of environments with stepwise regression. Their approach enabled yield levels in various climates to be approximated. It did not explain, however, how potato dry matter production is determined by climatic variables such as solar radiation, photoperiod and temperature.

More explanatory in nature were the various approaches of Van der Zaag and Doornbos (1987), Haverkort and Harris (1987), Fahem and Haverkort(1988) and Spitters (1987), who analysed the yield of potato crops based on intercepted radiation, the efficiency of the use of this radiation for dry matter production, and the harvest index. They based their studies on data from one climatic zone or on data from experiments carried out differently. Under crop growth conditions without limiting water or nutrients and in the absence of pests diseases and weeds, they found that the differences between cultivars could be explained primarily by the difference in light interception. Light use efficiency was considered to be a second explanatory factor.

This paper reports the results of eleven field trials, with 8 cultivars carried out at six sites in the Netherlands, Tunisia and Rwanda in 1991 and 1992, to analyse the variation in tuber dry matter production between sites and cultivars. The objective of this study was to find the sources of variation in tuber dry matter production and to ascertain how the climatological parameters temperature, photoperiod and radiation intensity influence these sources.

MATERIALS AND METHODS

The eleven field trials were carried out in two years at six different sites: in Rwanda at Kinigi (2350 m) and Rubona (1650 m), in Tunisia (three different growing season at two locations, spring and autumn in Saida and winter in Monastir) and in the Netherlands (Wageningen, summer). The details of the sites and growing seasons are given in Table 4.1. Except for the Tunisian winter trial all trials were carried out twice. The trials had two replicates in Tunisia and three replicates at the other sites. The sites were chosen to represent the wide range of temperature and daylength conditions in which potatoes are grown. The eight cultivars used here were chosen because of their difference in lateness in the Netherlands. They ranged from early (Première) to very late (Producent, Table 4.2). The seed potatoes used in the trials were in the 35 to 45 mm grade class, certified class "A" and originated from the 'Noord-Oost polder' in the Netherlands, with the exception of the seed tubers used in the Tunisian autumn and winter seasons, which were multiplied locally in spring. After harvest in June the local Tunisian seed was stored in a cold store at 4 °C. Before planting in the field, seed tubers were presprouted and the number and length of sprouts was recorded. In the spring crops no differences in sprouting between sites were found but for the Tunisian autumn crop sprouting varied between cultivars. The seed was planted in rows 0.75 m apart and at 0.30 m distance within the row. The management of the crop at each site was aimed at maximum tuber yields. The crops in the Netherlands and in Tunisia were irrigated when needed. The crops in Rwanda were grown in the rainy season, with ample supply of water.

Table 4.1 Locations and growings seasons of experiments. The averages given are the average over the complete growing season.

Country	Netherlands		Rwanda				Tunisia				
Site	Wageningen		Kinigi		Rubona		Saida				Monastir
Season	Summer		Rainy		Rainy		Spring		Autumn		Winter
Latitude (°N)	52		-1		-2		37		37		35
Longitude (°E)	6		30		30		10		10		11
Altitude (m above sealevel)	7		2350		1350		328		328		0
Irrigation	sprinkler		rainfed		rainfed		furrow		furrow		furrow
Seed source	Netherlands		Netherlands		Netherlands		Netherlands		Tunisia spring		Tunisia spring
years	1991	1992	1991	1992	1991	1992	1991	1992	1991	1992	1991/1992
Day of planting	113	113	74	59	67	65	61	64	248	250	316
Day of last harvest	296	272	179	176	168	195	171	168	358	351	77
Maximum season length (d)	183	159	105	117	101	130	110	104	110	101	126
Number of harvests	4	4	4	5	4	4	3	6	4	6	5
Nr. of crop Fractions	4	3	4	4	4	4	4	4	2	4	2
Average Temperature (°C)	13.8	16.2	15.6	15.8	19.9	19.4	15.8	17.1	17.6	19.8	12.5
Average Daylength (h)	14.4	14.9	12.0	12.0	11.9	11.9	13.2	13.3	10.7	10.6	9.9
Average PAR (MJ m^{-2} d^{-1})	6.9	8.0	6.2	6.6	8.6	10.7	11.7	11.2	6.6	8.0	4.6

Weather data

Daily values of global radiation, minimum and maximum temperature were recorded at the experimental site or at nearby weather stations. Photosynthetically Active Radiation (PAR, 400-700 nm) was calculated as 0.5 times the global radiation. PAR, the daily average temperature (henceforth referred to as 'temperature') and the daylength at each site and for each growing season are given in figure 4.1.

Sites and growing seasons

The Netherlands

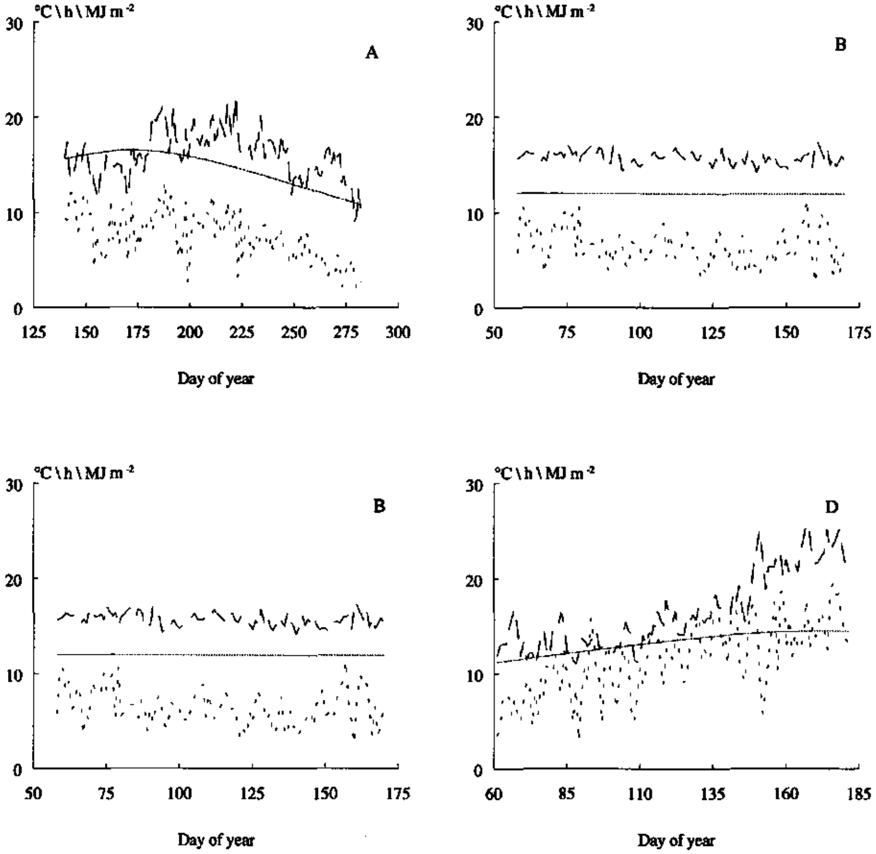
In the Netherlands the potato crop is grown in summer, from April to October. Wageningen has a temperate maritime climate with a cool summer. The growing season is limited by frost in spring and autumn.

The trials were planted mid April to avoid the risk of night frost. The earliest cultivars were harvested at the end of August and the latest cultivars at the beginning of October. The average temperature during the growing season ranged from about 5 °C in April to 17 °C in July. The days were long (14 - 17.5 h) and the daily amount of PAR varied from 2 MJ m^{-2} d^{-1} on an overcast day to 13 MJ m^{-2} d^{-1} on a clear summer day (Fig. 4.1a).

Rwanda

In Rwanda, potatoes are usually grown above 2000 m, and in two growing seasons per year corresponding the two rainy seasons (Haverkort, 1986). The growing season in Kinigi (in northern Rwanda) was determined by the rainy season which started early March and lasted until early June. The crop was planted just before the rain started. During the rainy season, soil moisture did not limit potato growth. Kinigi is located at 2350 m above sea level and is relatively cool with temperatures of about 17 °C and little variation in the growing season (Fig. 4.1b). The daylength was 12 hours and the daily amount of PAR ranged from 2 to 15 MJ m^{-2} d^{-1} depending on the cloudiness.

Rubona (Fig. 4.1c) in the south of Rwanda has climatic conditions similar to Kinigi but as it is lower (1650 m above sea level) the temperatures are higher (21 °C) and due to less cloudiness PAR is higher (about 20 MJ m^{-2}). In some years the rainy season starts later than in Kinigi and the crop emergence can then be delayed by lack of moisture.



Tunisia

Potato crops in Tunisia are mainly grown in two seasons; in spring and in autumn. An additional crop may be grown in winter in the coastal area. Potatoes cannot be grown in summer in the lowlands because of high temperatures nor in the winter in continental areas due to risk of frost (Fahem and Haverkort, 1988).

The Tunisian spring season at Saida (near Tunis) is limited by night frosts until February and by temperatures above 30 °C from the end of June onwards. The growing season had low temperatures (12 °C) and short days (11 h) at the beginning and high temperatures (27 °C) and relatively long days (14 h) at the end (Fig. 4.1d). The daily PAR increased towards the end of the season and varied from 4 to 15 MJ m^{-2} d^{-1}.

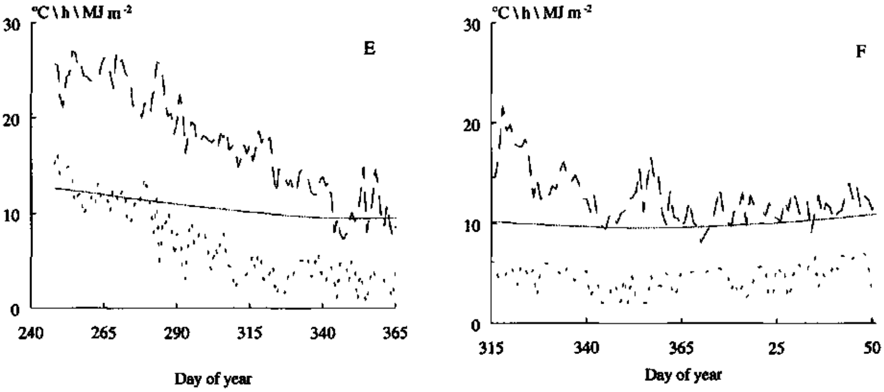


Figure 4.1. The daily amount of photosynthetically active radiation in MJ d^{-1} (- - - -), daily average temperature in °C (— —) and the daylength in hours (——) of Wageningen (A), Kinigi (B), Rubona (C), Tunisia spring (D), Tunisia autumn (E) and Tunisia winter (F).

The autumn crop was planted in September at Saida when temperatures were sufficiently low (below 30 °C) to allow potato production. The season lasted until the first half of December when crop growth ceased due to night frosts and low radiation. In the first week of September the temperature was about 26°C (Fig. 4.1e) , the daylength was about 12.5 h and the amount of PAR was about 15 MJ m^{-2} d^{-1}. In December these values had decreased to respectively 8 °C, 9.5 h and 4 MJ m^{-2} d^{-1}.

The winter crop in Tunisia was grown at Monastir near the Mediterranean Sea. The influence of the sea minimizes the risk of night frost, so potato crops can be grown from September until June. The crop was planted in November and harvested in March. This growing season was characterized by low temperatures (11 °C), short days (about 10 h) and low levels of solar radiation (5 MJ m^{-2} d^{-1} PAR) (Fig. 4.1f).

Data collection.

The proportion of the ground covered with green foliage was recorded with the aid of a metal grid divided into 100 rectangles, viewed directly from above (Haverkort et al. 1990). The dimensions of the frame were a multiple of the planting pattern: 0.75 m x 0.90 m. Observations were carried out at least once every 10 days. Three to six periodic harvests were carried out per growing season (Table 4.1). In the Tunisian spring season of 1991 only three periodic harvests were carried out because this growing season was relatively short due to late emergence of the crop. At Kinigi 1992, and the Tunisian winter season 5 harvests out and in the 1992 Tunisian spring and autumn seasons 6 periodic harvests were carried out.

In the Netherlands twice as many plants were lifted per harvest than at the other sites (12 plants versus 6 plants, and, at the final harvest, 24 versus 12 plants). In the major part of the trials the plant material was divided into foliage and tubers or into leaves, stems, tubers and an underground part (Table 4.1). In the Netherlands 1992, Tunisian autumn 1992 and the Tunisian winter trials the crop was separated into either tubers, foliage and underground parts, or into tubers and the rest. The fresh and dry weight of each organ were determined. Dry weight was determined by drying samples of the plants for 24 hours at 105 °C.

Data analysis

The amount of PAR intercepted by the canopy was calculated as the product of the fraction soil cover and the daily amount of PAR. Subsequently the average light-use efficiency (LUE) was determined by linear regression of the cumulative intercepted PAR and total dry weight. For the calculations during the period when the amount of foliage decreased the maximum amount of foliage recorded was taken as total foliage production.

The relation developed by Spitters (1987, 1990) (Fig. 4.2, Eq 1) was used to describe the course of the light interception during the growing season

$$F_t = \frac{F_0 M}{F_0 + (M - F_0)e^{-R_0 t}} \qquad \text{Equation 1a}$$

Where F_t is the fraction of soil covered with green foliage, F_0 the initial fraction of light intercepted at crop emergence, R_0 (°Cd^{-1}) the relative increase rate for light interception and t (°Cd) the thermal time with a base temperature of 2°C. The decline of light interception was assumed to be linear. (Eq. 1b, Fig. 4.2) This is the simplest way to describe this decline and is adequate for use in this study. A more complex function, such as a logistic decrease improves the precision slightly but requires more parameters.

$$F_t = 0.5 - \frac{t - t_{50}}{d} \qquad \text{Equation 1b}$$

t_{50} (°Cd) is the moment when the fraction of light intercepted is reduced to 50 per cent (Fig. 4.2), a parameter easily observed in the field, and d (°Cd) is twice the duration from t_{50} until cessation of light interception.

This function allows us to quantify the light interception over the season and to analyse the light interception in terms of the function parameters. Spitters(1990) distinguished two phases in the growing season: firstly the increase of light interception capacity towards maximum ground cover and secondly the decline of light interception. He described the first phase of light interception as a logistic function of thermal time, starting at emergence, and since potato crops in the Netherlands usually reach full ground cover, a maximum value (M) of 1. This situation is represented by line a in Figure 2. In other climatological conditions full ground cover is not always reached, hence ground cover may develop according to line b (Fig. 4.2). Therefore the maximum of 1 was replaced with a variable maximum M in the relation (Equation 1a.)

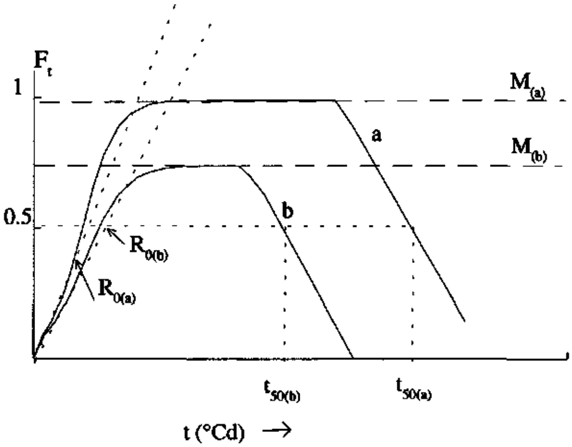


Figure 4.2. The development of the fraction of the ground covered with green leaves (F) during the growing season when the crop reaches full ground cover (a) and when the crop does not reach full ground cover. (b) R_0 is the relative increase rate for light interception, M the maximum ground cover and t_{50} the time when the ground cover is reduced to 50% of full ground cover.

Table 2. Observed values of total dry matter production in kg m^{-2}, tuber dry matter production kg m^{-2}, harvest index, cumulative intercepted PAR (PARINT in MJ m^{-2}),Ground cover duration (GCD in days),Ground cover duration (GCT in degree days) and days from planting to emergence (PL-EM in days).

Site	Cultivar	Dry matter production (kg m^{-2})	Tuber dry matter (kg m^{-2})	Harvest index	PARINT (MJ m^{-2})	GCD (d)	GCT (°Cd)	PL-EM (d)
Netherlands	Alpha	1.68	1.29	0.77	732	93	1385	26.5
	Bintje	1.52	1.22	0.81	611	83	1128	27.5
	Désirée	1.55	1.21	0.78	630	79	1178	24.5
	Diamant	1.64	1.30	0.79	666	84	1253	27.5
	Escort	1.76	1.44	0.82	664	81	1230	27.5
	Première	1.34	1.02	0.77	548	65	983	27
	Producent	1.99	1.63	0.82	758	100	1459	25.5
	Spunta	1.41	1.07	0.77	622	77	1156	24
Rwanda Kinigi	Alpha	1.11	0.90	0.81	386	65	870	18.5
	Bintje	0.65	0.54	0.83	298	54	728	17.5
	Désirée	0.86	0.70	0.81	364	64	853	16.5
	Diamant	1.09	0.88	0.81	391	66	889	16
	Escort	0.98	0.80	0.81	362	62	837	17
	Première	0.80	0.67	0.85	326	59	789	13
	Producent	1.03	0.85	0.83	383	65	879	14.5
	Spunta	0.86	0.68	0.79	383	66	883	15
Rwanda Rubona	Alpha	1.02	0.74	0.79	431	50	871	24
	Bintje	0.76	0.60	0.81	308	37	642	28
	Désirée	0.87	0.64	0.76	414	49	855	20.5
	Diamant	0.91	0.69	0.76	385	44	760	22
	Escort	0.94	0.73	0.78	384	56	909	26
	Première	0.79	0.55	0.83	339	41	710	23.5
	Producent	1.02	0.85	0.82	396	54	909	22
	Spunta	0.88	0.66	0.78	396	50	867	23.5
Tunisia autumn	Alpha	0.39	0.38	0.62	112	31	334	37
	Bintje	0.55	0.41	0.51	153	39	476	35.13
	Désirée	0.72	0.40	0.54	201	50	597	36
	Diamant	0.75	0.33	0.60	198	50	591	36

continue Table 4.2.

Site	Cultivar	Dry matter production (kg m^{-2})	Tuber dry matter (kg m^{-2})	Harvest index	PARINT (MJ m^{-2})	GCD (d)	GCT (°Cd)	PL-EM (d)
Tunisia	Escort	0.88	0.51	0.64	263	57	723	29
	Première	0.56	0.36	0.61	230	49	624	24
	Producent	0.64	0.38	0.57	227	54	649	29
	Spunta	0.54	0.36	0.63	158	39	460	35
Tunisia spring	Alpha	0.87	0.71	0.82	476	45	743	32
	Bintje	0.97	0.81	0.84	462	45	717	27
	Désirée	0.98	0.81	0.82	501	47	759	29
	Diamant	0.92	0.75	0.82	469	45	720	26.5
	Escort	0.90	0.76	0.85	437	44	701	27.5
	Première	0.91	0.74	0.83	431	38	620	30
	Producent	0.84	0.74	0.88	399	36	591	28
	Spunta	0.84	0.71	0.85	439	43	686	29
Tunisia winter	Alpha	0.36	0.24	0.66	233	66	542	25
	Bintje	0.76	0.50	0.65	193	55	431	42
	Désirée	0.62	0.46	0.74	201	87	728	29
	Diamant	0.77	0.45	0.61	228	80	656	28
	Escort	0.63	0.42	0.67	219	70	558	37
	Première	0.60	0.38	0.64	194	57	478	27
	Producent	0.38	0.27	0.70	169	70	586	28
	Spunta	0.72	0.51	0.71	228	98	817	27
LSD 5%								
Cultivars between locations		0.36	0.33	0.14	121	19	238	12
Cultivars between locations with Tunisian winter and autumn		0.44	0.47	0.20	148	24	291	27
Cultivars within location		0.22	0.20	0.06	53	7	88	6
Cultivars within Tunisian winter and autumn		0.31	0.34	0.10	75	9	124	8

When the curve is fitted to the observed data with non-linear regression the light interception over the growing season is described by only three parameters, R_0 as a measure for initial growth, M as a measure for maximum light interception and t_{50} for the length of the growing period. Neither the duration of senescence (d) nor the initial light interception (F_0) were considered. At 50 % emergence the light interception did not differ in the experiments so F_0 was assumed to be constant. When the light interception has fallen to 50 % of full light interception no substantial production takes place any more, and therefore the length of the growth period could be described well by using t_{50} only. An analysis of variance was done on the total dry matter production, tuber dry matter production, harvest index, total amount of intercepted radiation, ground cover duration in days and cumulated thermal time, the days from planting to emergence, estimates of R_0, M, t_{50} , D_{50} (days from emergence to t_{50}) and the light-use efficiency (Table 4.3). The trials were analysed as a split plot experiment with the sites in the main plots, the cultivars in the subplots and years as replicates. The Genstat statistical package (Genstat 5 committee, 1987) was used for the analysis of variance and the regressions.

RESULTS

The results of the trials are represented in the tables 4.2 and 4.4. Table 4.2 gives the observed values of total dry matter production, intercepted photosynthetically active radiation, ground cover duration in days (GCD), ground cover duration in thermal time (GCT) and the number of days from planting to emergence. Table 4.4 gives the calculated values of the light interception curve (R_0, M, t_{50}), the time in days until t_{50} (D_{50}) and the light-use efficiency for dry matter production (LUE). The values are the averages over 1991 and 1992 per location per cultivar. The 1991 Tunisian autumn season was excluded from statistical analysis since the emergence, and subsequent crop growth was irregular, probably because the seed used at this location was physiologically too young, therefore only the values for Tunisian autumn 1992 are given in Tables 4.2 and 4.4. The trial in Tunisian winter was carried out once only, so the values presented are for the 1991-1992 season. The LSD's for the different comparisons are given at the bottom of the tables.

The sites could be divided into three groups on the basis of total dry matter production; the first group contained Wageningen, the second group Kinigi, Rubona and the Tunisian spring season and the third group Tunisian autumn and winter seasons. Within the groups the yields of a particular cultivar did not differ statistically significant between sites. Total dry matter production was always highest in Wageningen, ranging from 1.34 kg m^{-2} for

Première to 1.99 kg m^{-2} for Producent (Table 4.2). The difference between Wageningen and the other sites was statistically significant for all cultivars. In the second group the total dry matter production ranged from 0.76 kg m^{-2} to 1.11 kg m^{-2} except for Bintje producing only 0.65 kg m^{-2} at Kinigi. The third group produced less dry matter than the second group (0.36-0.88 kg m^{-2}), although the difference was not statistically significant for all cultivars.

The harvest index varied between 0.51 in Tunisian autumn and 0.85 in Kinigi. In the Tunisian autumn experiment the harvest differed statistically significant from the other sites. No statistically significant difference was found between these sites (Table 4.2). Tuber yield was the result of total yield and harvest index. Since no difference in harvest

Table 4.3 Significance in analysis of variance for the following parameters: total dry matter production, tuber dry matter production, harvest index, cumulative amount of intercepted PAR (PARINT), ground cover duration in days (GCD) and in thermal time (GCT), time from planting to emergence (PL-EM), initial increase rate of light interception (R_0), maximum interception (M), Days (D_{50}) and thermal time (T_{50}) until the ground cover has fallen to 50 % of full ground cover and light-use efficiency (LUE).

