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Adaptation of a Crop-growth Model and its Extension by a Tuber Size Function for Use in a Seed Potato Forecasting System

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ABSTRACT

The crop-growth model for potatoes by Johnson et al. *(1986) was adapted for use within a decision support and forecasting system for seed potato production and coupled to a soil water-balance model in order to simulate growth under suboptimal hydrological conditions. The original model produced outputs that deviated largely from field data for cultivars grown in Switzerland. To achieve a better fit of these data, we adapted the model by estimating a new set of parameters. Furthermore, we needed to calculate the tuber size distribution, which is not done in the original model. For this purpose we introduced a tuber size output function. These modifications together with the corresponding validation results are described in this study. To simulate plant growth of many cultivars with a minimum of different parameter values, the cultivars were grouped into three maturity classes, which differ in the tuber initiation age, the tuber dry matter content at maturity and the leaf age at senescence. Tuber dry matter content is calculated as a function of physiological time. The tuber weight distribution is modelled by a Weibull distribution; its shape parameter α is kept constant, whereas the scale parameter β is a function of the average tuber weight. Before calculating the weight distribution, the tuber grades are transformed into tuber weights by accounting for the cultivar-specific shape of the tubers. The overall agreement of the model generated output with the corresponding field data was satisfactory. The mean absolute deviation between simulated and observed data was 15% of the average of the field*

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data in the case of total fresh yield, 17% for leaf dry weight, 25% for seed yield and 35% for ware yield. The agreements for stem and root dry masses were not as good, but simulated values were in the same order of magnitude as observed ones. We conclude that the model meets the objectives and can be used within the forecasting system.

INTRODUCTION

The production of seed potatoes in Switzerland, similar to other countries, presents difficult decisions every year. To keep infection by viruses low, haulms of potato crops used for seed production are destroyed between the end of June and the end of July (Häni & Winiger, 1987; Schwärzel & Gehriger, 1989). Haulm destruction is compulsory and its date is determined every year by the Federal Agricultural Research Stations. However, the date of haulm destruction has to be determined with great care, because tuber yield and infection of the tubers by viruses often rise quickly at this time. After 10 years of field experiments and several years of simulation and modelling studies (Nemecek, 1993), we developed a decision support system for seed potatoes, called TUBERPRO (= *Solanum **tuber**osum* **pro**gnosis; Nemecek *et al.*, 1994). In order to optimize haulm destruction dates, the system forecasts virus infection and graded tuber yields. Furthermore, it carries out a risk analysis.

The core of TUBERPRO consists of the simulation model EPOVIR (= **e**pidemiology of **po**tato **vir**uses), which is composed of four submodels: a potato crop-growth submodel, a soil water-balance submodel, a virus inoculation submodel and a virus infection submodel; the latter two submodels together form the virus epidemic model (Fig. 1A, Nemecek, 1993; Nemecek *et al.*, 1994, 1995). For the sake of simplicity, we will use the term "model" instead of submodel throughout this text.

A potato crop model was needed, to calculate yield and to simulate adequately the influence of the potato crop on virus infection, multiplication and translocation and on the aphid populations that transmit the viruses (Nemecek *et al.*, 1995). We found that the potato crop model of Johnson *et al.* (1986, 1987) meets most of our objectives. However, its outputs deviated largely from our field data for cultivars grown in Switzerland. We tried to achieve a satisfactory behaviour mainly by changing parameter values. The original model used soil moisture data as inputs, which we did not have in all our experiments. These measurements were replaced by a soil water-balance submodel (Fig. 1B). Further, we needed to know the tuber size distribution, because the grade of seed tubers is often very critical. For this purpose a tuber size output function was

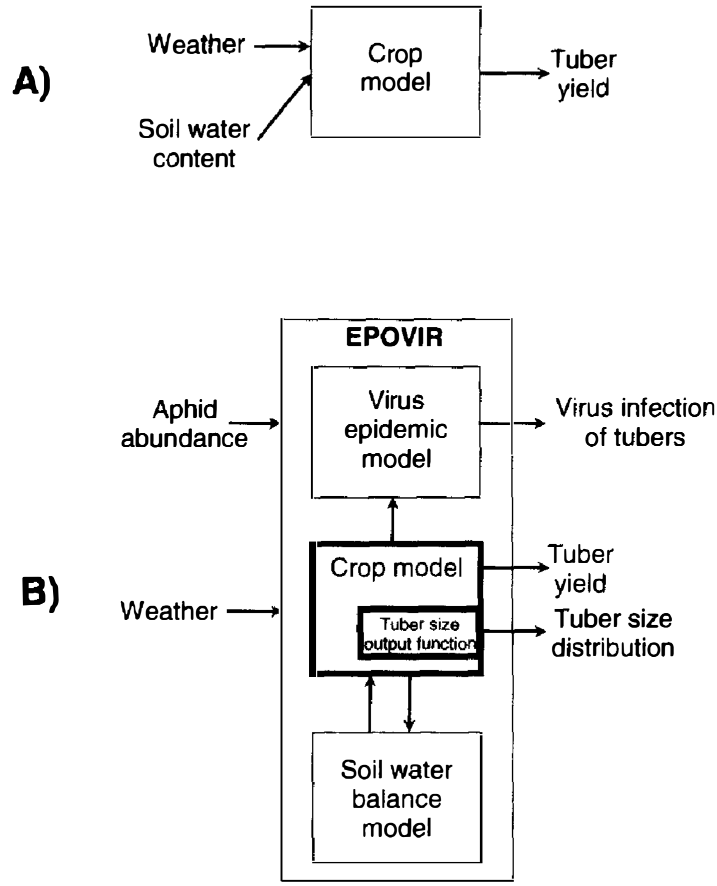

Fig. 1. Schematic representation of the original potato crop model of Johnson *et al.* (1986) (A) and the adapted crop model as used within EPOVIR (B). The boxes drawn with a bold line indicate the model parts treated in this paper.

introduced. After performing these modifications, the model needed to be validated by using independent data sets. These changes and validations of the model are presented in this paper. The aims of the model are to forecast total and graded potato yields and to simulate the leaf mass realistically. The latter is needed in the virus epidemic model, because the leaf area influences the behaviour of the aphid vectors, and the physiological age of the leaves is used in the calculation of the age resistance against virus infections (Nemecek, 1993; Nemecek *et al.*, 1995).

