Modelling

and

Parameterization of the Soil-Plant-Atmosphere

System

A Comparison of Potato Growth Models

Editors

P. Kabat B. Marshall B.J. van den Broek J. Vos H. van Keulen



IV-3: Coherent set of models to simulate potato growth

P.L. KOOMAN AND C.J.T. SPITTERS

1 Introduction

Crop growth models are used to predict yields or to gain insight into the processes determining crop growth.

When 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.

A single universal model describing all aspects of potato crop growth and able to answer any question would, if it were ever realized, necessarily be very detailed. Such a model also has the disadvantage of an unpredictable error behaviour. It has an excess of detail for each single research question, it requires substantial effort for the user and it is virtually impossible to parameterize for a particular condition. The development of a coherent set of models simulating the different processes of plant production at a different level of detail is a more promising approach.

The approach of simulation on different levels of complexity is illustrated in this paper. 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 are available for each of these main processes. A limited, but coherent set is presented here.

More comprehensive models, which simulate the growth of single organs (Ng & Loomis, 1984), are available. To illustrate the approach of a coherent set of models, however, such detail is not required. The performance of the combination of the coherent set of models is not only shown for the simulation of potential production, but also with a stress factor that limits production. Here we focus on drought and not on nutrients. The objective of this study is to compare and analyze the behaviour and performance of models, defined at different levels of detail.

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

2 Model descriptions

2.1 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 suboptimal 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 submodels. In this study an example of drought stress is given. The list of variables of the coherent set of models is given in Table 1.

Table 1. List of variable

Variable	Meaning	Units
A _m	the light saturated photosynthesis rate	$(g CO_2 m^{-2} leaf h^{-1})$
Α	CO ₂ assimilation rate	$(g m^{-2} d^{-1})$
C _f	conversion efficiency	$(g g^{-1} CH_2 0)$
D	daylength	$(h d^{-1})$
d	duration of leaf senescence	(°C d)
E	soil evaporation	(mm d ⁻¹)
E _r	evaporation for 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}	cropfactor with a value of 1.1	
F _{LINT}	light interception	(MJ m ⁻²)
HIm	asymptotic maximum harvest index	
HI	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 selfshading	$(m^2 m^2)$
LAI(t)	LAI at time t (in day degrees after emergence)	$(m^2 m^{-2})$
LUE	average light use efficiency	(g MJ ⁻¹)

Continue Table 1.		
Variable	Meaning	Units
LUE _{tb}	light use efficience for tuber growth	(g MJ ⁻¹)
N	plant density	(m ⁻²)
Р	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	
Piv	partitioning factor for leaves	
P _{rt}	partitioning factor for roots	
P _{st}	partitioning factor for stems	
P _{tb}	partitioning factor for tubers	
R ₀	initial relative growth rate	$(^{\circ}C^{-1}d^{-1})$
RDR	relative death rate	$(^{\circ}C^{-1}d^{-1})$
RDR _{dv}	death rate due to development	$(^{\circ}C^{-1}d^{-1})$
RDR _{sh}	death rate due to selfshading	$(^{\circ}C^{-1}d^{-1})$
R	relative leaf area growth rate	$(^{\circ}C^{-1}d^{-1})$
R _m	maintenance respiration	$(g CH_2 0 m^{-2} d^{-1})$
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	$(cm^{3} cm^{-3})$
SMa	moisture content at air dryness	$(cm^{3} cm^{-3})$
SMf	moisture content at field capacity	$(cm^{3} cm^{-3})$
t	thermal time	(°C d)
Т	crop transpiration	(mm d ⁻¹)
t ₅₀	thermal time when 50 percent of the leaves	
	has died	(°Cd)
W	total dry matter	(g m ⁻²)
Wi	organ dry matter	$(g m^{-2})$
W_{lv}	dry matter of total leaves	$(g m^{-2})$
Wivg	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	$(g m^{-2} d^{-1})$
3	initial efficiency for single leaf	(g CO ₂ J ⁻¹)

2.2 Governing equations

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2.2.1 Development of leaf area and interception of light

Interception of light by the foliage may be described at three levels of complexity (Table 2). The simplest approach is to describe the fractional interception of PAR as a function of the phenological development stage.