	Site	Cultivar	Site * Cultivar
Tuber dry matter production (kg m^{-2})	**	**	*
Total dry matter production (kg m^{-2})	**	**	**
Harvest Index	*	ns	ns
PARINT (MJ m^{-2})	**	**	**
LUE (g MJ^{-1})	*	ns	**
GCD (d)	*	**	**
GCT (°Cd)	**	**	**
R_0 (°$C^{-1}d^{-1}$)	ns	ns	ns
M_0	ns	ns	ns
T_{50} (°Cd)	ns	**	**
D_{50} (d)	*	**	**
PL-EM (d)	ns	*	ns

** =P < 0.01, * = P<0.05, ns=not significant.

index was found, tuber yield showed the same trends as total yields. Here Wageningen had the highest production, between 1.02 kg m^{-2} for Première and 1.63 kg m^{-2} for Producent. The lowest production occurred in the Tunisian autumn and winter seasons. Total production was low and the harvest index was also at the lower end of the range found in the trials.

No single cultivar gave the highest tuber or total dry matter production at all locations and the order with respect to dry matter production differed per location. Producent was the highest yielding cultivar in Wageningen, whereas in the Tunisian spring and winter trials Producent ranked among the lowest producing cultivars (Table 4.2). The stability of the cultivars is best analysed by examining the relative dry matter production with Wageningen as reference. Première and Désirée were relatively stable and produced between 40 and 65 percent of their Wageningen production Rwanda and Tunisia. Alpha and Producent had a much larger variation, ranging between 20 and 65 percent of their production at Wageningen.

The light-use efficiency was not constant when the different sites were compared. In Wageningen, Rubona and Kinigi the efficiency was about 2.5 g MJ^{-1} , in the Tunisian autumn and Tunisian winter trials high LUE values were found, respectively 2.96 and 3.20 g MJ^{-1} average. In the Tunisian spring trial the LUE was low: 1.95 g MJ^{-1}. Statistically significant differences were found between Tunisian spring and Tunisian autumn and winter season, except in for Première and Producent, which had relatively low values in the Tunisian winter and autumn trials. Diamant had very high LUE values in the winter and autumn seasons which differed statistically significant from those found in the Dutch and Rwandese locations. Within the locations, statistically significant differences between cultivars were only found in Tunisian winter and autumn. In these seasons the variation in LUE between cultivars large high compared to the other locations.

The cumulative amount of intercepted light proved to be more important for dry matter production than the LUE (Tables 4.2 and 4.4). The amount of intercepted light was highest in Wageningen, ranging from 548 MJ m^{-2} for the early cultivar Première up to 758 MJ m^{-2} for the late cultivar Producent. At the other locations the crops intercepted substantially less radiation. The Tunisian spring season ranked second for all cultivars, with 399 MJ m^{-2} for Producent to 501 MJ m^{-2} for Désirée. The Tunisian spring was followed directly by Rubona and Kinigi, except that Diamant intercepted more radiation at Kinigi. The differences between Rubona, Kinigi and Tunisian spring were small and only statistically significant in Bintje. Least radiation was intercepted by the Tunisian winter and autumn crops: about 225 MJ m^{-2} only.

The differences in light interception between sites are attributable to the combined result of the differences in light intensity and differences in ground cover duration. Differences between cultivars at a site solely caused by the ground cover duration. Figure 4.1 shows that a part of the difference in light interception was explained by the intensity and the course of the solar radiation at the different sites. The highest intensity was found in the Tunisian spring, especially towards the end of the growing season. Wageningen and Rubona followed close behind with Kinigi somewhat later. In the Tunisian winter the entire growing season had a low level of light intensity whereas in the Tunisian autumn the beginning of the season had a similar intensity as Wageningen and Rubona, but at the end of the growing season the intensity had fallen to low levels.

Figure 4.3 shows the time course of ground cover of the cultivars with the highest and lowest ground cover duration for Wageningen and the Tunisian spring season. The ground cover duration in °Cd (GCT) is represented by the area under the ground cover curves. Wageningen always had the longest ground cover duration, Kinigi was always second, followed by Rubona, Tunisian spring and Tunisian autumn and Tunisian winter

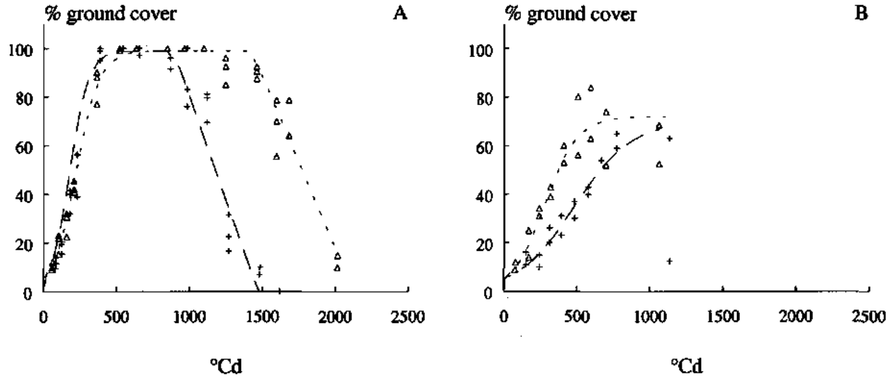


Figure 4.3 Observed and fitted ground cover for the best (— —, Δ) and worst (- - - -, +) performing cultivar in Wageningen(a) and Tunisian spring(b).

Table 4.4 Calculated values of initial increase rate of light interception (R_0), maximum interception (M), days (D_{50}) and thermal time (T_{50}) until the ground cover has fallen to 50 % of full ground cover and light-use efficiency (LUE).

Site	cultivar	R_0 (10^{-2} °$C^{-1}d^{-1}$)	M	T_{50} (°Cd)	D_{50} (d)	LUE (g MJ^{-1})
Netherlands	Alpha	1.09	0.97	1707	119	2.31
	Bintje	1.09	0.98	1418	97	2.60
	Désirée	1.03	0.95	1502	105	2.47
	Diamant	1.17	0.97	1530	105	2.50
	Escort	1.29	0.98	1490	101	2.68
	Première	1.36	0.98	1221	84	2.52
	Producent	1.07	0.98	1794	127	2.67
	Spunta	1.16	0.96	1441	101	2.28
Rwanda Kinigi	Alpha	1.49	1.00	1087	81	2.77
	Bintje	1.37	0.91	1014	76	2.13
	Désirée	1.46	0.97	1095	81	2.30
	Diamant	1.56	0.99	1092	81	2.75
	Escort	1.63	0.94	1098	82	2.55
	Première	1.57	0.90	1047	78	2.31
	Producent	1.47	0.98	1105	82	2.59
	Spunta	1.44	0.96	1121	84	2.18
Rwanda Rubona	Alpha	1.35	1.02	1101	63	2.41
	Bintje	1.99	0.93	873	50	2.45
	Désirée	1.12	0.99	1129	65	2.32
	Diamant	0.89	1.00	1107	64	2.52
	Escort	1.10	1.00	1296	75	2.66
	Première	1.38	0.91	990	57	2.45
	Producent	0.90	1.00	1283	74	2.56
	Spunta	1.88	0.96	1118	64	2.43

Continue Table 4.4

Site	cultivar	R_0 (10^{-2} °$C^{-1}d^{-1}$)	M	T_{50} (°Cd)	D_{50} (d)	LUE (g MJ^{-1})
Tunisia autumn	Alpha	0.75	0.74	891	73	3.52
	Bintje	1.11	0.95	860	68	3.06
	Désirée	1.16	1.05	914	74	3.35
	Diamant	1.12	1.01	914	74	3.36
	Escort	1.06	1.01	1055	81	2.69
	Première	0.69	1.05	1163	86	2.21
	Producent	1.21	0.99	938	76	2.51
	Spunta	0.87	0.88	938	75	2.98
Tunisia spring	Alpha	1.14	0.83	1141	67	1.77
	Bintje	1.12	0.77	1195	72	2.04
	Désirée	1.13	0.83	1169	70	2.00
	Diamant	1.12	0.76	1200	72	1.85
	Escort	1.02	0.76	1187	71	1.97
	Première	0.91	0.74	1159	69	2.00
	Producent	0.81	0.72	1185	59	2.13
	Spunta	1.14	0.74	1170	70	1.88
Tunisia winter	Alpha	1.62	0.93	821	102	1.54
	Bintje	1.40	0.96	655	67	4.40
	Désirée	1.35	0.81	793	97	3.46
	Diamant	1.32	0.92	799	116	3.63
	Escort	1.73	0.93	739	83	3.27
	Première	1.17	0.78	804	98	3.33
	Producent	1.75	0.61	799	98	2.49
	Spunta	1.31	0.93	799	98	3.53
LSD 5%						
Cultivars between locations				331	25	0.59
Cultivars between locations with Tunisian winter and autumn				406	30	0.73
Cultivars within location				146	12	0.41
Cultivars within Tunisian winter and autumn				206	16	0.58

depending on the cultivar. The difference between cultivars was largest in Wageningen (Fig. 4.3a) about 476°Cd or 35 days. In the Tunisian spring the difference in GCT between cultivars was smallest (Fig. 4.3b) 168 °Cd or 11 days only, and not statistically significant. When the ground cover duration was expressed in days the overall picture was less clear. The highest values of ground cover duration were again found in Wageningen followed by the Tunisian winter and Kinigi. Tunisian spring had the lowest values but only differed statistically significant from the Tunisian winter and Wageningen.

Ground cover duration is the integral of the ground cover over time. Variation in ground cover duration can therefore be explained in variation of the parameters which describe the light interception curve (Eq. 1). From these parameters only the length of the growth cycle varied significantly. Linear regression analysis showed that D_{50} accounted for 74 percent (Fig. 4.4) of the variation in ground cover duration, whereas M and R_0 each accounted for less than 10 %. Although the maximum ground cover (M) and rate of ground cover increase (R_0) did not differ statistically significantly, they did influence the ground cover duration.

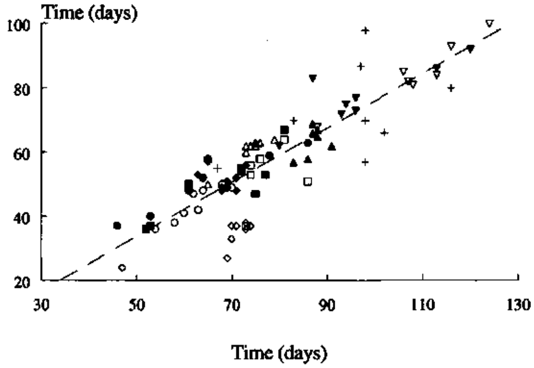


Figure 4.4 The relation between length of the growing season and ground cover duration. Wageningen(∇), Kinigi (Δ), Rubona (●), Tunisia autumn (■), Tunisia spring (◆) and Tunisia winter (+). The open symbols are values for 1991, the closed for 1992.

DISCUSSION

Except for the Tunisian autumn season there was no difference in the physiological age of the seed potatoes that might have influenced the crop growth in the trials. The seed was homogeneous and no statistically significant difference was found in sprout length between locations. The period between emergence and planting differed statistically significant between the cultivars in the Tunisian autumn only.

The Tunisian winter crop may have been damaged slightly by a night frost in early January. The 1991 Tunisian spring season and the 1992 crop in Rubona had a delayed emergence. The Tunisian spring crop had a delayed planting and subsequently emergence because conditions were too wet. The Rubona crop had too dry conditions just after planting, retarding emergence. No statistically significant effects were found although the moisture stress may have influenced the value of D_{50}, which might have been higher if conditions had been optimal.

In the Netherlands and Rwanda the last harvest took place when the vines were dead. In Tunisia the crops were harvested before complete senescence, so the value for D_{50} could not always be assessed. In practice the last harvest represents D_{50}, since the crop growth ceased very quickly after this date. In the Tunisian summer season this would happen because of high temperatures and in the Tunisian autumn season production almost ceased after this date, because of the low radiation; therefore for these seasons the last harvest was taken as D_{50}.

Of all the experiments, only the harvest index of the Tunisian autumn trial was statistically significantly lower and no difference was found between the other sites. We attributed this to the fact that at all sites except Tunisian autumn the growth cycle of the crop was completed. In Tunisian autumn the radiation levels dropped quickly at the end of the growing season and tuber bulking stopped, resulting in the low harvest indices. The low harvest index found in Tunisian autumn agrees with the results obtained by Fahem and Haverkort (1988). When a growth cycle is completed, tuber dry matter production is mainly determined by the total dry matter production.

Variation in total dry matter production of the crop could well be expressed in terms of light interception and light-use efficiency. The light-use efficiency at the different sites was not constant but the values found were similar to those found by others. Haverkort and Harris (1987) found values for Rwanda ranging from 2.29 g MJ^{-1} to 3.06 g MJ^{-1} , at Rubona and

Kinigi we found respectively 2.44 and 2.47 g MJ^{-1}. In Tunisian spring the same values (1.9 g MJ^{-1}) were found as recorded by Fahem and Haverkort (1988) and Fahem (1991), whereas in Tunisian autumn the values were higher (about 3.1 g MJ^{-1} compared with 2.2 g MJ^{-1} for both Fahem and Haverkort (1988) and Fahem (1991)). The values of about 2.45 in Wageningen were in line with the values found by van der Zaag and Doornbos (1987) and Spitters (1987) for different trials in the Netherlands. Therefore the values for the light-use efficiency found in this study are representative for the sites. Differences were caused by differences in environmental conditions at the experimental sites.

Light-use efficiency correlates negatively with temperature, radiation intensity and vapour pressure deficit (Manrique et al. 1991, Haverkort and Harris, 1987). In this study no relation was found between average seasonal temperature and light-use efficiency. In Fig. 4.5 the light-use efficiency for 88 combinations of year x cultivar x site are plotted against the average seasonal light intensity expressed per hour, to correct for daylength. The values of Tunisian autumn 1991 are given in Fig. 4.5 (■) but were not included in the regression line.

Light-use efficiency correlated negatively with the light intensity, similar to the findings of Haverkort and Harris (1987) and Manrique et al. (1991). This negative correlation can be explained by a larger part of the foliage being light saturated and therefore less efficient during a larger part of the season under high light intensities. The correlation we found

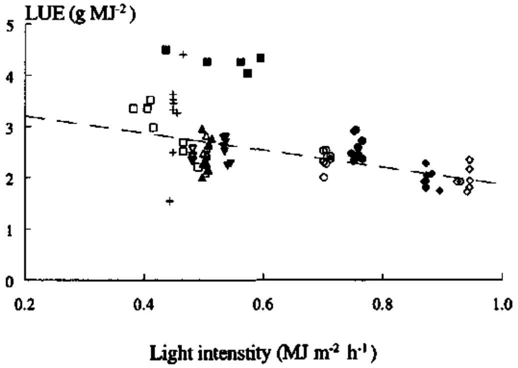


Figure 4.5 The relation between average light intensity during the growing season and the light-use efficiency. (symbols as in Fig. 4.4)

was rather weak. There are various possible explanations for this. Firstly the largest variation in light-use efficiency was found at low radiation levels. At these levels the distribution between direct and diffuse radiation changes more during the growing season, thus creating a more variable growing environment for the crop. Experimental errors also have a larger effect at low radiation levels; at 4 MJ m^{-2} an overestimation of the total dry matter production has three times the effect it has at 12 MJ m^{-2}. Secondly, for this study, average seasonal values for light intensity were used and those values had a different history at every location, with its consequences for crop growth. For example, Wageningen and Tunisian autumn did not differ much in average light intensity (Table 4.1) but the length of the growing season and the development during the season were completely different (Fig. 4.1). In Wageningen the highest values of light intensity were found in the middle of the growing season and diminished towards the end. In the Tunisian autumn however, the intensity fell sharply during the growing season.

The differences in light interception were the result of differences in light intensity between the sites (Fig. 4.1) and the ground cover duration which was affected by both site and cultivar. Light intensity correlated negatively with light-use efficiency so the effect of these two parameters on dry matter production was reduced this way correspondingly. This leaves the ground cover duration as the major parameter explaining total dry matter production. Similar results were found by Van der Zaag and Doornbos (1987) and Spitters (1987). In Fig. 4.4 we saw that the ground cover duration was determined mainly by the length of the growing season. Temperature alone could not explain the variation in length of the growing season. When the growth duration was expressed in thermal time, the individual cultivars differed statistically significantly between sites . Not only temperature but also daylength influences the duration of growth (e.g. Bodlaender,1960, Haverkort,1990). Table 4.5 shows the results of linear regression between length of the growth cycle in °Cd (t_{50}) and the daylength at emergence for the 8 cultivars. The general picture is of a growth period becoming shorter at a shorter daylength. The regression parameters show a large difference in sensitivity to daylength between cultivars. Producent appeared to be sensitive and Première insensitive, suggesting that late cultivars are more sensitive to daylength than early cultivars. (Bodlaender, 1968) The relation was not equally strong for every cultivar. Première and Bintje especially had low R-values.

We concluded that the main factor determining yield was the length of the growth period. When cultivars were transported from one climate to another they all reacted in a similar

Table 4.5 Regression parameters (n=11) of the relation between daylength at emergence and length of the growing season in °Cd.

	constant (°Cd)	slope (°Cd h^{-1})	coefficient of determination r
Alpha	-597	142	0.93
Bintje	-879	151	0.68
Désirée	-318	118	0.94
Diamant	-508	132	0.89
Escort	-148	107	0.81
Première	271	63	0.70
Producent	-934	174	0.92
Spunta	-123	102	0.93

way. Both a higher average temperature during the growing season and a shorter daylength at emergence resulted in a shorter duration of growth. However, the extent of these effects differed between cultivars, affecting the stability for total dry matter production, and thus tuber production between sites. These differences in reaction may be important in plant breeding. Breeding for high yields at one location does not guarantee high yields at other locations. We even found the opposite; in our study, the late cultivars in Wageningen seemed to be more sensitive than the early cultivars.

By analysing the crop in terms of cumulative light interception and average light-use efficiency a major part of the variation in yield between the cultivars and between sites could be explained and related to daylength and temperature. Growth duration is the result of underlying processes as crop growth, dry matter allocation and leaf senescence (Chapter 2). Insight into the background of these relations enables best cultivar for a given environment to be selected rationally or crop management to be directed in such a way that less adapted cultivars give higher yields.

GENOTYPE-ENVIRONMENT INTERACTION IN POTATO 2: DRY MATTER ALLOCATION AND DURATION OF THE GROWTH CYCLE

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ABSTRACT

The total growth and tuber dry matter production of a potato crop are mainly determined by the duration of its growth cycle. This in turn depends on climate, cultivar and crop management. The influence of the climate factors defining crop growth and the timing of this influence were analysed by dividing the growth cycle into three phases and relating these phases to temperature, daylength and radiation. The variation in the length of all three phases contributed to the variation in the duration of the growth cycle and thus to the variation in tuber yield. The variation in the first phase (between emergence and tuber initiation) was best explained by the meteorological variables observed. Both higher temperatures and shorter daylengths hastened the development in this phase. The magnitude of the change depended on the cultivar. In the second phase, from tuber initiation to end of leaf growth, temperature and daylength had similar effects but they were less clear and the variation in the duration of phase 2 could not be explained as well as the variation in phase 1. The last phase from end of leaf growth to end of crop growth was shortened by high temperatures and radiation levels. A small part of the variation in the duration of this phase was explained. At this level of crop analysis, the effect of climate on crop development was explained best for the first phase, which is the most important phase. Quantitative understanding of the processes involved is required to be able to explain the effect of-climate during the various phases of the growth cycle.

INTRODUCTION

The dry matter production of potato crops is mainly determined by the length of their growth cycles (Spitters 1987; Moll et al. 1987; Allen and Scott 1980). The variation in the duration of the growth cycle depends on site and cultivar (Kooman et al., chapter 4). Under non-limiting growth conditions, temperature and daylength determine the differences between sites. Short daylengths reduce the duration of the growth cycle (Haverkort 1990; Menzel 1985a; Kooman et al., chapter 4). High temperatures (> 25 °C) may have two effects. One is to extend the period of leaf growth and hence prolong the growth cycle (Marinus and Bodlaender, 1975). But high temperatures also increase the leaf senescence rate (Menzel 1985a) and through this they shorten the growth cycle of a crop. Thus depending on the relative importance of both processes, higher temperatures either prolong or curtail the growth cycle. The period of leaf growth varies among cultivars, and so does the influence of daylength and temperature on their vegetative growth (Spitters 1987; Kooman et al., chapter 4).

Leaf growth is the result of daily dry matter accumulation by the crop and the allocation of this dry matter to the leaves. Figure 5.1a shows the pattern of dry matter allocation of a standard potato crop in the Netherlands (after van Heemst, 1986). Roots are not included because accurate data are seldomly available. Three phases in the allocation of daily accumulated dry matter can be distinguished. Initially, dry matter is divided between stems and leaves. In the second phase, which starts at tuber initiation, an increasing part is allocated to the tubers and a decreasing fraction to the leaves. In the third phase all assimilates are allocated to the tubers. Then leaf growth stops, and the light interception of the crop will cease because of leaf senescence.

Environmental factors influence all three phases in the development of a potato crop. The duration of the first phase, between emergence and tuber initiation is shortened by short days (Ewing and Struik, 1992; Wheeler and Tibbits, 1987; Gregory, 1956; Haverkort 1990) and at temperatures under 20°C, tuber initiation is faster than at temperatures above 20 °C (Bodlaender, 1960; Gregory, 1956; Ewing, 1981; Ewing and Struik, 1992). The length of the second phase, between tuber initiation and allocation of all accumulated daily dry matter to the tubers, is influenced by temperature, with an optimum between 16 and 18 °C (van Heemst, 1986) or 14 and 22 °C (Ingram and Mccloud, 1984) and by solar radiation. The third and last phase of crop senescence is shortened by high temperatures, especially temperatures above 30 °C (Midmore, 1990; Fahem and Haverkort, 1988).

The objective of this study was to establish the relationship between the duration of the 3 phases and temperature, daylength and global radiation. This information may explain the variation between tuber yields of different cultivars under different climatological conditions and give quantitative information to be used in a potato growth model.

MATERIAL AND METHODS

Eleven field trials were carried out in two years at six sites. The sites were chosen such that their climatic conditions covered a broad range of temperature and daylength conditions in which potatoes are produced (Table 4.1, Kooman et al., chapter 4). Eight cultivars were planted at each site. These cultivars were chosen because of their difference in lateness in the Netherlands, ranging from early (Première) to very late (Producent) (Table 5.1). Except for the Tunisian winter trial, all trials were carried out twice.