MATERIAL AND METHODS

The field data used for model calibration and validation were collected during 10 years at various sites in Western Switzerland. These experiments (Nemecek & Derron, 1994) encompass all cultivars of the official list (Reust, 1993). Furthermore, data were collected by the seed grower organization "Association Suisse des Sélectionneurs" from 1988 to 1992 (unpublished). Five groups of five neighbouring plants in the same row were sampled per field. We have used the averages per cultivar to validate the tuber size output function. The field data were subdivided into "calibration data", used for parameter estimation, and "validation data", only used for validation purposes.

The model is implemented in the programming language Modula-2 (Wirth, 1985) by using the simulation environment "ModelWorks" (Fischlin *et al.*, 1994).

THE MODEL AND ITS MODIFICATIONS

Model outline

Johnson *et al.* (1986, 1987) used measurements of soil moisture as inputs for their model (Fig. 1A). Such measurements are often not available, which was also the case in many of our experiments. In order to calculate the water stress of the plants from weather data only, a soil water-balance model is required. Such a model was built and coupled to the potato crop model (Fig. 1B). The coupled crop-growth and soil water-balance models are described in detail by Roth *et al.* (1995). Here we give only a brief outline of the two models.

The crop-growth model simulates the dry mass of leaves, stems, roots, tubers and assimilates of an average plant in the field. The physiological scale, which is used to calculate phenological development and net assimilation, is derived from Sands *et al.* (1979). Net assimilation is calculated by intercepted global radiation, radiation use efficiency (RUE), water stress, leaf age and the increase in physiological age. Partitioning of assimilates is defined by a set of equations of the Michaelis–Menten type. Simulation starts at 50% crop emergence and stops at haulm destruction.

The soil water-balance model, which is based on the work of van Keulen and Wolf (1986), simulates the water content in the root zone by treating the soil as a single layer. The water stress factor is calculated as the ratio of actual to potential transpiration and used in the crop model. The output of the coupled models showed a satisfactory agreement with data for cv. Maris Piper and soil water data from Scotland, collected under wet and dry conditions (Roth *et al.*, 1995).

Because the yield reduction due to viruses is very small in seed potato production, it has been ignored in the model EPOVIR. Therefore the crop-growth and soil water-balance models do not depend on the virus epidemic model and are thus validated independently.

Changes in model equations

In the original model, tuber fresh yield (*tuberFW* [dt/ha]) was calculated as the product of tuber dry weight (*tuber* [g/plant]), plant density and a constant conversion factor (*tuberDWtoFW* [–]). As we are interested not only in final yield, but also in the development of tuber yield in the early growth phases, the assumption of a constant tuber dry matter content is not valid, because it increases during crop growth. Although of high practical relevance, most potato crop models do not calculate tuber fresh yield or do so by using a constant conversion factor. Only Jefferies and Heilbronn (1991) formulated tuber dry matter content as a quadratic function of physiological age by accounting for the amount of available soil water. This appeared to be too complicated for our study. We thus assumed that dry matter content increases linearly with physiological age after tuber initiation up to a maximum value:

$$tuberDWtoFW = \begin{matrix} 1/dmCont & \text{if } dmCont < maxDMCont \\ 1/maxDMCont & \text{if } dmCont \geq maxDMCont \end{matrix} \quad (1)$$

$$dmCont = minDMCont + (pA - tuberInitPA)\ dmIncr,$$

where *minDMCont* and *maxDMCont* [–] are the tuber dry matter contents at tuber initiation and maturity, respectively, *pA* is the current physiological age of the plant (phys. age units after emergence [pA], max. increase is 10 units per day), *tuberInitPA* [pA] is the physiological age at tuber initiation, *tubDMIncr* [%/(100 pA)] is the rate of tuber dry matter increase and *dmCont* [–] is an auxiliary variable.

The parameter *maxPlantPA* [pA] (age of complete senescence) has been dropped from the model because plant growth is already limited by haulm destruction or leaf senescence.

The only change in the soil water-balance model (Roth *et al.*, 1995) consists of the calculation of the potential transpiration TM (mm/d), where we use now the same parameter values as in the equation for light interception in the crop model.

Tuber size output function

Description

The purpose of this function is to calculate the tuber size distribution, i.e. the fraction of tubers in different size grades by using the average tuber weight and a factor for tuber shape. This information is needed to know which fraction of the total yield can be used for seed and other purposes, respectively.

In the literature, tuber weight and tuber size are sometimes used as synonyms. We will reserve "tuber weight" for the (fresh) weight of individual tubers (g) and tuber size for their grade or diameter (cm). Different approaches have been used to model the tuber grade distribution: some authors have modelled the *tuber weight* distribution (Marshall, 1986; Marshall *et al.*, 1993; Sands & Regel, 1983), and others the *tuber size* distribution (Hide & Welham, 1992; Travis, 1987; Wurr *et al.*, 1993). As the crop model calculates tuber weight, we decided to follow the first approach. However, the tubers are graded according to their diameter by using a square mesh, so we had to calculate tuber weight as a function of tuber size.

Two statistical distributions have been used: a normal distribution (Marshall, 1986; Sands & Regel, 1983; Travis, 1987; Wurr *et al.*, 1993) or a mixture of two normal distributions (Hide & Welham, 1992) and a log-normal distribution (Marshall *et al.*, 1993). The normal distribution is usually truncated at 0, which is not necessary, if the log-normal distribution is used.