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Table 2. Characterization of the models differing in complexity and detail (levels).

	level 1	level 2	level 3
Light interception	Fractional	Based on LAI	Based on LAI and light profile
•	(Equation 1)	(Equation 7)	(Equation 7)
Light utilization	Efficiency	Efficiency	Photosynthesis and Respiration
	(Equation 8)	(Equation 8)	(Equation 9)
Dry matter	Harvest	Distribution	Distribution
distribution	Index	pattern	pattern
	(Equation 12)	(Equation 13)	(Equation 13)

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 (Equation 1). The decrease towards maturity is assumed to be linear inversely proportional to the increase in temperature sum (Equation 2). The actual interception of PAR is the minimum of both functions:

$$F_{\text{LINT}} = \frac{NF_0 e^{R_0 t}}{NF_0 e^{R_0 t} + 1 - NF_0}$$
(1)

$$F_{\text{LINT}} = 0.5 - \frac{t - t_{50}}{d}$$
(2)

In both models of the second and third level of complexity (Table 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:

 $\Delta LAI = SLA \ \Delta W_{lv} \tag{3}$

Equation 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 then can be described with an exponential function of the temperature sum from plant emergence:

$$LAI_{t} = NL_{0}e^{R_{1}t}$$
 $t \le 450$ $LAI \le 0.75$ (4)

The decrease in leaf area in this most detailed approach is obtained by multiplying the amount of green leaf area with 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 3) and self shading (RDR_{sh}). The development is quantified by thermal time and dying of leaves occurs after 810 degree days. (Table 3). Dying of the leaves due to selfshading occurs only when and as long as the critical LAI (LAI_c) is exceeded (Table 3). In the model the maximum of both RDR_{dv} and RDR_{sh} is chosen as actual death rate (Equation 5).

$$RDR = MAX \left| RDR_{dv}, RDR_{sh} \right|$$
⁽⁵⁾

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

$$\Delta LAI = LAI RDR$$

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 (Equation 7) as is done at level 2 (Table 2):

$$F_{lint} = 1 - e^{-kLAI}$$

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, distinction is also made between profiles for the direct solar beam from the sun and for diffuse radiation. (e.g. de Wit, 1965; Spitters, 1986; Goudriaan, this volume).

2.2.2 The use of intercepted PAR for dry matter production

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

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):

$\Delta W = LUE F_{lint} PAR$

(8)

LUE changes with the development stage of the crop. Equation 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 the levels 2 and 3 (Table 2).

(6)

(7)

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
light interception	2	d (°C d)	duration of leaf senescence	600	regression	Spitters (1987)	regression	325
	1	F ₀ (MJ d ⁻¹)	initial light inter- ception 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	ι 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	literature	Spitters et al. (1989)	no change	
	1	R _o (°C ⁻¹ d ⁻¹)	initial relative leaf growth rate	0.014	regression	Spitters (1990)	regression	0.0119
	5	RDR _{dv} (°C ⁻¹ d ⁻¹)	relative death rate due to development	0.000968 * t * exp (0.002867* (t-725)) for Bintje	literature	Spitters et al. (1989)	calibration	0.000512 * t * exp (0.002867 *(t-810))
	5	RDR _{sh} (°C ⁻¹ d ⁻¹)	relative death rate due to self shading	0.03 * (LAI-5.2) /5.2))	calibration	Spitters unpublished	no change	

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Table 3. Parameter estimates for the set of crop growth models.

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Continue Table 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
	4	R ₁ (C ⁻¹ d ⁻¹)	relative leaf area growth rate	0.012	literature	Spitters et al. (1989)	no change	
	3	SLA (m ² g ⁻¹)	specific leaf area of new leaf	0.3	literature	Spitters et al. (1989)	calibration	(200+0.33) * 10 ⁻⁵
dry matter assimilation		A _m (g CO ₂ m ⁻² leaf h ⁻¹)	light saturated photosynthesis rate	30	literature	Spitters et al. (1989)	optimisation	30.85
	8	LUE (g MJ ⁻¹)	average light use efficiency	2.35 t≤i 2.35 + 0.00092(t-i) i <t<i+380 2.70 t≥i+380</t<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	literature	Spitters et al. (1989)	optimisation	0.4
dry matter distribution	12	HI _m	asymptotic maxi- mum 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
	13	P _{Iv}	partitioning factor for the leaves	0.75-(t-i/430) (0 <p<sub>1v<0.75)</p<sub>	literature	Spitters et al. (1989)	regression	0.48*exp (-0.0050 (t-158))

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Continue Table 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
	13	P _n	partitioning factor for the roots	1-0.8 + 0.2 * P _{tb} (0 <p<sub>rt<1)</p<sub>			no change	
	13	P _{st}	partitioning factor for the stems	1 - P _{iv} - P _{tb}	literature	Spitters et al. (1989)	no change	-
	13	P _{tb}	partitioning factor for the tubers	(t-i/430) (0 <p<sub>tb<1)</p<sub>	literature	Spitters et al. (1989)	regression	1-cxp (-0.00453 (t-158))
	12	s (°C ⁻¹ d ⁻¹)	initial slope of the harvest index curve	0.00322 for Bintjc	regression	Spitters (1987)	regression	0.00272
water relations	16	F _{cr}	crop specific factor for transpiration	1.1			no change	
	-	SW _{fc} (kg H ₂ 0 m ⁻³)	volumetric soil moisture content at field capacity				estimated	300
	-	SW _{wp} (kg H ₂ 0 m ⁻³)	volumetric soil moisture content at wilting point				estimated	60 _
	-	SW _{ad} (kg H ₂ 0 m ⁻³)	volumetric soil moisture content at air dryness				estimated	20

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

$\Delta W_{tb} = LUE_{tb} F_{lint} PAR$

In the second approach, as used at level 3 (Table 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.