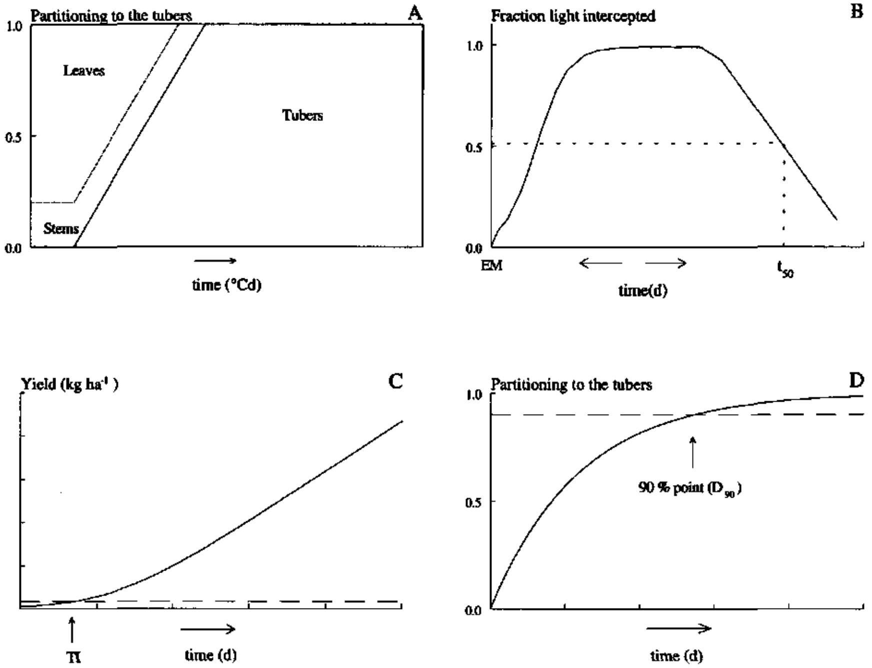


Figure 5.1 (A) Relationship between dry matter partitioning between tubers, leaves and stems and thermal time (°Cd) for a potato crop in the Netherlands. (After van Heemst 1986). The fractional light interception with time of a potato crop during the growing season (B, EM is moment of emergence, t_{50} is moment that light interception has decreased to 50 %). The dry matter production of potato tubers during the growing season, described by an expolinear relation (C, TI is moment of tuber initiation). The dry matter partitioning to the tubers against time, described by a negative exponential function (D, D_{90} is moment that 90% of assimilates is partitioned to the tubers).

In all experiments seed potatoes were planted in rows 0.75 m apart and at 0.30 m spacing within the row. The management of the crop at each site was aimed at maximal tuber yields The crops in the Netherlands and in Tunisia were irrigated. The crops in Rwanda were grown in the rainy season, with ample supply of water. The trials had two replicates in Tunisia and three replicates at the other sites.

Data collection

The duration of the growth cycle was measured by using a grid to record the proportion of ground covered with green leaves (Haverkort 1990; Kooman et al. chapter 4). Observations were carried out about once every 10 days. Three to six periodic harvests were carried out per growing season (Table 4.1). In the Tunisian spring season of 1991 only three periodic harvests were carried out, because this growing season was extremely short as a result of the late crop emergence. At Kinigi in 1992, and in the Tunisian winter season, five harvests were carried out. In the 1992 Tunisian spring and autumn seasons six periodic harvests were carried out. In the Netherlands 12 plants were lifted at each periodic harvest and at the final harvest 24 plants were lifted. At the other sites, 6 plants were lifted at the periodic harvests and 12 at the final harvest. In most trials, plant material was divided into leaves, stems, tubers and other underground parts. In the Netherlands 1992, Tunisian autumn 1992 and the Tunisian winter trials, the crop was separated into tubers, foliage and underground parts. The fresh and dry weight of each plant fraction were determined. Dry weight was determined by drying samples of the plants for 24 hours at 105 °C.

Data analysis

Four characteristic points in the growth cycle were determined for each combination of site and cultivar : emergence, tuber initiation, end of leaf growth and end of crop growth. *Emergence* was defined as the day by which 50 % of the plants had emerged. The *end of crop growth* was defined as the day when the ground cover was reduced to 50 % of total ground cover, after which little or no tuber production takes place.(Fig. 5.1b). If the crop was harvested before this day, the last harvest was defined as the end of crop growth. *Tuber initiation* was estimated from the growth curve of the tubers using the following procedure. When tuber dry matter is plotted against time, the first phase of tuber growth is exponential and later in the season the tuber growth is linear. These two phases together were described with an expolinear function (Fig. 5.1c) (Goudriaan and Monteith, 1990). The relative growth rate in the exponential stage was taken from Ingram and McCloud (1984) at the value of 0.37 $g\ g^{-1}\ m^{-2}\ d^{-1}$. The other parameters were estimated through nonlinear regression. The calculated moment when the tuber dry mass was equal to 1 $g\ m^{-2}$ was defined as the tuber initiation. A negative exponential relation best described the dry matter distribution between tubers and foliage with time (Fig. 5.1d). When 90 % of the dry matter is allocated to the tubers, leaf growth has practically ceased, therefore this moment was defined as the *end of leaf growth*.

Table 5.1 The duration of the period, from emergence to tuber initiation, from tuber initiation to end of leaf growth and from end of leaf growth to end of crop growth (days)

Location	Cultivar	Emergence-tuber initiation (d)	Tuber initiation - end leaf growth (d)	End of leaf growth-end of crop growth (d)
Wageningen	Alpha	25	43	50
	Bintje	21	30	49
	Désirée	22	31	53
	Diamant	24	35	49
	Escort	21	26	50
	Première	19	28	38
	Producent	21	40	65
	Spunta	26	34	44
Kinigi	Alpha	18	27	38
	Bintje	13	25	38
	Désirée	15	32	35
	Diamant	15	29	37
	Escort	13	27	42
	Première	14	15	50
	Producent	13	28	42
	Spunta	18	32	32
Rubona	Alpha	12	24	28
	Bintje	12	24	15
	Désirée	9	26	30
	Diamant	9	16	40
	Escort	11	17	58
	Première	6	33	29
	Producent	11	22	42
	Spunta	11	23	30

Continue Table 5.1

Location	Cultivar	Emergence-tuber initiation (d)	Tuber initiation - end leaf growth (d)	End of leaf growth-end of crop growth (d)
Tunisia autumn	Alpha	25	31	28
	Bintje	17	40	25
	Désirée	16	49	8
	Diamant	7	38	19
	Escort	13	35	30
	Première	14	33	28
	Producent	13	36	11
	Spunta	17	31	27
Tunisia spring	Alpha	15	27	21
	Bintje	15	26	26
	Désirée	19	35	16
	Diamant	18	31	24
	Escort	15	29	28
	Première	24	24	22
	Producent	21	21	35
	Spunta	20	28	21
Tunisia Winter	Alpha	42	14	46
	Bintje	14	16	38
	Désirée	26	29	42
	Diamant	26	24	66
	Escort	19	34	31
	Première	27	18	47
	Producent	22	23	51
	Spunta	26	25	47

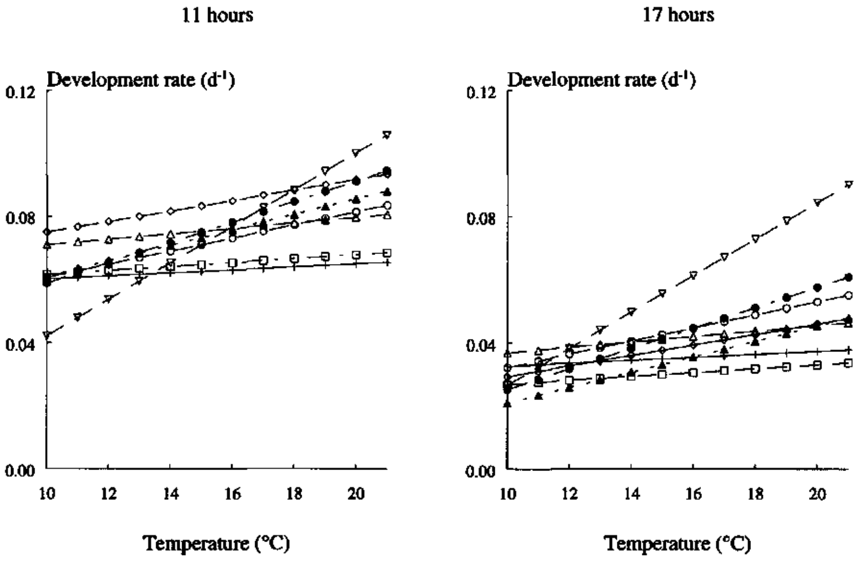


Figure 5.2 The development rate (d^{-1}) during phase 1, from emergence to tuber initiation against temperature (°C) for Alpha (+), Bintje (Δ), Désirée(O), Diamant(▲), Escort(●), Première(∇), Producent (◊) and Spunta (□) at two daylengths.

For the first and the third phases (between emergence and tuber initiation, and between end of leaf growth and end crop of growth) the development rate was calculated as the inverse of its duration. For the second phase (between tuber initiation and end of leaf growth) the initial slope of the curve in Fig. 5.1d was taken as the development rate (d^{-1})

Relation between length of phases and climatic factors

The development rate of each phase was related to the climatic factors that determine crop growth and development under non-limiting conditions. The climatic factors tested were radiation intensity, temperature and daylength. Temperature and radiation were averaged over each phase and daylength was taken at the start of each phase. For each day, the average radiation intensity was calculated by dividing the total daily radiation by the length of the photoperiod.

Table 5.2a Significance of the effect of Temperature (T), daylength at emergence (D) and Radiation intensity (R) on the rate of development during phase 1: from emergence to the tuber initiation. (** P < 1 %, * P < 5 %, - not significant)

Cultivar	T	D	R
Alpha	*	**	*
Bintje	*	-	*
Désirée	**	**	-
Diamant	*	**	-
Escort	*	*	-
Première	*	-	-
Producent	-	*	-
Spunta	-	**	-

Table 5.2b Regression parameters of the effect of Temperature (T), daylength at emergence (D) on the rate of development during phase 1: from emergence to the tuber initiation. (1/duration = development rate = C + aT+bD)

Cultivar	C	a ($^{\circ}C^{-1} * 10^{-3}$)	b ($h^{-1} * 10^{-3}$)	r^2_{adj}
Alpha	0.106	0.47	-4.59	98.3
Bintje	0.125	0.86	-5.69	30.3
Désirée	0.092	2.07	-4.73	92.1
Diamant	0.110	2.45	-6.68	95.8
Escort	0.088	3.23	-5.59	78.7
Première	0.013	5.77	-2.59	44.2
Producent	0.142	1.66	-7.60	66.0
Spunta	0.119	0.62	-5.78	88.8

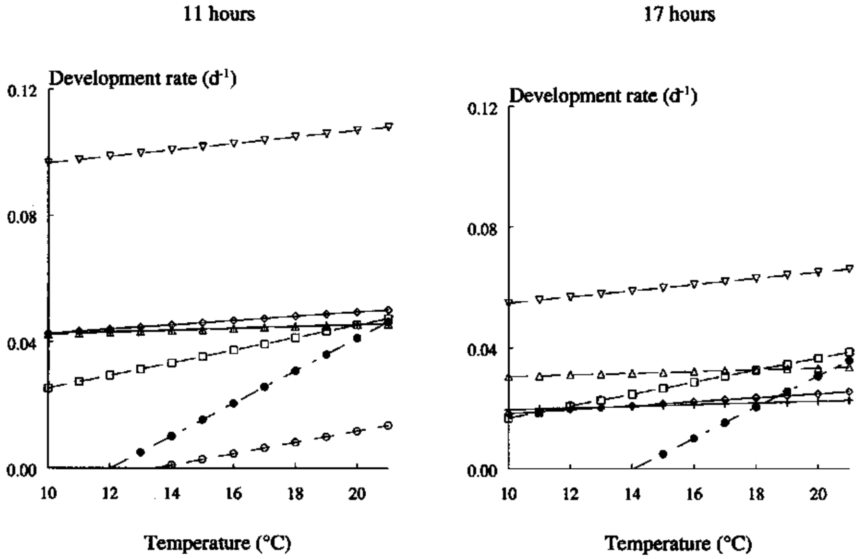


Figure 5.3 The development rate (d^{-1}) during phase 2, from tuber initiation to end of leaf growth against temperature (°C) for Alpha (+), Bintje (Δ), Désirée(O), Diamant(▲), Escort(●), Première(∇), Producent (◊) and Spunta (☐) at two daylengths.

First, a multiple regression equation was derived by selecting the combination of explanatory factors with the highest R^2, adjusted for degrees of freedom. Secondly, the significance of the various factors was expressed as the t-value for their contribution to the multiple regression equation. In this analysis the experiments of the Tunisian autumn and winter were excluded because of the different physiological age of the seed tubers. Rubona 1992 was excluded because of an irregular emergence of the crop as a result of a dry spell. The premise of undisturbed growth was not fulfilled in these trials.

RESULTS

Phase 1: Emergence to tuber initiation

In the Netherlands, the phase between emergence and the tuber initiation lasted about 22 days. In the Tunisian spring, phase 1 was a little shorter, about 20 days and in the Tunisian winter the average duration of this phase was 25 days. At Kinigi and in the Tunisian autumn this phase lasted respectively 13 and 14 days and the duration in

Table 5.3a Significance of the effect of Temperature (T), daylength at emergence (D) and Radiation intensity (R) on the rate of development during phase 2: from the tuber initiation to end of leaf growth. (** $P < 1$ %, * $P < 5$ %, - not significant)

Cultivar	T	D	R
Alpha	-	**	-
Bintje	-	*	-
Désirée	*	*	-
Diamant	*	-	**
Escort	*	-	-
Première	-	*	-
Producent	-	*	*
Spunta	*	-	-

Table 5.3b Regression parameters of the effect of Temperature (T) and daylength at tuber initiation (D) on the rate of development during phase 2: from the tuber initiation to the end of leaf growth. (1/duration= development rate = C + aT+bD)

Cultivar	C	a ($°C^{-1} * 10^{-3}$)	b ($h^{-1} * 10^{-3}$)	r^2_{adj}
Alpha	0.0822	0.29	-3.86	65.6
Bintje	0.0614	0.29	-1.99	36.0
Désirée	0.0078	1.80	-2.91	41.0
Diamant	-0.1050	3.10	-5.02	27.0
Escort	-0.0432	5.17	-1.73	90.0
Première	0.163	1.03	-6.97	-
Producent	0.0810	0.67	-4.09	54.1
Spunta	0.0212	2.00	-1.44	45.4

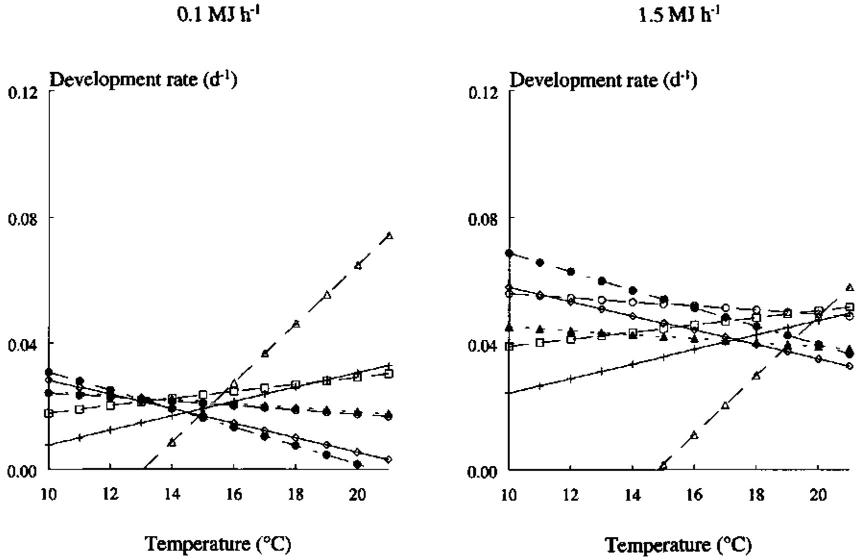


Figure 5.4 The development rate (d^{-1}) during phase 3, from end of leaf growth to end of crop growth against temperature (°C) for Alpha (+), Bintje (Δ), Désirée(O), Diamant(▲), Escort(●), Première(∇), Producent (◊) and Spunta (□) at two light intensities.

Rubona 1991 was about 10 days. Table 5.2a shows that the length of the period between emergence and tuber initiation in most of the cultivars was affected by temperature and daylength but not by radiation. The lowest coefficients of determination occurred in Bintje and Première, which were the earliest cultivars in the Netherlands. In the other cultivars, more than 70 % of the variation in phase 1 was explained by the influence of temperature and daylength.

Figure 5.2 shows the fitted relations between the rate of development and temperature at respectively 11 and 17 hours daylength for the eight cultivars. Higher temperatures shortened the duration of phase 1 in all cultivars. Least sensitive to temperature were Alpha, Spunta and Bintje (Table 5.2b, Fig. 5.2). For these cultivars the largest difference in development rate found was about 0.006 d^{-1} between the highest and lowest temperatures. When the temperature rose from 10 to 21 °C the development rate between emergence and tuber initiation of Première increased tenfold compared to that of Alpha, Spunta and Bintje.

Table 5.4a Significance of the effect of Temperature (T), daylength at emergence (D) and Radiation intensity (R) on the rate of development during phase 3: from end of leaf growth to end of crop growth. (** $P < 1$ %, * $P < 5$ %, - not significant)

Cultivar	T	D	R
Alpha	-	-	-
Bintje	*	*	-
Désirée	*	-	*
Diamant	-	-	*
Escort	*	-	*
Première	-	-	-
Producent	*	-	*
Spunta	*	-	*

Table 5.4b Regression parameters of the effect of Temperature (T) and radiation intensity (R) on the rate of development during phase 3: from the end of leaf growth to the end of crop growth. (1/duration= development rate = C + aT+bR)

Cultivar	C	a ($°C^{-1} * 10^{-3}$)	b ($MJ^{-1} h^{-1} * 10^{-2}$)	r^2_{adj}
Alpha	-0.0165	2.30	1.19	35.3
Bintje	-0.1217	9.39	-1.16	31.5
Désirée	0.0285	-0.66	2.27	70.7
Diamant	0.0296	-0.64	1.48	49.5
Escort	0.0572	-2.91	2.71	82.9
Première	-0.0250	-2.85	0.83	38.6
Producent	0.04894	-2.28	2.12	74.0
Spunta	0.0049	1.14	1.52	67.2

Longer days retarded tuber initiation. The cultivars differed less in daylength reaction than in temperature reaction. In this experiment, where daylength varied from 11 to 17 hours, the largest effect of daylength on the duration of phase 1 was 0.046 d^{-1} for Producent and the smallest for Première (0.015 d^{-1}). The rates of development between cultivars differed least between 12 and 16 °C and most at high temperatures in combination with long days

Phase 2: Tuber initiation to end of leaf growth

Phase 2 was longer than phase 1. It ranged from about 37 days in the Tunisian autumn, 33 days in Wageningen, about 28 days in the Tunisian spring and Kinigi, to 22 and 24 days in Rubona and Tunisian winter. The variation was largest in the Tunisian winter (Table 5.1). On average, this phase was longest for Désirée and shortest for Première. Higher temperatures increased the development rate during phase 2 statistically significantly in four of the eight cultivars (Table 5.3a). For daylength, the increase in development rate during this phase was statistically significant in five of the eight cultivars. Radiation intensity had a statistically significant effect on the development rate in phase 2 in Diamant and Producent only. Based on these data we conclude that daylength and temperature are the major factors influencing development rate in this phase. The percentage of variation accounted for was lower in the second phase than in the first phase. On average it was 45 %, with 0 % for Première and 90 % for Escort as extremes.

As in phase 1, high temperatures and short days shortened the length of phase 2 (Table 5.3b, Fig. 5.3). The effects of daylength and temperature were in the same order. The cultivars in which temperature had no statistically significantly effect had low coefficients for this factor (Table 5.3b) and thus were relatively insensitive to temperature. The largest increase in development rate was found in Escort, 0.06 d^{-1} between 10 and 21 °C. The effect of daylength showed less variation between cultivars than the effect of temperature. The largest increase due to short days was found in Première and the smallest in Spunta and Escort. During phase 2 the difference in development rate between cultivars was larger under short days than under long days.

Phase 3: End of leaf growth to end of crop growth

The duration of the third phase of the growth cycle showed more variation between sites and cultivars than phases 1 and 2. In the Netherlands, Phase 3 lasted about 50 days, compared with only about 23 days in the Tunisian spring and autumn seasons (Table 5.1).

On average this phase was longest for Escort and shortest for Désirée. Phase 3 was affected by both temperature and radiation intensity but not by daylength (Table 5.4a). The effect of temperature was not as clear as the effect of radiation intensity. In five cases the temperature effect was negative, indicating that senescence slowed down under higher temperatures. Only Bintje showed an acceleration of senescence at higher temperatures. High radiation levels hastened senescence in all cultivars except for Bintje. The rate of development during phase 3 increased by 0.012 d^{-1} for Première to 0.038 d^{-1} for Escort when the average hourly light intensity increased from 0.1 to 1.5 MJ h^{-1} (Fig. 5.4).

DISCUSSION

In an earlier paper (Kooman et al., chapter 4) it was demonstrated that the major factor determining tuber yield was the length of the growth period. The division of this period into three phases enables the timing and magnitude of temperature and daylength effects on tuber yield to be analysed.

Phase 1 was the shortest phase, with an average duration of 17 days, and its direct influence on the length of the growth cycle was relatively small. Within the range studied, both higher temperatures and shorter days hastened tuber initiation and thus shortened the duration of phase 1. The relation between the length of phase 1 and temperature and daylength explained the largest part of the variation in the duration of this phase. Therefore the relation between the duration of this phase and temperature and daylength could be better quantified than the following phases. The relation found in this phase coincided well with results found by others in previous studies. Development rate increases with higher temperatures, and maximum development rates have been reported between 14 and 22°C (Driver and Hawkes, 1943; Yamaguchi et al, 1964). This wide range can be narrowed down to values between 18 and 21°C (Marinus and Bodlaender 1975; Sands et al, 1979; Manrique, 1992). When the temperature exceeds the optimum, the development rate slows down and no tuber initiation takes place above temperatures between 23 and 30°C. (e.g., Bodlaender, 1963; Epstein, 1966; Menzel, 1985b; Manrique, 1992). Most of the trials in the present study were executed below or near the optimum temperature. This explains why development rate was found to increase with higher temperatures.

The effect of daylength found in this study corresponds with the hastened tuber initiation at shorter days found by Gregory (1956) or postponed tuber initiation at longer days found by Ewing and Struik (1992). Differences in daylength sensitivity between cultivars were reported by Ewing (1981) and Menzel (1985b). They expressed this as a difference in critical photoperiod (i.e. the photoperiod that still permits tuber initiation). In contrast with this concept, the data in the present study indicate a gradual effect of daylength. Note that the Wageningen experiments exert a relative large influence on the sensitivity for daylength because here the days were much longer than at the other locations (17 compared with 10.5 to 13 h).

The second phase lasted about 29 days on average with, a minimum of 14 and a maximum of 49 days (Table 4.1, Fig. 5.3). The effects of temperature and daylength on the duration of phase 2 could explain less of the variation between cultivars and locations than in the first phase. This means that the temperature and daylength have a minor influence on allocation of assimilates to the tubers once tuber growth is established, given the range in temperature and daylength in the experiments.