We decided to use the Weibull distribution as an alternative for several reasons. Tuber weight distributions were fitted better by the Weibull distribution than by the truncated normal distribution (Sands & Regel, 1983). The two distributions were compared on 57 samples of cv. Bintje, where five grades were separated. The distributions were fitted by a non-linear estimation procedure, by minimizing the squared deviations between the observed and the calculated distributions. In 38 cases (67%) the Weibull distribution gave a better fit than the truncated normal distribution; in the other cases, the truncated normal distribution performed better. On average, the squared deviations were 18% smaller for the Weibull than for the truncated normal distribution. Because the Weibull distribution is limited to positive values, no truncation is necessary. The values of the Weibull distribution function can be calculated by a simple formula (3), whereas those of the normal or log-normal distributions have to be calculated by numerical integration algorithms.

The tuber yield (fresh weight) of a certain grade is calculated in several steps:

1. The size limits are transformed into fresh weight limits (eqn (2)) at the beginning of each simulation run by accounting for the cultivar-specific tuber shape.
2. The scale parameter β of the Weibull distribution is calculated from the average tuber fresh weight (eqn (10)) at each integration step.
3. The fraction of tuber yield between the weight limits is calculated by the integral of the Weibull function and multiplied by the total yield (eqn (5)) at each integration step.

The relationship between tuber fresh weight w (g) and diameter d (cm) (definition see below) is derived from the formula for the volume of a sphere:

$$w = k4\pi/3(d/2)^3 \tag{2}$$

where k (g/cm^3) is a parameter accounting for the shape of the tuber as well as its specific gravity ($k > 1$). The fraction of tuber yield below a weight limit w_u is given by the Weibull distribution function with the parameters α and β:

$$P(w \leq w_u) = 1 - e^{-(w_u/\beta)^{\alpha}} \tag{3}$$

and the fraction between a lower weight limit w_l and an upper one w_u is:

$$P(w_l \leq w \leq w_u) = e^{-(w_l/\beta)^{\alpha}} - e^{-(w_u/\beta)^{\alpha}}. \tag{4}$$

Multiplying P by the total tuber yield *tuberFW* gives the tuber yield between the limits:

$$tuberFW(w_l \leq w \leq w_u) = tuberFW(e^{-(w_l/\beta)^{\alpha}} - e^{-(w_u/\beta)^{\alpha}}). \tag{5}$$

The weight limits w_l and w_u are given by eqn (2).

Parameter estimation

The tuber shape parameter k (Table 1) was derived from measurements of the tuber length a, the greatest breadth b, the least breadth c and the weight w of 50 tubers for each cultivar. k can be calculated by eqn (2), substituting $d = (b + c)/2$. d is closely related to the grade of a tuber as determined by a square mesh. The cultivars were grouped by Tukey's multiple comparison test. The values of k were transformed to natural logarithm to make the variances equal and the distributions normal. No significant differences at the 5% level were found within the groups shown

TABLE 1

Classes of Tuber Shape for the Tuber Size Model

Class	*Description of tuber shape*	k ± *CI*	*Cultivars*
I	Roundish	1·37 ± 0·03	Erntestolz, Hertha, Sirtema
II	Short oval	1·46 ± 0·02	Aula, Granola, Hermes, Panda
III	Oval	1·59 ± 0·03	Eba, Matilda, Ostara, Saturna
IV	Long oval	1·74 ± 0·03	Agria, Bintje, Christa, Désirée, Ukama, Urgenta
V	Long	1·96 ± 0·08	Nicola
VI	Very long	2·12 ± 0·06	Charlotte, Stella

k, tuber shape parameter; CI, half confidence interval (95%) for the estimate.

in Table 1. An alternative estimation procedure for k is to measure only a and b and to calculate:

$$k = -0 \cdot 07 + 1 \cdot 26a/b, \quad (6)$$

which is simpler and gives values very close to those obtained by the first method ($r^2 = 0{\cdot}97$). The parameters of the Weibull distributions were derived from graded yields by linear regression. The Weibull distribution function was linearized by:

$$\ln(-\ln(1 - P)) = b_0 + b_1 \ln(w), \quad (7)$$

where P is the cumulated weight distribution function and w the tuber weight. The Weibull parameters are given by:

$$\alpha = b_1 \quad (8)$$
$$\beta = e^{-b_0/b_1}$$

Estimates for α were found to vary little, which is in agreement with the findings of Marshall (1986) that the coefficient of variation (CV) is fairly constant in most situations. The CV of the Weibull distribution is a function of α (Hastings & Peacock, 1975). For our calibration data we found a value of $\alpha = 2{\cdot}3$, which gives CV = 46%, the same value as found by Marshall (1986). The parameter β was reestimated by eqns (7) and (8) for each situation by setting α resp. b_1 equal to 2·3. Finally, the resulting values of β were related to the average tuber fresh weight $\bar{w}$ (g). The relationship between the two variables was non-linear, and the variance of β increased with increasing $\bar{w}$, which was corrected by transforming the two variables to natural logarithms:

$$\ln(\beta) = c_0 + c_1 \ln(\bar{w}), \quad (9)$$

which resulted in the following relationship:

$$\beta = e^{(1 \cdot 17 + 0 \cdot 84 \ln(\bar{w}))}, \quad (10)$$

where $\bar{w}$ is given by the total fresh yield (g/plant) divided by the number of tuber sets per plant, i.e. tubers that are not resorbed and are likely to yield marketable or harvestable tubers (Ewing & Struik, 1992).