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

$$\Delta W = C_f \left(\frac{30}{44} A - R_M \right) \tag{10}$$

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 it is a weighted mean, determined by relative allocations of incremental dry matter to component plant parts: per unit increment in dry leaf dry matter 1.46 units substrate are required; likewise each unit of stem, root and tuber material requires 1.51, 1.44 and 1.28 units of substrate (Spitters et al., 1989).

A numerical approach is used in the more comprehensive model for the calculation of daily crop photosynthesis and consists of an asymptotic exponential function for the momentary photosynthesis light response of the individual leaves. The photosynthesis light response of individual leaves is characterised 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 distinguishing between a shaded area, receiving only diffuse radiation, and a sunlit area receiving 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 Equation 10) and respiration related to the conversion of assimilates into structural plant material (growth respiration 1- C_f , Equation 10) (McCree, 1970). The maintenance respiration is calculated by multiplying the weights of the organs with a specific factor, and allowing for a temperature effect:

(9)

$$R_{m} = \left(0.03W_{lv} + 0.015W_{st} + 0.015W_{rt} + 0.0045W_{tb}\right) F(t) \frac{W_{lvg}}{W_{lv}}$$
(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).

2.2.3 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):

$$HI_{t} = HI_{m} \left(1 - e^{\frac{-s(t-i)}{HI_{m}}} \right)$$
(12)

At level 2 and 3 (Table 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.

$$\Delta W_i = P_i \Delta W \tag{13}$$

In most experiments the root weight is not determined, so in our coherent set (levels 2 and 3 (Table 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 (Figure 1, Table 3).

2.2.4 Crop growth under water restricted conditions

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 submodel.

Water balance. Many models are published which calculate the amount of available soil water for the plant over time (Hanks & Rasmussen, 1982). A simple method is used for a free drained soil profile, based on the continuity equations. More detailed approaches are easily included into the modular structure of the model.



Figure 1. Schematic representation of the fractional 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:

$$\Delta S = I_n - P - E - T \tag{14}$$

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

$$E = E_r \left(e^{-0.7 k LAI} \right) f_{sm2} \tag{15}$$

where

 E_r = reference evapotranspiration according to Makkink (1957)

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

$$T = E_{r}F_{cr}\frac{1 - e^{-0.7kLAI}}{1 - e^{0.7k4}} \frac{SM - SM_{a}}{SM_{f} - SM_{a}}$$
(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_o) 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_o 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 below ground parts (Brouwer, 1983) as described by van Keulen et al. (1982).

2.3 Input and output of the model

The input parameters are summarized in Table 4. The potential version of the model required daily radiation and daily minimum and maximum temperature. The models which have water relations built in require also the early morning vapour pressure and the daily rainfall. The timestep 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 every state or rate variable is used in the model.

Table 4. Model characteristics.

Language	:	Fortran							
Shell	:	Fortran Simula	ortran Simulation Environment. (FSE)						
Timestep	:	1 Day	Day						
Timescale	:	1 season							
Input	:	Daily values of	of weather	data					
-		Radiation		(kJm ⁻² d ⁻¹)		• . •			
		Temperature	MIN	(°C)					
		•	MAX	(°C)					
		Vapour pressu	ire	(KPa)					
		Windspeed		(m s ⁻¹)					
		Rain		(mm d ⁻¹)					

3 Parameterization and calibration

3.1 Original parameterization and calibration

The set of models was initially parameterized for Bintje under Dutch conditions. The data in Table 3 which did not change were estimated under these conditions. Only parameters dependent on variety and location 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 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 the DRY treatment in 1986 were used to parameterize the versions in which water relations

were included. The 240 N treatment in 1985 and the WET and DRY treatment in 1987 are be predicted.

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	. 9

Table 5. Experiments and treatments used in this study.