Temperature affects dry matter allocation, but its effect is strongest at high temperatures (around 30 °C)(Ben Khedher and Ewing, 1985; Kraus and Marschner, 1984; Ng and Loomis, 1984) and low temperatures (below 10 °C)(Spitters et al., 1989; Van Heemst 1986). Near the optimum temperature, reported to be 18 °C (Van Heemst 1986) or 21 °C (Sands et al., 1979; Sale, 1979), little variation in allocation to the tubers is found. Ingram and McCloud (1984) found little reaction of tuber growth rate between 12 and 25 °C. The small effects in the present study, where the temperature ranged between 10 and 21°C, agree with these data. The effect of daylength in this phase may be the result of the promoted tuber initiation at shorter days.

The length of the third and last phase in the growth cycle showed the greatest variation between sites and cultivars. In the Netherlands, where temperatures and radiation levels were low during Phase 3 and the crop senesced slowly, it took about 50 days on average for the crop to die completely. In the Tunisian autumn similar conditions were found and here the crop was harvested when the crop growth ceased in response to radiation levels, although the leaves were still green. In this case, the phase was shortened artificially by harvesting. In the Tunisian spring and at Rubona at the end of the growing season the temperatures and the radiation intensity were high and the crop senesced quickly. Fahem and Haverkort (1988) also found this for the Tunisian spring season. In our study we found contradictory effects of temperature on the duration of phase 3. This may be explained by the fact that high temperatures can have two effects on the potato crop in this phase.The first effect is that the sink strength of the tubers is less at higher temperatures resulting in a slower leaf senescence rate and a prolonging of phase 3. The second effect is that the leaf senescence is hastened by higher temperatures (Marinus and Bodlaender, 1975) and phase 3 is shortened. An analysis at process level is needed to reveal these effects.

Higher light intensities tended to hasten crop senescence. It may well be, however, that crop transpiration rates increase at higher light intensities, as they tend to be associated with higher temperatures and greater vapour pressure deficits. Senescence is then accelerated because of higher leaf temperatures and the exhaustion of the amount of soil moisture available to the crop.

The effects of temperature and daylength on the duration of the phases after tuber initiation are less clear than on the phase before tuber initiation and seem to be overruled by other factors such as the availability of water and nutrients. Shortages of water and nutrients become increasingly important later in the growing season because the crop reacts by increasing the allocation to the tubers (Spitters and Schapendonk, 1990) and accelerating senescence (Devaux and Haverkort, 1987). During phases 2 and 3 the effect of shortages will exert more influence on the phase duration than in phase 1. It will therefore be more difficult to reveal relations with climatic factors at this level of analysis.

From this study we conclude that temperature and daylength exert the greatest influence on the duration of the crop growth cycle (and thus on final yields), mainly through their effect on the period between emergence and tuber initiation. The duration of this phase is

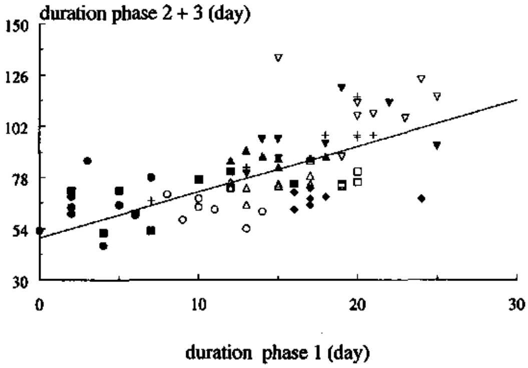


Figure 5.5 The duration of phase 1 against the joined duration of phase 2 and 3 for all cultivar x location combinations in the experiments.

of crucial importance for the total duration of the growth cycle. Figure 5.5 shows that an increase of phase 1 results in a twice as large increase in phases 2 and 3 combined. This can be explained by the fact that the early tuber initiation results in less foliage biomass production. Plants with a small amount of foliage biomass distribute relatively more of the assimilates to the tuber, thus phase 2 is shortened, and senescence is accelerated, resulting in a shortening of phase 3. (Kooman chapter 2; Sale, 1973a; Sale, 1973b; Moorby, 1978).

The results of this analysis of crop growth and development divided into three crucial phases will be used in the model described in chapter 5. This model is used to calculate potential yields for a given growing season and to indicate the cultivar characteristics with regard to responses to temperature and daylength necessary to achieve such yields.

CHAPTER 6

MODELLING DEVELOPMENT AND GROWTH OF THE POTATO CROP INFLUENCED BY TEMPERATURE AND DAYLENGTH: LINTUL-POTATO

P.L. Kooman and A . J. Haverkort

ABSTRACT

A model "LINTUL-POTATO" is described which bases total dry matter production on light-use efficiency of intercepted light by a potato crop. The course of light interception by green leaves initially is temperature-sum dependent and is also steered by influences of daylength and temperature on assimilate partitioning. Dry matter allocation to the foliage, which determines the final length of the growing period, is determined by a daylength and temperature dependent period between emergence and tuber initiation and subsequent partitioning of dry matter to the tubers. Once the tuber daily growth rate equals total crop dry matter accumulation, no more foliage is formed and the crop senesces faster at higher temperatures. The aim of this paper is to explain effects of temperature and daylength on total tuber production from the effects of these environmental factors on the underlying processes. The relative effect of temperature on rates of emergence, light-use efficiency, tuber initiation and tuber growth, and, the effect of daylength on development rate until tuber initiation are represented quantitatively. Potential tuber production at some temperature and daylength regimes is calculated exploratively and compared with results from the literature. The model can be used to simulate tuber dry matter production in specific environments and to select cultivars for such environments with suitable temperature and daylength reactions on tuber initiation and dry matter partitioning so as to maximise yields.

INTRODUCTION

The model LINTUL-POTATO is described in this chapter. This model simulates the Light INTerception and UtiLisation, temperature and daylength reactions of POTATO crops grown in different climates. The model is based on the light interception and utilisation model described by Spitters (1987) and Spitters and Schapendonk (1990) and adds temperature and daylength relations. A number of models simulating development and yield of potato have been described, which all perform relatively well under temperate long day conditions (Kabat et al., 1994). Such models, however, do not perform well in (sub)tropical conditions. In such climates, high temperatures during part of the year in lowland areas make the period or area unsuitable for potato growth. In addition to high temperatures, the prevailing short days, sometimes shorter than 11 h, also strongly affect the development of the crop, and often lead to inadequate yields (Haverkort, 1990). Models developed under tropical conditions (e.g. Haverkort and Harris, 1987) cannot be used under temperate conditions for similar reasons. There is a need for a model that includes crop reactions to temperature and daylength on those crucial processes that determine the length of the growth cycle and therefore the yield of the crop (chapters 4 and 5; Allen and Scott, 1980). Exploration of the yielding ability of crops in different agro-ecological zones (van Keulen and Stol, 1995) can then be carried out more accurately. Such a model may also offer breeders the scope to breed for cultivars which make the most effective use of a given environment described in terms of the yield-defining factors daylength, temperature and solar radiation which cannot be altered by the grower. Growers can affect yield limiting factors through irrigation and fertilisation and they can affect yield reducing factors through crop protection measures. The effect of yield limiting and yield reducing factors on crop growth and development are not included in LINTUL-POTATO.

In chapter 4 and 5 the effect of temperature and daylength on growth and development of 8 cultivars in different environments in the Netherlands, Tunisia and Rwanda is described. Temperature and daylength affected crop production in different ways (see also Struik and Ewing, 1995). Temperature influences dry matter production directly through its influence on daily growth rate. Temperature and daylength influence production indirectly through their influence on development, thus limiting the duration of the growth cycle and

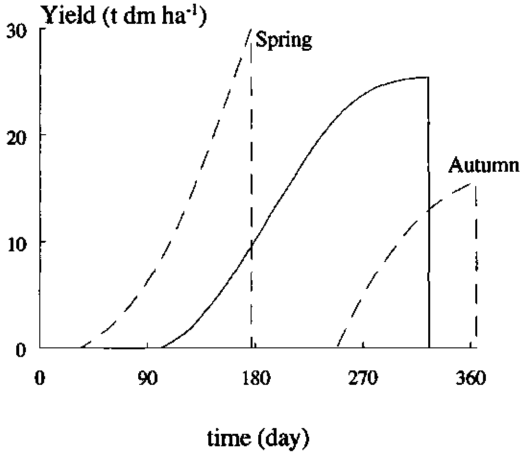


Figure 6.1 Potential total crop dry matter production in the Netherlands (———) and Tunisia (— —)

yielding ability of the crop. This is illustrated in Figure 6.1 with long-term temperature and solar radiation data from Tunisia and the Netherlands. One single season in the Netherlands and two distinct growing seasons in Tunisia occur, assuming that no potato crop growth is possible below 2 °C and above 30 °C (van Keulen and Stol, 1995). During winter, minimum daily temperatures in the Netherlands are constantly below 2 °C and below 28 °C in summer allowing a single, relatively long growing season of about six months. There is roughly one month period with temperatures that are too low and a three month period with mean daily maximum temperatures above 28 °C, leading to two annual seasons suitable for potato production. With a potential light-use efficiency of 2.5 g MJ^{-1} based on PAR. Figure 6.1 illustrates that potential dry matter production in the Tunisian spring is higher than in the temperate summer, that such a dry matter production can be achieved in much less time and that, in the Mediterranean area, potential yields in the autumn season are about half those in the spring season as was found by Fahem and Haverkort (1988). LINTUL-POTATO simulates potential dry matter production in different environments through the relative effect of temperature on rates of emergence, light-use efficiency, tuber initiation and tuber growth. Moreover, the effect of daylength on development rate until tuber initiation is quantitatively represented and potential tuber dry matter production is calculated exploratively under some regimes of temperature and daylength .

An analysis of the system of tuber yield formation enables an approach that may be used in areas with widely varying temperature and daylength regimes. Total crop dry matter production is determined by the length of the growth cycle which is divided into four phases each starting and ending by a characteristic stage of development. Phase 0 starts at planting and ends at emergence. Phase 1 , when only foliar growth takes place, is from emergence to tuber initiation. Phase 2 is from tuber initiation until the end of leaf growth (defined as the moment when 90 % of the assimilates which are produced daily, are partitioned to the tubers). In this Phase 2 there is competition for assimilates between tubers and foliage. Phase 3, finally, is from the end of leaf growth until the end of crop growth. In Phase 3 all assimilates are partitioned to the tubers. The development of radiation interception and of the daily partitioning of dry matter to the tubers is represented schematically in Figure 6.2. The system is conveniently divided into the four phases, each with its own key processes described by variables and parameters with values depending on temperature and/or daylength:

- Phase 0 between planting and emergence (when 50 % of the plants have emerged) the duration of which is determined by the sprout growth rate which depends on temperature;
- Phase 1 between emergence and tuber initiation (also defined as the start of tuber growth) the duration of which depends on the development rate until tuber initiation. In the Phases 1 through 3 the crop growth rate is calculated using foliar expansion rate, while the light-use efficiency determines the total amount of dry matter produced;
- Phase 2 between tuber initiation and the moment when 90 % of the daily acquired assimilates are partitioned to the tubers. This value is arbitrarily chosen as 100 % partitioning is only reached asymptotically and, as such, cannot be determined precisely. The length of Phase 2 depends on the relative tuber growth rate which determines partitioning of dry matter between the tubers and the rest of the plant;
- Phase 3 lasts until the end of crop growth. The length of the period of Phase 3 is determined by the leaf senescence rate.

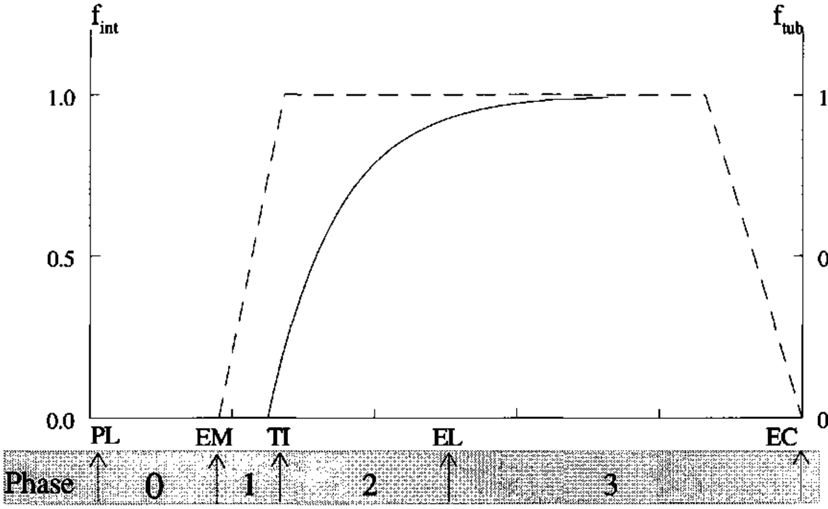


Figure 6.2 Schematic representation of the fraction of solar radiation intercepted by the crop (— —, f_{int}) and the fraction of the daily assimilate that is partitioned to the tubers (———, f_{tub}) from planting (PL) to emergence (EM), the start of tuber growth (TI), the moment that f_{tub} reaches the value of 0.9 (EL) until the end of crop growth (EC)

LINTUL-POTATO explains the effect of temperature and daylength on final tuber dry matter production through the quantification and integration of temperature and daylength effects on the major growth and development processes described in the Phases 0-3. The model is also aimed at simulating tuber dry matter production in specific environments and to select cultivars for such environments with suitable temperature and daylength reactions on tuber initiation and dry matter partitioning to maximise yields.

Temperature and daylength relations in LINTUL-POTATO

Phase 0

Rate of emergence: temperature relations Under temperate conditions with low temperatures limiting potato growth in spring, the date of emergence may be calculated from planting depth, initial sprout length, soil temperature (often not available so in LINTUL-POTATO we use the mean daily air temperature) and the sprout growth rate of 1 mm per °Cd above a base temperature of 2 °C (MacKerron and Waister, 1985). Daylength does not influence the sprout growth rate. At sub -optimal temperatures, whether low (Klemke and Moll, 1990) or high (Sale, 1979; Midmore, 1984 and 1988, Vander Zaag et al., 1986) sprout growth rate is reduced. Figure 6.3a shows the relative effect of temperature on the sprout growth rate compounded from the data collected by these authors: at a relative rate of 1.0, the sprout growth rate is 1 mm per °Cd.

Phase 1

Rate of foliar expansion: relation to daylength Daylength is reported to influence above-ground behaviour of potato plants and crops. Menzel (1985a), Ewing and Struik (1992) and Lorenzen and Ewing (1990) reported that short days reduce stem length, branching and weight, the number and weight of leaves and to increase the size of the leaflets and the leaf/stem weight ratio. Haverkort (1990) showed that shorter days reduce the vegetative growth and lead to earlier crop senescence. These observations agree with those of Demagante and Vander Zaag (1988) who observed that lengthening the photoperiod from 11.5 to 16 h increased branching, flowering and secondary growth. At the crop level, no clear influence on light interception and leaf growth was found in chapter 4 between the various climates and cultivars tested. Since the final maximum amount of foliage differed at the various locations, It can be concluded that the observations result from a shift in tuber initiation: shorter days increase the tuber initiation rate, thus reducing the length of phase 1 in Figure 6.2 and bringing forward phase 2 and 3 leading to an earlier crop. LINTUL-POTATO, therefore, has no relation linking foliar development to daylength.

Rate of foliar expansion: relation to temperature Marinus and Bodlaender (1975) observed that foliar growth increased with temperature at low temperatures and Midmore (1984) and Vander Zaag et al. (1986) observed that foliar growth decreased with temperature at high temperatures. MacKerron and Waister (1985) linearly correlated leaf expansion from emergence to temperature above a base temperature of 2.4 °C, Spitters (1987) and Spitters and Schapendonk (1990) used a similar approach with a base temperature of 2 °C. Often minimum (0 - 7 °C), optimum (20 - 28 °C) and maximum temperatures for leaf growth have been recorded (e.g. Borah and Milthorpe, 1962; Benoit et al, 1983; Manrique, 1992). Maximum temperatures for leaf expansion have been reported as 30 °C by Ingram and McCloud (1984), 40 °C by Ng and Loomis (1984) and 35 °C by Benoit et al. (1983). We conclude from these literature data that at temperatures below 24 °C foliar expansion is linearly correlated to temperature and that it is zero again at 35 °C, as such it is simulated in LINTUL-POTATO with optimum rate shown in Table 6.2.

Development rate until tuber initiation: relation to daylength Shorter days have been reported to increase the development rate until tuber initiation defined as the inverse of the number of days between emergence and the start of tuber growth. Some authors (e.g. Regel and Sands, 1983) reported the existence of a 'critical photoperiod' of 14.1 h for cv. Sebago and 15.5 h for cv. Kennebec above which tuber formation is retarded. Others (e.g. Lorenzen and Ewing, 1990 and Struik et al., 1988) reported that a shift from long (16 - 18 h) to short (10 - 12) days increased the development rate until tuber initiation and that short days compared to long days lead to earlier tuber initiation (Snyder and Ewing, 1989; Wolf et al., 1990a and Ewing and Struik, 1992). This was confirmed under field conditions in chapter 5, where a negative relation between development rate until tuber initiation and the photoperiod prevailing at emergence of the crop was reported. The relative effect of daylength (example of 11 h and 17 h) on development rate until tuber initiation as it is included in LINTUL-POTATO is shown in Figure 6.3c with optimum rate shown in Table 6.2.

Development rate until tuber initiation: relation to temperature Under temperate conditions higher temperatures increase the tuberisation rate (Menzel, 1983 and Hay and Allen, 1978) so that thermal time from planting with a base temperature of 0 °C describes the tuberisation rate well (Jefferies and MacKerron, 1987). There is, however, an optimum as many reports on the relation between tuber initiation and temperature concern the observation that high temperatures retard tuber initiation under tropical conditions (Sands et al., 1979, Manrique and Hodges, 1989; Struik et al., 1989a,b, Reynolds and Ewing, 1989) Minimum (0-7 °C), optimum (15 to 20 °C) and maximum (25-30 °C) temperatures for tuber initiation rates have been reported by Borah and Milthorpe, 1962, Sale, 1979; Manrique and Hodges, 1989 and by Ingram and McCloud (1984). The effect of photoperiod was found by Struik and Ewing (1992) to be more pronounced at higher temperatures. This was corroborated in chapter 5, where a decrease of the length of the period of Phase 1 between emergence and tuber initiation (i.e. increased development rate until tuber initiation) at temperatures between 10 and 21 °C was found. Depending on cultivar and location, this period lasted between 8 and 40 days. These observations allow us to simulate the relative effect of temperature on development rate until tuber initiation in LINTUL-POTATO as shown in Figure 6.3c with an optimum rate as given in Table 6.2.

Phase 2

Tuber growth rate: daylength relation Photoperiod has been reported to have an influence on the amount of dry matter allocated to the tuber after tuber initiation. Experimental results are often interpreted as "short days favouring the partitioning of dry matter to the tubers" (e.g. Lorenzen and Ewing, 1990; Ewing and Struik, 1992; Menzel, 1985b; Haynes et al, 1988). A shorter duration of Phase 2 under short days than under long days was found in chapter 5. This was attributed to an earlier tuber initiation (Phase 1) leading to higher tuber growth rates (not *relative* tuber growth rates) early in the season. This finding agrees with Wheeler and Tibbits (1987) as they reported similar dry matter allocation of tubers growing at 12 and 24 h daylength. No effect of daylength on tuber growth rate is included in LINTUL-POTATO .

Tuber growth rate: temperature relation In LINTUL-POTATO, the relative tuber growth rate is only dependent on temperature. As with the development rate until tuber initiation, there are reports on the decrease of tuber growth rate at high temperatures leading to a shift in assimilate allocation from the tubers to the foliage, e.g. Krauss and Marschner, 1984; Menzel, 1985b; Epstein 1966; Randeni and Caesar, 1986 As with development rate until tuber initiation, so minimum (0 - 4.4 °C), optimum (15 - 22 °C) and maximum (25 - 35 °C) temperatures have been observed for tuber growth rates (Borah and Milthorpe, 1962; Yandell et al., 1988; Manrique, 1992) The last, for instance assumed a maximum tuber growth rate between 16 and 24 °C. At 10 and 30 °C the growth rate was half of that at optimum and at 4 and 35 °C the tuber growth rates were 0. A shorter duration of Phase 2 with increasing temperature, up to the temperature of about 22 °C was reported in chapter 5. Based on these observations we simulate the relative effect of temperature on the relative tuber growth rate in LINTUL-POTATO as shown in Figure 6.3d with maximum rate shown in Table 6.2.

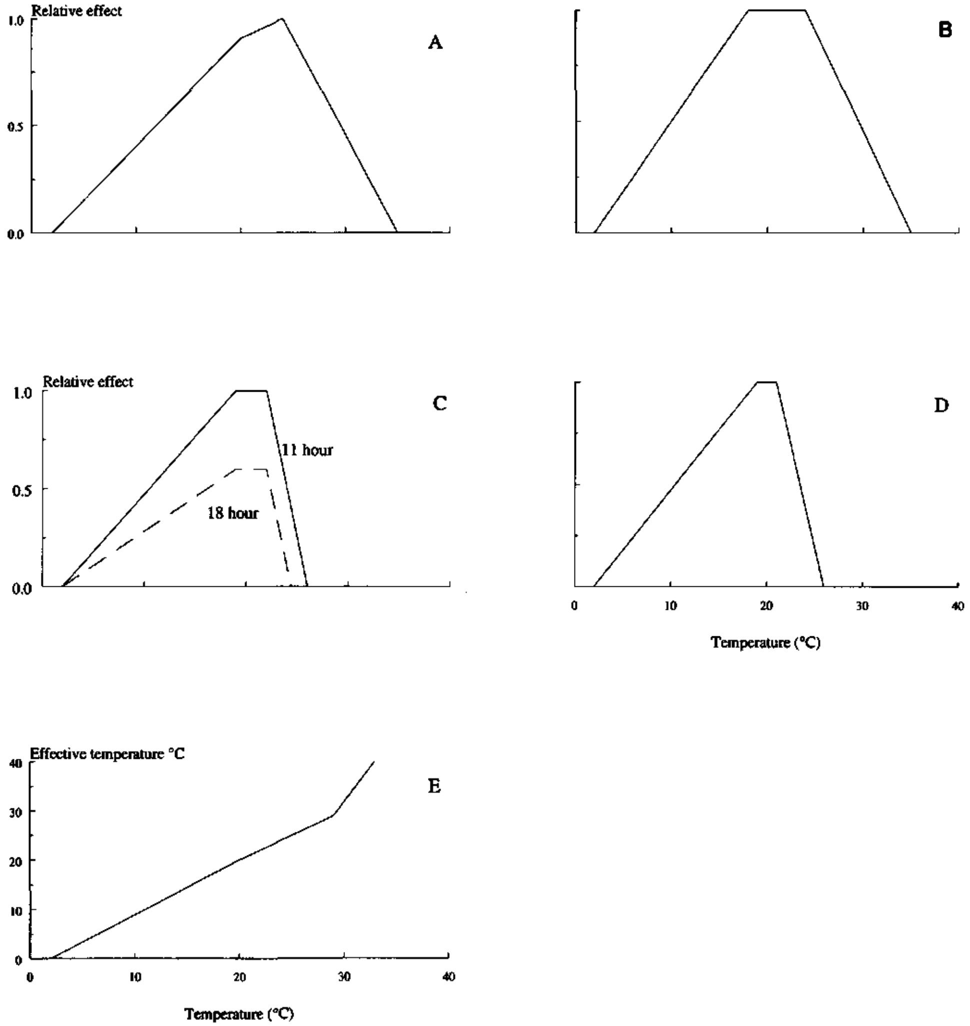


Figure 6.3 The relative effect of temperature in LINTUL-POTATO on the rates of sprout growth (A), light-use efficiency (B), tuber initiation (C, —— at 11 h and — — at 18 h daylength) and tuber growth (D), and leaf senescence (E)

Phase 3

Crop senescence rate: relation to temperature. Crop senescence takes place earlier at higher temperatures (Menzel, 1985a) although the total length of the growing period may last longer because the total period of leaf formation may increase (Marinus and Bodlaender, 1975). Leaf longevity has been recorded to last between 1440 and 1760 °Cd (Vos and Oyarzun, 1987). A leaf formed was estimated to be functional for about 23 days at 20 °C and 12 days at 30 °C by Ingram and McCloud (1984) under conditions in Florida. In chapter 3, leaf longevity was estimated under conditions in the Netherlands to be between 1000 and 1700 °Cd, depending on cultivar. In LINTUL-POTATO we incorporated the effect of temperature as shown in Figure 6.3e: doubling the effective temperature for leaf senescence rate from 30 °C onward, adequately accommodates the reductions observed in foliar development at high temperatures.