Changes in parameters

We adapted the crop-growth parameters first to cv. Bintje. The parameter values (Table 2) were derived directly from field data, by graphical and statistical comparison of model output with field data or by an optimization algorithm (see Roth *et al.*, 1995). Thereafter, we adapted them to all cultivars grown in Switzerland. For this purpose, we grouped the cultivars into three maturity classes (early, medium, late) according to the Swiss cultivar list (Reust, 1993). Within these classes the differences in tuber dry yield were mostly not significant. The maturity classes differed in following parameters: tuber initiation age *tuberInitPA*, leaf age at senescence *maxLeafPA*, highest leaf age with optimal photosynthesis *lpAge1*, tuber dry matter content at maturity *maxDMCont* and the partitioning parameter for stems μS. Table 2 lists the values of parameters that differ either from Johnson *et al.* (1986) or from Roth *et al.* (1995). Situation-specific parameters were taken from the field data (only the range of values is given): row distance (constant at 0·75 m), distance between plants in rows (0·24–0·35 m), dates of emergence (23 April to 21 May) and haulm destruction (25 June to 15 August) and the seed piece weight (30–63 g). The number of tubers (tuber sets) was estimated from the tuber samples for each field experiment. The samples during the phase when the number of tubers was still increasing were ignored for the estimation of the number of tubers per plant.

Parameter values of the soil water-balance model are given by Roth *et al.* (1995). The situation-specific parameters were also taken from field data (ranges in parentheses): soil type (loam to silty clay), proportion of stones (0–13%), latitude (46·6–46·8° Northern latitude), altitude (430–710 m) and slope of field (0–16%).

RESULTS

In a first step, the tuber size output function was validated independently from the other parts of the crop model (Figs 2 and 3, Table 3). This validation should show whether the output function calculates graded yields accurately enough, given the total tuber fresh weight and the number of tubers per plant.

The following statistics have been calculated: the mean deviation (MD) shows whether there was a systematic over- resp. underestimation, and the mean absolute deviation (MAD) indicates how much the calculated values deviated from the observed ones (absolute differences, see Table 3 for the formulas). The r^2 (squared correlation coefficient) gives similar information, but is very sensitive to the range of values; for instance a wide range tends to give higher correlation coefficients. In certain experiments, several samples were taken at regular intervals. These samples are not independent. Therefore we calculate only descriptive statistics. Table 3 shows that the correlations were high for both grades. The model tended to

TABLE 2
Parameter Values of the Potato Crop-growth Model

Parameter	*Meaning*	*Unit*	*Original value*	*New value*	*Source for new value*
K	Michaelis–Menten half saturation	g/pl	50	60	Field data for Bintje 1985–87 (optimization)
μL	Max. growth rate of leaves	—	1	1	—
μS	Max. growth rate of stems	—	6	15/15/13	Field data for Bintje 1985–87 (optimization)
μR	Max. growth rate of roots	—	1	6	Field data for Bintje 1985–87 (optimization)
μT	Max. growth rate of tubers	—	6	13	Field data for Bintje 1985–87 (optimization)
tuberInitPA	Start of tuber growth	pA	200–225	80/100/120	Field data for Bintje 1985–87, Sirtema (early) and Eba (late) 1992 (interpolation)
maxLeafPA	Leaf age at senescence	pA	350–400	480/600/710	Field data for early, medium and late cultivars 1986–89
maxPotNetGR	Maximal net dry matter assimilation rate (max. radiation use eff.)	g/MJ	1·5	1·6	Field data for Bintje 1985–87
lpAge1	Highest leaf age with maximal net assimilation	pA	160	240/300/300	Field data for Bintje 1985–87, Sirtema (early) and Eba (late) 1992 (optimization)
lpAge2	Lowest leaf age with maximal net assimilation	pA	80	120	Field data for Bintje 1985–87 (optimization)
averagePA	Average phys. age increase per day	pA	8	8	Weather data Changins 1980–89, May–July
specLA	Specific leaf area	m^2/g	0·023	0·023	Field data for Bintje 1985–87
pASeedCont	Duration of assimilate contribution from seed tuber	pA	200	120	Field data for Bintje 1985–87
propBefE	Proportion of mother tuber assimilates allocated before emergence	—	0·2	0·4	Field data for Bintje 1985–87
propAftE	Proportion of mother tuber assimilates allocated after emergence	—	0·6	0·45	Field data for Bintje 1985–87
propInLeaf	Proportion of mother tuber assimilates allocated to leaves	—	0·2	0·35	Greenhouse data for Bintje
propInStem	Proportion of mother tuber assimilates allocated to stems	—	0·4	0·45	Greenhouse data for Bintje
propInRoot	Proportion of mother tuber assimilates allocated to roots	—	0·4	0·2	Greenhouse data for Bintje
minGrT	Minimal growth temperature	°C	7	4	Ng and Loomis (1984)

cont.

TABLE 2

cont.

optGrT	Optimal growth temperature	°C	21	20	Ng and Loomis (1984)
maxGrT	Maximal growth temperature	°C	30	30	Sands *et al.* (1979)
extCoeff	Extinction coefficient for light interception	—	0·5	0·7	Field data for Bintje, Sirtema and Eba (1986, 1987 and 1993, non-linear regression)
minDMCont	Tuber dry matter content at tuber initiation	—	—	0·06	Wilcockson (1986) and field data for Bintje 1985–87
dmIncr	Increase in tuber dry matter content	1/ pA	—	0·00046	Field data for Bintje 1985–87
maxDMCont	Tuber dry matter content at maturity	—	—	0·2/0·22/0·26	Means of early, medium resp. late cultivars (1986–89)
α	Parameter of Weibull function of tuber weight distribution	—	—	2·3	Data for Bintjc (1991)

The original value in the model of Johnson *et al.* (1986, 1987) is listed in addition to the new one(s) used in the model EPOVIR. Where only onc new value is given, it is used for all cultivars; where three values are given, they refer to early, medium and late cultivars, respectively. The parameter names are adopted from Roth *et al.* (1995). pl, Plant; pA, physiological age unit.