3.2 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 on level 1 (Equation 1) and a lower value of R_1 on level 2 and 3 (Equation 4). Maris Piper had a later senescence compared to Bintje so the t_{50} on level 1 (Equation 2) was raised and the RDR_{dy} function on level 2 and 3 (Equation 5) had to start later and had to progress slower. Subsequently the allocation of assimilates to the different plant organs was studied. Compared to Bintje, Maris Piper initiated the tubers later. In the beginning of the season Maris Piper allocates a smaller fraction to the tubers. Therefore the slope and the maximum of the harvest index function on level 1 (Equation 12) were assigned a lower value. For the partitioning to the tubers and leaves on level 2 and 3, new relations are derived from the data. 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 3) which results in a partitioning pattern as given in Figure 1 and in a better prediction of yield.

Finally the conversion from light to assimilates was evaluated. On level 1 and 2 the LUE was made sink dependent (Table 3) because the presence of tubers increases the photosynthesis rate (Ng & Loomis, 1984). The parameters for this relation could be derived from regression analysis. On level 3 the A_m and ε could not be derived directly and were obtained with an optimization method based on the algorithm of Price (1979) as applied in crop growth models by Klepper & Rouse (1991). In the optimization procedure, 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 on the different levels is very small. The simulation of total dry matter and tuber dry matter in the year 1984 N4 treatment (Fig 2a) followed the observed data well, especially in the beginning of the season. On levels 2 and 3 the model tended to underestimate the production towards the end of the season. On these levels (2 and 3), the leaf dry matter production was predicted well but the stem dry matter was underestimated a little (data not shown). The model with different levels of complexity gave comparable results for the WET treatment in 1986, but the estimates were not as good as those for 1984. Figure 2b (1986 WET treatment) shows that at the beginning of the season the tuber dry matter was underestimated while the total dry matter was estimated rather well, whereas at the end of the season the simulated tuber dry matter yields compared well with the measured data while 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 directly related to the leaf dry matter and 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 on the levels 2 and 3.



Figure 2a. Simulated and observed production of total dry matter and tuber dry matter for the 1984 N4 treatment (calibration).



Figure 2b. Simulated and observed production of total dry matter and tuber dry matter for the 1986 WET treatment (calibration).



Figure 2c. Simulated and observed production of total dry matter and tuber dry matter for the 1986 DRY treatment (calibration).

In the DRY treatment of 1986 (Figure 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.

4 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 the 1985 N4 treatment (Figure 3a for levels 1, 2 and 3). The simulated deviations for level 1 were mainly due to too low an estimated value for the light use efficiency. Figure 3b shows a large underestimation of simulated stem dry weight but a good agreement between simulated and measured leaf dry weight for level 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 3c (levels 1, 2 and 3 without waterbalance and levels 2 and 3 with a waterbalance) as explained



Figure 3a. Simulated and observed production of total dry matter and tuber dry matter for the 1985 N4 treatment (verification).



Figure 3b. Simulated and observed production of leaf dry matter and stem dry matter for the 1985 N4 treatment (verification).



Figure 3c. Simulated and observed production of total dry matter and tuber dry matter for the 1987 WET treatment (verification).

in Section 2.2.4. with model level 1 showing the largest deviations from the observations. Figure 3d 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 waterbalance performed the same as levels 2 and 3 without waterbalance.

The 1987 DRY treatment was simulated with levels 2 and 3 with the waterbalance. There was a good agreement between simulated and observed values for both the total dry weight and tuber dry weight (Figure 3e), whereas leaf and stem dry weights were largely overestimated by the model (Figure 3f).

5 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 is varied in this study by using different levels of complexity for the main processes which determine crop growth. The level of complexity appeared not to be important 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).



Figure 3d. Simulated and observed production of leaf dry matter and stem dry matter for the 1987 WET treatment (verification).



Figure 3e. Simulated and observed production of total dry matter and tuber dry matter for the 1987 DRY treatment (verification).



Figure 3f. Simulated and observed production of leaf dry matter and stem dry matter for the 1987 DRY treatment (verification).

For predictive purposes this model (level 1) seems to be most suitable whereas with the inclusion of water relations, the more complex models are needed.

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. Different authors 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 they are included into the models may improve the performance.

The second facet of modelling is the parameterization of the models. Not all parameters used in the models are independent of variety and location. In this study the parameter estimation took place using the 1984 and 1986 data sets. Both the 1984 N4 treatment and the 1986 WET treatment were considered to be without stress. 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 pointed in the direction of stress at the beginning of the season. The parameters which were estimated using the 1986 data resulted in an underestimation of crop dry matter production. The effect of drought was large on the simulated results of 1986, probably due to a too simple description of the soil waterbalance. It was assumed that there was a free draining profile with no capillary rise from the groundwater. Nevertheless, the predictions for total and tuber dry weight for the 1987 DRY treatment were satisfactory.

In conclusion, the presented study illustrates the advantages of the use of 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 the use of more complicated models which independently describe crop growth processes in detail are needed when an explanation of the influence of the environment on crop growth is required.

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