Phases 1, 2 and 3

Light-use efficiency : temperature relations Daily crop growth per unit leaf area or unit soil covered by green foliage results from photosynthesis and respiration both of which are temperature dependent. Minimum (between 0 and 7 ° C), optimum (16 to 25 °C) and maximum (40 °C) temperatures for photosynthesis in potato crops have been reported by Ku et al. (1977); Dwelle (1985); Manrique (1992); Midmore (1992) and Hammes and Jager (1990). The highest total daily crop growth are reported between temperatures of 15 and 23 °C (Ben Kheder and Ewing, 1985; Nishibe et al., 1988). A strong increase of respiration with temperature, especially above about 25 °C (e.g. Sale, 1974; Midmore 1992) could contribute to the difference between optimum for photosynthesis and for crop growth rate and to the often observed reduction of the light-use efficiency at increasing temperatures. Haverkort and Harris, (1987) and Manrique et al.(1991) presented linear correlations between the observed reduction of crop light-use efficiencies and temperatures above 20 °C, with a slope of about -0.02 g MJ^{-1} $°C^{-1}$. Combining the various evidence, in LINTUL-POTATO we simulate the effect of temperature on the light-use efficiency as shown in Figure 6.3b with the optimum rate of 2.5 g MJ^{-1}. We assume that there is no influence of daylength on light-use efficiency. Rather than using a negative linear relation between light-use efficiency and total daily radiation to accommodate for light saturation of the canopy, LINTUL-POTATO only uses daily values up to a maximum of 12 MJ m^{-2} (chapter 4), disregarding radiation in excess of this value .

Model structure of LINTUL-POTATO

LINTUL-POTATO is partly based on models describing dry matter accumulation as a function of light interception and light-use efficiency (Spitters, 1990; Chapter 2 and Spitters and Schapendonk, 1990) and the dry matter allocation governed by a dominant tuber sink (Chapter 3). Part of the model was described in chapter 3 and the complete set of equations is given here in Table 6.1 with Table 6.2 describing the meaning of the acronyms and the (initial or optimum) values of the variables and parameters used.

The development of the crop starts at planting. The planting depth and the effective temperature (Fig. 6.3a) determine the time between planting and emergence (Eq 1). In the early stages of crop growth, temperatures rather than assimilates determine leaf area expansion and is therefore modelled according to Eq. 6.2. When the temperature sum from emergence exceeds 450 °Cd or the leaf area index exceeds 0.75, the increase of leaf area is determined by the availability of assimilates and is calculated as the product of leaf dry weight and specific leaf area (Eq. 6.3 from Spitters, 1990 and Spitters and Schapendonk, 1990). Leaves are divided into classes based on the day in which the leaves are formed in. These daily classes senesce when the temperature sum integrated by the class exceeds the leaf longevity or when the leaf area above the leaf layer is such that shading is too strong (Eq. 6.15 and Eq. 6.19). The leaf longevity is also influenced by tuber growth such that fast growing tubers reduce leaf longevity (Eq. 6.17). Crop growth ceases when the leaves in the latest class have senesced.

The daily amount of dry matter produced is calculated from the amount of photosynthetically active radiation intercepted by the canopy calculated from the leaf area index (LAI, Eq. 6.3 and Eq. 6.4) and its conversion efficiency for dry matter production (Eq 6.5, Fig. 6.3b). The growth of the different plant parts is calculated from the total dry matter production and the partition coefficients to the parts (Eqs. 6.6-6.11, 6.13 and 6.14). To obtain the cumulative amount of dry matter produced, the daily growth is integrated over the growing period (Eqs. 6.16-6.21).

After emergence the development rate until tuber initiation is determined by temperature and daylength (Eq. 6.12 and Fig. 6.3d). Assimilate allocation to the tubers receives priority after tuber initiation: TI in Figure 6.2. Initially, tuber growth is sink-limited and results from the product of the relative growth rate and the tuber weight. Thereafter, tubers become an increasing sink as they become larger, however, in this phase the source is not large enough to deliver all assimilates needed to maintain simultaneously exponential tuber

Table 6.1 Sequence of equations describing development and growth in LINTUL-POTATO, ("V " = if)

Development	Growth
Emergence.	Leaf area.
$t_{em} = t_{pl} + \frac{P_d}{G_s} * T_{eff}$ (6.1)	$LAI = LAI_0 * e^{\left(R_L * \Sigma T_{LUE}\right)} \quad \begin{matrix} LAI < 0.75 \\ \vee \\ \Sigma T_{LUE} < 450° Cd \end{matrix}$ (6.2)
	$LAI = W_l * SLA \quad \begin{matrix} LAI \geq 0.75 \\ \vee \\ \Sigma T_{LUE} \geq 450° Cd \end{matrix}$ (6.3)
	Light interception.
	$I = I_0 * e^{(-k*LAI)} \quad I_0 \leq 12\ MJ\ \ m^{-2}$ (6.4)
	Total growth.
	$dW_{Tot}/dt = I * LUE * E_{T,I}$ (6.5)
	Partitioning and daily growth of the foliage.
	$dW_{sht}/dt = f_{sht} * dW_{Tot}/dt$ (6.6) $f_{sht} = 1 - f_{Tub}$ (6.7)
	$dW_l/dt = f_l * dW_{sht}/dt$ (6.8) $f_l = f_{l0} - (.5 - f_{Tub})$ (6.9)
	$dW_{st}/dt = f_{st} * dW_{sht}/dt$ (6.10) $f_{st} = 1 - f_l$ (6.11)

Tuber initiation.

$$R_{ti} = ST_T * T_{Tub} - ST_p * P + ST_c \qquad t \rangle t_{em} \qquad (6.12)$$

Partitioning and daily growth of the tubers.

$$dW_{Tub}/dt = f_{Tub} * dW_{Tot}/dt \qquad (6.13)$$

$$f_{Tub} = \frac{rgr_{Tub} * W_{Tub} * E_{Tub}}{dW/dt + rgr_{Tub} * W_{Tub} * E_{Tub}} \qquad W_{Tub} \geq W_{Tub_0} \qquad (6.14)$$

Leaf senescence.

$$dW_{ld}/dt = \sum W_{l,i} \qquad \forall_i \begin{array}{c} \Sigma T_{s,i} \rangle S_t \\ \vee \\ S_{sh} \rangle 1 \end{array} \qquad (6.15)$$

$$S_t = A_{l0} - dW_{Tub}/dt * S_{Tub} \qquad (6.17)$$

$$S_{sh,i} = R_{sh} * \frac{LAI - LAI_c}{LAI_c} \qquad LAI \rangle LAI_c \qquad (6.19)$$

Crop biomass.

$$W_{Tub}(t) = \int_{ti}^{t} dW_{Tub}/dt \qquad (6.16)$$

$$W_l(t) = \int_{em}^{t} dW_l/dt \qquad (6.18)$$

$$W_{st}(t) = \int_{em}^{t} dW_{st}/dt \qquad (6.20)$$

$$W_{Tot}(t) = W_l(t) + W_{st}(t) + W_{Tub}(t) \qquad (6.21)$$

growth and leaf growth, resulting in an increasing part of the daily assimilates allocated to the tubers. Finally, tuber growth becomes source-limited and all assimilates produced go to the tubers. This course of tuber growth is described by Equation 6.17 and the relative effect of temperature on the relative tuber growth rate is given in Figure 6.3d. Assimilates not allocated to the tubers are allocated to the shoot and divided between the leaves and stems (Eq. 6.7 to 6.11). Root biomass is not taken into account as precise experimental measurements of roots in the field experiments are rare.

Simulation of temperature and daylength responses with LINTUL-POTATO

LINTUL-POTATO, as it is presented here, can be used for two main purposes.

Firstly, the values of variables and parameters in LINTUL-POTATO as they are presented here (Fig. 6.3 and Table 6.2) are mean values taken from literature and, where needed, adjusted by data given in chapter 4 and 5. In these chapters parameter values of 8 *Solanum tuberosum* cultivars varying in earliness and grown in the Netherlands, Tunisia (winter, spring and autumn seasons) and Rwanda (2 altitudes), represent a range of values for Dutch cultivars that are currently grown. Given a specific environment of temperature and daylength, desired cultivar characteristics for responses to these (especially on tuber initiation and tuber growth rates) can be evaluated by the model to calculate the potential tuber production in such an environment .

Secondly, the estimation of potential tuber yields in various regions (Fig. 6.1) can be improved considerably by the use of a dynamic dry matter allocation as in the model, rather than assuming a fixed harvest index of about 0.75 at crop senescence. LINTUL-POTATO takes into account prohibitive low or high temperatures for sprout growth before emergence in Phase 0 (Fig. 6.2). The parameters related to the tuber initiation rate (Phase 1), which is temperature and daylength dependent, can be given values such that the length of Phases 2 and 3 are sufficiently long so that the total length of the growing season fits in the period suitable for potato growth, between 2 and 30 °C.

Table 6.2 List of acronyms and equations used in LINTUL-POTATO

Acronym	Meaning and source	Value	Unit
A_{l0}	Initial longevity of a daily leaf class.(Chapter 3)	1000	°Cd
day	Julian day	Input	d
$E_{T.l}$	Relative effect of temperature on light-use efficiency	Fig. 6.3b	-
$E_{T.s}$	Relative effect of temperature on rate of leaf senescence	Fig. 6.3e	-
$E_{T.ti}$	Relative effect of temperature on development rate until tuber initiation	Fig. 6.3c	-
$E_{T.t}$	Relative effect of temperature on relative tuber growth rate	Fig. 6.3d	
$\mathrm{E}_{\mathrm{T.e}}$	Relative effect of temperature on sprout growth rate	Fig. 6.3a	
f_l	Fraction of daily shoot dry matter production allocated to the leaves	Output	-
f_{l0}	Initial fraction of daily shoot dry matter production allocated tothe leaves (Chapter 3)	0.8	-
f_{sht}	Fraction of daily total dry matter production allocated to the foliage	Output	-
f_{st}	Fraction of daily shoot dry matter production allocated to the stems	Output	-
f_{tub}	Fraction of daily total dry matter production allocated to the tubers	Output	-
G_s	Sprout growth rate (MacKerron and Waister,1985)	1	mm °Cd^{-1}
i	Index daily leaf class	Index	d
I	Intercepted PAR	Output	MJ m^{-2}
I_0	Total incident PAR	Input	MJ m^{-2}
k	Extinction coefficient (Spitters and Schapendonk, 1990)	1	-
LAI	Leaf Area Index	Output	m^2 m^{-2}
LAI_c	Critical leaf area Index (Chapter 3)	6.0	m^2 m^{-2}
LAI_0	Initial leaf area Index (Spitters and Schapendonk, 1990)	0.0155*NPL	m^2 m^{-2}
LUE	Light-use efficiency (Chapter 4)	2.5	g MJ^{-1}
NPL	number of plants	4.4	# m^{-1}
P	Photoperiod	Input	h
P_d	Planting depth	Input	cm
rgr_{tub}	Relative growth rate of tubers (Ingram and McCloud, 1984)	0.37	g g^{-1} d^{-1}

Acronym	Meaning and source	Value	Unit
R_l	Relative increase rate leaf area (Spitters and Schapendonk, 1990)	0.012	$m^2\,m^{-2}\,d^{-1}$
R_{sh}	Senescence rate due to shade (Chapter 3)	0.1	d^{-1}
R_{ti}	Development rate until tuber initiation	Calculated	
SLA	Specific leaf area (van Oijen et al. 1995)	0.0023	$m^2\,g^{-1}$
S_t	Leaf longevity	Output	
S_{sh}	Senescence due to shading	Output	
ST_C	Constant in calculating start tuber growth (Chapter 5)	0.119	
ST_P	Daylength parameter calculating start tuber growth (Chapter 5)	$6.2\ 10^{-4}$	h^{-1}
ST_T	Temperature parameter in calculating start tuber growth (Chapter 5)	$-5.8\ 10^{-3}$	$°C^{-1}$
t	time	Input	d
t_{em}	Day of emergence	Output	d

The effect of different temperatures and daylengths on the length of the growing season, expressed as the period when the ground is (partially) covered by green foliage is shown in figure 6.4 together with the development of the proportion of light interception, the fractional daily assimilates partitioning to the tubers, and tuber dry matter production, using the standard values of LINTUL-POTATO as presented in Table 6.2. and assuming a daily solar radiation level of 9 MJ m^{-2} throughout the season. The figure shows the effect of growing potatoes at mean daily temperatures of 10, 17 and 25 °C throughout the growing season at daylengths at emergence of 11 and 17 h.

At 10 °C the rates of emergence and initial light interception are low. Emergence takes place on day 21 and the start of tuber growth takes place on day 33 which is too early to enable the crop to reach full ground cover. Ground cover reaches a maximum of about 60 %. Because of the subsequent low total growth rate the fraction of dry matter allocated to the tubers increases rapidly and it takes about 40 days from tuber initiation until 90 % of the dry matter is allocated to the tubers (Table 6.3). The rate of senescence of the crop is low, resulting in a relative long growth cycle of about 270 days. Because of the low ground cover and the low growth rate at 10 °C the tuber dry matter production is only 12.3 t ha^{-1}.

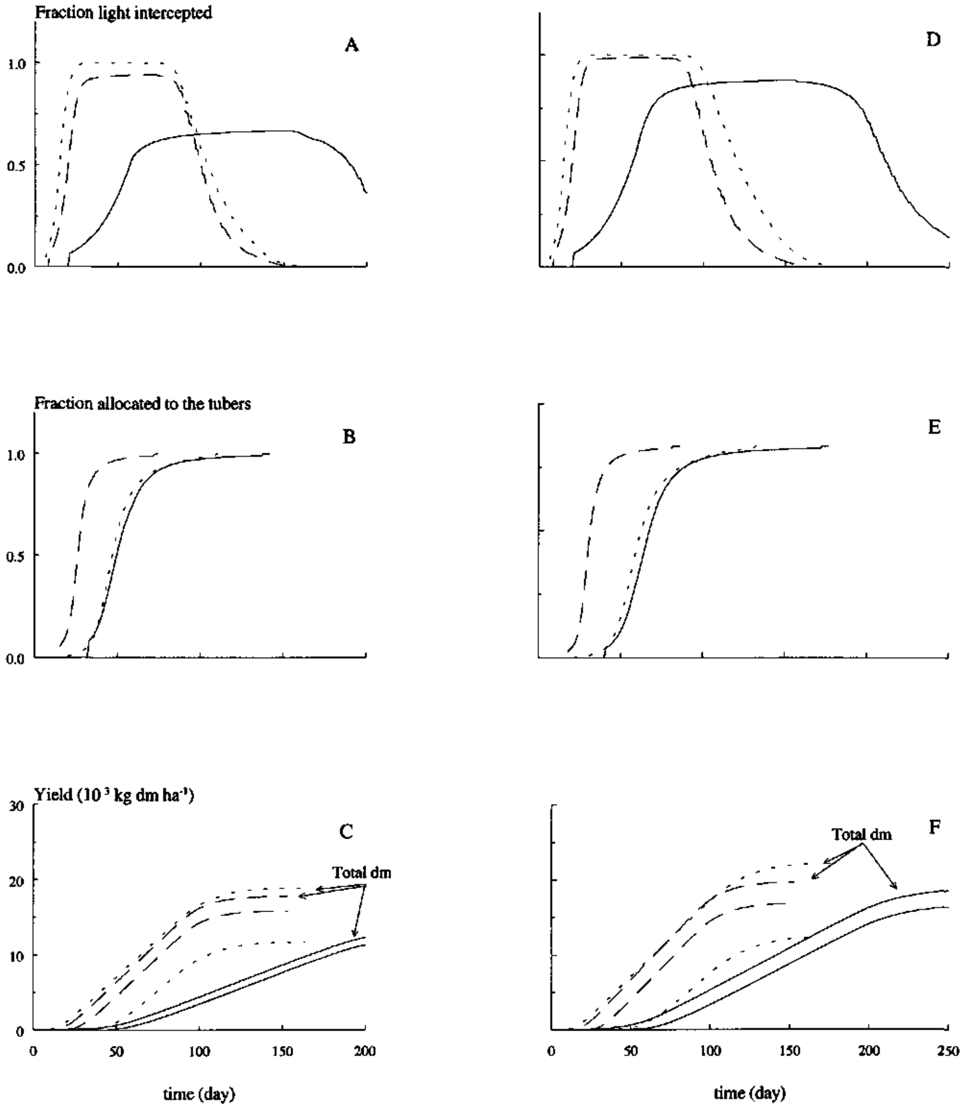


Figure 6.4 Simulated development of light interception (A,D), dry matter partitioning to the tubers (B,E), total and tuber dry matter production (C,F) at 10 (——), 17 (— —) and 25 °C (- - -) and at daylengths of 11 (A,B,C) and 17 h (D,E,F)

At 17 °C, emergence and initial growth are faster than at 10 °C. Emergence is brought forward by 12 days and the start tuber growth is 18 days earlier. The higher crop growth rate at 17 °C allows the crop to reach 95 % ground cover. Both tuber growth rate and leaf senescence rates are higher at 17 °C than at 10 °C leading to a reduction in the senescence period to 37 days. The total length of the growth cycle of the crop grown at 17 °C crop is 153 days. Due to the high growth rates and the early allocation of dry matter to the tubers, this crop produced 16 t ha^{-1} tuber dry matter by the end of the growing season. At 25 °C emergence takes place after 7 days but tuber initiation is not brought forward (see Fig. 6.3c) but takes place two days later than at 17 °C. The initial tuber growth is very slow and, therefore, the end leaf growth (end of phase 2, Fig. 6.2) is only reached on day 70. The total growth cycle is as long as at 17 °C . The greater rate of senescence counteracts the effect of increased foliar development because of a reduced fraction of dry matter allocated to the tuber which also explains why tuber dry matter production does not exceed 12 t ha^{-1}.

Carrying out the simulation for 17 h (Fig. 6.4 D,E,F) rather than for a daylength of 11 hour (Fig. 6.4 A,B,C) shows that the lengths of the growth cycles are increased and that a greater amount of light is intercepted. The increased growth cycle resulted from a delay in tuber initiation (Table 6.3), which delays dry matter allocation to the tubers. The increased growth cycle increased total dry matter production in t ha^{-1} from 13.3 (at 10 °C) and 18.9 (at 25 °C) at 11 hour daylength to 19.0 and 22.1 at 17 hour. The tuber dry matter production increased less than total dry matter production. The increase was largest at 10 °C (4.6 t) and smallest at 25 °C (0.6 t)

Table 6.3. Simulated end of phase 1,2 and 3 (Days After Planting, DAP), total and tuber yield at the end of the growth cycle at daylengths of 11 and 17 hour.

Temperature	phase 1 (DAP)		phase 2 (DAP)		phase 3 (DAP)		total yield (t ha^{-1})		tuber yield (t ha^{-1})	
	Photoperiod		Photoperiod		Photoperiod		Photoperiod		Photoperiod	
	11 h	17 h	11 h	17 h	11 h	17 h	11 h	17 h	11 h	17 h
10 °C	33	41	72	89	274	300	13.3	19.0	12.3	16.9
17 °C	15	18	32	42	153	162	17.8	19.7	15.9	16.9
25 °C	15	23	70	87	162	173	18.9	22.1	11.7	12.3

The model is not yet fully validated here. Comparison with independent data is carried out in chapter 7. LINTUL-POTATO simulates the trends in tuber dry matter production and crop behaviour as reported in literature: earlier tuber initiation under short days leads to earlier senescence (Haverkort, 1990; Ewing and Struik, 1992). At 10 °C total dry matter production was lower than at 17 °C which agrees with literature data from Ng and Loomis (1984), Ingram and McCloud (1984) and Spitters (1990) who reported optimal yields between 15 and 22 °C. Total dry matter differed only slightly between 17 and 25 °C as was also found by Marinus and Bodlaender (1975) comparing plant performance at 16, 22 and 28 °C. In long days, the growing season is longer at 25 than at 17 °C but the tuber dry matter production is lower due to reduced harvest indices at higher temperatures (Ben Kheder and Ewing, 1985 and Manrique, 1992).

We also used LINTUL-POTATO to determine the optimum temperature for potato growth at varying daylengths. The range of temperatures tested throughout the growing season varied from 2 to 28 °C and the simulations were carried out for daylengths of 11, 14 and 17 h. The resulting total tuber dry matter production is presented in figure 6.5. The highest tuber dry matter production at the 11 h daylength is achieved at about 17 °C. Longer days (e.g. 17 h) broaden the optimum range of temperatures and centre it at about 14 °C.

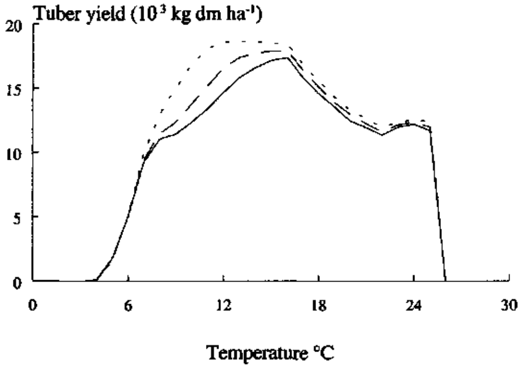


Figure 6.5 Simulated relation between tuber dry matter production by the time of crop senescence versus mean daily temperature throughout the growing season at daylengths of 11(——), 14 (— —) and 17 h (- - -).

The range of optimum temperatures for potato production calculated by LINTUL-POTATO shown in Figure 6.5 includes the optimum temperatures reported in literature: 13 °C by Spitters (1987), 14-22 °C by Ingram and McCloud (1984), 16-24 °C by Ng and Loomis (1984), 18 °C by Borah and Milthorpe (1962), 15-22 °C by Midmore (1992), 18-20 °C by Manrique (1992) and 21 °C by Sands et al. (1979).