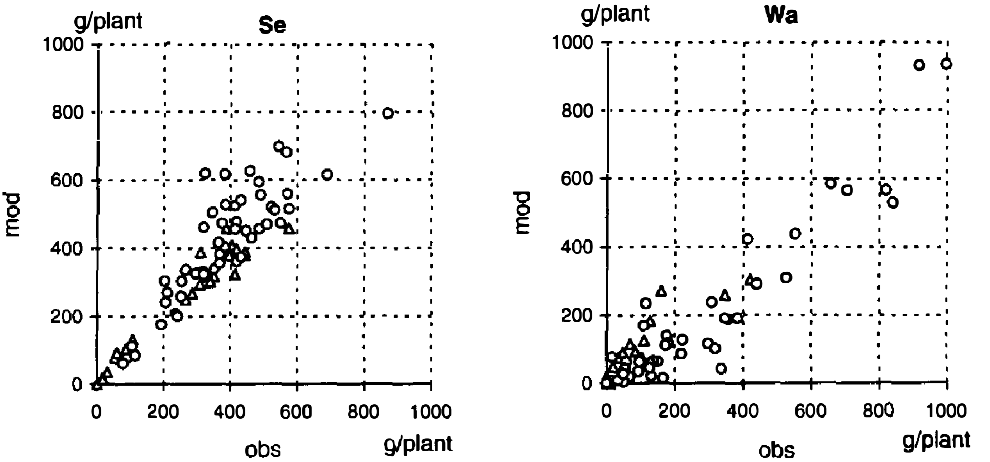

Fig. 2. Comparison of values calculated by the tuber size output function with data from field experiments with cv. Bintje: mod, model; obs, experiment ("observation"); Se, seed grade (32–45 mm); Wa, ware grade (> 45 mm); triangles, calibration data; circles, validation data.

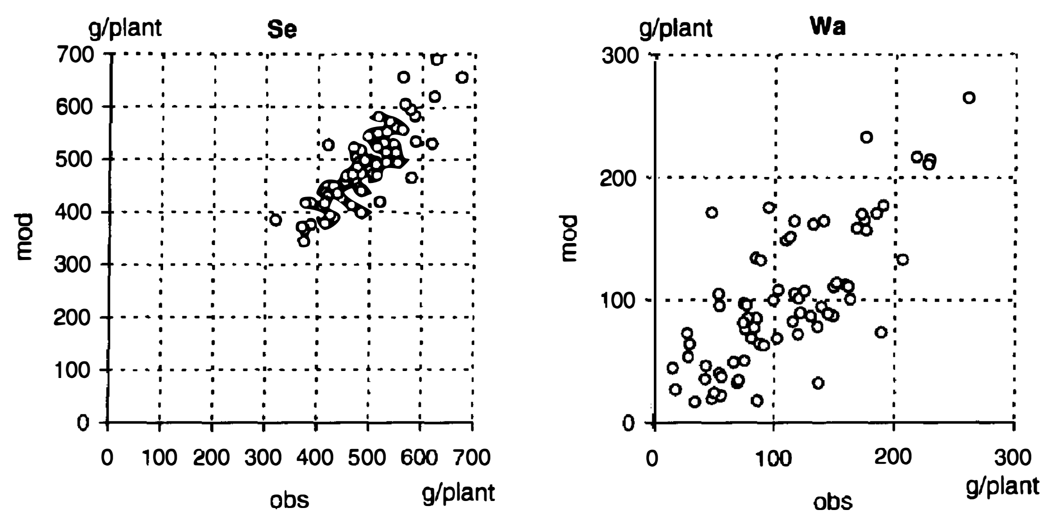

Fig. 3. Comparison of the tuber size output function with experimental data for all cultivars (only validation data): mod, model; obs, experiment; Se, seed grade; Wa, ware grade (sizes depend on cultivar).

overestimate the seed yield and to underestimate the ware yield (Fig. 2, Table 3A). A validation with mean values of 18 cultivars grown during 5 years showed a fairly good agreement for the seed grade and a worse one for the ware grade (Fig. 3, Table 3B). The absolute deviations were negatively correlated to the sample size, which indicates that these deviations can be partly explained by sampling errors.

Finally, the output of the entire crop-growth model was validated. Contrary to the preceding validation, the tuber size distribution was calculated

TABLE 3
Comparison of Validation and Calibration Data with the Results of the Tuber Size Output Function

	A		*B*	
Variable	*Se*	*Wa*	*Se*	*Wa*
Unit	g/pl	g/pl	g/pl	g/pl
N	74	74	74	74
MD	+20·01	−49·86	−2·33	−8·96
MD%	+6%	−27%	−0%	−8%
MAD	53·07	67·07	30·24	31·56
MAD%	16%	36%	6%	29%
r^2	0·84	0·88	0·70	0·55

N, number of observations; MD, mean deviation; MD%, MD in % of observed average; MAD, mean absolute deviation; MAD%, MAD in % of observed average; r, coefficient of simple correlation; A, data for Bintje (see Fig. 2); B, means per cultivar (see Fig. 3); Se, seed grade; Wa, ware grade. Formulas:

$$\mathrm{MD} = \frac{\sum_{i=1}^{N} y_i - x_i}{N}$$

$$\mathrm{MAD} = \frac{\sum_{i=1}^{N} |y_i - x_i|}{N}$$

$$\mathrm{MD\%} = 100\frac{\mathrm{MD}}{\text{Ø}}$$

$$\mathrm{MAD\%} = 100\frac{\mathrm{MAD}}{\text{Ø}}$$

$$\text{Ø} = \frac{\sum_{i=1}^{N} x_i}{N}$$

Legend: Ø = average of observed values; y_i = simulated value: x_i = observed value.

from the simulated tuber yield and not from the observed one. Figure 4 shows an example of a field experiment with the corresponding simulations. In the early growth phases the leaf mass was simulated well, but underestimated afterwards. The stem mass was overestimated in the beginning and underestimated in the later phases. Simulated dry and fresh weights of tubers were close to the experimental data. The seed yield was overestimated after the end of June and consequently, the ware yield was

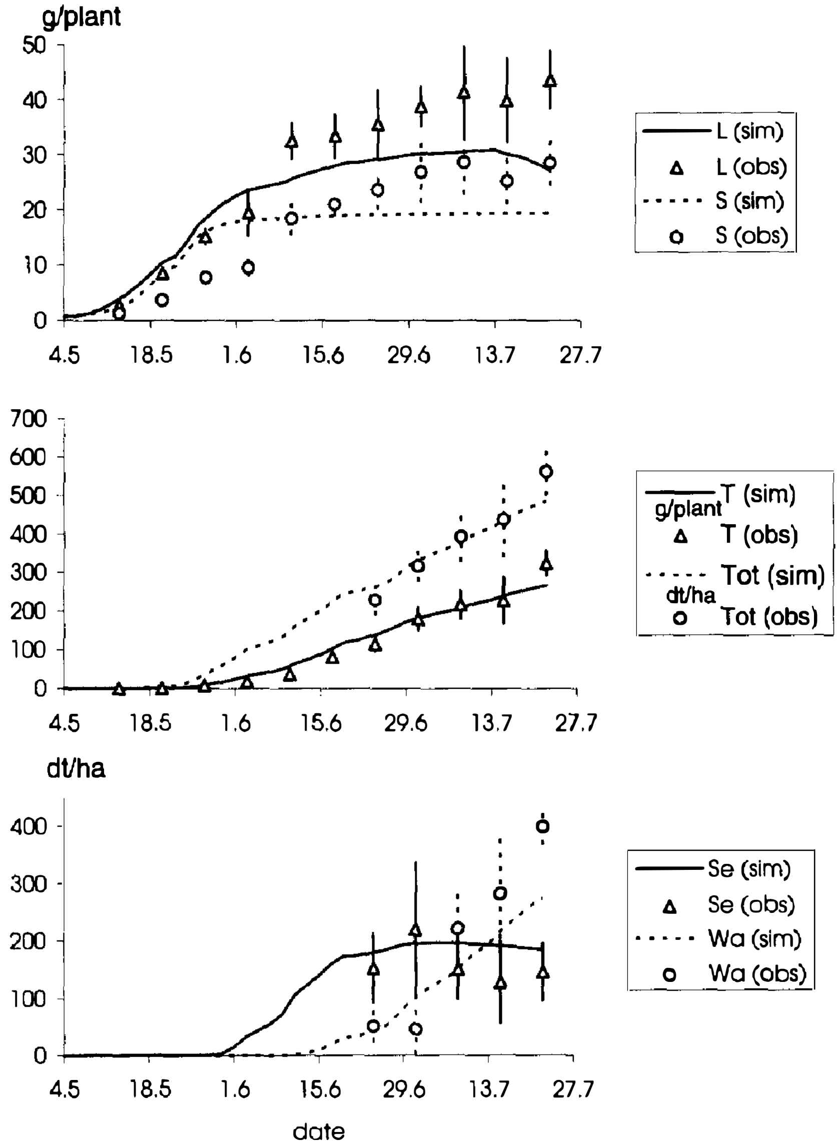

Fig. 4. Development of a potato crop cv. Bintje in Changins in 1992: dry weights (g/plant) of leaves (*L*), stems (*S*) and tubers (*T*) and tuber fresh yields (dt/ha): total (Tot); seed grade (Se, 32–45 mm) and ware grade (Wa, >45 mm). Sim, simulation; obs, experiment with 95% confidence intervals.

underestimated. The statistics for all calibration and validation data are summarized in Table 4. For corresponding graphs see Nemecek and Derron (1994). Tuber dry mass showed the best agreement of all plant organs, followed by leaf dry mass. The agreement for stems and roots was worse, but the MAD did not exceed one-third of the observed mean. The deviations of tuber fresh weight were slightly larger than those of tuber dry weight, and those of graded yields were the largest of the tuber yield variables.

TABLE 4

Comparison of Validation and Calibration Data with Outputs of the Potato Growth Model

Variable *Unit*	L *g/plant*	S *g/plant*	R *g/plant*	T *g/plant*	*Tot* *dt/ha*	*Se* *dt/ha*	*Wa* *dt/ha*
N	113	113	24	121	103	97	97
MD	−1·18	+0·86	+0·11	−0·53	+4·57	−12·7	+10·9
MD%	−5%	+6%	+8%	−1%	+2%	−9%	+10%
MAD	3·97	4·74	0·33	15·3	43·3	35·5	39·6
MAD%	17%	34%	25%	15%	15%	25%	35%
r^2	0·81	0·53	0·53	0·94	0·82	0·62	0·83

Dry weight of leaves (*L*), stems (*S*), roots (*R*) and tubers (*T*) and tuber fresh yield. Total (Tot), seed grade (Se, 32–45 mm) and ware grade (Wa, >45 mm) (for other symbols see Table 3).