The wider range of optimum temperatures in long days than in short days is explained as follows. The optimum crop growth rate is between 18 and 24 °C (Fig. 6.3B) and is not affected by daylength. Short days bring forward tuber initiation and reduce the total length of the growth cycle and/or the maximum level of light interception, hence total and tuber dry matter production. Longer days at low temperatures however, retard tuber initiation to such an extent (Fig. 6.3C) that it leads to longer growth cycles and/or higher maximum levels of light interception resulting in higher total and tuber production.

The phenomenon of a wider optimum temperature range for growth of the crop in longer days, may well explain the adaptability of potato to a wide range of climates. Besides its short day and low temperature origin, the crop also performs well in ecoregions with higher temperatures such as the Mediterranean area and the continental summer, because the prevailing daylength during the growing season here is longer than in the centre of origin.

Compared to experimental research LINTUL-POTATO yields more commonly applicable information. In experiments the lateness of a crop is beside daylength, affected by other factors such as cultivar and seed age. The optimum temperature for tuber production, assessed in an experiment, therefore, is always specific for that experiment. Which may explain the differences in optimum temperatures reported in literature.

The model LINTUL-POTATO simulated temperature and daylength responses similar to those reported in literature. The concept of dry matter allocation therfore is a valid tool to explain variation in potato production under different climate conditions. Accurate quantification of the variables for cultivars differing in lateness and comparison of the model with independent data is reported in chapter 7.

CHAPTER 7

EXPLORATION OF IDEOTYPES FOR POTENTIAL TUBER DRY MATTER PRODUCTION

P.L. Kooman and R.Rabbinge

ABSTRACT

In this paper a crop simulation model for potato (LINTUL-POTATO, Chapter 6) is parameterized with data from a series of trials in various countries at different latitudes and longitudes and is then validated against independent data. It is subsequently used to evaluate the constraints for higher potato yields in non limiting conditions. LINTUL-POTATO incorporates the effects of temperature and daylength. It simulates the variation between locations well but is less successful at simulating the observed variation among cultivars. Experiments carried out under optimal conditions for tuber dry matter production were simulated better than experiments under adverse conditions. This was attributable to side effects under high temperatures and the more critical role of crop management in these situations: neither of these factors was included in the simulation.

After validation, LINTUL-POTATO was used to explore the yielding abilities of and constraints to potato production, using meteorological data from each tenth degree between 0 and 60° latitude at 0, 1000 and 2000 m above sea level. The highest tuber yields in a single growth cycle were calculated to be at 30 °N and 2000 m above sea level. Southwards or at lower altitudes, it was not the length of the growing season but the growth cycle that was shortened by high temperatures. Northwards the growing season contracted because of low temperatures in winter. The length of the growth cycle was determined by the moment of tuber initiation and the temperature at the beginning of the growing season. The cultivars used to parameterize the model covered only a small range of the variation in the potato gene pool. In tropical montane climates, tuber initiation was such that full light interception was reached and maximum tuber yields were obtained from the given cultivars. In the subtropics at sea level the cultivars used to parameterize the model tended to be too early, leading to sub-maximal light interception which in its turn resulted in sub-maximal tuber dry matter production. In short growing seasons the tuber initiation of these cultivars was often too late and the growing season ended before the growth cycle was completed. This resulted in too much dry matter being allocated to the foliage and led to low harvest indices and tuber yields.

It is concluded that the model is a useful tool for calculating attainable tuber yields and for identifying the desirable genetic traits for potato at various geographical locations.

INTRODUCTION

Tuber yields in potato are influenced substantially by temperature and daylength. Variation in sensitivity to these factors among cultivars has been described by various authors (Ben Kedher and Ewing, 1985; Ewing and Struik, 1992; chapter 5). However, it is difficult to select potato cultivars according to temperature and daylength as yield-determining factors because temperature and daylength are not constant over the growing season and their interaction with other environmental conditions cannot be ruled out. Temperature and daylength affect various physiological and morphological characteristics of the potato crop. Therefore the response of the crop growth and tuber dry matter production to temperature will vary from year to year and from location to location. For example, Fahem and Haverkort (1988) found a large difference in crop reactions between crops grown in a Mediterranean spring and a Mediterranean autumn, whereas the average temperature between these growing seasons hardly differed. More important than the average temperature was the seasonal course of the temperature: increasing during the spring and decreasing in autumn.

Crop growth models enable the environmental effects at the level of single plant organs to extrapolated to the growth of a complete crop over the season in a continuously changing environment (Spitters and Schapendonk 1990). In the present study the crop model LINTUL-POTATO was used to elucidate the reaction of the potato crop to temperature and daylength and to reveal how potential tuber production is restricted by genetic and environmental factors. The LINTUL-POTATO model was first compared to the data sets used to build the it (parameterization), and its usability was then studied by comparing it with independent datasets (validation). The validated model was used in a feasibility study, in a wide range of environments between 0 and 60 ° latitude and at 0, 1000 and 2000 m above sea level.

Model description

The model used in this study is schematically represented in Figure 7.1 and has been described in detail in chapter 6. It calculates total dry matter production from the amount of incident photosynthetically active radiation and the light-use efficiency. The fraction of PAR intercepted is a function of the leaf area index. Tuber yield is calculated from the total dry matter increment and the fraction of dry matter allocated to the tubers. The allocation to the tubers starts at tuber initiation and depends on the amount of biomass in

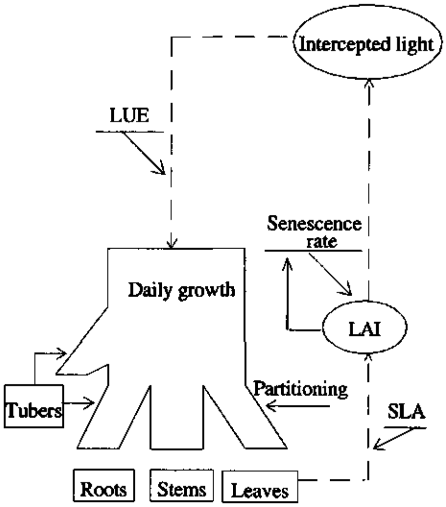


Figure 7.1 Schematic representation of the LINTUL-POTATO crop growth model. (LUE is the light-use efficiency, SLA the specific leaf area and LAI the leaf are index)

the tubers, their relative sink strength, temperature and the total dry matter increment. The dry matter that is not allocated to the tubers, is used for stem and leaf growth. In the model leaf senescence depends on temperature and on the amount of leaf formed, to take into account reallocation effects.

Parameterization

The LINTUL-POTATO parameter values in the present study have been partly derived from literature and partly from empirical data (Table 5.2). The model part that calculates total dry matter production and initial leaf growth has been taken from Spitters (1987). The dry matter allocation part and the temperature dependent leaf senescence are developed initially to explain differences in earliness under temperate conditions in the Netherlands (chapter 3). In chapter 3 it was found that differences in earliness between cultivars were explained not only by differences in dry matter allocation, but needed a correction in leaf senescence rate, depending on the amount of leaves formed.

The parameter values of the major processes that are influenced by temperature (total growth, sink strength of the tuber and leaf senescence rate) have been taken from Kooman

Table 7.1 Experiments used to parameterize LINTUL-POTATO. (For a complete description of the experiments, see chapters 4 and 5)

Land	Place	season	years	latitude	longitude
Netherlands	Wageningen	summer	1991,1992	51°58' N	5°49' E
Rwanda	Kinigi	Wet	1991,1992	1°49' S	29°73' E
	Rubona	Wet	1991,1992	2°45' S	29°73' E
Tunisia	Saiida	Spring	1991,1992	36°30' N	10° 0' E
		Autumn	1991,1992		
	Monastir	Winter	1991/92	34°52' N	10°59' E

and Haverkort (chapter 6). The parameter values of the relation between cultivar and climate are expressed in the effect of temperature and daylength on the tuber initiation rate (Table 4.2). In the model differences in location are assumed to be determined by weather and the latitude.

The simulation of the crop started at emergence. The other model parameters are kept constant over cultivars and locations. After parameterisation the observed values for tuber initiation date and tuber dry matter production in the experiments were compared with the simulated values.

Validation

The usability of LINTUL-POTATO was tested by running the model against empirical data obtained at locations and experiments other than those used to parameterize the model. The experiments used for the validation are summarized in Table 7.2. They were gathered from literature and personal communications and were selected to cover a wide range of climatological conditions, Désirée was used mostly but data on Alpha and Spunta were also available in some experiments.

The minimum set of data for a location consisted of monthly data on temperature and radiation; usually daily data were available. The daylength was calculated from the date and the location (Spitters et al., 1989). The simulation of the experiments started at the day of emergence and depended on the cultivar-specific tuber initiation parameters.

The validation is incomplete because experimental factors such as age and quality of tuber seed may have influenced the behaviour of the crop. In the experiments on which the model was based (Table 4.2), production was aimed at maximum tuber yields. Not all experiments used for validation (Table 7.2) had this objective.

Table 7.2 Data sets used for validation of the model.

Cultivar	Location	Experiment	Reference.
Alpha	Netherlands	Cultivar trials.	Gmelig-Meyling and Bodlaender 1981
Alpha	Netherlands	Cultivar trials	Caesar et. al. 1981
Désirée	Hawaii	Altitude trials	Manrique et al. 1989.
Désirée	Peru	Drought trials	Versteeg 1985.
Désirée	Philippines	Mulching	Vander Zaag et al. 1986
Désirée	Philippines	Shading and daylength	Vander Zaag and Demagante 1987
Désirée	Tunisia	planting date	Fahem 1991
Spunta	Tunisia	seed age	Fahem 1991
Alpha Désirée Spunta	Israel	Cultivar and Planting date	*Levy personal communication* unpublished.
Alpha Désirée	Netherlands	Cultivar	Kooman, own data unpublished.

Exploration of interactions between genotype and climate.

Weather data. For the evaluation of climates by means of simulation with LINTUL-POTATO, 7 weather stations were chosen from a weather database (Müller, 1982, 1987) at approximately each 10° latitude between 0° and 60° N (Table 7.3). The stations were all from continental climates to exclude maritime influence. At each weather station the mean monthly values averaged over a period of 30 years were available for minimum temperature, maximum temperature and daily global radiation. For the calculations, mean monthly values were assigned to the days in the middle of the month and daily values were derived by means of linear interpolation. Subsequently the temperature was normalized at sea level using an adiabatic lapse rate of 6°C per 1000 metre increase of altitude (Seeman et al. 1979). Thus the sensitivity of potato to temperature was tested by reducing the daily minimum and maximum temperature by 6 and 12 °C, coinciding with temperatures at approximately 1000 and 2000 m above sea level. Radiation levels were not changed with altitude in this sensitivity analysis.

Table 7.3 Locations of weather stations.

Country	Place	Longitude	Latitude
Burundi	Bujumbura	29° 21' E	3° 23' S
Sudan	Malakal	31° 39' E	9° 33' N
Niger	Bilma	13° 23' E	18° 39' N
Jordan	Amman	35° 57' E	31° 57' N
Spain	Madrid	3° 24' W	40° 25' N
Poland	Warsaw	20° 59' E	52° 09' N
Russia	Petrograd	30° 18' E	59° 58' N

Potential length of the growing season. For the three altitudes, the length of the growing season at every weather station was calculated. Under non-limited conditions the growth is restricted by temperature only. Three temperature constraints were used to determine the potential growing season. Firstly the minimum temperature had to be above 5 °C, because below this temperature there is a risk of night frost. Secondly, the maximum temperature had to be below 35 °C because higher temperature may cause heat damage. The final constraint was that the average temperature had to be below 28 °C, because at higher average temperatures respiration rate is higher than the photosynthesis and it would not be rational to grow potatoes at these temperatures. After determining the length of a growing season the potential dry matter production in such a season was calculated by multiplying the amount of photosynthetically active radiation (PAR = 0.5 * global radiation) using a maximum light-use efficiency of 2.5 g MJ^{-1} as a function of temperature (chapter 6).

Determination of ideotype. The ideotype with respect to temperature and daylength at a given location is defined as the cultivar with a moment of tuber initiation such that the maximum tuber dry matter production is reached. If tubers are initiated before this moment, not enough foliage is formed to sustain the subsequent tuber growth. Tuber initiation after the ideal moment leads to too much dry matter being allocated to the leaves at the expense of tuber yield. The ideotype was determined by varying the tuber initiation date and calculating the resulting tuber dry matter production. The emergence date was set on the first day that temperature did not restrict potato growth.

RESULTS AND DISCUSSION

Parameterization

The results of the model simulation were compared with the data from locations and years used to construct the model. Some of the trials were not used because they did not fulfil the prerequisite that growth and development were not affected by factors other than temperature and daylength (chapter 5). These were Tunisian autumn 1991 and 1992 because the seed was too young, Tunisian winter because of night frost and variable seed age, and Rubona 1992 because of a dry spell at the start of the growing season. Two model results, time of tuber initiation (Fig. 7.2a) and tuber dry matter production (Fig. 7.2b), were compared with actually observed data.

The time between emergence and tuber initiation determines the length of the growth cycle and tuber yield. (chapter 4, Ewing and Struik, 1992). The model assumes that tuber initiation is affected by daylength and temperature but that temperature influences other processes too (chapter 6). The general trend in the moment of tuber initiation is simulated well, but on average, a little late (Fig. 7.2a). The difference between locations and years (between different temperature and daylength regimes) were simulated better than differences between cultivars.

The variation among cultivars per location was simulated less well than the variation between locations. Generally the ranking in earliness was simulated well but the differences between cultivars were smaller than observed. For example in the "Netherlands 1991" trial, tuber initiation was observed between 14 and 26 days after emergence and was simulated between 21 and 28 days. When the observed values showed little variation at a location, such as in Kinigi for example, the simulated variation was also less.

The three experiments which were not used to estimate the relations in the model show the greatest differences between observed and simulated. For the "Tunisian autumn" trials the simulated variation among cultivars was between 10 and 17 days whereas the observed values ranged between 3 and 11 days in 1991 and between 11 and 20 in 1992. The large observed variation in this growing season was attributable to the relatively young seed. The seed originated from the Tunisian spring season and was too young, resulting in an irregular and slow emergence with a large variation. This was also found by Fahem (1991). In the "Tunisian winter" trial, seed from the same source was used but at planting the seed was older; in this case the model simulated tuber initiation too early.

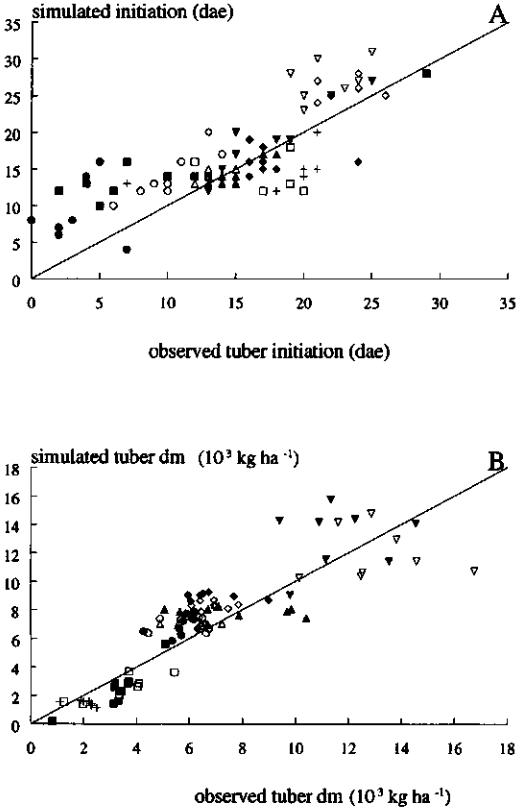


Figure 7.2 Simulated versus observed values for tuber initiation (dae: days after emergence, 7.2a) and tuber dry matter production (ton ha^{-1}, 7.2b) for the experiments used to parameterize the model. The symbols represent the locations: the Netherlands (▽), Kinigi (△), Rubona (○), Tunisian Spring(◇), Tunisian Autumn (□) and Tunisian Winter (+). The open symbols are for values 1991 and the solid ones values for 1992.

In Rubona 1992, a dry spell at the beginning of the season retarded emergence; after emergence this resulted in a fast tuber initiation which led to the length of the period between emergence and tuber initiation being overestimated by the model. On average, the tuber dry matter production was slightly overestimated but the differences in tuber dry matter production between locations were simulated well (Fig. 7.2b).

The lower simulated variation in tuber initiation date and the partly simulated variation in leaf longevity per growing season resulted in less simulated variation in tuber dry matter production, among cultivars than was actually observed. In the "Tunisian autumn" and "winter" trials, total and tuber dry matter production were underestimated by the model for two reasons. The crops here grew under low light intensities and therefore light was used more efficiently, leading to higher production than estimated (Haverkort and Harris, 1988; Manrique et al., 1991). Secondly the model tended to simulate tuber initiation date a few days too late, which had severe repercussions for tuber dry matter production, especially, since the growing season is short.

Validation

Figure 7.3 shows the comparison of the simulated tuber dry matter with the observed values of the experiments in Table 7.2. LINTUL-POTATO overestimated most of the experimental yields. In low-yielding trials the tuber dry matter production was overestimated more than in high-yielding trials. At the top end of the range, tuber dry matter production was underestimated. Closer examination of the data clarifies these results. The underestimated data are from trials with the late cultivar Alpha in the Netherlands in experiments of Gmelig Meyling and Bodlaender (1981) and Caesar et al. (1981). These were all aimed at maximum tuber production. In the parameterization section of this chapter it was explained that the model tended to underestimate late cultivars in temperate climate zones, so this result was expected. The lowest yields were found in the Philippines (Vander Zaag et al. 1986; Vander Zaag and Demagante 1987) and in Tunisia (Fahem, 1991). The experiments in the Philippines were carried out at relatively high temperatures and were not aimed at maximum tuber yields. The experiments in Tunisia included seed age effects, which were not included in the model. In the Israeli spring season, seed imported from the Netherlands was planted in three dates. Later planting affected the crop in two ways: firstly the seed was older, and secondly as the spring progressed the temperature rose and the conditions for potato worsened. The decreased growth later in the season was simulated by the model but the decrease in the observed tuber production was much stronger than simulated. This is partly attributable to the age of the seed but is largely the result of the environmental conditions. Later in the spring both temperature and radiation increased sharply. The crop in the experiment was affected more by unfavourable temperatures than simulated by the model, probably because high temperatures are associated with a high evaporative

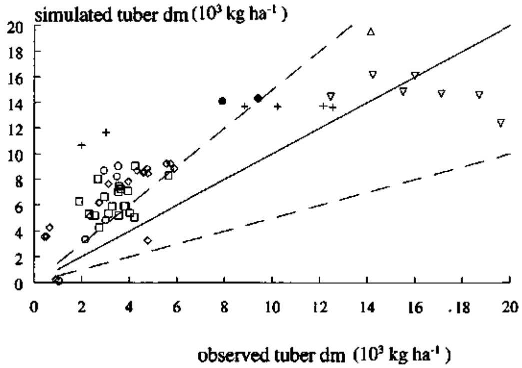


Figure 7.3 Simulated tuber dry matter versus observed tuber dry matter for a series of experiments in different climates (table 7.2), including planting date and seed-tuber age treatments. The 'simulated = observed' line is the solid line and the dotted lines show the range between 50 % overestimation and 50 % underestimation.

demand at the end of the growing season (Levy 1986a, 1986b) which reduces crop growth (Manrique 1991). Experimentally unfavourable conditions give lower yields and more variation (Grashoff 1990), even when management is optimal.

Exploration of interactions between genotype and climate

The length of the growth cycle is the crop characteristic that determines the total dry matter production (chapter 4). In the following section first the total dry matter production for a series of growing seasons in different climates is evaluated and then the ideotype for each season is determined by varying the tuber initiation date. This analysis enables the constraints to potential tuber yield to be examined. Finally, the day of tuber initiation for the cultivars used to build the model is calculated as a function of temperature and daylength and compared with the ideotypes.

Potential dry matter production and length of the growing season. The potential dry matter production is defined as the production by a closed canopy during the period that potato growth is possible. Temperature restricted the growing season and affected the light-use efficiency. In Figure 7.5a the figures for potential dry matter production are given for 0 to 60° latitude North at temperatures expected at approximately 0, 1000 and 2000 metre above sea level.

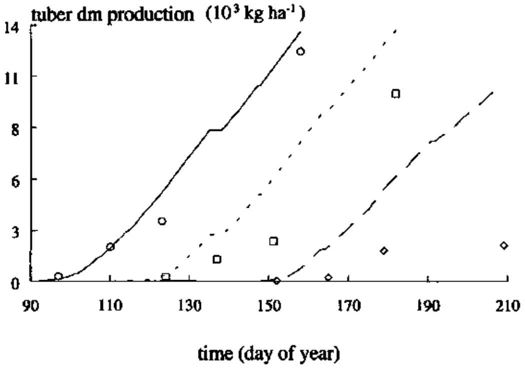


Figure 7.4 Simulated and observed tuber dry matter production of cultivar Alpha in Israel at three different planting dates (day numbers 46(——, O), 76 (····, □) and 106 (— —,◊)).

First, production seasons at sea level were evaluated. At the equator and 10 °N the temperatures are too high for growth. At 30 °N in the winter season the temperatures are sufficiently low to allow a short growing season of about 90 days resulting in a production of 19 t ha^{-1} total dry matter. Northwards, two growing seasons per year appeared, a spring and an autumn season, bounded by low temperatures in winter and high temperatures in summer. The spring season has higher radiation levels and yielded about 30 t ha^{-1}. The autumn season starts slowly because of high temperatures innitially and the growth rate levels off quickly because of low radiation levels in late autumn and winter. At 50 and 60 °N the production shifts to the summer season. LINTUL-POTATO calculated a maximum total dry matter production of 30 t ha^{-1} at 50°N and 20 t ha^{-1} at 60 °N .

If the minimum and maximum temperatures were lowered by 6 °C corresponding with an altitude of 1000 m above sea level, at the equator and at 10 °N potato growth was possible throughout the year. This led to year-round potato dry matter production potentials of about 90 t ha^{-1}. northwards the season became shorter because of cold winter periods. The potential production diminished until a potential of only about 6 tons of dry matter per hectare remained at 60 °N. If the temperatures were lowered by 12 °C, corresponding with an altitude of 2000 m above sea level, a similar trend is found. At the equator, year round production is possible and Northwards the growing season became shorter until at 50 °N no potato production was possible at these low temperatures. These results correspond well with those obtained by Haverkort (1990).