DISCUSSION

When we compare our model version to the original one, the following sensitive model parameters have been modified: the extinction coefficient *extCoeff* has been increased, tuber initiation (*tuberInitPA*) occurs much earlier and the leaf age-RUE parameters (*maxLeafPA*, *maxPotNetGR*, *lpAge1* and *lpAge2*) have been adapted (see Table 2). The higher extinction coefficient leads to higher light interception and consequently to higher crop productivity. The value of 0·7, which we found in our experiments, is consistent with published results (Haverkort *et al.*, 1991; Spitters, 1987). The change of the age at which tuber growth starts has many consequences, because stems and roots react sensitively to it (Johnson *et al.*, 1986). We based our parameters on field experiments and found 80–120 physiological age units for *tuberInitPA*, whereas Johnson *et al.* (1986) found 200–225 units. After tuber initiation, stem and root growth ceases quickly, while leaves continue growing for some time. The change in tuber initiation age also made significant changes in the distribution parameters necessary. The leaf age at senescence *maxLeafPA* has been increased in accordance with phenological observations. The differences in parameter values are probably mainly due to cultivar differences, and to a less extent to different cultural practices (e.g. pre-sprouting practised in Switzerland).

The fit of the main model outputs is sufficient for our objectives (Table 4, Nemecek & Derron, 1994). Of the four plant organs, tubers were simulated best, followed by the leaves, which is in accordance with the needs of the forecasting system TuberPro. The fact that the stem and root masses showed less agreement with experimental data has no practical relevance. A better fit of the stem mass would have required major changes in model equations. As the orders of magnitude were correct for all plant organs, we judged such changes not necessary regarding our objectives.

The different degrees of agreement between simulations and field data of the tuber yield variables are due to their mode of calculation. Tuber fresh mass is calculated from the tuber dry mass by assuming a very simple function for tuber dry matter content (eqn (1)). In reality, the dry matter content of tubers depends not only on the physiological age, but also on water availability (Jefferies & Heilbronn, 1991; Jefferies, 1995) and tuber size (Wilcockson, 1986; Wurr *et al.*, 1978). Wilcockson (1986) further showed that tuber dry matter content decreases after haulm destruction, but the amount of this decrease depends on the method of canopy destruction and on water availability. Unfortunately there is only limited information available which could be used to determine the parameters for different cultivars. In our model the dry matter content at maturity *maxDMCont* depends on the maturity class: it is 20% for early, 22% for medium and 26% for late cultivars. Contrary to the results of Wurr *et al.* (1978), we found a clear relationship between the tuber dry matter content and the maturity class for the cultivars considered in our study, whereas the differences within the classes were mostly not significant.

Graded yields are calculated from total yield. Errors in the estimation of total yield usually cause larger errors in graded yields, particularly in ware yields. The tuber size distribution was found to be sensitive to the number of tubers per plant. A fraction of the tubers does not grow or is even resorbed (Ewing & Struik, 1992). These tubers are irrelevant for the tuber size distribution and should be excluded during sampling. The seed yield tended to be overestimated at the expense of the ware yield (Fig. 2 and Table 3), because all sampled tubers were used to estimate the number of tubers. A large number of tubers gives a small average tuber size and favours the smaller grade. It would be desirable to predict the number of tubers per plant from seed size, plant density, storage conditions and weather during the early growth phases. However, this currently seems impossible with the required accuracy (Haverkort *et al.*, 1990).

The Weibull distribution was revealed to be a valuable alternative to the normal and log-normal distributions used by other authors to describe tuber weight or tuber size distributions. The differences between the distributions for the current parameter values are not very large. However, for our data the Weibull distribution gave a better fit than the truncated normal distribution. We have mainly used tuber samples of seed potato crops. It should be verified whether the Weibull distribution can be used equally well, when tubers are sampled from more mature crops. The Weibull distribution can be calculated by a single formula, with no need to truncate and to use numerical integration algorithms. The Weibull distribution also has two parameters like the other distributions, which means that it does not introduce a more complex model. The presented tuber size function can equally well be applied in situations where tubers are graded by weight and by size, respectively. It can be easily adapted to different cultivars, by estimating the tuber shape parameter k on a small sample of tubers (eqns (2) or (6)). In some years, however, tuber shape deviates largely from typical values, e.g. dry years tend to yield short tubers. In these situations the model will perform less well.

As the model outputs total tuber yield, graded tuber yield and leaf mass are generally well simulated by the model, we conclude that the model can be used within the forecasting and decision support system TuberPro. The present study showed that it is possible to adapt the potato crop model of Johnson *et al.* (1986, 1987) to different conditions. It has been sufficient to adapt the parameter values to different cultivars. The changes in model equations have been limited to minor adaptations. The inclusion of a tuber size output function yields more information, but has no effect on the other parts of the model, i.e. tuber dry and fresh mass are not affected by this function.

The crop-growth model has the following limitations: the model operates on production level 2 (Penning de Vries & van Laar, 1982), which means that plant growth is limited by weather and water availability, but that nutrient supply is optimal and that weeds, pests and diseases do not affect plant growth. If one of these assumptions is violated, the model will overestimate yield. Furthermore, the partitioning of the assimilates could be altered if the temperature regime is very different from that in our experiments (Wolf *et al.*, 1990). The parameter values given in Table 2 should be valid for the cultivars investigated in the temperate zones under similar cultural practices.

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REFERENCES

Ewing, E. E. & Struik, P. C. (1992). Tuber formation in potato: induction, initiation and growth. *Plant Breeding Reviews*, **14**, 89–198.

Fischlin, A., Gyalistras, D., Roth, O., Ulrich, M., Thöny, J., Nemecek, T., Bugmann, H. & Thommen, F. (1994). ModelWorks 2.2: An interactive simulation environment for personal computers and workstations. Internal Report No. 14, Systems Ecology, ETH Zurich, Switzerland, 324 pp.

Häni, A. & Winiger, F. A. (1987). Wie produziert die Schweiz Pflanzkartoffeln ohne Blattlausbehandlung?. *Kartoffelbau*, **38**, 273–276.

Hastings, N. A. J. & Peacock, J. B. (1975). *Statistical Distributions — a Handbook for Students and Practitioners*. John Wiley and Sons, New York, USA, 130 pp.

Haverkort, A. J., van de Waart, M. & Bodlaender, K. B. A. (1990). Interrelationships of the number of initial sprouts, stems, stolons and tubers per potato plant. *Potato Research*, **33**, 269–274.