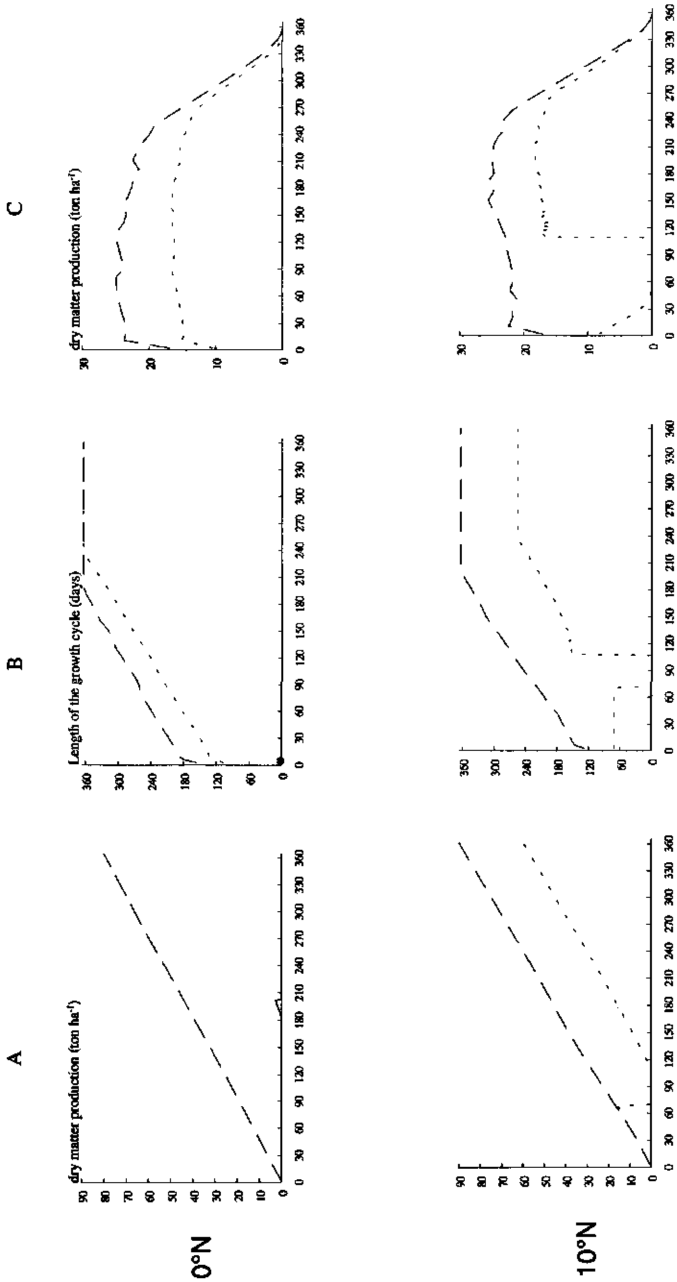
Determination of ideotype and constraints to potential tuber yield. An ideotype is the potato cultivar that given the growing season has such a tuber initiation date that enables maximum tuber dry matter production to be obtained. Varying the tuber initiation date over the growing season and calculating the associated length of the growth cycle and tuber dry matter production reveals the ideotype.

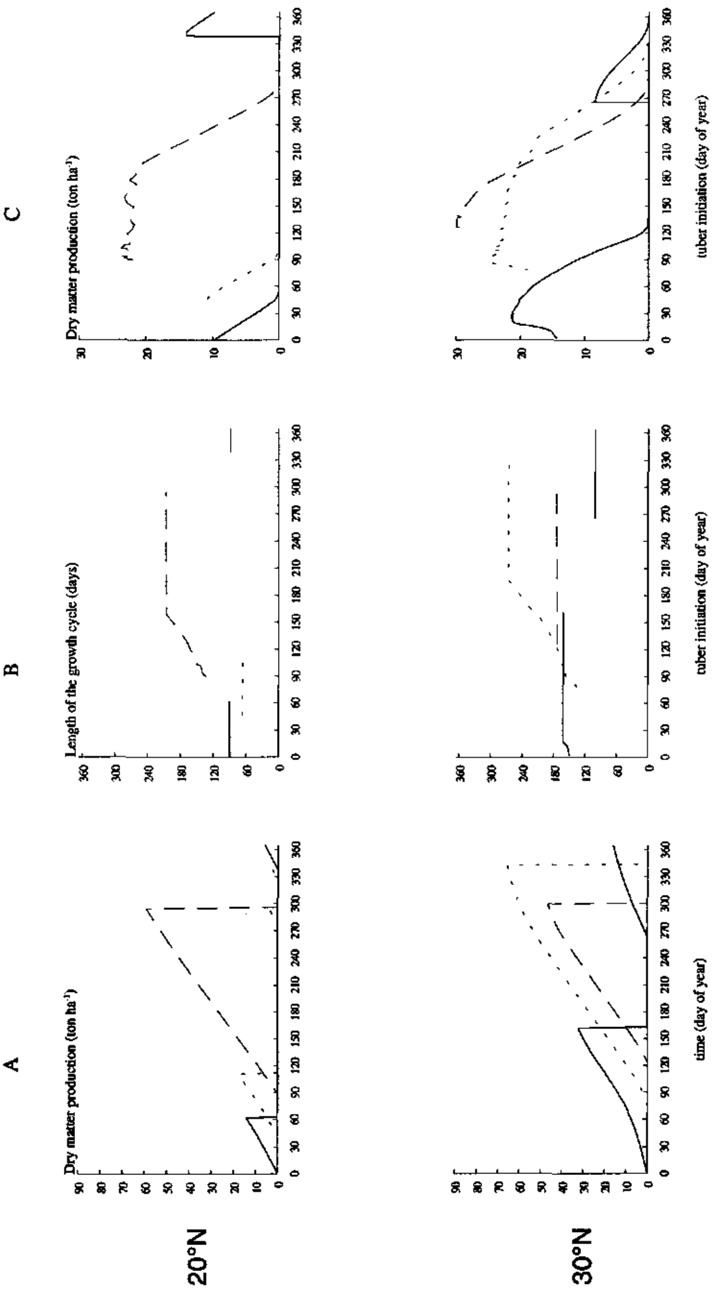
The growing seasons in Table 7.3 were examined to identify the factors restricting tuber dry matter production. Figures 7.5b and 7.5c show the length of the growth cycle and the accompanying tuber dry matter production. At sea level up to 20 °N the length of the growing season limited the dry matter production. At 0 and 10 °N no potato growth was possible. At 20 °N the tuber dry matter production decreased with later tuber initiation (Fig. 7.5c, 20°), and the growth cycle was cut off at the end of the growing season (Fig. 7.5b, 20°). This agrees with results found by Haverkort (1990). In the autumn season at 30 and 40 °N a similar situation occurs, the growing season is fully used and tuber dry matter production decreases with later tuber initiation. In the spring season at these latitudes an optimum appears. Here, early tuber initiation results in a restricted leaf growth and the growth cycle is shorter than the growing season. At the optimum, the growth cycle equals the growing season and if tuber initiation occurs later, the growth cycle is cut off at the end of the growing season. This was found in experiments in the Mediterranean area by Levy (1986a) and Fahem (1991). Further North at 50 and 60 °N the seasons shorten and the optimum moment shifts to earlier in the season. In Dutch experiments, Van Heemst (1986) and Spitters (1987) found that earlier tuber initiation resulted in lower yields, which means that all cultivars in these experiments had their tuber initiation before the optimum date.

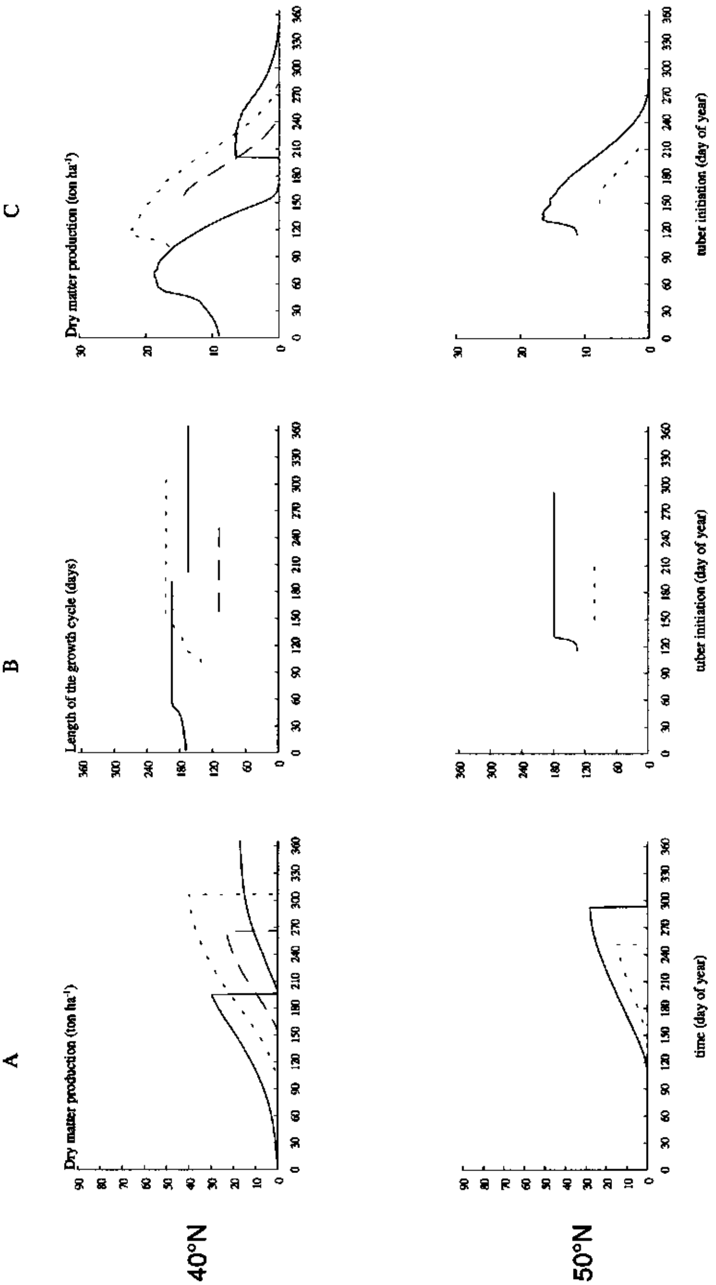
At higher altitudes the growing season shorten with increasing distance from the equator. At the equator the growing season enables a full growth cycle and maximum tuber yields. At 2000 metres altitude the season becomes too short to accommodate the growth cycle and this restricts dry matter production at latitudes north of 30 °N. At 1000 metres altitude, at 20 °N, the season length restricts tuber production because of a warm period in summer and above 50 °N the restriction is caused by the long cold winter. At the other locations the growth cycle fits into the growing season.

To be able to define an ideotype, three situations have to be considered with regard to conditions at the start of the growing season and the length of the growing season.

1) tuber initiation may limit only the length of the growth cycle and not tuber yield (at 0° latitude, Fig. 7.5b, 7.5c, 0°),
2) it may limit both the growth cycle and tuber yield (for example at 40 °N, 1000 and 2000 m Fig. 7.5b, 7.5c 40°) and
3) it may restrict tuber yield but not influence the growth cycle (60 °N Fig. 7.5b, 7.5c 60°).


A
B
C
0°N
10°N
dry matter production (ton ha-1)
Length of the growth cycle (days)
dry matter production (ton ha-1)
time (day of year)
tuber initiation (day of year)
tuber initiation (day of year)
0 30 60 90 120 150 180 210 240 270 300 330 360
0 10 20 30 40 50 60 70 80 90
0 60 120 180 240 300 360
0 10 20 30


A
B
C
20°N
30°N
Dry matter production (ton ha^{-1})
Length of the growth cycle (days)
Dry matter production (ton ha^{-1})
0
10
20
30
40
50
60
70
80
90
0
60
120
180
240
300
360
0
10
20
30
0
30
60
90
120
150
180
210
240
270
300
330
360
time (day of year)
tuber initiation (day of year)
tuber initiation (day of year)


40°N
50°N
A
B
C
Dry matter production (ton ha^{-1})
Length of the growth cycle (days)
Dry matter production (ton ha^{-1})
time (day of year)
tuber initiation (day of year)
tuber initiation (day of year)
0 10 20 30 40 50 60 70 80 90
0 60 120 180 240 300 360
0 10 20 30
0 30 60 90 120 150 180 210 240 270 300 330 360

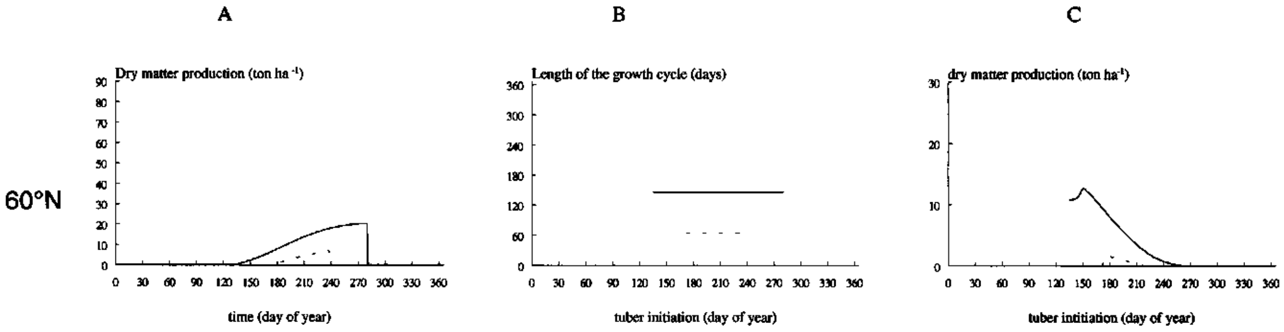


Figure 7.5 Potential dry matter production (A)at 0 , 10 , 20, 30, 40, 50 and 60 degrees north latitude at sea level (——), 1000 m (— —) and 2000 m(·····), and length of the growth cycle, (B) and tuber dry matter production (C) in relation to the tuber initiation date at these altitudes and latitudes.

If only the length of the growth cycle is restricted (first situation), the ideotype initiates its tubers so early that the maximum tuber yield is reached at the minimum length of the growth cycle. A shorter growth cycle reduces the risks that occur during the season and allows a second crop to be planted. (Haverkort 1990). The ideotype in the second situation initiates its tubers on the day that enables the crop to fill the growing season. In the third situation, tuber yields are restricted by early tuber initiation because the total amount of leaves formed do enable to full light interception so the ideotype initiates its tubers at the moment that there is a balance between maximum light interception and a high harvest index.

CONCLUSIONS

LINTUL-POTATO simulated the variation in the observed data well. The effect of daylength and temperature appeared to be the main factors affecting tuber initiation. A later start of tuber growth led to an extension of crop growth because of a combination of prolonged leaf growth and slower leaf senescence which explains a considerable part of the variation in yield. The differences between locations were simulated better than the variation among cultivars at a location.

When the model was compared with independent data sets, the simulations agreed more with the observed values if the tuber yields were higher. These higher yields agree with more favourable conditions for potato production and this must be taken into account when these models are compared with empirical data. It remains to be seen if simulated yields ever can be attained in the tropical environments in spite of the side-effects of high temperatures such as high disease pressure and a high vapour pressure deficit.

Exploration with LINTUL-POTATO showed that the desired traits of ideotypes for different latitudes and altitudes concern the onset and the duration of the growing season. In long growing seasons the growth cycle limited potential tuber production. Therefore the potential tuber production differed less than the total dry matter production among different climates.

The model is based on a small genetic selection of cultivars bred in temperate climates. The maximum range of likely possibilities is not covered in this study but the general trends simulated in this study are representative for potato. In conclusion: the model LINTUL-POTATO is a useful tool for identifying the constraints to tuber production potentials.

CHAPTER 8

GENERAL DISCUSSION

The research presented in the previous chapters focused on one central question:

What is the influence of radiation, temperature and daylength on the potential tuber dry matter production in potato ?

An examination of the literature reveals that there have been two types of study to date: Those that relate tuber dry matter production directly to climatic factors and those that relate crop processes to temperature and daylength. The former have resulted in various rules of thumb (e.g. high temperatures give lower yields, short days give higher yields - see Haverkort 1990) but do not unravel the mechanisms involved in the interaction between crop and environment and therefore yield little explanation. Studies of the second type, such as the extensive research on the interaction between climatic factors and tuber initiation as reviewed by Ewing and Struik (1992), demonstrate the interaction between plant processes and environment but do not explain the impact of this interaction on final tuber production.

The present study combined the positive aspects of these two types of research. It unravelled the processes underlying tuber yield and demonstrated the interaction between plant growth and development processes and climate. Subsequently the importance of this interaction for tuber dry matter production was assessed. Thus this study is an example of production ecology research. The advantage of this type of research is that it studies crop and environment as an integrated system. The conclusions drawn therefore be applied to a broad range of environmental conditions.

Combining genotype-environment experiments with systems analysis, a useful approach

In this study, empirical results and models were combined, to analyse the interaction between potato dry matter production and climatic factors. Experiments were used to determine processes that are important for tuber dry matter production (chapter 3). Subsequently the relation of these processes to the climatic factors radiation, temperature and daylength and the genetic variation in these processes were quantified (chapters 4 and 5). The quantitative information from the experiments was used in a simulation model to assess the effect of the separate processes on tuber dry matter production. Figure 8.1 shows the sequence of steps followed in this study.

Systems analysis, a way to gain insight in relations between crop processes

A series of models that simulate potato crop growth and development already existed (e.g. Ng and Loomis, 1984; MacKerron and Waister, 1985; Haverkort and Harris, 1987; Spitters and Schapendonk, 1990). These models were constructed to handle specific problems at specific locations, as is apparent from their differing levels of complexity and processes they included. The present study required a model that could be applied over a wide range of climates. Testing various Dutch models over a series of years in Scotland (chapter 2) revealed that there was no difference in their ability to simulate tuber dry matter production accurately. However, all the models, needed to be reparameterized. This was easier in the simple models that included fewer processes than in the complex models but the latter better explained the processes involved. There was no difference in simulation ability between the levels of complexity, so concentration could be focused on the processes needed to explain variation over climates. In the models tested dry matter partitioning was driven by temperature-dependent development. This descriptive way of modelling could not account for the differences between climates and did not explain why tuber yields differed.

Differences in tuber dry matter production between cultivars are attributed to differences in earliness (Moll et al., 1987; Spitters, 1987). When a potato starts to allocate dry matter to the tubers early in the season, it does so at the expense of the leaves, and leaf growth ceases early, resulting in a short growth cycle and a low tuber dry matter production. Starting allocation to the tubers later, will result in abundant leaf growth, a short period of tuber growth and low tuber yields. To establish which processes affect earliness in potato the following hypothesis was formulated: differences in earliness are due to differences in dry matter allocation, and a dominant tuber sink governs this dry matter allocation (chapter 3). This hypothesis was included in a simulation model. In a series of experiments the dry matter allocation was recorded and subsequently simulated with the model which yielded earliness and tuber dry matter production. Much of the variation in earliness and tuber yield could be explained in this way. Three parameters affecting the earliness in a potato crop were identified. In addition to the timing of tuber initiation, it was found that relative tuber sink strength and leaf longevity also contributed to the explanation of the variation in tuber dry matter production between cultivars. Early tuber initiation, a strong tuber sink and short leaf longevity lead to a shorter growth cycle and less tuber dry matter production.

Figure 8.1 Aims and conclusions of the chapters in this thesis.

Chapter 1	**Aim:** To determine and quantify the effect of climate on potential tuber dry matter production and the variation in total dry matter production among cultivars.	
[illegible]		
Chapter 2	**Aim:** To determine the level of detail needed to predict tuber yield and to assess the general applicability of existing models.	**Conclusion:** Different levels of complexity do not differ in their ability to predict tuber yield. Explanation is less satisfactory in simple models and parameterization is more difficult in complex models.
Question: [illegible]		
Chapter 3	**Aim:** To test the hypothesis that earliness is determined by dry matter allocation.	**Conclusion:** Tuber initiation, leaf longevity and tuber sink strength, are the major crop characteristics that determine the earliness of a potato crop.
Question: Which crop characteristics are influenced by the climate		
Chapter 4	**Aim:** To analyse the variation in tuber dry matter production among cultivars and locations, and the influence of temperature, daylength and radiation on this variation.	**Conclusion:** Variation in length of the growth cycle is the main factor explaining variation in tuber dry matter production, and this factor is affected by temperature and daylength.
[illegible]		
Chapter 5	**Aim:** To analyse the influence of temperature and daylength on the length of the growth cycle.	**Conclusion:** The influence of temperature and daylength was strongest during the phase from emergence to tuber initiation. The shift in sink priorities in this phase also affected the subsequent phases.

[illegible]		
Chapter 6	**Aim:** To integrate the effect of temperature and daylength of separate plant processes in a model to explain variation in tuber dry matter production.	**Conclusion:** Integration provides information on the interaction between daylength and temperature on tuber production and explains the differences in tuber dry matter production reported in the literature.
[illegible]		
Chapter 7	**Aim:** To test the usability of the model, to define ideotypes in relation to the climate and to evaluate constraints to potato production.	**Conclusion:** LINTUL-POTATO simulates differences between locations better than differences between cultivars. The favourable situations for potato production are simulated better than unfavourable ones. The ideotype of potato depends on conditions at the beginning of the growth cycle and the length of the growing season.

Systems analysis enabled us to detect the flaws in the existing models and to clarify the relation between dry matter allocation and tuber production. However the relation to climate is not revealed, and therefore the simulation model could not be applied over a wide range of climates. To obtain this information, experimental research needs to be done on how the variation in dry matter allocation is affected by climate.

Systems analysis and experiments in different climates, a way to elucidate in the relations between crop and climate.

Temperature, daylength and radiation determine potential dry matter production. Previous studies often covered only a limited range of climates (Manrique, 1989a; Haverkort and Harris, 1987) or did cover a wide range of climates but compared only a limited number of processes (Tai and Young, 1989; Van der Zaag and Doornbos, 1987) or a limited number of cultivars (Manrique 1989b).

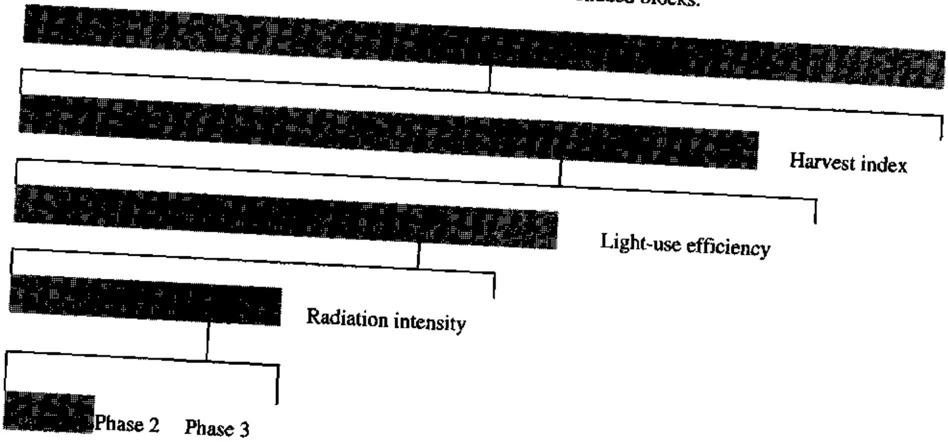
In the present study the variation between cultivars and climates was analysed step by step, reaching a greater level of detail at each step (chapters 4 and 5). The shaded blocks in Figure 8.2 indicate the most important factors identified in each step of the analysis. Tuber dry matter was determined by total dry matter, and the variation of that was accounted for mainly by the variation in light interception, which in turn was explained by duration of light interception. When this duration was divided into three phases, the first phase was found to be most important although the variation in the other phases also contributed to the variation in light interception. These phases can be determined well in experiments since they coincide with the periods of leaf growth, competition between leaf and tuber growth and leaf senescence (chapter 5). Relating the length of these phases to temperature and daylength enables the effects of these factors to be quantified.

The first phase, before tuber initiation, was shortened by higher temperatures and shorter days. In phases 2 and 3 the effect of temperature and daylength was less clear. The variation in the length of phase 1 was caused by a shift in sink priorities between tubers and leaves. When phase 1 was shorter fewer leaves were formed and these leaves lasted shorter. This explained part of the variation in phases 2 and 3. Differences between cultivars could be attributed to differences in the sensitivity to temperature and daylength for the length of phase 1.

The variation in tuber yield between locations was explained best. Only in the Netherlands was the variation between cultivars found to be significant. Here the variation in tuber initiation data was largest, resulting in an asynchronous development of the different cultivars under differing weather conditions. This led to a variation in earliness between cultivars and to differences in tuber dry matter production. At the other locations the daylength was relatively short and the short day advanced the time of tuber initiation and diminished the variation in tuber initiation date between cultivars. The cultivars were more synchronized and therefore the differences in earliness between cultivars were found to be no longer statistically significant.

Systematically analysing the crop, step by step identifies the processes that play are crucial at each level of analysis and reveals their relation within the crop. If only one level is studied, there is a risk that the processes studied are only of minor importance or that they do not yield the information required. The processes found in a stepwise analysis will be determinative for potato production irrespective of location and cultivar.

Figure 8.2 Stepwise analysis of tuber dry matter production in potato. At each level of the analysis the most important crop characteristic is shown in the shaded blocks.



Crop ecology research in a broad range of climates has the advantage that the conclusions are valid over a broad area and there is less risk of generalizing site-specific conclusions The range of cultivars used gives some idea of the genetic variation in the pool from which the cultivars are drawn. Although the cultivars used in this study cover only a small part of the genetic variation, differences in reaction to climatic factors were found.

Explanation of yielding ability of potato crops in different environments

The potential dry matter production of a potato cultivar is determined by climatic factors and the genotype. In this study a systematic procedure was developed that evaluates the growing season and determines the ideotype for that growing season (chapter 7).

The first step was to define the growing season. Potato production is not possible below 5 °C and above 28°C (van Keulen & Stol, 1995), the growing season is defined as the period during which temperatures are in between these extremes. The length of this season also defines potential total dry matter production. The next step was to compare the duration of the growth cycle of a cultivar with the duration of the growing season. When the growing season is just long enough to accommodate the growth cycle of the ideotype, later cultivars lead to a longer growth cycle without higher production. An early cultivar leads to a low production, especially if the temperature in the beginning of the season is low and tuber growth has a relative advantage over foliage growth. If the growing season is too short to allow a full growth cycle, early tuber initiation leads to low yields, especially if the conditions favour tuber growth. Late tuber initiation also leads to low yields because too much dry matter is invested in the leaves at the cost of the tubers.

Let us consider three actual situations. The first is tropical highlands. Here, year-round potato growth is possible, so the growing season is extremely long and the potential for dry matter production is high in theory. However, the cultivars use only a small part of the available growing season, and the use of late cultivars leads to more partitioning to the leaves and only slightly higher tuber yield. In tropical highlands, genetic restrictions are responsible for the large difference between potential dry matter production in a growing season and in a growth cycle. In the second situation, a temperate maritime climate, the growing season is shorter than in tropical highlands. The potential yields are therefore lower than in the tropics. The growth cycle of the ideotype, however, fits neatly in the growing season and therefore it is easy to obtain yields close to potential production of the growing season. The reason that tuber yields are high in temperate climates is that the growth cycle fits in well with the length of the growing season. The third situation is found in the Mediterranean spring season. The growing season is relatively short, but because of favourable temperatures and radiation levels during the season the potential production is high. However, the growing season is too short to accommodate a growth cycle. Even the ideotype for this growing season does not finish its growth cycle, but earlier tuber initiation means that too few leaves are formed to maintain an adequate daily dry matter production. Hence, timing is more important here and if a cultivar is slightly too early or too late, this has major repercussions for tuber yield. Because of the more difficult situation and the year to year variability in the weather, yields seldom approach potential production here.

This study has shown that no single cultivar attains the highest yields at every location. Potato's sensitivity to temperature and daylength means that a cultivar gives the highest yields in only a limited range of environments. In practice some cultivars (for example, Désirée) are distributed over an area that covers a wider range of climates than expected from the results of this study. This is because these cultivars give farmers an acceptable yield in all these climates. Other properties such as adequate resistance to diseases, tolerance of abiotic factors and an adequate dormant period often play a greater role than yielding ability.

Application of the model in the development and introduction of new cultivars

The knowledge obtained in this study about the crop-climate system can be used in the introduction of new cultivars. Three phases can be distinguished. The first phase is making crosses and selecting of new genotypes. Subsequently, genotypes and new cultivars are introduced by an international organization such as the International Potato Centre (CIP) or by commercial companies such as those found in the Netherlands, Schotland and France. The final phase is the widespread adaptation of a cultivar by farmers. In each phase, different components of the genotype-environment system are of importance. The breeder changes physiological characteristics; with the introduction of a new cultivar both crop characteristics and environment have to be considered; and in crop management , it is only the environment during the growing season that matters (Fig. 8.3). In each phase, models can be used to support decisions, but in each phase systems analysis will play a different role.

Plant breeding

The first phase in the creation of a new cultivar is plant breeding. The aim of plant breeding is to improve physiological and morphological characteristics so that a cultivar fits the growing environment. Presently it is difficult to breed cultivars for a certain target

Figure 8.3 Activities related to elements in the crop environment system during different phases of the development and implementation of a new cultivar.

Activities		Elements of the crop - environment system
Breeding	↔	Crop physiology
Introduction of cultivar	↔	Crop and environment
Crop management	↔	Environment

climate because it is not properly understood which traits determine tuber yield in relation to climate. After a laborious selection procedure a genotype that is suitable for a given climate is identified. Systems analysis may be of help to rationalize breeding and improve its efficiency. It helps in identifying ideotypes and the plant characteristics that can be used as a selection criterion. One advantage of a simulation model is that hypothetical genotypes can be evaluated and used to give direction to breeding. Additionally, it shows the interaction with other plant characteristics and how a change in plant characteristics affects final yield. For example: the ideotype in this study had a moment of tuber initiation that led to maximization of tuber yields (chapter 7). The selection criterion in the study presented in chapter 7 was the date of tuber initiation, because in the experiments genetic variation was found in this crop characteristic. If genetic variation is found in other crop characteristics (such as the rate of dry matter allocation to the tuber, and leaf longevity) this may be included in the definition of ideotypes. The effect of earlier tuber initiation could be undone by a longer leaf longevity. Insight into these kinds of relations will give the breeder more possibilities of breeding for higher tuber dry matter production.

Defining ideotypes and selection criteria is not the only way systems analysis is useful. It also enables the sensitivity of the different cultivar parameters to climate to be established in parental lines. Once it is known how this sensitivity is inherited, the performance of newly bred cultivars can be evaluated with a simulation model in the early stages of a breeding programme. This enables cultivars to be bred and evaluated for different climates without testing them in all these climates and therefore makes breeding more efficient.

Introduction of cultivars

At present, the introduction of a new cultivar demands an enormous amount of work. It is common to test a series of genotypes in a wide range of locations so tons of seed tubers are sent all over the world so that genotypes can be tested and selected for their suitability in these situations. The idea behind systems analysis and modelling is to establish relations which are valid beyond the conditions in which these relations are derived. This means that it is not necessary to test new cultivars at every location, but that a series of well-chosen locations can be used to derive the relation between climate and the crop. With the help of a simulation model it is then calculated how the crops behave at other locations or in other growing seasons. In this study we derived the parameters that were important for potential tuber production and using the parameters derived at the test locations we were able to give an overview of the potential production of potato in climates between the equator and 60 °N. Cultivars will always have to be tested at various locations to confirm model results and to obtain information about features not included in the model. However, a cultivar that is expected to give low yields can be excluded from experimental screening and this makes the testing of new cultivars more efficient.

A model is also useful when screening cultivars in the field. The outcome of a screening experiment is always influenced by climate and crop management. For example; long days, young seed, too much nitrogen and a slight water shortage at the beginning of the growing season have a similar effect on dry matter allocation in the crop (Ewing and Struik, 1992; Haverkort, 1990). By calculating the potential yields as defined by the climate and comparing these with the experimental results, the effects of climate and crop management can be isolated, and this makes it easier to infer the right conclusions. At this stage of introduction of new genotypes, the ideotype for a given location can be used to direct management in such a way that an existing genotype approaches the ideotype as much as possible. An early cultivar can be made later by applying more nitrogen or using younger seed. In situations where the genotype deviates only slightly from the ideotype, this way of improving yield is much faster than breeding a new genotype.

Management of the crop

Crop management depends on environmental parameters once the cultivar is chosen. In a potato crop, yield can be improved by a wide range of measures. A model can help in various ways to ensure that appropriate decisions are made in crop management. Thus before planting the crop, risks that may damage the crop can be estimated and the management adjusted so that yields are maximized at an acceptable risk. For example, the planting of early potato crops in the Netherlands is seriously affected by the risk of night frost. Using historical weather data the risk of frost damage can be evaluated with a simulation model. The trade-off between lower yields at later planting and accepting a greater risk of frost is then determined and gives a criterion for deciding an appropriate stategy.

During the growing season the crop management can be adjusted on the basis of information from the field and an analysis done with the help of a model. For example, if the beginning of the growing season has been colder than usual, which was the case in North-western Europe in 1994. This has repercussions for crop growth during the rest of the growing season because of a lagging growth and a change in sink priorities. Using a model, the expected maximum yield is estimated and the amount of e.g. nitrogen needed to support this can be adjusted accordingly.

At the end of the season the actual growth of the crop is compared with model calculations. The difference between calculated and observed values is analysed and the causes of this difference are identified. In subsequent growing seasons these causes can be taken away leading to a higher production, a more efficient use of resources and less pressure on the environment.

Final remarks

More information on variation among cultivars is needed to improve the potential for using system analysis in breeding and crop management. As the research presented in this thesis shows, at present LINTUL-POTATO is best suited for use in the introduction and testing of cultivars at different locations. If supported with sufficient experimental information this model is a useful tool for determining **what** cultivar to breed, **where and when** to grow it and **how** to grow it.

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SAMENVATTING

Oorsprong en verspreiding

Aardappelen komen oorspronkelijk uit het Andesgebied in Zuid-Amerika. Aan het eind van de 16e eeuw werden ze geïntroduceerd in Spanje en van daaruit verspreidde het gewas zich door de rest van Europa. In de rest van de wereld zijn aardappelen in de meeste gevallen geïntroduceerd vanuit Europa. Missionarissen en kolonisten namen de knollen vanaf het begin van de 17^e eeuw mee naar tropische en subtropische gebieden. Aanvankelijk werden ze in deze gebieden alleen gegeten door de Europeanen. Lokale bewoners begonnen vaak pas aardappelen te eten in tijden van voedselschaarste en dan vaak alleen nog in gebieden waar de aardappel makkelijk te telen was (Horton 1987).

Sinds het begin van de zestiger jaren is de met aardappelen beteelde oppervlakte in tropische en subtropische klimaten toegenomen met 70 % en zijn de opbrengsten per hectare ongeveer verdubbeld. Mede door de afgenomen produktie in de gematigde klimaatsgebieden is het relatieve belang van deze tropische en subtropische gebieden toegenomen. De consumptie hier is echter nog laag door de relatief hoge prijs van aardappelen in vergelijking met ander voedsel. Er worden meer aardappelen geconsumeerd wanneer de produktiekosten omlaag gaan hetgeen bereikt kan worden door meer aardappelen te produceren tegen lagere kosten per eenheid produkt (Midmore 1992). De huidige lage opbrengsten kunnen meerdere oorzaken hebben waaronder met name de slechte aangepastheid van aardappelen aan warme klimaten (Haverkort, 1990).

Doel van het onderzoek

Alhoewel de aardappel in bijna alle klimaatsgebieden geteeld wordt, lijkt hij toch het best aangepast te zijn aan gematigde klimaten met een lange dag. De hoogste knolopbrengsten worden dan ook verkregen in noordwest Europa en noordwest Amerika (van der Zaag 1984; Stol et al. 1991). Op dit moment zijn de opbrengsten in tropische en subtropische klimaten laag en weinig stabiel. Om te bepalen of dit komt door de gebrekkige aanpassing van het gewas aan de omstandigheden in de tropen en subtropen, is het effect van het klimaat op de potentiële produktie bestudeerd. De studie die in dit proefschrift beschreven is, exploreert de potentiële en haalbare opbrengsten van de aardappel en heeft als doel het effect van de klimaatsfactoren (temperatuur, daglengte en zonnestraling) op de potentiële knolproduktie te bepalen en te kwantificeren. Daarnaast heeft deze studie tot doel de genetische variatie in de reactie op de klimaatsfactoren te analyseren en te verklaren, en de verworven inzichten te benutten bij de ontwikkeling en introduktie van aardappelrassen.

De aanpak van het onderzoek

In het verleden zijn verscheidene studies gedaan naar de interactie tussen de groei van aardappel en het klimaat. Deze studies zijn in twee groepen te verdelen. De eerste relateert de knolopbrengst direct aan klimaatsfactoren; de resultaten uit zulke studies bieden vuistregels maar geven weinig inzicht in hoe de opbrengst tot stand komt. Dit wordt geïllustreerd met de knolopbrengsten. Bij hoge temperaturen en korte dag is de opbrengst lager is dan bij lange dag en lage temperaturen (Tai en Young, 1989). Andere studies relateren individuele karakteristieken van de plant aan temperatuur en daglengte. Een voorbeeld hiervan is het overzicht van Ewing en Struik (1992) dat ondermeer de relatie tussen knolinitiatie en verschillende klimaatsfactoren bespreekt. Zulk type onderzoek geeft aan hoe de plant wordt beïnvloed door klimaatsfactoren maar geeft niet aan hoe deze invloed doorwerkt op de uiteindelijke knolopbrengst.

Hoofdstuk 1 van dit proefschrift geeft aan dat men meer inzicht in het gedrag van een gewas en de variatie in knolopbrengsten krijgt wanneer het gewas en zijn omgeving als een geïntegreerd geheel wordt bestudeerd. Daartoe worden aspecten van eerdere studies gecombineerd. Na vaststelling van de invloed van het klimaat op cruciale processen in de plant zijn de gevolgen van deze invloed op de uiteindelijke knolopbrengst bepaald. De op deze manier beredeneerde conclusies hebben een brede geldigheid .

Om de invloed van het klimaat op het gewas te onderzoeken in deze studie, is experimenteel onderzoek gecombineerd met het gebruik van simulatiemodellen. Om te bepalen welk simulatiemodel het best voldoet, zijn een serie in Nederland ontwikkelde modellen, getest onder Schotse omstandigheden (hoofdstuk 2). Na herparameterisatie bleken al deze modellen, onafhankelijk van hun complexiteit, de drogestofopbrengst juist te kunnen simuleren. De modellen waren echter niet overdraagbaar naar andere klimaten met substantieel verschillende temperaturen en daglengten. In alle geteste modellen werd de drogestofverdeling aangestuurd door een temperatuurgestuurde ontwikkeling. Dit was een te simpele weergave voor het doel van de onderhavige studie en daarom was een nieuwe relatie nodig die de drogestofverdeling beschrijft. Om de toepasbaarheid van de tot dan bestaande modellen te vergroten zijn de cruciale processen bestudeerd die de drogestofproduktie bepalen. Op basis van literatuur (Moll et al., 1987; Spitters, 1987) is gehypothetiseerd (hoofdstuk 3) dat de lengte van een groeicyclus (en dus de opbrengst) afhangt van de drogestofverdeling naar de knol. Deze hypothese is modelmatig getest met behulp van een serie experimenten die in Nederland werden uitgevoerd. En inderdaad, op basis van de geformuleerde hypothese werd de drogestofverdeling goed gesimuleerd. De variatie in drogestofopbrengst onder verschillende omstandigheden wordt echter niet geheel verklaard uit de variatie in drogestofverdeling, want naast de drogestofverdeling blijkt de levensduur van de bladeren ook van belang.

Om de effecten van temperatuur, daglengte, en straling op de drogestofproduktie van aardappelen te bepalen zijn veldproeven in het kader van deze studie uitgevoerd in Rwanda (op 2 hoogten), in Tunesië (in het voorjaar, herfst en winter) en in Nederland (in de zomer). Om de interactie tussen het klimaat en de genotypen te bestuderen zijn acht Nederlandse rassen van verschillende vroegheid getoetst. De totale drogestofproduktie en knolopbrengsten zijn geanalyseerd in termen van lichtonderschepping en de omzetting van dit onderschepte licht naar drogestof (hoofdstuk 4). De variatie in knol- en totale produktie bleek merendeels te verklaren uit de verschillen in de hoeveelheid onderschept licht. De hoeveelheid onderschept licht is opgedeeld in lichtintensiteit en de lengte van de groeicyclus. De efficiëntie van de omzetting naar drogestof van het onderschepte licht was lager bij hogere straling. De belangrijkste variabele die uiteindelijk de variatie in lichtonderschepping (dus in knolopbrengst) verklaart, is de lengte van de groeicyclus. Korte dagen bij opkomst en hoge temperaturen tijdens het groeiseizoen verkorten de groeicyclus.

Om de relatie tussen knolopbrengst en de klimaatsfactoren (temperatuur, daglengte en straling) te kwantificeren is de groeicylus in drie fasen opgedeeld (hoofdstuk 5). Door de lengte van elke fase aan temperatuur, daglengte en straling te relateren is de invloed van deze klimaatsfactoren op de groei en ontwikkeling duidelijk gemaakt. Hoge temperaturen en korte dagen verkorten de eerste fase tussen opkomst en knolinitiatie; de mate waarin is rasafhankelijk. In de tweede fase, van begin knolgroei tot einde loofgroei, heeft de temperatuur nog enig effect op de drogestofverdeling. De laatste fase, van eind loofgroei tot eind gewasgroei, wordt verkort door hoge temperaturen en straling. De lengte van fase 1 is medebepalend voor de lengte van de latere fasen.

De informatie uit de veldproeven in Nederland, Tunesië en Rwanda is gecombineerd met informatie uit de literatuur om het overzicht te completeren van de relaties die de invloed per fase beschrijven van temperatuur, straling en daglengte op de drogestofaccumulatie en -verdeling. Dit resulteerde in het model LINTUL-POTATO dat is beschreven in hoofdstuk 6. LINTUL-POTATO is gebruikt om de gevolgen van verschillende combinaties van temperatuur en daglengte voor een 'standaard' aardappelgewas te verkennen. LINTUL-POTATO simuleerde waarden van drogestofopbrengsten die overeenkomen met die gevonden in de literatuur. Het model laat bovendien zien dat de aardappel onder lange dag beter aangepast is aan een breed bereik van temperaturen dan bij korte dag hetgeen mede verklaart waarom een grote spreiding in optimale temperaturen voor knolgroei gevonden wordt.

In hoofdstuk 7 zijn berekeningen met LINTUL-POTATO vergeleken met uitkomsten van de veldproeven die zijn gebruikt voor de ontwikkeling ervan (verificatie). Tevens vond validatie plaats met onafhankelijke data afkomstig van die proeven die op verschillende locaties in de wereld waren uitgevoerd (e.g. Fahem, 1991; vander Zaag 1986; Manrique et al. 1989). Door het opnemen van temperatuur- en daglengterelaties is het model goed in staat om verschillen in drogestofopbrengst tussen verschillende locaties te verklaren. De verschillen in drogestofopbrengst tussen de rassen worden minder goed gesimuleerd, mede doordat in de veldproeven die de parameterwaarden opleverden, de variatie tussen rassen op de (sub)tropische locaties gering bleek. Bij de validatie van LINTUL-POTATO bleek dat de overeenkomst tussen gesimuleerde en waargenomen waarden beter was naarmate de opbrengsten hoger waren. Het is duidelijk dat bij lage waargenomen opbrengsten van in de literatuur gerapporteerde proeven, naast de opbrengstdefiniërende factoren (temperatuur, licht en daglengte), groeibeperkende en groeikortende factoren een rol speelden bij de opbrengstvorming.

Het model LINTUL-POTATO biedt goede mogelijkheden om de opbrengsten voor een groot bereik van klimaten te verkennen. In hoofdstuk 7 is voor elk klimaat voor elke 10° tussen de evenaar en 60° noorderbreedte op zeeniveau, 1000 en 2000 meter hoogte, de knol- en de totale drogestofproduktie, en het ideotype bepaald. De lengte van het beschikbare groei<u>seizoen</u> bepaalt de totale drogestofopbrengst terwijl de lengte van de groei<u>cyclus</u> de knolopbrengst bepaalt. Knolopbrengsten zijn relatief laag indien het groeiseizoen korter is dan de groeicyclus als gevolg van een te late knolinitiatie en indien de groeicyclus korter is dan het groeiseizoen als gevolg van een te vroege knolinitiatie. Deze verkenning verklaart waarom de potentiële opbrengsten in het tropisch hoogland veel sterker afwijken van de opbrengsten die alleen op grond van temperatuur en straling kunnen worden gerealiseerd dan in gematigde klimaatsgebieden. De hoge opbrengsten in de gematigde gebieden laten zich verklaren doordat de lengte van de groeicyclus van de gebruikte rassen goed aansluit op de lengte van het groeiseizoen.

In hoofdstuk 8, tenslotte, zijn de voordelen van de gebruikte benadering (systeemanalyse, veldproeven, modelbouw en verkenningen) bij de ontwikkeling en introductie van nieuwe rassen besproken. De verworven inzichten kunnen gebruikt worden om ideotypen te ontwerpen, om selectieprocedures efficiënter te maken en om verschillen tussen potentiële en actuele opbrengsten te verklaren.

CURRICULUM VITAE

Pieter Leendert (Peter) Kooman werd op 3 februari 1964 te Westenschouwen geboren. Na het behalen van zijn HAVO diploma in 1981 en zijn Atheneum diploma in 1983 aan de "Professor Zeeman" scholengemeenschap te Zierikzee, begon hij in augustus 1983 met de studie Landbouwplantenteelt aan de toenmalige Landbouwhogeschool te Wageningen. In Augustus 1989 behaalde hij het doctoraalexamen aan de Landbouw Universiteit met als doctoraalvakken Landbouwplantenteelt, Informatica, Vegetatiekunde en Theoretische Productie Ecologie. Zijn stage bracht hij door aan the University of California, te Davis (USA). Per 1 februari 1990 trad hij in dienst van de vakgroep Theoretische Produktie-Ecologie (TPE) van waaruit hij gedetacheerd werd bij het toenmalige Centrum voor Agrobiologisch Onderzoek (CABO), het huidige DLO-Instituut voor Agrobiologisch en Bodemvruchtbaarheidsonderzoek (AB-DLO). Tot december 1994 werkte hij hier als assistent in opleiding aan het onderzoek dat beschreven is in dit proefschrift.

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