Haverkort, A. J., Uenk, D., Veroude, H. & van de Waart, M. (1991). Relationships between ground cover, intercepted solar radiation, leaf area index and infrared reflectance of potato crops. *Potato Research*, **34**, 113–121.

Hide, G. A. & Welham, S. J. (1992). Observations on the bulking and development of tuber size distribution in maincrop potatoes at Rothamsted in 1964–75. *Potato Research*, **35**, 235–247.

Jefferies, R. A. (1995). Physiology of crop response to drought. In *Potato Ecology and Modelling of Crops under Conditions Limiting Growth*, eds A. J. Haverkort & D. K. L. MacKerron. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 61–74.

Jefferies, R. A. & Heilbronn, T. D. (1991). Water stress as a constraint on growth in the potato crop. 1. Model development. *Agricultural and Forest Meteorology*, **53**, 185–196.

Johnson, K. B., Johnson, S. B. & Teng, P. S. (1986). Development of a simple potato growth model for use in crop-pest management. *Agricultural Systems*, **19**, 189–209.

Johnson, K. B., Teng, P. S. & Radcliffe, E. B. (1987). Coupling feeding effects of potato leafhopper, *Empoasca fabae* (Homoptera: Cicadellidae), nymphs to a model of potato growth. *Environmental Entomology*, **16**, 250–258.

Marshall, B. (1986). Tuber size. *Aspects of Applied Biology*, **13**, 393–396.

Marshall, B., Holwerda, H. T. & Struik, P. C. (1993). Synchronisation of tuber growth in potato (*Solanum tuberosum*): a statistical model. *Field Crops Research*, **32**, 343–357.

Nemecek, T. (1993). The role of aphid behaviour in the epidemiology of potato virus Y: a simulation study. Diss. No. 10086, ETH Zurich, Switzerland, 232 pp.

Nemecek, T. & Derron, J. O. (1994). Validation et application d'un modèle de croissance de la pomme de terre. *Revue Suisse d'Agriculture*, **26**, 311–315.

Nemecek, T., Derron, J. O., Schwärzel, R., Fischlin, A. & Roth, O. (1994). Un modèle de simulation au service des producteurs de plants de pommes de terre. *Revue Suisse d'Agriculture*, **26**, 17–20.

Nemecek, T., Derron, J. O., Fischlin, A. & Roth, O. (1995). Use of a crop-growth model coupled to an epidemic model to forecast yield and virus infection in seed potatoes. In *Potato Ecology and Modelling of Crops Under Conditions Limiting Growth*, eds A. J. Haverkort & D. K. L. MacKerron. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 281–290.

Ng, E. & Loomis, R. S. (1984). Simulation of growth and yield of the potato crop. Simulation Monographs, Pudoc Wageningen, The Netherlands, 147 pp.

Penning de Vries, F. W. T. & van Laar, H. H. (eds) (1982). *Simulation of Plant Growth and Crop Production.* Pudoc, Wageningen, The Netherlands, 308 pp.
Reust, W. (1993). Liste officielle suisse des variétés de pomme de terre 1994. *Revue Suisse d'Agriculture*, **25**, I–VI.
Roth, O., Derron, J., Fischlin, A., Nemecek, T. & Ulrich, M. (1995). Implementation and parameter adaptation of a potato crop simulation model combined with a soil water subsystem. In *Modelling and Parametrization of the Soil–Plant–Atmosphere System — a Comparison of Potato Growth Models*, eds P. Kabat, B. Marshall, B. J. van den Broek, J. Vos & H. van Keulen. Wageningen Pers, The Netherlands, pp. 371–399.
Sands, P. J., Hackett, C. & Nix, H. A. (1979). A model of the development and bulking of potatoes (*Solanum tuberosum* L.) I. Derivation from well-managed field crops. *Field Crops Research*, **2**, 309–331.
Sands, P. J. & Regel, P. A. (1983). A model of the development and bulking of potatoes (*Solanum tuberosum* L.) V. A simple model for predicting graded yields. *Field Crops Research*, **6**, 25–40.
Schwärzel, R. & Gehriger, W. (1989). La certification des plants de pommes de terre. *Revue Suisse d'Agriculture*, **21**, 67–69.
Spitters, C. J. T. (1987). An analysis of variation in yield among potato cultivars in terms of light absoption, light utilization and dry matter partitioning. *Acta Horticulturae*, **214**, 71–84.
Travis, K. Z. (1987). Use of a simple model to study factors affecting the size distribution of tubers in potato crops. *Journal of Agricultural Science, Cambridge*, **109**, 563–571.
van Keulen, H. & Wolf, J. (eds) (1986). *Modelling of Agricultural Production: Weather, Soils and Crops.* Pudoc, Wageningen, The Netherlands, 479 pp.
Wilcockson, S. J. (1986). Effects of defoliation and time of harvest on tuber dry-matter percentage of Pentland Crown potatoes. *Journal of Agricultural Science, Cambridge*, **107**, 723–733.
Wirth, N. (1985). *Programming in Modula-2*, 3rd edn. Springer-Verlag, Berlin, Germany, 202 pp.
Wolf, S., Marani, A. & Rudich, J. (1990). Effects of temperature and photoperiod on assimilate partitioning in potato plants. *Annals of Botany*, **66**, 513–520.
Wurr, D. C. E., Bean, J. N. & Allen, E. J. (1978). Effects of variety and date of harvest on the tuber dry-matter percentage of potatoes. *Journal of Agricultural Science, Cambridge*, **90**, 597–604.
Wurr, D. C. E., Fellows, J. R., Lynn, J. R. & Allen, E. J. (1993). The impact of some agronomic factors on the variability of potato tuber size distribution. *Potato Research*, **36**, 237–245.